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Phytoplanktonic productivity and nutrients in five Mediterranean lagoons

Coastal lagoons
Flushing time
Nutrients
Primary productivity
Eutrophication
Lagunes côtières
Temps de séjour
Sels nutritifs
Production primaire
Eutrophisation

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ABSTRACT

Phytoplankton and nutrients have been studied in relation to hydrological parameters in five Mediterranean lagoons. Some methods and concepts borrowed from limnology (annual budgets, limiting factors...) have been used to establish simple relationships between phytoplankton biomass (as measured by chlorophyll), nutrient concentrations and nutrient inputs. These relationships demonstrate that the response of lagoons to given loading conditions can differ from that of lakes, due in particular to the marine origin of phytoplankton species, the dilution of lagoon water by nutrient-poor seawater and N-limitation rather than P-limitation.

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RÉSUMÉ

Production phytoplanctonique et sels nutritifs dans cinq lagunes méditerranéennes.

Le phytoplancton et les sels nutritifs ont été étudiés dans cinq lagunes méditerranéennes en relation avec les paramètres hydrologiques. L'application des méthodes et concepts utilisés en limnologie (bilan annuel des apports, facteurs limitants...) a permis de mettre en relation biomasse phytoplanctonique (mesurée par la teneur en chlorophylle) d'une part et concentrations et apports externes en sels nutritifs d'autre part. Les relations observées démontrent que les lagunes ne répondent pas de la même manière que les lacs aux apports de sels nutritifs en raison de l'origine marine des espèces phytoplanctoniques présentes, d'une dilution de l'eau lagunaire par une eau marine pauvre en sels nutritifs et d'une limitation par l'azote plutôt que par le phosphore.

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INTRODUCTION

Brackish lagoons occupy a significant part of the shore line in some areas of the world. Because of efficient mixing and sediment proximity, these shallow water bodies often sustain a very high productivity (Mee, 1978; Nixon, 1982). Mediterranean lagoons show very peculiar features due to their geographical position. The lack of tides in the Mediterranean Sea reduces exchanges between the lagoons and the outlying marine waters. The Mediterranean climate, which is characterized by a low level of precipitation concentrated in a short time span during autumn and spring, results in a high degree of variability in water catchment inputs.

The present paper describes some of the processes that govern phytoplankton productivity in five Mediterranean lagoons located along the south coast of France. We shall show that some of the concepts and methods used in limnology (loading and flushing rates, single nutrient limitation) can be applied to lagoons as well. However the marine character of lagoons may cause responses which are qualitatively and quantitatively different from those pertaining to lakes.

METHODS

Phytoplankton surveys were conducted in five French lagoons from 1976 to 1979. In each lagoon, 5 to 10 stations (Fig. 1) were sampled at the surface with a frequency of once every two weeks to once every 3 months, for at least one full year. Salinity was determined using an electronic salinometer (Electronic Switchgear — MC5). Nitrate and phosphate concentrations were measured as described in Strickland and Parsons (1968). Species composition was obtained using the Utermöhl sedimentation method. Chlorophyll *a* was determined after GF/C filtration by the fluorimetric method of Yentsch and Menzel (1963): no correction was made for phaeophytin *a*. Primary productivity

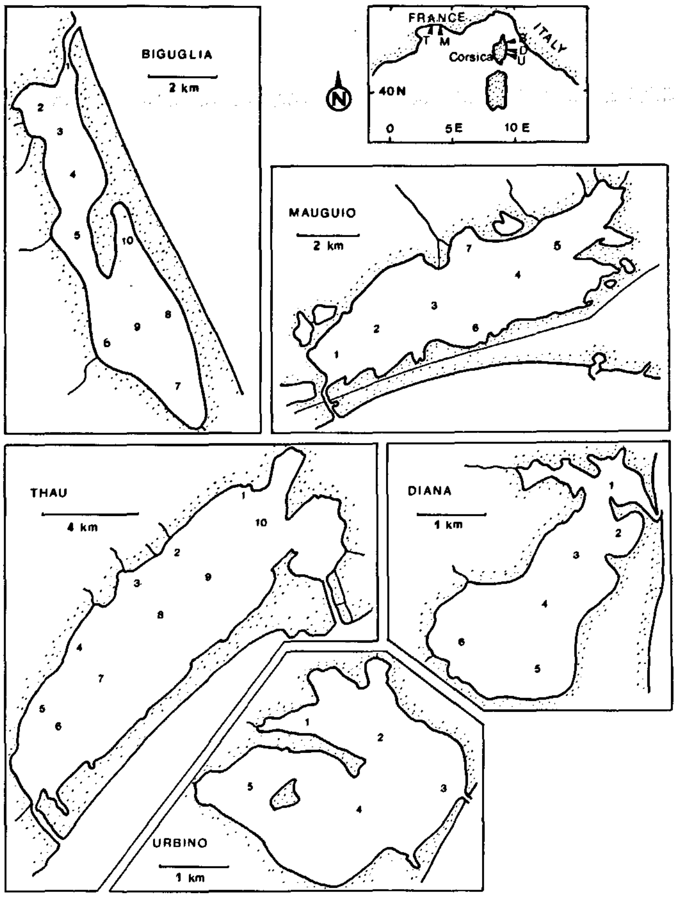

Figure 1
Localization of the five Mediterranean lagoons: Thau (T), Mauguio (M), Biguglia (B), Diana (D) and Urbino (U). Numbers on each lagoon map refer to sampling stations.

was measured by the ^{14}C method (Steeman-Nielsen, 1952); 100 ml samples, inoculated with $H^{14}CO_3Na$ (2 μCi activity) were incubated for 4 hours *in situ* and then filtered on a 0.45 μm Sartorius filter. Filter activity was measured with a Packard 3375 liquid scintillation counter. For regression analysis, the least squares method as described in Snedecor and Cochran (1980), and the partial regression method as described in Legendre and Legendre (1980), were used.

RESULTS

Morphology, circulation and water budgets

The five lagoons considered in this study are shallow (maximum depth = 10 m; Tab. 1) and communicate with the Mediterranean Sea for either all or part of the year. Mauguio and Biguglia, the two shallowest (average dept = 1 to 2 m; Tab. 1), have poor horizontal mixing and are clearly brackish (average salinity = 10; Tab. 2). Thau, Diana and Urbino, which are deeper (average depth = 4 to 6 m; Tab. 1) and well mixed horizontally, have a salinity much closer to that of the Mediterranean Sea (33–36; Tab. 2). The two main sources of water inputs are precipitations and exchanges with the sea. The very small tidal amplitudes in the Golfe du Lion (0.14 m on the average) result in very weak residual tidal currents (less than 0.10 m/s in Thau; Audouin, 1962). The wind is therefore primarily responsible for exchanges with the sea and for water circulation within the lagoons (Armengau, Burkhalter, 1978).

Assuming that mixing is complete between lagoon and incoming sea water, salinity can be used as a tracer to evaluate annual water inputs and outputs. The data from Table 1 permit the estimation of three quantities (Tab. 2); Q_f, the water catchment input, Q_r, the direct rain input and Q_e, the evaporation output, all expressed in $m^3 . year^{-1}$, according to the set of equations:

$$Q_f = P \cdot (1 - C_{sr}) \cdot A_d = 0.4 \cdot P \cdot A_d \tag{1}$$

$$Q_r = P \cdot A_0 \tag{2}$$

$$Q_e = E \cdot A_0, \tag{3}$$

Where A_d is the water catchment area (m^2), A_o, the lagoon area (m^2), C_{sr}, the soil retention coefficient (0.6 on the average in Mediterranean regions), E, the annual evaporation ($m.year^{-1}$) and P the annual rainfall ($m.year^{-1}$). Then the annual volume of sea water (Q_s) necessary to maintain the salt balance is computed as:

$$Q_s = (Q_f + Q_r - Q_e) \cdot S_l / (S_s - S_l), \tag{4}$$

where S_l and S_s are the mean salinities of the lagoon and the sea respectively. The annual output from the lagoon (Q_e) necessary to ensure the water balance is obtained as:

$$Q_l = Q_s + Q_f + Q_r - Q_e \tag{5}$$

Table 1
Morphometric data for the five Mediterranean lagoons.
Données morphométriques pour les cinq lagunes méditerranéennes.

	Lagoon area A_o ($10^6 m^2$)	Lagoon volume V ($10^6 m^3$)	Mean depth Z (m)	Maximum depth Z max (m)	Water catchment area Ad ($10^6 m^2$)	Period of communication with Mediterranean Sea (nb of months/year)
MAUGUIO	31.6	31.6	1.0	1.3	313.0	12
BIGUGLIA	14.5	21.8	1.5	1.8	166.0	6
THAU	75.0	337.0	4.5	10.0	350.0	12
DIANA	5.7	33.4	6.0	11.0	56.3	12
URBINO	7.9	38.5	5.0	9.0	23.1	2

Table 2

Meteorological and hydrological data for the five Mediterranean lagoons. Derivation of the computed quantities is given in the text.

Données météorologiques et hydrologiques pour les cinq lagunes méditerranéennes. La dérivation des quantités calculées est donnée dans le texte.

		Precipitation	Evaporation	Sea salinity	Lagoon salinity	Water catchment inflow	Direct rain inflow	Evaporation outflow	Sea-water inflow	Lagoon outflow	Water catchment influence	Sea influence	Mean residence time
		P (m/y)	E (m/y)	S*s* (%o)	S*l* (%o)	Q*f* (10⁶m³/y)	Q*r* (10⁶m³/y)	Q*e* (10⁶m³/y)	Q*s* (10⁶m³/y)	Q*l* (10⁶m³/y)	Q*f*/V (y⁻¹)	Q*s*/V (y⁻¹)	V/Q*l* (y)
MAUGUIO	1977	0.740	1.200	37.1	11.8	92.0	23.0	38.0	36.0	113	2.91	1.14	0.28
BIGUBLIA	1978	0.637	1.450	38.0	12.8	42.0	10.0	21.0	16.0	48	1.93	0.74	0.46
THAU	1976	0.750	1.200	37.5	36.7	105.0	56.0	90.0	3257.0	3328	0.31	9.66	0.10
	1977	0.742	1.200	37.1	33.9	104.0	56.0	90.0	744.0	814	0.31	2.21	0.41
	1978	0.727	1.093	36.6	35.1	101.0	55.0	82.0	1721.0	1795	0.30	5.11	0.19
	1979	0.886	1.130	37.4	33.2	124.0	66.0	85.0	832.0	937	0.37	2.47	0.36
DIANA	1976	0.806	1.450	38.0	35.8	18.0	4.6	8.2	237.0	252	0.54	7.14	0.13
URBINO	1978	0.942	1.450	38.0	32.9	8.7	7.4	11.5	28.4	33	0.20	0.74	1.17

R.N.O. data

These estimates are not very precise when lagoon and sea salinities are very close, as in Thau and Diana, since the relative error on Q_s is large when $(S_s - S_l)/S_l$ is small. Other potential sources of errors include the use of the same average soil retention coefficient ($C_{sr} = 0.6$) for all lagoons and the variability of the annual rainfall over each water catchment. However, the only existing field measurement of exchanges volumes between a lagoon (Thau) and the Mediterranean Sea provides a range for Q_l from 800 to 1200 $10^6.m^3.year^{-1}$ for 1979 (Armengau, pers. comm.), a figure quite comparable to our estimate (937 $10^6.m^3.year^{-1}$; Tab. 2). The water residence time (computed as V/Q_l, where V is the lagoon volume in m^3; Tab. 2) permits a distinction between closed systems with an average residence time of a year, such as Urbino, and opened systems, where the average residence time is only a few months, which may be under the dependence of either the water catchment (Mauguio, Biguglia) or the sea (Thau, Diana).

Nutrients

Only oxydized nutrient forms, *i.e.* nitrates and phosphates, have been collected over all the lagoons. Measurements of the reduced forms in some lagoons indicate however that, on an annual average basis, oxydized forms dominate the dissolved inorganic fractions: 74% for $N\text{-}NO_3$ and 70% for $P\text{-}PO_4$ (Frisoni, 1984).

Mean nutrient levels inside the lagoons can be very high: for example $N\text{-}NO_3$ can reach 15 µg-at.l^{-1} in Mauguio and $P\text{-}PO_4$, 1.5 µg-at.l^{-1} in Thau. These levels are determined by the dilution of land inputs of high nutrient concentration by marine inputs of low nutrient concentration. In nearshore waters, mean annual concentrations range from 1 to 3 µg-at.l^{-1} for $N\text{-}NO_3$ and from 0.2 to 0.6 µg-at.l^{-1} for $P\text{-}PO_4$ (RNO, 1980) resulting in low N/P ratios (5:1). Water catchment inputs are two fold. The bulk of rainy season inputs comes from leaching of the watersheds occupied by agriculture (vineyards), providing essentially nitrates at typical concentrations of 100-200 µg-at.l^{-1} $N\text{-}NO_3$ in tributaries (Frisoni, 1984). During the dry season, urban wastes, which are important only for Mauguio, Biguglia and Thau, are the main sources of outside nutrients; they bring ammonia, dissolved organic nitrogen and especially phosphates.

As a consequence, one may expect average annual nitrate concentrations in the lagoons to be related to the annual nitrogen input which originates mainly from the watershed and can thus be taken as proportional to the water catchment area (A_d), divided by the lagoon volume (V) and corrected for dilution by the residence time (V/Q_l; Fisher *et al.*, 1979), such that:

$$N\text{-}NO_3 = k_N . A_d . 1/V . V/Q_l + N\text{-}NO_{3\,0} \qquad (6\ a)$$

Which may be rewritten as:

$$N\text{-}NO_3 = k_N . A_d/Q_l + N\text{-}NO_{3\,0}, \qquad (6\ b)$$

Where $N\text{-}NO_{30}$ is the ordinate intercept and k_N a proportionality constant. A good correlation (Fig. 2)

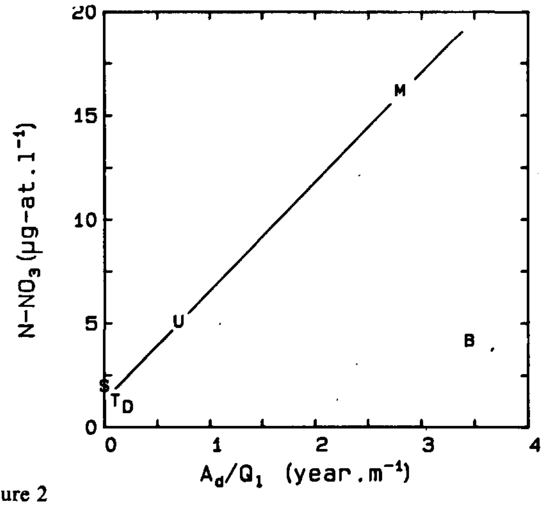

Figure 2

Mean annual nitrate ($N\text{-}NO_3$) concentrations vs. water catchment area (A_d) divided by the annual outflow (Q_l), for Thau (T), Mauguio (M), Biguglia (B), Diana (D), Urbino (U) and the Mediterranean Sea (S). The straight line was drawn by inspection.

Moyennes annuelles de la concentration de nitrates ($N\text{-}NO_3$) en fonction de l'aire du bassin versant (A_d) divisée par le débit annuel quittant l'étang (Q_l) pour Thau (T), Mauguio (M), Biguglia (B), Diana (D), Urbino (U) et la mer Méditerranée (S). La ligne droite a été tracée par inspection.

is observed if Biguglia is not included: in the latter lagoon the sampling scheme missed the rainy periods, when nitrate inputs are very important (Frisoni, 1984), and thus the nitrate concentration may have been underestimated. Similarly to what has been observed in Lake Washington (Edmondson, Lehman, 1981), waste water nitrogen does not seem to affect nitrate economy in these lagoons: Thau, which is largely urbanized, has even lower $N\text{-}NO_3$ concentrations than the sea (Fig. 2).

In contrast, phosphate concentrations (Fig. 3) seem related to the mean annual population (Pop = 4/12 summer population + 8/12 winter population), which can be taken as a rough measure of waste water inflows, such that:

$$P\text{-}PO_4 = k_p . \mathrm{Pop} + P\text{-}PO_{4\,0}, \qquad (7)$$

Where $P\text{-}PO_{40}$ and k_p have the same meaning as $N\text{-}NO_{30}$ and k_N in equations (6). The good fit observed and the absence of correction for flushing, in contrast to nitrates, indicate that phosphorus might enter the lagoons in particulate form and settle rapidly or that, alternatively, it might be immediately assimilated by phytoplankton.

In equations (6) and (7), $N\text{-}NO_{30}$ and $P\text{-}PO_{40}$ are very close to the marine concentrations, reflecting the importance of marine inputs for lagoons which receive neither water catchment nor urban inputs.

Phytoplankton productivity

Annual areal productivity of the Mediterranean lagoons is very high ranging from 100 to 300 $gC.m^{-2}.year^{-1}$. Daily production amounts up to as much as 4 $gC.m^{-2}.d^{-1}$ in Mauguio. In terms of seasonal variations (Fig. 4), some lagoons (Mauguio, Biguglia) reach a maximum of productivity during spring while others (Thau, Diana, Urbino) do so during summer. This parallels the morphological differences between lagoons (*see* above). The timing of maximum productivity depends upon nutrient availability and competition for nutrients. For example, Mauguio and Biguglia, which are shallow and water catchment dependent, have their maximum of phytoplankton productivity in the spring, when nutrient inputs are high, and their minimum in the summer, when phytoplankton compete with macrophytes for nutrients (Denizot, Riouall, 1979). On a finer time scale (Fig. 4: Thau), short successive blooms, probably linked to the high nutrient levels (Kalff, Knoechel, 1978) encountered in the lagoons, are observed.

Diatoms and dinoflagellates dominate the microphytoplankton while dinoflagellates, cryptophycae and chrysophycae are the main components of the nannoplankton. Marine influence is favorable to centric diatoms, while pennate diatoms of periphytic and benthic origin are important in areas influenced by fresh water and in shallow lagoons. Dinoflagellates favor areas which either receive freshwater inputs, or have low renewal rates (Urbino). Species which bloom have in general a marine origin: diatoms (*Skeletonema costatum*, *Asterionella japonica*, *Nitzschia* sp.) during winter, dinoflagellates (*Exuviella compressa*, *Gymnodinium nelsoni*) and small flagellates during summer. On a finer time scale, the relative abundance of these groups oscillates (Fig. 5) in parallel with productivity (Fig. 4).

DISCUSSION

In lakes, empirical relationships have been established between biological, chemical and physical variables (Smith, 1979; Lund, 1970; Nichols, Dillon, 1978; Schindler, 1978). Do the same relationships apply to lagoons and, if not, how do the differences between lagoons and lakes reflect their respective specificities?

In order to answer these questions, we used regression analysis to determine the relations existing between the annual mean values of five parameters (productivity, chlorophyll, $N\text{-}NO_3$, $P\text{-}PO_4$ and salinity) over the complete set of the sampled stations (Tab. 3). Six simple determination coefficients and only two partial ones are significant at the one per cent level. This indicates that some of the relations which appear to exist between two parameters after a simple regression analy-

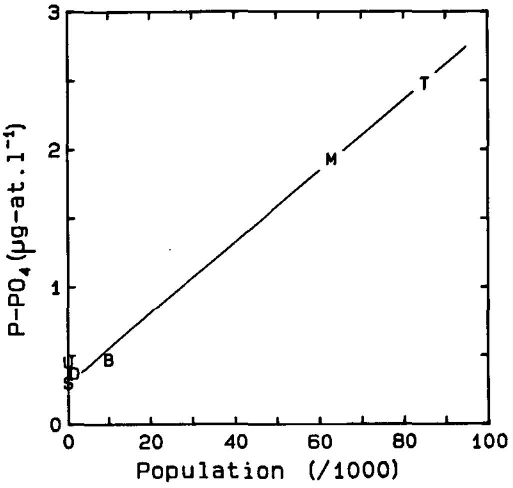

Figure 3
Mean annual phosphate ($P\text{-}PO_4$) *concentration vs. mean population on the water catchment. Symbols as in Figure 2.*

Moyenne annuelle de la concentration de phosphates ($P\text{-}PO_4$) en fonction de la population moyenne sur le bassin versant. Les symboles sont identiques à ceux de la figure 2.

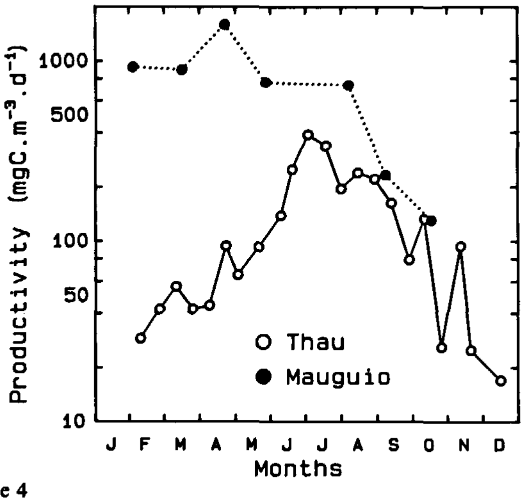

Figure 4
Seasonal evolution of the mean primary productivity in Thau (solid line) and Mauguio (dashed line) lagoons.

Évolution saisonnière de la production primaire moyenne dans les étangs de Thau (ligne continue) et de Mauguio (ligne pointillée).

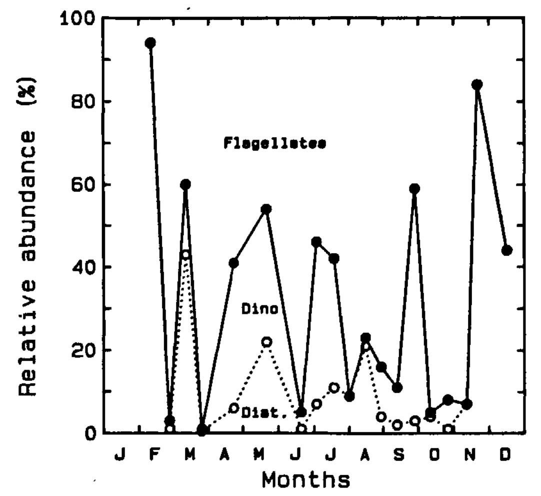

Figure 5

Seasonal evolution of the cumulated relative abundances of diatoms (diat.), dinoflagellates (dino.) and small flagellates in Thau lagoon.

Évolution saisonnière des abondances relatives cumulées des diatomées (diat.), dinoflagellés (dino.) et petits flagellés (flagellates) dans l'étang de Thau.

sis are mere artefacts, resulting from a common link to a third parameter: for example, the good correlation observed between productivity and nitrates results from their common link to biomass. The emerging pattern correlates productivity to chlorophyll; the latter is in turn correlated to nutrients. Productivity appears moreover to be an inverse function of salinity.

A plot of the mean annual productivity versus chlorophyll at each station (Fig. 6) reveals that Mauguio has a much lower photosynthetic rate (defined as the ratio productivity/chlorophyll) than the other lagoons, while sustaining a much higher biomass. A linear regression analysis for the two sets of stations brings:

$$\text{Mauguio:Prod} = 12.\text{Chl} - 33 \quad r^2 = 0.89\ (P = 0.01) \qquad (8)$$

$$\text{Others:Prod} = 104.\text{Chl} - 28 \quad r^2 = 0.78\ (P = 0.01), \qquad (9)$$

where Prod represents the primary productivity, Chl the chlorophyll (mg.m^{-3}). The low photosynthetic rate of Mauguio might result from its high biomass which induces self-shading (Smith, 1979) and from a limitation by temperature and light in winter and early spring (Bruno *et al.*, 1979; Parsons *et al.*, 1977), periods of maximum productivity in Mauguio. It is interesting to compare these data for lagoons with lacustrine and marine data. In freshwater lakes (Fig. 6, dashed line), Smith (1979), using data from the growing season, found that:

$$\text{Prod} = 22.9.\text{Chl} - 42.6 \quad r^2 = 0.81. \qquad (10)$$

Freshwater lakes thus appear to have an average photosynthetic rate five times lower than the Mediterranean lagoons under study, Mauguio excluded (equation 9). For marine temperate waters, Parsons *et al.* (1977) indicate values for assimilation numbers (Pmax) ranging from 1.5 to 6 $\text{mgC.mgChl}^{-1}.\text{hour}^{-1}$. A reasonable estimate for the maximum daily photosynthetic rate is thus 72 $\text{mgC.mgChl}^{-1}.\text{year}^{-1}$, assuming an assimilation number of 6 maintained for 12 hours. This figure is smaller than the mean photosynthetic rate for lagoons in equation (9). The Mediterranean lagoons thus appear to have a very good photosynthetic efficiency, on the average, when compared to both lakes and marine waters. This could result from an increase in photosynthetic capacity at low salinities for some species (Quasim *et al.*, 1972) and from a more intense cycling of nutrients in lagoons than in lakes and oceans due in particular to sediment proximity (Nixon, 1982).

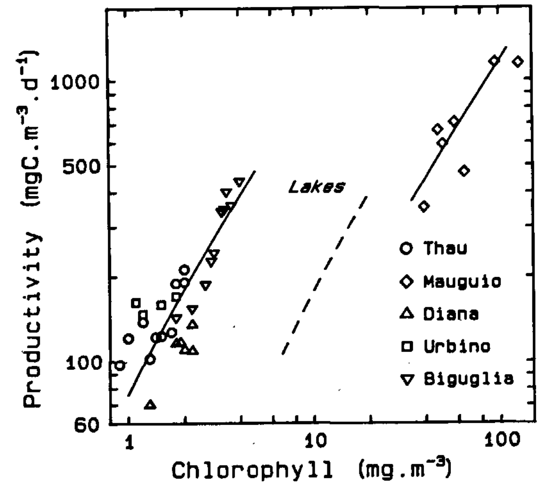

Figure 6

Mean annual primary productivity vs. mean annual chlorophyll concentration at each station. The two solid lines are for Mauguio (equation 8 in text) and for the other lagoons (equation 9). The dashed line is from Smith (1980) for freshwater lakes (equation 10).

Moyenne annuelle de la production primaire en fonction de la concentration en chlorophylle à chaque station. Les deux lignes continues correspondent respectivement à Mauguio (équation 8 dans le texte) et aux autres lagunes (équation 9). La ligne pointillée a été établie par Smith (1980) pour les lacs d'eau douce (équation 10).

Table 3

Simple (lower half matrix, d.f. = 35) and partial (upper half matrix – d.f. = 32) determination coefficients computed for the five measured parameters. Correlation sign is given within brackets.

Coefficients de détermination simple (demi-matrice inférieure, degrès de liberté = 35) et partielle (demi-matrice supérieure, degrés de liberté = 32) calculés pour les cinq paramètres mesurés. Le signe de la corrélation est indiqué entre parenthèses.

	Productivity	Chla	N-NO$_3$	P-PO$_4$	Salinity
Productivity		0.79$^{\Delta}$	0.02	0.12	0.17$^{\nabla}$
Chla	0.88$^{\Delta}$ (+)		0.18$^{\nabla}$	0.24$^{\Delta}$	0.07
N-NO$_3$	0.55$^{\Delta}$ (+)	0.58$^{\Delta}$ (+)		0.04	0.12
P-PO$_4$	0.01 (+)	0.07 (+)	0		0.02
Salinity	0.42$^{\Delta}$ (–)	0.28$^{\Delta}$	0.38$^{\Delta}$ (–)	0.03	

$^{\Delta}r^2 \neq 0$ ($P < 0.01$)
$r^2 \neq 0$ ($P < 0.02$)

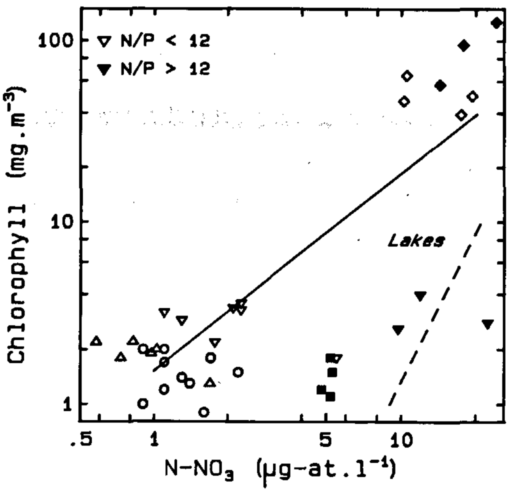

Figure 7
Mean annual chlorophyll concentration vs. mean annual N-BO$_3$concentration at each station. Symbols are as in Figure 6. The regression line takes into account stations where N-NO$_3$/P-PO$_4$ is less than 12 (open symbols). The dashed line is for lakes (Lund, 1970).

Moyennes annuelles de la concentration en chlorophylle en fonction de la concentration en N-NO$_3$ à chaque station. Les symboles sont les mêmes que pour la figure 6. La droite de régression ne prend en compte que les stations où le rapport N-NO$_3$/P-PO$_4$, est inférieur à 12 (symboles vides). La ligne pointillée a été établie par Lund (1970) pour les lacs d'eau douce.

The mean annual chlorophyll concentration at each station is clearly related to both nitrates (Fig. 7) and phosphates (Fig. 8). However in order to obtain good correlations, one must exclude all the stations where the N/P ratio is more than 12 for the chlorophyll-nitrates relationship and less than 2 for the chlorophyll-phosphates relationship (Fig. 7 and 8). This would suggest that the mean annual biomass is limited by nitrates for N/P<2, by phosphates for N/P>12 and by both for intermediary ratios. The large dispersion observed between the different stations within each lagoon (Fig. 7 and 8) indicates the importance of local effects (shore proximity, source inputs, zones of accumulation, zooplankton grazing; Harris, 1980), especially important in lagoons where horizontal mixing is poor (Mauguio, Biguglia). In several English lakes, Lund (1970) related the maximum summer biomass to the maximum winter N-NO$_3$ and P-PO$_4$ (Fig. 7 and 8: dashed lines). In comparison to lakes, lagoons seem thus to convert more efficiently nitrates, and less efficiently phosphates, to phytoplankton biomass. Since Lund's study (1970), investigations have been conducted on a larger scale for lakes (Nichols, Dillon, 1978; Schindler, 1978; Smith, 1979), but they take into account total phosphorus and nitrogen, whose concentrations are unfortunately not available for all the lagoons considered here.

As a conclusion, it might be interesting to examine some of the implications of the relationships observed between nutrient and lagoon characteristics for lagoon management. As shown above, biomass can be related to either nitrates or phosphates depending upon the value of the N/P ratio. Combining equations (6) and (7) brings:

$$\text{N-NO}_3/\text{P-PO}_4 = k_N/k_p . A_d/\text{Pop} . 1/Q_1 \qquad (11\,a)$$

$$= k . 1/D_{pop} . 1/Q_1, \qquad (11\,b)$$

where D_{pop} is the population density (habitants.m^{-2}) and k a proportionality constant. Thus if a lagoon is surrounded by dense urbanization, *i.e.* if D_{pop} is large, N/P will be low and the phytoplankton biomass will be related to N-NO$_3$. Diversion or treatment of the phosphorus-rich waste water will have little effect on biomass until a threshold is reached, such that N/P becomes larger than 12. Conversely if a lagoon receives little waste water, N/P will be high and biomass will be related to P-PO$_4$. Diversion of waste water will have then immediate effects on lagoon annual phytoplankton biomass. Paradoxically, waste water treatment and effluent diversion can be more important for lagoons which receive little waste water than for those which receive heavy loads. Nitrogen inputs are in general less manageable than phosphorus ones since they occur in dissolved form (Recknow, Simpson, 1980). In the case of lagoons, it is possible to counteract the effects of nitrogen inputs from the watershed by increasing outflow (Q_l), *i.e.* by favoring exchanges with the sea. This may however result in salinity changes and increased sedimentation, damaging to the lagoon fauna.

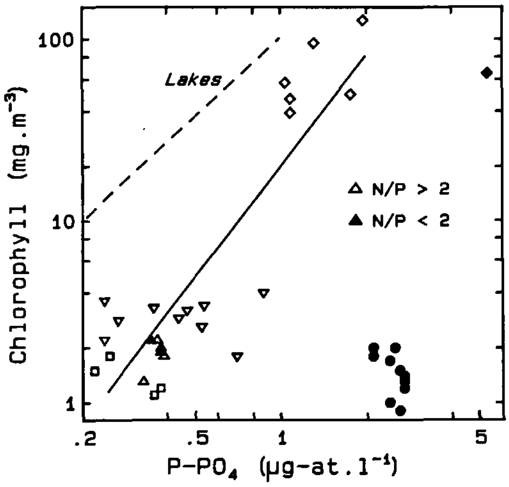

Figure 8
Annual chlorophyll concentration vs. mean annual P-PO$_4$ concentration at each station. Symbols are as in Figure 6. The regression line takes into account stations where N-NO$_3$/P-PO$_4$ is larger than 2 (open symbols). The dashed line is for lakes (Lund, 1970).

Moyennes annuelles de la concentration en chlorophylle en fonction de la concentration en P-PO$_4$ à chaque station. Les symboles sont les mêmes que pour la figure 6. La droite de régression ne prend en compte que les stations où le rapport N-NO$_3$/P-PO$_4$ est supérieur à 2 (symboles vides). La ligne pointillée a été établie par Lund (1970) pour les lacs d'eau douce.

The conclusions of this study have to be taken with a number of caveats. We only considered nitrate and phosphate forms. Both ammonia and particulate forms of nitrogen and phosphorus may be very important in lagoons (Nixon, 1982). We did not consider in details the interactions between phytoplankton and its competitors (macrophytes) and predators (zooplankton, fish), which can play a major role to regulate phytoplankton biomass (Timms, Moss, 1984). The conclusions drawn here concerning lagoon management might not be applicable to other lagoons where input conditions are different: industrial pollution, occupation of the water catchment by activities other than agriculture... Further, blooms and dystrophic crisis might be more important considerations for lagoon management than average biomass levels. For instance in Thau, the average annual biomass is not limited by $P\text{-}PO_4$; nevertheless high phosphorus levels during summer can result in large phytoplankton blooms followed by oxygen depletion and massive shellfish kills (Tournier *et al.*, 1979).

Despite these limitations the data presented in this paper illustrate the very high levels of phytoplankton biomass and productivity reached in these Mediterranean lagoons, and provide some basis to interpret the differences observed between the various lagoons in terms of nutrient loading and water residence time.

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