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Primary production under hypertrophic conditions and its relationship with bacterial production

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Abstract In shallow hypertrophic lakes where light availability restricts the growth of macrophytes and benthic phytoplankton, pelagic phytoplankton modulates importantly ecosystem production and the energy transfer to heterotrophic bacteria. Diel and seasonal variations in primary production (PP) were studied in the hypertrophic Albufera de Valencia (Spain). Additionally, the relationship between PP and heterotrophic bacterial production (BP) was assessed. PP was extremely high, exceeding most values reported for hypertrophic lakes to date. PP displayed marked diurnal variations defined by the solar radiation curve. Likewise, PP changed importantly across seasons. Minimum PP coincided with maximum water transparency and short water residence times in winter, whereas maximum PP was observed in late spring associated with high chlorophyll *a*. The spring PP maximum contrasted with the summer maximum often observed in hypertrophic lakes. When compared to spring PP values, summer PP values were lower as a result of strong nitrogen limitation. In contrast to PP, BP remained fairly constant across seasons. Nonetheless, there was a joint diminution during increased water transparency followed by an increase in early spring. Phytoplankton was always the most relevant input to particulate carbon production, but the BP/PP ratio showed clear seasonal variations. The BP/PP ratio was minimum in spring, low in summer and highest in winter. The extracellular dissolved organic carbon released by phytoplankton was sufficient to meet bacterial carbon demand in all experimental dates, suggesting that allochthonous carbon sources play a minor role in sustaining BP, though they cannot be excluded. However, we hypothesize that high availability of dissolved organic carbon might explain the lack of coupling observed between BP and PP.

Keywords Eutrophication · Shallow lagoon · Phytoplankton productivity · Bacterial production · Carbon flux

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Introduction

Phytoplankton plays a key role in aquatic food webs, constituting a food source for higher trophic levels and supplying dissolved organic carbon (DOC) to heterotrophic bacteria (Cole et al. 1982; Baines and Pace 1991). In clear-water shallow lakes and lagoons with high light availability, the benthic food web tends to be

of greater relevance than the pelagic one. Conversely, in turbid shallow hypertrophic lakes and lagoons, where light availability is restricted to the surface layer limiting the growth of submerged macrophytes, epiphyton or phytobenthos, the contribution of pelagic algae to ecosystem production becomes more important (Hart and Lovvorn 2000; Liboriussen and Jeppesen 2003; Blindow et al. 2006). Temporal changes in phytoplankton biomass and productivity both at the daily and seasonal scale are expected to significantly affect crucial ecological processes such as the trophic interactions and energy transfer among the lower components of the aquatic food web (Kamjunke et al. 1997; Kisand and Noges 1998; Winter et al. 2004).

The supply of DOC to heterotrophic bacteria is assumed to mediate the correlation observed between primary production (PP) and heterotrophic bacterial production (BP) in pelagic ecosystems (Bird and Kalff 1984; Cole et al. 1988). However, this correlation appears to vary with trophic status, specifically, a tight relationship might be awaited in oligotrophic waters where DOC is limiting, whereas a weak connection might be anticipated in eutrophic waters with higher DOC availability (Pugnetti et al. 2010).

The linkage between PP and BP provides valuable information about the interactions within the food web. Further, these interactions are essential in assessing the importance of heterotrophic bacteria in consuming PP and in providing organic matter and energy for higher trophic levels in pelagic ecosystems (Cole et al. 1988). Despite the relationship between PP and BP has been investigated in a wide range of marine and freshwater ecosystems, data on hypertrophic lagoons are scarce. The contribution of bacteria to community biomass has been found to decrease as lake productivity increases. Namely, bacterial numbers have been found to increase slower than algal biomass with eutrophication, with a possible explanation being high grazing pressure (Bird and Kalff 1984; Sommaruga and Robarts 1997). This could imply a lesser role of bacteria within the lake food web if bacterial production per unit of bacterial biomass does not increase with system productivity, but again, evidence based on highly enriched systems with Chlorophyll-*a* (Chl-*a*) concentrations >120 μg L^{-1} is limited.

Albufera de Valencia constitutes a representative study case for such ecosystems. This shallow lagoon initially populated by submerged vegetation, shifted from a clear to a turbid state as a result of an intense eutrophication process that started in the 1960s (Vicente and Miracle 1992; Romo et al. 2005). At present, this ecosystem is in a turbid state dominated by phytoplankton, mainly filamentous cyanobacteria. The lagoon, subjected to strong management, is "flushed" in winter when the water contained in the surrounding paddies flows through its basin into the sea, driving "clear-water" events characterized by reduced water turbidity. Several studies have emphasized the role of flushing rates in diminishing phytoplankton biomass and primary productivity in lakes (Dickman 1969; Søballe and Kimmel 1987; Padisák et al. 1999; Jones and Elliott 2007). Though the flushing-associated changes in phytoplankton biomass, abundance and community composition have been extensively studied in Albufera de Valencia (Villena and Romo 2003; Romo et al. 2008), the variations in PP have not been investigated. Likewise, no information is available on the coupling between primary and secondary producers or the carbon transfer concerning these trophic levels.

The goals of this study were (1) to assess diurnal changes in PP and physicochemical parameters in hypertrophic lakes and (2) to investigate the seasonal variations in PP, especially in relation to changes in water turbidity. We hypothesize that lower PP values should be found during periods in which phytoplankton biomass is reduced as a consequence of winter lake flushing, which in turn results in an overall decrease in water turbidity. Based on existing bacterial production data on the study site (Onandia et al. 2014), the relationship between PP and BP was explored. Namely, we aim to test whether PP and BP respond similarly to fluctuations in water turbidity. If the variations in BP described by Onandia et al. (2014) are driven by the availability of extracellular dissolved organic carbon (EDOC) released by phytoplankton, BP and PP should be coupled and a common response to water turbidity variations should be observed. Finally, we intend to test whether the observations that bacterial abundance does not increase as rapidly as algal biomass with increasing nutrient concentration (e.g., Bird and Kalff 1984) apply to the particular case of the hypertrophic Albufera de Valencia (with Chl-*a* concentrations >120 μg L^{-1}), anticipating that our data will support this hypothesis. By addressing

these questions, we aim to improve the understanding of the food web relationships in hypertrophic lakes, considered the ultimate stage of eutrophication.

Materials and methods

Site of study, sampling and experimental design

Albufera de Valencia is an oligohaline (salinity $\approx$ 1 PSU) lagoon of approximately 24 km^2 located on the Mediterranean coast, south of Valencia (Spain). This shallow lagoon (mean depth $\approx$ 1 m) is hypertrophic and at present is in a turbid state dominated by phytoplankton, mainly cyanobacteria (Romo et al. 2008). During the study period, total phosphorus ranged from 106 to 348 μg L^{-1}, whereas total nitrogen ranged from 3.2 to 5.5 mg L^{-1} (Onandia et al. 2014). The water column is well mixed to the bottom as a result of the frequent windy conditions, which favor sediment resuspension. A detailed study on wind data during April 24–25 and May 7–8, 2012, showed that wind speed increased from 5 to 10 km h^{-1} in the early morning to a maximum of 25–30 km h^{-1} in the afternoon and subsequently fell to 0 km h^{-1} in the evening (AEMET, unpublished results). The lake is surrounded by a large area where rice is cultivated. Numerous irrigation ditches cross this area and flow into the lagoon, separated from the sea by a sand bar 500–1,000 m wide. Three outlet channels with sluice gates connect the lake with the Mediterranean Sea and allow water level regulation. A period of high water renewal rate takes place in late winter, when rice paddies, which have been flooded since late autumn (November), are drained through the lagoon. Then, agricultural works are undertaken in the dry paddies before rice sowing in May, when paddies are flooded again, defining a period of low water renewal until rice harvesting in mid-September.

PP as well as a number of relevant biological and physicochemical variables was measured in a central location of the lagoon (39° 20′53 N 0° 19′23 W) on February 23–25, 2011, August 2–3, 2011, January 24–25, 2012, and February 22, 2012. Each experimental date included two measurements, performed in the noon and in the afternoon, respectively, at the depths of 0.2, 0.8 and 1.1 m. In spring, namely on April 24–25 and May 7–8, 2012, PP diel cycles consisting of three measurements (performed during light hours within a 24-h interval) were followed at the depths of 0.2 and 0.6 m on the east shore of the lagoon (39° 20′38 N 0° 20′27 W). Physicochemical and biological variables were measured throughout the diel cycles at 4 h intervals. Additionally, the selected variables were measured on January 13, 2011, April 27, 2011, May 18, 2011, and July 21, 2012. Therefore, this work comprises winter, summer and spring data on the corresponding months of two consecutive years.

Physicochemical variables

A multiparameter WTW 350i probe was used to measure in situ temperature (T), pH, oxygen saturation (O_2 %), conductivity and salinity. Vertical profiles of photosynthetic active radiation (PAR, μE $m^{-2}s^{-1}$) were obtained during the experiments with a flat-faced quantum sensor (LiCor Li-1000). The acquired values (at 0.1 m depth intervals) were used to calculate the vertical light attenuation coefficient K_d (m^{-1}) of PAR. Global incident solar radiation data (I, KJ m^{-2} h^{-1}), based on measurements at Valencia's Airport Station ($\approx$20 km from Albufera de Valencia), were provided by Meteorological State Agency (AEMET). Water subsamples were filtered on glass fiber filters (GF/F, Whatman) upon arrival in the lab for the determination of dissolved inorganic nutrients and dissolved organic and inorganic carbon. Suspended solids (SS), loss of ignition (LOI), soluble reactive phosphorus (SRP), total phosphorus (TP), ammonia (NH_4), nitrate (NO_3), nitrite (NO_2) and total nitrogen (TN), as well as alkalinity (Alk), were measured as described in APHA (1992) and specified in Onandia et al. (2014). Dissolved inorganic nitrogen (DIN) was calculated as the sum of NH_4, NO_3 and NO_2. Water turbidity (WT) was determined spectrophotometrically as described in ISO (1999). A total organic carbon analyzer (Shimadzu TOC-VCSH) was used to determine total and dissolved forms of organic and inorganic carbon (TOC, TIC, DOC, DIC) by high-temperature combustion, as described in ISO (1997). A standard solution of potassium hydrogen phthalate or sodium carbonate diluted in Mili-Q water was used for calibration of organic and inorganic forms, respectively. Chl-*a* collected onto glass fiber filters (GF/F, Whatman) was measured spectrophotometrically as described in Shoaf and Lium (1976).

Biological variables

Samples for algal cell counts were preserved in Lugol's solution and enumerated with an inverted microscope at 1000X in a 3-ml sedimentation chamber. Cell biovolume was calculated as described by Hillebrand et al. (1999) and transformed to biomass using a conversion factor of 0.225 pgC μm^{-3} for mixed phytoplankton populations (Reynolds 2006). Particulate primary production (PP) and dark assimilation were measured following the ^{14}C uptake method (Steeman-Nielsen 1952). For each depth, the collected water was distributed into two transparent and three opaque flat-shaped cell culture 62.5-mL bottles (Nunclon® Surface). In one of the opaque bottles, formalin (final concentration 0.6 %) was added immediately after water to be used as a control. Approximately 3 μCi of $NaH^{14}CO_3$ (specific activity 39,035 kBq mL^{-1}) was added to the bottles, which were hanged horizontally at the sampling depth. Incubations lasted 1 h and were stopped with formalin (final concentration 0.6 %). Bottles were immediately placed in the dark and cold, and as soon as possible, 10 mL sample aliquots were filtered through a Whatman GF/F glass fiber filter and the filtrate was collected in scintillation vials. Filters were rinsed three times with HCl (0.005 N), placed in open scintillation vials and dried at 25 °C for 24 h. Thereafter, 10 mL of scintillation cocktail (Sigma-Fluor LSC cocktail for non-aqueous samples, S-3898) was added to the vials, and they were capped. The dissolved primary production (extracellular dissolved organic carbon, EDOC) was estimated from the 10 ml sample filtrate mentioned above as described by Mague et al. (1980). Radioactivity was measured with a PerkinElmer LSA Tri-Carb 2810TR liquid scintillation counter. The percentage EDOC contribution to total primary production was estimated as PER = EDOC/(PP + EDOC).

Hourly areal primary production (HPP, mgC m^{-2} h^{-1}) was calculated following the equations derived from the light–photosynthesis relationship (Jacoby and Welch 2004) and assuming maximum photosynthesis at 0.2 m, except for the experiment performed in the morning on February 2012, where PP was fairly constant along the water column and the trapezoidal method was used (both methods were found to be comparable, yielding results that did not differ more than 1 % in the afternoon experiment on the mentioned date). Daily areal primary production (DPP) for winter and summer experiments was calculated based on noon HPP values using Platt's factor (Callieri and Stockner 2002). For spring experiments, DPP was estimated as in Wetzel and Likens (2000), i.e., PP was assumed to be proportional to light and scaled to daily values using the ratio between total daily irradiance and irradiance during the incubation period. Chl-*a*-specific PP was obtained dividing maximum primary production (PP_{max}) by Chl-*a* at the corresponding depth. BP values simultaneously obtained at the study site (Onandia et al. 2014) were used to calculate bacterial growth efficiency (BGE) using the empirical model BGE = (0.037 + 0.65 × BP)/(1.8 + BP) described by del Giorgio and Cole (1998). Bacterial gross production (BP plus bacterial respiration), hereinafter referred as bacterial carbon demand (BCD), was subsequently estimated as BP/BGE. Ultimately, we explored the relationship between PP and BP by evaluating whether EDOC was able to meet BCD. Additionally, hourly and daily bacterial production values (HBP and DBP) as well as bacterial biomass values reported by Onandia et al. (2014) were used to explore the relationship with HPP, DPP and phytoplankton biomass (algal biomass). To this aim, the DBP/DPP ratio and bacteria/phytoplankton biomass ratio were calculated.

Statistical analyses

Normality of data and homogeneity of variance were checked with Kolmogorov–Smirnov test and Levene's test, respectively, before data analysis. One-way ANOVA or the nonparametric Kruskal–Wallis test was used to analyze significant differences ($p < 0.05$) in the selected variables between seasons and depths. The found differences were further explored with post hoc analyses using either Tukey-b or Mann–Whitney tests. Correlation between variables was estimated with Pearson's correlation coefficient (r) applying a Bonferroni correction to the alpha level ($\alpha = 0.05$). SPSS Statistics 20.0 software was used for all mentioned analyses.

Results

Conductivity varied slightly across seasons (1,380–2,020 μS cm^{-1}). Water temperature showed pronounced seasonality (28 and 10 °C at midday in August 2011 and

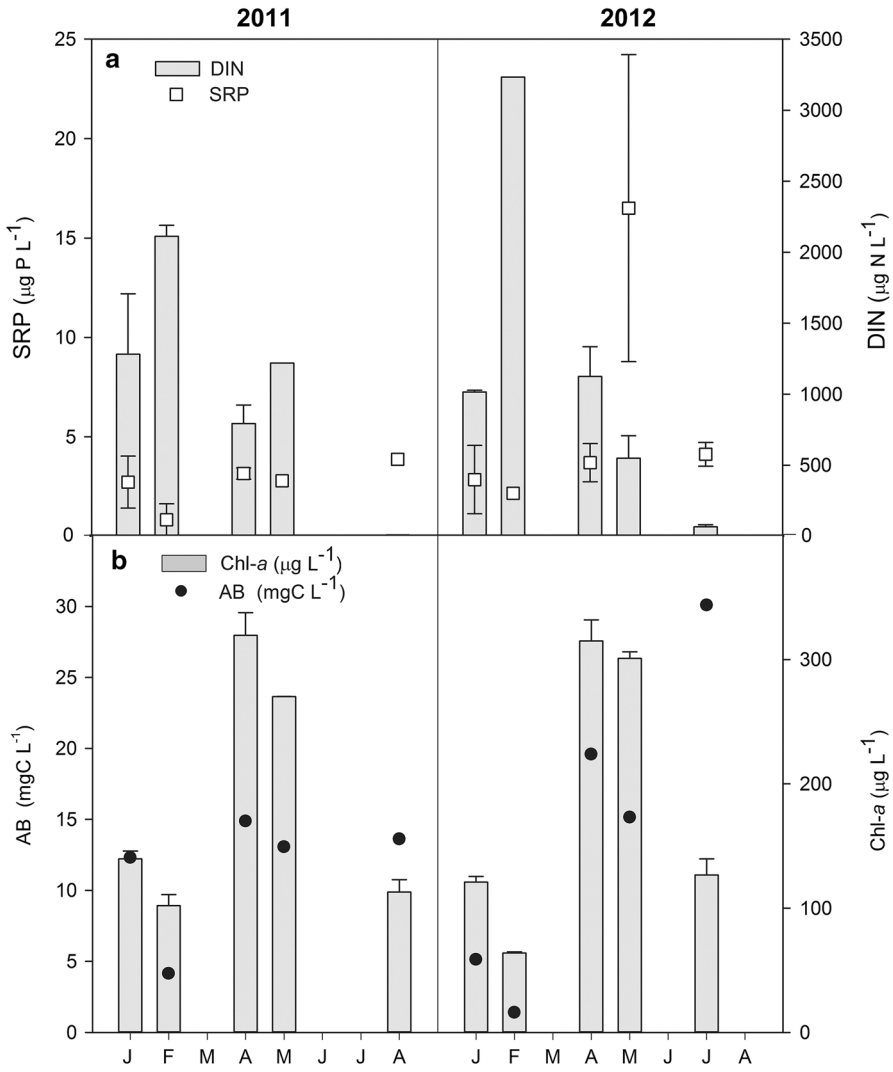

Fig. 1 **a** Chl-*a* along algal biomass (AB), **b** dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) concentrations in sampling dates. *Bar* and *points* are mean concentrations for all depths and times on each sampling campaign. *Error bars* represent standard deviation

February 2012, respectively). Both pH and O_2 % clearly increased with PP, showing highest values in spring. On the other hand, TIC and DIC (which were nearly equal) diminished with increasing PP and were lowest in this season. Values for K_d, WT and SS (Online Resource 1) illustrate the high turbidity of the lake. These parameters varied concurrently across seasons, showing maximum in spring and minimum in February 2012.

Both TP and SRP were highest in spring. While the former ranged from 106 to 392 µg L^{-1}, the latter averaged 4.3 ± 4.4 µg L^{-1} (Fig. 1a). The SRP/TP ratio ranged from 0.004 to 0.01 (with the exception of values in May 2012: average 0.05 ± 0.03), which is in good agreement with the constant SRP/TP ratio (1:20 or <5 %) found across the temperate zone (Wetzel and Likens 2001). Likewise, the observed TP values are typical values for hypertrophic lakes (Wetzel and Likens 2001), as well as TN concentrations, which ranged from 3.2 to 5.6 mg L^{-1}. DIN displayed remarkably high values during the clear-water event in February 2012 and declined dramatically in summer (Fig. 1a), which resulted in a decreased DIN/SRP ratio in this season. DOC and TOC were considerably higher in summer than in the other seasons (Online Resource 1).

Chl-*a* was around 100 µg L^{-1} in winter and halved during the clear-water event in late winter 2012, to reach very high values in spring (≈300 µg L^{-1}). It is noteworthy that there was practically a fivefold increase between February and April 2012 (Fig. 1b).

Table 1 Significant correlations found between the studied variables

	Alk		DIC		pH		WT		SS		AA		*n*
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	
Chl-*a*	−0.78	***	−0.8	***		ns	0.95	***	0.95	***	0.63	***	36
PP_{max}		ns	−0.77	**	0.89	***		ns		ns		ns	14
Chl-a-specific PP		ns		ns		ns		ns		ns		ns	14
	TN		TP		NO_3		NO_2		EDOC				
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*			
Chl-*a*	0.74	***	0.95	***		ns		ns		ns			26
PP_{max}		ns		ns		ns		ns	0.93[2]	**			10
PP		ns		ns		ns		ns	0.95[1]	***			26
Dark assimilation		ns		ns	−0.78	***	−0.67	***		ns			26

Pearson's correlation coefficient (*r*) after applying Bonferroni's correction is shown, along level of significance (ns not significant, * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$) and sample size (*n*). See text for abbreviations

[1] $n = 14$; [2] $n = 8$

Thereafter, in summer, algal biomass was still very high and Chl-*a* diminished to 100 μg L^{-1}. The significant correlations found between Chl-*a* and physicochemical parameters are shown in Table 1. The similarity of the variables among depths (data not shown) indicated that the water column was well mixed.

Both phytoplankton abundance (algal abundance, AA) and biomass were markedly variable among seasons. Abundance and biomass were very high, reaching 15×10^6 cells mL^{-1} and 133.7×10^6 - μm^{-3} mL^{-1} in summer, but decreased substantially in winter during flushing (Online Resource 1; Fig. 2). Because temporal variations in Chl-*a* and biomass differed, the Chl-*a*/biovolume ratio varied across seasons, being highest in the clear-water event and lowest in summer (Online Resource 1). Similarly, the composition of the phytoplankton community displayed important seasonal variations (Fig. 2). In summer, cyanobacteria made up for 90 % of phytoplankton biomass. Most frequent species were filamentous oscillatoriales (*Planktolyngbya* sp.), mucilaginous colonial chroococcales (*Aphanothece* sp., *Merismopedia* sp.) and heterocystous cyanobacteria as *Cylindrospermopsis raciborskii*, which especially in 2012 represented a very large biomass fraction. In winter, cyanobacteria dominance decreased substantially in terms of biomass, although they remained as the most abundant group. *Pseudanabaena galeata*, of bigger size than summer oscillatoriales, accounted for most of the cyanobacterial biomass. Diatoms, chlorophytes and cryptophytes, with larger cell dimensions than cyanobacteria, as well as small-sized chrysophytes, became also distinctly abundant. In spring, except in April 2011, bacillariophytes were the major contributors to biomass, making up for 40–50 % of the total pool. *Fragilaria* sp. dominated in the phytoplankton assemblage. Chlorophytes were also relevant (up to 30 %), especially in April 2011. Nonetheless, cyanobacteria accounted for an important part of biomass (35–55 %) in spring, with most numerous species being *P. galeata*, closely followed by *Merismopedia* sp. Autotrophic picoplankton biomass was always scarce: ≈1 % of total picoplankton abundance estimated by epifluorescence from DAPI-stained samples micrographs (Onandia et al. 2014).

At the daily scale, only minor variations in phytoplankton biomass, abundance and the relative proportion of the different taxonomic groups were observed. Coefficients of variation for phytoplankton abundance were 23 and 21 % in April and May 2012, respectively. In the case of biomass, these coefficients were 13 % in April and 16 % in May 2012. Likewise, phytoplankton abundance, biomass and community structure did not change with depth.

PP followed the expected behavior with depth in relation to light intensity, i.e., the fast light extinction with depth translated in a notable PP decrease along the water column (Fig. 3). Highest values were consistently

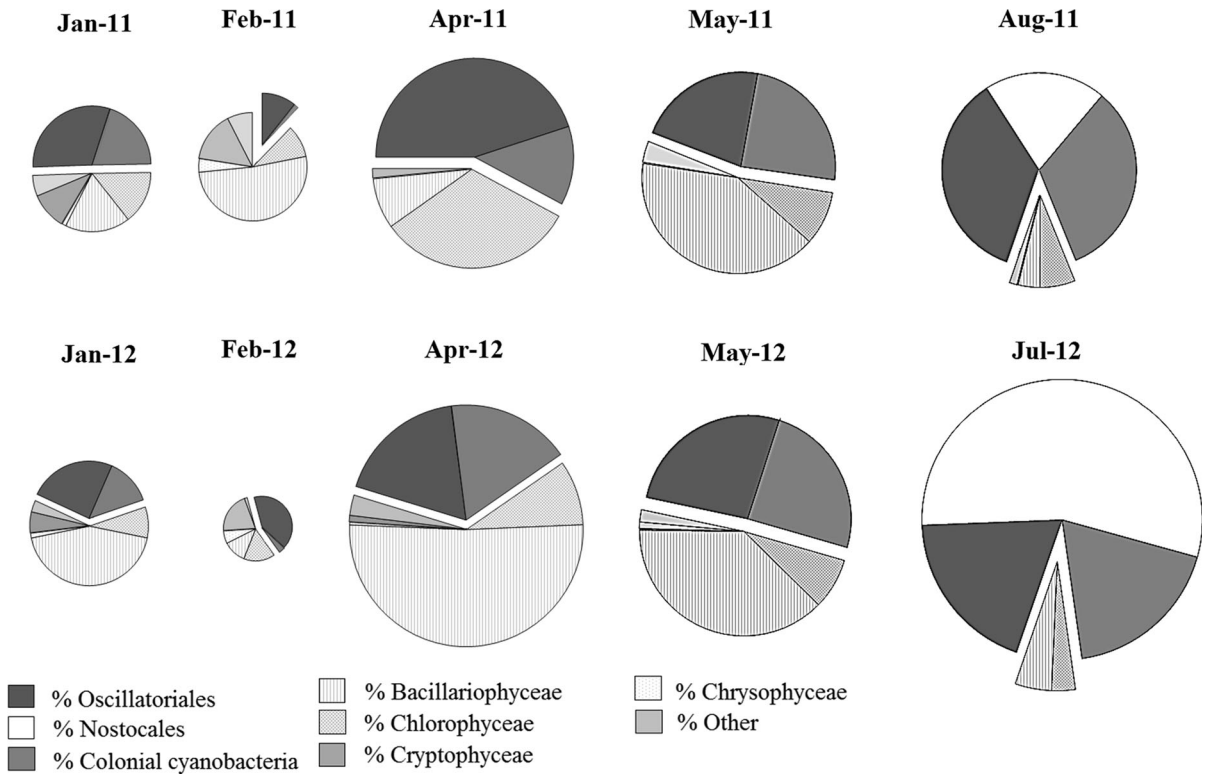

Fig. 2 Contribution of main phytoplankton groups to total algal biomass. Cyanobacteria *vs* other algae are displayed as separate clusters in the pie graphs. Pie radius is equivalent to the square root of phytoplankton biomass at the corresponding experimental campaign. Biomass and contribution are average values for all depths and times on each sampling campaign

observed at 0.2 m with the exception of February 2012, when water transparency increased and light penetrated deeper into the water column causing photoinhibition at noon. In all experimental dates, PP showed evident diurnal variations defined by solar radiation, being highest around noon (Figs. 3, 4). PP_{max} was significantly correlated to EDOC and other variables (Table 1).

The seasonal PP dynamics differed from that of the biomass. The minimum was observed in winter, but whereas biomass was lowest in February 2012, PP was smallest in January 2012. Maximum biomass was recorded in summer, but PP was highest in spring. An important PP increase was observed as this season advanced, with noon PP values in May being twice as much noon values in April. In summer, despite phytoplankton biomass remained high, areal PP and Chl-*a* diminished. Chl-*a*-specific PP varied between 2.2 and 9.8 μgC L^{-1}: μgChl-*a* L^{-1} h^{-1}, with the minimum in January 2012 and the maximum in May (Table 2).

EDOC ranged from 1.86 to 222 mgC m^{-3} h^{-1} and was strongly correlated to PP (Table 1). PER ranged between 6 and 21 %, averaging 7, 12, 16 and 19 % in May, April and February and January 2012, respectively. PER did not differ between depths ($p > 0.05$, $n = 14$, ANOVA test) but varied among seasons, being significantly higher in January and February than in May, when PP was maximum ($p < 0.01$, $n = 14$, ANOVA test; Tukey-b test).

Dark assimilation ranged from 0.02 to 25.3 mgC m^{-3} h^{-1} and was correlated to NO_2 and NO_3 (Table 1). Dark assimilation did not differ significantly between depths ($p > 0.05$, $n = 35$, ANOVA test). Nonetheless, seasonal differences were found ($p < 0.05$, Kruskal–Wallis test). Specifically, dark assimilation was significantly higher in summer than in winter and spring, and spring values were significantly higher than those found in winter (Mann–Whitney test). Daily integrated values ranged from 33 to 400 mgC m^{-2} d^{-1}. The dark assimilation/PP ratio expressed as daily integrated values (mgC m^{-2} d^{-1}) ranged from 2 to 13 %.

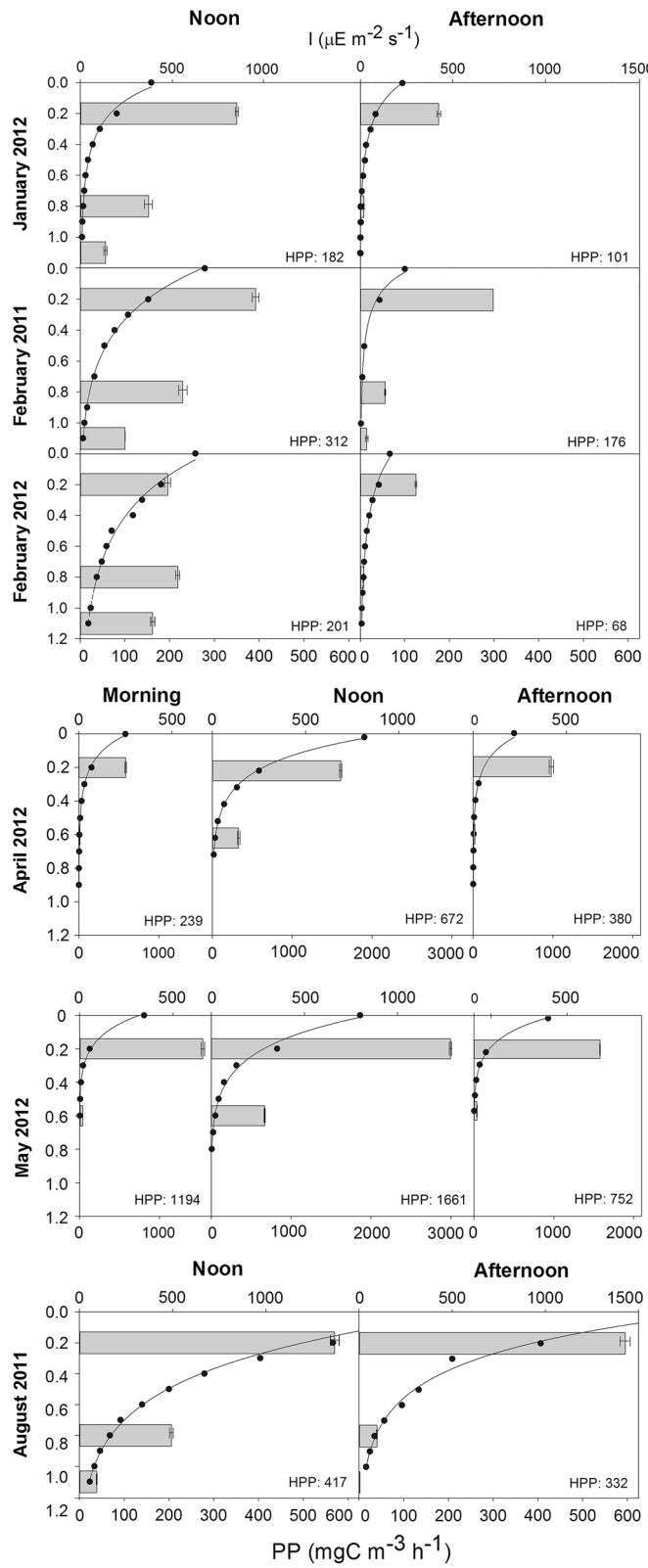

Fig. 3 Primary production (PP) along the water column in winter, summer and spring. *Bars* represent average PP of duplicate samples at each depth, and *error bars* indicate the range of variation between them. PAR attenuation as a function of depth, fitted to logarithmic (second order) trend lines ($r = 0.99$, $p < 0.01$), is also shown. Hourly areal primary production (HPP, mgC m^{-2} h^{-1}) is shown in the bottom right corner of each panel

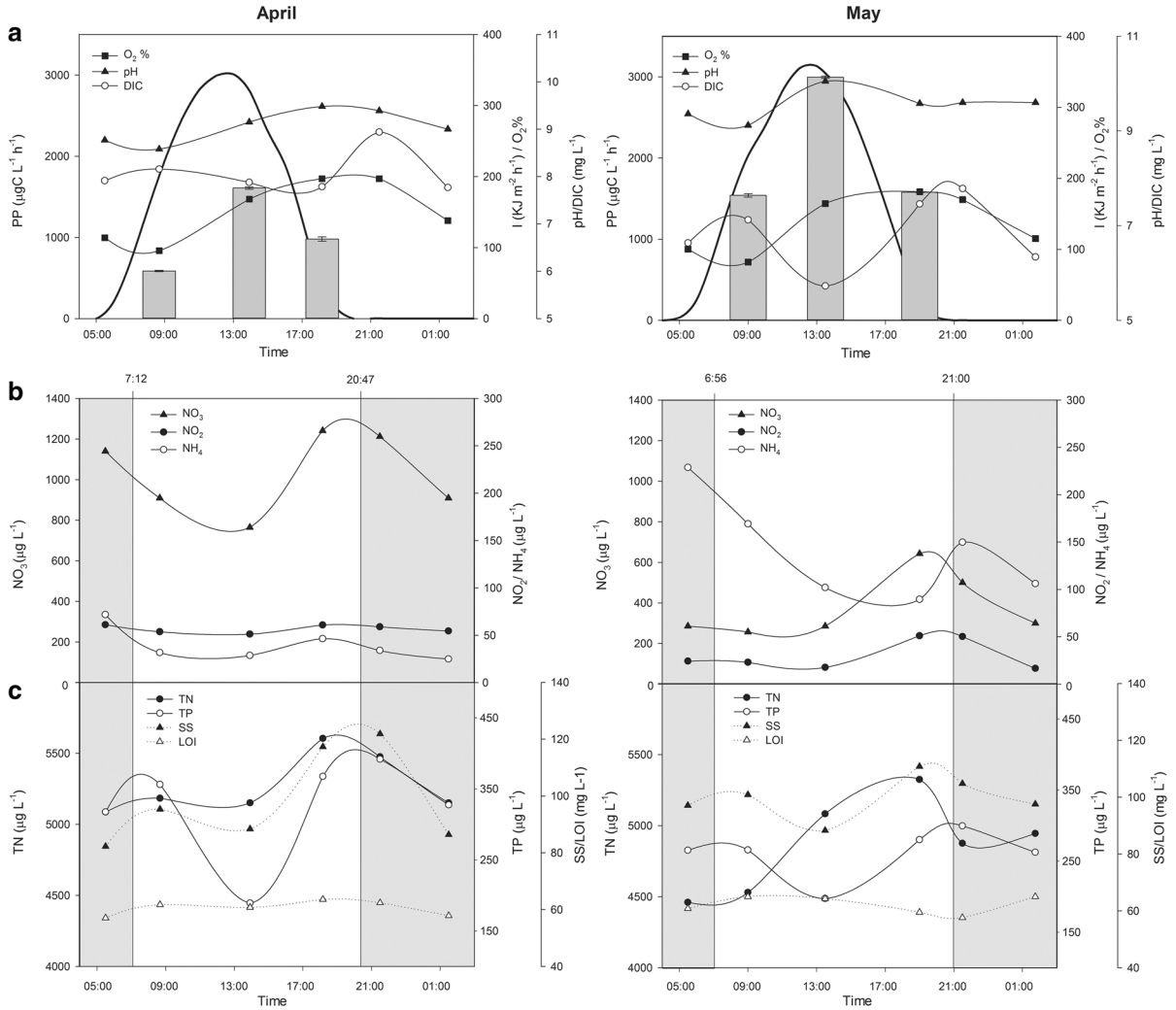

Fig. 4 **a** Diel changes in primary production (PP) at 0.2 m during two diel cycles. *Bars* represent average PP of duplicate samples at each day time, and *error bars* indicate the range of variation between them. Diel changes in oxygen saturation (O2 %), pH and dissolved inorganic carbon (DIC) are also shown, along with global solar radiation (I), **b** diel changes in NO_2, NO_3 and NH_4 and **c** diel changes in TN, TP, suspended solids (SS) and loss of ignition (LOI). Time scales have been standardized to obtain a better comparison. Shaded area in b and c represents night periods. Local times for sunset and sunrise (in hour: minutes) are indicated at the top of the panels

Results from the diel cycle experiments performed in spring showed the strong impact of the PP cycle in its associated variables. DIC showed a minor peak around early morning (8:30), decreased along the light hours and increased markedly after sunset (21:30) during both diel cycles (Fig. 4a). Oxygen supersaturation, caused by the high photosynthetic activity, fell to 80–95 % at daybreak, but reached 180–200 % after sunset (Fig. 4a). Likewise, pH started rising around 8:30, was higher in the afternoon and decreased throughout the night (Fig. 4a). Similar temporal dynamics were observed for all inorganic forms of nitrogen along the day, and the diel pattern was the same during both cycles (Fig. 4b). All forms peaked around 5:30, decreased until 8:30 to increase until 18:00, when they decreased again until 1:30. NO_2 concentration variation was smaller in both cycles. TP started to decrease at sunrise to reach the minimum around noon and then increased to peak shortly after sunset, when it started falling over. TN increased throughout the day and peaked before sunset, to moderately decrease until 1:30 (Fig. 4c). Whereas LOI displayed only minor variations, SS followed a diel pattern similar to that of TP (Fig. 4c).

Table 2 Mean and SD of primary and bacterial production related parameters for each sampling campaign in 2011 and 2012

	Jan-12 Mean ± SD	Feb-11 Mean ± SD	Feb-12 Mean ± SD	Apr-12 Mean ± SD	May-12 Mean ± SD	Aug-11 Mean ± SD
Chl-*a*-specific PP (μgC L^{-1}:μgChl-*a* L^{-1} h^{-1})	2.2 ± 1	3.3 ± 0.9	2.5 ± 0.8	3.5 ± 0.9	6.7 ± 3.2	5.3 ± 0.2
Dark assimilation (mgC m^{-3} h^{-1})	3.2 ± 0.7	1.5 ± 0.6	0.3 ± 0.2	8.9 ± 0.9	9.9 ± 5.8	18.4 ± 4.3
EDOC (mgC m^{-2} h^{-1}) morning	–	–	–	37	65	–
EDOC (mgC m^{-2} h^{-1}) noon	35	–	46	137	164	–
EDOC (mgC m^{-2} h^{-1}) afternoon	19	–	23	64	79	–
BCD (mgC m^{-2} h^{-1}) morning	–	–	–	10	6	–
BCD (mgC m^{-2} h^{-1}) noon	26	15	8	15	9	14
BCD (mgC m^{-2} h^{-1}) afternoon	21	14	9	10	9	8
BGE (%)	56 ± 3	52 ± 3	49 ± 4	44 ± 5	44 ± 2	47 ± 5

EDOC extracellular dissolved organic carbon; *BCD* bacterial carbon demand; *BGE* bacterial growth efficiency

Bacterial production: relationship with primary production

There was no significant correlation between DBP and DPP. Similarly, no significant correlation was found when hourly areal values were compared. As a percentage of DPP, DBP represented between 1.7 and 38.2 % and averaged 16 % (Fig. 5a). This fraction was relatively small in spring and summer. The winter DBP/DPP ratio remarkably greater, though some differences existed between sampling dates. The ratio was higher in January 2012 than in February 2011 and February 2012. The bacteria/phytoplankton biomass ratio showed the same pattern as the DBP/DPP ratio. Higher ratios were found in winter (concurrent to increased water flow and lower Chl-*a* concentrations) when compared to spring and summer (Fig. 5b), characterized by longer water retention times.

Bacterial growth efficiency (BGE) was high (namely around 50 %) and did not differ importantly across seasons (Table 2). BCD was low in February 2012 during flushing, but also in May 2012 after a marked increase in April 2012. BCD represented a highly variable fraction of EDOC. This fraction was highest in winter and lowest in spring (Table 2).

Discussion

Phytoplankton biomass and Chl-*a* underwent big seasonal fluctuations in Albufera de Valencia (Fig. 1b). A marked decrease of both variables took place in late winter, subsequent to lake flushing, i.e., increased water flow through the lagoon during paddies draining allowed by the opening of the sluice gates placed in the "golas," which connect the lagoon with the sea. Throughout this period, maximum water transparency was achieved. The phytoplankton community, dominated by cyanobacteria during most of the annual cycle, shifted to a community with a lesser cyanobacterial dominance and a greater contribution of cryptophytes, chrysophytes and diatoms (Fig. 2). In spring, the flow through the lagoon, controlled by the sluice gates, was severely reduced. Both Chl-*a* and phytoplankton biomass increased during this season and attained very high values in April. At the end of the spring, cyanobacteria dominance was practically reestablished. Thereafter, in late summer, cyanobacterial dominance was nearly absolute and phytoplankton biomass remained high (2011) or even increased (2012), but Chl-*a* diminished. During this period, characterized by DIN depletion, heterocystous cyanobacteria became also important. Despite cyanobacteria have dominated the phytoplankton assemblage over the last 40 years, species composition has varied greatly in the lagoon partly as a consequence of a sewage purification plan implemented in the 1990s. For instance, there has been a decrease in filamentous cyanobacteria and an increase in chroococcal cyanobacteria, and species such as *Microcystis aeruginosa* or *C. raciborskii* have become increasingly abundant (Vicente and Miracle 1992; Romo et al. 2005, 2008). Nonetheless, the overall described Chl-*a* and biomass trends could be observed since the lagoon shifted to a hypertrophic state, i.e., marked spring and autumn peaks.

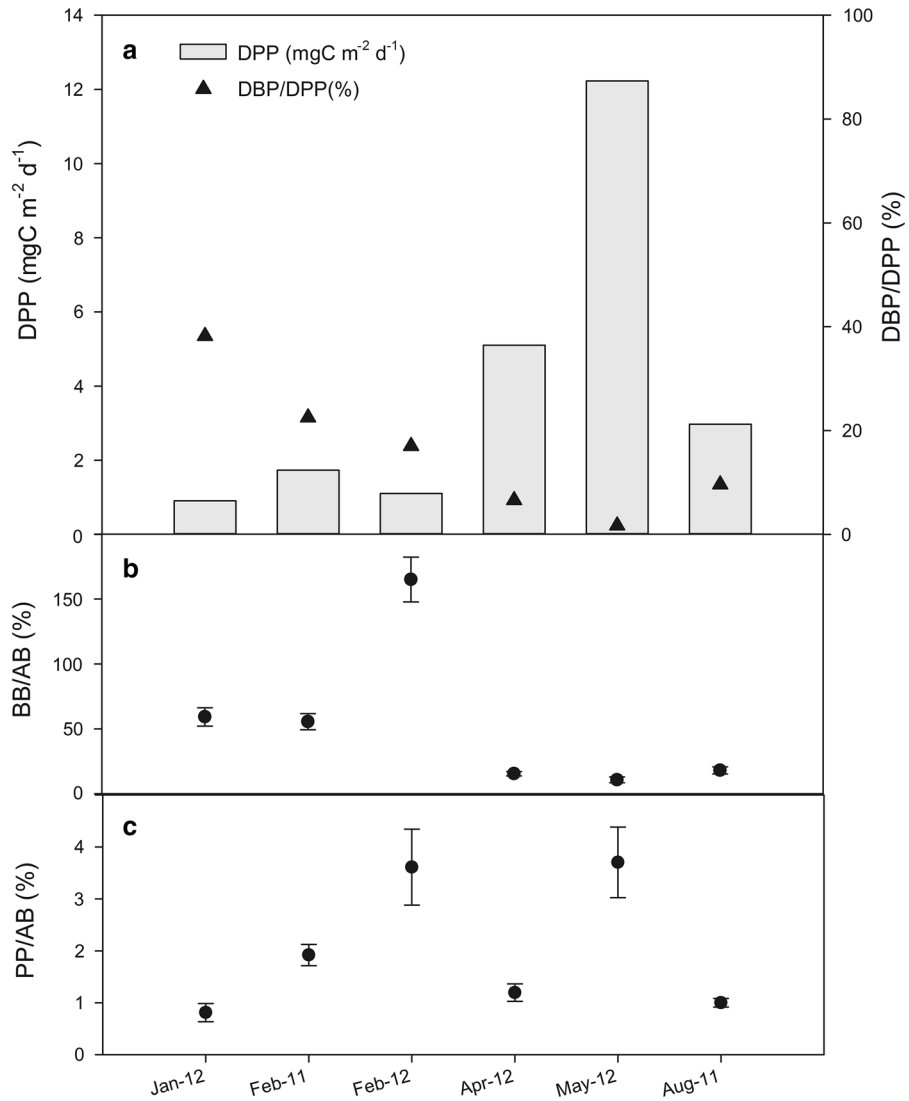

Fig. 5 **a** Daily areal primary production (DPP) along with the daily bacterial production (DBP) to DPP ratio, **b** bacterial biomass (BB) to algal biomass ratio (AB), *error bars* indicate standard deviation and **c** PP to phytoplankton biomass ratio in each sampling campaign

Variations in PP and physicochemical parameters will be discussed in relation to the three distinct seasonal periods described above: winter, spring and summer. Winter differs from other periods mainly by its higher water transparency (smaller WT, K_d, SS and Chl-*a*), but also by lower temperature and incident solar radiation, together with higher TIC. PP had the expected lower values in this season as a consequence of lower solar radiation, but mainly because of reduced algal density caused by flushing, especially in February 2012. This suggests that the reduction of water residence time by flushing could be used as a potentially effective action to alleviate eutrophication, which coincides with results from similar ecosystems (Padisák et al. 1999; Moustaka-Gouni et al. 2006). Chl-*a*-specific PP was noticeably lower in winter (Table 2). Enhanced Chl-*a* synthesis at low light intensities has been reported for both prokaryote and eukaryote algae (Falkowski and Laroche 1991) which might explain our observed low Chl-*a*-specific PP values in winter, when irradiance was lowest. Similarly, the change in community composition, with a substantial decrease in cyanobacteria biomass, possibly contributed to the observed variations in this variable.

Maximum PP values should be expected in summer, since solar radiation, temperature and phytoplankton abundance were at peak this time of the year. However, maximum values for PP, DPP or Chl-*a*-specific PP were consistently observed in spring (Figs. 1, 3; Table 2). The lower summer PP values were most likely caused by inorganic nutrient limitation. There was a dramatic decrease in DIN and in the DIN/SRP ratio (Fig. 1a) as the result of high phytoplankton growth during spring and early summer. This decline was probably also due to the denitrification in the sediment–water interface (Seitzinger 1988), where oxygen, that fluctuated markedly along the diel cycle, became almost exhausted at night in summer (author's unpublished data). Summer was further characterized by higher DOC and TOC concentrations (Online Resource 1), which might be attributed to the production of mucilage by the dominant algae, namely filamentous and colonial cyanobacteria. This mucilage very likely consists of unused photosynthetic derivatives, which indicates nutrient deficiency or C, N and P imbalance in the environment (Myklestad 1995; Margalef 1997; Fraga 2001; Reynolds 2006). Further, the fact that Chl-*a* values were close to those found in winter (aside from the low values observed during February 2012), but phytoplankton abundance and biomass were high indicates a low phytoplankton production/biomass ratio (Fig. 5c) characteristic of later successional stages (Margalef 1997), when resources become scarce. In agreement with our results, a decrease in Chl-*a* content in relation to high algal densities was found in four Korean reservoirs (Ahn et al. 2007).

In spring, both Chl-*a* and PP reached maximum values, favoured by the high solar radiation and nutrients levels. Water transparency was minimum in this season as illustrated by K_d, WT and SS (Online Resource 1). SRP and DIN were relatively high while a clear TIC decrease was observed due to enhanced photosynthesis. The present results agree with previous findings in a seasonal study in Albufera de Valencia, with the peak Chl-*a* concentrations and maximum PP measured in late spring, namely in May and June, respectively (Vicente and Miracle 1992), but surprisingly, they differ from those found in many hypertrophic systems, with maximum PP in summer (Kamjunke et al. 1997; Kisand and Noges 1998; Liboriussen and Jeppesen 2003; Schelske et al. 2003). This discrepancy was very likely caused by the fact that unlike most mentioned systems (located in the north-temperate zone), Albufera de Valencia presents favorable temperature conditions in spring ($\approx$20 °C). A similarly important factor might be the mentioned strong nitrogen limitation in summer, which overcame the role of high temperature and light availability in controlling phytoplankton photosynthetic rates during this season in the lagoon. Nonetheless, the seasonal variations in Chl-*a*-specific PP agreed with the seasonal variations described in the shallow hypertrophic coastal lake Zeekoevlei, with lower values in winter and greater values in spring (Harding 1997). Our Chl-*a*-specific PP values (Table 2) laid within the range of 1.6–7.9 μg C L^{-1} : μg Chl-a^{-1} m^{-3} h^{-1} reported in a study that included numerous productive lakes (Harding 1997), the range of 2–12 "μg C L^{-1} : μg Chl-a^{-1} m^{-3} h^{-1} found in a shallow hypertrophic subtropical lake (Schelske et al. 2003) and the range of approximately 1–14 μg C L^{-1} : μg Chl-a^{-1} m^{-3} h^{-1} observed in the shallow hypertrophic reservoir Maltañski (Joniak et al. 2003).

Maximum DPP (Fig. 5a) exceeded the DPP values reported by the aforementioned studies: 1–5 g C m^{-2} day^{-1} (Schelske et al. 2003) and 4.7 g C m^{-2} d^{-1} (Joniak et al. 2003). Moreover, among the results from numerous warm freshwater ecosystems compiled by Harding (1997), only Hartbeespoort Dam and Sri Lanka reservoirs surpassed the values observed in Albufera de Valencia, which reflects the considerably high productivity of this system.

We consider that in the present study, the misestimation of EDOC caused by heterotrophic bacterial uptake is very unlikely. Firstly, incubation time was short. Secondly, the proportion of labeled/unlabeled DOC is small given the high DOC concentrations naturally present in the environment, so we assume that the heterotrophic bacteria that might have been held in the filter had uptaken an insignificant fraction of labeled DOC and therefore did not cause an overestimation of EDOC. The strong correlation found between PP and EDOC has been widely observed in aquatic systems (Baines and Pace 1991) and indicates that in Albufera de Valencia PP is the major factor controlling EDOC. PER averaged 12 %, very close to the 13 % reported in the model of Baines and Pace (1991) and laid within the range described in that study. PER values also coincided with variations (0.6–32.4 %) observed in the euphotic zone of the

hypertrophic Hartbeesport Dam in South Africa (Robarts and Sephton 1989). In agreement with results from both marine and freshwater systems (Robarts and Sephton 1989; Morán et al. 2002), PER was found to decrease with increasing PP in the present study, suggesting that when photosynthesis is not light or nutrient-limited, the amount of EDOC is smaller.

Dark assimilation supposed a small contribution to pelagic production in comparison with PP. Because chemosynthesis occurs in layers having contact with anaerobic areas (Wetzel and Likens 2001), higher values are usually observed in the bottom layer in contact with the sediment, where oxygen is consumed by the decomposition of organic matter. However, the intense mixing of the water column in this shallow system prevented severe stratification and very likely explains the lack of differences with depth. Seasonal variations, however, did occur: Dark assimilation was lower in winter, intermediate in spring and very high in summer (Table 2), indicating the increase of chemosynthetic bacterial activity with raising temperatures. Nonetheless, these variations were probably also driven by the availability of reduced substrates produced by the organic matter decomposition, which increased alongside PP and temperature from winter to summer.

Diel patterns

As a result of diurnal changes in light availability, PP showed a marked diel pattern that followed the solar radiation curve with the maximum at noon (Figs. 3, 4). Given the remarkably high phytoplankton biomass in Albufera de Valencia, self-shading probably impeded light inhibition at 0.2 m depth and no depression in PP was observed around noon, in contrast to what it has been described in other studies (Oliver et al. 2003; Wu et al. 2011). The fact that photoinhibition was observed in February 2012 during the noon experiment as a consequence of the increased water transparency, driven in turn by the reduction in algal biomass (Fig. 3), supports the idea that self-shading plays a main role in shaping diurnal PP variations.

The high photosynthetic activity in Albufera de Valencia during spring drove very evident diurnal variations in physicochemical variables (Fig. 4a). Greater pH and O_2 % values were linked to higher photosynthetic rates during light hours. These values descended during the night and reached a minimum at dawn. As expected, DIC showed the opposite pattern with a decrease during the day and an increase at nightfall. However, the increase was followed by an unexpected diminution throughout the night. This decline might have been caused by CO_2 consumption by chemosynthetic bacteria. Then, there was a slight rise at daybreak immediately followed by the decrease that typically occurs during light hours. Previous observations in this lake with higher dark assimilation during night (Vicente and Miracle 1992) support the hypothesis of a higher activity of chemosynthetic bacteria in this period.

In an extremely shallow lake like Albufera de Valencia, nutrient diurnal fluctuations might partially respond to wind-induced vertical mixing patterns and convention currents due to day-night temperature changes. Higher NH_4 and NO_3 concentrations were observed during late afternoon and evening coinciding with higher SS, TP and TN levels, though the latter showed a weaker relation (Fig. 4b, c). The fact that unlike SS, organic matter (measured as LOI) showed no coupling with the different nitrogen and phosphorus forms, together with the increase in wind speed during late afternoon on spring experimental dates, indicates that sediment suspension caused the rise in NH_4 and NO_3 toward the evening. Low values of NH_4 and NO_3 coincided with maximum photosynthesis around noon and are very likely the result of phytoplankton consumption. The observed fluctuations in nitrogen forms during the night might be mediated by bacterial processes such as nitrification or ammonification, but further studies should be conducted in order to detangle these processes.

PP in relation to BP

The strong variations observed in phytoplankton biomass across seasons contrasted with the small bacterial biomass variations reported by Onandia et al. (2014) for the same sampling dates. These results agree with observations in other hypertrophic shallow lakes, such as the tropical lagoon Ciénaga Grande de Santa Marta in Colombia (Gocke et al. 2004). Seasonal variation of the bacteria/phytoplankton biomass ratio (Fig. 5b) responded to phytoplankton changes. This ratio was considerably low in spring and summer, indicating the predominance of the autotrophic component in the lagoon during these seasons, but increased in winter. Algal biomass was

higher than bacterial biomass values (BB/AB ratio, Fig. 5b), which is in agreement with previous results in eutrophic ecosystems (Simon et al. 1992; Moustaka-Gouni et al. 2006). However, there was one exception after intense flushing, when the increased flow provoked a drastic reduction in phytoplankton biomass accompanied by a less important diminution in bacterial biomass.

Whereas there was an approximately fivefold increase in Chl-*a* concentrations, bacterial numbers remained fairly constant (see bacteria densities in Table 1 in Onandia et al. 2014), supporting previous observations that bacterial abundance does not increase as rapidly as algal biomass with increasing nutrient concentration (Bird and Kalff 1984; Robarts 1988; Gao et al. 2007) and adding new evidence based on a hypertrophic system with Chl-*a* concentrations up to 300 $\mu g\ L^{-1}$.

Similarly, PP showed noticeable variations and increased in spring and summer alongside water turbidity-related parameters, though after the spring peak a diminution took place in summer as nutrients were exhausted. On the contrary, BP remained similar across seasons (see BP in Fig. 5 in Onandia et al. 2014). The different dynamics is illustrated by the variations in the share of DBP in DPP (Fig. 5a). In summer and spring, our values of DBP represented a low proportion of DPP similar to 2–5 % for a range of mesotrophic to hypertrophic lakes (Kamjunke et al. 1997 and references therein). The higher winter values were still in agreement with reported observations: 17 % in the hypertrophic Humboldt Lake or 31 % in the shallow eutrophic Frederiksborg Slotssø (Søndergaard 1993; Robarts et al. 1994). Interestingly, our mean DBP/DPP (16 %) was very close to the value of 15 % found for 21 freshwater systems (Fouilland and Mostajir 2010) with primary productivity (DPP 1–10 $gC\ m^{-2}\ d^{-1}$) similar to Albufera de Valencia. The DBP/DPP aforementioned data suggest that the role of bacteria within the food web decreased with increasing lake PP. This is further supported by the fact that bacterial carbon production per unit of biomass did not increase with lake primary productivity (author's unpublished data). These results do not necessarily contradict with the idea that microbial activities increase along nutrient availability (Auer et al. 2004), since other factors (such as predation) might be shaping PP–BP interaction in the lagoon. Similarly, the fact that all Chl-*a* values lay within the hypertrophic range might explain the discrepancy, though they could also point to a saturation in the relationship of increasing BP with PP. The ratio PP/BP can provide information about the base of the planktonic food web; PP/BP < 1 indicates that in terms of particulate carbon, heterotrophic bacteria make available more energy than primary producers for higher trophic levels. In all samplings, the DPP/DBP ratio was greater than one, indicating the autotrophic nature of the lagoon. In agreement with the observation that BGE generally increases with system productivity (del Giorgio and Cole 1998), BGE was high in the extremely productive Albufera de Valencia. Nonetheless, despite BGE was greater than reported values for the hypertrophic lakes Szymon and Taltowisko (Poland): 40 and 37 %, respectively (Chrost and Siuda 2006), it did not surpass maximum values (up to 80 %) reported for nutrient-rich lakes (del Giorgio and Cole 1998).

At the seasonal scale, neither on an hourly nor on a daily areal basis were BP and PP correlated. However, consecutive measurements as well as a time lag would be necessary to better assess this relationship. A potential explanation for the lack of coupling at the seasonal scale is that bacterial production might be related to the use of the standing stock of organic compounds rather than to the EDOC supplied by phytoplankton during contemporary photosynthesis. Further, EDOC supports 50 % or more of bacterial carbon demand in most pelagic systems (Chrost et al. 2000). In a highly productive system like Albufera de Valencia, we hypothesize that EDOC would be seldom limiting for heterotrophic bacteria, thus making more difficult to observe the coupling between BP and PP. As a matter of fact, contemporaneous EDOC was sufficient to meet BCD in all the experimental dates, indicating that algal photosynthesis would be able to support the great bacterial production rates observed in the lake and allochthonous organic matter inputs should be of little importance to heterotrophic bacteria, though they cannot be completely discarded as an additional carbon source. Similar results were found in shallow eutrophic Lake Võrtsjärv (Kisand and Noges 1998), where no tight coupling was found and PP could cover the carbon need of heterotrophic bacteria. However, in the eutrophic Bautzen reservoir (Kamjunke et al. 1997), EDOC only partially covered BCD and BP and PP were strongly correlated. These results indicate a stronger coupling in relation to lower

EDOC availability and support the hypothesis that a more tightly coupled community should be found where DOC is more scarce and a less tightly coupled situation should be found in relation to higher DOC availability (Gasol et al. 1998), though in the latter study concerning a marine ecosystem, the higher DOC availability proceeded from sources other than PP such as allochthonous carbon of continental origin.

In conclusion, PP and BP varied differently across seasons. Whereas the former showed important seasonal variations, the latter remained fairly constant. Nonetheless, there was a joint diminution during increased water transparency followed by an increase in early spring. The BP/PP ratio was higher in winter, coinciding with lower PP values. These data indicate that the role of bacteria within the lake food web might decrease as primary productivity increases in the lagoon. EDOC was sufficient to meet BCD in all the experimental dates, signifying that allochthonous carbon sources play a minor role in sustaining BP, though they cannot be excluded. However, we hypothesize that high availability of DOC might explain the lack of coupling observed between BP and PP.

Minimum PP values coincided with increased water flow in winter, suggesting that flushing management could be used to reduce eutrophication symptoms in the lagoon. PP/phytoplankton biomass ratio was higher in mid-spring when compared to summer values, which is in agreement with the theory of lower energy transfer along the annual phytoplankton succession (Margalef 1997). Our results show that in Albufera de Valencia, phytoplankton was always the most relevant input to particulate carbon production. However, because filamentous and colonial cyanobacteria are not edible for zooplankton, heterotrophic bacteria are probably an important energy source for higher trophic levels in hypertrophic lakes. Indeed, the bacterivory of rotifers (such as *Brachionus angularis* and *Anuraeopsis fissa*) has been described in Albufera de Valencia (Miracle et al. 2014), highlighting the relevance of the microbial food web in energy transfer. Future studies comprising the microbial loop as well as higher trophic levels as zooplankton would be needed better depict carbon flow pathways.

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References

Ahn C-Y, Joung S-H, Yoon S-K, Oh H-M (2007) Alternative alert system for cyanobacterial bloom, using phycocyanin as a level determinant. J Microbiol 45:98–104

APHA (1992) Standard methods for the examination of water and wastewater, 18th edn. American Public Health Association, Washington, DC

Auer B, Elzer U, Arndt H (2004) Comparison of pelagic food webs in lakes along a trophic gradient and with seasonal aspects: influence of resource and predation. J Plankton Res 26:697–709

Baines SB, Pace ML (1991) The production of dissolved organic-matter by phytoplankton and its importance to bacteria: patterns across marine and fresh-water systems. Limnol Oceanogr 36:1078–1090

Bird DF, Kalff J (1984) Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. Can J of Fish Aquat Sci 41:1015–1023. doi:10.1139/f84-118

Blindow I, Hargeby A, Meyercordt J, Schubert H (2006) Primary production in two shallow lakes with contrasting plant form dominance: a paradox of enrichment? Limnol Oceanogr 51:2711–2721

Callieri C, Stockner JG (2002) Freshwater autotrophic picoplankton: a review. J Limnol 61:1–14

Chrost RJ, Siuda W (2006) Microbial production, utilization, and enzymatic degradation of organic matter in the upper trophogenic layer in the pelagial zone of lakes along an eutrophication gradient. Limnol Oceanogr 51:749–762

Chrost RJ, Koton M, Siuda W (2000) Bacterial secondary production and bacterial biomass in four Mazurian lakes of differing trophic status. Pol J Environ Stud 9:255–266

Cole JJ, Likens GE, Strayer DL (1982) Photosynthetically produced dissolved organic carbon: an important carbon source for planktonic bacteria. Limnol Oceanogr 27:1080–1090

Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Mar Ecol Prog Ser 43:1–10. doi:10.3354/meps043001

del Giorgio PA, Cole JJ (1998) Bacterial growth efficiency in natural aquatic systems. Annu Rev Ecol Syst 29:503–541. doi:10.1146/annurev.ecolsys.29.1.503

Dickman M (1969) Some effects of lake renewal on phytoplankton productivity and species composition. Limnol Oceanogr 14:660–666

Falkowski PG, Laroche J (1991) Acclimation to spectral irradiance in algae. J Phycol 27:8–14. doi:10.1111/j.0022-3646.1991.00008.x

Fouilland E, Mostajir B (2010) Revisited phytoplanktonic carbon dependency of heterotrophic bacteria in freshwaters, transitional, coastal and oceanic waters. FEMS Microbiol Ecol 73:419–429. doi:10.1111/j.1574-6941.2010.00896.x

Fraga F (2001) Phytoplanktonic biomass synthesis: application to deviations from Redfield stoichiometry. Sci Mar 65:153–169

Gao G, Qin B, Sommaruga R, Psenner R (2007) The bacterioplankton of Lake Taihu, China: abundance, biomass, and production. Hydrobiologia 581:177–188. doi:10.1007/s10750-006-0511-7

Gasol JM, Doval MD, Pinhassi J, Calderon-Paz JI, Guixa-Boixareu N, Vaque D, Pedros-Alio C (1998) Diel variations in bacterial heterotrophic activity and growth in the northwestern Mediterranean Sea. Mar Ecol Prog Ser 164:107–124. doi:10.3354/meps164107

Gocke K, Hernandez C, Giesenhagen H, Hoppe HG (2004) Seasonal variations of bacterial abundance and biomass and their relation to phytoplankton in the hypertrophic tropical lagoon Cienaga Grande de Santa Marta, Colombia. J Plankton Res 26:1429–1439. doi:10.1093/plankt/fbh131

Harding WR (1997) Phytoplankton primary production in a shallow, well-mixed, hypertrophic South African lake. Hydrobiologia 344:87–102. doi:10.1023/a:1002954311328

Hart EA, Lovvorn JR (2000) Vegetation dynamics and primary production in saline, lacustrine wetlands of a Rocky Mountain basin. Aquat Bot 66:21–39

Hillebrand H, Durselen CD, Kirschtel D, Pollingher U, Zohary T (1999) Biovolume calculation for pelagic and benthic microalgae. J Phycol 35:403–424

ISO (International Organization for Standardization) (1997) Water analysis - Guidelines for the determination of total organic carbon (TOC) and dissolved organic carbon (DOC). ISO EN 1484.ISO, Geneva

ISO (International Organization for Standardization) (1999) Water quality - Determination of turbidity. ISO EN 7027, ISO, Geneva

Jacoby J, Welch E (2004) Pollutant effects in freshwater: applied limnology, 3rd edn. Spon Press, London

Jones I, Elliott J (2007) Modelling the effects of changing retention time on abundance and composition of phytoplankton species in a small lake. Freshw Biol 52:988–997

Joniak T, Goldyn R, Kozak A (2003) The primary production of phytoplankton in the restored Maltanski Reservoir in Poland. Hydrobiologia 506:311–316. doi:10.1023/b:hydr.0000008584.22153.86

Kamjunke N, Boing W, Voigt H (1997) Bacterial and primary production under hypertrophic conditions. Aquat Microb Ecol 13:29–35. doi:10.3354/ame013029

Kisand V, Noges T (1998) Seasonal dynamics of bacterio—and phytoplankton in large and shallow eutrophic Lake Vortsjarv, Estonia. Int Rev Hydrobiol 83:205–216. doi:10.1002/iroh.19980830304

Liboriussen L, Jeppesen E (2003) Temporal dynamics in epipelic, pelagic and epiphytic algal production in a clear and a turbid shallow lake. Freshw Biol 48:418–431. doi:10.1046/j.1365-2427.2003.01018.x

Mague TH, Friberg E, Hughes DJ, Morris I (1980) Extracellular release of carbon by marine phytoplankton; a physiolocial approach. Limnol Oceanogr 25:262–279

Margalef R (1997) Our biosphere. Excellence in ecology, vol 10. Oldenforf-Luhe, Germany

Miracle MR, Vicente E, Sarma S, Nandini S (2014) Planktonic rotifer feeding in hypertrophic conditions. Int Rev Hydrobiol 99:141–150

Morán X, Estrada M, Gasol J, Pedrós-Alió C (2002) Dissolved primary production and the strength of phytoplankton–bacterioplankton coupling in contrasting marine regions. Microb Ecol 44:217–223

Moustaka-Gouni M et al (2006) Plankton food web structure in a eutrophic polymictic lake with a history of toxic cyanobacterial blooms. Limnol Oceanogr 51:715–727

Myklestad SM (1995) Release of extracellular products by phytoplankton with special emphasis on polysaccharides. Sci Total Environ 165:155–164

Oliver RL, Whittington J, Lorenz Z, Webster IT (2003) The influence of vertical mixing on the photoinhibition of variable chlorophyll a fluorescence and its inclusion in a model of phytoplankton photosynthesis. J Plankton Res 25:1107–1129

Onandia G, Miracle MR, Blasco C, Vicente E (2014) Diel and seasonal variations in bacterial producation in a hypertrophic shallow lagoon. Aquat Microb Ecol 72:255–267

Padisák J, Köhler J, Hoeg S (1999) Effect of changing flushing rates on development of late summer Aphanizomenon and Microcystis populations in a shallow lake. Müggelsee, Berlin

Pugnetti A, Del Negro P, Giani M, Acri F, Aubry FB, Bianchi F, Berto D, Valeri A (2010) Phytoplankton–bacterioplankton interactions and carbon fluxes through microbial communities in a microtidal lagoon. FEMS Microbiol Ecol 72:153–164

Reynolds CS (2006) The ecology of phytoplankton, 1st edn. Cambridge University Press, New York

Robarts RD (1988) Heterotrophic bacterial activity and primary production in a hypertrophic African lake. Hydrobiologia 162:97–107. doi:10.1007/bf00014532

Robarts RD, Sephton LM (1989) Phytoplankton extracellular dissolved organic-carbon production in a hypertrophic African lake. Hydrobiologia 182:137–148. doi:10.1007/bf00006039

Robarts RD, Arts MT, Evans MS, Waiser MJ (1994) The coupling of heterotrophic bacterial and phytoplankton production in a hypertrophic, shallow prairie lake. Can J Fish Aquat Sci 51:2219–2226. doi:10.1139/f94-224

Romo S et al (2005) Response of a shallow Mediterranean lake to nutrient diversion: does it follow similar patterns as in northern shallow lakes? Freshw Biol 50:1706–1717. doi:10.1111/j.1365-2427.2005.01432.x

Romo S, Garcıa-Murcia A, Villena MJ, Balleste VSA (2008) Tendencias del fitoplancton en el lago de la Albufera de Valencia e implicaciones para su ecología, gestión y recuperación. Limnetica 27:11–28

Schelske CL, Aldridge FJ, Carrick HJ, Coveney MF (2003) Phytoplankton community photosynthesis and primary production in a hypereutrophic lake, Lake Apopka, Florida. Arch Hydrobiol 157:145–172. doi:10.1127/0003-9136/2003/0157-0145

Seitzinger SP (1988) Denitrification in fresh-water and coastal marine ecosystems: ecological and geochemical significance. Limnol Oceanogr 33:702–724

Shoaf TW, Lium BW (1976) Improved extraction of chlorophyll a and b from algae using dimethylsulphoxide. Limnol Oceanogr 21:926–928

Simon M, Cho BC, Azam F (1992) Significance of bacterial biomass in lakes and the ocean: comparison to phytoplankton biomass and biogeochemical implications. Mar Ecol-Prog Ser 86:103–110

Søballe D, Kimmel B (1987) A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. Ecology 68:1943–1954

Sommaruga R, Robarts RD (1997) The significance of autotrophic and heterotrophic picoplankton in hypertrophic ecosystems. FEMS Microbiol Ecol 24:187–200. doi:10.1111/j.1574-6941.1997.tb00436.x

Søndergaard M (1993) Organic carbon pools in two Danish lakes. Flow of carbon to bacterioplankton. Verh Int Ver Angew Theor Limnol 25:593–598

Steeman-Nielsen EJ (1952) The use of radioactive carbon (14C) for measuring organic production in the sea. J Cons Perm Int Pour l'Explor Mer 18:117–140

Vicente E, Miracle M (1992) The coastal lagoon Albufera de Valencia: an ecosystem under stress. Limnetica 8:87–100

Villena M-J, Romo S (2003) Temporal changes of cyanobacteria in the largest coastal Spanish lake. Algol Stud 109:593–608

Wetzel RG, Likens GE (2000) Limnological analyses, 3rd edn. Springer, New York

Wetzel RG, Likens GE (2001) Limnology: lake and river ecosystems, 3rd edn. Springer, San Diego

Winter C, Herndl GJ, Weinbauer MG (2004) Diel cycles in viral infection of bacterioplankton in the North Sea. Aquat Microb Ecol 35:207–216

Wu X, Kong F, Zhang M (2011) Photoinhibition of colonial and unicellular Microcystis cells in a summer bloom in Lake Taihu. Limnology 12:55–61