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Primary production, carbon export and nutrients availability in western and eastern Mediterranean Sea in early summer 1996 (MINOS cruise)

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Abstract

The distribution of primary production (PP), particulate carbon export from the photic zone to deeper layer, and nutrient concentrations are investigated in the Mediterranean Sea (MS) during May–June 1996. A decrease in integrated primary production, particulate carbon export and nutrient availability towards the eastern part of the Mediterranean sea was observed while integrated chlorophyll *a* remains rather constant. This pattern may be explained both by the adaptation of phytoplanktonic organisms to low light conditions and by a more efficient nutrient diffusion from the deeper layer in the east related to the position of the nutricline and density gradient. Integrated primary production ranging from 350 to 450 mgC m^{-2} day^{-1} in the west decreases toward the east to a value of about 150 mgC m^{-2} day^{-1}. The latter value may appear as a limit for primary production rates under strong oligotrophic conditions. Particulate carbon export represents $4.0 + 2.9\%$ of integrated primary production. Up to 90–95% of primary production is then sustained by internal recycling of organic matter. Evidence of a limitation of production by phosphate was obtained from differences between depth of nitracline and phosphacline and by enrichment experiments. The wide range of oligotrophic conditions in the Mediterranean Sea provides a case study for links between C, N and P-cycles.

Keywords: Primary production; Carbon export; Nutrients; Mediterranean Sea

1. Introduction

Carbon assimilation by phytoplankton or primary production (PP) in the ocean is one important variable for assessing the global carbon cycle and thus to evaluate the impact of the anthropogenic CO_2 input on climate change. Assessing the carbon export from the photic zone to the deep layer is central in the debate concerning the possibility of the ocean to absorb the anthropogenic CO_2 excess (Longhurst, 1991). Oceanic oligotrophic areas represent more than 75% of the global ocean and, according to recent estimations, about 40% of the total oceanic production (Berger, 1989). However, the functioning and productivity of oligotrophic systems are still much debated. The role of oligotrophic areas in overall export production is probably not very important, because the greatest part

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of photosynthesised carbon is recycled in the surface layer and rapidly re-exchanged with the atmosphere. Nevertheless, recycling may lead to dissolved organic carbon (DOC) accumulation (Thingstad et al., 1997) and it should be considered since accumulation and export of DOC in oligotrophic areas has been shown to be potentially more important than the transport via sinking particles (Copin-Montégut and Avril, 1993; Carlson et al., 1994).

Despite the high complexity of the plankton food-web in the pelagic ecosystem, it is obvious that the ultimate constraints for autotrophic PP are the abiotic factors: light and inorganic nutrients (De Baar, 1994). Unquestionably, variation of light is a dominant factor controlling the growth rate of algae. Nevertheless, light conditions at sea surface may be approximated with simple calculations (Kirk, 1994; see Moutin et al., 1999), and light conditions with depth may be seen as a consequence of biological activity in the open ocean. Consequently, assessing nutrients (included iron) availability appears as a key factor to understand and eventually predict the biological response (in terms of trophic structure and/or in terms of carbon fluxes) in the upper photic zone. PP rates vs. limiting nutrients availability is a first approach to that question.

The in situ ^{14}C method is now generally believed to give a good approximation of the rate of PP (Williams et al., 1979; Platt, 1984; Davies and Williams, 1984; Bender et al., 1987; Grande et al., 1989). This rate may be supported by new nutrients coming into the photic zone (new production) and by internal recycling of organic matter (regenerated production). Nutrient availability will then depend on hydrological conditions and on biological activity. Only new production can create an increase in biomass and subsequently it is a fundamental criterion for fertility (Minas et al., 1988).

The Mediterranean Sea (MS) is characterized by a general circulation largely influenced by the existence of straits with sills (Lacombe, 1988) and by large seasonal variability of hydrological structures, from a deep homogenisation of the water column in winter to a strong stratification in summer. During winter, deep nutrient-rich waters reach the surface allowing spring algal blooms to occur. Mediterranean production is then characterized by two annual extremes nutritive limits. The first corresponds to winter mixing, which determines the initial stock of nutrients. Quantity of nutrient brought in the photic zone will mainly depend on the depth reached by cooling waters. The second limit corresponds to the maximum summer stratification and to the lower availability of new nutrients.

The MINOS cruise (*Mediterranean INvestigation of Oligotrophic Systems*) was planned in early summer 1996 in the MS, which offers a wide range of oligotrophic conditions—ideal for studying productivity during low new nutrients availability. We studied the distribution of PP, particulate carbon export from the photic zone, and nutrients concentration. In addition, we examined whether phosphate may be a key factor for the control of productivity in the MS. Prediction of carbon export from physically, chemically and biologically constrained phosphate distribution is also discussed.

2. Material and method

The MINOS cruise was carried out from May 21 to June 29 (1996) on board the R/V *Le Suroît* in the MS (Fig. 1). Hydrological measurements and biological experiments were conducted at 20 stations that cover the central parts of the western and eastern basins. Nutrients, chlorophyll *a*, ^{14}C uptake rates, and sinking rates of carbon in particles within the 0–200 m layer were measured daily. The 1% light penetration depth (1% LPD) was calculated from a profile of photosynthetically active radiation (PAR) performed around noon using a biospheric instrument (LI-COR). Hydrographic measurements were done with a conductivity–temperature–oxygen–depth profiling system (CTOD Seabird, model 911+). Continuous multiparametric profiles obtained during the 0–200 m downcasts were examined to select 12 sampling depths for the upcasts in order to always encompass the chlorophyll *a* maximum. Samples were obtained with 12-l Niskin bottles with silicone rubber closures and tubing that had been carefully cleaned to avoid introducing toxic metals during sampling. Sample for nitrate and SRP were collected in polyethylene flasks and were analysed immediately after sampling on a Technicon AutoAnalyser according to Tréguer and LeCorre (1975). Samples for particulate organic nitrogen and phosphate (250 ml) and chlorophyll *a* (250 ml) were filtered using precombusted GF/F glass-fibre filters. Chlorophyll *a* concentration was determined by fluorimetry using the methanol extraction procedure (ana-

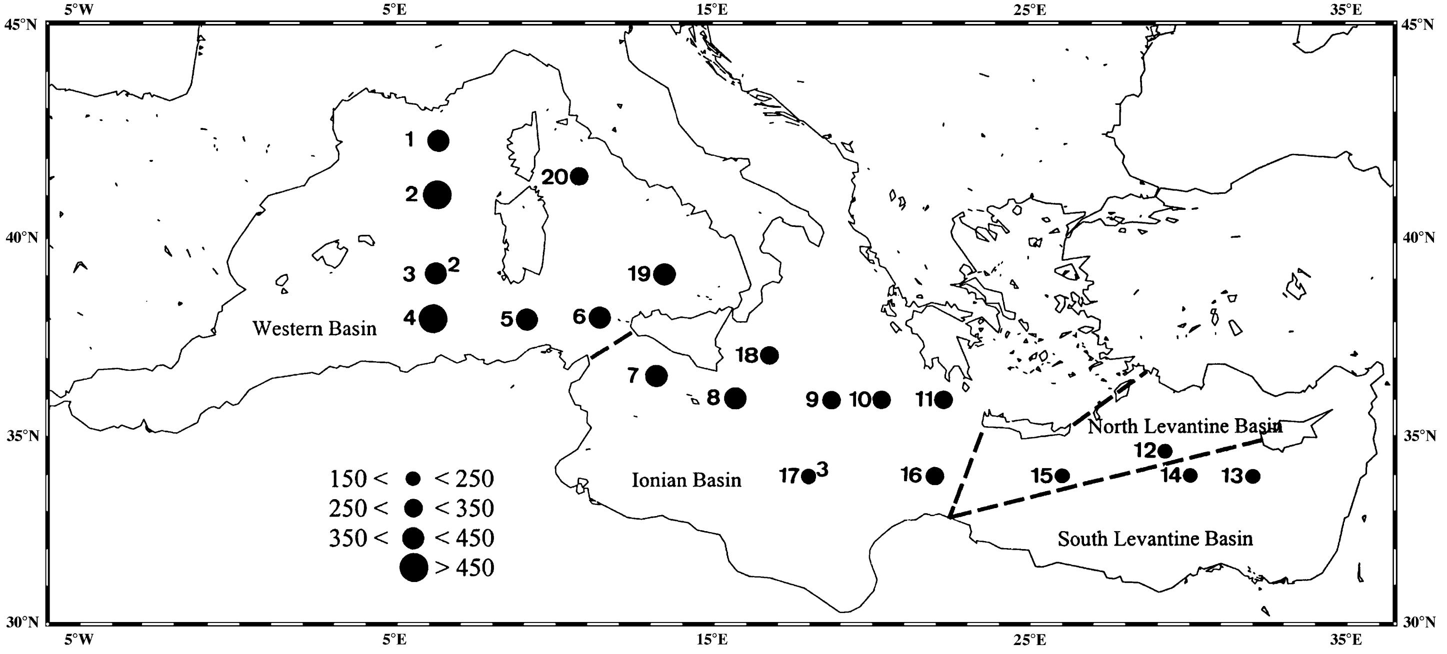

Fig. 1. Location of the 1–20 stations and integrated primary production (mgC m^{-2} day^{-1}) during the MINOS cruise (May–June 1996).

lytical precision and accuracy, 5% and 0.01 μg l^{-1}, respectively) as described by Raimbault et al. (1988). Dissolved and Particulate organic nitrogen and phosphate was determined using a persulfate wet-oxidation method (Valderrama, 1981; Pujo-Pay and Raimbault, 1994).

2.1. PP measurements

Carbon absorption has been quantified according to the experimental protocol recommended by France-JGOFS-P.F.O. (1991). Each sample (320-ml polycarbonate bottle, three light and one dark sample per depth) was collected before sunrise, inoculated with 250 μl of the ^{14}C working solution[1] just before sunrise, and then incubated in situ. At noon (1st LEG, from Marseilles to Heraklion, stations 1–11) or 24 h later (2nd LEG, from Heraklion to Marseilles, stations 13–20, station 12 was exceptionally shorter), the samples were filtered on GF/F filters to measure net absorption (A_N, mgC m^{-3}). Filters were immediately covered with 500 μl of HCl 0.5 M and stored for counting at the laboratory. Each day, three samples were filtered immediately after inoculation for t_o determination, and 250 μl of sample was taken at random from three bottles and stored with 250 μl of ethanolamine to determine the quantity of added tracer (Q_i). In the laboratory, samples were dried for 12 h at 60 °C, 10 ml of AQUASOL 2 (Packard) were added to the filters and dpm was counted after 24 h with a Packard Tri carb 2100 TR liquid scintillation analyser.[2]

Net absorption $A_{N(T_i;T)}$ for dark and light bottles was calculated from:

$$A_{N(T_i;T)}\ (\text{mgC m}^{-3}) = (\text{dpm} - \text{dpm}_{(t_o)})/(\text{dpm}_{(Q_i)} \times 1280) \times \text{TCO}_2$$

where T_i corresponds to the starting time of the incubation since dawn and T to the incubation duration.[3]

PP rates PP* (* = 24 h from dawn-to-dawn) were obtained from:

$$\text{PP*}\ (\text{mgC m}^{-3}\ \text{day}^{-1}) = A_{\text{Nlight}(T_i;T)}/\tau_{(T_i;T)} - (A_{\text{Nblack}(T)}/T) \times 24$$

Integrated PP, IPP* (mg m^{-2} day^{-1}) has been calculated with trapezium method assuming (1) that subsurface (about 5 m) rates are identical to surface rates (not measured) and (2) that rates are zero at 20 m below the deepest sampled depth.[4]

Remark: A comparison between GF/F and 0.2-μm Teflon filters for net carbon absorption measurements was carried out: $A_N(\text{GF/F}) = 0.93 \times A_N(0.2\ \mu\text{m}) \pm 0.04$ ($R^2 = 0.91$, $N = 48$, $\alpha = 0.05$). This result indicates that almost all carbon absorption is carried out by organism retained by GF/F filters at this period in the MS.

2.2. Downward fluxes of particulate matter

Downward fluxes of particulate matter were measured in free-floating sediment traps (PPS4) deployed at a depth of 200 m. These cylindrical sediment traps have a mouth area of 0.05 m^2, a height of 1.20 m. The trap material was concentrated in a polyvinyl receptacle (10 cm height) placed at the bottom of the trap. During launching and retrieval of the mooring, the flasks were isolated from further inputs by a valve that was activated by an electronic device with a timer. The collected flask was filled with filtered sea-water containing no preservatives. In order to minimise microbial degradation of the particulate matter, traps were deployed during short time intervals (8 h during the first part of the cruise, stations 1–11, and 24 h during the second LEG) in parallel with the in situ ^{14}C incubations. Estimates of the total particle flux was made gravimetrically. Particulate matter was filtered onto tared 25-mm precombusted GF/F filters immediately after recovery. Swimmers were scarce, but when present were immediately removed from the filter using forceps. To eliminate residual salt water, filters were given three brief rinses with deionized water.

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[1] Working solution: 12.5 ml of NaH^{14}CO$_3$ (25 mCi, 50–60 mCi/mmol, Amersham CFA3) was added to a solution containing 0.09 g of Na$_2$CO$_3$ (Aldrich 20,442-0) per 300 ml of sterilized milliQ water. This solution was stored in sealed 15-ml glass flasks.

[2] One milliliter of milli-Q water was added in Q_i samples.

[3] TCO$_2$ (mgC m^{-3}) was determined according to Copin-Montégut (1993).

[4] $\tau_{(T_i;T)}$ (conversion factor depending on the date and the latitudinal position) was determined according to Moutin et al. (1999). Applying this procedure allows to normalize PP rates obtained from incubation duration ≤ 24 h in a given region at a given date, to daily rates, thus allowing the comparison of data obtained from different experimental incubation durations.

Table 1

Primary production rates at surface and subsurface and standard deviations, depths corresponding to sub-surface maximum rates (in parentheses when weakly marked), integrated primary production, carbon export and standard deviation, 1% light depth (data from S. Maritorena), maximum of fluorescence and of chlorophyll *a*, integrated chlo *a*

Stations	Longitude	PP sea surface (mgC m^{-3} day^{-1})	S.D.	Max. PP sub-surface (mgC m^{-3} day^{-1})	S.D.	Depth (m)	IPP (mgC m^{-2} day^{-1})	Carbon export mean (mgC m^{-2} day^{-1})	S.D.	*N*	1% LPD	Max fluo depth (m) CTD	Max chlo *a* depth (m) bottles	Chlo *a* (mg m^{-2})
1	6.2	7.3	0.6	8.0	0.6	40	353	44.2	8.9	3		43.0	40	36
2	6.2	7.1	0.3	10.9	0.4	40	472	27.4	8.5	3		54.8	50	32
3	6.2	9.2, 5.9	0.9, 0.3	5.0, 6.5	0.8, 0.6	50	396, 401	6.3	1.0	6		74.4	71	36
4	6.2	9.0	1.2	42.3	3.8	50	996	13.1	1.0	2		61.8	60	116
5	9.0	4.6	0.3	7.2	0.9	50	378	20.7	3.2	2		78.0	70	29
6	11.3	4.2	0.4	11.6	0.9	51	441	20.0	1.0	2		57.5	50	43
7	13.3	5.4	0.4	7.1	0.1	71	419	28.7	8.3	2		71.5	71	30
8	15.8	4.1	0.4	6.5	0.4	71	402	19.0	2.0	2		86.9	80	55
9	18.8	3.6	0.3	(2.3)	0.1	(61)	255	8.6	3.0	2		108.7	110	27
10	20.3	3.3	0.4	6.4	0.1	50	313	10.1	1.8	2		71.6	60	32
11	22.3	3.5	0.6	5.3	0.3	50	325	9.2	0.3	2		79.2	60	33
12	29.2	3.3	0.1	(1.9)	0.7	(71)	221	20.5	2.5	3	85	80.6	70	29
13	32.0	3.2	0.4	2.8	0.3	101	192	7.4	6.3	3	104	116.3	100	34
14	30.0	2.4	0.2	(1.1)	0.1	(91)	168	5.4	1.0	3	101	122.4	111	31
15	26.0	2.02	0.03	1.2	0.1	90–100	174	4.5	1.2	3	114	140.1	130	28
16	22.0	3.9	1.4	3.0	0.3	81	303	4.2	0.8	3	96	96.3	100	34
17	18.0	3.6, 2.4, 3.4	0.04, 0.03, 0.37	(1.7, 1.6, 2.0)	(0.03, 0.04, 0.08)	(60, 50, 60)	210, 159, 242	4.5	2.7	7	108, 110, 110	134.4	120	(28, 25, 26)
18	16.9	3.6	0.2	3.1	0.2	61	296	3.5	0.7	2	91	103.2	100	37
19	13.3	5.0	0.2	9.4	0.5	60	395	7.4	1.6	3	79	71.1	60	57

They were then dried at 60 °C and placed in a dessicator with silica gel and stored dry until they could be re-weighted at laboratory. After weighting, filters were analysed with a CHN LECO 800 to determine the carbon content of the particulate matter. To facilitate comparisons with data from literature, all sediment fluxes were converted in daily rates assuming no significant influence of the photoperiod.

3. Results

PP (PP) sea-surface and sub-surface rates, as well as integrated PP (IPP), carbon export and relevant physical and biogeochemical variables measured during the MINOS cruise are presented in Tables 1 and 2.

3.1. Primary production distribution

Two examples of vertical profiles of the net carbon absorption obtained in the western and eastern MS are presented in Fig. 2. Dark net absorption is very low. It represents less than 4% of the light net absorption at sea surface, which is within the standard deviation calculated from the three light samples. The profile from the western basin depicted a surface and sub-surface (50–60 m) maximum rate (6 mgC m^{-3} day^{-1}). In the eastern Mediterranean profile, rates decrease regularly from the surface (3 mgC m^{-3} day^{-1}) down to zero (125 m), even if there is a small but significant increase of the production rate at 90 m. The 1% light depth which characterized the photic zone is around 70–80 m in the western basin and could reach 110 m in the eastern part of the MS (Table 1).

When considering the 20 stations sampled, PP profiles generally depicted a surface and sub-surface maximum rates (Table 1). At sea surface (5 m), PP rates varied from 2.0 mgC m^{-3} day^{-1} measured in the Levantine basin of the eastern MS to 9.2 mgC m^{-3} day^{-1} measured in the Western MS. At subsurface, these rates varied from 1.1 to 1.2 mgC m^{-3} day^{-1} measured at about 90 m depth in the Levantine basin to

Table 2
S and T from sea surface (5 m) and from D_{PO_4}, $\Delta\sigma$ between this two depths, characteristics of nutricline (slopes and depth where PO_4 or NO_3 reach zero), diffusive coefficient, PO_4 or NO_3 diffusive fluxes, equivalent carbon, integrated phosphate (0–150 m) and integrated particulate organic phosphate

Stations	Longitude	S	T	S	T	$\Delta\sigma$ (kg m^{-3})	Phosphacline S_{PO_4} (nM m^{-1})	D_{PO_4} (m)	N	r^2
		Sea surface		Depth of D_{PO_4}						
		PSU	°C	PSU	°C					
1	6.2	38.046	16.619	38.069	15.476	0.286	5.4	35	3	0.96
2	6.2	37.749	16.970	37.953	15.536	0.495	6.3	*43*	*3*	*0.86*
3	6.2	37.292	18.727	37.810	13.954	1.526	4.3	67	4	0.99
4	6.2	36.989	19.609	37.290	17.742	0.708	3.9	34	3	0.91
5	9.0	37.142	18.109	37.685	15.783	0.979	4.3	63	4	0.97
6	11.3	37.430	18.383	37.252	16.223	0.391	1.2	32	7	0.89
7	13.3	37.184	18.408	37.291	15.782	0.718	1.4	*51*	*4*	*0.71*
8	15.8	37.223	19.063	37.304	15.042	1.035	1.3	67	5	0.96
9	18.8	38.254	19.958	38.219	14.888	1.224	1	113	4	1.00
10	20.3	38.066	20.216	38.406	15.973	1.332	1.3	39	5	0.91
11	22.3	38.613	20.982	38.772	15.140	1.599	0.6	47	4	0.82
12	29.2	39.115	22.809	38.989	15.142	1.904	2.9	76	3	1.00
13	32.0	39.096	23.688	39.068	15.416	2.176	1.7	203	4	0.95
14	30.0	39.036	22.817	38.942	15.457	1.858	1	205	12	0.84
15	26.0	38.724	23.295	38.910	16.318	2.009	0.8	272	3	0.97
16	22.0	38.602	22.590	38.291	15.178	1.683	0.9	94	*6*	*0.87*
17	18.0	38.351	22.935	38.223	14.922	1.980	0.8	181	3	0.99
18	16.9	38.119	22.788	38.338	15.303	2.116	1.5	94	5	0.94
19	13.3	37.477	23.046	37.598	15.462	2.071	1.9	47	4	0.98
20	10.7	38.052	19.768	38.167	14.878	1.289	4.4	81	4	0.95

11.6 mgC m^{-3} day^{-1} measured at 50 m depth in the Western MS. An exceptionally high value of 42.3 was measured in the Algerian basin at 50 m depth (station 4), which is probably related to the Algerian current (see Raimbault et al., 1993). Surface salinity at this station is the lowest salinity measured (36.989). Subsurface maximum PP rates are generally higher than surface PP rates in the western part of the MS while the opposite is observed in the eastern part. The depths of subsurface maximum PP rates are strongly correlated to the depths of the chlorophyll *a* maximum (Table 1). The depths obtained from discrete sampling are in good agreement with depths of the maximum of fluorescence obtained with the CTD profile system. When discarding data from weakly marked subsurface maximum rates (in parentheses on Table 1), the following relation is obtained: $D_{\mathrm{maxChlo}} = 1.19 \times D_{\mathrm{maxPP}}$ ($R^2 = 0.73$, $n = 15$). Depths of the chlo *a* maximum are below the depths of PP subsurface maximum rates.

Integrated PP varied from 180 mgC m^{-2} day^{-1} in the South Levantine Basin to 996 mgC m^{-2} day^{-1} found north of Algerian coast (Fig. 1). Means and standard deviations were 398 ± 45 mgC m^{-2} day^{-1} ($n = 7$) for the western portion of the MS (omitted the highest value cited above) and 273 ± 85 mgC m^{-2} day^{-1} ($n = 12$) for the eastern basin. Three basins can be distinguished in the eastern part: the Ionian basin with 315 ± 71 mgC m^{-2} day^{-1} ($n = 8$), the North Levantine basin with 198 ± 33 mgC m^{-2} day^{-1} ($n = 2$), and the South Levantine basin with 180 ± 17 mgC m^{-2} day^{-1} ($n = 2$).

3.2. Export of particulate matter

Data obtained from sediment traps deployment are presented in Table 1. The mean C content (% of particulate matter weight/weight) was obtained with considering 35 samples: 14.1 (S.D. = 5.9). Then, the standard deviation for POC export presented in Table 1 corresponds to the S.D. calculated from three different weighting of particulate matter corresponding to three different samples. POC export varied from 3.5 to 44.2 mgC m^{-2} day^{-1} and represents between 1.2% and 12.5% of the 24-h integrated PP.

Nitracline S_{NO_3} (nM m^{-1})	D_{NO_3} (m)	*N*	r^2	K_z (m^2 day^{-1})	*N*	r^2	$Flux_{PO_4}$ (μmol m^{-2} day^{-1})	$Flux_{NO_3}$ (μmol m^{-2} day^{-1})	Equivalent-C (mgC m^{-2} day^{-1})	$\sum PO_4$	$\sum POP$
										(0–150 m)	
										mmol m^{-2}	mmol m^{-2}
103.8	13	3	*0.85*	0.2	3	0.88	0.9	17	1.1	24	
215.7	40	3	0.99	0.1	3	1.00	0.3	11	0.4	17	5.8
89.1	52	4	1.00	0.3	4	0.98	1.2	24	1.5	18	3.6
81.2	41	3	0.89	0.0	3	0.98	0.2	4	0.2	17	
115.7	65	4	0.97	0.1	4	1.00	0.5	13	0.6	10	
39.1	43	7	0.94	0.2	7	0.99	0.2	6	0.2	9	6.1
30.2	63	4	1.00	0.2	4	0.99	0.3	6	0.3	5	3.9
28.6	58	5	0.96	0.1	5	1.00	0.2	4	0.2	5	
26.2	102	4	0.96	0.5	4	0.97	0.5	12	0.6	1	3.3
61.7	39	5	0.92	0.2	5	0.97	0.3	14	0.4	8	3.0
26.2	33	5	0.94	1.4	*7*	*0.84*	0.9	38	1.1	4	3.7
92.7	57	3	0.92	0.6	3	0.91	1.8	57	2.3	7.4	3.3
34.9	160	4	0.97	2.0	4	1.00	3.4	69	4.3	1	3.6
19.9	111	12	0.98	1.8	12	0.95	1.8	35	2.2	1	3.1
21.8	218	3	0.93	0.8	3	0.88	0.7	18	0.8	1	4.1
29.1	101	6	0.99	0.5	6	0.95	0.4	14	0.6	2	4.5
19.6	129	3	0.93	0.5	3	0.87	0.4	11	0.6	0.3	3.6
61.2	94	5	1.00	0.3	5	0.98	0.4	16	0.5	3	5.3
61.1	54	4	0.99	0.2	4	0.98	0.4	12	0.5	8	4.7
73	59	4	0.98	0.4	4	0.99	1.7	29	2.2	10	

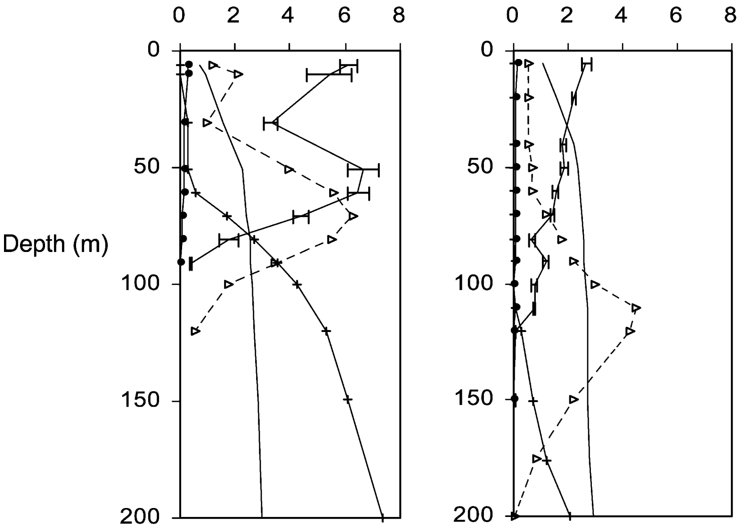

Fig. 2. Net carbon absorption for one dark (●: mgC m^{-3} day^{-1}) and three light samples (with standard deviation: mgC m^{-3} day^{-1}), chlorophyll $a \times 10$ (△: μg l^{-1}), nitrate concentration (+: μM) and $\sigma_\theta - 26$ (solid line: kg m^{-3}), at station 3 (Western basin) and station 14 (Eastern basin). Minos cruise (May–June 1996).

3.3. Nutrients distribution

Surface phosphate and nitrate concentrations were under chemical detection limits both in the western and in the eastern sections of the MS at this period. It may become measurable (>0.02 μM for PO_4 and >0.05 μM for NO_3) under 30-m depth in the west and deeper than 80 m in the east. As nutrient concentration against depth at the beginning of the nutricline may be linearized, we propose to characterize phosphacline and nitracline by their slopes (S) and the depth were PO_4 or NO_3 will be zero (D_{PO_4} and D_{NO_3}). In order to describe nutricline, this method is more precise for a discrete sampling vs. depth than the determination of the depth were nutrients become clearly measurable, particularly for phosphate ($[PO_4]>0.05$ μM). For $\alpha = 0.05$, only two linear regressions models concerning PO_4 have to be rejected (stations 2 and 7), data are indicated in italic in Table 2. D_{PO_4} varies from 32 m at station 6 in the western MS to 272 m in station 15 at the south Levantine basin of the eastern MS. Depths of nitracline are approximately the same as that of D_{PO_4} in the western basin while D_{PO_4} may be largely deeper than D_{NO_3} in the eastern part of the MS (Table 2).

Nitrate vs. phosphate concentration, data obtained in the whole MS during the MINOS cruise, are shown in Fig. 3 together with the classical Redfield ratio. When considering data above 0.1 μM of phosphate only, three linear relationships between NO_3 and PO_4 may be obtained for the three basins. For the western, the Ionian and the Levantine basins, slopes of 18.3–14.5–13.9 and intercepts of 1.6–2.3–2.6 μM with r^2 of 0.94–0.70–0.76 were obtained, respectively.

Nitrate/phosphate ratios may reach values of about 100 in the three basins considered (Fig. 4). Maximum values are obtained at an intermediate depth and a deepening of the depth where the maximum occur is observed from the west to the east. Under the maximum, NO_3/PO_4 ratios decrease with depth to finally reach value of about 20–30 near the bottom of the three basins. Above the maximum NO_3/PO_4 ratio, a slight decrease of the ratio is observed for the three basins. However, both NO_3 and PO_4 were close to the limits of the analytical precision in this depth range and therefore such ratios may not be reliable. Ratios were calculated only when phosphate and nitrate exceeded the detection limits of 0.02 and 0.05 μM, respectively.

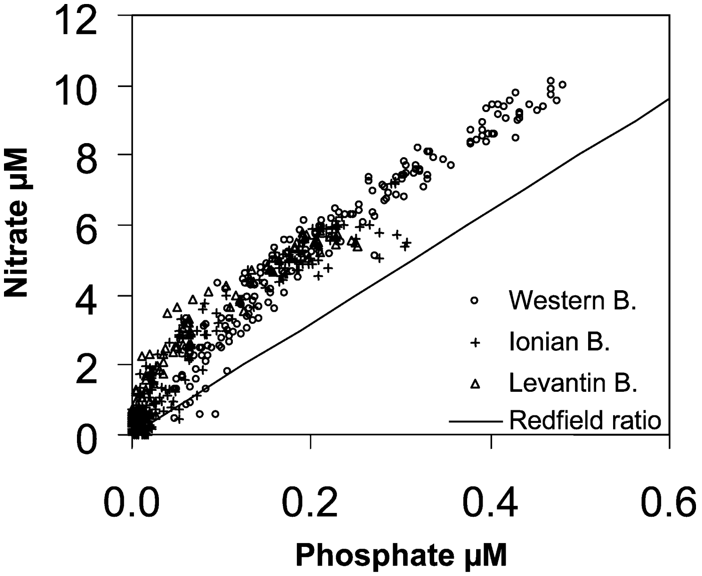

Fig. 3. Nitrate vs. phosphate concentration (µM) in the western (○), Ionian (+) and Levantine (△) basins. Minos cruise (May–June 1996).

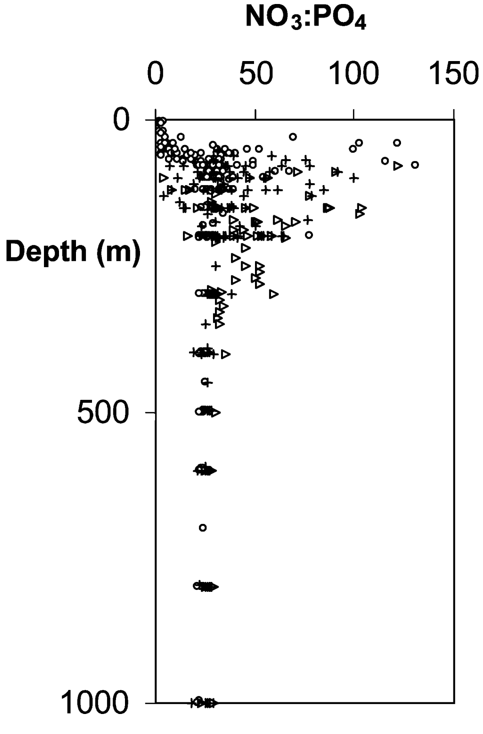

Fig. 4. Nitrate/phosphate ratio against depth in the western (○), Ionian (+) and Levantine (△) basins. Minos cruise (May–June 1996).

Surface (0–100 m), intermediate (300–500 m) and deep (>1000 m) N and P mean concentrations are presented in Table 3 for the western and eastern basins. Differences in nutrient concentrations along depth are larger than latitudinal variations at the scale of a basin, therefore it seems reasonable to present data from characteristic depth for each basin. Dissolved organic fractions represent the largest part of P and N both in western and eastern surface waters, always more than 50% of total nitrogen or phosphate. Intermediate depths nitrate and phosphate distributions are characterized by large standard deviations, particularly for phosphate, which is indicative of large latitudinal variations in nutrients concentrations at these depths. This has to be related to the varying vertical position of intermediate waters as well as to an increasing mineralisation of organic matter produced in the overlying water column. Effectively, a maximum nutrient concentration related to a minimum of oxygen concentration is generally observed at these depths (Minas, 1970). From 1000 to 3000 m, concentrations are relatively constant—which is indicated by weak standard deviations: deep mean nitrate and phosphate concentrations are respectively 8.54 ± 0.59 and 0.40 ± 0.04 µM in the western basin

Table 3
Surface (0–100 m), intermediate (300–500 m) and deep (>1000 m) N and P concentration (μM) in the western and eastern MS

		TP	PO_4	TOP	POP	DOP	TN	NO_3	TON	PON	DON
Western basin											
0–100 m	Mean	0.17	0.05	0.11	0.02	0.08	6.4	1.2	5.2	0.4	4.6
	S.D.	0.04	0.05	0.03	0.01	0.02	1.3	1.4	0.7	0.2	0.6
	n	49	49	49	23	23	49	49	49	23	23
300–500 m	Mean	0.40	0.35	0.05	0.00	0.06	11.2	8.0	3.2	0.1	3.1
	S.D.	0.07	0.07	0.02	0.00	0.01	1.4	1.3	0.3	0.0	0.3
	n	16	16	16	7	7	16	16	16	7	7
>1000 m	Mean	0.43	0.40	0.03	0.00	0.03	11.5	8.5	2.9	0.0	2.8
	S.D.	0.03	0.04	0.02	0.00	0.02	0.7	0.6	0.2	0.0	0.1
	n	18	18	18	6	6	18	18	18	6	6
Eastern basin											
0–100 m	Mean	0.10	0.01	0.09	0.02	0.06	5.4	0.3	5.0	0.4	4.5
	S.D.	0.03	0.02	0.03	0.01	0.03	0.7	0.7	0.6	0.2	0.6
	n	60	60	60	35	35	60	60	60	39	39
300–500 m	Mean	0.24	0.20	0.04	0.01	0.05	8.5	5.2	3.3	0.2	3.7
	S.D.	0.04	0.04	0.02	0.01	0.02	0.8	0.7	0.5	0.2	0.4
	n	21	21	21	6	6	21	21	21	6	6
>1000 m	Mean	0.24	0.21	0.03	0.00	0.05	8.1	5.0	3.0	0.0	3.3
	S.D.	0.03	0.04	0.02	0.01	0.02	0.6	0.4	0.4	0.0	0.3
	n	28	28	28	13	13	28	28	28	13	13

and 5.05 ± 0.44 and 0.21 ± 0.04 μM in the eastern basin (Table 3). NO_3/PO_4 ratios determined from the mean values are around 22 whatever the depth in the western basin while they decrease from 42 in surface waters to about 24 in the deep eastern waters. Dissolved organic concentrations decrease with depth to reach the same level in the two deep waters: about 0.03 μM for DOP (i.e., just above the detection limit) and 3 μM for DON (largely above the detection limit). It accounted for about 24% and 7% of total nitrogen and phosphate in the deep western basin and about 41% and 20% in the deep eastern basin.

4. Discussion

4.1. Availability of nutrients and primary production

The availability of the limiting nutrients for PP in the photic zone in summer will depend on several input, recycling and export fluxes. Nutrient concentration in the upper layer represents the equilibrium state between all those fluxes. As concentrations in the surface layers were below chemical detection limits, no direct relationship between nitrate or phosphate distributions and primary productivity level could be shown, although it may exist. An alternative way to discuss nutrient availability is to characterize the nutricline by *D* (depth when nutrient reach zero) and *S* (slope). *D* and *S* are essentially the result of biological consumption and physical export of nutrients from the photic to the deeper layers. They also indicate the potential ability of new nutrients to reach the photic zone by diffusion and advection. The higher *D* and the smaller *S*, the less new nutrients can reach the photic layer by vertical diffusion. Even if there is no simple direct influence of the nutricline on the 24-h PP in the MS at this period, as most of PP is likely supported by internal nutrient recycling in the photic layer, IPP varied in the same way as slopes and as the inverse of depth of nutriclines (Table 2). Higher IPP is observed in the western basin were *D* is low and lower IPP is observed in the LB were *D* is high (Fig. 5). Ionian basin IPP and *D* appeared as intermediate values. When *D* trends to zero, IPP may trend to its maximal value. Station 4, which was not represented in Fig. 5, gives an IPP of around 1 gC m^{-2} day^{-1} probably corresponding to special physical conditions due to the Algerian current. When *D* reaches extremely high values (above 150 m), it seems that IPP reaches a plateau: IPP never decreases under 150 mgC m^{-2} day^{-1} in these very oligotrophic waters. The same

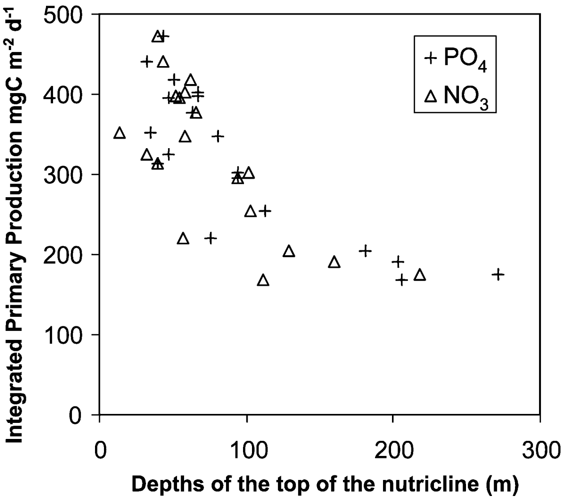

Fig. 5. Integrated Primary Production (mgC m^{-2} day^{-1}) against depths of the top of the nutricline (m). Minos cruise (May–June 1996).

tendency is observed for the depth of the maximum of fluorescence against *D*, in which depth is clearly related to the depth of the maximum of chlorophyll *a* (Table 1). An intuitive consequence would be that the biological nutrient-cycle in the photic layer may function with very low loss of nutrients in the eastern MS. Then, it would be possible to sustain a non-negligible PP rate for a long time and the value of 150 mgC m^{-2} day^{-1} may appear as a limit for PP rates under strong oligotrophic conditions.

D_{PO_4} is either the same or higher than D_{NO_3} (Table 2), which indicates a relatively higher depletion of phosphate than nitrate. Discrepancies between the depths of nitracline and phosphacline increase significantly in the east.

4.2. Nitrate vs. phosphate control of Primary production

In addition to the general depletion of nutrients observed, phosphate usually runs out slightly before nitrate when nutrients become depleted in surface waters (Fig. 3); that is, subsurface NO_3/PO_4 is significantly greater than the usual value of 14–16 generally found in most of the world ocean. Ratio of about 20–30 in the deep waters may reach around 100 at depths of around 50–150 m. High values for the NO_3/PO_4 ratio have already been observed in subsurface layers of the western Mediterranean (Raimbault and Coste, 1990). Krom et al. (1991) have measured ratios of up to 120 in the boundary of an eddy sampled in 1989 in the Levantine basin of the eastern MS. Intercept of the regression lines between nitrate and phosphate increase from 1.6 μM in the western basin to 2.6 μM in the Levantine basin. It may represent nitrate concentration when phosphate reach zero, i.e. when all phosphate would be taken up by planktonic species, and seems to indicate an increasing P limitation from the west to the east of the MS.

Several hypotheses have been proposed to explain the high nitrate vs. phosphate ratio of the MS. As far as deep water is concerned, nutrient exchanges at the straits of Gibraltar and Sicily in combination with the large vertical variation of nutrient concentrations appear as key factors to understand the nutrient budget of the MS. The influence of the exchange at the straits relative to that of river input of nutrients has been widely discussed and values from about 10% (Coste et al., 1988) to about 90% (Bethoux et al., 1998) have been proposed. Except hydrological fluxes, two largely different processes has been proposed to explain the typical NO_3/PO_4 ratios observed in deep waters. It concerns a biological process like unusually high rates of nitrogen (N_2) fixation (Bethoux and Copin-Montegut, 1986; Bonin et al., 1989; Sacchs and Repeta, 2000), which may lead to nitrogen accumulation in deep waters, and chemical process like the removal of phosphate by adsorption on iron-rich dust particles (Krom et al., 1991), which leads to increase in P depletion of the Mediterranean Sea. Both processes may explain the high nitrate vs. phosphate ratio observed in subsurface waters. Recently, Diaz et al. (2001) suggested that high subsurface ratios may be primarily attributed to the depletion in P relative to N in deep Mediterranean waters. Upward diffusion of deep nutrients taken up biologically in constant molar ratio of 1:16 may theoretically lead to ratios as high as those observed.

The biogeochemical evidence of high nitrate/phosphate ratios, and also direct evidence from bioassays (Fiala et al., 1976; Bonin et al., 1989; Justic et al., 1995) and from flow cytometric analysis (Vaulot et al., 1996) suggest that P is the most important limiting element for phytoplankton growth in Mediterranean stratified summer situations, as was already suggested in the western (Berland, 1980; Thingstad et al., 1998) and eastern MS (Krom et al., 1991). MacIsaac and Dugdale (1972) obtained an enhancement of NO_3 uptake while testing the response of a population of microplankton collected near Greece to the addition of phosphate. We also found that phosphate additions to samples of nutrients-poor surface water stimulate the uptake of nitrate and ammonium (Fig. 6).

4.3. PP and particulate carbon export

New production, defined as the fraction of PP driven by input of new nutrients (usually nitrate) into the euphotic zone (Dugdale and Goering, 1967), is assumed to be quantitatively equivalent to the organic matter that can be exported from the total production in the euphotic zone without the production system running down, and global new production is generally believed to balance the sinking flux of particulate organic matter to the deep ocean (Eppley and Petterson, 1979). As phosphate seems to control nitrate uptake in the MS, it could be interesting to attribute new carbon production to new phosphate entering the photic zone.

Export of particulate matter just below the photic zone has been estimated to represent between 1.2% and 12.5% of the 24-h integrated PP with a mean value of 4.0% (S.D. = 2.9). Typical upper oceanic export vs. PP ratios for the open ocean are about 5–10% (Buesseler, 1998). This biological drawdown of carbon does not include export via dissolved organic carbon. Consequently, if we assumed the following factors:

(1) An equilibrium state for PP and carbon export on a 24-h duration; i.e. that there is no more influence of the nutrients winter conditions; i.e. nutrients brought to the upper layer during winter have been lost after algal spring bloom; i.e. that we attain a typical oligotrophic status of productivity, as it is described for example in the tropical Atlantic ocean (Herbland et al., 1983);

(2) No effect of specific mesoscale hydrological events such as fronts, eddies and strong vertical shear;

(3) Negligible horizontal advection. Then new production should be at least equal to particulate export production: 3.5–44.2 mgC m^{-2} day^{-1}. As the secondary sources of phosphate for new production, like terrestrial or atmospheric inputs, are probably low when considering the central position of the stations (Fig. 1), the principal source of phosphate for new production would be diffusion from deeper water into the photic zone (if vertical advection is negligible). The vertical diffusive fluxes may be approximated by the Fick diffusion equation: $F = K_z \times \delta C/\delta z$ (Okubo, 1971). $\delta C/\delta z$ are the slopes of nutricline as previously described and eddy diffusion coefficients K_z (Table 2)

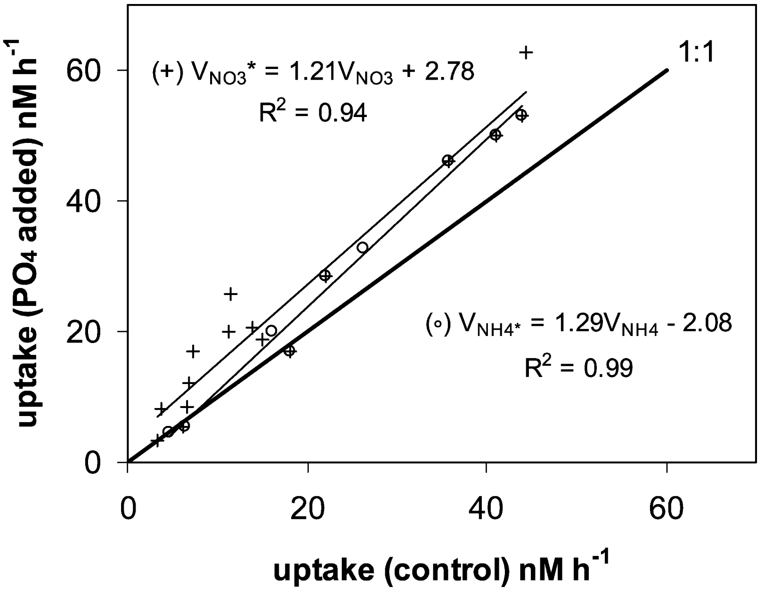

Fig. 6. Twenty-four-hour uptake rates of nitrate and ammonium, phosphate enriched samples against control.

were calculated at the same depth from the turbulent kinetic energy dissipation rate (ε) and the buoyancy frequency $N(z)$ according to Osborn (1980), $K = 0.25\varepsilon N^{-2}$ and $N^2(z) = g/\rho_w \, d\rho/dz$, considering $\rho_w = 1029$ kg m^{-3} and $\varepsilon = 7 \times 10^{-10}$ W kg^{-1}. The latter value was proposed by Gregg (1989) to be, within a factor of 2, the average dissipation rate attributable to internal waves. It was obtained after observations from six various sites in the mid-latitude thermocline.

The PO_4 and NO_3 diffusive fluxes (Table 2) were strongly correlated ($F_{PO_4} = 22.8 \times F_{NO_3}$, $r^2 = 0.83$). Even though the slopes of nutricline clearly decrease from the west to the east of the MS, the diffusive fluxes increase following the increase of K_z. This feature is due to the deepening of the nutricline from west to east: nutrient gradients correspond to lower density gradients in the east (Fig. 2). The same kinetic energy is then more efficient at creating turbulence. As a consequence, we established that new carbon production, which could be attributed to the diffusive fluxes (considering C/P = 106:1, which is a minimum value), is of the same order of magnitude as the export production in the east. The same calculation may lead to an explanation of only 1–20% of the export production in the west. This is probably related to the fact that ε may be largely greater than ε that is attributable only to internal waves (Denman and Gargett, 1983; Gregg, 1989). The effect of wind is probably higher in the west where nutriclines are shallower. Copin-Montégut (2000) use a value of 5×10^{-8} W kg^{-1} for the turbulent kinetic energy dissipation rate at the DYFAMED site in the northwestern MS in May 1995, which corresponds to an average for the thermocline (Denman and Gargett, 1983). When using this value of ε to determine K_z, we obtained nutrient fluxes and equivalent-C new production rates in the same order of magnitude or even larger than the export of particulate carbon in the western MS. Export production may be balanced by new production attributable to nutrients diffusion from deeper layer in the summer period but great uncertainty remains because of the large variations in estimations of K_z. Comparatively higher vertical diffusive fluxes of nutrients may explain the low decrease of PP under strong oligotrophic conditions (depth of nutricline above 150 m). It may support the high biomass (chlorophyll *a* concentration) measured in the east as deep as 150 m. This could be another explanation, different from that considering the adaptation to low light conditions, explaining the low decrease of integrated chlorophyll *a* concentration from the west to the east of the MS (Fig. 7). The role of predators might also be considered.

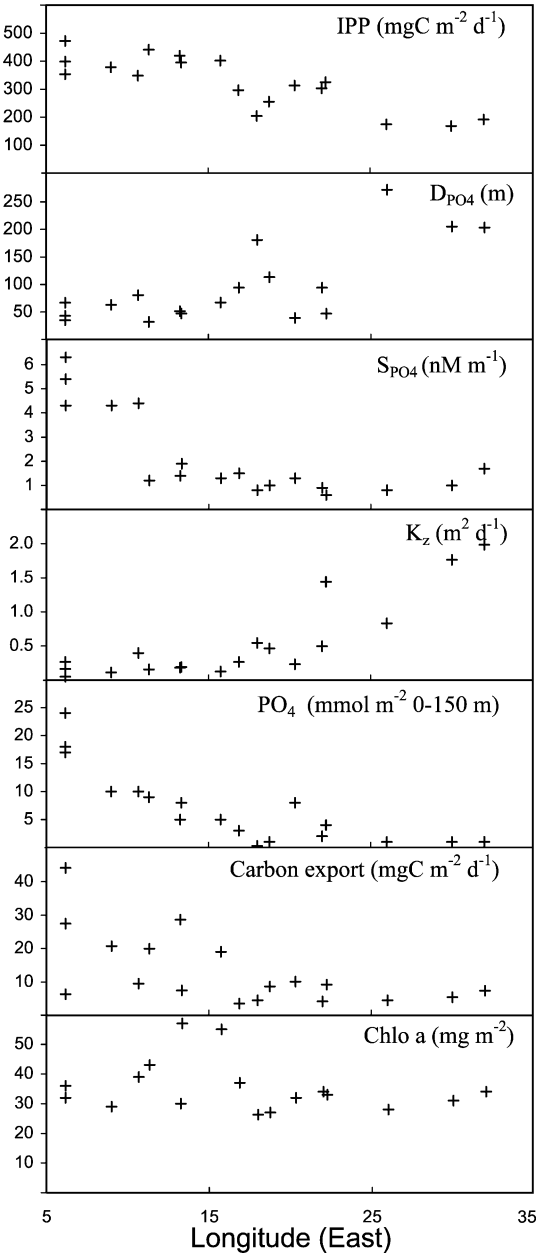

Fig. 7. Longitudinal trends of IPP, D_{PO_4}, S_{PO_4}, $\sum PO_4$, K_z, carbon export and integrated chlo *a* during the MINOS cruise (May–June 1996), stations 4 and 12 are omitted.

Recently, Herut et al. (1999) and Ridame and Guieu (submitted) suggested a non-negligible role of atmospheric inputs of new phosphate for primary production in the upper surface of the MS. The lack of measurements of nutrient fluxes from deeper to surface layers and large uncertainties of the estimations enable difficult comparison between downward and upward fluxes of new nutrients during stratified period. The quasi systematic presence of a deep PP maximum rate just above the deep chlorophyll *a* maximum may probably be related to new production attributable to new nutrients originating from deeper layers.

4.4. General trends

Integrated PP is higher in the western than in the eastern part of the MS during the period of the study, which is consistent with historical patterns showing the eastern MS as a zone of low production compared to the western MS (Sournia, 1973). Nutrient concentrations in the MS, largely under nutrients concentration from the adjacent Atlantic ocean, decrease across the different basins (Table 3). The same pattern was already observed by McGill (1961) and may explain the decrease of PP from west to east. This is in good agreement with the fact that the two major external sources of nutrients come in the Western part of the MS: the Rhône river input and the entry of the nutrients-rich Atlantic surface waters which gives the property of the Alboran sea and the Lion gulf to be the most productive areas in the MS (Antoine and Morel, 1995). The Nile river no longer represents a large nutrient enrichment in the MS since most of its water is now retained for irrigation.

Deep phosphate concentrations (>1000 m) in the western MS were found to be 0.40 ± 0.04 μM and were not significantly different from those previously observed in 1960 (Raimbault et al., 1995). Therefore, increasing nutrient river input as shown by Moutin et al. (1998) may not have had an impact on these concentrations as argued by Bethoux et al. (1998).

5. Conclusion

We have confirmed the relatively low primary productivity of the MS during summer characterized by thermal stratification and the increase of oligotrophy from west to east. Although mesoscale hydrological events may modify nutrient availability and, as a consequence, the biological response, it seems probable to give westward–eastward trends in nutrient availability and PP rates. These rates are mainly sustained by regeneration of nutrients through the food web of the surface waters (about 90%). New production attributable to diffusion of nutrients from deeper layers probably sustains the export of particulate organic carbon (1.2–12.5% of the 24-h PP rates, which correspond to typical open ocean values), but large uncertainties remain because of the wide range of available diffusive coefficients. The same induced turbulence may be more efficient in bringing nutrients upwards by diffusion in the east than in the west because of the lower density gradient at the depth of the nutricline in the former region. This is suggested to partly explain the relatively high biomass (chlorophyll *a*) and production in the east where nutricline reach values under 150 m. No integrated PP values lower than 150 mgC m^{-2} day^{-1} are observed, a value which may appear as a lower limit for PP rates under strong oligotrophic conditions.

We present additional evidence to that provided by enrichment experiments to confirm P limitation in the Mediterranean. The dynamics of the P-cycle is important for controlling productivity and should be considered as a key process to understand the food web systems in the MS. Gaining better understanding of what governs carbon fluxes seems likely to require improvement of chemical measurements of nutrients and particularly phosphate, which is below the classical detection limit during summer. New production, equal to carbon export if steady state is assumed, may be related to new phosphate entering in the photic zone.

N and P-cycle in the photic zone should be studied together to better understand the transfer of carbon to the ocean interior by biological processes (biological pump). The Mediterranean Sea give an exceptional range of trophic conditions which may be helpful to study links between C, N and P-cycles.

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