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Patterns in planktonic metabolism in the Mediterranean Sea

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Abstract

Planktonic gross community production (GPP), net community production (NCP) and community respiration (CR) across the Mediterranean Sea was examined in two cruises, THRESHOLDS 2006 and 2007, each crossing the Mediterranean from West to East to test for consistent variation along this longitudinal gradient. GPP averaged 2.4±0.4 mmol O_2 m^{-3} d^{-1}, CR averaged 3.8±0.5 mmol O_2 m^{-3} d^{-1}, and NCP averaged −0.8±0.6 mmol O_2 m^{-3} d^{-1}across the studied sections, indicative of a tendency for a net heterotrophic metabolism, prevalent across studied sections of the Mediterranean Sea as reflected in 70% of negative NCP estimates. The median *P/R* ratio was 0.58, also indicating a strong prevalence of heterotrophic communities ($P/R<1$) along the studied sections of the Mediterranean Sea. The communities tended to be net heterotrophic (i.e. $P/R<1$) at GPP less than 3.5 mmol O_2 m^{-3} d^{-1}. Although the Western Mediterranean supports a higher gross primary production than the Eastern basin does, it also supported a higher community respiration. The net heterotrophy nature of the studied sections of the Mediterranean Sea indicates that allochthonous carbon should be important to subsidise planktonic metabolism, and that the planktonic communities in the Mediterranean Sea acted as CO_2 sources to the atmosphere during the study.

1 Introduction

The Mediterranean Sea represents an anomaly in the world ocean because it ranks amongst the most oligotrophic areas of the world while receiving significant land-derived inputs of both natural and anthropogenic materials. The Mediterranean Sea receives nutrient inputs through atmospheric deposition across the entire basin, from riverine inputs (Martin et al., 1989; Bethoux and Gentili, 1999; Guerzoni et al., 1999), and from inputs with Atlantic water entering the Western basin. Hence, nutrient inputs are highest in the Western basin, which receives the largest riverine discharge (e.g. Rhône, France) compared to the eastern basin. Accordingly, the Mediterranean Sea has been reported to show a decreasing gradient in primary production from West to East, with primary production three times lower in the Eastern basin compared to the north-western basin (Turley, 1999). While nutrient inputs stimulate primary production, most of these inputs are accompanied by organic inputs as well, which may also stimulate planktonic respiration. Hence, it is unclear whether the reported gradient in primary production may lead to a similar west-east gradient in net community production. Yet, whether a West-East gradient in net community production exists in the Mediterranean Sea has not yet been resolved, due to a paucity of reports on planktonic metabolism in the Mediterranean Sea, particularly on the Eastern basin, as the bulk of the data available derive from the Western basin, with a dominance of studies in coastal waters (Gulf of Lions, Lefèvre et al., 1997; Bay of Blanes, Duarte et al., 2004; Lucea et al., 2005; Alboran Sea, Van Wambeke et al., 2004; Majorca Island, Gazeau et al., 2005; Navarro et al., 2004). Moreover, the magnitude of gross primary production and community respiration and the possible correlation between these processes in the Mediterranean Sea remains poorly resolved. Yet, the metabolic balance of planktonic communities is a key determinant of their role on biogeochemical cycle and, particularly, the role of planktonic communities as CO_2 sinks or sources affecting the atmosphere-sea CO_2 transfer (Duarte and Prairie, 2005).

Here we evaluate gross community production (GPP) and community respiration (CR) across the Mediterranean Sea and test the hypothesis that planktonic metabolism varies consistently along the West to East gradient in the Mediterranean Sea. We do so on the basis of two cruises across the Mediterranean Sea, THRESHOLDS 2006 and 2007, each crossing the Mediterranean from West to East and back. The first cruise covered a section from Majorca Island (Spain), Western Mediterranean, to the Black Sea, returning to Majorca Island, in June 2006, and the second cruise covered a section from Majorca Island to Alexandria (Egypt), returning to Majorca Island, in May 2007 (Fig. 1).

2 Materials and methods

The study was conducted on board of the Spanish R/V Garcia del Cid, involving two cruises: THRESHOLDS-2006 (4 June 2006–4 July 2006) and THRESHOLDS-2007 (6 May 2007–1 June 2007) occupying 36 and 23 stations, respectively. At each station, vertical profiles for temperature, salinity and fluorescence were taken with a Seabird CTD attached to a Rosette sampling system. The metabolism of the planktonic communities was measured in the THRESHOLDS-2006 and THRESHOLDS-2007 at 7 and 14 stations, respectively (Fig. 1).

Community metabolism (gross primary production, community respiration and net community production) was determined from changes in oxygen over 24 h in water samples containing communities sampled from the surface layer (5 m), the Deep Chlorophyll Maximum (DCM, typically between 40 and 120 m), and at an intermediate depth (20 m or 50 m) at each station. Water samples collected from these depths using 10-L Niskin bottles attached to a Rosette sampler system were carefully siphoned into narrow-mouth Winkler bottles. Seven replicates were used to determine the initial oxygen concentration, and seven replicates bottles were incubated for 24 h in the "dark" and in the "light". The Winkler bottles were incubated on deck at in situ temperature (temperature at 5 m depth), adjusting the incident natural irradiance to that received in situ using neutral density screens for "light" treatment or in the dark, in the case of the seven replicate "dark" bottles. The mean temperature difference observed between the surface layer and the DCM at the stations occupied was 3.8±0.4°C and the maximum difference was around 7.6°C. This difference may enhance somewhat metabolic rates of DCM samples when incubated at surface temperature. We calculated, using Q_{10} values for R of 1.60 and NCP of 1.51 (Raven and Geider, 1988; Robinson and Williams, 1993; López-Urrutia et al., 2006) that the metabolic rates presented here for the DCM layer may be 10% to 20% higher, on average, than those at the in situ temperature for the Western and the Eastern basin, respectively. This is within the error of the estimates and, therefore, no correction was considered necessary.

Net community production (NCP) and community respiration were measured by monitoring oxygen concentration changes in the light and dark bottles along the incubation (Carpenter, 1965, Carritt and Carpenter, 1966). Oxygen concentrations were analysed by Winkler titration using a potentiometric electrode and automated endpoint detection (Mettler Toledo, DL28 titrator) (Oudot et al., 1988). CR and NCP were calculated from changes in dissolved oxygen concentration after incubation of samples under "dark" and "light" conditions, respectively and GPP was calculated by solving the mass balance equation GPP=NCP–CR. The integrated metabolism rates were calculated by the trapezoid method, from the surface layer to the DCM. Samples of 250 ml for chlorophyll a determinations were filtered through Millipore GF/F filters (pressure < $0.3\,kg\,cm^{-2}$), frozen and then extracted for 24 h with 90% acetone. Fluorescence of the extracts was measured using a Shimadzu RF-5301 fluorometer (Yentsch and Menzel, 1963).

3 Results

Seawater temperature was relatively uniform across the Mediterranean, varying from 20°C to 23°C at 5 m depth, and from 10°C to 15°C at 100 m depth across the transects (data not shown). Chlorophyll a concentration was low, below $1.0\,\mu g\,L^{-1}$ over the entire water column (5 to 200 m) across the studied section, except in the Balearic Sea, where chlorophyll a concentration increased up to $4.5\,\mu g\,L^{-1}$ at 50 m depth during THRESHOLDS-2006 and up to $1.2\,\mu g\,L^{-1}$ at 70 m depth in the Sicily-Tunisia Strait, during THRESHOLDS-2007 (Fig. 2).

GPP averaged (±SE) 2.4±0.4 mmol $O_2\,m^{-3}\,d^{-1}$ across the sections (Table 1) and remained below 10 mmol $O_2\,m^{-3}\,d^{-1}$ in the euphotic zone (Fig. 3a, b), except for the subsurface maxima of the Aegean Sea (at 25.92° E) where GPP reached 15.1 mmol $O_2\,m^{-3}\,d^{-1}$. GPP differed significantly between the THRESHOLDS 2006 and 2007 (t-test, p=0.012) with higher rates observed in the THRESHOLDS 2006 cruise. GPP showed a diversity of vertical profiles, from lack of vertical structure

BGD

6, 8569–8588, 2009

to strong vertical heterogeneity with surface or deep maxima (Fig. 3b). CR averaged 3.8± 0.5 mmol O_2 m^{-3} d^{-1} and also remained, for the majority of stations, below 10 mmol O_2 m^{-3} d^{-1} throughout the sections (Table 1). CR was significantly higher in THRESHOLDS 2006 than in THRESHOLDS 2007 (Kruskal-Wallis test, p=0.031). CR also showed a diversity of vertical profile patterns across the stations, typically including a subsurface maximum (Fig. 3c).

NCP averaged –0.8±0.6 mmol O_2 m^{-3} d^{-1} across the sections (Table 1) and showed contrasting vertical patterns (Fig. 3a). NCP was similar between the THRESHOLDS 2006 and 2007 cruises and did not differ across the basins. NCP values were below 5 mmol O_2 m^{-3} d^{-1}, with a prevalence of negative values (70% of the estimates) indicative of a prevalence of net heterotrophic communities during the two cruises. The median *P/R* ratio was 0.6 indicating also a strong prevalence of heterotrophic communities (*P/R*<1) along the studied sections. The majority of the Mediterranean regions examined supported heterotrophic communities, except for the Ionian Sea with a *P/R* ratio of 1.35 (Table 3), where autotrophic communities prevailed.

The *P/R* ratio tended to increase significantly (r^2=0.36, p<0.05) with increasing gross primary production (Fig. 4) implying that the studied communities tended to be net heterotrophic (i.e. *P/R*<1) at low GPP and net autotrophic at high GPP. The volumetric GPP required for production to balance respiration (GPP at GPP=R) was 3.5 mmol O_2 m^{-3} d^{-1}, with the GPP threshold for the Western basin being 2-fold higher (GPP=7.6 mmol O_2 m^{-3} d^{-1}) than that for the Eastern basin (GPP=3.0 mmol O_2 m^{-3} d^{-1}).

4 Discussion

The two cruises presented here showed a broad range of planktonic metabolic rates across the Mediterranean. The volumetric GPP and CR, as well as the chlorophyll a concentration, were significantly higher during THRESHOLDS-2006 than THRESHOLDS-2007 (Kruskal-Wallis test, p<0.001). Whereas GPP and NCP tended to be somewhat higher in the western compared to the eastern basin, these differences were not statistical significant, so no significant West-East gradient in planktonic metabolism was supported by our data.

Planktonic communities across the studied sections tended to be heterotrophic during the early summer, consistent with available reports of metabolic seasonality for the NW Mediterranean littoral (Duarte et al., 2004; Navarro et al., 2004; Satta et al., 1996). The prevalence of heterotrophic conditions during the studied period was consistent with the supersaturation in CO_2 of surface Mediterranean waters across the THRESHOLDS 2006 cruise, with the mean pCO_2 in surface waters exceeding atmospheric equilibrium by, on average, 40±14 ppm (Vaquer-Sunyer, unpublished data). In contrast, the mean atmospheric pCO_2 during THRESHOLDS 2007 was 371 μatm (mean sea-air difference −18±4 ppm), implying that the Mediterranean Sea acted as a sink for atmospheric CO_2 (Alvarez, unpublished data), possibly a legacy from a spring bloom preceding this cruise. The *P/R* ratio increased with increasing GPP indicating that the most productive areas, associated with the Sicily-Tunisia Strait separating the West and East basins, tend to support net autotrophic planktonic communities.

Turley (2000) reported significant gradients between the western and the eastern basin in primary production (West to East ratio=3.33, p=0.018, t-test), bacterial production (West to East ratio=1.87, p=0.029) and bacterial growth rate (West to East ratio=2.27, p=0.007). Our data suggest a similar trend across basins for GPP (West to East ratio=1.37, p=0.68, t-test) and for CR (West to East ratio=1.74, p=0.37, t-test), consistent with the enhanced bacterial abundance and activity in the Western basin reported by Turley (2000). Hence, NCP in the Western basin tended to be more negative than that in the Eastern Basin (Table 2). However, the important variability within basins rendered these differences in metabolic rates not statistically significant (p=0.88, t-test). Although GPP seems to be enhanced in the less oligotrophic Western basin relative to the Eastern basin, CR is increased as well as riverine inputs are accompanied by important loads of organic matter (Lefèvre et al., 1997; Moutin et al., 1998; de Madron et al., 2002) that enhance community respiration. Accordingly, planktonic communities in the Western Mediterranean also tended to be heterotrophic in this study.

This study reports the first assessment of planktonic community metabolism across the Mediterranean, as previous reports focussed on particular regions, mostly coastal areas in the NW Mediterranean (Table 3, Fig. 5). Both the results reported here and all of the published reports of planktonic community metabolism in the Mediterranean, except that of Gazeau et al. (2005), report a negative mean NCP, indicative of a prevalence of heterotrophic communities in the Mediterranean Sea (Table 3, Fig. 5). In addition to riverine inputs, atmospheric inputs, which are high across the Mediterranean (Guerzoni et al., 1999), are an important source of organic carbon (Dachs et al., 2005; Jurado et al., 2008), providing, along with riverine inputs, the allochtonous carbon required to support net heterotrophic communities.

The metabolic rates observed in the THRESHOLDS cruises were somewhat higher than previously reported rates (Table 3). This could be explained by the fact that most previous studies were conducted during the winter and/or fall, whereas planktonic metabolic rates are highest, both for CR and GPP, in early summer, when an increase in metabolic rate per unit autotrophic and heterotrophic biomass is observed in the Mediterranean Sea (Satta et al., 1996; Duarte et al., 2004). Also some of the literature rates were derived from shallow littoral stations (Table 3), where vertically-integrated metabolic rates were constrained by the water column depth available.

Our study shows that net heterotrophic communities prevailed at GPP rates $<4\,\mathrm{mmol\,O_2\,m^{-3}\,d^{-1}}$ for the studied sections of the Mediterranean Sea. The GPP threshold for metabolic balance for this study is somewhat higher than those reported earlier for NW Mediterranean coastal areas (Bay of Palma: $2.8\,\mathrm{mmol\,O_2\,m^{-3}\,d^{-1}}$, Navarro et al., 2004; and Bay of Blanes: $3.8\,\mathrm{mmol\,O_2\,m^{-3}\,d^{-1}}$, Duarte et al., 2004) and well above that for the global ocean ($1.1\,\mathrm{mmol\,O_2\,m^{-3}\,d^{-1}}$, Duarte and Regaudie-de-Gioux, 2009), implying that the GPP necessary to balance community respiration for Mediterranean communities is three times higher than that for the global ocean. This suggests that a higher gross primary production is required to compensate for the excess respiration supported by the high inputs of allochthonous organic carbon to the Mediterranean Sea.

In conclusion, the study presented here provides evidence that the planktonic communities of the studied regions in the Mediterranean Sea tend to be net heterotrophic, as supported by previous reports from studies conducted mostly in coastal areas. Whereas the Western Mediterranean supports a higher gross primary production than the eastern basin does, it also supports higher community respiration rates, so that net community production tends to be more negative in the Western than in the Eastern basin. The net heterotrophy nature of the Mediterranean Sea indicates that the planktonic communities in the Mediterranean Sea should act as CO_2 sources, largely driven by the allochthonous organic carbon inputs that subsidise planktonic respiration. Hence, planktonic metabolism in the Mediterranean Sea is likely to be very sensitive to changes in organic carbon inputs. Regulation of major rivers (Rhône, Ebro, Nile, Po) discharging in the Mediterranean, changes in the aerosol load over the Mediterranean, and increased human population in the basin may all have affected community metabolism and the role of planktonic communities in the CO_2 budget of the Mediterranean Sea.

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Table 1. Mean, SE, Range and number of estimates of volumetric gross primary production (GPP), community respiration (CR) and net community production (NCP) rates (mmol $O_2\ m^{-3}\ d^{-1}$) in the western and eastern Mediterranean basins, during THRESHOLDS 2006 (1) and 2007 (2).

		Western Basin		Eastern Basin	
		1	2	1	2
GPP	Mean	4.5	2.9	4.9	1.2
	SE	2.3	1.1	1.3	0.2
	Minimum	2.1	0.6	1.1	0.1
	Maximum	9	8	15.1	2.9
	N	3	7	10	25
CR	Mean	6.4	6.2	4.8	2.4
	SE	3.4	2.3	0.8	0.4
	Minimum	2.4	0.6	0.9	0.1
	Maximum	13.1	16.9	8.9	8.2
	N	3	7	10	25
NCP	Mean	−2.6	−2.7	0.22	−0.4
	SE	9.5	1.4	1.3	0.6
	Minimum	−18.6	−8.9	−2.8	−6.4
	Maximum	11.1	1.4	11.8	8.1
	N	6	8	11	28

BGD

6, 8569–8588, 2009

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Table 2. Western to Eastern ratios of planktonic community components and processes integrated to the DCM (Deep Chlorophyll Maximum). Ratios for this study were calculated as the ration of the mean value for each basin.

Variable	West:East	References
Bacteria biomass ($mg\ C\ m^{-2}$)	0.75	Turley et al. (2000)
Bacterial production ($mg\ C\ m^{-2} d^{-1}$)	1.87	Turley et al. (2000)
Bacterial growth rate (d^{-1})	2.27	Turley et al. (2000)
Net Primary Production ($mg\ C\ m^{-2}\ d^{-1}$)	3.33	Turley et al. (2000)
Chlorophyll ($mg\ m^{-2}$)	1.13	Turley et al. (2000)
Chlorophyll a ($mg\ m^{-2}$)	1.55	This study
GPP ($mmol\ O_2\ m^{-2}\ d^{-1}$)	1.37	This study
CR ($mmol\ O_2\ m^{-2}\ d^{-1}$)	1.74	This study
NCP ($mmol\ O_2\ m^{-2}\ d^{-1}$)	1.46*	This study

* Mean net community production was negative, heterotrophic, so that the ratio >1 implies NCP to be more negative in the Western than in the Eastern basin.

Table 3. Geometric mean of the integrated (euphotic zone) planktonic metabolic rates (mmol O_2 m^{-2} d^{-1}) and of the *P/R* ratio for different studies of planktonic communities metabolism in the Mediterranean Sea (Fig. 1). The number of stations (N station) and number of individual volumetric estimates (N depth) in each study is also shown. We just took into account stations with metabolism analysed for 3 depths. a: data reported in carbon units convered to oxygen units assuming a 1.25 molar stoichiometry between O_2 and C. n.d. = not determined.

Ref.	Authors	Region	Date	Depth (m)	GPP	R	NCP	*P/R*	N stations	N depth
1	Lefèvre et al. (1997)	Gulf of Lions	12/1988 – 03/1992	53	72.2	72.7	−0.5	1	19	83
2	Duarte et al. (2004)	Bay of Blanes	03/1988 – 10/1994	5	12.9	23.4	−10.5	0.6	333	333
3	Lucea et al. (2005)	Bay of Blanes	01/1996 – 12/1997	15	28.3	41.3	−13.0	0.7	23	23
4	Lefèvre et al. (PANGEA 2001)	Alboran Sea	12/1997-01/1998	60	34.8	40.3	−5.5	0.9	8	40
5	VanWambeke et al. (2004)	Alboran Sea	12/2001 – 01/2002	80	25.9	33.0	−7.1	0.8	7	n.d.
6	Navarro et al. (2004)	Bay of Palma	06/2001 – 10/2002	7	23.2	27.9	−4.7	0.8	14	14
7	Gazeau et al. (2005)	Bay of Palma	03/2002 – 06/2002	26	68.0	54.0	15	1.3	4	32
8	Robinson (2000)	Aegean Sea	06/1996; 09/1996; 06/1997	7	25.2	130.2	−105.0	0.2	10	16
	This study	Western basin	06/2006; 05/2007	54	195.9	370.3	−155.4	0.6	3	9
	This study	Eastern basin	06/2006; 05/2007	63	118.6	156.9	−82.9	1.3	9	27

BGD
6, 8569–8588, 2009

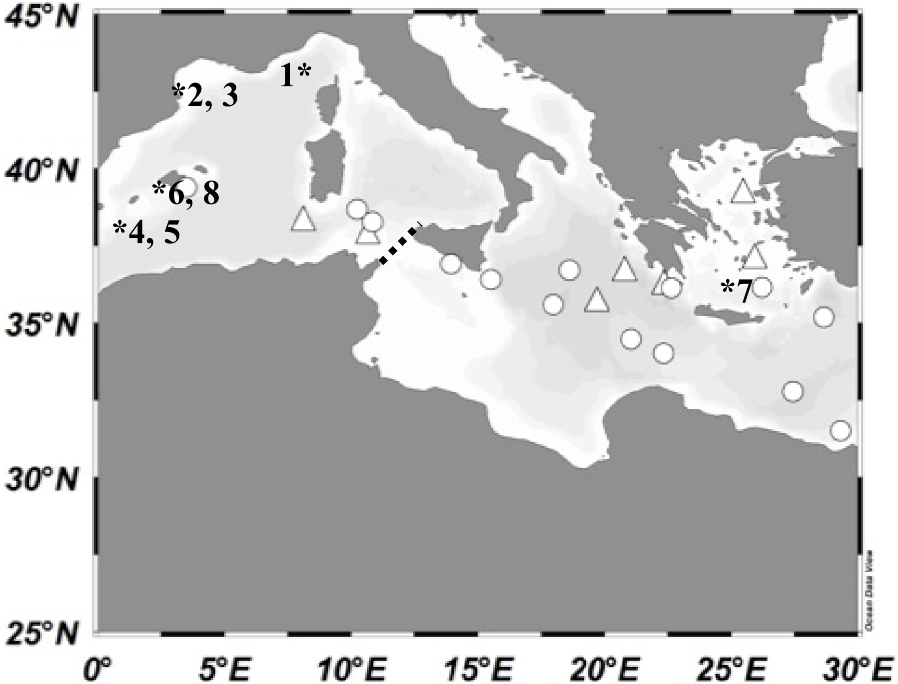

Fig. 1. Distribution of the stations occupied for planktonic metabolism determinations during the THRESHOLDS-2006 (triangles) and THRESHOLDS-2007 (circles) cruises. The dotted line delimits the western and the eastern basin across the Sicily-Tunisia Strait (SIS). Also shown the location of previous studies of community metabolism, marked with asterisks (*) with the reference number of the studies shown in Table 3.

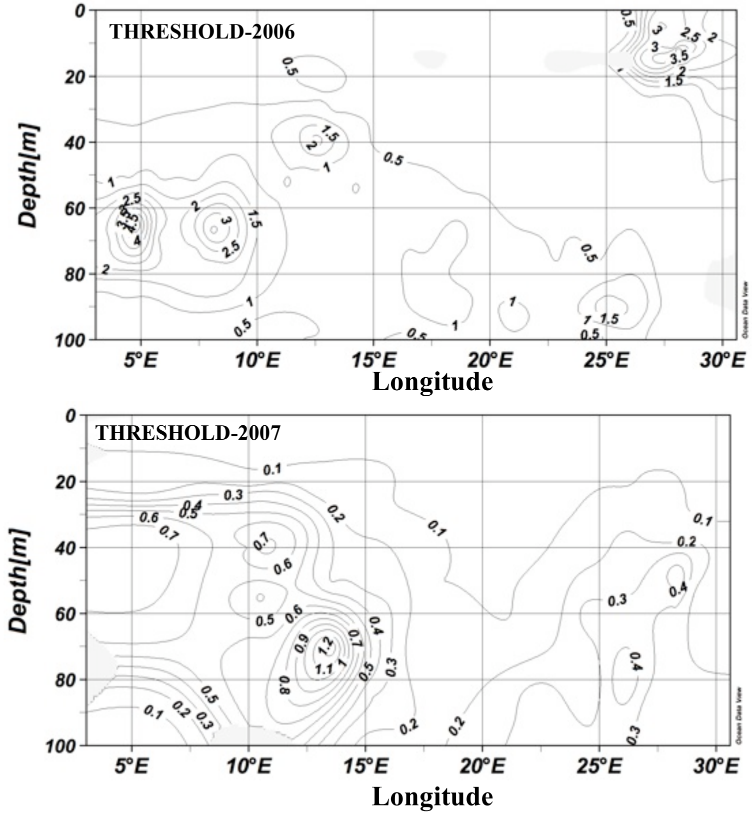

Fig. 2. Chlorophyll a (mg m^{-3}) profiles across the Mediterranean Sea during the THRESHOLDS-2006 and THRESHOLDS-2007 cruises.

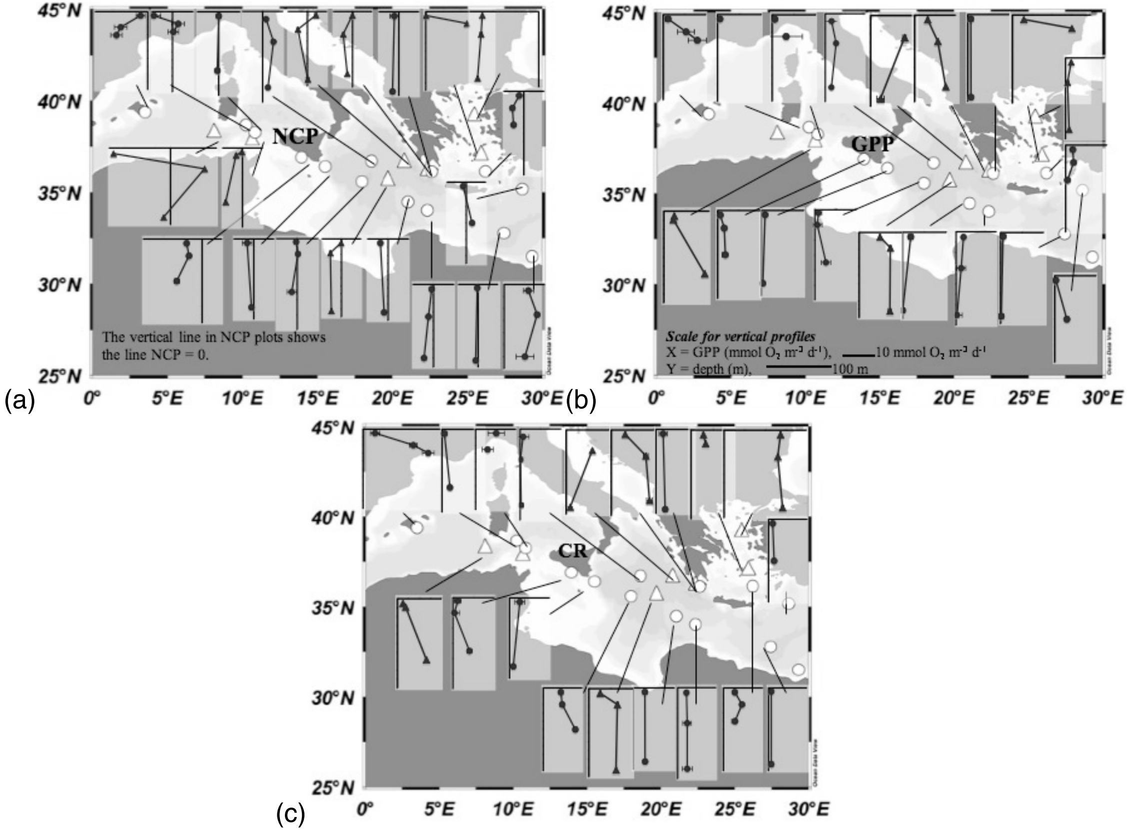

Fig. 3. Vertical profiles of gross primary production (GPP, mmol O_2 m^{-3} d^{-1}), community respiration (CR, mmol O_2 m^{-3} d^{-1}) and net community production (NCP) (mmol O_2 m^{-3} d^{-1}) profiles at each station along the Mediterranean studies combined for the THRESHOLD-2006 (triangles) and 2007 (circles) cruises.

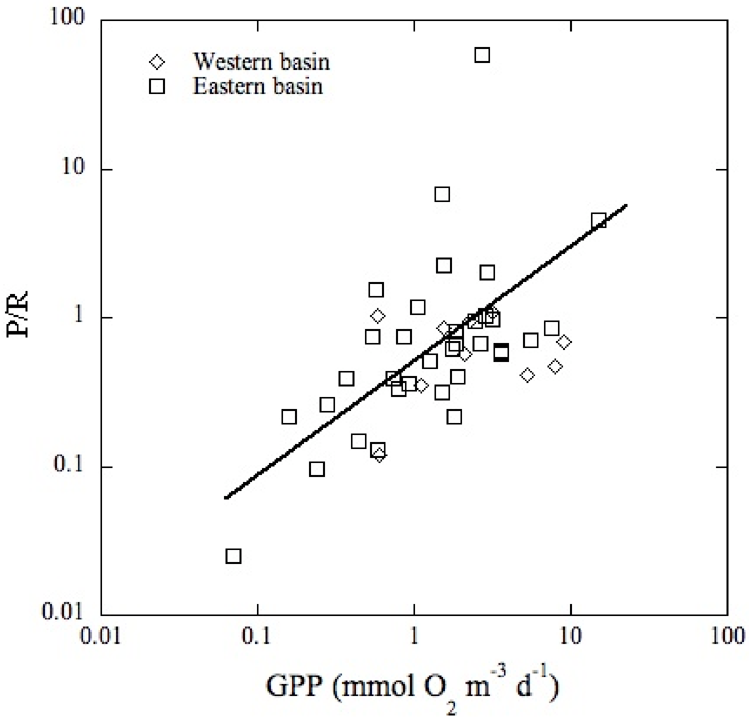

Fig. 4. The relationship between the gross primary production to community respiration ratio (*P/R*) and gross primary production (mmol O_2 m^{-3} d^{-1}) in the Western (diamonds) and Eastern (squares) basins of the Mediterranean Sea. The solid line shows the fitted linear regression model II equation (both basins): P/R=0.26(±0.03) GPP+0.09(±0.12) (r^2=0.36, p<0.05).

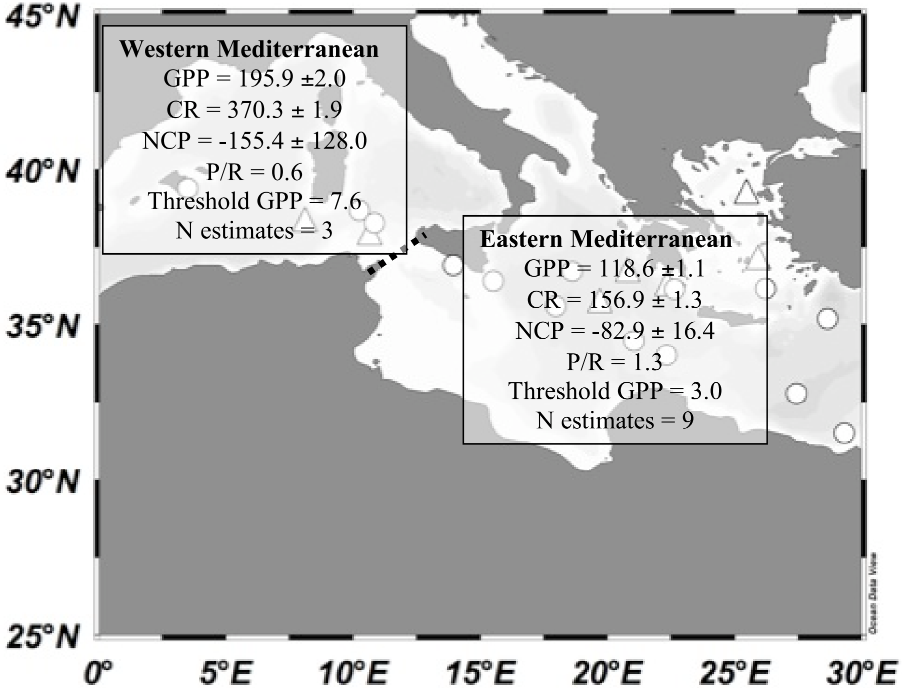

Fig. 5. Integrated (0–100 m) geometric mean (± SE) metabolic rates (mmol O_2 m^{-2} d^{-1}) in the western and eastern basins (N=22), along with the corresponding geometric mean *P/R* ratio, threshold GPP for GPP=R, and number of estimates (*N*) for this study. The Geometric means were calculated for stations with metabolism analysed at 3 depths.