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Photosynthetic rate and size structure of the phytoplankton community in transitional waters of the Northern Adriatic Sea

Olga Mangoni[1], Francesco Bolinesi[1*], Vincenzo Saggiomo[2], Maria Saggiomo[2]

[1]Department of Biology, University of Naples Federico II, Naples, Italy
[2]Stazione Zoologica Anton Dohrn, Naples, Italy
corresponding author e-mail: francesco.bolinesi@unina.it

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Abstract. Transitional waters are among the most productive systems of the earth, supporting high rates of metabolism and primary production processes and providing important ecosystem services.

In this study, we have investigated the effects of the freshwater input of the Po river on primary production processes in a coastal area influenced by the plume dispersion, using overall data derived from seven oceanographic cruises performed in seven different periods.

In order to do this, P*vs*E (maximum rate of photosynthesis, P – *vs* light irradiance, E) curves with ^{14}C were made for the determination of photosynthetic parameters, in association with the analyses of total phytoplankton biomass and size structure of the phytoplankton community, salinity and inorganic nutrient concentration. Stations were positioned according to salinity distribution from the coast to the off-shore waters.

Data revealed that the water stratification mainly influenced the maximum Chl-a normalized photosynthetic rate (P^B_{max}), total biomass and inorganic nutrients concentration. In the surface layer (0m), where the highest values of phytoplankton biomass were recorded, the micro- (>20µm) size class showed the highest photosynthetic rate and decreased toward off-shore waters. In the sub-surface layer, the nano- (>2 and <20µm) size class displayed the highest P^B_{max}, probably linked to its capability to well photosynthesize under low light irradiance. The structure of the community in terms of size-classes was similar in both surface and deeper layer.

Keywords: primary production; micro-, nano-, pico-phytoplankton; river plume

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Introduction

Transitional waters are ecotones between terrestrial, freshwater and marine ecosystems, characterized by high spatial heterogeneity and temporal variability. For this reasons, they provide essential ecosystem goods and services, such as shoreline protection, fishery resources and improvements to water quality, and are also very productive ecosystems, providing habitat and food for migratory and resident animals (Abbiati et al., 2010; Danovaro et al., 2016). In recent years, pressures on marine ecosystems increased with the maritime and coastal activities (Bertram and Rehdanz, 2013; Bertram et al., 2014; Dailianis et al., 2018) like fishing, aquaculture and maritime transport, together with high population density (Borja et al., 2013; Bellas, 2014; O'Higgins & Gilbert, 2014).

The Northern Adriatic Sea is among the most productive areas in Mediterranean Sea (Sournia, 1973) and seasonal and interannual variability of phytoplankton is mainly driven by riverine discharge of land-derived nutrients (Bortoluzzi et al., 1984; Degobbis and Gilmartin, 1990; Provini et al., 1992). This area mainly consists of lagoon–river delta systems, hosting a large number of transitional water bodies which differ in their environmental features.

These habitats range from the largest and most studied Lagoon of Venice to wetlands, estuaries, embayment and ponds, differing in their extent and connection with the sea (Abbiati et al., 2010). The coastal marine area is characterised by shallow waters and considerable freshwater input mainly coming from the Po River, which is the largest Italian river. The Po River strongly affects the thermohaline circulation in the northern Adriatic Sea delivering 52% of total freshwater inputs (mean flow 1500 m^3 s^{-1}; from 275 to 11,580 m^3 s^{-1}, Artegiani et al., 1997). Freshwater of the Po drives the so-called geostrophic coastal current flowing southwards along the Italian coast. The shallow depth of the whole northern region enhances benthic-pelagic interactions and nutrient recycling (Giordani et al., 1992). As a result, a productive (potentially eutrophic) shallow coastal area and oligotrophic conditions in the offshore waters characterize the basin year-round. Some evidence of oligotrophication in the northern Adriatic (Mozetic et al., 2010) and the potential of it being a net heterotrophic system (Fonda Umani et al., 2007) have opposed the general notion of the high primary productivity of the northern Adriatic basin. The review of studies on long-term series of river discharges, oceanographic features, plankton, fish and benthic compartments, collected since the 1970s, was made by Giani et al., (2012). Nevertheless, several studies have addressed phytoplankton distributions and composition (Smodlaka, 1986; Giordani et al., 1997; Pugnetti et al., 2006; Klöpper et al., 2013) with little attention to the underlying physiology (Mangoni et al., 2008; Talaber et al., 2014). Phytoplankton organisms provide important ecosystem services, such as primary production to be transferred to higher trophic levels, atmospheric CO_2 drawdown and climate regulation.

Phytoplankton is an efficient indicator of changes in nutrient loads, but is also effective in evaluating responses to many other environmental stressors, due to its fast population response to changes in water quality, hydrology or climate (Domingues et al., 2008) and may respond by shifting cell size and/or taxonomic composition (Rodríguez et al., 2001; Finkel et al., 2010). In coastal areas affected by seasonal upwelling as well as anthropogenic inputs, biological changes are even more pronounced, as nutrient-rich upwelled waters favour the dominance of large organisms (micro-phytoplankton, usually diatoms) and high levels of primary productivity (Tilstone et al., 2003; Cermeño et al., 2005). Given the multiplicity of anthropogenic, atmospheric and terrestrial forcing that drive physical and community dynamics of near-shore marine ecosystems, the absence of canonical phytoplankton patterns might be expected (Cloern and Jassby, 2008; Bolinesi et al., 2020). The high variability at small spatial and temporal scales requires a high capacity of the phytoplankton to rapidly acclimate to these ever-changing conditions. Photoacclimation involves alterations in the molecular structure of the photosynthetic apparatus, which occurs through two strategies (Falkowski & LaRoche, 1991). The first consists of an alteration in the size of light-harvesting antenna associated with each reaction center of the photosystem, and the second is an alteration in the number of cellular reaction centers, which drive the differences in the functional relationship between photosynthesis and irradiance (P*vs*E curve) among taxa (Falkowski and Owens, 1980; MacIntyre et al., 2002). The photosynthesis–irradiance relationship helps us understand their physiological response to light and other limiting factors of photosynthesis (Saksaug et al., 1997; Bouman et al., 2017). Furthermore, the P*vs*E relationship provides information for primary production modelling, which enables primary production estimates at large spatial and temporal scales (Sathyendranath et al., 1989; Bouman et al., 2018).

The main objective of this study was to analyze the photosynthetic parameters of phytoplankton community in different environmental conditions of the plume river dispersion. We discuss photosynthetic parameters taking into account the phytoplankton community in terms of size classes and physical-chemical properties of the water column (salinity, inorganic nutrient concentrations).

Material and Methods

In the frame of the PRISMA2 Project, seven oceanographic campaigns were carried out in the area off the Po River delta between 1996 and 1998 (Figure 1). Sampling activities were conducted in the following period and enumerated according to date: 1- (July, 18-22 1996); 2- (August, 31- September 3 1996); 3-(February, 13-14 1997); 4-(March, 12-13 1997); 5-(October, 1997); 6- (May, 14-15 1998); 7-(June, 20-21 1998). Sampling was performed by means of a carousel (Sea Bird Electronics) equipped with a CTD SBE 911 Plus, a fluorometer and twelve 12l Niskin bottles. Water depth was < 30m across the area of study. At each station, up to five sampling depths were selected on the basis of salinity and fluorescence profiles. Water samples for spectrofluorometric determination of (Chl-a) were filtered onto 25 mm GF/F Whatman glass fiber filters for the analysis of total phytoplankton biomass (total Chl-a), and for the determination of size fractions (micro-, nano- and pico-phytoplankton) following serial filtrations procedures reported in Mangoni et al. (2008). For each size fraction, and total biomass, 0.5 l of waters were filtered. Chl-a analyses were performed using a Spex, mod. Fluoromax spectrofluorometer (Jeffrey & Humphrey, 1975). The photosynthetic performance of phytoplankton community was analysed through P*vs*E experiments (Babin et al., 1994). PvsE experiments were conducted in a radial photosynthetron (Babin et al., 1994), containing four incubation chambers holding twelve

50ml bottles each, equipped with an HQI-T 250W/D Osram lamp. Each chamber was connected to a thermostat and *in situ* temperature was obtained by circulating seawater during incubations. Irradiance extinction curves were obtained measuring the light within each incubation bottle by means of a PAR sensor 4π (Biospherical Instruments, mod. QSL-101). For methodological details, see Mangoni et al. (2008). For each sampling depth, twelve subsamples were inoculated with 1 ml of $NaH^{14}CO_3$ solution (20mCi/ml). After 1h incubation, sub-samples were immediately filtered in dim light on GF/F Whatman filters that were transferred into scintillation vials and frozen until analyses carried out one week after the end of the campaign. The ^{14}C samples were acidified (200 µl 0.1N HCl for 12h), after adding 10ml of Aquasol-2 scintillation cocktail, read with a liquid scintillator (Packard Tri-Carb mod.2100TR). The photosynthetic parameters were derived from the model by Platt et al. (1980): $P^B(E) = P^B_s\ [1- \exp(-E/ P^B_s)]\ \exp(-\beta E/ P^B_s)$, were P^B_s [mg C (mg Chl-a)$^{-1}$ h^{-1}] is the potential light-saturated Chl-a normalized rate of photosynthesis in absence of photoinhibition; (alpha) [mg C (mg Chl-a)$^{-1}$ h^{-1}] represents the photosynthetic capacity; is the photoinhibition parameter [mg C (mg Chl-a)$^{-1}$ h^{-1} (µmol photons m^{-2}s^{-1})$^{-1}$].

Principal component analysis (PCA), based on a Spearman's correlation matrix, was performed in order to investigate the relationship between freshwater input (salinity) and the biological features (phytoplankton biomass, percentage contribution of size classes and main phytoplankton groups). The analyses were performed on a raw data set of 1239 total samples, excluded missing data that were estimated using the mean of the corresponding variables. Table 1 reports the Spearman's correlation matrix with values in bold that are different from 0 with a significant level alpha = 0.05. All analyses were performed using XLSTAT 2019 with results of the PCA that are presented using diagrams of factor loadings (projection of the variables on the factor-plane described by the 1st and 2nd principal factors) and scores (projection of the sampling cases on the factor-plane described the 1st and 2nd principal factors). Variables with the highest loadings have the greatest influence on the samples separation.

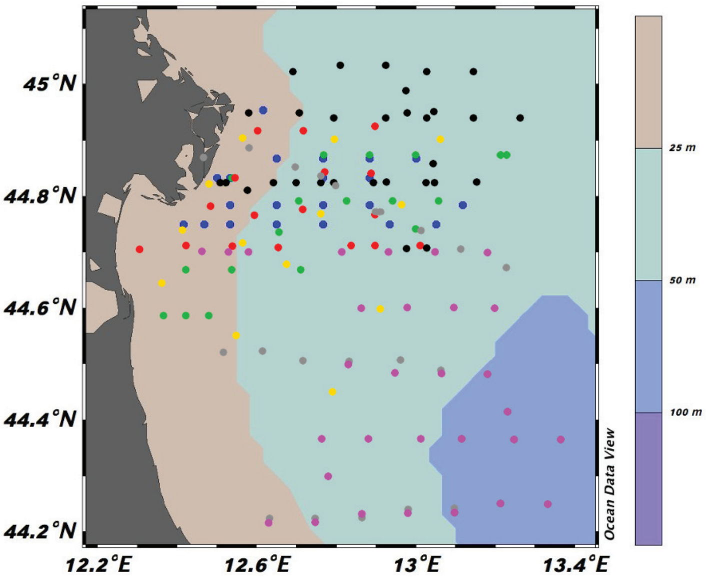

Figure 1. Map of the study area and location of the stations at different sampling times: blu = 1 (July '96), green = 2 (August '96), red=3 (February '97), yellow = 4 (March '97), black = 5 (October '97), grey = 6 (May '98) pink = 7 (June '98).

Results and discussion

Recurrent phytoplankton blooms are observed year-round in the Po river plume and accumulation of very high phytoplankton biomass occurs inside the front (Mangoni et al., 2008, 2013,2017). The set of data analysed in this study showed that the distribution of surface total Chl-a values (Figure 2) reached the highest concentrations especially at stations located near the coast, which are more subjected to river inputs. Although the magnitude and extension of the river input changed over time, this pattern of distribution was the same with the presence of two different productive areas.

The first one included coastal stations characterized by strong gradients of salinity, and the second one included stations in which salinity did not change as observed in the coastal area. The uncoupling between total Chl-a and salinity observed during sampling (4) was probably influenced by local mesoscale water circulation as reported by Mangoni et al. (2008).

The data set of salinity at 0 m and in the sub-surface layer was reported in Figure 3. The mean value of salinity at 0 m was 34, and presented a strong variability; in the sub-surface layer the mean value of salinity was 37 and changed less compared to the surface layer.

Chl-a reached the maximum of 15.77 µg/L in March, (sampling 4-) and the mean values of Chl-a (Figure 3) for the overall data set was 1.85 µg/L at 0 m and 1.07 µg/L in the sub-surface layer.

As for the size structure of the phytoplankton community, box plots in Figure 4 did not show significant differences between the surface and the sub-surface layer. At 0 m, the percentage contributions of size classes micro-, nano-, and pico-phytoplankton were 35%, 38% and 27% respectively compared to 32%, 38% and 30%, respectively, in the sub-surface layer.

In the coastal area directly influenced by the river plume, P^B_{max} reached 20 mgC (mgChl-*a*)$^{-1}$h^{-1} in August (period 2-), that is among the highest values ever reported in marine systems, and comparable to values reported in land-locked ecosystems (e.g. P^B_{max} =22) (Macedo et al., 2001). With the exception of such maximum value, the P^B_{max} reported in this area were similar to those found in temperate coastal waters. At the offshore stations, P^B_{max} ranged between 2 and 9 mgC (mgChl-a)$^{-1}$h^{-1} (Figure 5a). The variability of P^B_{max} was much less pronounced in the sub-surface layer where environmental conditions were more stable, and values were lower than those observed at 0 m (Figure 5b). Considering the whole set of data, the mean P^B_{max} was 7.42 mgC (mgChl-a)$^{-1}$h^{-1} at the surface layer and 5.0 mgC (mgChl-a)$^{-1}$h^{-1} at the sub-surface layer (Figure 3).

Table 1. Spearman correlation matrix with values in bold that are different from 0 with a significant level alpha = 0.05

Variables	P^B_{max}	Alpha	E_K	Salinity	Total Chl -a	Micro- (> 20 µm)	Nano- (20-2 µm)	Pico- (< 2 µm)	PO_4	$Si(OH)_4$	DIN
P^B_{max}	**1**	**0.667**	**0.374**	-0.152	0.057	**0.291**	-0.193	-0.210	0.057	**0.221**	**0.214**
alpha	**0.667**	**1**	**-0.382**	0.025	0.044	0.100	0.031	-0.194	-0.102	0.143	**0.410**
E_K	**0.374**	**-0.382**	**1**	**-0.220**	-0.042	0.144	**-0.307**	0.107	**0.257**	0.108	**-0.320**
Salinity	-0.152	0.025	**-0.220**	**1**	**-0.466**	**-0.469**	0.174	**0.451**	0.054	0.025	**-0.404**
Total Chl -a	0.057	0.044	-0.042	**-0.466**	**1**	**0.561**	0.027	**-0.742**	-0.127	0.155	**0.339**
Micro- (> 20 µm)	**0.291**	0.100	0.144	**-0.469**	**0.561**	**1**	**-0.608**	**-0.574**	-0.080	0.195	**0.308**
Nano- (20-2 µm)	-0.193	0.031	**-0.307**	0.174	0.027	**-0.608**	**1**	**-0.217**	0.107	-0.052	0.078
Pico- (< 2 µm)	-0.210	-0.194	0.107	**0.451**	**-0.742**	**-0.574**	**-0.217**	**1**	-0.092	-0.208	**-0.494**
PO_4	0.057	-0.102	**0.257**	0.054	-0.127	-0.080	0.107	-0.092	**1**	**0.292**	-0.008
$Si(OH)_4$	**0.221**	0.143	0.108	0.025	0.155	0.195	-0.052	-0.208	**0.292**	**1**	**0.307**
DIN	**0.214**	**0.410**	**-0.320**	**-0.404**	**0.339**	**0.308**	0.078	-0.494	-0.008	**0.307**	**1**

Values in bold are different from 0 with a significance level alpha=0.05

Variables	P^B_{max}	Alpha	E_K	Salinity	Total Chl -a	Micro- (> 20 µm)	Nano- (20-2 µm)	Pico- (< 2 µm)	PO_4	$Si(OH)_4$	DIN
P^B_{max}	**1**	**0.696**	**0.407**	-0.047	0.075	-0.188	0.342	-0.149	**0.456**	**-0.519**	**0.443**
alpha	**0.696**	**1**	-0.295	0.268	-0.091	-0.282	0.407	-0.086	0.253	-0.145	**0.489**
E_K	**0.407**	-0.295	**1**	**-0.407**	**0.363**	0.289	-0.159	-0.211	0.206	**-0.486**	-0.131
Salinity	-0.047	0.268	**-0.407**	**1**	**-0.670**	-0.179	-0.143	**0.377**	0.020	**0.391**	-0.041
Total Chl -a	0.075	-0.091	**0.363**	**-0.670**	**1**	**0.528**	0.079	**-0.765**	-0.252	-0.112	0.143
Micro- (> 20 µm)	-0.188	-0.282	0.289	-0.179	**0.528**	**1**	**-0.687**	**-0.476**	**-0.417**	0.099	-0.236
Nano- (20-2 µm)	**0.342**	**0.407**	-0.159	-0.143	0.079	**-0.687**	**1**	-0.213	0.253	-0.222	**0.666**
Pico- (< 2 µm)	-0.149	-0.086	-0.211	**0.377**	**-0.765**	**-0.476**	-0.213	**1**	0.204	0.143	**-0.324**
PO_4	**0.456**	0.253	0.206	0.020	-0.252	**-0.417**	0.253	0.204	**1**	**-0.654**	0.153
$Si(OH)_4$	**-0.519**	-0.145	-0.486	**0.391**	-0.112	0.099	-0.222	0.143	**-0.654**	**1**	-0.200
DIN	**0.443**	**0.489**	-0.131	-0.041	0.143	-0.236	**0.666**	**-0.324**	0.153	-0.200	**1**

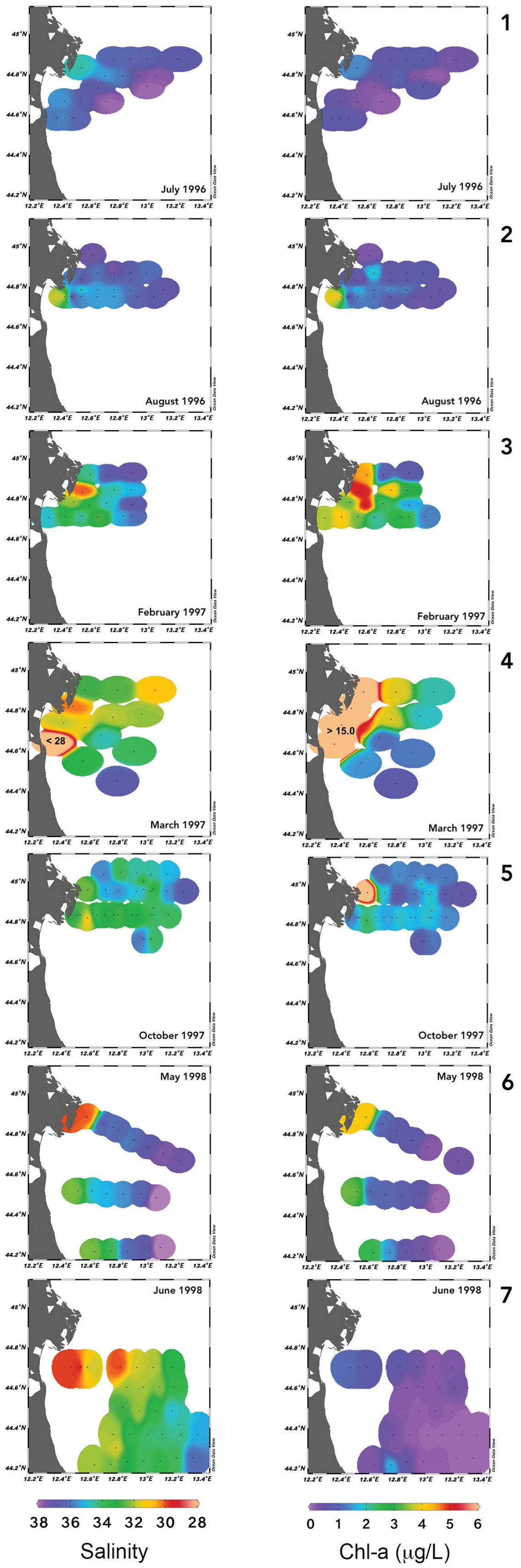

Figure 2. Surface distribution of salinity (left panel) and total Chl-a concentration (µg/L) (right panel) during the different sampling periods (July '96, August '96, February '97, March '97. October '97, May '98, June '98

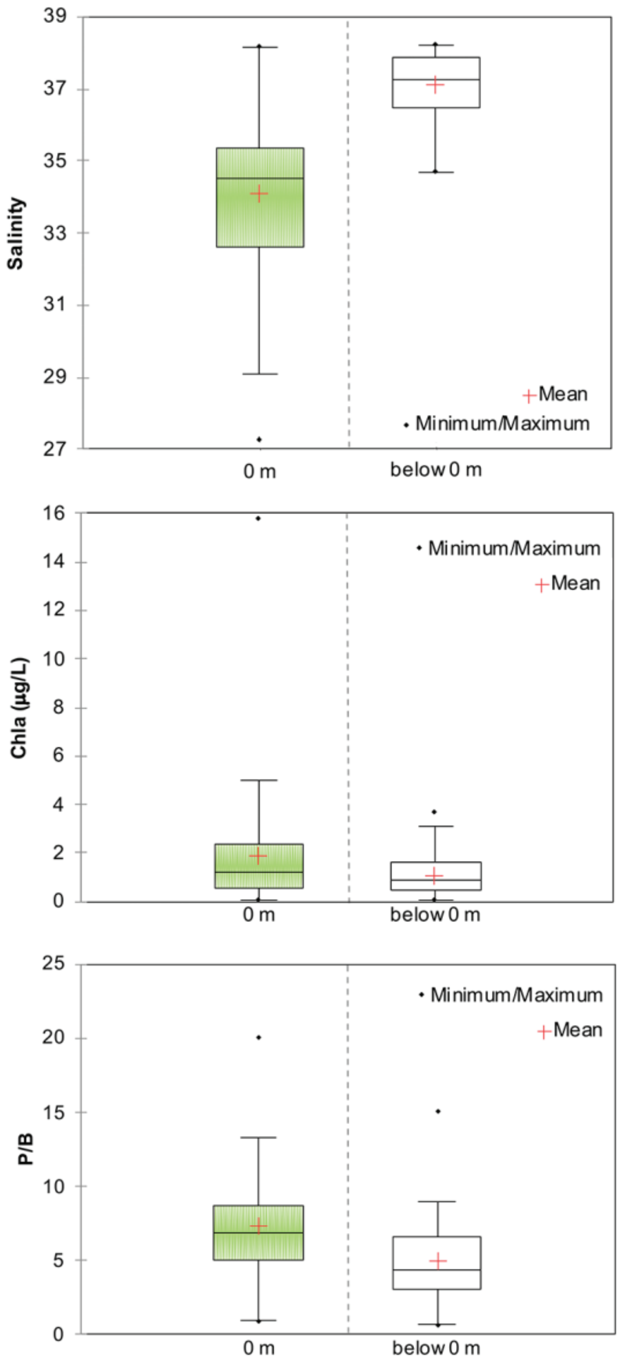

Figure 3. Mean, max, min, standard deviation of salinity, total phytoplankton biomass (Chl-a, µg/L) and P/B over the entire sampling period.

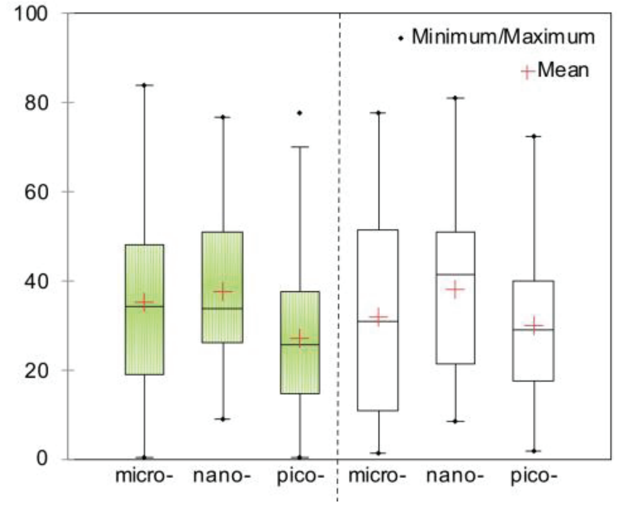

Figure 4. Mean, max, min, standard deviation of micro- (>20 μm), nano- (20-2 μm) and pico- (<2 μm) phytoplankton fractions (%) over the entire sampling period

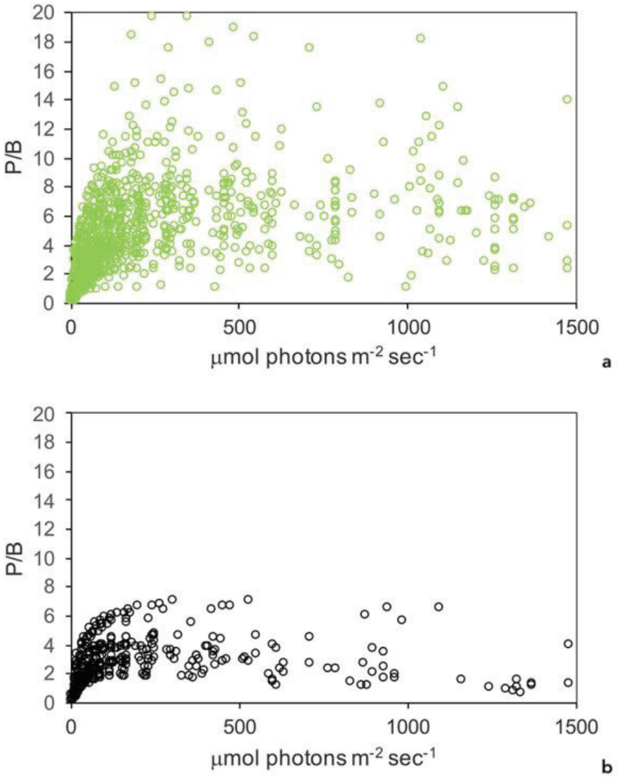

Figure 5. Photosynthesis-irradiance curves (PvsE): (a) at 0 m samples and (b) below 0 m

PCA of biological, physical and chemical variables at 0 m explained only 46.97% of total variance, with F1 axis accounting for 29.50% and F2 axis for 17.47% of total variance (Figure 6a). Chl-a, Dissolved Inorganic Nitrogen (DIN) and alpha were negatively correlated with F1 axis, and Chl-a was inversely correlated with pico-phytoplankton. Micro, $Si(OH)_4$ and P^B_{max} were strongly correlated among them in the fourth quadrant, while PO_4 and E_K (the light saturation parameter P^B_{max}/alpha) overlapped with positive axis F2, especially E_K. The salinity placed in the second quadrant, and was inversely correlated with micro, $Si(OH)_4$ and P^B_{max}. Nano-phytoplankton showed a strong negative correlation with F2 axis, placing into the second quadrant. The inverse correlation between E_k and nano-phtyoplankton, and the correlation of nano- and alpha along the negative axis F1, suggested the adaptation of nano-fraction to low light. The almost overlapping of P^B_{max} with micro-, both inversely correlated with salinity, suggest that at 0 m the large size displayed the highest photosynthetic rate, that decreased proportionally moving to areas with high salinity, where conversely the small size increased.

PCA of the sub-surface layer explained 56.75% of total variance, with F1 axis accounting for 29.79% and F2 for 26.95% of total variance, respectively (Figure 6b). Chl-a overlapped with positive F2 axis, and a similar correlation was observed also for E_k and micro- fraction. P^B_{max}, DIN, nano, PO_4 and alpha were all correlated with positive F1 axis. Pico- fraction and salinity placed in the third quadrant and were strongly correlated among them (almost overlapped) displaying an inverse correlation with E_k. $Si(OH)_4$ showed the same correlation of micro-fraction along the negative F1 axis, although displayed a negative correlation with F2 axis. The overall picture suggests that since nano-phytoplankton showed high photosynthetic rate (P^B_{max}) and high alpha values in the sub-surface layer, it was the most productive size-fraction adapted to low irradiance. Furthermore, data highlight the presence of higher concentrations of total Chl-a in the less salty water where the micro-phytoplankton dominated, and E_k values were higher, suggesting that biomass was adapted to high light, probably as a consequence of the stratification itself linked to the plume. In this context, productivity is driven by the nano-phytoplankton.

Environmental variability affects the photosynthetic response of the phytoplankton community, which is manifested by the variation of the photosynthetic parameters. Phytoplankton must adjust its photosynthetic output to match the environmental constraints and to optimize growth. Sakshaug et al. (1997) pointed out that the photosynthetic performance of phytoplankton, i.e. the physiological adaptation to environmental conditions may be more important than biomass concentrations to determine primary production.

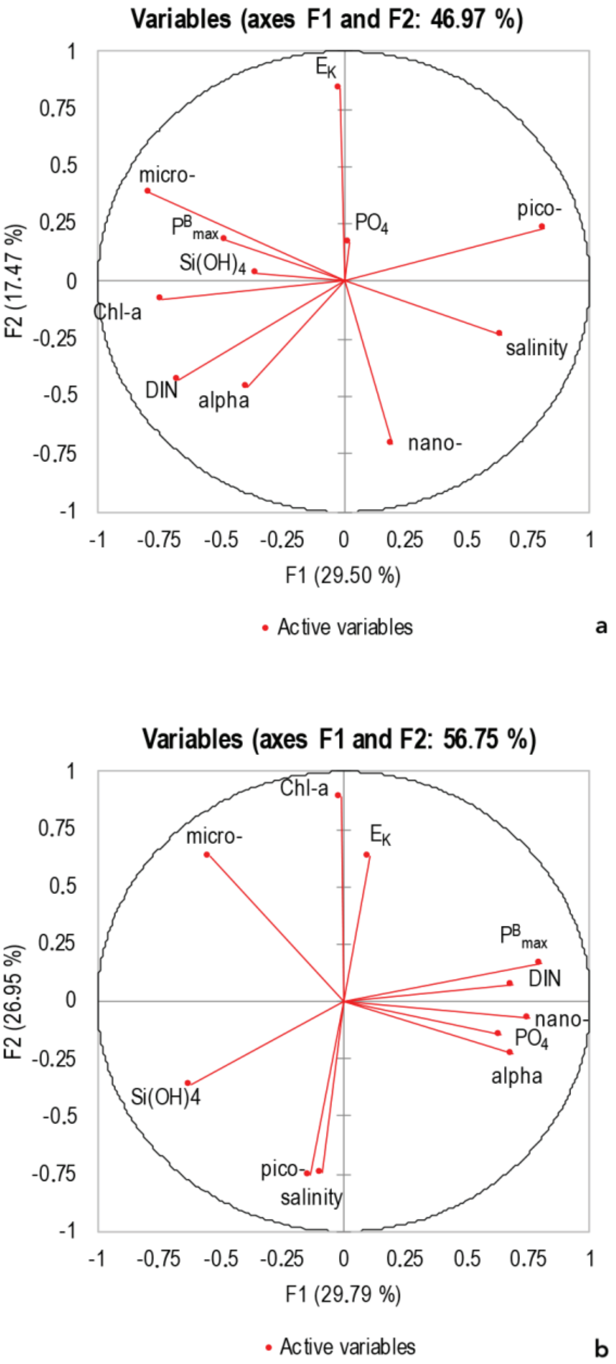

Figure 6. Principal component analysis (PCA) over the entire temporal and spatial dimensions at (a) 0 m and (b) below 0 m

The north Adriatic coastal areas are characterized by discontinuous pulses of nutrient-enriched freshwater (Harding et al., 1999) and any prediction of phytoplankton blooms and production in this area must be based on a physical model. Our findings suggest that in such a variable system, rapid environmental changes do not allow the replacement of phytoplankton that are better adapted to the variable conditions, as highlighted by the almost constant percentages of micro-, nano- and pico-phytoplankton. In surface and stratified waters, the micro- compartment exhibited the highest P^B_{max} while, in the sub-surface layer, the highest photosynthetic rate depended mostly on the nano-compartment. In addition, the recognised small-scale variability of P*vs*E parameters in coastal areas is frequently interpreted in the context of higher heterogeneity for the coastal and shelf environments (Moran and Estrada 2001; Mangoni et al. 2008; Gallegos, 2012), which highlights the importance of a finer resolution of sampling compared with the open ocean.

Conclusions

Two different sub-areas can be identified in a restricted sector of the north Adriatic coastal waters, near the delta of the Po river, in relation to the position of the ever-changing salinity front. The area more susceptible to the river inputs displayed higher values of biomass in both surface and sub-surface layers, while low biomass characterized the area outside the front.

The phytoplankton community was mainly dominated by classes micro- and nano- phytoplankton in the coastal area, while pico-phytoplankton increased with salinity moving toward off-shore waters; no differences in size classes emerged between the surface and sub-surface layer.

On the contrary, significant differences emerged in P^B_{max}. The micro-phytoplankton exhibited the highest photosynthetic rate at 0 m, that decreased with increasing salinity; in the sub-surface layer the higher photosynthetic rate was linked to the nano-phytoplankton, probably related to its capability to well photosynthesize under low light, and was less influenced by changes in salinity due to the relative stability of this layer.

Changes in the salinity front mainly affected the productivity of the micro- size compartment, that usually is channelled through short food chains, resulting in an increased efficiency of the biological pump in transporting carbon towards upper trophic levels (Cushing, 1989).

The authors emphasize the results of this study in light of current climate changes that, as observed in Antarctic coastal waters (Mangoni et al., 2017, 2019), could significantly alter the carrying capacity of the north Adriatic ecosystems which represents a fundamental part of marine resources in the entire Mediterranean Sea.

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