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Microplankton respiration and net community metabolism in a bay on the NW Mediterranean coast

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ABSTRACT: The seasonal variation in the respiration and net community metabolism of microplanktonic communities was examined in the Bay of Blanes, an exposed NW Mediterranean bay (NE Spanish coast) which receives intermittent inputs from a torrential river, based on estimates of respiration rates of microplanktonic communities obtained over 2 yr (March 1992 to March 1994). Community respiration rates (mean ± SE = 5.232 ± 0.9 µmol O_2 dm^{-3} d^{-1}) ranged over 2 orders of magnitude, showing a distinct seasonal pattern, with the highest respiration rates in summer and late winter. Differences in respiration rate were independent of ambient temperature but were closely related (r = 0.81) to the biomass of heterotrophic microplankton, which was dominated by bacteria and heterotrophic ciliates. The microplankton community in the Bay of Blanes tended to be net heterotrophic on the annual time scale, with demands exceeding autochthonous production. Net daily autotrophic metabolism was only observed during periods of very low respiration rates, and heterotrophic organisms played a dominant role in the metabolism of the NW Mediterranean littoral community studied, as evidenced by a strong correlation between net community metabolism and respiration rates. There was substantial interannual variation in metabolic rates between years, with average respiration rates in the first year twice as high as those in the second year (6.816 ± 1.728 and 3.672 ± 0.374 µmol O_2 dm^{-3} d^{-1}, respectively). This resulted in a more heterotrophic net daily community metabolism during the first than during the second year (−1.258 ± 0.94 and 0.978 ± 0.344 µmol O_2 dm^{-3} d^{-1}, respectively). The net heterotrophic nature of the microplanktonic community in the Bay of Blanes indicates that carbon demands should be partially satisfied from inputs from land, consistent with the much higher rainfall in the first, compared to the second, year. Variability in rainfall and the associated differences in carbon inputs from land are, therefore, major sources of interannual differences in the microplanktonic metabolism of the NW Mediterranean littoral.

KEY WORDS: Microplankton · Net production · Seasonal variation

INTRODUCTION

Planktonic primary production shows a distinct seasonality in temperate waters, coupled to seasonal changes in water-column dynamics (Sverdrup 1953, Ryther & Yentsch 1958, Jacques 1970, Kenney et al. 1988, Parsons & Lalli 1988). The seasonal variability of microplanktonic heterotrophic metabolism may be coupled to that of primary production as observed by some authors (Simon & Tilzer 1987, Hoch & Kirchman 1993), while others report no evidence of this coupling (Ducklow & Kirchman 1983, Coffin & Sharp 1987, Findlay et al. 1991). Coastal areas often show enhanced primary production, largely derived from nutrient inputs from land, which typically result in enhanced heterotrophic planktonic metabolism as well; however, inputs from land also include organic carbon and, as a result, heterotrophic metabolism and primary production may be uncoupled in coastal ecosystems.

The seasonal development of primary production off the Spanish Mediterranean coast involves the occurrence of several phytoplankton blooms, typically in

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autumn (October–November), late winter (late February–early March), and summer (mid-July) (Herrera & Margalef 1963, Coste et al. 1967, Margalef & Ballester 1967, Jacques 1970, San Feliu & Muñoz 1975, Nival et al. 1976, Williams & Robinson 1990, Mura et al. 1996, Satta et al. in press). Mediterranean coastal areas receive inputs from the discharge of torrential rivers which flow only after heavy rain. These inputs of land-derived carbon may enhance respiration but there is, however, remarkably little information on the seasonal variation of microplanktonic respiration (Williams & Robinson 1990, 1991). As a consequence, the seasonality in the metabolic balance of planktonic communities in the Mediterranean coast remains unresolved.

Here we examine the seasonal variation in microplankton (<200 µm) respiration and net community metabolism in the Bay of Blanes (NE Spanish coast), an exposed Mediterranean bay which receives intermittent inputs from a torrential river (Tordera river). We estimated the respiration rate of microplanktonic communities, sampled at 3 to 7 d intervals over 2 yr, and then combined it with estimates of gross primary production (also derived from oxygen evolution rates) reported elsewhere (Satta et al. in press) to characterise the seasonal evolution, as well as the annual balance, of the net planktonic metabolism in this Mediterranean coastal area.

METHODS

Subsurface water samples were collected at a fixed station (41° 39.90' N, 2° 48.03' E) at an average depth of about 15 m in the Bay of Blanes. The Bay is affected by the sporadic discharge of the Tordera river as well as by urban runoff following heavy rain (Cebrián et al. in press). The Bay of Blanes has relatively clear waters, with low nutrient concentrations and plankton biomass throughout most of the year (Table 1), and little, if any, vertical heterogeneity in water properties, since the thermocline is offshore from the Bay (about 50 m depth; Cebrián et al. in press). Sampling was carried out twice a week from March 1992 to March 1993 and once a week from March 1993 to March 1994. Sampling frequency was increased (to 1 or 0.5 d^{-1}) at the time of phytoplankton blooms.

Surface water was collected with clean 5 l bottles from an outboard motor boat and kept refrigerated while transported to the laboratory (within 30 min). In the laboratory, a variable water volume (50 to 500 ml, depending on phytoplankton biomass) was filtered through Whatman GF/F filters for fluorometric analysis of chlorophyll *a* concentration (Parsons et al. 1984). The filters were homogenised and kept refrigerated in the dark while pigments were extracted in 90% acetone for ca 6 h. Fluorescence was measured, following extraction, in a Turner Designs fluorometer calibrated with pure chlorophyll *a* (Sigma Co., Madrid, Spain) (Holm-Hansen & Riemann 1978).

Community respiration rates and net metabolism were calculated from oxygen variations after incubation of samples in 'light' and 'dark' bottles. Water samples for the measurement of respiration rates and net metabolism were bubbled with gaseous nitrogen to reduce the initial oxygen concentration whenever the water was oversaturated with oxygen (e.g. bloom periods) to avoid the formation of bubbles during incubation. Water was then filtered through a 200 µm mesh (to exclude larger zooplankton) and carefully siphoned into 125 ml narrow-mouth Winkler bottles. Respiration rates were calculated from changes in oxygen concentration after incubation of samples in the dark. Four replicate bottles were immediately used to determinate the initial oxygen concentration, and incubations of 'dark' and 'light' bottles were carried out using 5 replicates each. These bottles were incubated for 20 to 24 h at surface sea temperature in a thermostatic bath or in an incubator. The relatively long incubation times, similar to those used for plankton-poor waters (Williams & Jenkinson 1982), were necessary to obtain reliable estimates of oxygen changes in these sparse plankton communities (Mura et al. 1996). 'Light' bottles, used to calculate net metabolism, were incubated at 200 µmol photons m^{-2} s^{-1}. This light intensity suffices to saturate phytoplankton photosynthesis, which is light-saturated *in situ* throughout most of the year in the Bay of Blanes, as was concluded from an examination of photosynthesis-irradiance curves obtained in different seasons and *in situ* underwater irradiance (Satta et al. in press). The net community metabolism measured in this way was converted to diel (24 h) estimates by considering the length of the daytime and nighttime periods *in situ* for each sampling event.

Table 1. Summary of environmental conditions and relevant biotic properties in the water column of the Bay of Blanes. Values represent mean and range of total values from a 2 to 3 yr monitoring programme

Parameter	Mean	Max.	Min.
Chl *a* (µg l^{-1})	0.88	5.75	0.09
Bacteria (cells l^{-1})	0.48×10^9	1.45×10^9	0.24×10^8
Ciliates (cells l^{-1})	3.44×10^3	18.3×10^3	0.16×10^3
Flagellates (cells l^{-1})	7.86×10^5	39.4×10^5	0.92×10^5
NO_3 (µmol l^{-1})	1.34	5.57	0.02
PO_4 (µmol l^{-1})	0.28	5.31	0.01
Temperature (°C)	17.41	26.27	11.31
Attenuation coef.	0.11	0.15	0.07
Surface irradiance (µE m^{-2} s^{-1})	760.3	1282	174.0

Dissolved oxygen concentration was measured using a high-precision Winkler titration after Carritt & Carpenter (1966), using a Mettler DL-21 Autotitrator for the potentiometric (redox electrode) end-point detection (Oudot et al. 1988). The average coefficient of variation of the dissolved oxygen concentration was 0.5%, and the resulting detection limit for respiration rates was about 0.744 µmol O_2 dm^{-3} d^{-1}. An oxygen electrode (Orbisphere Laboratories, model 2607, sensor 2112) was used to measure dissolved oxygen during the first 2 mo of the study.

The abundance of bacteria and nanoflagellates was determined by epifluorescence microscopy, and that of ciliates using an inverted microscope. Duplicate water samples for bacteria and nanoflagellates were preserved with formaldehyde (0.5% final concentration) and glutaraldehyde (1% final concentration), respectively, and stained with 4',6-diamidino-2-phenylindole (DAPI; Porter & Feig 1980). A 100 ml sample was preserved in a 1% final concentration of Lugol's solution for enumeration of ciliates. Ciliates were counted after settling using an inverted microscope at 200× magnification. Biovolume of bacteria and protists was calculated from cell dimensions by approximation to the nearest geometric figures.

Table 2. Monthly mean, minimum (min.), and maximum (max.) instantaneous planktonic respiration and net production rates (all rates in µmol O_2 dm^{-3} d^{-1}) in the Bay of Blanes

Year	Month	Respiration			Net production		
		Mean	Min.	Max.	Mean	Min.	Max.
1992	Mar	21.15	6.37	45.00	−17.73	−38.77	−5.36
	Apr	10.87	6.75	15.00	−8.01	−10.77	−5.24
	May	4.93	0.61	10.43	−3.14	−6.17	0.60
	Jun	7.32	2.20	11.37	−3.04	−8.15	4.39
	Jul	12.35	2.48	21.67	−5.08	−16.33	4.40
	Aug	7.40	3.12	16.00	−5.88	−13.23	−2.10
	Sep	9.77	7.57	11.97	−9.56	−11.75	−7.37
	Oct	0.39	0.39	0.39	0.30	0.30	0.30
	Nov	3.44	1.18	5.71	1.58	−5.14	1.75
	Dec	0.55	0.55	0.55	0.63	0.63	0.63
1993	Jan	1.93	0.37	2.93	−1.02	−2.23	0.37
	Feb	2.26	0.72	4.63	0.84	−1.33	2.48
	Mar	3.23	0.28	7.53	−1.08	−4.09	1.11
	Apr	2.33	0.78	5.77	−1.10	−4.80	0.63
	May	4.05	2.50	6.06	−0.74	−2.91	0.40
	Jun	5.44	2.17	8.53	−1.84	−5.63	3.10
	Jul	5.92	3.67	9.26	−0.55	−3.55	5.97
	Aug	5.35	2.53	8.17	−2.57	−4.33	−0.81
	Sep	3.72	2.38	4.66	−1.84	−3.90	1.79
	Oct	2.31	0.52	3.76	0.92	−0.94	3.07
	Nov	2.12	0.42	3.80	−0.07	−2.99	1.25
	Dec	1.79	0.74	3.73	−0.86	−3.30	0.53
1994	Jan	2.15	1.06	3.82	−0.82	−1.12	−0.44
	Feb	2.45	0.05	5.70	0.39	−1.20	2.72
	Mar	5.17	1.20	9.22	−3.47	−7.12	0.53

RESULTS AND DISCUSSION

Microplankton (<200 µm) community respiration showed great variability during the study period, with a minimum of 0.05 µmol O_2 dm^{-3} d^{-1}, at levels where the method is inaccurate, and a maximum of 45.00 µmol O_2 dm^{-3} d^{-1} (Table 2). During the first year, the highest monthly average respiration was detected in March (Fig. 1). This value represented the highest individual rate measured over the 2 yr of study (Table 2) and corresponded with the highest chlorophyll *a* concentration observed in the 2 yr study (5.1 mg chl *a* m^{-3}). Other periods of enhanced respiration were detected in July and September 1992, while the minimum respiration rate was detected in October 1992 (Fig. 1). During the second year respiration remained low throughout winter and increased in summer with a maximum detected in July 1993, reduced values in autumn and early winter, and a subsequent increase in March 1994 (Fig. 1). These results suggest a consistent seasonal pattern in microplankton community respiration during both years, with increased respiration rates in summer (July) and late winter (March) and reduced rates during spring and autumn. This pattern deviates from the few available reports on the seasonality of plankton community respiration in other seas, which indicate a single period of enhanced respiration during summer in the coastal Atlantic sites studied (Randall & Day 1987, Kenney et al. 1988, Sampou & Kemp 1994). However, Williams & Robinson (1990), working in the French Mediterranean coastal area off the Rhone river, also found respiration rates to be as high in winter as they were in summer. This suggests that the seasonal pattern of microplanktonic respiration in the Mediterranean Sea, similar to that of gross production (Satta et al. in press), may deviate from that reported for other temperate waters. Respiration rates in the Bay of Blanes were between those reported for typically oligotrophic (Williams et al. 1983, Williams & Robinson 1990) and for eutrophic (Sand-Jensen et al. 1990, Sampou & Kemp 1994) waters.

The time course of respiration rate resembled that of microheterotroph biovolume (Fig. 1), suggesting a close association between community respiration rate and the biomass of microheterotrophs. The biomass of microheterotrophs (Fig. 1) was greatest following

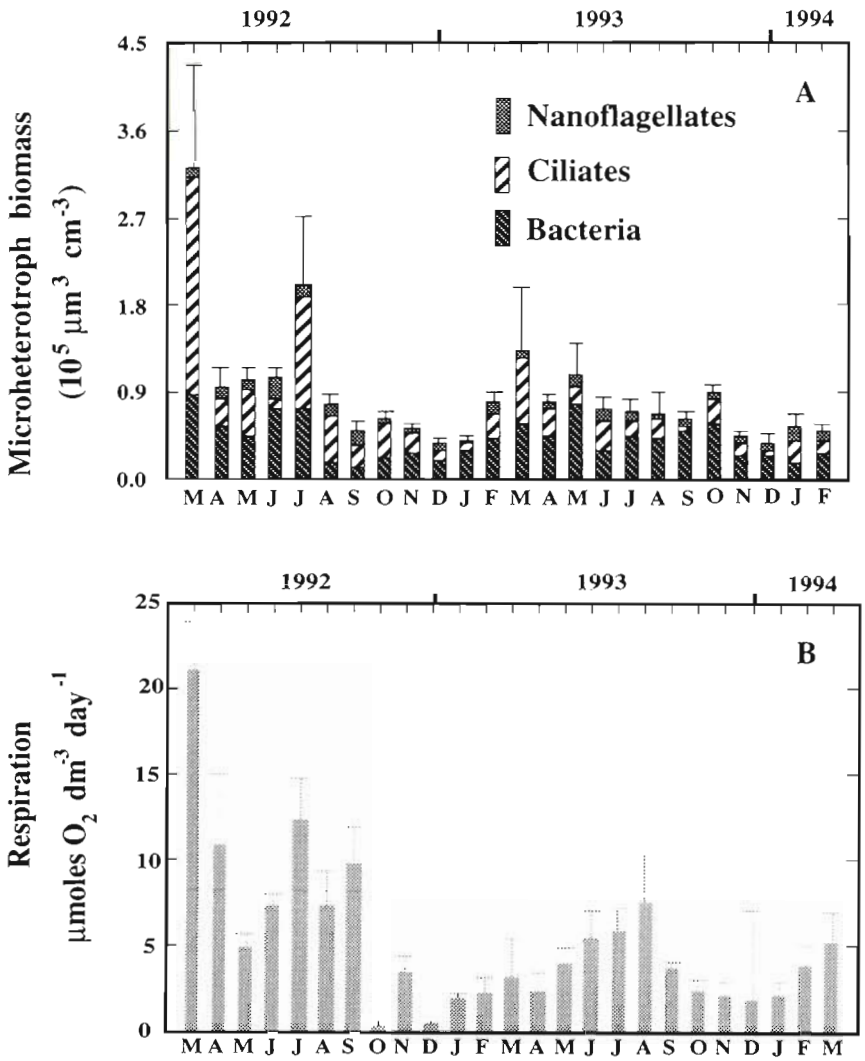

Fig. 1. Temporal variation in monthly mean (± SE) of the (A) biovolume of planktonic microherotrophs and (B) microplanktonic respiration rates in the Bay of Blanes from March 1992 to March 1994

phytoplankton blooms (cf. Vaqué in press). Bacteria generally dominated the biomass of microheterotrophs in the bay of Blanes (Vaqué 1996), although ciliates were also an important component in some periods, especially in summer (Fig. 1).

Differences in respiration rate between the 2 years were substantial, with average respiration rates twice as high during the first (6.816 ± 1.728 µmol O_2 dm^{-3} d^{-1}) than during the second (3.672 ± 0.374 µmol O_2 dm^{-3} d^{-1}) year. This considerable interannual variation in respiration rate are likely to be associated with the important interannual differences in meteorological and hydrographic events observed in the Bay of Blanes during the period of the study (Cebrián et al. in press). The most important difference was the substantially greater rainfall during the first year (annual rainfall of 927 and 636 dm^{-3} m^{-2} in 1992-93 and 1993-94, respectively), which involved unusually heavy storms during summer 1992, in addition to the typically heavy rain of spring and autumn (Cebrián et al. in press). These events involve the discharge of substantial loads of particulate and dissolved inorganic materials into the Bay, as reflected in a 4-fold increase, on average, in seston concentration after thunder storms (Duarte unpubl. data). The differences between years in rainfall and the associated input of land-derived materials to the littoral zone were reflected in a higher concentration of dissolved phosphorus during the first year (annual mean phosphate concentration 0.39 ± 0.06 and 0.09 ± 0.02 µmol dm^{-3} in 1992-93 and 1993-94, respectively), when high phosphate concentrations remained during the summer (Duarte unpubl. data).

Planktonic respiration rates were poorly, albeit significantly, correlated with chlorophyll *a* concentration and phytoplankton biomass ($r = 0.44$, $n = 121$, $p < 0.05$). However, the monthly average planktonic respiration rate was strongly correlated ($r = 0.81$, $n = 24$, $p < 0.0001$) with the total biovolume of the microhetero-

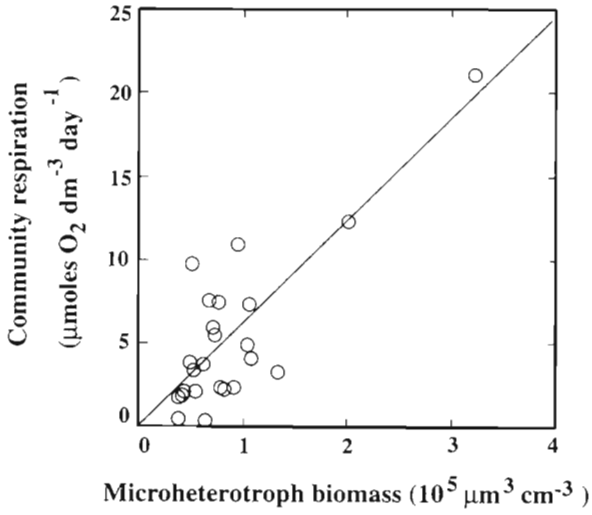

Fig. 2. Relationship between the monthly average microplanktonic respiration rates and biovolume of planktonic microherotrophs in the Bay of Blanes from March 1992 to March 1994

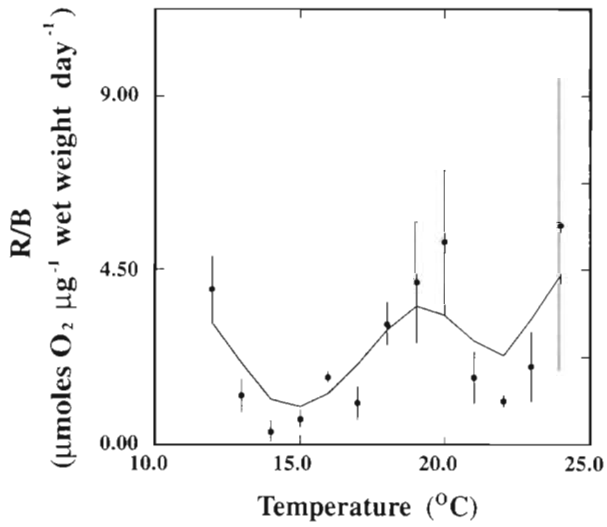

Fig. 3. Relationship between the average (± SE) biomass-specific respiration (R/B) and water temperature in the Bay of Blanes. Solid line represents the underlying tendency as represented by the LOWESS smoothing

trophic community (bacteria, heterotrophic flagellates and ciliates; Fig. 2). The relationship between community respiration (R) and the biovolume of planktonic microheterotrophs (B_h) was best described by the regression equation

$$R\ (\mu mol\ O_2\ dm^{-3}\ d^{-1}) = 0.0622 + 6.089 B_h\ (10^5\ \mu m^3\ ml^{-1})$$
$$r^2 = 0.64,\ n = 24,\ F = 42.5,\ p < 0.00001$$

which indicates that community respiration rises linearly with increasing biomass of microplanktonic heterotrophs. The individual estimates of the biomass-specific respiration rate varied greatly from 0.1008 to 16.903 µmol O_2 μg^{-1} wet wt d^{-1} and did not show any clear relationship with water temperature. There was, however, a tendency for specific respiration to increase with increasing temperature at temperatures ranging between 14°C and 20°C, although specific respiration was high at lower temperatures (Figs. 3 & 4), following the dominant phytoplankton bloom of the year (cf. Mura et al. 1996). This indicates that factors other than temperature, probably involving the availability of labile organic carbon to sustain heterotrophic activity, are most important in controlling the variation observed in biomass-specific microplanktonic respiration in the Bay of Blanes. The low sensitivity of specific respiration to temperature may reflect the fact that high levels of dissolved organic matter (DOM) could counteract the effect of low temperature (Pomeroy et al. 1991). Factors that explain the relatively high winter respiration rates in the Bay of Blanes include riverine inputs, which are associated with increased microheterotroph biomass (Vaqué in press), and the phytoplankton bloom that typically occurs in late winter (late February), the most important bloom of the year (Mura et al. in press, Satta et al. in press) and one that coincides with cold water temperatures (Fig. 4).

Microplankton respiration was poorly ($r = 0.39$, $n = 124$), albeit significantly ($p < 0.00001$), correlated to

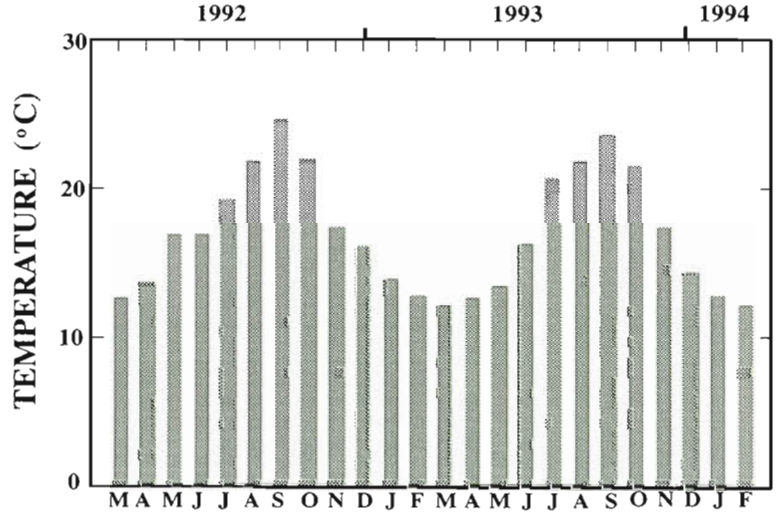

Fig. 4. Time course of monthly averaged water temperature in the Bay of Blanes

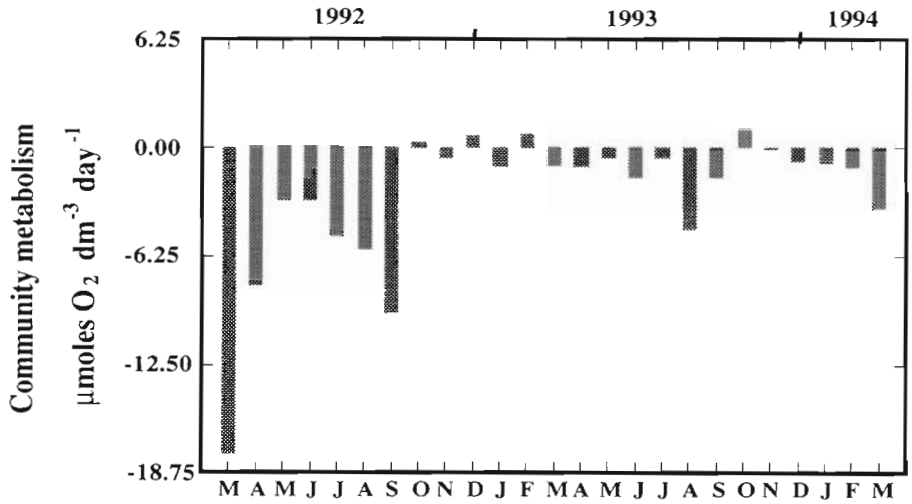

Fig. 5. Time course of monthly averaged net community metabolism in the Bay of Blanes

gross production. The resulting estimates of daily net community metabolism indicates, however, that the microplankton community is net heterotrophic during most of the year, with the communities being net autotrophic only during limited periods. These periods coincided with the months when respiration reached minimal values, usually autumn to early winter (Fig. 5), and with the late winter phytoplankton bloom (e.g. February 1993). As a result, the communities were net heterotrophic at the annual scale, with substantially more negative annual-average net community metabolism the first (-6.1406 ± 0.9406 µmol O_2 dm^{-3} d^{-1}) than the second (-0.9781 ± 0.3437 µmol O_2 dm^{-3} d^{-1}) year. The P/R ratio (the ratio of daily gross production to respiration), which reflects the degree of coupling between production and respiration, showed an average value <1 for the first year (0.58 ± 0.078), whereas it was close to a balance between production and respiration during the second year (0.98 ± 0.12). The changes in net microplankton metabolism over the study period were dominated by changes in community respiration rates, which explained 86% of the variance in net community metabolism ($R^2 = 0.86$, $n = 124$, $p < 0.0001$; Fig. 6). In contrast, we observed no significant correlation between net and gross production ($R^2 = 0.0004$, $n = 124$, $p > 0.9$). As a consequence, the P/R ratio was also negatively correlated with respiration ($R^2 = 0.34$, $n = 124$, $p < 0.0001$).

These results further demonstrate the dominant influence of heterotrophic processes in determining the magnitude and dynamics of planktonic metabolism in the Bay of Blanes. The inputs of land-derived organic and inorganic nutrients to the Bay of Blanes appear to enhance heterotrophic metabolism relative to primary production, driving the system to net heterotrophy, as expected for the coastal ocean in general (e.g Smith & Mackenzie 1987). Moreover, variability in these inputs associated with rainfall variability is likely to be responsible for the major differences in planktonic respiration rates among years. Similarly, Randall & Day (1987) observed a negative correlation between river flow and net production in a Louisiana (USA) estuary. Riverine inputs do not always enhance heterotrophic over autotrophic production. For example, Kenney et al. (1988) showed that net autotrophic production in a temperate estuary of North Carolina, USA, was positively correlated with riverine inputs, as observed by Williams & Robinson (1990) for a coastal NW Mediterranean zone receiving inputs from the Rhone river. The influence of river inputs on net pro-

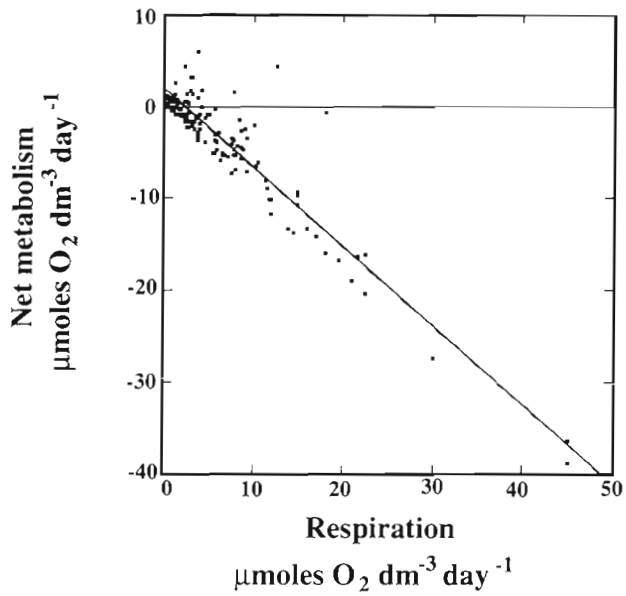

Fig. 6. Relationships between daily net microplanktonic metabolism and daily respiration in the Bay of Blanes. Solid lines represent the fitted least-squares regression equations

duction appears, therefore, to have a strong local component, probably associated with the balance between organic and inorganic nutrients in the discharge and with the nature of the factors limiting planktonic metabolism. Hence, experimental work has shown the phytoplankton community of the Bay of Blanes to be limited by grazers rather than nutrients (Mura et al. 1996), so that river discharge is unlikely to promote primary producers there.

That the microplankton community in the Bay of Blanes remained net heterotrophic over most of the 2 yr study indicates that community metabolism must be supported to a large extent by allochthonous (land-derived) production. The extent of dominance of heterotrophic metabolism also varies substantially among years, with a clear dominance of heterotrophic metabolism occurring during the period of heavy storms observed in 1992, which resulted in a very low annual average P/R. During the second year, however, the proximity of the P/R value to 1 (0.98) indicated a close balance between the carbon produced and that consumed, suggesting that heterotrophic metabolism was mostly dependent on autocthonous production that year. The dominant importance of heterotrophic metabolism in the littoral NW Mediterranean planktonic community studied suggests that nutrient recycling should generally exceed autotroph requirements. As a consequence, community metabolism and biomass in the Bay of Blanes do not appear to be controlled by inorganic resources (cf. Mura et al. 1996), but rather by the availability of organic carbon and its flow in the planktonic food web.

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