

Controls on planktonic metabolism in the Bay of Blanes, northwestern Mediterranean littoral

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Abstract

Long-term and experimental approaches were used to examine the metabolic balance of the planktonic community in the Bay of Blanes (Spanish Mediterranean). Incubation measurements at weekly intervals for 6 yr revealed that community respiration, R , was consistently larger than gross primary production (GPP) by a factor of 2. The plankton community was net heterotrophic for 2/3 of the study period, with a median P/R ratio of 0.65. The biomass of autotrophs comprised, on average, $41\% \pm 3\%$ of the planktonic biomass, and the total microplankton biomass was about 2.5-fold greater than that of the primary producers. The monthly average GPP and R were positively correlated with day length, and the planktonic respiration and gross production per unit microplankton biomass increased with increasing water temperature. Experimental nutrient additions had a greater effect on GPP than respiration rates; the increase in R along the nutrient gradient was $7.8\% (\pm 0.4\%)$ of the increase in GPP. As a result, net community production increased in parallel with GPP, shifting from net heterotrophic at low GPP to net autotrophic when GPP increased because of nutrient additions. Our results show that the R that would be supported by allochthonous inputs was $3.83 \pm 0.67 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$, and the average GPP required to shift the community from net heterotrophic to net autotrophic was about $4 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$. This is well above the average GPP recorded in the Bay of Blanes along this study ($2.56 \pm 0.13 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$), explaining the net heterotrophic nature of the community.

The metabolic status of ecosystems is dependent on the balance between the gross primary production (GPP) and the community respiration (R), such that ecosystems are characterized as net autotrophic whenever they support a positive net community production (NCP) (i.e., $\text{NCP} = \text{GPP} - R > 0$). In contrast, they are characterized as net heterotrophic whenever respiratory losses exceed inputs from autochthonous GPP (i.e., $\text{NCP} = \text{GPP} - R < 0$). Net heterotrophic ecosystems must be supported by allochthonous inputs of organic carbon (Cole 1999). Unproductive marine ecosystems have been often reported to support net heterotrophic planktonic communities (Duarte and Agustí 1998, Hopkinson and Smith in press). These communities are, therefore, dependent on allochthonous inputs of organic matter (Duarte and Agustí 1998). Coastal unproductive pelagic communities may re-

ceive significant inputs of organic matter from adjacent terrestrial and productive benthic ecosystems, often rendering coastal ecosystems net heterotrophic (Smith and Hollibaugh 1993; Caffrey 2004, Hopkinson and Smith in press). Yet, the current debate on the metabolic balance of planktonic communities is centered in open ocean communities, while that of unproductive coastal ecosystems has not received sufficient attention.

An additional reason why the present debate on the metabolic balance of oligotrophic marine ecosystems remains unresolved is the lack of high-resolution time series of pelagic metabolism. Because primary production may occur in pulses, the probability of encountering a productive event is low, resulting in a likely bias toward periods of moderate to low production in conventional cruises (e.g., Karl et al. 2003). Whereas the development of the high-resolution time series of open ocean pelagic metabolism necessary to reliably represent the pelagic metabolic balance remains cumbersome, ease of access to coastal ecosystems renders these possible. Time series of pelagic metabolism in productive coastal communities have shown that production and respiration may be in balance over annual time scales but uncoupled at seasonal ones (e.g., Sherr and Sherr 1996; Serret et al. 1999). Yet, there are at present no high-resolution time series of pelagic metabolism in unproductive coastal waters sustained over sufficient time as to allow balances to be drawn at time scales relevant to test whether the putative net heterotrophic nature of these communities (Duarte and Agustí 1998) is the result of undersampling or a reliable trait of these communities.

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Here we test the expected net heterotrophic nature of the planktonic community of an unproductive coastal ecosystem and test experimentally the expected relation between planktonic metabolism and productivity (Duarte and Agustí 1998). We do so on the basis of a 7-yr time series of planktonic metabolism and community structure resolved at weekly time intervals, and a manipulation experiment whereby the response of planktonic net community metabolism to increasing GPP, achieved through a gradient of nutrient inputs to mesocosms, was tested.

Methods

Sampling—The study was conducted in the Bay of Blanes located in the northwestern Mediterranean Spanish coast (Fig. 1; 41°40,19'N, 2°47,11'E), an open, oligotrophic coastal area (Lucea et al. in press). The Bay of Blanes receives terrestrial inputs from La Tordera River as well as urban runoff from the town of Blanes, which hosts a high number of tourists during summer.

The study extended from March 1992 to November 1998. Subsurface water samples were collected twice a week during 1992 and weekly between 1993 and 1998, from a permanent station 1 km offshore, at a depth of 15 m, where the water column remains well mixed throughout the year (Lucea et al. in press). Samples, collected in acid-washed polyethylene bottles, were taken to the laboratory and processed within 30 min from collection.

Analytical procedures—Water samples for the determination of planktonic metabolic rates were carefully siphoned into 15 125-ml narrow-mouthed Winkler bottles. Five of the bottles were immediately processed to measure the initial oxygen content present in the samples, five transparent ones were incubated for 24 h in the light ($200 \mu\text{mol photon m}^{-2} \text{s}^{-1}$), and the remaining five were incubated for 24 h in the dark at in situ temperature. Dissolved oxygen concentration was measured using high-precision Winkler titration using a Metrohm-682 titrator for the potentiometric (redox electrode) end-point detection (Oudot et al. 1988). The average coefficient of variation (C.V.) of the dissolved oxygen concentration was about 0.35% and the resulting detection limit for net production and respiration was about $0.02 \text{ mg O}_2 \text{ L}^{-1} \text{ d}^{-1}$. Oxygen evolution rates were converted to daily values using the observed corresponding photoperiod. Respiration rates (R) were determined from the oxygen change in the dark bottles, net community production (NCP) was determined from the oxygen change in the clear bottles, corrected for photoperiod, and GPP was calculated as the sum of R and NCP.

The abundance of autotrophic plankton was estimated using flow cytometry (since 1997) or epifluorescence microscopy (1992 to 1996) for picoplankton, epifluorescence microscopy for nanoflagellates and microplankton, and an inverted microscope on concentrated samples for microphytoplankton from the mesocosm experiments. Fresh seawater subsamples from the Bay and from the different experimental bags were filtered through a $50 \mu\text{m}$ mesh, maintained in the dark, and analyzed in a FACSCalibur (Becton Dickinson) flow cytometer for the quantification of picophytoplanktonic cells (Duarte et al. 2000). The cell volume of the cells was

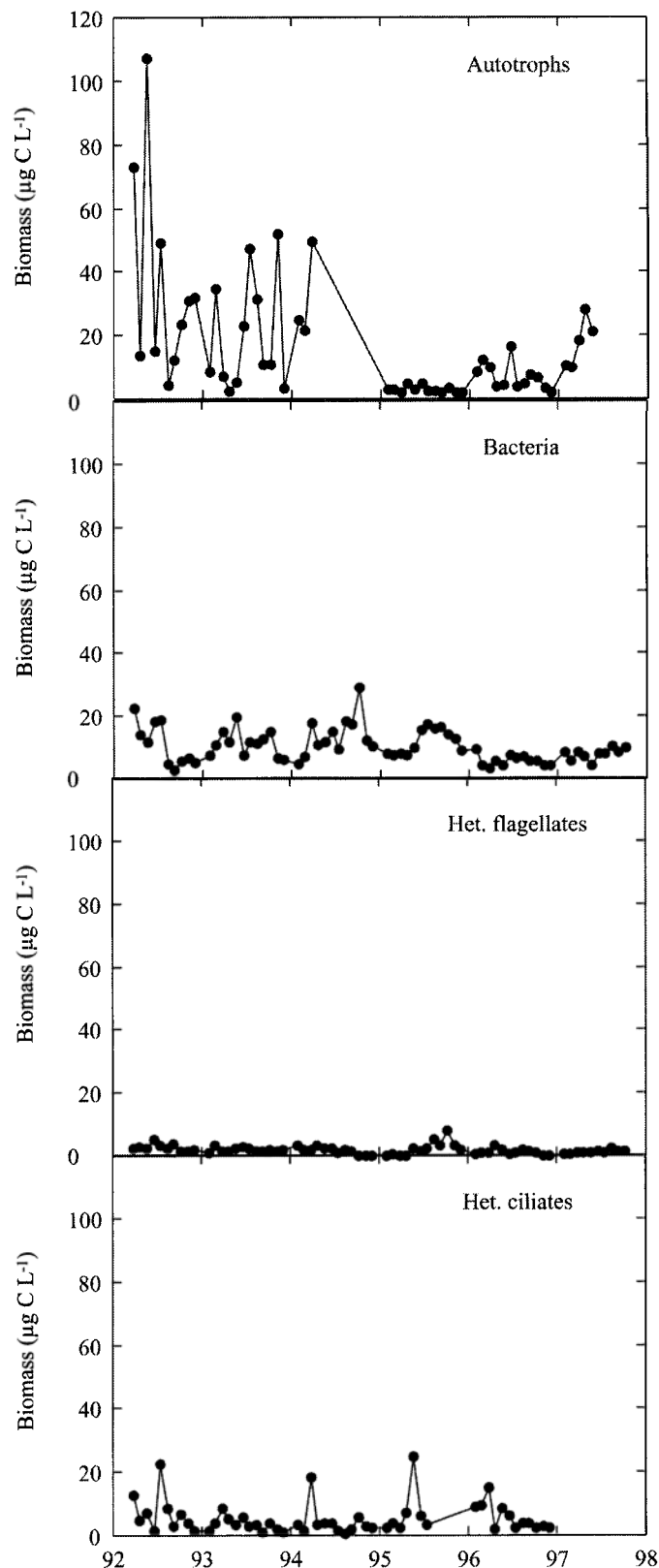


Fig. 1. Time series of the monthly average biomass of different components of the planktonic community in the Bay of Blanes.

Table 1. Average (SE), minimum, and maximum abundance of microplanktonic autotrophs and heterotrophs in the Bay of Blanes (1992–1997).

	Mean	SE	Min	Max
Autotrophs				
Cyanobacteria (cells ml ⁻¹)	10,208	1,446	39	51,320
Diatoms (cells ml ⁻¹)	102.3	17.5	1.5	707.3
Dinoflagellates (cells ml ⁻¹)	73.6	23.5	0	989.8
Flagellates (cells ml ⁻¹)	1,074.6	144.9	8	4,930.7
Heterotrophs				
Bacteria (10 ⁶ ml ⁻¹)	0.57	0.03	0.16	1.24
Het. nanoflagellates (cells ml ⁻¹)	314.8	24.5	16.3	1,220
Ciliates (cells ml ⁻¹)	3.42	0.26	0.61	11

estimated from the mean cell diameter, calculated from the mean forward scattering (FSC) signal of the populations using a calibration curve developed using cultured organisms and fluorescent beads of different diameters (FluoSpheres Size Kit #2, Molecular Probes). The regression equation derived was $\log \text{diameter } (\mu\text{m}) = -3.53 + 0.77 \log \text{FSC}$ ($R^2 = 0.96$, $n = 9$). Picophytoplankton, nanophytoplankton, and microphytoplankton samples, preserved in glutaraldehyde (1% final concentration), were filtered onto 0.6- μm Nucleopore filters and counted and measured at $\times 1,000$ magnification under an epifluorescence microscope. Microphytoplanktonic samples from the mesocosm bags (0.5 to 2 L, depending on density), preserved in glutaraldehyde (1% final concentration), were preconcentrated into 10 ml using a Millipore concentrator chamber with 5 μm pore size membranes and were enumerated and counted at $\times 200$ and $\times 320$ magnification under an inverted microscope (Duarte et al. 2000). Cell volume was calculated from microscopical measurements of the linear dimensions of the cells, and used to calculate phytoplankton biovolume as the product of cell abundance and cell volume. Autotrophic carbon was calculated from biovolume estimates by assuming cyanobacteria to contain 0.123 $\text{pg } \mu\text{m}^{-3}$ (Waterbury et al. 1986), and using the equations provided by Strathmann (1967) for the other groups.

Bacterioplankton samples, preserved in glutaraldehyde (1% final concentration), were filtered onto 0.2 μm Nucleopore filters and counted and measured at $\times 1000$ magnification under an epifluorescence microscope. Bacterial volume ($\mu\text{m}^3 \text{ cell}^{-1}$) was converted to weight using the carbon to volume relation derived by Norland (1993):

$$\text{pgC cell}^{-1} = 0.12 \text{ volume}^{0.7}$$

A 100-ml subsample from each seawater sample was preserved with cold glutaraldehyde (1%, final concentration) for 4', 6-diamidino-2-phenylindole (DAPI) counts of heterotrophic nanoflagellates by epifluorescence microscopy (Porter and Feig 1980). Subsamples of 10 to 15 ml were filtered, within 24 h of collection, through 0.6- μm black polycarbonate filters to collect nanoflagellates. These were stained with 1 $\mu\text{g ml}^{-1}$ final DAPI concentration for 5 min and mounted on microscope slides with nonfluorescent oil. The filters were kept frozen until microscope inspection, which occurred before 1 month of sampling. At least 100 cells were counted and measured in each sample. We distinguished col-

orless nanoflagellates, which we assumed were heterotrophic, from pigmented flagellates, which we assumed to be phototrophic. However, we are aware that some of the nanoflagellates that we considered phototrophic could be mixotrophic. Heterotrophic nanoflagellate biovolume was calculated as the product of cell abundance and cell volume, estimated from cell dimensions by approximation to the nearest geometrical figure. Carbon biomass was estimated assuming a carbon content of 0.22 $\text{pg } \mu\text{m}^{-3}$ (Børsheim & Bratbak 1987).

Ciliate abundance was examined in single 100-ml samples, which were preserved in a 1% final concentration of acidic Lugol solution, and sedimented in 100-ml chambers for at least 48 h before enumeration, at $\times 200$ or $\times 400$ magnification, using an inverted microscope attached to a video camera. Enumeration and sizing were performed from the images recorded in the videotape. Ciliate average size was determined after measuring all cells recorded per sample (from 50 to 200 cells). Ciliate cell volume was measured by approximation to the nearest geometric figure, and ciliate biovolume was calculated as the product of cell abundance and cell volume. To avoid the probable underestimation of ciliate volume due to fixation with Lugol solution (Leaky et al. 1994; Stoecker et al. 1994), the average cell volume was converted to carbon equivalents using the factor experimentally derived for Lugol's-fixed marine oligotrichs of 0.2 $\text{pg } \mu\text{m}^{-3}$ (Putt and Stoecker 1989), except for tintinnid carbon, which was estimated using the experimentally derived factor of 0.053 $\text{pg } \mu\text{m}^3$ of lorica volume (Verity and Langdon 1984).

Experimental design—To test the expected relation between the metabolic nature (autotrophic vs. heterotrophic) of the planktonic community and GPP, a manipulation experiment was conducted between 18 June and 8 July 1997 using large mesocosms receiving a gradient of nutrient inputs to achieve a range of primary production (Duarte et al. 2000). The experimental design involved a gradient of nutrient additions to mesocosms following a geometric series of nutrient inputs centered at the nutrient loading calculated for the Bay of Blanes, estimated to be about 5 $\text{mmol m}^{-2} \text{ d}^{-1}$ in summer (Duarte et al. 2000), hereafter referred to as a “nominal loading rate” control. Phosphorus and silicon were added to maintain their average summer stoichiometry with nitrogen in the sedimentary flux (20 N:7 Si:1 P; Duarte et

al. 2000). Nitrogen was added as ammonium, the dominant form of summer nitrogen inputs to the Blanes Bay.

We used a series of seven large (nominal and effective volume 50 and 33 m³, respectively) mesocosms, consisting of 14-m tall bags with a 4.2 m² cross-sectional area. One of the units (that receiving twice the nominal nutrient loading) was found to be damaged 4 d before the end of the experiment. Nutrients were added to the mesocosms on alternate days, following the collection of samples, as solutions of CINH₄, KH₂PO₄, and Na₂SiF₆, in seawater. The nutrient additions included a treatment equivalent to the nominal loading rate control, a treatment equivalent to half of that nutrient input, and enriched nutrient additions equivalent to 2-, 4-, 8-, and 16-fold the nominal loading rate control. In addition, we also used a mesocosm to which no nutrients were added. The nutrient input to this mesocosm unit, derived from wet and dry atmospheric deposition, was determined from short-term nutrient mass balances to be about 0.005 $\mu\text{mol L}^{-1} \text{d}^{-1}$ (Duarte et al. 2000). Additional details on the experimental design are reported in Duarte et al. (2000). Integrated water samples (0–13 m) to determine planktonic metabolism were collected on alternate days at 0700 h and transported within 30 min to the laboratory.

Results

The autotrophic component of the Bay of Blanes showed important interannual variability, with high biomasses in 1992–1994 and much lower biomass thereafter (Fig. 1), with autotrophic biomass being dominated by picoplankton, largely *Synechococcus* sp., and occasionally dinoflagellates (*Prorocentrum* sp., *Ceratium* sp., *Scirpsiella* sp., occasionally *Alexandrium* sp.) in the summer and diatoms (e.g., *Chaetoceros* sp., *Leptocylindrus* sp., *Nitzschia* sp.) in the winter (Table 1). The biomass and community structure of the heterotrophic components of the microplanktonic community were much more uniform along the study period. The biomass of microheterotrophs was dominated by bacteria and, secondarily, ciliates, both greatly exceeding the biomass of heterotrophic nanoflagellates (Fig. 1). The ciliate community was dominated by oligotrich ciliates, including heterotrophic (e.g., *Halteria*, *Strombidium*, *Scribneridium*) and mixotrophic ones (e.g., *Laboea* and *Tontonia*). The biomass of autotrophs comprised, on average, 41% ($\pm 3\%$) of the planktonic biomass, which was dominated, therefore, by microheterotrophs. This was particularly so during 1995, when microheterotrophs comprised, on average >80% of the planktonic biomass. Hence, the total microplankton biomass, all of which contributes to the respiration of the community, was about 2.5-fold greater than that of the primary producers.

Planktonic metabolism varied greatly along the studied period (Fig. 2), with 2/3 (227 of a total of 344 experiments) of the estimates indicative of a net heterotrophic metabolism. R and GPP showed distinct seasonal patterns, both positively correlated with those in mean monthly water temperature with a lag of 1 month (Fig. 3), except for relatively high values in February for gross production and March for respiration, associated with the late winter bloom characteristic

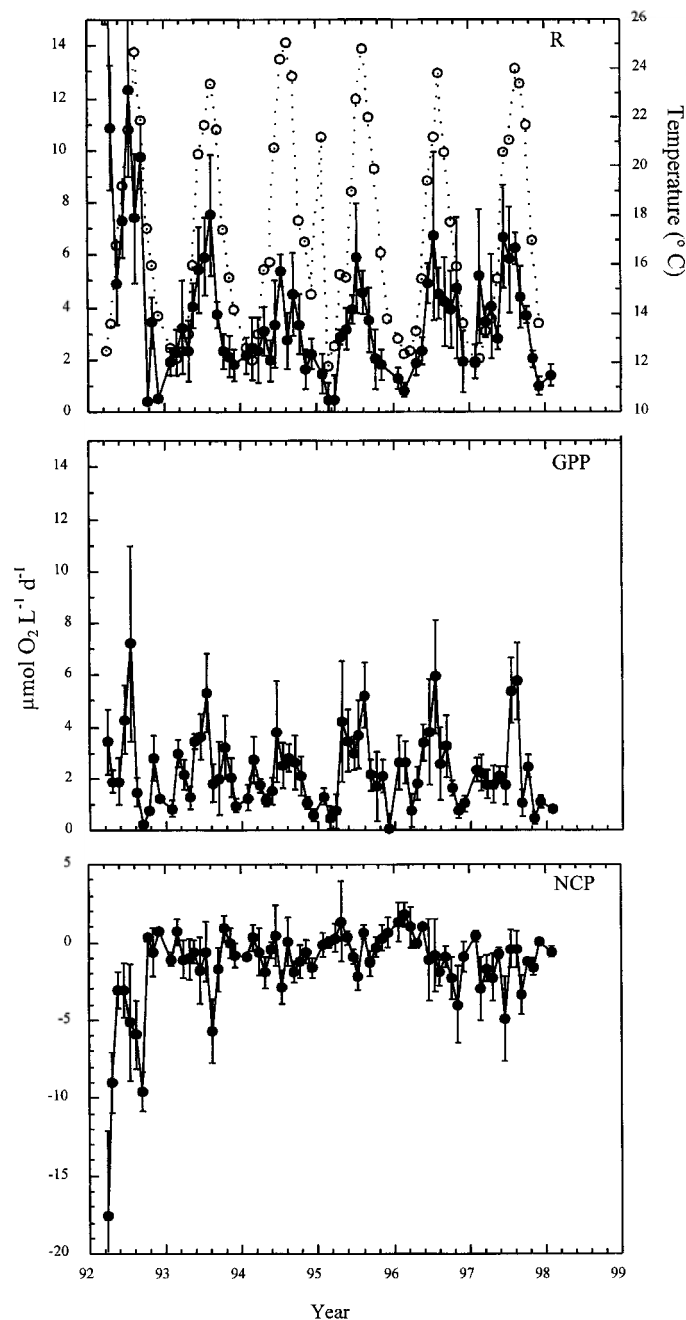


Fig. 2. Time series of the monthly average (\pm SE) community respiration (R), gross primary production (GPP), and net community production (NCP). Mean sea surface temperature is shown in the top panel with a broken line with open circles.

of this Bay (Agustí and Duarte 2000). Both the monthly average GPP and R were closely correlated with the duration of the day length (Table 2, Fig. 4). R was positively correlated with total microplankton biomass, with the respiration per unit microplankton biomass increasing with increasing water temperature (Table 2). Planktonic respiration per unit microplankton biomass increased, on average, 2.5-fold across the temperature range observed in the Bay of Blanes. Similarly, the specific GPP per unit autotrophic biomass increased with increasing water temperature (Table 2).

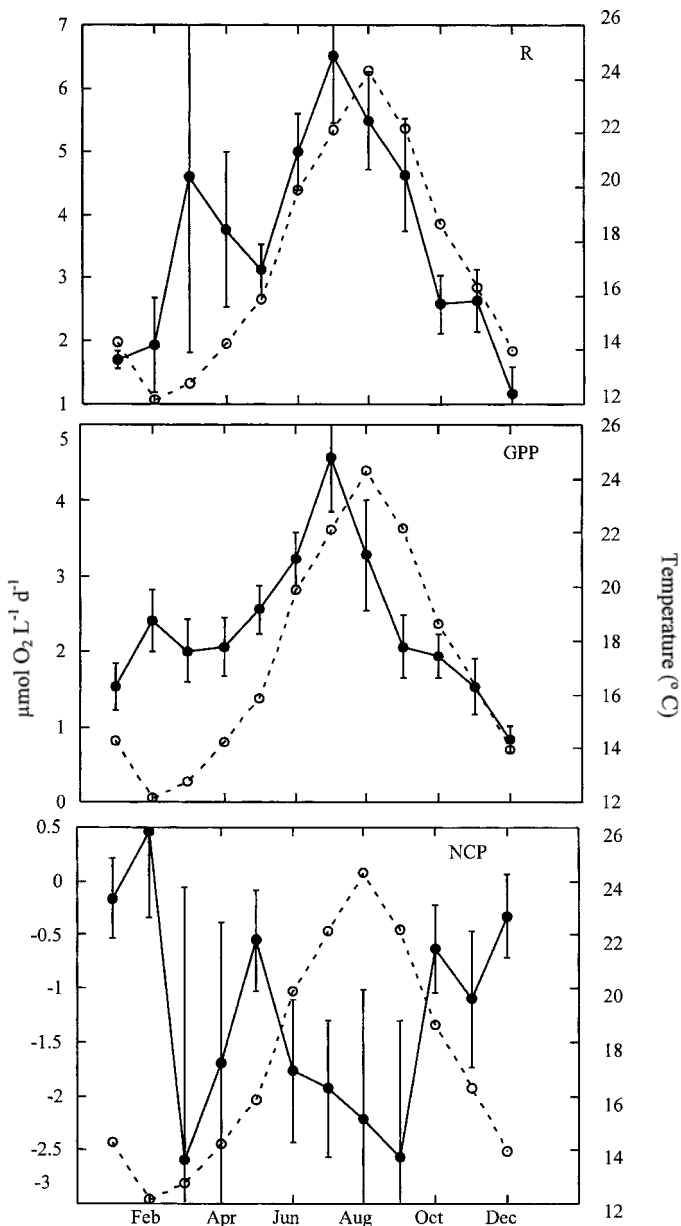


Fig. 3. Average (\pm SE) monthly community respiration (R), gross primary production (GPP), and net community production (NCP). Mean sea surface temperature is shown as a broken line with open circles.

Respiration rates were significantly correlated with gross production (Table 2), although the average respiration rate was significantly greater than the average gross production (*t*-test, $p < 0.001$, Fig. 5), yielding a median P/R ratio of 0.65. R was more variable than gross production (C.V. = 1.14 and 0.92, respectively, Fig. 5), driving the variability in the P/R ratio (Table 2). Accordingly, the plankton community in the Bay of Blanes was net heterotrophic at the annual time scale throughout the study period, except in 1995, when it was in metabolic balance (Fig. 6). There was a positive relation between the P/R ratio and GPP (Fig. 7), indicative of a threshold GPP of $3.95 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$ to reach a balanced metabolism (i.e., $P/R = 1$).

Table 2. Pearson correlation coefficient (r) and associated probability (p) between mean monthly gross primary production ($\text{GPP}_{\text{monthly}}$, $\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$) and respiration (R_{monthly} , $\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$), specific respiration per unit microplankton biomass (specific R, $\mu\text{mol O}_2 \mu\text{g C}^{-1} \text{ d}^{-1}$) and specific GPP per unit autotrophic biomass (specific GPP, $\mu\text{mol O}_2 \mu\text{g C}^{-1} \text{ d}^{-1}$), day length (h), and water temperature (T , $^{\circ}\text{C}$), and community respiration and gross primary production (R and GPP, respectively, $\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$), planktonic biomass ($B_{\text{microplankton}}$), and the GPP to respiration ratio (P/R).

Variables		r	p
$\text{GPP}_{\text{monthly}}$	Day length	0.82	0.006
R_{monthly}	Day length	0.82	0.006
R	$B_{\text{microplankton}}$	0.48	0.0004
Specific R	T	0.41	0.0007
Specific GPP	T	0.40	0.0008
R	GPP	0.41	0.0008
R	P/R	-0.85	<0.0001

Experimental nutrient additions greatly enhanced (up to 70-fold over the nominal loading rate control) GPP, following a time lag of about 6–8 d (Fig. 8). R rates also increased in response to increased nutrient additions, although the response was much less (up to 10-fold increase over the nominal loading rate control) than that of GPP (Fig. 8). Although the initially enclosed community was net heterotrophic, it shifted to highly autotrophic with increasing nutrient inputs (Fig. 8). Even the unamended community remained net heterotrophic over only half of the duration of the experiment, as the heterotrophic condition is not sustainable in the absence of the land inputs of organic matter received at the Bay of Blanes derived from enclosure of the community. Experimental nutrient additions had a much greater impact on GPP than they did on respiration rates, as the increase in R along the nutrient gradient represented 7.8% ($\pm 0.4\%$) of the increase in GPP (Fig. 9). As a result, net community production increased in parallel with increasing GPP, shifting from net heterotrophic at low GPP to net autotrophic as GPP increased because of nutrient additions (Fig. 9).

Discussion

The results presented show clear seasonal patterns in the planktonic metabolism in the Bay of Blanes, with highest rates of both respiration and GPP observed in summer, corresponding to an increase in the metabolic rate per unit autotrophic and heterotrophic biomass. Indeed, maximal GPP does not correspond with the period of highest autotrophic biomass, which occurs in late winter, when a diatom-dominated bloom occurs in this area (Agustí and Duarte 2000).

These results clearly depict the planktonic community in the oligotrophic Blanes Bay as a net heterotrophic one, with the average R rate along the study ($4.64 \pm 0.29 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$) exceeding the average GPP ($2.56 \pm 0.13 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$) by a factor of two. Yet, the R rate was not particularly high, as it was about half of the median value for coastal ecosystems (Hopkinson and Smith in press), leading to the conclusion that the net heterotrophic nature of the community is a result of the low planktonic primary pro-

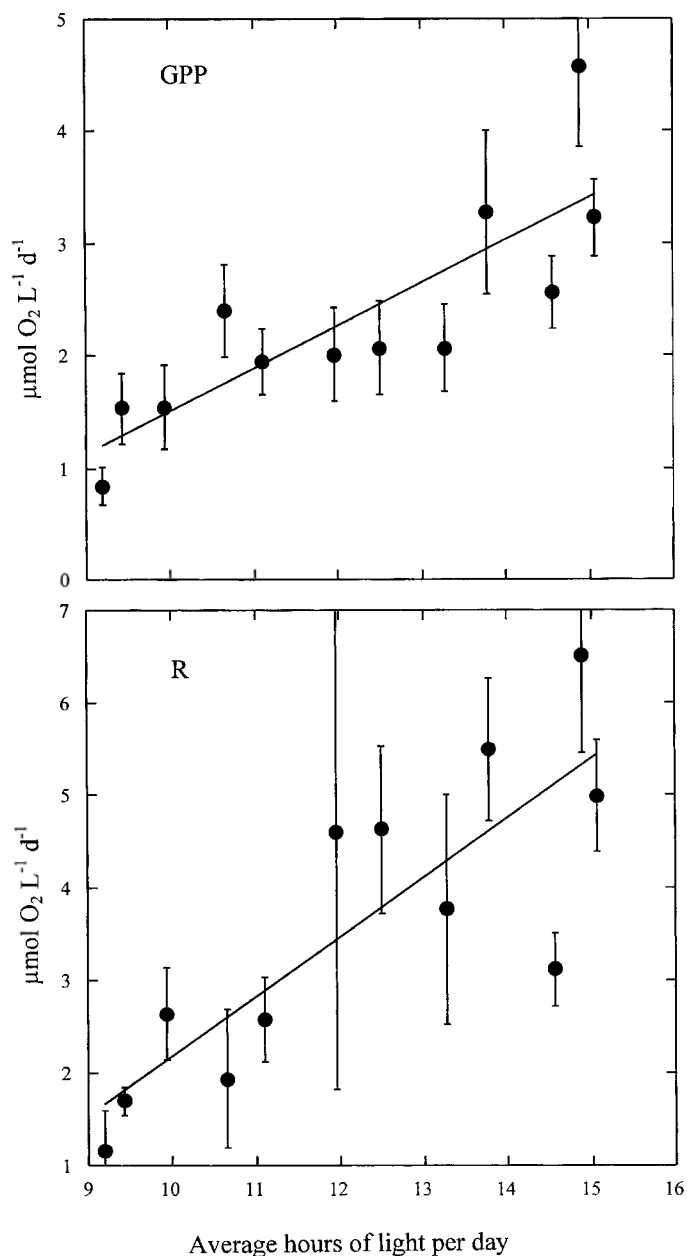


Fig. 4. The relation between the average ($\pm \text{SE}$) monthly gross primary production and community respiration of the planktonic community of the Bay of Blanes and the duration of the day length. Solid lines represent the fitted regression equations.

duction in the Bay. The high sampling frequency (twice a week in 1992, weekly during the rest of the study) sustained over 7 yr renders the conclusion that the planktonic community studied is net heterotrophic a robust one, as the high sampling frequency allows the capture of any net autotrophic event that may escape less intense sampling programs. Indeed, contrary to contentions that suggest the net heterotrophic nature of some planktonic communities to be an artifact derived from undersampling due to a pulsed behavior of GPP (Karl et al. 2003), our results, derived from a high-frequency sampling sustained over multiple years, suggest R

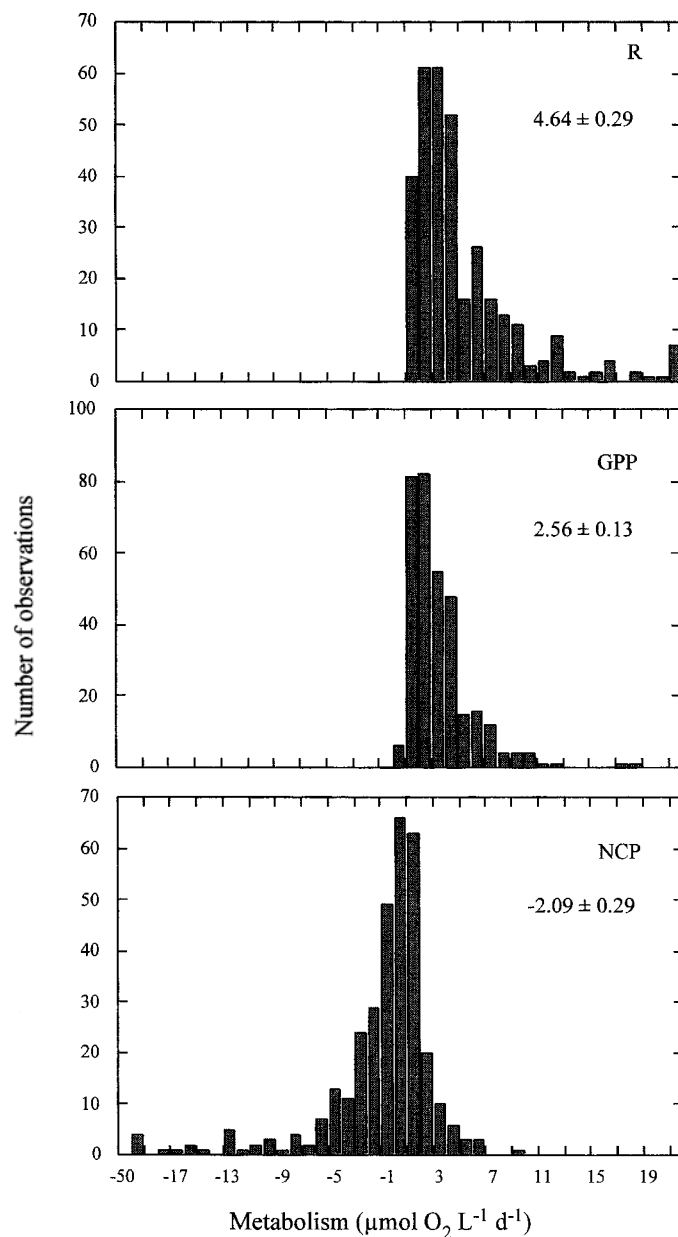


Fig. 5. Frequency distribution of estimates of community respiration (R), gross primary production (GPP), and net community production (NCP). The mean ($\pm \text{SE}$) value is given on panels.

to show a more pulsed behavior than GPP does in the Bay of Blanes.

The biomass structure of the plankton community, where autotrophs represent $<40\%$ of the biomass, consistent with the oligotrophic nature of the system (Gasol et al. 1997), is consistent with its net heterotrophic metabolism, supporting earlier contentions of a correspondence between the biomass structure and metabolism of planktonic communities (Agustí et al. 2001). The net heterotrophic nature of the planktonic community in the Bay of Blanes indicates that it must be supported by allochthonous inputs, derived from the riverine inputs from the adjacent La Tordera River, in agreement with results of Lucea et al. (in press).

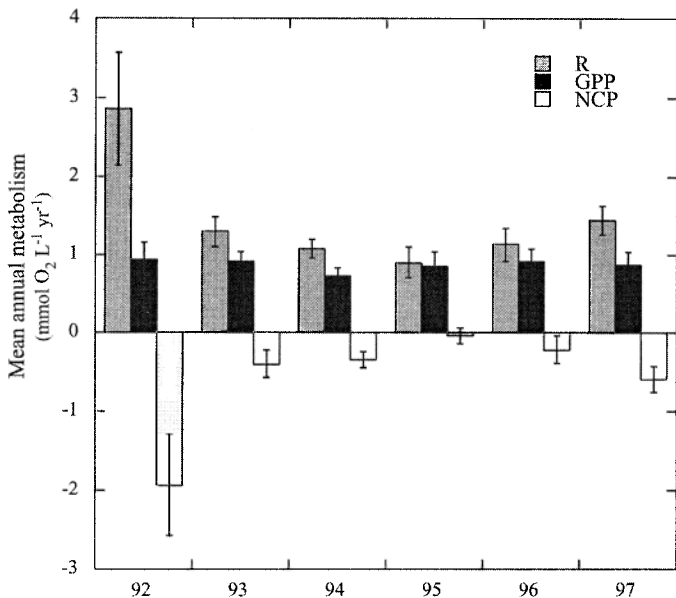


Fig. 6. Mean (\pm SE) annual gross primary production, community respiration, and net community production.

The manipulation experiment conducted further showed that the net heterotrophic nature of the Blanes Bay planktonic community is a result of the low GPP of this community relative to the background respiration rate that can be supported by allochthonous inputs. The results from the experiment showed that the R that would be supported by allochthonous inputs (i.e., in the absence of gross community production) can be estimated—as the intercept of the re-

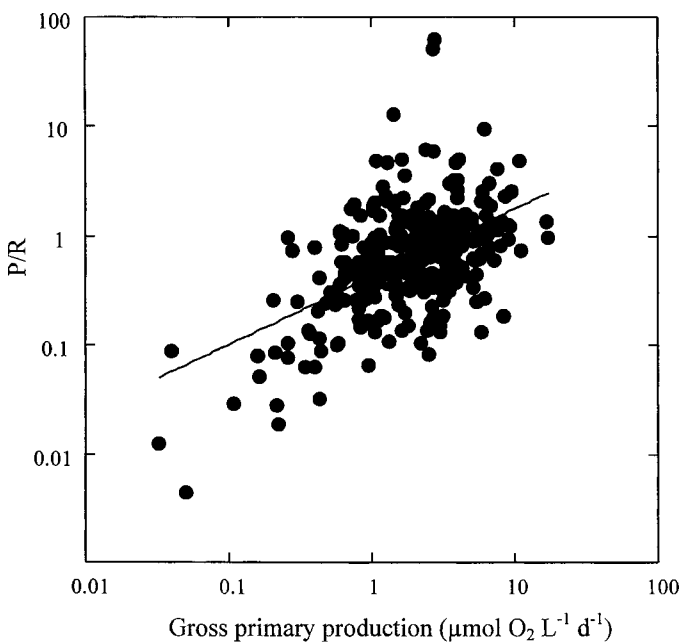


Fig. 7. Relation between the gross primary production to community respiration ratio (P/R) and gross primary production in the Bay of Blanes. The solid line shows the fitted regression equation $P/R = 0.42 \text{ GPP}^{-0.62} (\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1})$, $R^2 = 0.27$, $p < 0.001$.

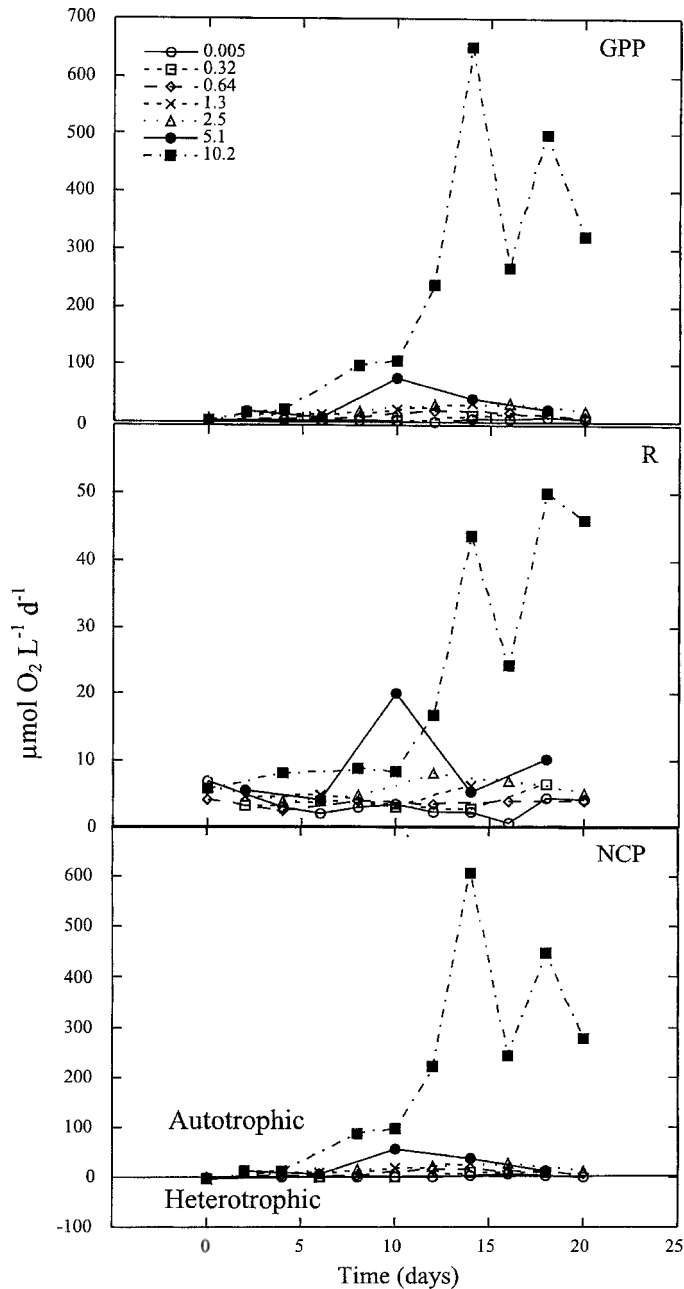


Fig. 8. Time series of gross primary production, community respiration, and net community production in mesocosms receiving different nutrient inputs (in $\mu\text{mol N L}^{-1} \text{ d}^{-1}$).

gression equations between NCP or R versus gross community production, with the standard error derived from the standard error of the regression estimates—to be $3.83 \pm 0.67 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$ (Fig. 9). In turn, the experimental results allowed calculation, from the fitted regression equation between GPP and R, of the average GPP required for the community to shift from net heterotrophic to net autotrophic (i.e., GPP at GPP = R) at $4.1 \pm 0.67 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$ (Fig. 9). This threshold is remarkably close to the long-term value of $3.95 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$ derived for the planktonic community

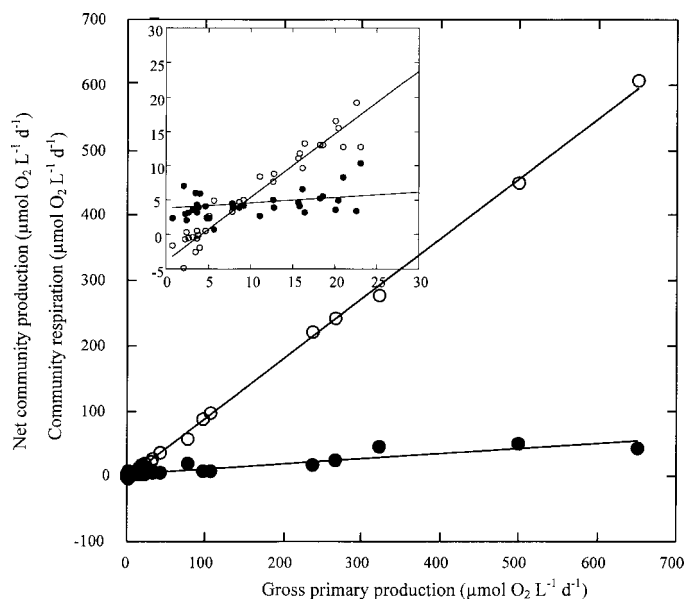


Fig. 9. Relation between the daily gross primary production (GPP) and the net community production (NCP) and community respiration (R) resulting from combining all results derived from the mesocosm experiment (i.e., each data point represents a daily value derived experimentally at one of the mesocosm units). The insert shows the relation at low gross community production. Solid lines depict the fitted least-squares regression equations: NCP ($\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$) = $-3.81 + 0.92 (\pm 0.004) \text{ GPP } (\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1})$, $R^2 = 0.99$; and R ($\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$) = $3.83 + 0.078 (\pm 0.004) \text{ GPP } (\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1})$, $R^2 = 0.87$.

in the Bay of Blanes, suggesting this threshold to hold predictive power for the community investigated. The average GPP required to render the community autotrophic is about 60% larger than the average GPP ($2.56 \pm 0.13 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$) recorded in the Bay of Blanes along the 7-yr study, which is lower than the estimated R that would be supported by allochthonous inputs, therefore explaining the net heterotrophic nature of the community. The increase in NCP as the experimental nutrient inputs increased indicates a dependence of NCP on nutrient supply, in agreement with recent findings derived from a comparative analysis of 44 North American estuaries (Caffrey 2004).

The average GPP required to render the community autotrophic in the Bay of Blanes is more than twice the threshold value of $1.62 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$ required to render oceanic planktonic communities net autotrophic (Duarte and Agustí 1998; Duarte et al. 2001; González et al. 2001). This further indicates the importance of allochthonous inputs of organic carbon in sustaining a relatively high background R rate, rendering the planktonic metabolism in the Mediterranean littoral system studied net heterotrophic. Allochthonous organic matter inputs have the greatest impact on coastal communities with low rates of GPP (Hopkinson and Smith in press). Hence, the results derived for the Bay of Blanes indicate that even modest allochthonous organic carbon inputs suffice to render oligotrophic planktonic coastal communities net heterotrophic.

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