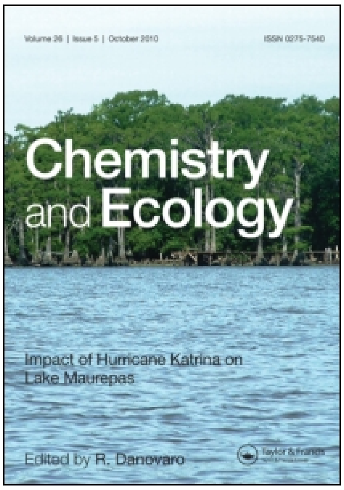

Chemistry and Ecology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713455114

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To cite this Article Pugnetti, Alessandra , Acri, Francesco , Alberighi, Luisa , Barletta, Donato , Bastianini, Mauro , Bernardi-Aubry, Fabrizio , Berton, Andrea , Bianchi, Franco , Socal, Giorgio and Totti, Cecilia(2004) 'Phytoplankton photosynthetic activity and growth rates in the NW Adriatic Sea', Chemistry and Ecology, 20: 6, 399 — 409

To link to this Article: DOI: 10.1080/02757540412331294902

URL: http://dx.doi.org/10.1080/02757540412331294902

Chemistry and Ecology
December 2004, Vol. 20(6), pp. 399–409

PHYTOPLANKTON PHOTOSYNTHETIC ACTIVITY AND GROWTH RATES IN THE NW ADRIATIC SEA

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(Received 15 May 2004; In final form 18 June 2004)

Taxonomic composition, biomass, primary production and growth rates of the phytoplankton community were studied in two stations in the NW Adriatic Sea on a seasonal basis, in areas characterized by differing hydrological and trophic conditions. The main differences between the two stations were quantitative rather than qualitative, most phytoplankton species being common to both stations. The effects of differing nutrient concentrations and plume spreading were evident. Biomass and primary production rates were significantly higher in the coastal station (S1), and the phytoplankton distribution in the water column was markedly stratified in S1 and more even in the offshore station (S3). However, chlorophyll *a* specific production, potential growth rate and production efficiencies were very similar in both stations, even when phosphorus concentrations were limiting. A discrepancy between potential and actual growth rate was observed: as a feature common to both stations, comparisons between potential and actual growth rates revealed that little carbon produced by phytoplankton accumulated as algal biomass; therefore, very high loss rates were estimated.

Keywords: NW Adriatic Sea; Phytoplankton; Primary production; Growth rate

1 INTRODUCTION

The volume and distribution of freshwater transported to the Northern Adriatic from the Po, the main Italian River, deeply influences the phytoplankton community in terms of supply of inorganic nutrients and seston, general circulation of the system, and vertical stability of the water column (Franco and Michelato, 1992; Boicourt *et al.*, 1999; Hopkins *et al.*, 1999).

Most previous studies on primary production in the Northern Adriatic refer to stations located offshore; only a few have considered the western coastal zone, where the effect of river runoff is higher (Heilmann and Richardson, 1999a, b; Bernardi Aubry *et al.*, 2002; Socal *et al.*, 2002; Vadrucci *et al.*, 2002). The area is characterized by marked temporal and spatial variability of the underwater light field, vertical stratification and mixing,

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ISSN 0275-7540 print; ISSN 1029-0370 online
DOI: 10.1080/02757540412331294902

and nutrient supply. These features are expected to have a marked influence on the photosynthetic performance of phytoplankton.

Our study concerned analysis of the phytoplankton community in two stations (Fig. 1), which may be considered as representative of two different hydrological and trophic conditions encountered in the NW Adriatic, *i.e.* the high, continuous *vs.* low, sporadic influence of the river Po.

Primary production may be viewed as the product of standing stock and growth rate; its variations depend on light availability and on the extent to which the nutrient supply limits phytoplankton standing stock, growth rate, or both (Caperon *et al.*, 1971; Cullen *et al.*, 1992; Malone *et al.*, 1996). This work analyses the relationships between *in situ* photosynthetic rates and phytoplankton biomass in the NW Adriatic with the purpose, first of all, of assessing if differing nutrient supplies control primary productivity by affecting standing stock or growth rate; then to evaluate if, for this area, specific production (production normalized to chlorophyll a, P^b) is reliable in reflecting the different nutritional status of the phytoplankton; and, lastly, to estimate if and how actual daily growth rates match potential growth rates.

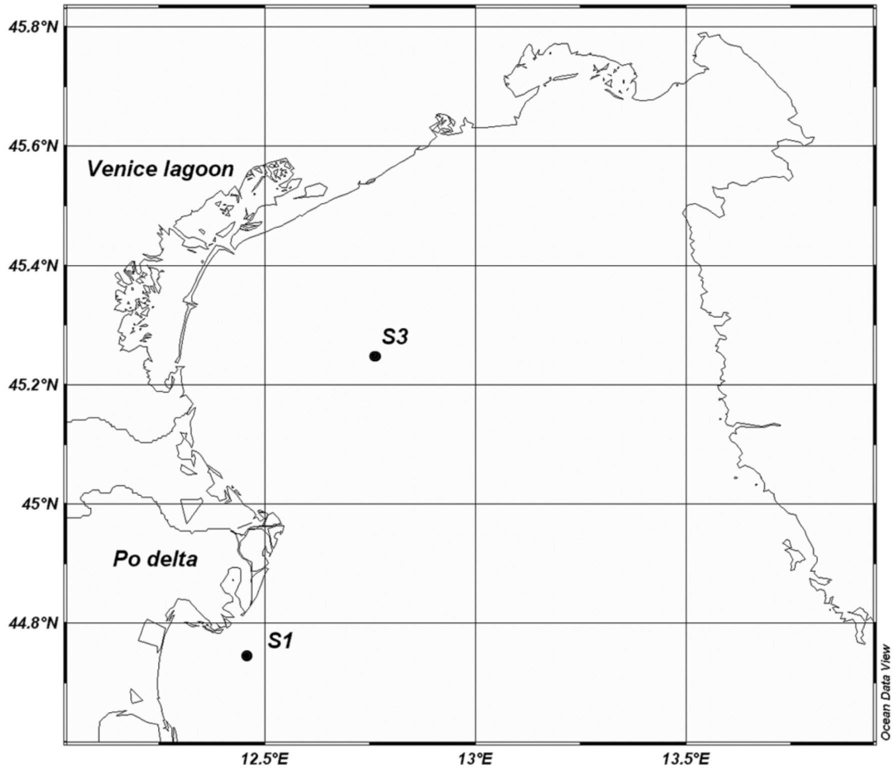

FIGURE 1 Location of sampling stations S1 and S3.

2 MATERIALS AND METHODS

Station S1 (44° 44.70′ N; 12° 27.41′ E; bottom depth 20 m) is located 5 nautical miles from the coast and is always affected by the plume of the river Po. Station S3 (45° 15.0′ N; 12° 45.60′ E; bottom depth 27 m) is about 20 nautical miles from the coast, is rarely influenced by fluvial inputs, and is representative of offshore waters in the NW Adriatic (Fig. 1).

Four surveys in each station were carried out seasonally in April, July and October 1995 and January 1996; during each survey, with the exception of station S3 in January, measurements were repeated on two consecutive days, at 24 h intervals.

Continuous vertical profiles of temperature and conductivity were performed with a CTD probe (Idronaut, mod. 801). Photosynthetically available radiation (PAR: 400–700 nm) was measured with a Biospherical quantum scalar irradiance meter. Samples were collected at fixed depths along the whole water column (S1: surface, 1, 5, 10, 15 and 20 m; S3: surface, 1, 5, 10, 15, 20 and 27 m). Dissolved inorganic nutrients (Grasshoff *et al.*, 1983), phytoplankton chlorophyll *a* (Holm-Hansen *et al.*, 1965), species composition, abundance (Utermöhl, 1958), biomass (Smetacek, 1975; Edler, 1979) and primary production (Steemann Nielsen, 1952) were analysed. Phytoplankton taxonomic composition was defined according to Tomas (1997); the nanoflagellate group included the cells of various taxa, with sizes ranging mainly between 3 and 5 μm, and were often undetermined. The mean phytoplankton community cell size was estimated from the ratio between total biovolume and total abundance.

Samples for primary production measurement were incubated *in situ* for 4 h around noon, in 150 ml duplicate light and dark bottles inoculated with a 148 kBq $NaH^{14}CO_3$ solution; they were then passed through GF/F filters and placed in scintillation vials after removal of ^{14}C by addition of 0.2 ml of HCl 0.5 N. A scintillation cocktail (Instagel-Packard) was added to the dried filters, which were left in the dark for 24 h, before being counted on a Beckman scintillation counter. CO_2 was measured by potentiometric titration (Johannson and Wedborg, 1982).

Daily production (ΔC, mg C m^{-2} d^{-1}) was estimated according to Platt (1971). Potential ($\mu = \ln\,(1 + \Delta C/Cp_{t1})$) and actual ($k = \ln\,(Cp_{t2} - Cp_{t1})/(t_2 - t_1)$) growth rates and loss ($\lambda = \mu - k$) rates for the phytoplankton community were calculated, on a daily basis, from the daily production (ΔC) and from the total phytoplankton biomass (Cp: mg C m^{-2}), according to Tilzer (1984).

3 RESULTS AND DISCUSSION

A general overview of the main hydrological characteristics and of the phytoplankton community in the two stations is presented in Tables I–III. The dominant phytoplankton groups were nanoflagellates and diatoms in both stations (Tab. III), a feature generally observed in the NW Adriatic (Bernardi Aubry *et al.*, 2002). However, the mean relative abundance of diatoms was higher in station S3, where dinoflagellates (in April and July) and coccolithophorids (in January) also had some importance. The relevance of coccolithophorids was clearly related to high salinity.

TABLE I Main hydrological parameters: comparison between the two stations (one-way ANOVA on the whole data set).

	Station S1 *Mean ± S.D.*	*Station S3* *Mean ± S.D.*	*P*
Water density (γ_t)	24.4 ± 5.9	27.4 ± 1.7	<0.01
Water column stratification	Saline	Thermal	
Dissolved inorganic nitrogen, DIN (μM)	25.3 ± 34.3	3.7 ± 2.0	<0.01
Silicates (μM)	13.3 ± 28.1	4.0 ± 3.6	<0.01
Phosphates (μM)	0.2 ± 0.3	0.03 ± 0.03	<0.01
N/P	$\gg 16$	$\gg 16$	
PAR attenuation coefficient, k_0 (m^{-1})	0.5 ± 0.7	0.2 ± 0.2	<0.05

Most phytoplankton groups observed with the highest abundance (Tab. III), *i.e.* small flagellates (3–5 µm) and filamentous or radial colonial diatoms (*Pseudo-nitzschia delicatissima*, *Skeletonema costatum*, *Asterionellopis glacialis*) were common to both stations. This observation is in accordance with long-term series studies, indicating that most taxa blooming in the NW Adriatic are common to both coastal and offshore areas.

Small (6–7 µm, as maximum linear dimension, MLD) single-cell centric diatoms (*Chaetoceros* spp.) were found preferentially in station S1, and large (MLD: 20–25 µm) single-cell diatoms (*Proboscia alata*), colonial diatoms (*Cerataulina pelagica*) and large (MLD: 20–25 µm) motile dinoflagellates (*Prorocentrum* spp.) in station S3. In any case, the mean community cell size was lower in station S1, as a consequence of the greater importance of nanoflagellates and the lack of large species.

Water column stratification and PAR attenuation were different in the two stations, leading to evident dissimilarities in the vertical distribution of phytoplankton production and biomass (Figs. 2 and 3). In all seasons, minimum values of phytoplankton biomass

TABLE II Main phytoplankton community characteristics in the two stations, in the euphotic layer (one-way ANOVA on the whole data set).

	Station S1 *Mean ± S.D.*	*Station S3* *Mean ± S.D.*	*P*
Nanoflagellates (% total abundance)	69 ± 20	48 ± 26	<0.05
Diatoms (% total abundance)	28 ± 20	39 ± 31	<0.05
Dinoflagellates (% total abundance)	1 ± 1	5 ± 8	<0.05
Coccolithophorids (% total abundance)	0.2 ± 0.5	6 ± 11	<0.05
Phytoplankton abundances, Ab_p (cells ml^{-1})	8150 ± 7810	1180 ± 2970	<0.01
Phytoplankton carbon, Cp (μg l^{-1})	148 ± 140	28 ± 59	<0.01
Chlorophyll *a*, chl (μg l^{-1})	3.2 ± 4.5	0.5 ± 0.3	<0.01
Mean community biovolume (μm^3)	150 ± 126	369 ± 331	<0.01
Primary production, PP (mg C m^{-3} h^{-1})	30 ± 59	3 ± 2	<0.01
Specific production, P^b (mg C mg chl a^{-1} h^{-1})	7.2 ± 5.8	6.6 ± 4.8	n.s.
Production efficiency, P^b/PAR (mg C (mg chl a)$^{-1}$ h^{-1} (μE m^{-2} s^{-1})$^{-1}$)	0.05 ± 0.07	0.05 ± 0.03	n.s.
Potential growth rate, μ (d^{-1})	0.47 ± 0.42	1.0 ± 0.7	<0.05
Actual growth rate, k (d^{-1})	0.05 ± 0.3	0.5 ± 1.1 (coastal inputs)	<0.05
Loss rate, λ (d^{-1})	0.40 ± 0.40	0.28 ± 1.2	n.s.

Note: n.s.: not significant.

TABLE III Phytoplankton taxonomic composition in the two stations (taxa whose relative abundance is higher than 2%).

April	*July*	*October*	*January*
Station S1			
Nanoflagellates	Nanoflagellates	Nanoflagellates	Nanoflagellates
Pseudo-nitzschia delicatissima complex	*Chaetoceros calcitrans*	*Asterionellopsis glacialis*	
Skeletonema costatum	*Pseudo-nitzschia delicatissima* complex	*Skeletonema costatum*	
		Leptocylindrus danicus *Leptocylindrus minimus* *Pseudo-nitzschia delicatissima* complex	
Station S3			
Nanoflagellates	Nanoflagellates	Nanoflagellates	Nanoflagellates
Pseudo-nitzschia delicatissima complex	*Pseudo-nitzschia seriata* complex	*Asterionellopsis glacialis*	*Emiliania huxleyi*
Skeletonema costatum	*Pseudo-nitzschia delicatissima* complex *Proboscia alata* *Cerataulina pelagica* *Emiliania huxleyi* *Prorocentrum* spp.	*Pseudo-nitzschia delicatissima* complex *Leptocilyndrus danicus*	*Cylindrotheca closterium*

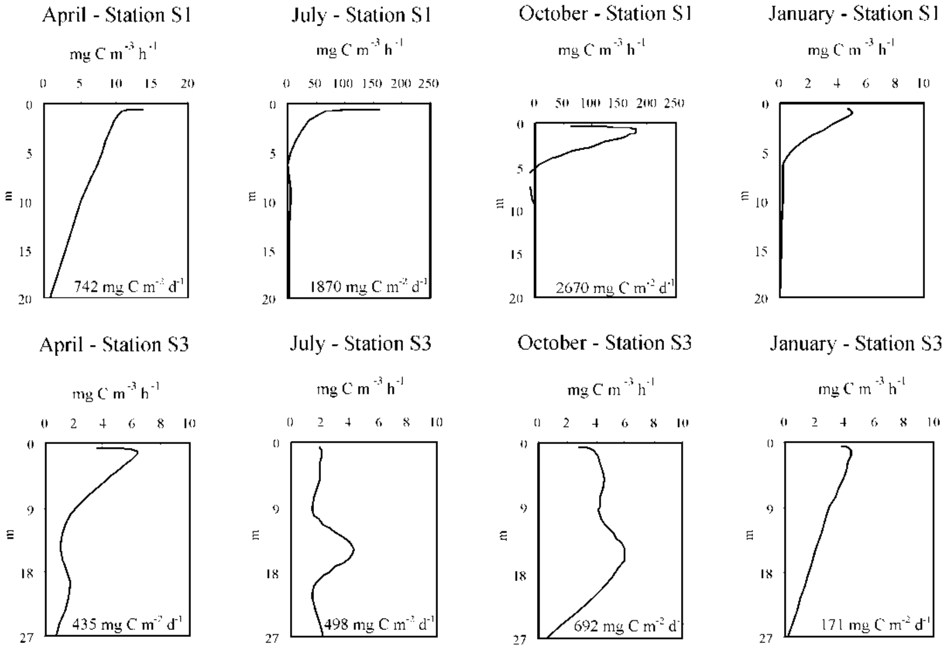

FIGURE 2 Vertical profiles of primary productivity in the two stations.

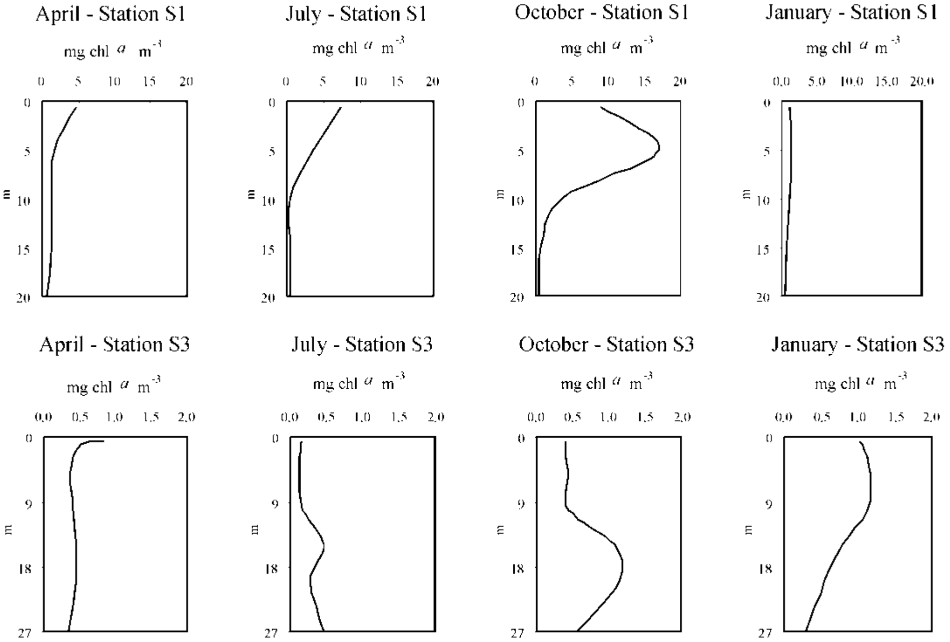

FIGURE 3 Vertical profiles of chlorophyll *a* concentrations in the two stations.

and production occurred in the bottom layers at both stations, less than 1 mg chl *a* m^{-3} and 1 mg C m^{-3} h^{-1}, respectively. In station S1, as a result of strong vertical salinity gradients, low vertical mixing of the water column, and confinement of bottom waters (Giani *et al.*, 2001), primary production (maximum values: 15 mg C m^{-3} h^{-1}, in April; 170 in July; 240 in October; 5 in January) and chlorophyll *a* (maximum values: 7 mg m^{-3} in April; 7.6 in July; 20 in October; 1.4 in January) differed markedly between the upper and lower layers. The water column was aphotic below 5 m in October and January, and the water-column productivity was obviously light-limited. In station S3, the water column was always euphotic; the values and the range of vertical variations of phytoplankton productivity (maximum values: 11 mg C m^{-3} h^{-1} in April; 6 in July; 8 in October; 5 in January) and chlorophyll *a* (maximum values: 1.4 mg m^{-3} in April; 0.6 in July; 1.3 in October; 1.2 in January) were much smaller than those observed in station S1. Subsurface peaks of both productivity and chlorophyll *a* were observed in every sampling, with the exception of January. Dissimilarities in production in the two stations were greater in the upper 5 m; values were similar or even higher in the offshore station in the layers below. The mean (Tab. II) and integrated production values of the water column (Fig. 2) were higher in station S1, with the exception of January.

The elevated productivity rates observed in station S1 were mostly related to higher biomass rather than to higher specific production (P^{b}) and potential growth rates (μ, Tab. II): the offshore station appeared to be more oligotrophic as regards standing stock (Tab. II) and nutrient concentrations (Tab. I), but it was characterized by P^{b} and μ similar to or higher than those measured in the coastal station (Tab. II). The main effect of different nutrient concentrations therefore seemed to concern control of standing stock rather than growth rates. Also, production efficiency (production normalized to chlorophyll and PAR) did not differ significantly between the two stations (Tab. II). Similar results were also obtained in other works carried out in the northern Adriatic (Heilmann and Richardson, 1999b; Bernardi Aubry *et al.*, 2002; Vadrucci *et al.*, 2002).

Phosphorus has often been indicated as the limiting nutrient in the northern Adriatic (Harding *et al.*, 1999; Degobbis *et al.*, 2000). In the present study, phosphorus concentrations ranged between 0.01 and 1.2 μM in station S1 and between 0.01 and 0.2 μM in station S3. Very high N/P values, considerably higher than the Redfield ratio, are commonly observed in the northern Adriatic, and nitrogen excess can be considered as an intrinsic characteristic of Adriatic waters. Phosphorus regeneration and the role played by dissolved organic phosphorus are considered highly significant for phytoplankton growth (Degobbis *et al.*, 2000; Cozzi *et al.*, 2002), particularly in offshore waters. Dissolved inorganic nitrogen ranged between 3 and 135 μM and between 2 and 8 μM, respectively in station S1 and S3. Our data implied potential P limitation ($N{:}P \gg 16$), in most cases in both stations. The daily inorganic phosphorus demand, estimated from the daily production and from the Redfield ratio (Tab. IV), indicated, however, that in station S3, the phosphorus demand was usually reasonably well balanced with ambient concentrations, while severe ortophosphate limitation seemed to occur in the upper layers of stations S1 in April and July. In any case, in the periods and at the depths at which this potential phosphorus limitation might occur, both the primary production and the chlorophyll specific production remained high (Tab. IV), falling in a range that did not indicate nutrient limitation (Cotè and Platt, 1983; Lohrenz *et al.*, 1994). This observation suggests, on the one hand, that phytoplankton production might be sustained by sources of phosphorus other than orthophosphate (e.g. phosphorus stored in the phytoplankton cells) and/or by fast regeneration processes from zooplankton and bacteria; on the other hand, it could indicate the existence of a discoupling between photosynthetic activity and new biomass formation. Indeed, comparisons between potential and actual growth rates indicated that very little carbon produced by phytoplankton accumulates as algal biomass in the 24 h, a feature common to both stations (Fig. 4). In station S3, a daily biomass increase was observed only in April, concomitant with a pulse of diluted waters, and was therefore presumably determined by allochthonous inputs. In station S1, the biomass increased after 24 h only in July, in the whole water column.

The ^{14}C uptake rarely results in the equivalent new phytoplankton carbon after 24 h: discrepancies between potential and real growth rates have commonly been observed in other aquatic environments (Banse, 2002) and are mainly explained by loss processes (lateral advection, sedimentation, respiration, excretion, grazing and lysis). The loss processes have not been estimated in the present study, but an analysis has been attempted, based on the few literature data available for the area. Data concerning currents and downward fluxes of carbon in the two stations indicated that losses due to lateral advection and sedimentation were relatively unimportant (Giani *et al.*, 2001): the mean current was weak in both stations (<2 and $<1\ \mathrm{cm\ s^{-1}}$, respectively in stations S3 and S1) and the export of organic carbon to the bottom was estimated at between 2 and 9% of primary production in both stations.

Information about grazing activity comes from studies carried out in another coastal area of the northern Adriatic, the Gulf of Trieste. The dominant herbivorous copepods (*Acartia clausii* and *Temora* spp.) graze, at most, 12% of available chlorophyll of the larger (>10 μm) phytoplankton (Lipej *et al.*, 1997). *Penilia avirostris* has been reported

TABLE IV Phosphorus concentrations (P-PO_4, μM), daily theoretical phosphorus uptake (ΔP, μM), primary production (*PP*, mg C m^{-3} h^{-1}) and specific production (P^b, mg C (mg chl *a*)$^{-1}$ h^{-1}) in the euphotic zone.

Station	*Period*	*Depth (m)*	*P-PO$_4$*	ΔP	ΔP/*P-PO$_4$*	*PP*	P^b
S1	April	0.5	0.02	0.08	6.0	13.9	4.2
		5	0.03	0.05	1.7	8.0	5.1
		10	0.02	0.03	2.2	5.2	4.4
		15	0.02	0.02	0.8	3.1	2.5
		20	0.02	0.01	0.3	0.9	1.2
S1	July	0.5	0.11	1.1	10.0	162.3	21.9
		5	0.03	0.03	1.2	4.5	11.5
		10	0.02	0.03	1.3	4.1	12.3
		15	0.04	0.02	0.6	3.1	8.3
		20	0.15	0.01	0.2	2.3	8.0
S1	October	0.5	0.6	0.3	0.7	61.5	6.8
		5	0.9	0.01	0.1	177.9	10.2
S1	January	0.5	1.2	0.02	0.01	4.7	4.2
		5	0.4	0.01	0.01	5.0	3.7
S3	April	0.5	0.04	0.02	0.8	3.6	5.1
		5	0.05	0.02	0.7	4.2	11.3
		10	0.03	0.01	0.4	1.8	4.4
		15	0.04	0.06	0.2	1.1	2.5
		20	0.05	0.01	0.2	1.7	3.7
		27	0.04	0.004	0.1	0.8	2.1
S3	July	0.5	0.02	0.01	1.1	1.9	13.0
		5	0.02	0.01	0.6	1.9	15.4
		10	0.03	0.01	0.7	1.6	9.9
		15	0.04	0.03	0.7	4.3	9.4
		20	0.03	0.01	0.3	1.6	5.6
		27	0.03	0.14	0.6	2.2	4.8
S3	October	0.5	0.02	0.01	0.7	2.7	6.9
		5	0.02	0.02	1.1	4.5	10.0
		10	0.02	0.02	1.0	4.2	9.5
		15	0.02	0.03	1.5	6.0	5.5
		20	0.02	0.02	1.1	4.4	4.1
		27	0.14	0.003	0.02	0.6	1.1
S3	January	0.5	0.02	0.02	0.9	3.8	4.0
		5	0.02	0.02	0.8	3.9	3.2
		10	0.03	0.01	0.3	2.8	2.0
		15	0.02	0.004	0.2	2.1	1.1
		20	0.04	0.001	0.03	1.3	0.6
		27	0.09	0.001	0.002	0.5	0.2

Note: The N/P ratio is always $\gg 16$.

to be the dominant zooplankton in Adriatic coastal waters during summer, and this was the case also in the present study (Comaschi *et al.*, 1998). *P. avirostris* feeds on particles <15 μm with a highly variable grazing impact, from 5 to 100% of the available chlorophyll, in relation to phytoplankton community size and biomass (Lipej *et al.*, 1997). The grazing impact of the microzooplankton in the coastal waters of the Gulf of Trieste (Fonda Umani and Beran, 2003) on the nano-sized prey, varied from 5 to 100%. In the present study, indirect estimates of the grazing activity were obtained from the ratio phaeopigments/chlorophyll *a*. This ratio was mostly below 1 (with the highest values close to the bottom)

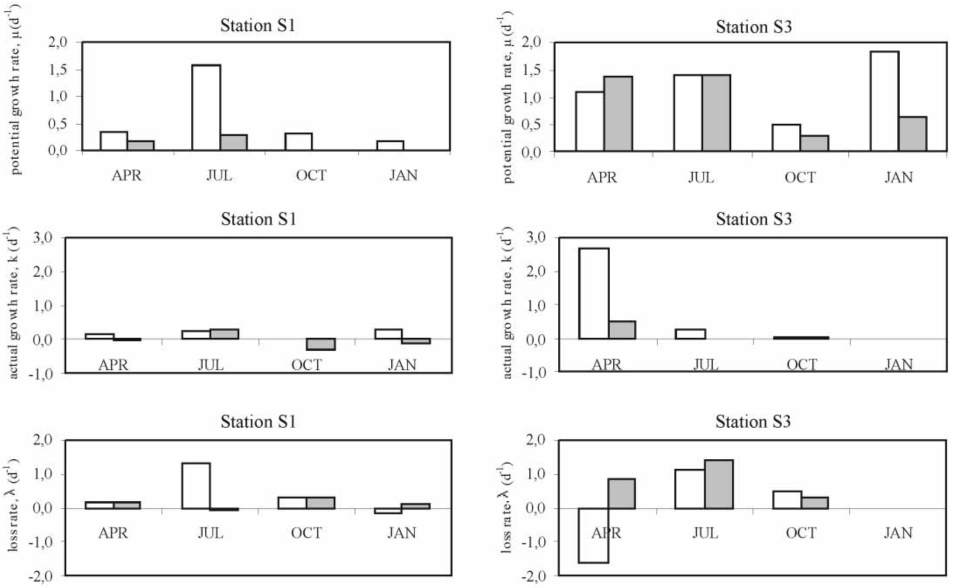

FIGURE 4 Potential (μ) and actual (k) growth and loss rates (λ) in upper (0–5 m) and lower (5 m bottom) layers in the two stations.

and, therefore, did not indicate active removal of biomass by grazing. Moreover, the phaeopigment concentrations never increased over the 24 h. According to the relationship between primary production and mesozooplankton grazing proposed by Calbet (2001) and Calbet and Prairie (2003) the estimated percentage of daily primary production ingested could vary between 2 and 20% in station S1 and between 6 and 15% in station S3.

The role of the bacterial community in the carbon cycle appears to be very significant in the northern Adriatic coastal waters, and the bacteria-phytoplankton coupling seems very tight: in the two stations, during the most productive periods, 40–80% of the carbon synthesized by phytoplankton was processed by the bacterial community (Puddu *et al.*, 1998). Other important losses can be attributed to respiration and carbon excretion, but there does not appear to be any information about these processes for this area. The high bacterial carbon demand may indicate that direct exudation of dissolved organic carbon by phytoplankton can represent an important process in this area.

4 CONCLUSION

Most of the phytoplankton species were common to both stations. The variability of the system seems to favour the spread of tolerant species, and a qualitative differentiation of the phytoplankton community between the two stations concerned mainly the relative importance of the different taxa.

The most evident effect of differing nutrient concentrations and of plume spreading was on total phytoplankton biomass and production and on their distribution in the water column. In contrast, the two stations could not be distinguished for their specific production and potential growth rates. A discrepancy between similar specific production and different biomass and primary production was evident. The different nutrient supply set the limit for the standing stock (high in station S1 and low in station S3) but not for potential growth rates and chlorophyll specific production. The chlorophyll *a* specific production values were quite high and, therefore, not indicative of nutrient limitation. However, a large discrepancy between the potential for growth and the actual production of new biomass was evident. This observation has profound implications whenever the significance of primary production processes in this ecosystem is considered, and therefore further studies aimed at quantifying the different loss processes will be important.

Acknowledgements

The present research was carried out in the framework of the PRISMA project (phase 1), financially supported by MURST. The authors acknowledge A. Cesca, F. Cioce, A. Locatelli, M. Marin, G. Penzo and S. Tortato, for their helpful assistance in the field, and the crew of research vessels *U. D'Ancona* and *S. Lo Bianco*.

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