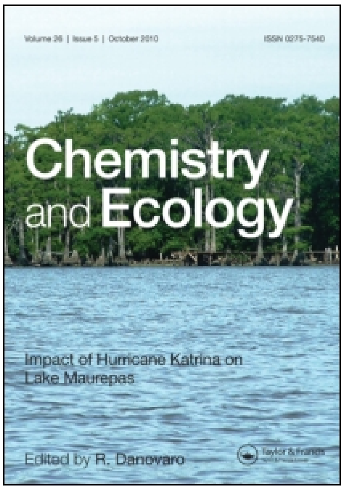

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Phytoplankton production in Italian freshwater and marine ecosystems: State of the art and perspectives

Alessandra Pugnetti[a]; Elisa Camatti[a]; Olga Mangoni[b]; Giuseppe Morabito[c]; Alessandro Oggioni[c]; Vincenzo Saggiomo[d]
[a] CNR, Istituto di Scienze Marine (ISMAR), Venice, Italy [b] Dipartimento di Zoologia, Università di Napoli Federico II, Naples, Italy [c] CNR, Istituto per lo Studio degli Ecosistemi, Verbania-Pallanza, Italy [d] Laboratorio di Oceanografia Biologica, Naples, Italy

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Phytoplankton production in Italian freshwater and marine ecosystems: State of the art and perspectives

ALESSANDRA PUGNETTI*†, ELISA CAMATTI†, OLGA MANGONI‡, GIUSEPPE MORABITO§, ALESSANDRO OGGIONI§ and VINCENZO SAGGIOMO¶

†CNR, Istituto di Scienze Marine (ISMAR), Sezione di Venezia, Castello 1364/A, I-30122 Venice, Italy
‡Dipartimento di Zoologia, Università di Napoli Federico II, Naples, Italy
§CNR, Istituto per lo Studio degli Ecosistemi, Sezione di Idrobiologia ed Ecologia delle Acque Interne, Largo Tonolli 50-52, I-28922 Verbania-Pallanza, Italy
¶Laboratorio di Oceanografia Biologica, Stazione Zoologica 'A. Dohrn', Villa Comunale, I-80121 Naples, Italy

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The present work aims at evaluating the state of art of phytoplankton production research in Italy. We present a synthesis of the main results achieved in three ecosystems where primary production studies have been carried out most intensively: a large subalpine lake (Lago Maggiore, LM), a shallow marine ecosystem with strong fluvial influence (the Northern Adriatic Sea, NAS), and a coastal area of the Southern Tyrrhenian Sea (the Gulf of Naples, GoN). The present yearly production values are around 150 g C m^{-2} yr^{-1} in LM and GoN; this ranges between 80 (offshore) and 150 g C m^{-2} yr^{-1} (coast) in the NAS. The temporal and spatial variations of phytoplankton production appeared, in each ecosystem, in accordance with the trophic changes. Significant correlations between production, chlorophyll, and light were generally observed for LM and for GoN. On the contrary, these parameters were poorly correlated in the NAS, hampering the use of predictive models in this ecosystem. Discrepancies between primary production and the actual phytoplankton biomass changes were observed across trophic gradients: the largest part of the carbon that is photosynthetically produced does not seem to be transformed into new phytoplankton biomass, strongly affecting the interpretation of the production figures in the ecosystems.

Keywords: Phytoplankton production; Trophic state; Lago Maggiore; Northern Adriatic Sea; Gulf of Naples

1. Introduction

The general concern about the global carbon cycle has provided a foreground position to primary production studies in the aquatic environment [1, 2]. Marine production represents approximately 40% of total primary production on earth [3], and the phytoplankton community may produce up to 50 Gt of carbon per year [4, 5], contributing up to 90% of total marine

*Corresponding author. Email: alessandra.pugnetti@ismar.cnr.it

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production [6]. Moreover, the quantification of the carbon fluxes and the definition of the role of aquatic ecosystems as a source or sink of CO_2 assume particular importance in the current environmental emergencies, especially those concerning climate change; in this context, the role of the biological pump plays a central role in the global carbon cycle [7].

The Italian perspective shows that considerable information on phytoplankton production in the Mediterranean aquatic ecosystems is accessible; however, measurements have been carried out only in a few freshwater and marine environments on appropriate spatial and temporal scales.

In this work we present a synthesis of the main results achieved in three ecosystems, where the phytoplankton production has been studied intensively: a large subalpine lake (Lago Maggiore), a shallow marine ecosystem, strongly influenced by coastal inputs (the Northern Adriatic Sea), and a coastal area of the Southern Tyrrhenian Sea (the Gulf of Naples). Despite obvious differences, these three ecosystems share similar eutrophication histories, related to consistent effects of anthropogenic nutrient loading and alterations of watersheds.

Our main goals are, first of all, to define the present state of the art and to assess the relations between primary production and the trophic state in these ecosystems, presenting a review of the main results as well as through a critical analysis of the available literature. Second, the examination of the relationships between production and the main environmental factors (e.g. light, nutrients, and physical dynamics of the water column) will supply a helpful insight into some physiological aspects that could be used for the development of models. Finally, we will examine the predictive power of ^{14}C measurements to obtain the actual rate of temporal changes in phytoplankton biomass.

2. Study sites

2.1 *Lago Maggiore*

Lago Maggiore, the second largest Italian subalpine lake (figure 1 and table 1), was originally oligotrophic, as testified by early limnological studies [8–10] and by the analysis of sedimentary pigments [11, 12]. The eutrophication process started in the 1960s [13–15]; the lake reached a trophic state close to eutrophy in the late 1970s (maximum in-lake total phosphorus concentration during winter mixing around $30\,\mu g\,l^{-1}$) [16]. Since that time, the phosphorus loads have been gradually reduced by various means, among which the adoption of treatment plants and the reduction in total phosphorus in detergents were the most important. As a result, the values of TP during winter mixing gradually declined, reaching values around $10\,\mu g\,l^{-1}$ in recent years [17].

First reports on Lago Maggiore primary productivity date back to 1957 [18], just a few years after the publication of Steeman-Nielsen's famous paper describing the ^{14}C method for the measurement of organic carbon production in phytoplankton samples [19]. Until the early 1980s, this parameter was frequently measured. Among the most noticeable papers, Gerletti [20] provided a unique picture of the spatial distribution of primary productivity along the longitudinal axis of the lake; Goldman *et al.* [21] explored, from an holistic point of view, the relationship between primary productivity and several environmental variables; Gerletti [22] described the decadal trend of primary productivity according to the trophic evolution of the lake, and finally, Ruggiu and Saraceni [13, 23] and Ruggiu *et al.* [24–26] reconsidered the historical data and analysed the factors controlling the photosynthetic process at the time of maximum trophic level in Lago Maggiore. The phytoplankton productivity measurements ceased until the middle of the 1990s: the new data collected during those

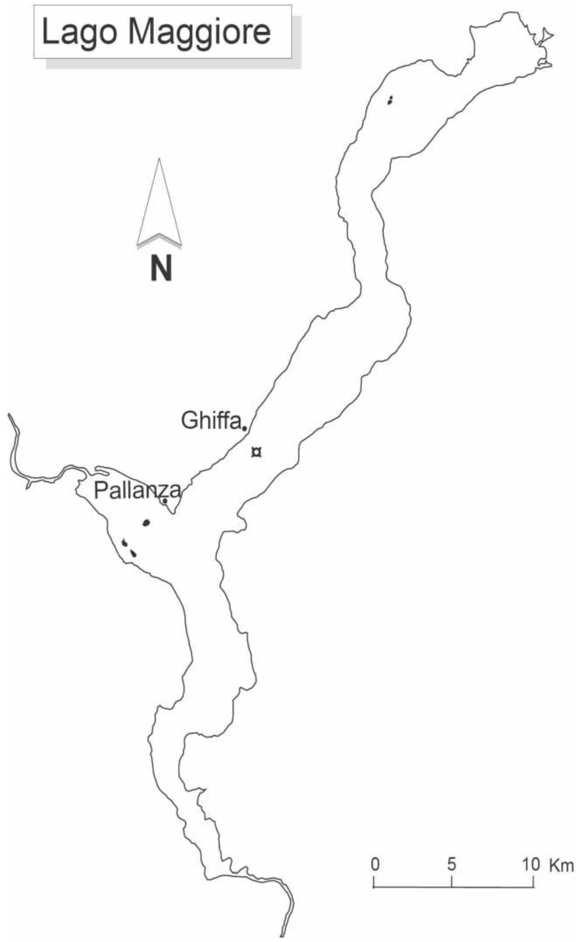

Figure 1. Map of Lago Maggiore. The sampling station is indicated by an asterisk.

years [27] showed a decline in the annual productivity, now close to the values measured during the 1950s (around $150\,g\,C\,m^{-2}\,yr^{-1}$) and indicated the change in relationship between primary productivity and some environmental parameters, as a consequence of the ever more oligotrophic conditions [15]. Recent measurements ($150\,g\,C\,m^{-2}\,yr^{-1}$), carried out in 2002 (Morabito and Oggioni, unpublished data), confirm the recent oligotrophic state of the lake (table 2). The long-term trend of annual productivity, although discontinuous (figure 2), clearly

Table 1. Main morphometric and hydrological features of Lago Maggiore.

Altitude (m a.s.l.)	194
Latitude	45°57′ N
Longitude	8°38′ E
Drainage basin area (km^2)	6599
Volume (m^3 × 10^6)	37 500
Area (km^2)	212
Max depth (m)	370
Mean depth (m)	177.5
Turn over time (yr)	4.1

Table 2. Recent primary production values in the three ecosystems.

	Lago Maggiore	Gulf of Naples	Northern Adriatic coast	Northern Adriatic offshore
Yearly production ($g\,C\,m^{-2}\,yr^{-1}$)	150	151	150	80
Daily production ($mg\,C\,m^{-2}\,d^{-1}$): avg ± SD	480 ± 250	757 ± 518	625 ± 415	235 ± 119
Daily production ($mg\,C\,m^{-2}\,d^{-1}$): min and max	16–900	92–1518	144–1480	26–440
Yearly production ($mg\,C\,m^{-3}\,h^{-1}$): avg ± SD	7.0 ± 4.4	19.2 ± 17.0	17.6 ± 18.3	1.3 ± 0.8
Yearly production ($mg\,C\,m^{-3}\,h^{-1}$): min and max	0.9–15.5	0.15–67	1.5–100	0.2–4.7

mirrors the trophic evolution of Lago Maggiore, although it must be considered that factors other than the nutrient availability can account for the yearly amount of productivity. The decrease in phosphorus does not necessarily imply a parallel decrease in pelagic productivity, as shown by the long-term trends observed in Lake Constance, where the effect of the phosphorus load reduction on the productivity rates was delayed by 10 more years [28].

The decline in primary productivity in Lago Maggiore was coupled with a decrease in phytoplankton biomass and with a rearrangement of the algal biocoenosis, increasingly dominated by smaller organisms [29]. A deep analysis of the long-term changes inside the phytoplankton assemblage is still to be done.

2.2 *Gulf of Naples*

The Gulf of Naples (GoN) is a coastal embayment with an average depth of 170 m (figure 3). The GoN is characterized by two subsystems: a eutrophic inner shelf area influenced by land runoff and an oligotrophic area with characteristics similar to those found in offshore Tyrrhenian waters. The two subsystems are strongly coupled due to the general physiography and bottom topography and a highly dynamic circulation of the water masses [30–33]. The

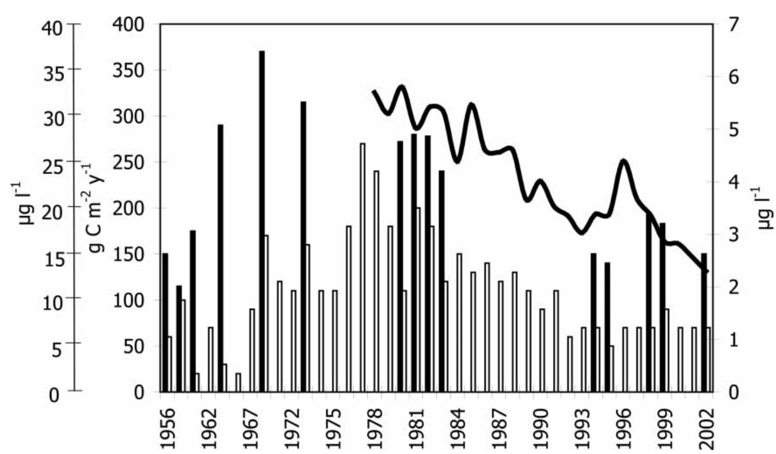

Figure 2. Lago Maggiore: long-term trend of annual primary productivity (black bars, left inner scale), total phosphorus concentration at mixing time (white bars, left outer scale) and chlorophyll *a* annual average (line, right scale).

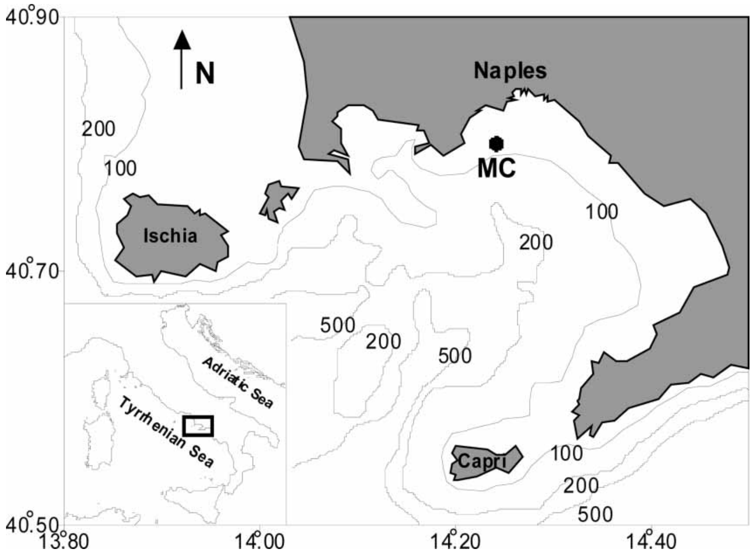

Figure 3. Gulf of Naples. Study site, denominated Marechiara (MC), (40°48.5′ N and 14°15.0′ E).

GoN represents one of the most intensely studied marine areas. However, interdisciplinary studies on the appropriate temporal and spatial scale have been carried out only since the late 1970s. In particular, the pronounced variability of hydrological and biological parameters was described in the early 1980s [30], and the first studies on primary production processes in the GoN were reported in [34]. From January 1984 to the present, hydrographical and biological sampling has been performed at a coastal station located 2 nautical miles from the coast (figure 3). This time series represents one of the most important datasets on the ecology and long-term evolution of phyto- and zooplankton as related to chemical and physical parameters in the Mediterranean [35, 36]. During the first years of this study, we observed the typical pattern of seasonal variation in phytoplankton concentrations of a Mediterranean coastal area with a strong anthropic impact. In terms of primary production (284 g C m^{-2} yr^{-1}; [35]), the GoN appeared to be the most productive area of the Mediterranean Sea. This was probably because primary production measurements were carried out on appropriate timescales only for this area. A further observation in the GoN, similar to that reported in other temperate coastal areas, is a phytoplankton bloom in autumn during a period of time called 'St. Martin's summer', characterized by a period of stable atmospheric pressure [37]. In the GoN, the phytoplankton assemblages show a very high biodiversity of mainly diatoms and phytoflagellates all year round [38, 39]; a minor but fairly constant contribution is provided by the picoplankton [40]. Analyses of the 1984–2000 dataset have shown that the trophic conditions of the GoN have changed over the period of study, which might be related both to climate change and to a decrease in the anthropic input to the area [41]. A sharp decrease in annual means of phytoplankton biomass (Chl *a*) has occurred; integrated Chl *a* concentrations are 30% less in the 0–60 m interval and 50% less in the surface layer in the period 1997–2000 as compared with the 1984–1991 values. Also, annual primary production is considerably lower in the second period than in the first period (151 and 266 g C m^{-2} yr^{-1}, respectively). The variations of primary production analysed in recent years are reported in table 2. These values are quite similar to those reported for Narragansett Bay [42] and Bedford Basin [43]. Furthermore, the phytoplankton size spectrum and species composition have changed also. Since 1995, an increase in phytoplankton cell numbers was observed as well as a decrease in cell size; the

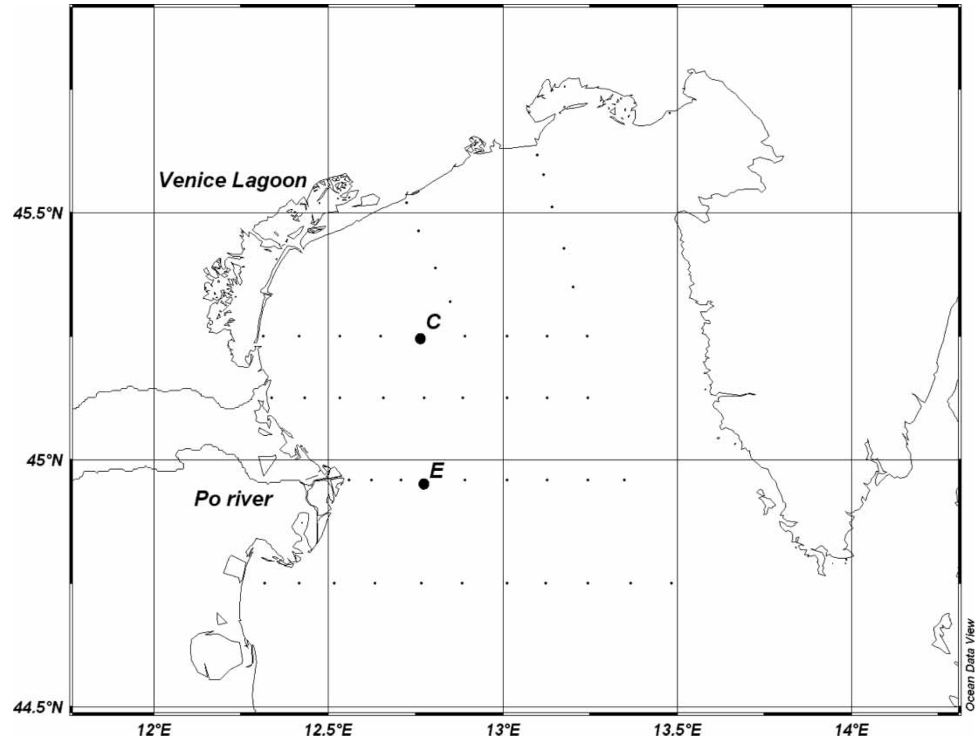

Figure 4. Northern Adriatic Sea. The main sampling stations (C and E) are shown.

phytoplankton is now dominated by small diatoms and undetermined coccoid species [36]. At present, instead of the typical annual cycle of temperate areas, phytoplankton concentrations and primary production are now related to occasional and discontinuous anthropic input.

2.3 *Northern Adriatic Sea*

The Northern Adriatic Sea (figure 4 and table 3) is a shallow basin characterized by a dominant cyclonic circulation and by the inputs of several rivers, of which the Po, by far the largest Italian river, and the Adige provide major contributions to the total freshwater inputs. On the other hand, at its southeastern end, the Northern Adriatic receives highly saline and oligotrophic waters from the southern Adriatic basin.

The annual cycles of phytoplankton biomass and primary production are mainly driven by freshwater flow and by nutrients inputs from the major rivers: in particular, a strong salinity and nutrient gradient, decreasing from north-west to south-east, is typically recognized, and the western side represents an area of enhanced biological activity.

Table 3. Range of average values of some hydrological parameters in the Northern Adriatic Sea.

Salinity	35.6–38.4
Dissolved inorganic nitrogen (μM)	0.7–8.3
Dissolved inorganic phosphorus (μM)	0.05–0.1
Chlorophyll *a* (mg m^{-3})	0.2–3.0

High N/P values, far above the Redfield ratio, are considered an intrinsic characteristic of the Northern Adriatic waters [44–46]. However, rapid variations of nutrient availability, with alternating N and P limitation, might occur, in relation to abrupt changes in Po River flow and to phytoplankton uptake [47, 48]. The complex hydrodynamics and the seasonal alternation of vertical mixing and stratification make this system highly heterogeneous, in both time and space [49, 50].

Several short-term studies on phytoplankton production have been performed on the Northern Adriatic Sea since the 1970s, by different working groups and in the framework of several research projects. Most of these studies are reviewed and reported in Harding *et al.* [46], but see also the papers by Franco [51, 52], Zoppini *et al.*, [45], Heilman and Richardson [53], and Cantoni *et al.* [54]. The main focus of the present paper will be on the data gathered by CNR ISMAR since the early 1990s [55–59].

In the Northern Adriatic Sea, major primary production variations occur along the trophic gradient (table 2), and typically a negative correlation between phytoplankton production and salinity has been reported [46, 51, 52, 57]. The range of phytoplankton production is considerable: annual values between 60 and 90 and between 130 and 210 g C m^{-2} yr^{-1} for offshore and coastal waters, respectively, have been recorded [44, 45, 53, 56, 60, 61]. A similar gradient can be observed also for hourly and daily production value: maxima up to 100 mg C m^{-3} h^{-1} and 3 g C m^{-2} d^{-1} were reported at stations close to the Po River delta, while production maxima at

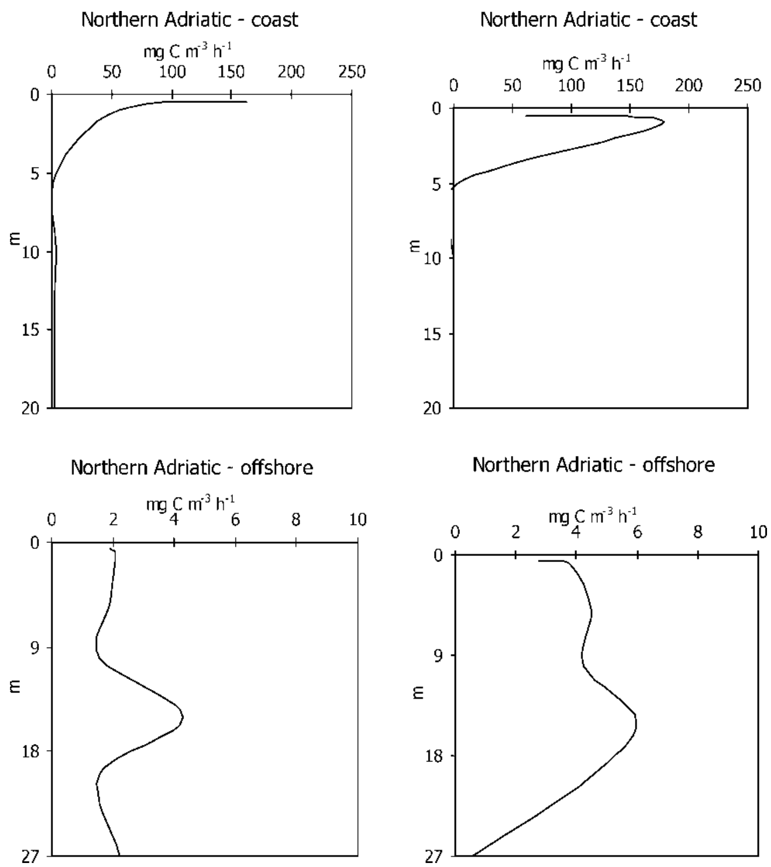

Figure 5. Northern Adriatic Sea: examples of vertical distribution of primary production at a coastal and an offshore station.

the offshore stations rarely attain 5 mg C m^{-3} h^{-1} and 600 mg C m^{-2} d^{-1} [45, 53, 54, 57–59]. Major differences in the vertical distribution of primary production between coastal and offshore area were generally observed (figure 5). The productive layer was restricted to the upper metres in the coastal stations, mainly as the result of strong vertical salinity gradient and irradiance attenuation, while offshore the productive layer frequently includes the entire water column with peaks in primary productivity that may occur close to the bottom [55, 57–59].

3. Methods

At the three study sites, primary production was measured by means of the classic ^{14}C technique [19]. In the present paper, the methods will be described only briefly; for details, refer to previous papers.

3.1 *Lago Maggiore*

Since the end of the 1970s, sampling of physical, chemical, and biological parameters was performed at a site, where maximum depth (370 m) occurs, located in front of the town of Ghiffa. To measure the primary productivity, the samples were taken at five depths, corresponding to 100%, 50%, 25%, 10%, and 1% of subsurface PAR. *In situ* incubations were carried out, for 4 h around noon, at a shallower site, in front of the town of Pallanza. Sampling frequency was, in most cases, fortnightly during the period March–October and monthly in January, February, November, and December. The same method was used from 1970 to the present [19], and only minor changes in the protocol have been introduced during that period (activity of the ^{14}C added, type of filters employed and the scintillation counting procedure). This permits fairly reliable comparisons between primary production measurements throughout the 30 year dataset. The productivity was always measured as particulate organic carbon collected on filters. In the most recent years, the incubation of dark bottles was omitted, and a blank correction, based on the activity incorporated by a non-incubated sample, was introduced.

3.2 *Gulf of Naples*

In the GoN, primary production measurements were carried out by the end of the 1970s on seven different light levels (from 100% to 1% of incident PAR) in the two subsystems described in section 2. Since January 1984, long-term sampling has been carried out at a station, Marechiara (MC), located 2 nautical miles off the coast at a depth of 80 m (figure 3). Physical, chemical, and biological parameters were measured every 2 weeks until 1991; after an interruption, since February 1995 to date, sampling has been performed on a weekly basis. Primary production measurements were conducted from 1984 to 1988 on standard hydrographical levels (0, 2, 5, 10, 20, 40, and 60 m). Since 1998, photosynthetic parameters have been determined regularly at four levels (0, 10, 20, and 40 m) by means of the classical C^{14} method (P vs. *E* experiments) and by means of modulated fluorescence (FRRF and PhytoPAM). Primary production measurements were conducted in situ from 10 a.m. to 2 p.m. according to the same protocol as that employed in Lago Maggiore. During the incubations, two light profiles were recorded with underwater LI-COR 2π quantum sensors equipped with a reference surface sensor. P vs. *E* measurements were performed according to Babin *et al.* [62] at four depths. At each depth, sub-samples of 50 ml were collected in 12 Corning culture flasks and inoculated with 740 kBq of $NaH^{14}CO_3$. Incubations were carried out for 1 h in an artificial thermostat light gradient incubator (Osram HQI-T 250 W/D lamp). In order to check for dark fixation, for each sample one subsample was placed in the dark, inside the incubator, with four drops of saturated seawater DCMU solution [63]. The irradiance in each incubation bottle was measured using a 4π sensor QLS-101 (Biospherical Instruments, San Diego, CA). The P vs. E data were derived from the model of Platt *et al.* [64].

3.3 *Northern Adriatic Sea*

In this paper, we will refer mainly to the data that were gathered by the CNR ISMAR, during 1994–2002, in the framework of the monitoring and research projects PRISMA1 [59], PRISMA2 [57], INTERREG2 [58], and MAT [65]. Sampling frequency varied from monthly to seasonal, depending on the aim and on the sampling design of the projects. In general, phytoplankton photosynthetic activity was measured by means of *in situ* incubations of the whole phytoplankton community in both coastal and offshore stations, at three to five depths in the euphotic zone, for 2–4 h around noon. Throughout the study period, productivity was measured as both particulate organic carbon collected on filters and total production, after acidification and stirring of duplicate 5 ml subsamples.

At each station, besides production measurements, vertical profiles of temperature and salinity (CTD profiler) and PAR irradiance (quantum scalar irradiance meter, Biospherical) were always performed, and water samples were collected for the determination of dissolved inorganic nutrients [66], chlorophyll *a* (fluorometric method) [67], and phytoplankton [68].

4. Environmental factors controlling primary productivity across trophic gradients

Irradiance and chlorophyll concentration are the parameters which best explain the fluctuations of primary productivity in aquatic environments [69]. Considerable research effort has been devoted worldwide to quantify the relationships between phytoplankton photosynthesis, light, and chlorophyll, to model the mathematical relationships between these variables, and to identify the environmental constraints causing the temporal variations of the parameters describing the photosynthesis-irradiance curves [70].

4.1 *Lago Maggiore*

The relationships between irradiance, chlorophyll, and production, and how these parameters have changed during the trophic evolution of the lake have been recently discussed [15]. Here, we would like to summarize the main findings: first, the photosynthetic activity in Lago Maggiore is strongly influenced by light availability, regardless of the trophic state. The relationship between these two variables (figure 6) measured at the time of maximum trophic state (1978–1981) and in the oligotrophic phase (1994–1995) remained almost unchanged, as indicated by the slopes of the regression lines (figure 6). On the other hand, the relationship between daily primary productivity and chlorophyll *a* (as an average in the euphotic zone) showed an interesting pattern, moving from the poor relationship measured in 1978–1981 to the good regression observed with the 1994–1995 data (figure 6). These findings suggest that during the period of meso-eutrophy, other factors were more important than chlorophyll in controlling the fluctuations of primary production. The opposite seems to be true in the more recent period, when we hypothesize a stronger coupling between photosynthesis and biomass, as indicated by the difference in slopes for the two regression lines (figure 6). Following oligotrophication, the system evolved towards an increasing nutrient limitation; accordingly, the amount of in-lake

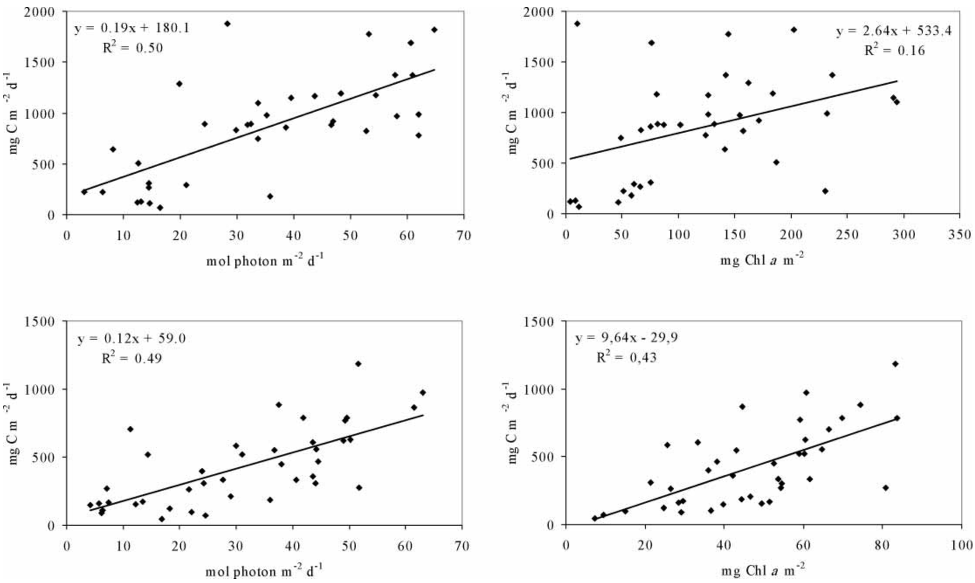

Figure 6. Lago Maggiore: regression curves of daily primary production vs. incident daily solar radiation (left panels) and daily primary production vs. euphotic chlorophyll *a* concentration (right panels) during 1978–1981 (upper panels) and 1994–1995 (lower panels).

biomass is now strictly controlled by the low nutrient availability, which prevents high production rates. The complete overturn of the water column observed in February 1999 may confirm our hypothesis: an exceptional amount of nutrients refuelled the euphotic layers and, in March, productivity values close to 1500 mg C m^{-2} d^{-1}, comparable with those recorded during the 1970s, were measured [71]. To give a rough idea of the impact of the complete mixing, in March 2002 the highest peak was 900 mg C m^{-2} d^{-1}, corresponding to the annual maximum. As a more general pattern, the mixing regime of the lake can reasonably affect the spring phytoplankton dynamics through the amount of nutrient available for growth, as suggested by the relationship between mixing depth (calculated according to Ambrosetti *et al.* [72]) and total phosphorus concentration at mixing time (figure 7). The relationship, although not

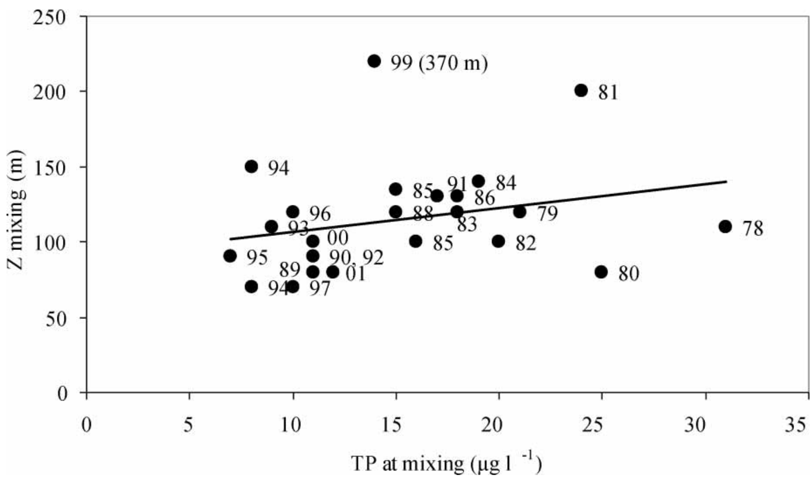

Figure 7. Lago Maggiore: relationship between depth of winter mixing and total phosphorus concentration at overturn, from 1981 to 2001.

significant ($r = 0.14$, $P = 0.51$), indicates a trend towards an increase in nutrient supply when the mixing depth is higher: the eutrophicating effect of the 1999 deep mixing is very clear.

An increase in the internal loading due to a deeper winter mixing can be normal in the deep oligotrophic lakes: for instance, the long-term data recorded in Lake Tahoe show a strong effect of the mixing depth on the interannual and seasonal variability of the algal productivity [73].

The effect of the complete overturn indicated the key role of meteo-climatic events in controlling the primary productivity in Lago Maggiore. In the course of the lake's trophic evolution, anomalous events in the algal succession, such as peaks or depressions of the annual average chlorophyll concentration, have often been interpreted as indications of important trophic changes, while most of them were later explained by the occurrence of peculiar meteorological conditions that modified the physics and chemistry of the water column. A recent analysis of the long-term phytoplankton data showed that the fluctuations of the local climate could deeply affect the annual algal dynamics [74].

4.2 *Gulf of Naples*

During the period 1984–2002, the first annual phytoplankton bloom in the GoN occurred in January–February during stable weather conditions; despite isopycnal conditions of the water column and an even vertical distribution of phytoplankton biomass in the photic layer, integrated primary production values recorded in this period were comparatively high. Notably, in relation to the well-mixed conditions of the water column, the photosynthetic parameters were essentially the same at all depths (table 4) indicating the acclimation of phytoplankton cells to the average irradiance levels of the water column. The lack of thermal or aline water column stratification allows for a continuous nutrient input, thus providing ideal conditions for primary production processes in terms of both photosynthetic capacity and efficiency. Along with short day lengths, the relatively low winter temperatures might limit primary production to some extent.

The variations in primary production were strongly correlated with phytoplankton concentrations throughout the year, while the relation to irradiance was less clear (figure 8).

Up until the mid-1990s, eutrophic conditions characterized the inner part of the GoN due to frequent terrestrial discharge. Subsequently, the discontinuous land runoff as well as climate changes have determined a change towards mesotrophic conditions [36, 41]. Such a change is also reflected in the specific composition and in the size spectrum of the phytoplankton assemblages as observed since the mid-1990s as compared with those reported in the mid-1980s. In this complex scenario, the photosynthetic parameters recorded in recent years differ from those found in 1984–1988. During that period, the relation between primary production and phytoplankton biomass (P/B) was extremely variable with an average ratio >10 mgC (mgChl $a)^{-1}$ h^{-1} in the surface layer, indicating that with continuous anthropic discharge nutrients were generally not a limiting factor for phytoplankton production. In recent years

Table 4. Photosynthetic parameters of the Gulf of Naples in well-mixed conditions (February).

Depth m	P^b_{max} mg C (mg chl $a)^{-1}$ h^{-1}	α mg (mg chl $a)^{-1}$ h^{-1} (μ mol photons m^{-2} s$^{-1})^{-1}$	β mg C (mg chl $a)^{-1}$ h^{-1} (μ mol photons m^{-2} s$^{-1})^{-1}$	E_k μ mol photons m^{-2} s^{-1}	Chl a μg l^{-1}
0	4.24	0.0498	0.0032	85	0.56
10	4.07	0.0563	0.001	72	0.55
20	4.25	0.0596	0.0026	71	0.54
40	3.41	0.0605	0.0016	56	0.56

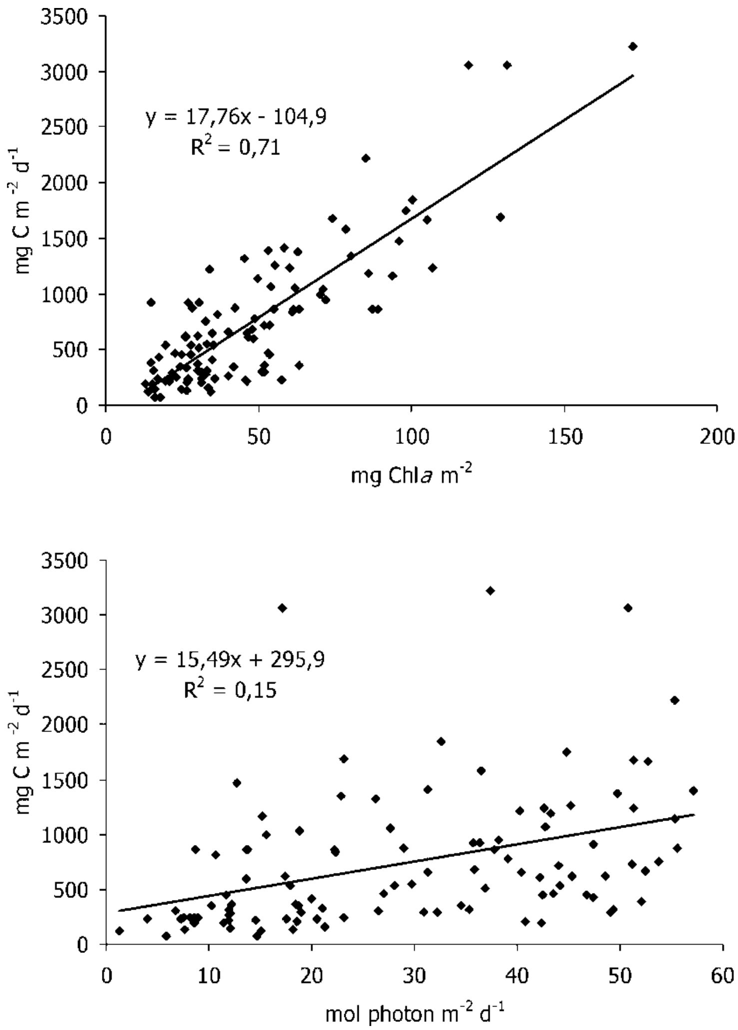

Figure 8. Gulf of Naples: linear regression between daily primary production, chlorophyll *a* concentration (upper panel) and incident solar radiation (lower panel).

(2003–04) the average P/B ratio was lower (8 mgC (mgChl a)$^{-1}$ h^{-1}) and steadier than in the previous time period, probably as a consequence of the observed trophic change. At present, the main limiting factor of phytoplankton production in GoN appears to be nutrient concentrations, as observed in all mesotrophic areas. This aspect is further emphasized by the relatively low nutrient concentrations recorded at all depths also in completely mixed water column conditions. Finally, the strong correlation between phytoplankton biomass and production is expected in an efficient system, and such a regional feature allows for the construction of reasonably reliable primary production models.

4.3 *Northern Adriatic Sea*

A strong correlation between phytoplankton production, chlorophyll *a*, and irradiance is generally found in estuaries where nutrients do not limit production. Changes in production over periods of weeks to years can therefore be estimated simply from phytoplankton biomass and light [75, 76].

This general statement does not seem to hold for the Northern Adriatic waters. In the offshore area of the Northern Adriatic Sea, primary production throughout the water column appears to be significantly correlated, although not always so, with the incident PAR, but not with chlorophyll *a* (figure 9). The highest values of water column productivity are predominantly observed during the spring and summer [46, 58] in most cases due to an increase in the extension of the productive layer, rather than of higher production values. At the coastal stations, production was not significantly correlated with light or chlorophyll *a* (figure 9).

The parameters obtained from photosynthesis-irradiance experiments in the Northern Adriatic Sea show a conspicuous range of variation in the coastal waters directly influenced by the Po river plume; in offshore waters, the variability in photosynthetic parameters was much less pronounced (figure 10). The classical models that allow the prediction of production from irradiance and chlorophyll rely on the definition of stable relations between production, chlorophyll, and light, and stable parameters of the photosynthesis/light curves. The use and the predictive power of these models in the Northern Adriatic Sea therefore appear hampered.

Specific production frequently exceeding 5 mg C mg Chl a^{-1} h^{-1}, with peaks up to 20 mg C mg Chl a^{-1} h^{-1}, are commonly observed in the Northern Adriatic waters [53, 58, 59], as well as dramatic changes in P^b_{max} [77]. Extremely high P^b values, among the highest reported so far for marine systems, were recorded during the early-phase phytoplankton blooms followed by a rapid decline, due to nutrient exhaustion [78]. Nutrient dynamics appear to play a key role in the relations between production and chlorophyll: the largest part of the Northern Adriatic waters is, indeed, characterized by rapid variations of nutrient availability, with alternating N and P limitation, in relation to abrupt changes in Po River flow, to nutrient distribution in the basin and to phytoplankton uptake [47].

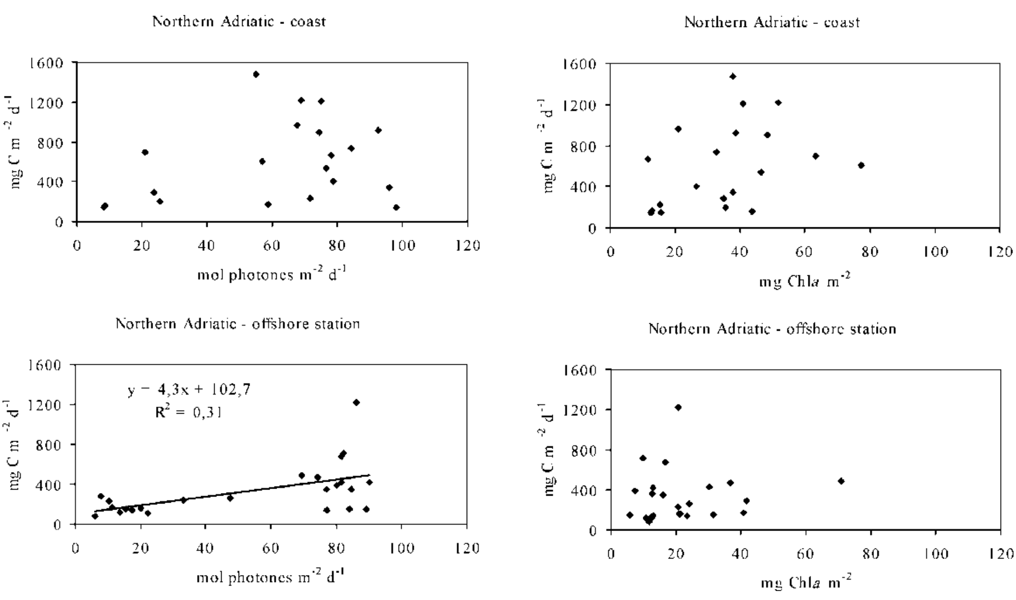

Figure 9. Northern Adriatic Sea: correlations between daily primary production, incident PAR and chlorophyll *a* at a coastal and an offshore station.

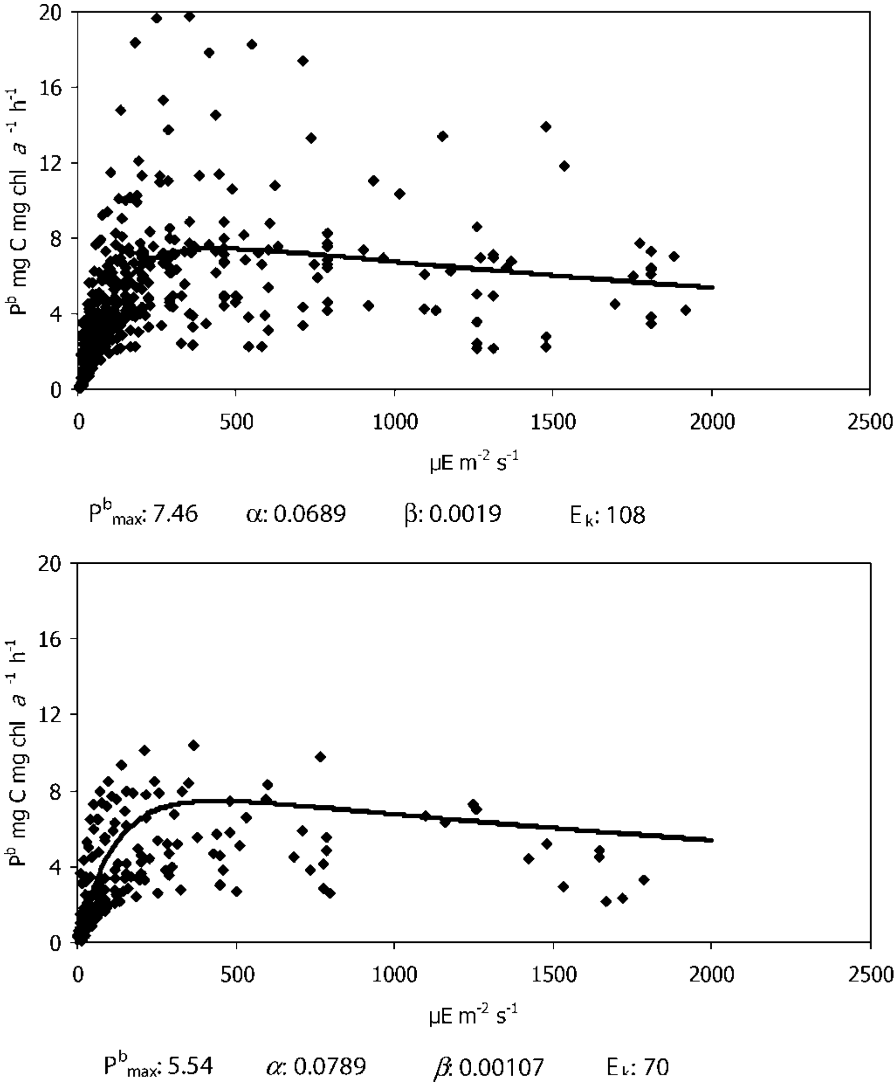

Figure 10. Northern Adriatic Sea: P vs. *E* experiments in the surface layer. The photosynthetic parameters and the curve represent the average of 40 experiments in the coastal area (upper panel) and of 15 experiments in the offshore area (lower panel). P^b_{max}: mg C (mg chl *a*)$^{-1}$ h^{-1}; α: mg C (mg chl *a*)$^{-1}$ h^{-1} (μ mol photons m^{-2} s^{-1})$^{-1}$; β: mg C (mg chl *a*)$^{-1}$ h^{-1} (μ mol photons m^{-2} s^{-1})$^{-1}$; E_k: μ mol photons m^{-2} s^{-1}.

5. Primary productivity and biomass growth

Only a minor part of the carbon fixed by photosynthesis is incorporated into new algal biomass [79–82], especially if nutrient resources are deficient. The ^{14}C uptake rarely results in the equivalent new phytoplankton carbon biomass after 24 h: discrepancies between potential and real growth rates have commonly been observed in many aquatic environments [83], and these are mainly explained by the prevalence of loss processes (lateral advection, sedimentation, respiration, excretion, grazing, and lyses).

As reviewed by Dubinsky and Berman-Frank [84], uncoupling of photosynthesis from growth is a commonly observed phenomenon in nature, whenever photosynthetic assimilation of carbon by algae exceeds that usable for biomass synthesis. In such conditions, carbon assimilation rates will exceed those needed for cell building, and photosynthesis will become uncoupled from cell growth: the excess carbon may be respired and excreted, but also employed for the synthesis of various compounds containing carbon, most of which provide an evolutionary or co-evolutionary important advantage, such as the photoprotective pigments, the ballast carbohydrates, or the protective spore walls.

The annual fluctuations of potential growth rate (μ), loss rate (λ) and rate of daily biomass change (K), calculated for two different periods (1981 and 1999), according to Tilzer [85] for the trophic evolution of Lago Maggiore, show almost the same trend (figure 11): for most of the year, the daily rate of biomass change is close to zero, because of the high loss rate, always reaching the potential growth rate, except for a short spring period, when the phytoplankton populations display a net positive growth. Even though the algae grow faster in oligotrophic conditions, losses are still very high.

In the Northern Adriatic Sea, comparisons between potential and actual growth rates (calculated, as for LM, according to Tilzer [85]) indicated that very little carbon produced by

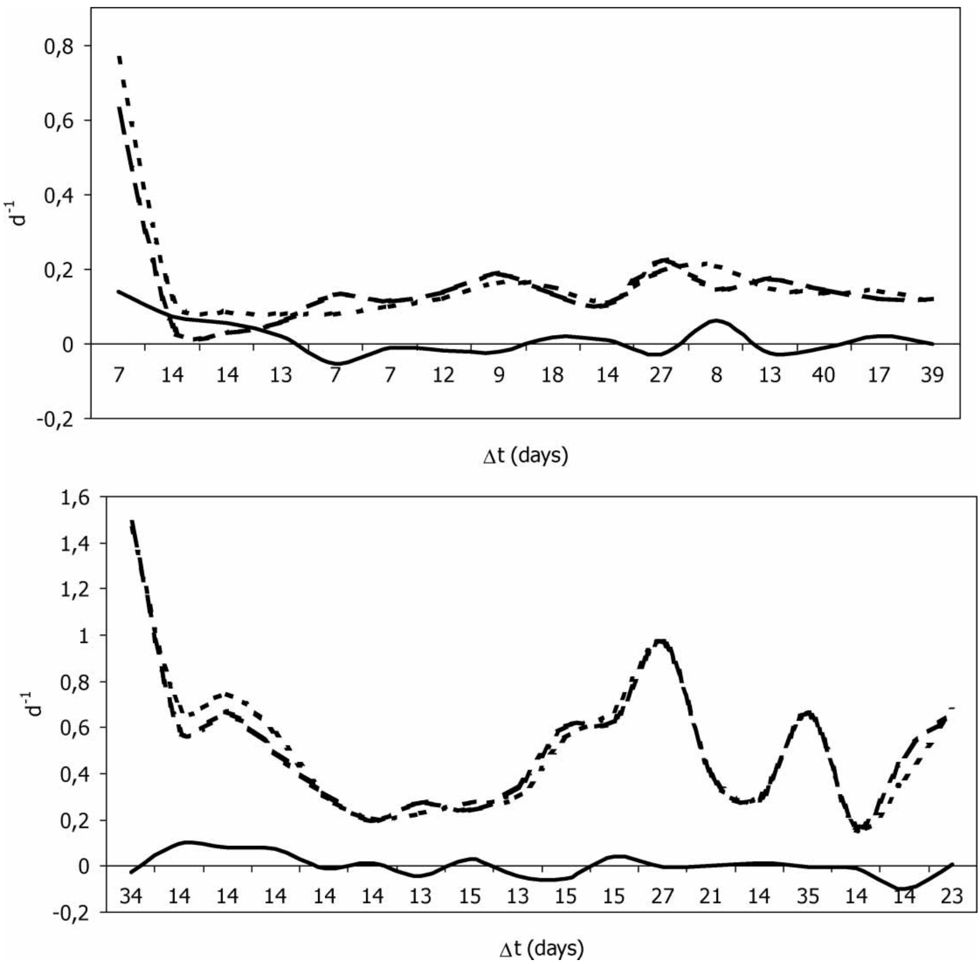

Figure 11. Lago Maggiore: rates of phytoplankton growth (μ, dotted line), biomass change (k, solid line), and loss (λ, dashed line) in 1981 (upper panel) and 1999 (lower panel).

phytoplankton accumulates daily as algal biomass (figure 12). A daily biomass increase was observed only in concomitance with pulses of diluted waters and was therefore mainly determined by allochthonous inputs [59]. Among the loss processes, respiration and release of exudates were supposed to have a major importance [59]. Respiration rates as high as 70% of total production have been measured (Pugnetti *et al.*, unpublished data); the average short-term carbon exudates release in the Northern Adriatic Sea, estimated from in situ measurements, is indeed higher than 20% of total production, with maxima up to 70%, [65].

According to Wood and Van Valen [86], algal exudation allows the algal cells to keep their photosynthetic metabolism active, in environments, such as Lago Maggiore and the Northern Adriatic Sea, where nutrient availability is highly variable and not always adequate for phytoplankton growth requirements. This may lead to an uncoupling between photosynthesis and growth [87, 88] and to high specific production and release of exudates. In the Northern Adriatic Sea, the nutrient supply dynamics might induce the shift from biomass growth to pure polysaccharide production, not requiring nitrogen and phosphorus. Indeed,

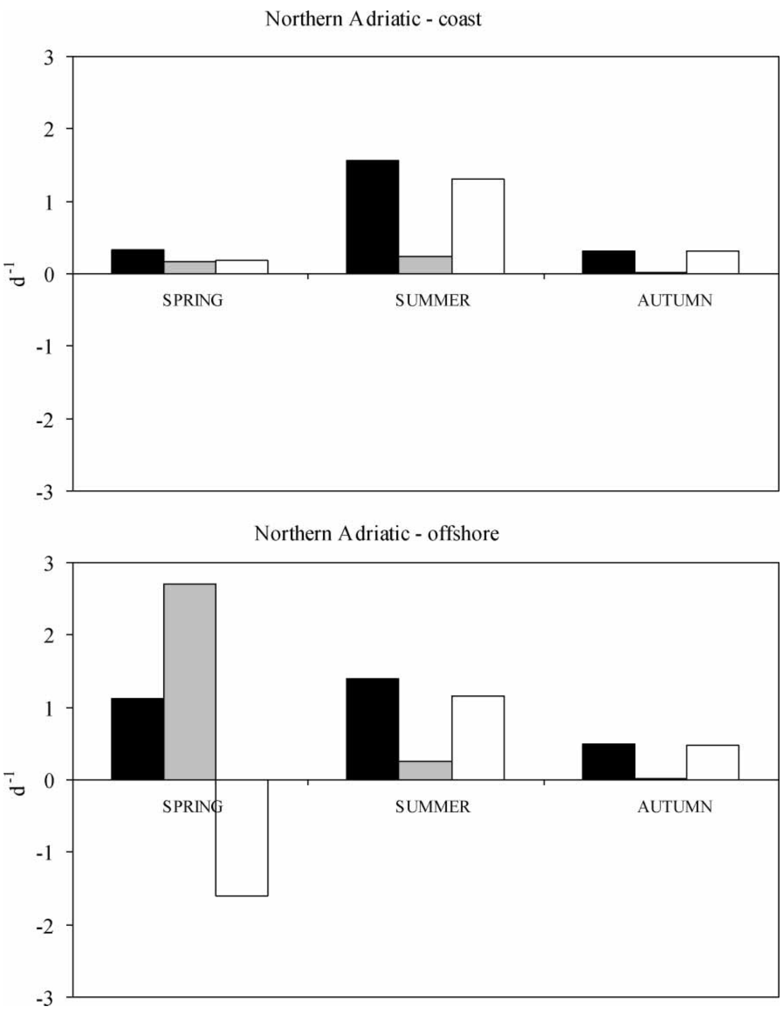

Figure 12. Northern Adriatic Sea: rates of phytoplankton growth (μ, black bars), biomass change (k, grey bars), and loss (λ, white bars) at a coastal and offshore station.

the decreasing gradient of phytoplankton production in the Northern Adriatic is mostly associated with decreasing phytoplankton biomass rather than with decreasing P^b [53, 58, 59]: the nutrient concentration seems to limit the total phytoplankton biomass rather than the specific production of organic carbon.

The average short-term percentage carbon exudate release in the Northern Adriatic Sea is close to the highest values reported in the literature for marine and/or lacustrine environments [65]. Several diatom species, commonly encountered in Northern Adriatic phytoplankton assemblages (e.g. *Skeletonema costatum*, *Chaetoceros* spp. and *Cylindrotheca closterium*), are known, from laboratory experiments, to produce a large amount of extracellular polysaccharides [88–93], and this process is enhanced under P-limitation reported in the Adriatic basin. The extracellular release of polysaccharides is considered to be one of the main mechanisms triggering the mucilage phenomenon [89, 90, 94].

Uncoupling of the processes regulating biomass yields and production rates is also common in large lakes, as suggested previously [21, 95] when a low biomass was responsible for a daily productivity exceeding $1\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$.

Apart from the physiological explanations given above, another reason for these discrepancies might be the difficulty in accurately estimating the carbon content of phytoplankton biomass [96].

6. Open questions and perspectives

The considerable data set available for the three ecosystems considered in this work allowed, first of all, a good estimation of daily and annual primary production. Phytoplankton production appears, in each ecosystem, a good indicator of the trophic changes, on both the temporal and spatial scale. However, large discrepancies between primary production values and the actual phytoplankton biomass changes are observed across the trophic gradient: the loss rates appear to be as high as the production rate, so the largest part of C produced is not transformed into new phytoplankton biomass. As already emphasized by other authors, the evaluation of the role of phytoplankton in marine and freshwater ecosystems and of the ecological meaning of the production figures requires an examination of the fate of the carbon that is photosynthetically produced. Major efforts should therefore be devoted to the estimation of the loss rates, in particular of respiration, and to the evaluation of the pathways of the photosynthesized carbon, in relation to the dominant (microbial or grazing) food web.

Considerable research efforts to understand the dynamics of phytoplankton production have been devoted worldwide to quantifying the relationships of phytoplankton photosynthesis with light and chlorophyll and to the identification of the environmental constraints causing the temporal variations of the photosynthesis/light curve parameters. The possibility of predicting daily production from the analysis of simple covariables (such as light and chlorophyll) requires the ability to parametrize the production processes. This opportunity seems realistic for the Lago Maggiore and the Gulf of Naples where good correlations between production, chlorophyll, and light have been established. Opposite indications come from the analysis of the data of the Northern Adriatic Sea, where photosynthesis, light, and chlorophyll were poorly correlated. This characteristic has profound implications for the general understanding of the Northern Adriatic ecosystem and the possibility of using predictive models.

The ^{14}C method for the measurement of PP has been around for 50 years, the existing database at a global scale is very large, and the method will undoubtedly remain a standard in freshwater and marine research. However, discordances and uncertainties about the accuracy and the interpretation of the measurements still exist. Problems related to bottle effects, incubation procedures, and, more generally, the comparability of the results, as well as the cost of ship time required for extended in situ incubations and for waste treatment, have stimulated basic research on alternative methods for estimating phytoplankton photosynthesis. One of the major challenges for the future research on primary production in Italy should be to integrate the classic ^{14}C data with the results from other methods. An analysis of alternative methods to ^{14}C is beyond the scope of this paper: each of these techniques obviously has merits, limits, and constraints, and is not suitable for universal application. However, we should mention the in situ measurements based on fluorescence: this technique can provide a significant amount of information on biophysical parameters related to photosynthesis, in real time, with high temporal and spatial resolution, thus increasing the accuracy of predictive models and providing a further insight into the interactions between primary production, nutrient availability, and hydrodynamics.

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