The spatial distribution of phytoplankton in a Mediterranean lagoon (Étang de Thau)

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ABSTRACT

A network of 63 stations situated 1 km apart was sampled on four occasions (June and October 1986, February and May 1987), to study the spatial distribution of phytoplankton in the Thau lagoon. The distribution of Chl a showed a positive gradient along the principal SW-NE axis of the lagoon over a 20 km length, levels varying from 1.0 to 1.7 mg.m^{-3} in the southwestern third, from 1.7 to 2.4 mg.m^{-3} in the middle area, and from 2.4 to 3.8 mg.m^{-3} at the mouths of the Sète channels which connect the lagoon to the Mediterranean Sea. The variations in Chl b demonstrated at times local blooms of the Chlorophyceae, but their maximal abundance was always lower than those of the diatoms. Although input from the land is low, nutrient concentrations were significantly higher than those in the Golfe du Lion, with means of 7 µM for nitrate and 1.3 µM for phosphate. The distribution of biomass was dependent both on physical forcing (wind, exchanges with the sea, exchanges with sediment) and on nutrients. The shellfish breeding zones (where the annual commercial production is about 20 000 tons of oysters) constitute a significant chlorophyll sink.

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RÉSUMÉ

Répartition du phytoplancton dans un étang méditerranéen (Étang de Thau)

Un réseau de 63 stations réparties selon un maillage carré de 1 km de côté a permis en quatre occasions (juin et octobre 1986, février et mai 1987) d'étudier la répartition spatiale du phytoplancton de l'étang de Thau. La répartition de la Chl a met en évidence un gradient positif le long des 20 km de l'axe principal SO-NE de l'étang; les teneurs varient de 1,0 à 1,7 mg.m^{-3} dans le tiers sud-ouest, de 1,7 à 2,4 mg.m^{-3} dans la partie médiane et de 2,4 à 3,8 mg.m^{-3} au débouché des canaux de Sète qui assurent la communication avec la Méditerranée. Les variations de la Chl b indiquent parfois des floraisons locales de chlorophycées dont les concentrations restent cependant inférieures à celles des diatomées. Bien que les apports du bassin versant soient faibles, les teneurs en sels nutritifs sont nettement supérieures à celles du Golfe du Lion: en moyenne 7 µM pour les nitrates et 1,3 µM pour les phosphates. La répartition de la biomasse dépend à la fois du forçage physique (vents, échanges avec la mer, échanges avec le sédiment) et des apports nutritifs. Les zones conchylicoles qui produisent annuellement 20 000 tonnes d'huîtres représentent des «puits» pour la chlorophylle.

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INTRODUCTION

The Thau lagoon (Fig. 1 *a*) covers a surface of 75 km^2 and measures 20 km at its longest and 4.5 km at its widest points. It receives very little inflow from the continent. The 35 000 hectares drainage basin possesses a single permanent stream, La Vène. The lagoon is connected to the Mediterranean Sea through a channel, the "grau de Pisses-Saumes" and mainly through the channels of the Sète harbour (mean flow rate 15 to 20 times that of the "grau de Pisses-Saumes").

The earliest studies of the phytoplankton of the Thau lagoon, performed at the beginning of the century (Pavillard, 1905), were particularly focussed on the species composition of the communities which appeared very similar to those of the neighbouring marine neritic zone. Thau lagoon is described as an ecosystem dominated by diatoms (Hénard, 1978; Laffont, 1985): *Skeletonema costatum* is the typical diatom of the winter bloom; through the other seasons, a succession of species belonging to the genera *Chaetoceros* and *Nitzchia* are found. However, nanoflagellates can also be at the origin of blooms. Dinoflagellates are also present but, even during their maximum development, they never reach a biomass comparable with that of the diatoms.

The Thau lagoon is the site of intense shellfish breeding with an annual commercial production of 20 000 tons. The previous works (Tournier *et al.*, 1982, Tournier and Pichot, 1987) relied on a small number of stations generally situated in the shellfish breeding zone, covering a third of the lagoon. The biomass of phytoplankton is often below 3 mg Chl *a*.m^{-3}; this can rise above 5 mg.m^{-3} during transient but regular winter blooms. Apart from these bloom periods, the mean chlorophyll level is maximal between May and October. The spatial distribution of the phytoplankton is not uniform, partly due to the filtration of the molluscs, and the shellfish breeding zones constitute a sink for the phytoplankton. The only measurements of phytoplankton productivity were conducted by Hénard (1978).

The primary objective of the Ecothau programme (Amanieu *et al.*, 1989) was to define the type of station-network, the timetable and the variables to be monitored in order to understand the internal processes in each trophic compartment of the food web. It is, however, evident that the repetition, on four occasions, of a network of 63 stations while analyzing 28 variables produces an exceptional quantity of information which permits an accurate description of the spatial distribution. We also examined the influence of physical factors (hydrodynamics), chemical factors (nutrients) and shellfish predation upon the distribution of the phytoplankton.

MATERIAL AND METHODS

Sampling

According to the sampling strategy (Amanieu *et al.*, 1989) four field trips were undertaken in June 1986, October 1986, February 1987 and May 1987. The 63 stations, forming a grid with stations 1 km apart (Fig. 1 *b*), were visited in the morning, within a 4-6 hour time period by three boats operating simultaneously. Samples were collected 50 cm below the surface, using Niskin bottles.

Chlorophylls

The chlorophylls were assayed using the spectrofluorometric method according to Neveux and Panouse (1987). Fluorescence was measured at six coupled wavelengths (excitation, emission) on an Aminco-Bowman spectrofluorometer. Each coupled wavelength corresponds to the fluorescence excitation and emission
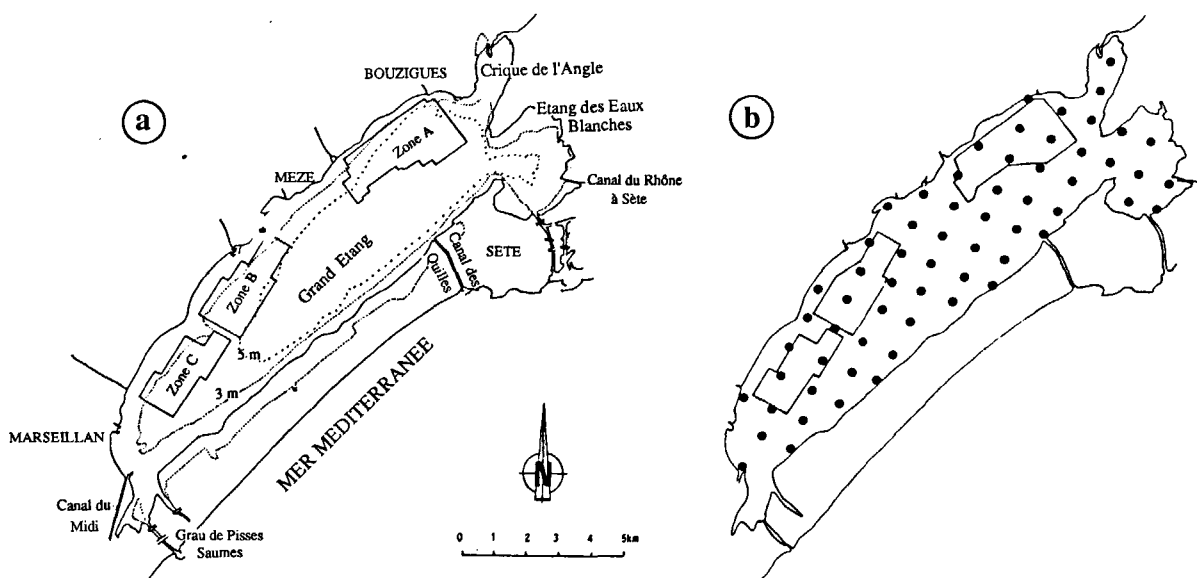

Figure 1

General profile of the Thau lagoon (1 a) and position of the 63 network stations (1 b) used in the four Ecothau field trips of 1986-1987 to determine the spatial distribution of the phytoplankton. Zones A, B and C show the shellfish breeding areas.

maxima of each pigment to be analyzed. The fluorescence data were corrected for changes in the response of the spectrofluorometer using a solid sample of phaeophytin $\searrow a$ in polymethylmethacrylate as reference. Calibration was conducted with solutions of freshly prepared purified pigments using column chromatography according to Neveux and Panouse (1987) for Chl a and Chl b and Jeffrey (1972) for Chl c. The concentrations of the standard stock solutions were determined by spectrophotometry using specific absorption coefficients of Jeffrey and Humphrey (1975) for Chl a and Chl b, and Jeffrey (1972) for Chl c (mean of Chl c_1 and Chl c_2). Phaeophytin a, phaeophytin b and phaeoporphyrin c were prepared from the corresponding chlorophylls by acidification with 1 N HCl.

Extensive precautions were taken to protect the pigments from light during the different stages of the assay. The method comprised the following steps: filtration of 50 ml through a glass-fibre membrane Whatman GF/F; manual grinding of the filter in 90% acetone, extraction at 5°C for two hours; centrifugation at 3 000 rpm for 5 minutes.

Phytoplankton populations

Species composition was analysed at 17 of the network stations (2 km grid) using Utermöhl's method.

Nutrients

Nitrates and phosphates were assayed using the Auto Analyser method (Tréguer and Le Corre, 1975) by the Laboratoire d'Hydrologie et d'Hygiène (Faculté de Pharmacie, Montpellier).

Data processing

Maps describing the distribution of different variables

We employed a numeric interpolation technique, the kriging technique (Matheron, 1962) based on time-related changes in the variance in relation to space (variogram). The variogram model which best described the information concerning the variable under study in space was used for the cartography (software package Unimap, European Software Contractors A/S). This approach produces a continuous spatial representation and also an evaluation of the variance associated with the interpolations between each sampling station.

Graphic representation of the lagoon in homogeneous zones

This was carried out using a grouping method with spatial constraints (Legendre and Legendre, 1984; Legendre, 1987; Legendre et al., 1989). The programmes employed are part of the "R" software package (Legendre, 1985). For each of the homogeneous zones, the 95% confidence interval was calculated. Here the term "homogeneous zone" is used to describe a contiguous region in space which shows statistically comparable values for Chl a.

RESULTS

Distribution of phytoplankton pigments

Chl a is representative of the total phytoplankton biomass. The relative proportions of the different chlorophylls a, b and c give an indication of the principal components of the populations present. Apart from a few Prasinophyceae which contain both Chl b and Chl c (Wilhelm et al., 1986). these two pigments are found independently in the plant kingdom. Chl b identifies green algae (Chlorophyceae, Prasinophyceae or Euglenophyceae) from all other groups (Diatomophyceae, Cryptophyceae, Dinophyceae, Chrysophyceae), which generally contain Chl c. Data interpretation was relatively complex due to various factors: the same concentrations of Chl b and Chl c were not related to the same biomass in term of Chl a. Furthermore, in
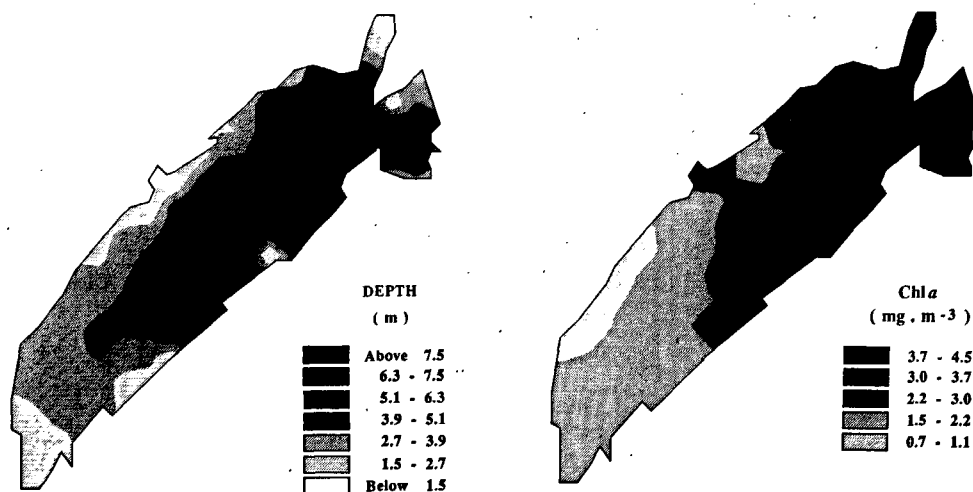

Figure 2

Bathymetry and mean spatial distribution of the phytoplankton biomass (Chl a) in the four field trips. Note the similarities between the distribution of Chl a (positive gradient SW-NE and diagonal aspect of the isopleths) and the bathymetric map.

the case of a dominance of cyanobacteria, the ratios Chl b/Chl a and Chl c/Chl a decrease, as this group does not possess accessory chlorophylls.

Chlorophyll a

The mean distribution of the surface chlorophyll (Fig. 2) reveals a positive gradient along the principal SW-NE axis of the lagoon, with isopleths crossing the axis diagonally. Levels varied from 1.0 to 1.7mg.m^{-3} in the southwestern third of the lagoon, from 1.7 to 2.4mg.m^{-3} in the middle area, and from 2.4 to 3.8mg.m^{-3} toward the "Etang des Eaux-Blanches" where the channels from Sète harbour enter the lagoon. The detailed distribution of Chl a during each field trip showed some deviations from these mean results (Fig. 3):

— in June 1986, two zones of high biomass ($>4.5 \text{mg.m}^{-3}$) appeared; one in the "parcs de Bouzigues", the other in the "Crique de l'Angle". The lagoon is cut into two equal parts by the $2 \text{mg Chl } a.\text{m}^{-3}$ isopleth;

— in October 1986, most of the lagoon is occupied by waters containing less than $2 \text{mg Chl } a.\text{m}^{-3}$, the distribution being almost identical to that given by the mean results;

— in February 1987, during the diatom bloom, high levels appeared ($>4.5 \text{mg Chl } a.\text{m}^{-3}$) near Sète and off Bouzigues;

— in May 1987, although the values were lower (between 0.7 and 2.2mg.m^{-3}), the spatial structure

persisted, forming a decreasing gradient from Sète to Marseillan. The graphic representation of homogeneous zones shows three large zones in the southwestern region of the lagoon between Mèze and Marseillan (Fig. 4). In the northeastern regions, between Mèze and Sète, four smaller zones can be identified, which points to a greater spatio-temporal variability in the biomass due to the complexity of the hydrodynamic circulation (Millet, 1989). Moreover, the highest Chl a concentrations were observed in the area of highest energy dissipation as described by Millet (1989). This was true for all of the four sampling field trips, as significant correlations were noted between values for chlorophyll a and the energy group values (Table 1).

Table 1

Correlation (Kendall levels) between the three energy zones (Millet, 1989) and chlorophyll a concentrations determined during the four sampling field trips. The value attributed to each station is that corresponding to the zone number.

Field trip	June 86	October 86	February 87	May 87	86-87
Kendall levels	0.34	0.21	0.27	0.35	0.35
Probability	$p<0.001$	$p<0.05$	$p<0.01$	$p<0.05$	$p<0.001$

In the Thau lagoon, such a positive relation is usually observed between the primary production (and consequently of the biomass) and the available external energy *i.e.* the fraction of the energy flux that does not flow through the photosynthetic path (Margalef, 1978; 1985). As the thickness of the euphotic layer is always greater than that of the mixed layer, this energy
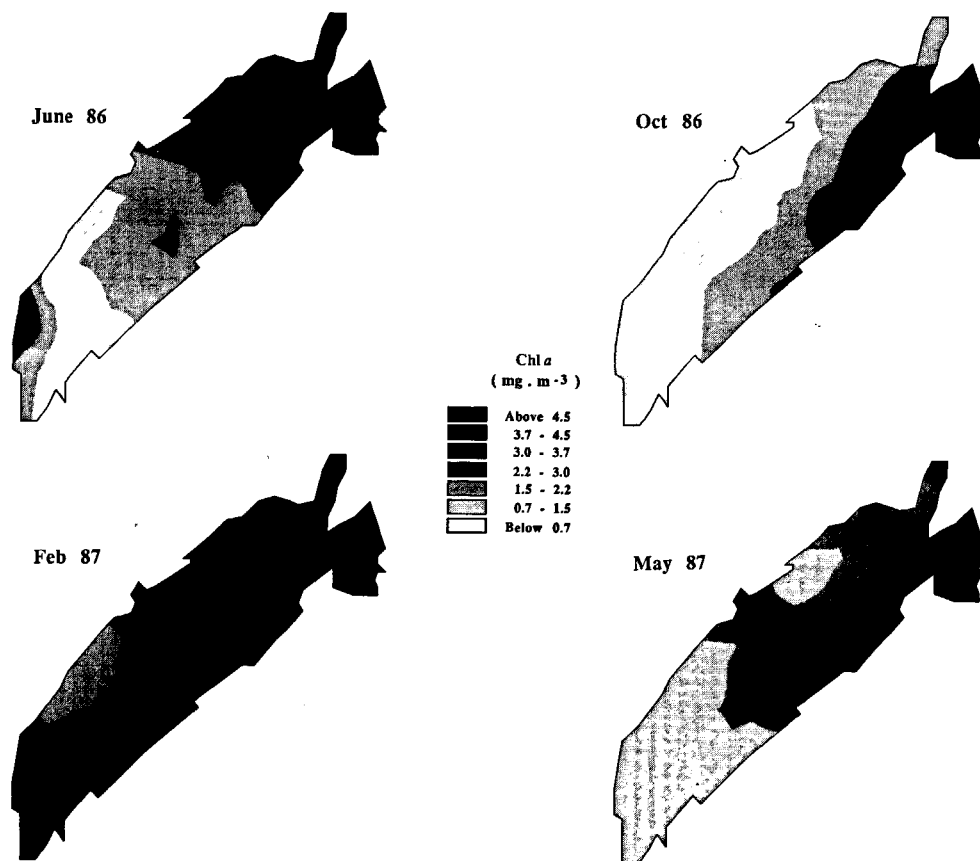

Figure 3
Spatial distribution of Chl a during each of the four field trips.

(a) — undefined zone

(1) Spatial homogeneity and variations within the lowest part of energy range
(2) Spatial homogeneity and variations within a narrow range of low energy
(3) Spatial heterogeneity and stability through the entire range of energy

(b)
2,98 ± 1,50 (n=12)
2,74 ± 1,44 (n=8)
2,40 ± 0,32 (n=56)
3,23 ± 0,26 (n=26)
1,32 ± 0,17 (n=68)
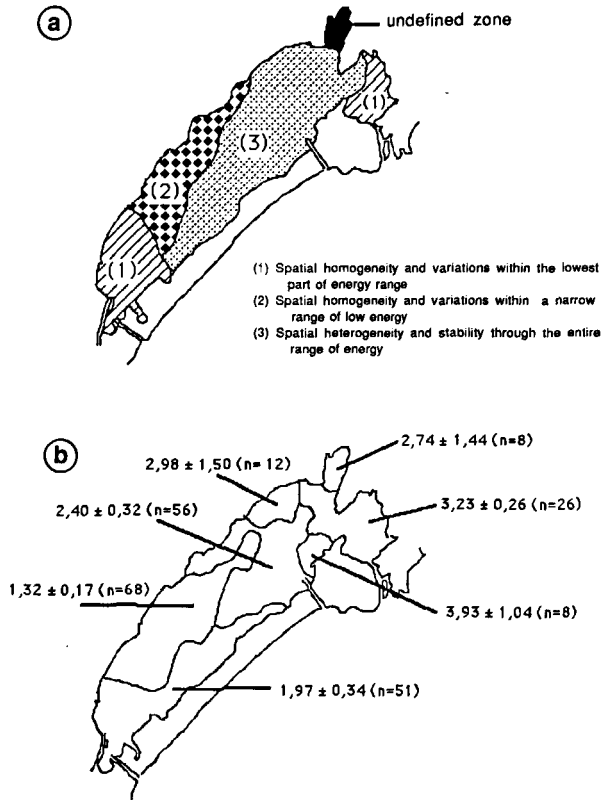3,93 ± 1,04 (n=8)
1,97 ± 0,34 (n=51)

Figure 4

Subdivision of the Thau lagoon into statistically homogeneous zones: in terms of characteristic energy levels (4a), after Millet (1989); in terms of yearly averaged Chl a after grouping through spatial contraints (4b). The values shown are the mean concentrations of Chl a $(mg.m^{-3})$ and their confidence intervals.

facilates renewal from the bottom of the nutrient supply and prevents phytoplankton sedimentation.

Pigment composition and population structure

If the four field trips are taken together, the Chl b/Chl a ratio (Fig. 5) shows a more extended range (0.00 to 0.38) than Chl c/Chl a (0.08 to 0.22). This demonstrates a high variability of the Chlorophyceae which, however, never reach a high concentration. Note that the high ratios of Chl b/Chl a generally appear when biomass is low, e. g. in May 1987 (Fig. 5).

In June 1986, the contrast is particularly marked: Chl b/Chl a ratios were close to 0.15 in the southwest of the lagoon, around 0.10 in the major part of the lagoon and only 0.02 in the "Etang des Eaux-Blanches". Conversely, the Chl c/Chl a ratio was relatively constant over most of the lagoon but gave minimal values (<0.08) in the southwest. This is in agreement with the dominance of the diatoms (*Chaetoceros laciniosus*, *Rhizosolenia setigera*) in the "Etang des Eaux-Blanches», the eastern region of the "Grand Etang" and along the barrier beach, whereas the nanoflagellates occupied the western region with a preponderance of Chlorophyceae and Cryptophyceae.

In October, the situation was not very different, with a restricted range of variations: from 0.02 to 0.17 for the Chl b/Chl a ratio and from 0.09 to 0.14 for the Chl c/Chl a ratio. The population, basically nanoplankton, was more homogeneous: Cryptophyceae dominated, accompanied by Chlorophyceae and some naked

June 86
Chl b / Chl a

Above 0.220
0.176 - 0.220
0.132 - 0.176
0.089 - 0.132
0.045 - 0.089
0.001 - 0.045
Below 0.001

Oct 86
Chl b / Chl a

Above 0.10
0.09 - 0.10
0.08 - 0.09
0.07 - 0.08
0.06 - 0.07
0.05 - 0.06
Below 0.05

Feb 87
Chl b / Chl a

Above 0.018
0.015 - 0.018
0.011 - 0.015
0.008 - 0.011
0.004 - 0.008
0.001 - 0.004
Below 0.001

May 87
Chl b / Chl a

Above 0.275
0.247 - 0.275
0.219 - 0.247
0.191 - 0.219
0.163 - 0.191
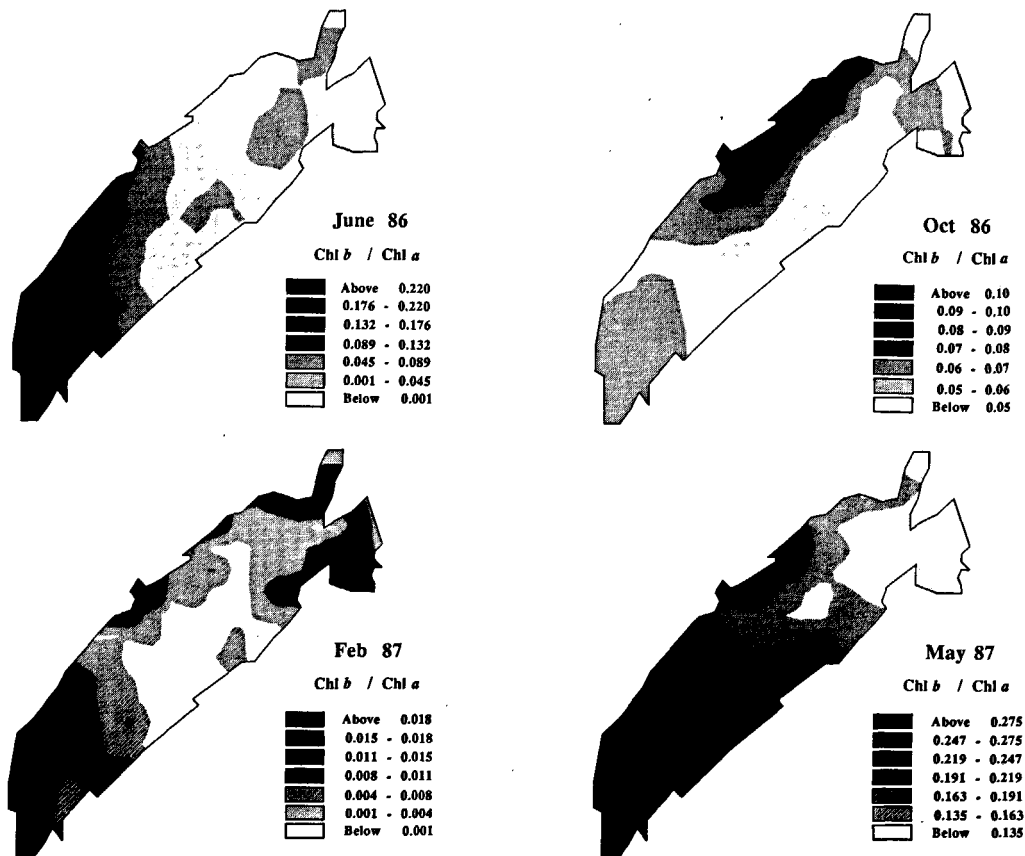0.135 - 0.163
Below 0.135

Figure 5

Spatial distribution of the Chl b/Chl a ratio during each of the four field trips.

dinoflagellates belonging to the genera *Amphidinium* and *Gymnodinium*.

The field trip undertaken in February 1987 revealed low levels of Chl *b*; the Chl *b*/Chl *a* ratio was very low, but significant (0.04 to 0.07) at only five stations, principally found at the edges of the lagoon. An analysis of the populations showed blooms of the diatom *Skeletonema costatum* throughout the lagoon, except in a few peripherical zones.

Finally, in May 1987, the situation was reversed, with relatively high concentrations of Chl *b*. Throughout the lagoon, the Chl *b*/Chl *a* ratio was above 0.10, and above 0.20 in the "parc" zones and along the coast, reaching a maximum of 0.38. Minimum values were noted in the "Etang des Eaux-Blanches". Population characteristics were very similar to those observed in June 1986, though the mixed population of nanoflagellates covered a larger area; *Chaetoceros laciniosus* dominated, especially in the northeastern region of the lagoon.

Interpretation of the spatial distribution

The distribution of phytoplankton biomass in the lagoon results from interactions between various physical (climatology, hydrodynamics, light), chemical (nutrients, pollutants), and biological (algal growth rate, grazing rate by herbivores, mineralization by bacteria) factors.

Physical variables

Phytoplankton, which float freely in the water and are able to respond to any exterior stimulation because of rapid turnover, are directly dependent on solar energy (photosynthesis) and auxiliary energy sources (temperature, wind, turbulence) derived from it.

In this study, we employ a model of the circulation within the lagoon and exchanges with the sea. These factors are themselves dependent on meteorological conditions such as wind and barometric pressure. As tides are virtually insignificant in the Mediterranean Sea, the only influence related to the sea level may stem from storm-surges occurring during very strong and long lasting gales of onshore winds; this being an uncommon event, the only forcing source of energy taken into account in the hydrodynamic model of Mil-

let (1989) has been the wind. Instead of the normal outputs of this model, which are the water-level elevation field and the velocity field over the basin, we have used the spatial distribution of the non-directional term $H^2 V^2$ defined in each mesh of the grid as the product of two factors: the squared local depth and the squared mean over the whole column of the water velocity. Owing to the factor V^2, the term $H^2 V^2$ is representative of the cinetic energy with a strong influence of bathymetry; the dimensions of this term are $L^4 . T^{-2}$ *i.e.* $m^4 . s^{-2}$ according to the international system of units, but we have used the MKS notation throughout this paper for the sake of simplicity.

From a climatic point of view, the year in which the study was carried out can be considered as normal with 41% of total winds in the NW and 24% in the E. These values are similar to the mean values determined over a 24-year period (Millet, 1989).

Currents, winds and exchanges with the sea influence the plankton in two ways:

— by acting on the spatial distribution: input and output of biomass through the "grau" (channel), vertical stratification or homogenization, creation of poor or rich phytoplankton zones,

— and by modulating production: through turbulence, which, apart from its mechanical action, modifies the quantity of light received by the algae. Due to the shallow depth of this lagoon this effect is obviously less pronounced than in deep water, but the decrease of light penetration is further reduced because turbulence also brings the sediment back into suspension;

through modifications in nutrient supply, either by input from the sea enriched with waste from Sète harbour, remineralization from the sediment, or changes in land-derived inputs during periods of rain. To understand fully the effects of physical factors on the distribution of phytoplankton, it is necessary to analyse the climatic and hydrologic (tides, atmospheric pressure, rainfall) conditions in the periods just prior to the sampling (Table 2).

The major part of the lagoon-Mediterranean Sea exchange takes place through the channels at Sète harbour; this "marine" influence is marked (among other signs) by the dominance of centric diatoms in the NE region of the lagoon. Due to the lack of nutrient of

Table 2

Climatic and hydrodynamic conditions during the week preceding each field trip.

Field trip 1 (17 June 1986)	— Zero rainfall
	— Moderate SE winds until the 16th, turning to NW and strengthening on the 17th.
	— Tide filling the lagoon from the 11th to 16th; the net result of exchanges in the two weeks preceding the field trip is positive: +12 million m³.
	⇒ Type of circulation not determined, on account of fluctuations and (or) insufficient wind strength.
Field trip 2 (21 October 1986)	— Considerable rainfall (150-300 mm), stopped on 20th.
	— Wind W, then NW between 18th and 20th.
	— Considerable input of seawater from 11th to 14th, with simultaneous continental input.
	⇒ Three circulation cells (Millet, 1989).
Field trip 3 (6 February 1987)	— Considerable rainfall from 2nd to 4th with 80% of monthly amount.
	— Tramontane (local dominant wind) strong W-NW from 4th to 6th.
	— Tide resulting in marked emptying of lagoon from 4th.
	⇒ Three circulation, cells.
Field trip 4 (19 May 1987)	— Very slight rainfall the 17th May.
	· — Moderate N-NW wind from 18th.
	— Filling of lagoon ceased the 11th, without marked effect on exchanges.
	⇒ Type of circulation not determined, on account of fluctuations and (or) insufficient wind strength.

Chl *a* data for the harbour waters, enrichment through the sea-lagoon flow remains hypothetical.

When there is no firmly established wind direction, as in the field trips of June 1986 and May 1987, the circulation has little effect on the distribution of Chl *a*. The cartography was different during the October and February field trips, which were preceded by W-NW winds creating three circulation cells (Millet, 1989), the first in the "Etang des Eaux-Blanches" and the other two bisecting the "Grand Etang" along its principal axis. In October, the chlorophyll isopleths followed this circulation scheme, as they were practically parallel to the barrier beach. It should, however, be noted that the positive gradient from Marseillan to Sète remains clearly visible, being based on a permanent production dynamic. The distribution observed in February under similar climatic conditions is less clear although it presents analogous trends.

Nutrients

Nutrient concentration (Picot *et al.*, in preparation) are in agreement with the mean seasonal values previously determined for the Thau lagoon (Tournier and Pichot, 1987; Hénard, 1978). Maximum levels are observed in autumn and winter for nitrates and in summer and early autumn for phosphates (Table 3). As observed for other Mediterranean lagoons (Fiala, 1972-73; Vaulot and Frisoni, 1986), the Thau lagoon waters are nutrient-rich compared with the neighbouring marine environment.

Mean phosphate concentrations are $1.3\,\mu M$ and the minimum is never below $0.2\,\mu M$, a value equivalent to the mean in Mediterranean sea water. Irrespective of the season, the spatial distribution of phosphates is relatively homogeneous (Casellas *et al.*, submitted), with a single unexplained exception: above $9\,\mu M$ to the north-east of Mèze in June 1986. On the other hand, seasonal variations in nitrate levels are considerable. In winter, concentrations are 50 to 100 times those noted in summer (Table 3). Furthermore, unlike the phosphate values, those recorded for nitrates during each trip showed a sharp SW-NE gradient. The highest concentrations were found in the "Crique de l'Angle"

Table 3

Mean nutrient levels throughout the Thau lagoon during each field trip (according to Picot et al., in preparation).

	June 86	October 86	February 87	May 87	General Mean
Nitrate (μM)	1.97	10.45	15.22	0.16	6.95
Phosphate (μM)	1.83	2.09	0.86	0.42	1.30
N/P ratio	1.08	5.00	17.70	0.38	6.04
Chl *a* (mg.m^{-3})	2.39	1.72	3.34	1.55	2.25

and in the "Etang des Eaux-Blanches", with mean concentrations between 8 and $15\,\mu M$ (Fig. 6) and maximum values of 35 to $70\,\mu M$ recorded at the mouths of the Sète channels in February 1987. Nitrates decrease progressively towards the southwest: $4\text{-}6\,\mu M$ in the central region and $2\text{-}4\,\mu M$ between Mèze and Bouzigues. The nitrogenous compounds in the lagoon probably spread from a source in the northern part, near the outlets of the various channels in the vicinity of Sète. These inputs are episodic and probably linked to
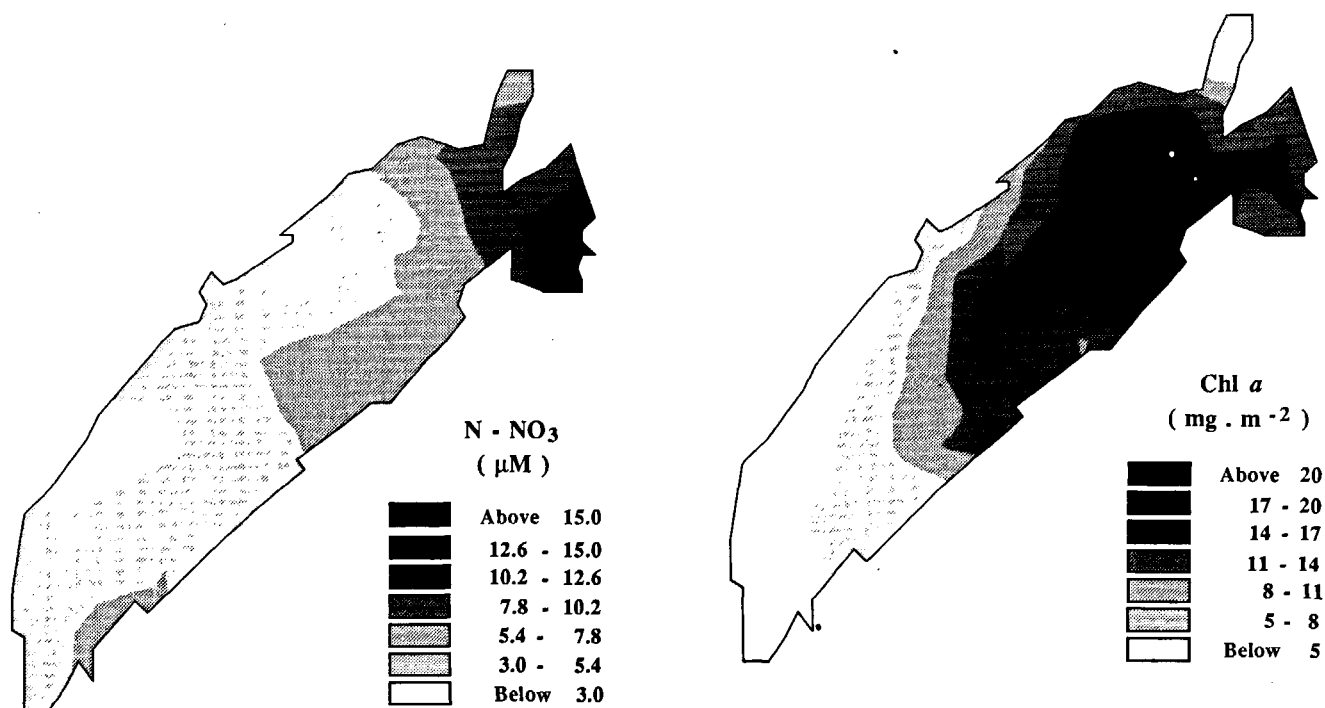

N - NO₃
(µM)

Above 15.0
12.6 - 15.0
10.2 - 12.6
7.8 - 10.2
5.4 - 7.8
3.0 - 5.4
Below 3.0

Chl *a*
(mg . m⁻²)

Above 20
17 - 20
14 - 17
11 - 14
8 - 11
5 - 8
Below 5

Figure 6

Mean spatial distribution of surface nitrate for the four field trips. Note the similarities between the increasing SW-NE gradients of nitrate and Chl a *(see also Fig. 3).*

the agricultural or industrial activities, such as the nitrogenous fertilizer plant near Sète.

The mean surface distribution of nitrates and Chl a were similar, showing a richer area in the northeastern part of the lagoon (Fig. 6), with a maximum near Sète. This phenomenon was strongest in October and February, with significant correlations between nitrate and Chl a ($r=0.38$ and $r=0.56$ respectively, $p=0.05$). Nitrogen depletion in June, illustrated by very low N/P values (Table 3) was probably the cause of the limited phytoplankton development.

Influence of shellfish breeding zones ("parcs") on the distribution of pigments

Shellfish breeding is concentrated in three zones along the north coast of the Thau lagoon (Fig. 1); zone A between Mèze and Bouzigues in the northeastern part, zones B and C between Mèze and Marseillan in the southwestern part. The Ecothau programme was designed to describe the whole of the lagoon, so the grid system employed did not favour the shellfish breeding zones. From twenty-six of the sixty-three stations influenced by the parcs, only eight were within the parcs themselves: four in zone A, two in zone B and two in zone C. In order to determine the influence of the parcs, we compared stations inside them with adjacent ones.

Mean chlorophyll concentrations within the parcs (Table 4) were 8 to 31% lower than those in adjacent stations. Overall, the three shellfish breeding zones

Table 4

Mean levels of Chl a ($mg.m^{-3}$) in the shellfish breeding zone. This table gives the mean value for each zone during each field trip (columns 1 to 4) and for the four field trips taken together (column 5). Zone A is in the NE part of the lagoon, zones B and C in the SW. It should be noted, as a reference, that mean Chl a concentrations for the entire lagoon were between $1.55\,mg.m^{-3}$ in May 1987 and $3.34\,mg.m^{-3}$ in February 1987, the mean value for the four field trips being $2.25\,mg.m^{-3}$. The value in brackets is the coefficient of variation.

	06/86	10/86	02/87	05/87	86-87
Breeding zone A					
Parc	3.87	0.79	3.82	0.85	2.33
	(38)	(22)	(28)	(31)	(76)
Adjacent areas	3.21	1.54	4.09	1.73	2.64
	(56)	(79)	(30)	(43)	(68)
NE lagoon	2.95	1.92	3.91	1.65	2.61
	(47)	(78)	(23)	(39)	(56)
Breeding zone B					
Parcs	1.06	0.34	1.56	0.80	0.94
	(15)	(5)	(1)	(22)	(49)
Adjacent areas	1.62	0.75	1.92	1.21	1.37
	(23)	(23)	(15)	(11)	(39)
SW lagoon	1.56	1.17	2.66	1.23	1.68
	(64)	(69)	(33)	(67)	(64)
Breeding zone C					
Parcs	0.81	0.73	2.12	0.92	1.14
	(1)	(24)	(13)	(28)	(53)
Adjacent areas	1.81	0.67	2.82	0.80	1.57
	(106)	(36)	(31)	(38)	(89)
SW lagoon	1.56	1.17	2.66	1.23	1.68
	(64)	(69)	(33)	(67)	(64)

presented values 13 to 25% lower than those in the rest of the lagoon. There were, however, some exceptions: see, for example, zone A in June 1986. It is interesting to follow changes in the pigment ratios within and outside the parcs as this indicates which phytoplankton

group was dominant. The stations within the parcs generally gave ratios Chl b/ Chl a 15 to 30% higher than those in adjacent area; the same kind of results were noted when comparing the shellfish breeding zones with the rest of the lagoon (Table 5). This effect was not noted in February, as there was a total disappearance of Chl b in zone A as well as in the northeastern part of the lagoon. Elsewhere, the ratio was only slightly higher (<0.06). The shellfish breeding zones are characterized by a lower energy hydrodynamic environment which could favor flagellate species (Chlorophyceae, in the case of the Thau lagoon) because of their greater capacity to resist sedimentation (Sournia, 1982).

Table 5

Chl b/Chl a ratio within and outside the parc zones.

	06/86	10/86	02/87	05/87	86-87
Breeding zone A					
Parcs	0.02	0.08	0.00	0.23	0.09
Adjacent areas	0.03	0.08	0.00	0.17	0.07
NE lagoon	0.04	0.07	0.00	0.19	0.07
Breeding zone B					
Parcs	0.08	0.09	0.01	0.31	0.12
Adjacent areas	0.08	0.06	0.00	0.23	0.09
SW lagoon	0.11	0.06	0.01	0.24	0.11
Breeding zone C					
Parcs	0.21	0.07	0.03	0.31	0.15
Adjacent areas	0.19	0.06	0.01	0.27	0.13
SW lagoon	0.11	0.06	0.01	0.24	0.11

DISCUSSION AND CONCLUSION

The pigment ratios give a biochemical image of the taxonomic composition and underline the heterogeneity of the distribution of phytoplankton in the Thau lagoon. Centric diatoms, indicative of either a direct supply of nutrients (new production) or a marine "importation" via the channels of Sète, dominate in the "Etang des Eaux-Blanches", and invade to a greater or lesser extent the "Grand Etang". Conversely, in the shallower and more continental areas, the phytoplankton assemblage is dominated by small forms, the nanoplankton generally indicating rapid recycling of mineral elements.

The Thau lagoon appears to be separated into two parts by a diagonal demarcation line:
— to the southwest, a shallow zone of low energy presents a low biomass and a high Chl b/Chl a ratio (>0.15);
— to the northeast, a deep zone of high turbulent energy is the main biomass reservoir, mainly composed of centric diatoms.

This heterogeneity (increasing biomass gradient SW-NE in spite of active circulation), which was not expected, is a consequence of the different energy ranges involved. For each of the four field trips, there is a significant positive correlation between the levels of Chl a and energy values ($H^2 V^2$) (Millet, 1989). The northeastern third of the lagoon (characterized by four small homogeneous chlorophyll zones which demon-

strate the high spatio-temporal variability involved) receives the highest quantity of energy and contains the major part of the biomass. On the other hand, the southwestern two-thirds of the lagoon receives less energy and are divided into three chlorophyll zones, more homogeneous and oligotrophic.

This distribution influences the growth of filter feeders; the most productive shellfish breeding zone lies in the area of high chlorophyll supply through the general circulation. Owing to the consumption of the phytoplankton by the shellfish, there is a chlorophyll sink in these zones with chlorophyll levels often reduced by 50%. One can infer that mollusc filtration mainly selects for diatoms whose dimensions are above $10 \mu m$, resulting in a relative "excess" of smaller phytoplankton. Recent data (Neveux, unpublished) show that phytoplankton species smaller than $1 \mu m$ (Chlorophyceae) can constitute more than 45% of the total biomass in the parc zones. The effects of shellfish predation can also be observed in terms of stability of biomass (Dajoz, 1974), the coefficients of variation being generally lower within than outside the parcs (Table 4).

The abundance of bivalves leads to physico-chemical modifications in the environment which constitute a favorable factor for the phytoplankton:

— either indirectly, the feces and pseudo-feces enrich the sediment in organic matter, a fraction of which (mineralized or not) returns into the water column;

— or directly, the bivalves liberate mineral nitrogen and phosphorus compounds in different degrees of oxidation and also organic molecules such as taurin which is excreted in significant quantities and used preferentially by the microflagellates (Vincendeau, 1986).

These phenomena concerning the enhancement of the primary productivity of plankton and microphytobenthos in waters containing shellfish, are now fully elucidated. (Robert et al., 1982). From measurements of the excretion of ammonia carried out in the oyster *Crassostrea gigas* of the Thau lagoon, it can be estimated that the population of 20000 tons excretes approximately 750 kg of ammonium nitrogen every year (Outin et al., submitted). This, however, is a closed circuit: ingestion of phytoplankton by the filterers ⇒ excretion of nitrogen — and phosphorus-containing molecules ⇒ increase in phytoplankton productivity. The potential of the lagoon in terms of biomass is certainly better indicated by the external sources of nutrients, namely nitrogen compounds which constitute the principal limiting nutrient.

In the Thau lagoon, the nutrient input has its principal source in the northeastern part: the "Crique de l'Angle" and — above all — Sète harbour. It seems likely that the high winter and spring concentrations of nitrogen are the result of the degradation of organic material of urban and harbour origin.

This study confirms the existence of gradients in chlorophyll and nutrient distributions; they illustrate the extent to which the Thau lagoon is influenced by the various nutrient inputs, the most important being those related to the marine environment through the channels of Sète harbour. Although the main fertilizing sources are generally the nutrient inputs of terrestrial origin (Dufour, 1984; Frisoni, 1987), one of the main features of the Thau lagoon is, as in most of those situated in the Mediterranean area (Guélorget & Perthuisot, 1983), the existence of a strong marine influence. Any diminution of the marine input leads to a decrease of the taxonomic diversity and an increase in the relative abundance of flagellates, mainly nanoplanktonic forms (Frisoni, 1984).

The Mediterranean lagoon ecosystem, in spite of a large diversity in terms of chlorophyll amount and species composition (Frisoni, 1984; Vaulot and Frisoni, 1986), generally displays a phytoplankton biomass higher ($> 1 \, mg \, Chl \, a . m^{-3}$) than that usually found in the neighbouring marine environment; thus the relative abundance of diatoms supports the growth of shellfish. This high chlorophyll concentration is due to the high hydrodynamic energy level and the associated high nutrient concentration: among them, nitrogen appears to be the limiting factor for phytoplankton growth in the Thau lagoon.

Acknowledgements

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