



HAL
open science

Temporal and seasonal scale variations of phytoplankton biomass control in the Gulf of Gabes

M. Bel Hassen, A. Hamza, A. Zouari, Z. Drira, F. Akrouf, S. Messaoudi

► **To cite this version:**

M. Bel Hassen, A. Hamza, A. Zouari, Z. Drira, F. Akrouf, et al.. Temporal and seasonal scale variations of phytoplankton biomass control in the Gulf of Gabes. *Vie et Milieu / Life & Environment*, 2010, pp.17-26. hal-03261941

HAL Id: hal-03261941

<https://hal.sorbonne-universite.fr/hal-03261941v1>

Submitted on 16 Jun 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

TEMPORAL AND SEASONAL SCALE VARIATIONS OF PHYTOPLANKTON BIOMASS CONTROL IN THE GULF OF GABES

M. BEL HASSEN, A. HAMZA, A. ZOUARI, Z. DRIRA, F. AKROUT, S. MESSAOUDI

Institut National des Sciences et Technologies de la Mer
28 rue 2 mars 1934, 2025 Salammbô, Tunisia
Corresponding author: belhassen.malika@instm.rnrt.tn

CHLOROPHYLL *a*
NUTRIENT
TOTAL SUSPENDED SEDIMENT
HYDROGRAPHIC FEATURES
GULF OF GABES

ABSTRACT. – We investigated the phytoplankton biomass and its relationships with nutrient, suspended sediment and hydrographic characteristics, during three oceanographic cruises in May-June 2006, September 2006 and March 2007 in the Gulf of Gabes (south-eastern Mediterranean). The May-June cruise coincided with the beginning of the summer stratification, a strong stratification occurred in September and a well-mixed water column marked March cruise. Results allow characterizing the phytoplankton biomass potential limitation during hydrological transition between vertical mixing and strong stratification. The potential nutrient limitation on the phytoplankton biomass showed seasonal and spatial patterns. N-limitation was preponderant during winter mixing conditions. Potential Si and P-limitation were associated with oligotrophic signatures such as, low chlorophyll and high organic suspended solid during enhanced summer stratification. A transition period characterized by N-limitation in the coastal area and Si-limitation in the offshore area characterized the beginning of the water stratification. General opposition patterns existed between organic suspended matter and chlorophyll *a* vertical distributions suggesting a potential control of phytoplankton biomass by top down processes. Our observations revealed the seasonal scale variations in the physical/biological coupling in the Gulf of Gabes and the implications for nutrient, organic suspended solid and phytoplankton standing stock.

INTRODUCTION

The hydrological regime of the Mediterranean Sea has been extensively studied. The water column is well stratified in summer, mixed in winter with transition periods of stratification occurring during late spring and early winter (Béthoux & Prieur 1983). These seasonal dynamics have a manifest influence on the water column nutrient availability. Particularly, the winter mixing is revealed to be a major nutrient input to the surface layer (Estratda *et al.* 1991, Marty *et al.* 2002). Moreover, the formation in the western Mediterranean basin of dense water in winter leads to intense vertical mixing; thus nutrients are transported to the surface layer, allowing spring blooms to occur (Béthoux 1989). In contrast, due to the strong stratification of the upper layer, the surface waters in the summer are not enriched by deep water nutrients (Marty *et al.* 2002, Bustillos-Guzman *et al.* 1995) and the coastal waters become more strongly affected by continental inputs.

The seasonal variations in phytoplankton biomass occur primarily due to changes in environmental variables, such as nutrient and light availability. Some authors suggested that surface waters of the western basin are N-limited (Andersen & Nival 1988, Owens *et al.* 1989), whilst others suggest that P-limitation is more likely (Béthoux *et al.* 1992, Béthoux *et al.* 1998, Thingstad *et*

al. 1998). The evidence for P-limitation of the eastern basin is stronger (Herut *et al.* 1999, Krom *et al.* 1991) and the limitation in the western basin may shift from N to P, according to the spatio-temporal trophic conditions (Klein *et al.* 1997). The shifts of phytoplankton biomass in higher trophic levels are also among the factor of regulation of this biomass (Gómez *et al.* 2001).

Identifying the ecological variables that regulate the seasonal fluctuations of phytoplankton standing stock is essential for understanding the consequences of the potential physical chemical and effects on the biological response of the ecosystem. The phytoplankton community structure has been investigated and discussed in the Gulf of Gabes with regard to the environmental variability during three characteristic periods (Bel Hassen *et al.* 2008, Bel Hassen *et al.* 2009a, Bel Hassen *et al.* 2009b). However, the seasonal transition of the factors regulating the phytoplankton standing stocks, especially the nutrient availability and the potential degradation of phytoplankton biomass, have not yet been approached. The main objective of this work is to investigate the spatial and seasonal patterns of the phytoplankton biomass control in the Gulf of Gabes continental shelf area based on analyses of physical processes, nutrient concentrations, stoichiometric ratios, suspended solid concentrations, and chlorophyll *a* concentrations.

METHODS

The studied area: The Gulf of Gabes occupies a wide continental shelf area. The water dynamics is influenced by the regional water circulation. Particularly, the dynamics of the Sicily Straits studied by Béranger *et al.* (2004) showed that the Atlantic Water (AW) in the western Mediterranean enters the Straits of Sicily and splits into two branches: one flowing to the south-eastern Mediterranean and the second flowing to the south and directly affecting the circulation at the mouth of the Gulf of Gabes. These authors pointed out a seasonal variability along the Tunisian coast, observing that the AW was generally stronger during the winter and flowed in the upper 100 m, while they revealed a weakening of the advection during the summer. Similar observations were reported by Poulain & Zambianchi (2007) using Lagrangian drifters data. They particularly showed that, during winter, the AW strongly flowed along the Tunisian coast through the shallow Gulf of Gabes. Recent observations have shown in a study carried out during late winter in the Gulf of Gabes that the AW flows within the continental shelf area between 50 m and 100 m isobaths (Bel Hassen *et al.* 2009a), whereas it exhibited a weak advection as summer stratification was established (Bel Hassen *et al.* 2008).

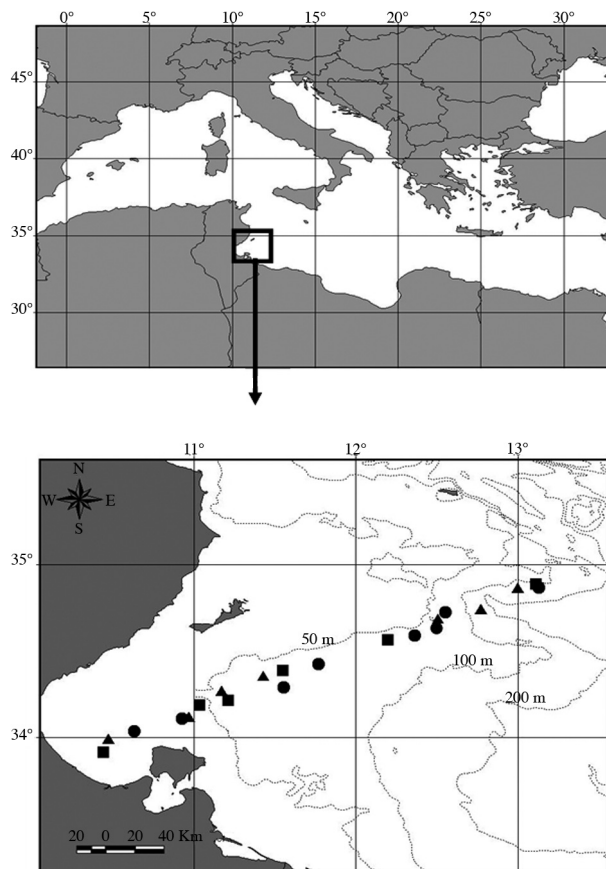


Fig. 1. – Sampling locations and the 50 m, 100 m and 200 m isobaths in the Gulf of Gabes. Squares are sites investigated in the May-June cruise, circles are sites visited in the September cruise and triangles are sites sampled in the March cruise.

Sampling: The study area encompassed the continental shelf area between 20 m and over 100 m. of depth (Fig. 1). Three cruises aboard the ‘R/V Hannibal’ were conducted during 2006-2007 labelled herein as (May-June), (September) and (March). The first cruise (26 May-6 June) was carried out at the end of spring and the beginning of the summer stratification, the second (7-11 September) coincided with a well-established water column while the third (16-19 March) corresponded to a well-mixed water column. Due to the difference in the hydrological forcing, mainly ascribed to the AW advection, different sampling designs were conducted during the three cruises (Bel Hassen *et al.* 2008, Bel Hassen *et al.* 2009a, Bel Hassen *et al.* 2009b). To highlight the difference in the hydrological regime between the cruises, we have retained in the present study the sampling locations situated along a seaward transect which also characterized the variability across the AW, the main hydrological forcing factor in this area. The station locations along the transect, although not exactly at the same positions for each cruise due to slight differences in the sampling designs, were rather well distributed along the transect.

For each station a vertical profile of temperature and salinity was made with a Seabird conductivity-temperature-depth (CTD) sensor (SBE 9, Seabird Electronics, USA) equipped with a 12l-Niskin rosette. Discrete samples were collected at three depths (2 m, 25 m and near bottom) in stations less than 50 m in depth and from five depths in stations above 50 m in depth (2 m, 10 m, 20 m, 50 m and near bottom). Sub-samples (2L) for pigment analyses were filtered with 47 mm-diameter glass fibre filter Whatman, GF/F. Filters for chlorophyll *a* analyses were immediately stored at -20°C for subsequent analyses. Samples for nutrient analyses were preserved immediately upon collection (-20°C , in the dark) and analysed within 15 days. Sub-samples (1L) of seawater were filtered with Whatman GF/F membrane filters for determination of the suspended solid concentrations.

The Secchi disk measurements were achieved during daylight. Vertical light attenuation coefficients were estimated according to Holmes (1970), and the euphotic zone depth was calculated assuming that irradiance at the bottom was 1 % of surface irradiance (Cloern 1987).

Sample analysis and criteria for stoichiometric and potential nutrient limitations: Nutrient analyses were performed with an automatic analyser type 3 (BRAN + LUEBBE) using standard methods (Tréguer & Le Corre 1975). The combinations of N, P and Si ratios were established to investigate potential nutrient limitations. Criteria for stoichiometric nutrient limitation were developed based on nutrient requirements of diatoms established by Redfield *et al.* (1963).

The total suspended solids (TSS) concentrations were based on dry weight filters after drying at 50°C for 48 h. The organic suspended solid (OSS) fraction was determined by weighing after incineration for 5 h at 450°C . Mineral suspended sediment (MSS) was thus deduced as the difference between (TSS) and (OSS) concentrations.

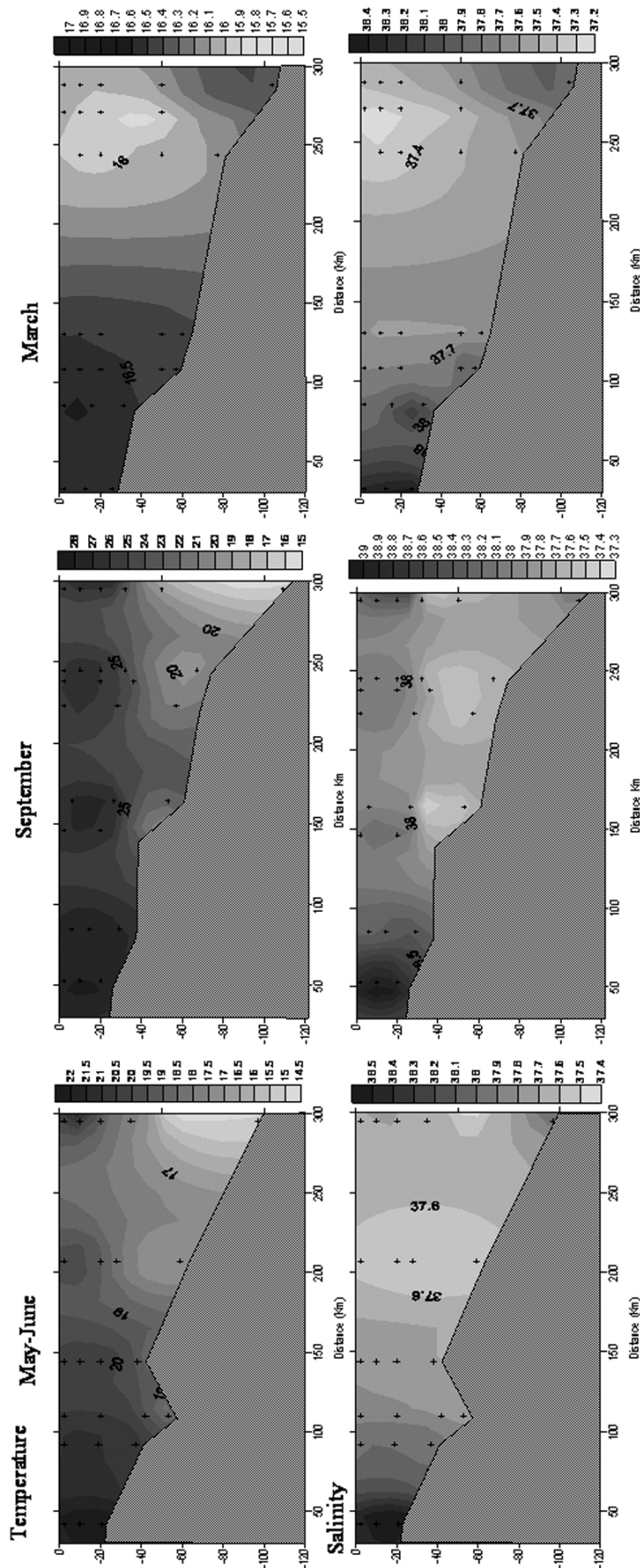


Fig. 2. – Vertical profiles of temperature (°C) and salinity (PSU) according to the sampled coast-offshore transect for the three sampled periods.

Chlorophyll-*a* analyses were performed by HPLC according to Pinckney *et al.* (2001), the analytical method was fully described in Bel Hassen *et al.* (2009a).

Statistical analysis: The original data collected were analyzed using the principal component analysis to understand the influence of various factors on the biological component of the system. Physical (temperature, salinity, suspended matter), chemical (Nitrate +Nitrite (NN), phosphate (P) and silicate (Si)) and “biological parameters” (chlorophyll-*a*) assessed over the three sampled periods were considered. The normality of the sampling distribution was first tested using the Kolmogorov-Smirnov test and the potential relationships between variables were tested by Pearson’s correlation coefficient.

RESULTS

Physical data

The vertical profile of the temperature measured along the transect showed variations between surface and bottom waters of about 6° C in May-June, 10° C in September and 1° C in March. In May-June, the thermocline depth ranged from 10 m in offshore samples to more than 30 m in coastal samples. In September, the water stratification was more pronounced and the thermocline established at a depth of more than 30 m. Surface salinity exhibited a decreased gradient along the transect (Fig. 2). The salinity minima (< 37.5) were observed in the offshore surface water in May-June and March, whereas they were situated between -50 m and -60 m of depth in September.

Nutrient data

Table I gives the mean nutrient concentrations and standard deviations and Fig. 3 shows the pattern of nutrient distribution along the transect. NN and P concentrated more in May-June than in September and March, while Si concentrations were higher in March than in the other investigated periods. In May-June, NN were mainly recorded in local patches from the surface layer to 20m of depth. P concentrations were higher in the offshore

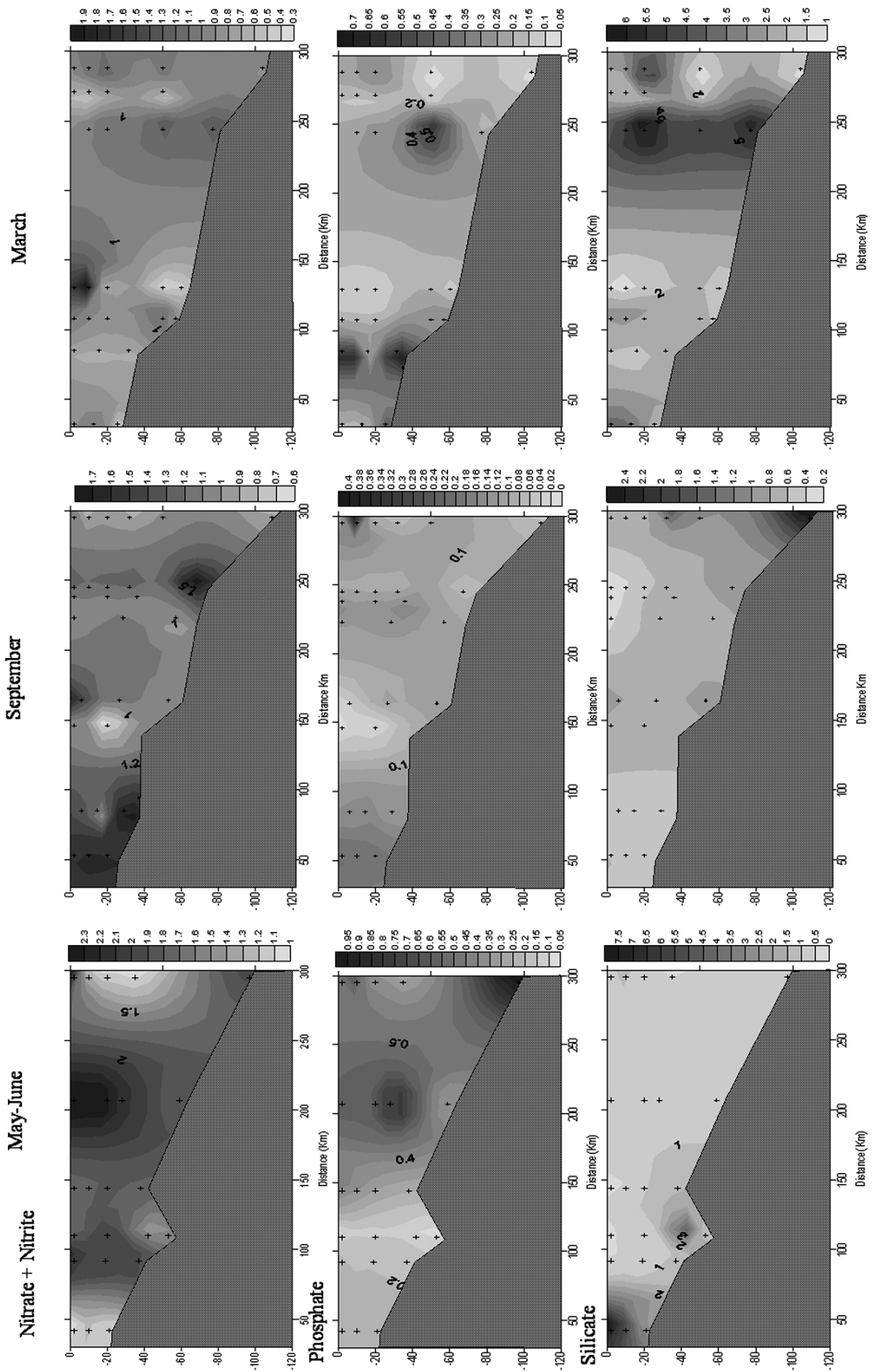


Fig. 3. – Vertical profiles of nitrate plus nitrite (μM), phosphate (μM) and Silicate (μM) according to the sampled coast-offshore transect for the three sampled periods.

Table I. – The mean (plus the standard deviation) values for nutrient, chlorophyll *a* and suspended solid concentrations recorded during the sampled periods.

	May-June	September	March
NN (μM)	1.71 ± 0.53	1.18 ± 0.37	0.92 ± 0.48
P (μM)	0.35 ± 0.27	0.11 ± 0.08	0.23 ± 0.23
Si (μM)	1.50 ± 2.36	0.71 ± 0.49	2.76 ± 1.96
Chl <i>a</i> ($\mu\text{g l}^{-1}$)	0.30 ± 0.26	0.10 ± 0.12	0.10 ± 0.11
TSS (mg l^{-1})	46.10 ± 16.17	54.47 ± 28.08	26.88 ± 10.54
OSS (mg l^{-1})	37.15 ± 124.5	42.79 ± 22.25	21.19 ± 8.77
MSS (mg l^{-1})	8.95 ± 4.04	11.68 ± 7.34	4.68 ± 1.88

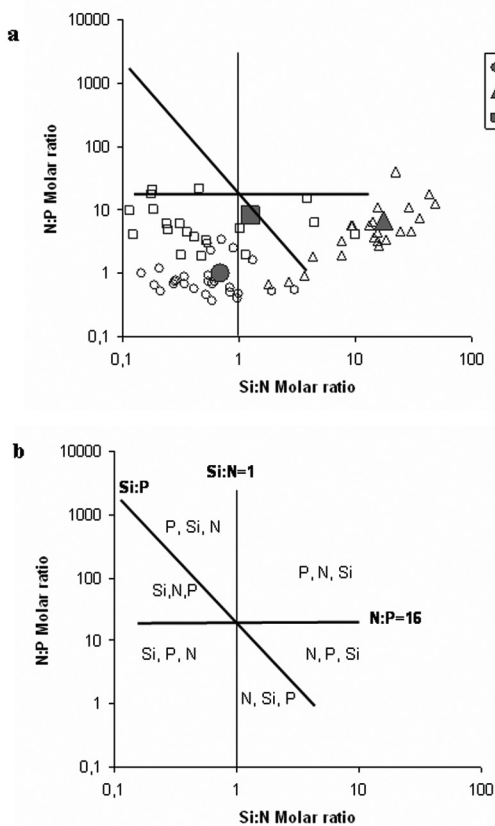


Fig. 4. – a, Si:N:P molar ratios in the water column of Gulf of Gabes in May-June, September and March. Grey symbols: average values from the total stations during a specific cruise; smaller, white symbols: individual measurements at every sampled station. b, Figure key: molar quotients between the concentrations of potentially limiting nutrients are delimited in this logarithmic plot ($\log \text{Si:N}$ vs $\log \text{N:P}$) by the $\text{Si:N} = 1$; $\text{N:P} = 16$ and $\text{Si:P} = 16$ lines, which define six different areas within the plot, with each one characterized by the potentially limiting nutrients in order of priority (Rocha *et al.* 2002).

stations at 30m depth and in bottom water, while Si concentrations were higher in the coastal stations. In September, NN occupied the whole water column in the coastal stations, while they concentrated more at 70 m depth in the offshore stations. P was mainly present in subsurface water in the offshore area; by contrast Si concentrations

were higher in the bottom offshore area. In March, NN were mainly present in local zones, in the subsurface coastal area and in bottom offshore areas. A depth-related trend was also observed for P and Si but at varying depth levels (Fig. 3).

The accepted standard molar ratios between N, Si and P for marine diatom biomass growth is $\text{Si:N:P} = 16:16:1$ (Redfield *et al.* 1963). The molar quotients between the *in situ* concentrations of potentially limiting nutrients are delimited by the $\text{Si:N} = 1$, $\text{N:P} = 16$ and $\text{Si:P} = 16$ lines (Fig. 4). These define 6 different areas, each one characterized by the potentially limiting nutrients in order of priority (Fig. 4b). The relative proportions of available nutrients evidenced a consistent temporal pattern. In March nutrient ratios fell in the region in which N limitation was most likely to occur. In May-June, nutrient ratio fell within different potential limiting areas. Particularly, in the regions in which Si-limitation, and to a lesser degree N-limitation, were likely to occur. During September strong stratified conditions, nutrient ratios fell in the region in which Si-limitation and to a lesser degree P-limitations were more likely to occur.

Total suspended sediment and organic suspended sediment

The TSS concentrations were higher in September than in May-June and March (Table I). The OSS represented about 81.15 %, 78.88 % and 82.50 % of TSS concentrations in May-June, September and March, respectively. TSS vertical distribution along the transect (Fig. 5) showed that the highest concentrations were mainly observed in the offshore stations in May-June and September but at varying depths, between 10 m and 30 m depth and in bottom water in May-June, while between 10 m and 50 m depth in September. In March, at the exception of a local patch observed at 60 m depth in the offshore area; the highest concentrations were mainly recorded in the coastal stations.

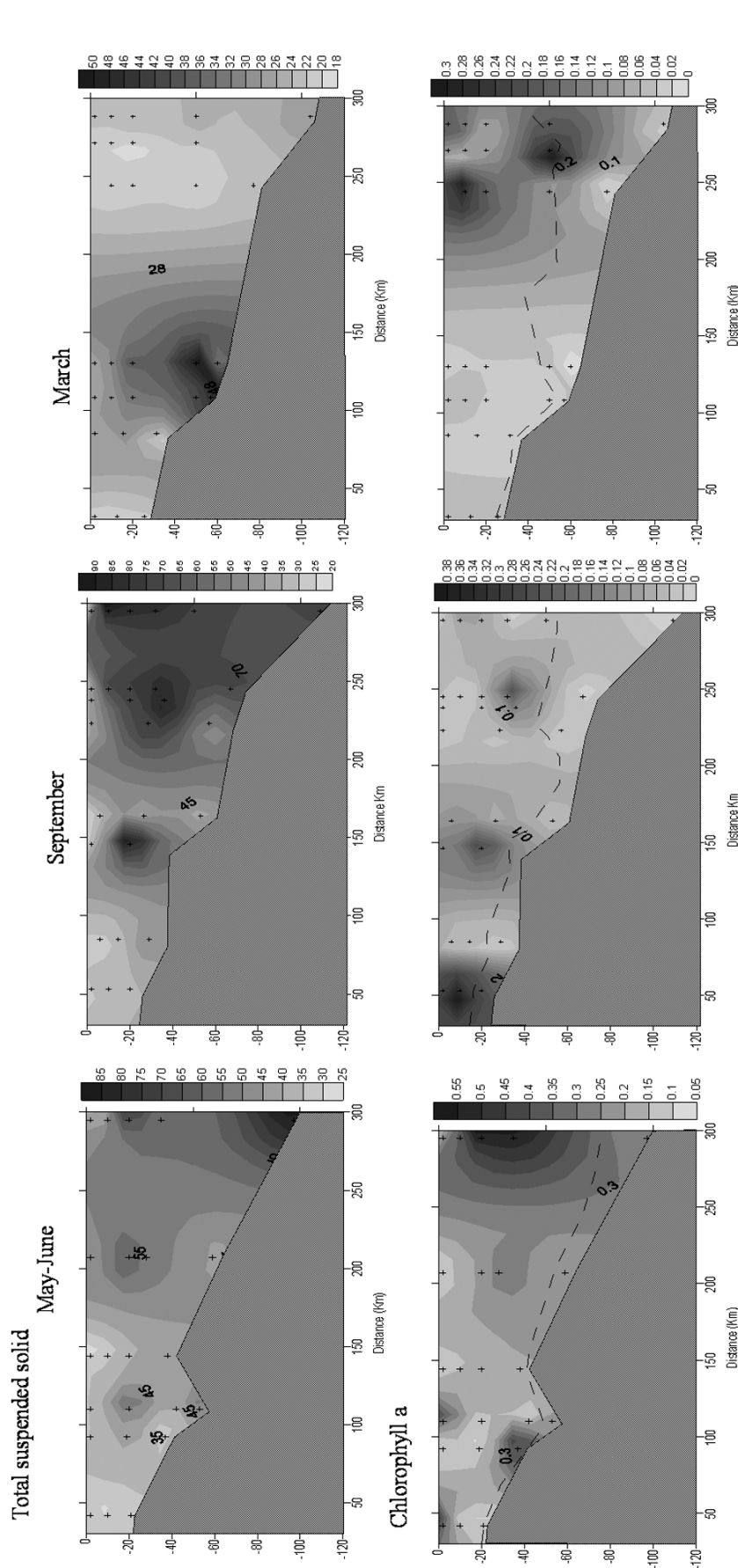


Fig. 5. – Vertical profiles of Total suspended solid (mg l^{-1}) and Chlorophyll a ($\mu\text{g l}^{-1}$) according to the sampled coast-offshore transect for the three sampled periods. Dashed line indicates the depth of the euphotic zone.

Phytoplankton biomasses

Chlorophyll a concentrations were generally less than $0.5 \mu\text{g l}^{-1}$ (Table I), the highest value was recorded in May-June ($1.2 \mu\text{g l}^{-1}$). The coast-offshore transect allowed identification of zones of chlorophyll maxima in both coastal and offshore areas (Fig. 5). In May-June, the euphotic depth deepened to more than 70 m in the offshore stations and local chlorophyll maxima were recorded at surface levels in the coastal area and between 20 m and 40 m depth in the offshore area. In September the chlorophyll maximum was observed in the coastal area at 10m of depth, while in the offshore station concentrations higher than $0.1 \mu\text{g l}^{-1}$ were recorded at 40 m depth. In March chlorophyll maxima were located in the surface offshore stations and at 50 m depth coinciding with the limit of the euphotic layer.

Relationships between physical, chemical and biological parameters

The PCA of water quality variables for the period May-June indicated that together the first two axes explained 59.75 % of the total variance (Fig. 6). Factor 1 accounted for 34.95 % of the total variance and was associated with positive loadings of temperature and Si and a negative loading of NN. In this factor Si correlated positively with temperature and negatively with NN (Table II). Factor 2 accounted for 24.8 % of the total variance and was associated with a positive loading of chlorophyll a and negative loadings of NN, TSS

Table II. – Pearson's correlation coefficients of biological, chemical and hydrographical variables at all sampled stations for the three cruises. Significant correlations ($P < 0.05$) are reported.

May-June	TSS	OSS	MSS	Chl <i>a</i>	Temp	Sal	NO ₂ NO ₃	PO ₄	Si
TSS	1								
OSS	0.994	1							
MSS	0.940	0.894	1						
Chl <i>a</i>				1					
Temp	-0.669	-0.671	-0.612		1				
Sal					0.526	1			
NO ₂ NO ₃							1		
PO ₄		0,515						1	
Si					0.523		-0.471		1
September									
TSS	1								
OSS	0,984	1							
MSS	0,837	0,725	1						
Chl <i>a</i>				1					
Temp					1				
Sal					0,463	1			
NO ₂ NO ₃							1		
PO ₄								1	
Si					-0.682				1
March									
TSS	1								
OSS	0.977	1							
MSS	0.944	0.918	1						
Chl <i>a</i>				1					
Temp				-0.516	1				
Sal					0.616	1			
NO ₂ NO ₃							1		
PO ₄								1	
Si					-0.373				1

and salinity. In this factor neither the relationship between chlorophyll *a* and TSS nor between chlorophyll *a* and NN were statistically significant (Table II).

In September, the PCA results indicated that the two first axes explained 54.25 % of the total variance, with factor 1 accounting for 36.68 % of the total variance. Factor 1 was associated with positive loadings of temperature and salinity and a negative loading of Si. In this factor Si was negatively correlated with temperature and positively correlated with salinity. Factor 2 accounted for 17.57 % of the total variance and was associated with positive

loadings of chlorophyll *a* and TSS and negative loading of NN.

In March, the two first axes explained 54.18 % of the total variance, with factor 1 accounting for 32.80 % of the total variance. Factor 1 was associated with positive loadings of temperature, salinity and TSS and negative loadings of chlorophyll *a* and Si. In this factor temperature was negatively correlated with chlorophyll *a* and Si. Factor 2 accounted for 21.38 % of the total variance and was associated with a positive loading of Si and negative loadings of NN and P.

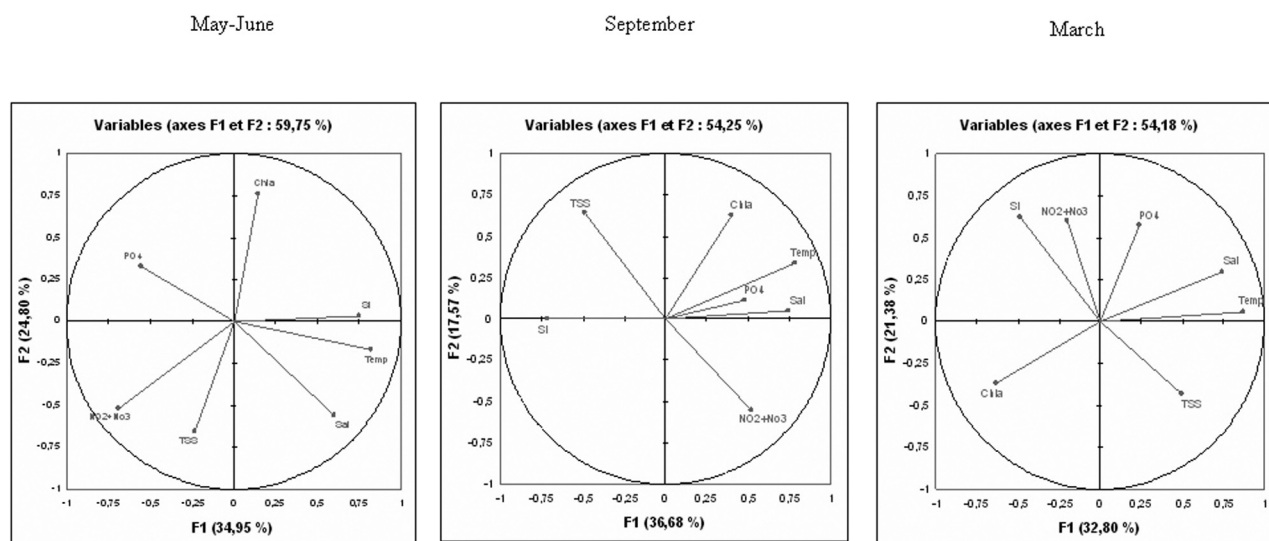


Fig. 6. – Results of Principal Component Analysis (PCA) (Axis I and II) of the physical, chemical and biological factors in the three sampled periods.

DISCUSSION

The region showed a high variability level in physical properties at seasonal and spatial scales. The March cruise corresponded to the winter-spring transition with a well-mixed water column, a strong advection of the Atlantic Water (Bel Hassen *et al.* 2009a) and a reduction of the euphotic layer likely induced by decreased day-length. The May-June cruise coincided with the beginning of the thermal stratification, which was established differently between the coast and the offshore areas. This was more likely explained by the influence of the AW advection, which interfered with the thermocline establishment in the offshore area. The September cruise fell in the well-established summer hydrological conditions. The thermocline deepened to more than 30 m in depth and the Atlantic water occupied the lower layer of the water column. Similar vertical water distribution was reported in this area during July 2005 subjected to a weak advection (Bel Hassen *et al.* 2008). These authors suspected the AW to be the residual of an enhanced spring circulation having therefore a stronger oligotrophy than the freshly advected water.

NN depletion was revealed during a water mixing condition, whereas general Si and P deficiencies characterized the strong stratification with a subsequent decrease of chlorophyll *a* concentrations (Table I). The potential resource limitation effect on phytoplankton growth will be discussed in regard to the marine diatoms requirements. During the mixing conditions whereas N-limitation was likely to occur, Si was particularly available suggesting that the potential N-limitation of diatoms growth might explain an incomplete utilization of silica by diatoms. During this period the chlorophyll *a* concentrations correlated significantly with temperature (Table II), supporting

the results that AW, characterised by low temperature and salinity, contributed to the phytoplankton biomass accumulation in this area (Bel Hassen *et al.* 2009a). With the beginning of stratification, Si-limitation and N-limitation, were likely to occur. These two nutrients exhibited different spatial distributions (Fig. 4). This was also associated with different relationships to temperature (Table II). We infer that the N-limitation occurred at coastal stations whereas Si-limitation occurred at offshore stations. This statement can find support in the scarcity of diatoms during May-June semi-mixed conditions in the offshore compartment and particularly at the deep chlorophyll maximum (Drira *et al.* 2009a).

The strong stratified conditions were characterized by a general Si deficiency (Table I). The Si was mainly available in the bottom offshore water, thus situated well below the euphotic area. In addition, P depletion was also observed, which was consistent with reports of P limitation in the Mediterranean Sea during the summer (Jacques *et al.* 1973, Minas *et al.* 1988, Thingstad & Rassoulzadegan 1995, Thingstad *et al.* 1998). This situation was also accompanied by low chlorophyll *a* concentrations. Unexpectedly, the highest chlorophyll *a* concentrations occurred in the coastal regions particularly marked by the scarcity of the potentially limiting nutrients (i.e., Si and P). This suggests that other factors than nutrient availability, would regulate the phytoplankton standing stock and/or that the phytoplankton composition was adapted to overcome these limiting conditions. Indeed, the micro-phytoplankton composition structure, studied during this period revealed the dominance of non-siliceous species (Drira *et al.* 2009a). In addition, associated phytoplankton pigments composition data showed that 87 % of the chlorophyll *a* was contributed by pico- and nano phytoplankton classes, among them cyanobacteria, prochlorophytes

and prasinophytes were the most important (Bel Hassen *et al.* 2009b). This indicates that these small phytoplankton cells were less opportunistic with regard to nutrient requirements than large cells, thus they were better adapted to oligotrophic conditions (Fogg 1991, Gómez *et al.* 2001).

The striking findings of this work were the high concentrations, throughout the cruises, of suspended matter with high proportions of organic components. Surprisingly, the highest concentrations were recorded in stratified offshore stations, while we expected higher concentrations in the coastal stations, mainly due to the water column vertical mixing. As the Gulf of Gabes has one of the largest trawlable shelf areas in the SE Mediterranean, the trawling-induced re-suspension of sediment (Durrieu de Madron *et al.* 2005) was a likely factor justifying the high TSS concentrations. In addition, the physical mechanisms associated with the formation of the AW at bottom layer depth during enhanced stratification, although it is not yet well elucidated and documented, could also have an impact on shelf sediment erosion as suggested by Bourrin *et al.* (2008) in the Gulf of Lions. These physical processes tended to generate high TSS concentrations in the bottom layer depth. However, the highest concentrations were recorded at subsurface levels and at the thermocline depth inferring that the TSS depth-related distribution might not depend on purely physical processes. Indeed, almost 80 % of TSS had organic origin which suggests that many other important biological factors considerably influenced the TSS vertical distribution patterns.

TSS and chlorophyll *a* vertical distributions exhibited general opposition patterns (Fig. 5). These opposing trends were also reflected in the PCA plots during the three cruises (Fig. 6). This suggests that high TSS concentrations might limit chlorophyll *a* biomass by constraining sunlight penetration through the water column (Cloern 1987, Irigoien & Castel 1997). Nevertheless, this is unlikely to occur due to the deepening of the euphotic layer well below the depth of the highest TSS concentrations. Moreover, these opposing trends between TSS and chlorophyll *a* is a very relevant information and could contribute to the calibration of a remote sensing algorithm in this area, since most of the algorithms used at the Mediterranean basin scale are not always appropriate for the Gulf of Gabes water (Bosc *et al.* 2004).

The absence of significant relationships between chlorophyll *a* and TSS indicates that phytoplankton biomass did not directly contribute to the TSS. However, zooplankton organisms were particularly abundant during summer stratification corresponding to the highest TSS concentrations (Drira *et al.* 2009b). These metazoans were mainly represented by copepods, averaging 80 % of the total zooplankton biomass (Drira *et al.* 2009b). Furthermore, the study of the ciliate community showed that ciliates also concentrated in the coastal area of the Gulf of Gabes (Hannachi *et al.* 2009). We suspect predation

by zooplankton and protozoan ciliates as being among the most important factors regulating the phytoplankton biomass in this area and this could therefore justify the inverse trend between TSS and Chlorophyll *a*. Moreover, zooplankton ingestion is followed by egesting of faecal pellets, which could significantly increase the TSS concentrations (Krivtsov *et al.* 2001).

The results of the present study show a seasonal pattern of potential nutrient limitation on the phytoplankton biomass. Particularly, Si deficiency which started in early stratification and increased with well-established stratification should be carefully considered and monitored as it could mark the transition to a non-siliceous phytoplankton-dominated ecosystem with its long-term effects on water quality and on the economical value of the resources.

The bottom down processes seems to play a major role in shaping the phytoplankton composition structure in this area. Nevertheless, the top down processes, mainly the grazing by protozoan ciliates and zooplankters, although not deeply investigated, were suspected to play a significant role in regulating the phytoplankton standing stocks. Therefore, their functional roles in the trophic transfer within the food chain remain to be determined.

ACKNOWLEDGMENTS. – This work was supported by the Tunisian funded project POEMM (LR02INSTM04), which was conducted in the National Institute of Marine Sciences and Technologies (INSTM). The authors wish to thank the crew of the ‘RV Hannibal’ for their assistance.

REFERENCES

- Andersen V, Nival P 1988. Modèles d'écosystème pélagique des eaux côtières de la mer Ligure. In Minas HJ, Nival P (eds), Océanographie Pélagique Méditerranéenne. *Oceanol Acta* 9: 211-217.
- Bel Hassen M, Drira Z, Hamza A, Ayadi H, Akrouf F, Issaoui H 2008. Summer phytoplankton pigments and community composition related to water mass properties in the Gulf of Gabes. *Estuar Coast Shelf Sci* 77: 645-656.
- Bel Hassen M, Drira Z, Hamza A, Ayadi H, Akrouf F, Messaoudi S, Issaoui H, Aleya L, Bouaïn A 2009a. Phytoplankton dynamics related to water mass properties in the Gulf of Gabes: Ecological implications. *J Mar Syst* 75: 216-226.
- Bel Hassen M, Hamza A, Drira Z, Zouari A, Akrouf F, Messaoudi S, Aleya L, Ayadi H 2009b. Phytoplankton-pigment signatures and their relationship to spring-summer stratification in the Gulf of Gabes. *Estuar Coast Shelf Sci* 88: 296-306.
- Béranger K, Mortier L, Gasparini GP, Gervasio L, Astraldi M, Crepon M 2004. The dynamics of the Sicily Strait: a comprehensive study from observations and models. *Deep-Sea Res II* 51: 411-440.
- Béthoux JP 1989. Oxygen consumption, new production, vertical advection and environmental evolution in the Mediterranean Sea. *Deep-Sea Res* 36:769-781.
- Béthoux JP, Prieur L 1983. Hydrologie et circulation en Méditerranée nord-occidentale. *Petrol Tech* 299: 25-34.

- Béthoux JP, Morin P, Madec C, Gentili B 1992. Phosphorus and nitrogen behaviour in the Mediterranean Sea. *Deep Sea Res* 39:1641-1654.
- Béthoux JP, Morin P, Chaumery C, Connan O, Gentili B, Ruiz-Pino D 1998. Nutrients in the Mediterranean Sea, mass balance and statistical analysis of concentrations with respect to environmental change. *Mar Chem* 63:155-169.
- Bosc E, Bricaud A, Antoine D 2004. Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. Global biogeochemical cycles, doi: 10.1029/2003GB002034.
- Bourrin F, Friend PL, Amos CL, Manca E, Ulses C, Palanques A, Durrieu de Madron X, Thompson CEL 2008. Sediment dispersal from a typical Mediterranean flood: The Têt River, Gulf of Lions. *Cont Shelf Res* 28:1895-1910.
- Bustillos-Guzman J, Claustre H, Marty JC 1995. Specific phytoplankton signatures and their relationship to hydrographic conditions in the coastal northwestern Mediterranean Sea. *Mar Ecol Progr Ser* 124: 247-258.
- Cloern JE 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. *Cont Shelf Res* 7: 1367-1381
- Drira Z, Bel Hassen M, Hamza A, Ayadi H, Rebai A, Bouain A, Aleya L 2009a. Spatial and temporal variations of microphytoplankton composition related to hydrographic conditions in the Gulf of Gabes. *J Mar Biol Ass UK*: doi:10.1017/S002531540900023.
- Drira Z, Bel Hassen M, Ayadi H, Hamza A, Zarrad R, Bouain A, Aleya L 2009b. Copepod community structure from a summer cruise in the Gulf of Gabes (Tunisia, Eastern Mediterranean Sea). *J Mar Biol Ass UK* 90: 145-157.
- Durrieu de Madron X, Ferré B, Le Corre G, Grenz C, Conan P, Pujo-Pay M, Buscaïl R, Bodiou O 2005. Trawling-induced resuspension and dispersal of muddy sediments and dissolved elements in the Gulf of Lions (NW Mediterranean). *Cont Shelf Res* 25: 2387-2409.
- Estrada M 1991. Phytoplankton assemblages across a NW Mediterranean front: changes from winter mixing to spring stratification. In Ros JD, Prat N eds, *Homage to Ramon Margalef; or, Why there is such pleasure in studying nature. Oecol Aquat* 10: 157-185.
- Fogg GE 1991. The phytoplankton way of life. *New Phytol* 118: 191-232.
- Goomez F, Gorsky G, Striby L, Vargas JM, Gonzalez N, Picheral M, Garcia-Lafuente J, Varela M, Goutx M 2001. Small-scale temporal variations in biogeochemical features in the Strait of Gibraltar, Mediterranean side. The role of NACW and the interface oscillation. *J Mar Syst* 30: 207-220.
- Hannachi I, Drira Z, Bel Hassen M, Hamza A, Ayadi H, Bouain A, Aleya L 2009. Abundance and biomass of the ciliate community during a spring cruise in the Gulf of Gabes (East Mediterranean Sea, Tunisia). *Acta Protozool* 47: 209-305.
- Herut B, Krom MD, Pan G, Mortimer R 1999. Atmospheric input of nitrogen and phosphorus to the southeast Mediterranean: sources, fluxes and possible impact. *Limnol Oceanogr* 44: 1683-1692.
- Holmes RW 1970. The Secchi disk in turbid coastal waters. *Limnol Oceanogr* 15: 688-694.
- Irigoién X, Castel J 1997. Light limitation and distribution of chlorophyll pigments in a highly turbid estuary: the Gironde (SW France). *Estuar Coast Shelf Sci* 44: 507-517.
- Jacquet S, Havskum H, Thingstad FT, Vaulot D 2002. Effects of inorganic and organic nutrient addition on coastal microbial community (Isefjord, Denmark). *Mar Ecol Progr Ser* 228: 3-14.
- Klein C, Dolan JR, Rassoulzadegan F 1997. Experimental examination of the effects of rainwater on microbial communities in the surface layer of the NW Mediterranean Sea. *Mar Ecol Progr Ser* 158: 41-50.
- Krivtsov V, Goldspink C, Sigeo DC, Bellinger EG 2001. Expansion of the model 'Rostherne' for fish and zooplankton: role of top-down effects in modifying the prevailing pattern of ecosystem functioning. *Ecol Model* 138: 153-171.
- Krom N, Kress S, Gordon LI 1991. Phosphorus limitation of primary productivity in the eastern Mediterranean Sea. *Limnol Oceanogr* 36: 424-432
- Marty JC, Chiaverini J, Pizay MD Avril B 2002. Seasonal and inter-annual dynamics of nutrients and phytoplankton pigments in the western Mediterranean Sea at the DYFAMED time-series station (1991-1999). *Deep-Sea Res II* 49: 1965-1985.
- Minas HJ, Minas M, Coste M, Gostan P, Nival P, Bonin MC 1988. Production de base et recyclage ; une revue de la problématique en Méditerranée nord-occidentale. *Oceanol Acta* 9: 155-162.
- Owens NJP, Rees AP, Woodward EMS, Mantoura RFC 1989. Size-fractionated primary production and nitrogen assimilation in the northwest Mediterranean Sea during January 1989. *Water Poll Res Bull* 13: 126-135.
- Pinckney JL, Richardson TL, Millie DF, Paerl HW 2001. Application of photopigment biomarkers for quantifying microalgal community composition and in situ growth rates. *Org Geochem* 32: 585 - 595.
- Poulain PM, Zambianchi E 2007. Near-surface circulation in the central Mediterranean Sea as deduced from Lagrangian drifters in the 1990's. *Cont Shelf Res* 27: 981-1001.
- Redfield AC, Ketchum BH, Richards FA 1963. The influence of organisms in the composition of seawater. In Hill MN ed, *The Sea, Vol II*, Wiley, New York: 26-77.
- Rocha C, Galvao H, Barbosa A 2002. Role of transient silicon limitation in the development of cyanobacteria blooms in the Guadiana estuary, south-western Iberia. *Mar Ecol Progr Ser* 228: 35-45.
- Thingstad TF, Rassoulzadegan F 1995. Nutrient limitations, microbial food webs, and "biological C-pumps": suggested interactions in a P-limited Mediterranean. *Mar Ecol Progr Ser* 117: 299-306.
- Thingstad TF, Zweifel UL, Rassoulzadegan F 1998. P limitation of heterotrophic bacteria and phytoplankton in the northwest Mediterranean. *Limnol Oceanogr* 43: 88-94.
- Tréguer P, LeCorre P 1975. Manuel d'analyse des sels nutritifs dans l'eau de mer, Université de Bretagne Occidentale, Brest, France, 110 p.

Received May 15, 2009
 Accepted March 30, 2010
 Associate Editor: J Boissier