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M. R. Vadrucci^a; A. Basset^a; F. Decembrini^b

^a Dipartimento di Biologia, Università di Lecce, Lecce, Italy ^b Istituto Sperimentale Talassografico Spianata San Ranieri, Messina, Italy

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QUANTITATIVE RELATIONSHIPS AMONG PHYTOPLANKTON BODY SIZE CLASSES AND PRODUCTION PROCESSES IN THE NORTH ADRIATIC FRONTAL REGION

M.R. VADRUCCI^a, A. BASSET^{a,*} and F. DECEMRINI^b

^a*Dipartimento di Biologia-Università di Lecce Via Prov. Lecce-Monteroni, 73100 Lecce, Italy;*

^b*Istituto Sperimentale Talassografico Spianata San Ranieri,
86 98100 Messina, Italy*

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The variation patterns of phytoplankton standing crop and productivity in the North Adriatic frontal region and the relative importance of pico-, nano-, micro-phytoplankton are shown. Data of standing crop (chlorophyll *a* – Chl*a*) and productivity (¹⁴C assimilation) and PAR radiation ($\mu\text{Em}^{-2}\text{s}^{-1}$) were collected during the four oceanographic cruises of the PRISMA II project. Average standing crop and productivity in the study area were $1.41 \pm 0.42 \text{ mg m}^{-3} \text{ Chl}a$ and $1.23 \pm 0.37 \text{ mg C m}^{-3} \text{ h}^{-1}$; average assimilation number (P/B) was $0.872 \pm 0.589 \text{ mg C (mg-Chl}a)^{-1} \text{ h}^{-1}$ and average photosynthetic efficiency (PE) was $0.020 \pm 0.054 \text{ (mg C(mg-Chl}a)^{-1} \text{ h}^{-1}) [\mu\text{Em}^{-2}\text{s}^{-1}]^{-1}$. Phytoplankton biomass and productivity showed significant patterns of variation with the distance from the coast, with increasing depth and decreasing light intensity. The same patterns were shown by the three phytoplankton size classes. The spatio-temporal variations were significantly larger within the microplankton than within the pico- and nano-plankton size classes. Planktonic guilds were dominated by picoplankton, both as standing crop and productivity, in the northern stations ($0.539 \pm 0.21 \text{ mg m}^{-3} \text{ Chl}a$ and $0.572 \pm 0.25 \text{ mg C m}^{-3} \text{ h}^{-1}$) and in those more offshore, while microplankton was more important in the coastal and southern stations ($0.727 \pm 0.58 \text{ mg m}^{-3} \text{ Chl}a$ and $0.63 \pm 0.28 \text{ mg C m}^{-3} \text{ h}^{-1}$). In relative terms, picoplankton accounts for the 53% and 46% of biomass and primary production, while the microplankton account for the 43.6% and 48%.

Assimilation number and photosynthetic efficiency did not show spatio-temporal variations but PE was inversely related with PAR radiation for all the size classes. Data suggest that the spatio-temporal patterns observed in this study are affected by the competitive relationships among body size classes in the phytoplankton guilds.

Keywords: Phytoplankton; Body size; Primary productivity

INTRODUCTION

Phytoplankton production accounts for 40% approximately of the global carbon fixation, even though its biomass represents only the 2% of the total plant carbon. This high production/biomass ratio of the phytoplankton is mainly related to its small individual body size and high photosynthetic efficiency (Falkowski, 1996). Commonly, marine coastal frontal zones are marine area characterised by high phytoplankton biomass and productivity, because of

*Corresponding author. E-mail: abasset@ilenic.unile.it

the nutrient supply either from the continental fresh water inputs and from the bottom sediments (Parson *et al.*, 1984). Nutrients are also a main factor affecting the structure and organization of the phytoplanktonic guilds (Fogg, 1995; Zuccarello *et al.*, 1996); however, the competitive relationships among species or groups of species are still unclear and the role of the coexistence mechanisms on the productivity of phytoplanktonic guilds is relatively unknown.

Recent studies on the organization of phytoplanktonic guilds emphasized the different importance that the various size classes (pico-, nano-, micro-phytoplankton) have in the carbon cycle (Carrik and Schelske, 1997; Beaty and Parker, 1996; Magazzù and Decembrini, 1995; Fogg, 1995). As already observed for other guilds (*i.e.*, fresh water invertebrate guilds; Basset, 1995a) the relative importance of the different size classes (micro- vs. pico-plankton) seems to be affected by the overall availability of resources (e.g., nutrient concentration; Carrik and Schelske, 1997; Magazzù *et al.*, 1996). Body size-related competition and energy partitioning (Basset, 1995a) could therefore be a relevant mechanism affecting the organization of the marine phytoplankton guilds.

The three main objectives of this study were: (1) to describe the pattern of spatio-temporal distribution of both biomass and productivity of phytoplankton guilds in two areas across the frontal system of North Adriatic Sea; (2) to analyze the relative importance of pico-, nano- and micro-plankton in terms of biomass, photosynthetic efficiency and photosynthetic rate; (3) to evaluate the role of the biotic interactions on the organization of body size structure of phytoplankton guilds in the study area.

MATERIALS AND METHODS

Study Area and Samplings

Data on fractionated phytoplankton biomass (expressed as Chlorophyll *a*) and primary production (expressed as ^{14}C uptake rate) were collected in the North Adriatic Sea during four oceanographic cruises of the PRISMA II project carried out in summer (June, 1996 and June, 1997) and winter (February, 1997 and February, 1998) periods. Two sampling areas were selected: one close to the river Po mouth (Northern Zone), the second close to the Conero promontory (Southern Zone). In each area, there were sampled at 4 to 8 stations located along 2 to 4 transects across the frontal system. The geographical position of the sampling transects varied among cruises according to the position of the frontal system. Samples were collected using Niskin 10 l bottles at five «optical depths» corresponding respectively to the 100, 30, 12, 4 and 1% of the surface active photosynthetic radiations (Surface PAR). Light penetration was determined by a quantum meter PNF-300 (Biospherical Instruments).

Autotrophic Biomass

Samples were filtered immediately after their collection to separate three size classes of autotrophic plankton: pico- (mean particle size between 0.5–2 μm) nano- (mean particle size between 2–10 μm) and micro-plankton (mean particle >10 μm).

Nucleopore polycarbonate filters with 10 μm and 2 μm porosity and GF/F (0.5 μm) were used for differential filtration according to Magazzù *et al.*, 1996.

Filters were stored at -20°C until the analysis. Chlorophyll *a* was extracted in 90% acetone, for 24 h in the dark, and determined with a spectrofluorometer SHIMATZU-1051 before and after acidification with hydrochloric acid 0.5 N. Excitation and emission wavelengths (429 nm and 669 nm) were selected after standardization with a solution of chlorophyll *a* extracted from *Anacistys nidulans* (Sigma Co). The turnover time (B/P) was evaluated assuming that Chla was on average the 1.5% of the phytoplankton biomass.

Primary Production

Primary production was assessed with the standard ^{14}C radioisotopic technique. Two samples from each optical depth were placed into a light and a dark 450 ml polycarbonate bottle. Bottles received 1 ml of a sodium carbonate solution (activity density of about $20\ \mu\text{Ci ml}^{-1}$) and were incubated in continuous flow deck incubators covered by selective screens, in order to reproduce the original light intensities. After four hours of exposure samples were filtered as described above. Filters were transferred to 20 ml scintillation vials and radioactivity was assessed on a Beckman LS1801 β -counter using a 10 ml «Aquasol» scintillation cocktail (Magazzù and Decembrini, 1990). Six readings of each sample were performed. Alkalinity was measured on board using the potentiometric method and the available total carbon dioxide was determined from the tables given by Strickland and Parson (1972).

Data Treatment

Data analysis were performed on data pooled either among optical quotes and/or stations placed at the same position with respect to the front zone. t-Student and F-Fisher tests were used to compare means and variances. Regression analysis was used to evaluate the statistical power of the variation patterns observed on the coast-offshore and the depth gradients.

RESULTS

Mean phytoplankton standing crop was $1.41 \pm 0.42\ \text{mg m}^{-3}$ Chla and average productivity $1.23 \pm 0.37\ \text{mg C m}^{-3}\ \text{h}^{-1}$ (Fig. 1).

Assimilation number (P/B) presented a mean value of $0.872 \pm 0.589\ \text{mg C}(\text{mg-Chla})^{-1}\ \text{h}^{-1}$. Photosynthetic efficiency (PE) was similar, on average, in the two study areas (northern, $0.022\ (\text{mg C}(\text{mg-Chla})^{-1}\ \text{h}^{-1})\ [\mu\text{Em}^{-2}\ \text{s}^{-1}]^{-1}$; southern $0.018\ (\text{mg C}(\text{mg-Chla})^{-1}\ \text{h}^{-1})\ [\mu\text{Em}^{-2}\ \text{s}^{-1}]^{-1}$) but the maximum value was measured in the northern area. The ratio between phytoplankton biomass and productivity indicated an average turnover time (biomass – mg m^{-3} /production – $\text{mg C m}^{-3}\ \text{h}^{-1}$) of the plankton guilds equal to 5.16 ± 1.60 days. Much lower values (2.79 ± 0.93 days) were observed only during a winter period in the northern area, probably corresponding to the beginning of an algal bloom.

The standing crop of plankton guilds varied significantly with the distance from the coast of the sampling stations ($y = 2.816x^{-0.466}$, $P = 0.001$, $n = 67$) (Fig. 2). Biomass was also inversely related to salinity, particularly in the second winter cruise (northern zone: $r = 0.77$, $P < 0.001$; southern zone: $r = 0.97$, $P < 0.001$). Productivity also decreased according to a negative exponential model, with increasing distance from the coast and with increasing salinity. The largest variations on the salinity gradient were observed in the second winter cruise

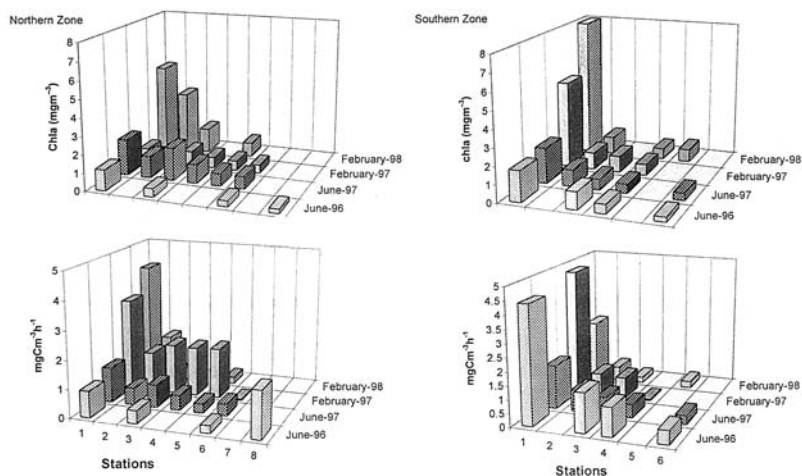


FIGURE 1 Biomass ($\text{Chla}\text{-mg m}^{-3}$) and primary productivity ($\text{mg C m}^{-3} \text{h}^{-1}$) of phytoplankton during the four PRISMA II oceanographic cruises (integrated water column values).

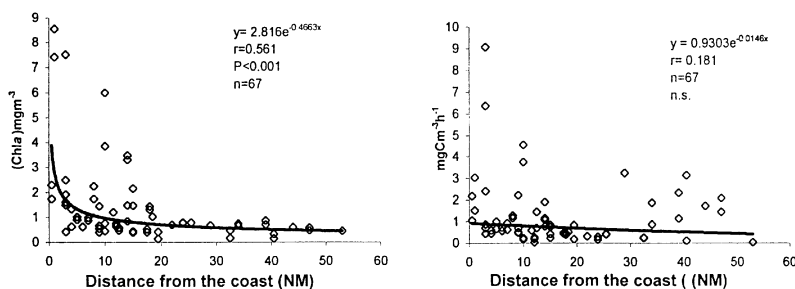


FIGURE 2 Inshore-offshore patterns of variation of the phytoplankton biomass and primary production (integrated water column values).

(northern zone: $r = 0.82$, $P < 0.001$; southern zone: $r = 0.61$, $P < 0.001$). The photosynthetic parameters (P/B and PE) were related to salinity in a single case (northern zone, second winter cruise $r = 0.51$, $P < 0.05$) and only PE showed a significant temporal variation; the highest mean value ($0.033 \text{ (mg C(mg-Chla)}^{-1} \text{h}^{-1}) [\mu\text{Em}^{-2} \text{h}^{-1}]^{-1}$) was observed in February and was associated to low PAR light intensity. On average, assimilation number showed higher values in the southern than in the northern area, attributable to the microplankton, but the highest value, attributable to the nanoplankton, was observed in the northern area ($15.8 \text{ mg C(mg-Chla)}^{-1} \text{h}^{-1}$).

In terms of biomass, pico- and micro-plankton dominated the phytoplanktonic guilds (38.8% and 38.7%). The biomass of the microplankton component showed a significantly higher variation, with respect to the picoplanktonic component (F-Fisher test, $F_{66,66} = 2.628$, $P < 0.001$). Nanoplankton biomass was significantly lower than the picoplanktonic one (t-Student test, $P < 0.05$) while it was not statistically different from the microplankton one. Nanoplankton also showed a biomass variation in space and time significantly lower than those of both picoplankton (F-Fisher test, $F_{66,66} = 5.847$, $P < 0.001$) and microplankton (F-Fisher test, $F_{66,66} = 15.75$, $P < 0.001$). In both the study areas, the biomass of each of the three size classes was inversely and statistically related

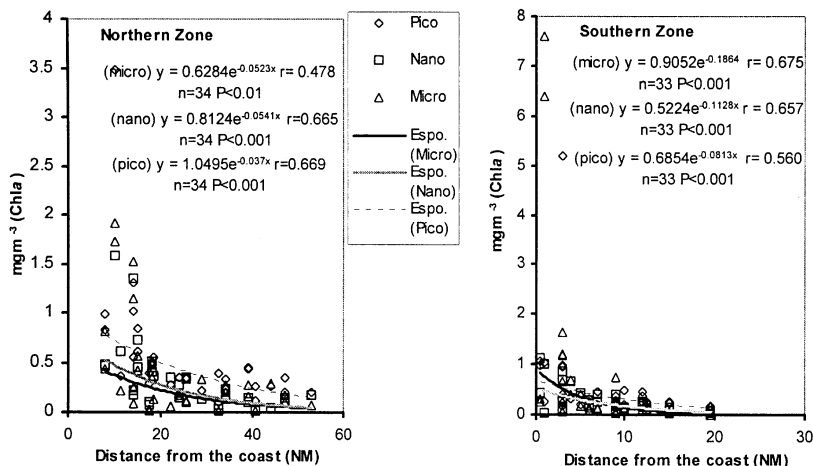


FIGURE 3 Patterns of biomass (Chla-mg m^{-3}) variation of the phytoplankton body size classes (integrated values of four oceanographic cruises).

to the distance from the coast, according to exponential equations (Fig. 3). Micro- and nano-plankton always showed higher slopes than picoplankton. A larger difference was observed in the southern area; there, the difference between the slopes was statistically significant between micro- and pico-plankton (test of parallelism, $t = 2.687$, g.l. = 64, $P < 0.01$) and the ratio between micro- and pico-plankton varied inversely with the distance from the coast, according to a negative exponential equation ($y = 1.28e^{-0.103x}$; $r = 0.4$, $P < 0.02$) (Fig. 5).

In terms of productivity, pico- and micro-plankton dominated the phytoplankton guilds, too (37.9%; 40%). The primary production of the microplankton did not show a spatio-temporal variation larger than that of the picoplanktonic component ($F_{66,66} = 0.96$), but both of

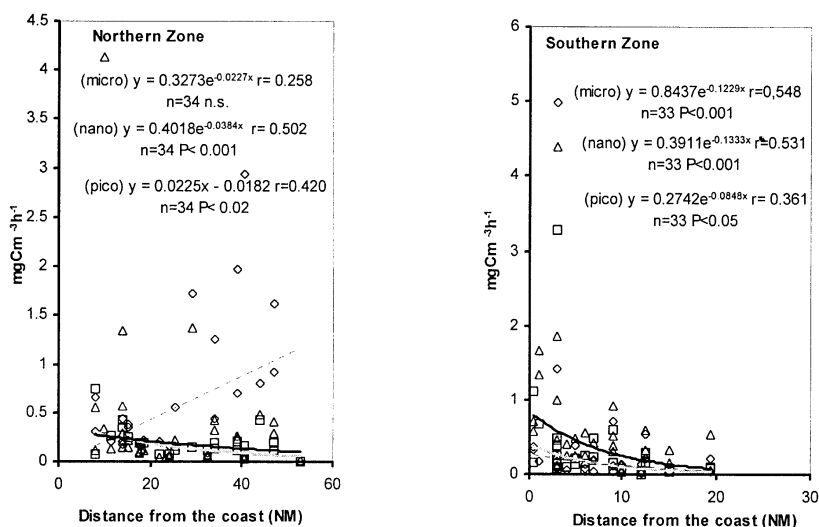


FIGURE 4 Patterns of primary production ($\text{mgC m}^{-3} \text{h}^{-1}$) variation of the phytoplankton body size classes (integrated values of four oceanographic cruises).

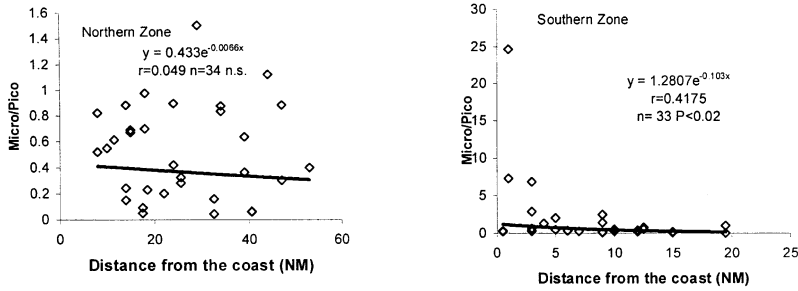


FIGURE 5 Spatial variation of the ratio between micro- and pico-phytoplankton biomass in two study areas.

them showed higher variability than the nanoplankton ($F_{66,66} = 3.18$, $P < 0.001$; $F_{66,66} = 3.32$, $P < 0.001$). Variations with the distance from the coast were observed also for the primary production, even though the pattern was less clear. As regards the micro-planktonic size class, a significant variation was observed only in the southern area ($y = 0.8437e^{-0.1229x}$; $r = 0.548$, $P < 0.001$) (Fig. 4).

In terms of photosynthetic efficiency, pico-phytoplankton was the most efficient size fraction, with a maximum peak value in February, 1997 in the southern area ($2.1 \text{ mg C}(\text{mg-Chl}a)^{-1} \text{ h}^{-1}$) [$\mu\text{Em}^{-2} \text{ h}^{-1}$] $^{-1}$.

Patterns of variation have also been analyzed with respect to the optical depth. Globally only primary productivity showed a direct logarithmic relationship with the optical depth (Fig. 6).

DISCUSSION

In the past decade many studies addressed the structure and functions of phytoplankton guilds in the Northern Adriatic area (Revelante and Gilmartin, 1995; Zuccarello *et al.*, 1996). The values of the primary production and phytoplankton biomass described here are in the range of published data (Zoppini *et al.*, 1995; Alberighi *et al.*, 1996). Particularly, values observed seem to be lower as regard with coastal area, where the influence of the river Po input is greater, while phytoplankton biomass and primary production in the offshore

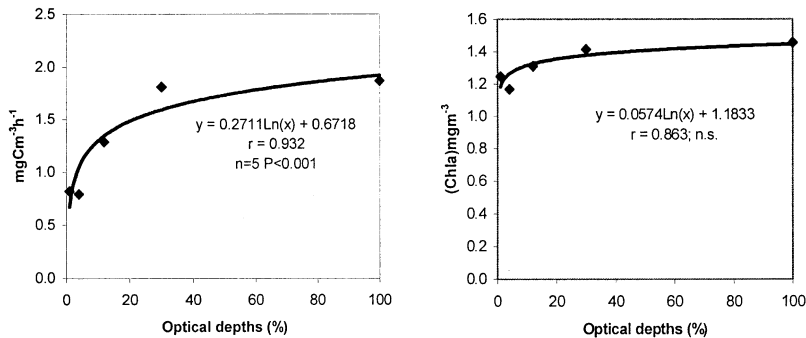


FIGURE 6 Patterns of variation of average phytoplankton production and biomass with the optical depths.

areas are comparable with those observed by other authors (De Gobbi *et al.*, 1996; Revelante and Gilmartin; 1995).

The location of sampling sites can be partially responsible of the difference of primary production values observed in the coastal areas. In fact, coastal stations (0–2 nautical miles from the coast) were sampled only in the southern zone while phytoplankton biomass and productivity showed significant negative exponential model of variation with the distance from the coast. The low values of primary production, could also depend on the analytical method selected which measures only the particulate net primary production, directly flowing into the grazing food webs. This is also suggested by the evidence that both assimilation numbers and photosynthetic efficiencies in the studied areas are lower than those observed for other Italian marine areas (Decembrini and Magazzù, 1990) or different marine ecosystems (Bransfield Strait, Antarctic; Cabrera and Montalcino, 1990; temperate estuarine and coastal environments; Malone and Neale, 1991). On the other hand, it emphasizes that the direct carbon flux in the grazing food webs is relatively slower in the studied areas with compared to other Italian seas.

The evidence collected in the present study seem to focus on a central role of nutrients and interspecific competition on both structure and functions of the planktonic guilds in the studied areas. First of all, it is supported by the variation patterns of phytoplankton biomass and primary production with the distance from the coast, in agreement with the important influence of the river Po inputs also reported by other research groups. Moreover, stations in the southern area which are more close to the coast, also show on average, higher phytoplankton biomass and productivity.

Secondly, the relevance of the microplankton size class, which has the highest requirements per individual, is higher in the southern zone with respect to the northern one and in the coastal station with respect to the offshore ones. Consistently the microplankton showed the highest assimilation numbers, indicating higher rates of production per unit of biomass and therefore higher competitive effects.

Third, picoplankton dominates the autotrophic guilds in the northern area and in the offshore stations, consistently with the observed higher photosynthetic efficiency of this size class with respect to the others. This supports higher response competitive ability of picoplankton (see Aarssen, 1983). Therefore, the observed variations are in agreement with the more recent theories of size related coexistence (Basset, 1995b). The low biomass and production of nanoplankton could also be due to competitive compression by the other size classes as observed in other guilds (Basset and Rossi, 1990; Basset, 1992).

The relations within the phytoplankton guilds are probably affected by nutrients, even though also temporal variability (Carrick and Schelske, 1997) and predation (Fogg, 1995) were proposed as potential causal factors. Nutrients are in fact a most relevant component of the Po input and they are likely to vary on a coast-offshore gradient, as will be discussed by other research groups. Moreover, it was already observed that pico-phytoplankton dominated in oligotrophic conditions and under pulse nutrient supply, such as upwelling zones in the oceans (Carrick and Schelske, 1997) while the microplankton dominated in eutrophic conditions and in manipulative experiments after nutrient additions (Carrick and Schelske, 1997; Beaty and Parker, 1996).

In conclusion structure and functions of phytoplankton guilds in the study areas seem to be controlled by nutrient inflow and competitive interreaction among body size classes.

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