

Long term response of six diatom species to eutrophication

Diatoms Abundance Periodicity Patterns Eutrophication Diatomées

Abondance Périodicité Modèles Eutrophisation

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ABSTRACT	An investigation has been made on the abundance and annual periodicity patterns of six diatom species, using samples collected during the period 1977-1981 from Saronicos Gulf, Aegean Sea. The data comprised counts of the species Chaetoceros affine, Chaetoceros curvisetum, Chaetoceros didymum, Rhizosolenia fragilissima, Rhizosolenia stolterfothii, and Skeletonema costatum in samples collected from eutrophic and oligo- trophic waters. The frequency distribution for abundance and the autocorrelation analysis were used for explaining the intraspecific and interspecific differences in growth and annual periodicity patterns of the above species. It is postulated that this procedure can be followed for defining on a quantitative basis the sensitivity of phytoplanktonic species to water enrichment.
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RÉSUMÉ	Réaction à long terme de six espèces de diatomées à l'eutrophisation
	Une étude a été faite sur les modèles d'abondance et de périodicité annuelle de six espèces de diatomées, en se servant d'échantillons récoltés pendant la période 1977-1981 dans le Golfe Saronique de la Mer Égée. Les données correspondant aux espèces <i>Chaetoceros affine, Chaetoceros curvisetum, Chaetoceros didymum, Rhizosolenia fragilis-</i> <i>sima, Rhizosolenia stolterfothii,</i> et <i>Skeletonema costatum</i> provenant d'eaux eutrophiques et oligotrophiques. Les analyses de la fréquence de distribution sur l'abondance et l'autocorrélation ont été utilisées pour expliquer les différences intraspécifiques et interspécifiques sur les modèles d'abondance et la périodicité annuelle de ces espèces. Nous en concluons que ce procédé peut être utilisé afin de définir sur une base quantitative la sensibilité des espèces phytoplanctoniques envers l'enrichissement de l'eau.
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INTRODUCTION

Our understanding of eutrophication is mainly derived from information about the impact of water enrichment on the community structure. Common criteria for evaluation of the phytoplankton response to changes in the trophic nature of the marine environment are indices that utilize population size classes (Eppley, Weiler, 1979), production rates (Hooper, 1969) and species diversity (Cook, 1976).

The information concerning the ecological effects of the enrichment process on each of the component species of a phytoplanktonic community is scanty (Hooper, 1969; Kilham, Kilham, 1980). The essential problem is the identification of those members of the population that are most sensitive to eutrophication and have suffered essential changes in abundance or seasonality. A few reports on the relationship between algal species and water quality in freshwater environment (Palmer, 1969; Williams, 1972) are based on empirical experience.

The main objective of this investigation is to present and interpret a series of five-year data for abundance and periodicity of six diatom species grown in eutrophic and oligotrophic waters of the marine environment. Two different approaches have been used for the analysis of the data. First, log-normal statistics are applied for the analysis of the frequency distribution for abundance of the examined species (Cassie, 1962).

The second analysis consists of the use of autocorrelation technique (Legendre, Legendre, 1979) which is a method of numerical analysis exploring the internal structure of a series by measuring the relationship between the successive terms of a series with a view to determining its oscillation pattern.

It is hoped that these analyses will help elucidate the long term responses of the examined species to eutrophication and furthermore that they may serve as a procedure to be followed for defining the sensitivity of phytoplanktonic species to water enrichment.

MATERIALS AND METHODS

Data presented here were collected during a series of 60 monthly cruises from January 1977 to December 1981 in the Saronicos Gulf, Aegean Sea. Two stations were occupied: one (S_1) eutrophic which was located near the sewage outfall and the second (S_3) oligotrophic lying 12 miles apart from the outfall. The topography of the stations is described elsewhere (Karydis *et al.*, 1983).

Sampling was performed by van Dorn bottle at 1 m depth where diatoms have good quantitative and qualitative representation (Ignatiades, 1969; 1979; 1983; Ignatiades *et al.*, 1983). Samples for chlorophyll *a* determinations were filtered on board through millipore (0.8 μ m pore size) filters and treated according to Strickland and Parsons (1968). The filtrates of all samples were deep frozen and analysed in the laboratory for P-PO₄ and N-NO₃ (Strickland, Parsons, 1968). Temperature and salinity were also recorded on each sampling date.

Phytoplankton samples were preserved by lugol solution and counted in an inverted microscope. Six species of diatoms were chosen for this investigation: Chaetoceros affine, Chaetoceros curvisetum, Chaetoceros didymum, Rhizosolenia fragilissima, Rhizosolenia stolterfothii, and Skeletonema costatum. These species were recorded at both stations S_1 and S_3 at almost all sampling periods. The data of cell abundances of the above species were transformed logarithmically and analysed as follows:

Frequency distribution analysis

The frequency distribution of abundance of each species was analysed by the truncated log-normal distribution model (Cassie, 1962).

It is based on the following equation (Thompson, 1951):

$$y_{r} = \frac{1}{\sigma \sqrt{(2\pi)}} \int_{\log r}^{\log (r+1)} \exp\left(-\frac{(x-\mu)^{2}}{2\sigma^{2}}\right) dx, \sum_{r=0}^{\infty} y_{r} = 1,$$

where y_r is the frequency of r counts, log (r+1) is the normalizing function (logarithms to base 10), μ is the mean and σ is the standard deviation of the parent normal distribution. The simplified maximum likelihood method of Cohen (1959) was applied for estimating. the above parameters. With these estimates, the expected frequencies were calculated and compared with the observed frequencies of the truncated sample by χ^2 (Bliss, 1967). Tests of equality of standard deviations (t-test) and homogeneity of frequencies (interaction χ^2 test) were also performed (Steel, Torrie, 1969).

Serial correlation analysis

Serial correlation analysis or autocorrelation was used to determine the oscillations in abundance of the examined species during the five year period (Legendre, Legendre, 1979). The serial correlation coefficients between the consequent abundances of each species at regular monthly intervals t=1,2...n were calculated from the following equation (Poole, 1974):

$$r_{t} = \left[\frac{n}{n-t}\right] \left[\frac{\sum_{i=1}^{n-1} X_{i} X_{i+t} - (n-t)^{-1} \sum_{i=1}^{n-t} X_{i} \sum_{i=t+1}^{n} X_{i}}{\sum_{i=1}^{n} X_{i}^{2} - n^{-1} (\sum_{i=1}^{n} X_{i})^{2}}\right]$$

where *n* is the number of observations from i=1 to *n* (where n=60), X_i is one of the observations and r_t is the serial correlation or autocorrelation.

The original data after being logarithmically transformed were tested for trend by the Kendall rank correlation test and detrended by the method of the moving averages (Legendre, Legendre, 1979). Confidence intervals were computed (Cox, Lewis, 1966) and drawn on the correlograms in order to test whether the autocorrelation is significantly different from zero. A computer programme (Davies, 1971) was used for the estimation of autocorrelation.

RESULTS

Inspection of the raw data of physical and chemical parameters showed:

1) Temperature fluctuated regularly with time whereas salinity fluctuated irregularly (Fig. 1). The ranges and means of these parameters for the 5-year period did not differ between stations (Tab. 1).

2) The eutrophic character of station S_1 is indicated by the range and mean (P-PO₄: 1.57 µg-at/l; N-NO₃: 2.05 µg-at/l) of nutrients for the 5-year period (Tab. 1). At the oligotrophic station S_3 the 5-year range and means (P-PO₄: 0.16 µg-at/l; N-NO₃: 0.49 µg-at/l) are much lower. The observed annual variations in the concentrations of nutrients at each station (Fig. 1) do not allow an exact evaluation of their fluctuation pattern in the time series.

3) The difference in nutrient levels between the experimental stations were accompanied by quantitative (Tab. 1) differences in phytoplanktonic populations. Station S_1 was richer in chlorophyll *a* concentration (mean: 5.08 mg/m³) and total cells (mean: 3.01×10^6 cells/l) in relation to station S_3 (mean chl *a*: 0.73 mg/m³; mean total cells: 2.68×10^5 cells/l).

4) The information derived from the graphical presentation of the quantitative variability with time of the species Sk. costatum, Ch. didymum, Ch. affine, Ch.



Figure 1

Raw data of temperature, salinity, phosphate and nitrate in eutrophic (S_1) and oligotrophic (S_3) waters during the period 1977-1981.

curvisetum, Rh. fragilissima and Rh. stolterfothii (Fig. 2, Fig. 3) at the two stations is quite obscure, *i.e.*, the differences in abundance levels of these species between stations as well as their fluctuation patterns in the time series are not clear. Thus, an attempt was made to interpret the series of the 5-year data for abundance and periodical variability by the log-normal distribution and the autocorrelation analysis correspondly.

The primary value of the log-normal distribution is to summarize the sample data so that any given species population may be described by a few parameters which are readily comparable with the corresponding parameters of another population.

Values of the log-normal statistics for each species and station sampled are given in Table 2. It is seen that in



Figure 2

Raw data of cell concentrations of the species Sk. costatum, Ch. affine and Ch. didymum in eutrophic (S_1) and oligotrophic (S_3) waters during the period 1977-1981.





Raw data of cell concentrations of the species Rh. stolterfothii, Rh. fragilissima and Ch. curvisetum in eutrophic (S_1) and oligotrophic (S_3) waters during the period 1977-1981.

Table 1

Range and mean of selected hydrographic and biological parameters in 1 m depth of Saronicos Gulf, during the period 1977-1981.

Station	Temperature °C	Salinity	P-PO ₄ μg-at/l	N-NO3 µg-at/l	Chl a mg/m ³	Total cells cells/l
*S ₁	12.5-27.4	36.80-38.99	0.04-13.72	0.13-9.97	0.19-32.40	1.7×10^4 -2.9 × 10 ⁷
	19.76	38.10	1.57	2.05	5.08	3.01 × 10 ⁶
*S ₃	12.8-27.6	36.80-38.90	0.01-0.56	0.01-2.18	0.07-7.01	$\overline{3.1 \times 10^{3} - 4.8 \times 10^{6}}$
	19.85	38.32	0.16	0.49	0.73	2.68 × 10 ⁵

* Both stations S₁ and S₃ had maximum depth about 40 m.

Table 2		
Log normal distributions of six diat	om species from Saronico	s Gulf Aegean Sea

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Species	Station	μ	σ	N	Ñ	χ.,	V (μ̂)	V(ớ)	df	χ²	$P(\chi^2)$
Chaetoceros	S ₁	· 2.57	1.18	47	70.14	0.44	0.29	0.079	5	3.62	0.60
affine	S ₃	2.96	0.82	47	54.23	1.11	0.04	0.019	5	8.52	0.20
Chaetoceros	S_1	3.93	0.57	57	59.68		0.01	0.007	6	6.13	0.40
curvisetum	S_3	3.38	0.49	54	55.67		0.01	0.003	4	4.79	0.30
Chaetoceros	S ₁	2.93	1.24	46	60.44	0.71	0.18	0.069	7	8.95	0.20
didymum	S ₃	2.98	0.69	46	47.30	1.93	0.01	0.008	4	0.60	0.95
Rhizosolenia	S ₁	3.00	1.20	56	71.31	0.80	0.12	0.046	6	6.45	0.40
fragilissima	S ₃	2.85	0.94	56	60.09	1.49	0.02	0.011	6	3.56	0.70
Rhizosolenia	S_1	2.68	0.62	49	58.07	1.02	0.03	0.012	4	6.05	0.20
stolterfothii	S_3	2.79	0.63	49	50.78	1.82	0.01	0.006	4	4.22	0.40
Skeletonema	S_1	3.30	1.63	55	70.57	0.77	0.22	0.088	10	10.02	0.40
costatum	S_3	3.17	0.91	32	35.85	1.24	0.06	0.033	6	8.69	0.20

 $\mu = \log$ mean abundance; $\sigma = \log$ standard deviation; N=total number of observed frequencies; $\hat{N} = \text{total number of expected frequencies};$ $\chi_o = \text{truncation point; } V(\hat{\mu}) = \text{variance of the mean; } V(\hat{\sigma}) = \text{variance of the standard deviation; } df = \text{degrees of freedom; } P(\chi^2) = \text{percentage points}$ of the χ^2 distribution.

all cases the frequency distribution for abundance was truncated: N (total number of observed frequencies) was always lower than \hat{N} (total number of expected frequencies). This is due to the fact that all species measurements lacked the abundance values which were smaller than some limiting value. Sampling and count-

ing errors may explain the truncated character of the frequency distribution for abundance. Values of the percentage points of the χ^2 distribution P (χ^2) ranged from 0.20 to 0.95, indicating that in all cases the lognormal distribution provided a reasonable fit to the data. The examination of the curves (Fig. 4, 5) shows

Figure 4

Frequency distributions of the species Sk. costatum, Ch. affine and Ch. didymum in eutrophic (S_1) and oligotrophic (S_3) waters during the period 1977-1981.





Figure 5

Frequency distributions of the species Rh. stolterfothii, Rh. fragilissima and Ch. curvisetum in eutrophic (S_1) and oligotrophic (S_3) waters during the period 1977-1981. also that they may likely to be a fairly adequate representation of the log-normal distribution. The area under the truncated sample curve represents the sum of frequencies for abundance of each species.

The steepness or shallowness of the curve depends on the distribution of abundance within the recorded frequencies. The parameter σ (standard deviation, Tab. 2) is a measure of the rate of decent of the curve, *i.e.*, it determines the location and the shape of the distribution (Sokal, Rohlf, 1969).

An attempt has been made to illustrate the effects of changes in the trophic environment on the shape of the log-normal curves. A comparison of the two curves (Fig. 4, 5) for each species corresponding to its growth in eutrophic (station S_1) and oligotrophic (station S_3) waters may indicate the following:

1) For species Sk. costatum, Ch. didymum and Ch. affine (Fig. 4) the growth seems to be distinctly influenced by the trophic regime. In eutrophic waters the area under the curve is wider than in oligotrophic waters and the values of σ (Tab. 2) at station S₁ and S_3 respectively are for Sk. costatum 1.63 vs 0.91, for Ch. didymum 1.24 vs 0.69 and for Ch. affine 1.18 vs 0.82 and they differ statistically (Tab. 3). Also, in eutrophic waters the curves were extended to higher abundances (up to 1.47×10^7 cells/l for Sk. costatum, 5.71×10^5 cells/l for Ch. didymum and 7.38×10^4 cells/l for Ch. affine) in contrast to the oligotrophic waters where the maximum abundance of these species decreased $(4.05 \times 10^5 \text{ cells/l} \text{ for } Sk. \text{ costatum},$ 2.26×10^4 cells/l for Ch. didymum and 3.40×10^4 cells/l for Ch. affine).

2) The differences in nutrient concentrations did not seem to affect the growth pattern of *Ch. curvisetum*, *Rh. fragilissima* and *Rh. stolterfothii* at the two stations (Fig. 5). The width of the curves (σ) does not differ statistically between stations (Tab. 3) having the values at stations S₁ and S₃ respectively for *Ch. curvisetum* 0.57 vs 0.49, for *Rh. fragilissima* 1.20 vs 0.94 and for *Rh. stolterfothii* 0.62 vs 0.63 (Tab. 2). The maximum values in cell concentrations for *Ch. curvisetum* were 5.54×10^5 cells/l (station S₁) and 1.47×10^5 cells/l (station S₃), for *Rh. fragilissima* were 2.58×10^5 cells/l (S₁) and 2.64×10^5 cells/l (S₃) and for *Rh. stolterfothii* they were 1.47×10^4 cells/l (S₁) and 1.61×10^4 cells/l (S₃).

The time variability in abundance of the examined species is given in Figure 6 and Figure 7. The graphic display of the data (correlograms) gives us a general idea of the time series and enables us to detect the presence of seasonal fluctuations. Pielou (1974) discriminated the fluctuations in time as a) regular with period of approximately constant length (periodic or oscillatory) and b) irregular or aperiodic.

The inspection of the two correlograms of each species corresponding to its growth in eutrophic (station S_1) and oligotrophic (station S_3) waters may indicate the following:

Ch. didymum

For this species the evidence is that there is a dominant oscillation of the order of 11 months at station S_1 but this information is not quite as clear for station S_3 .

Ch. affine-Ch. curvisetum

These species show similar behaviour in variability of abundance with time. At station S_1 the fluctuations of both species seem to be aperiodic. On the other hand, at station S_3 the oscillation of both species is better defined and it is on the order of 12 months.

Sk. costatum-Rh. fragilissima

These species also exhibited similar fluctuations in abundance with time. At station S_1 the abundance of both species oscillated regularly on the order of 12 months but at station S_3 it fluctuated irregularly and could be characterized as aperiodic.

Rh. stolterfothii

The pattern of fluctuations at both stations were similar with a weak evidence of an oscillation of the order of 11 months.

It must be noted that the application of the Kendall test to the raw data revealed the existence of trend (Fig. 2) in only one instance (species *Ch. affine*, station S_1) and the data for this species were detrended.

Table 3

Testing the difference of standard deviations (t-test) and the homogeneity of frequencies (interaction χ^2 test) for the six species.

		t-test	Interaction χ^2		
Species	df	t	t.05	df	χ²
Chaetoceros affine	92	4.67*	1.983	1	0.89
Chaetoceros curvisetum	109	1.11	1.982	1	0.01
Chaetoceros didymum	90	3.69*	1.983	1	0.74
Rhizosolenia fragilissina	110	1.78	1.982	1	0.44
Rhizosolenia stolterfothii	96	1.12	1. 981	1	0.23
Skeletonema costatum	85	35.75*	1.994	1	0.20

df=degrees of freedom: $\chi^2_{.05 (1)}$ =3.841; * exceeds value expected at 0.05 significance level.

DISCUSSION

The use of frequency distribution models in zooplankton ecology has been discussed by Cassie (1962) who demonstrated that the frequency for abundance (counts) of the copepod *Paracalanus parvus* fitted the log-normal distribution.

In phytoplankton ecology, log-normal statistics have been used to describe community structure (Hohn, 1961; Patrick, Strawbridge, 1963) or to define a measure of species diversity (Edden, 1971; Tett, Igna-

Figure 6

AUTOCORRELATION

the species Sk. costatum, Ch. affine and Ch. didymum in eutrophic (S_1) and oligotrophic (S_3) waters during the period 1977-1981. Dashed lines indicate the confidence interval for a probability of 0.05.



tiades, 1976). A reference to the log-normal distribution of diatom species in polluted rivers has been made by McArthur (1960). The mechanisms generating the log-normal distribution have been discussed by Koch (1966) who showed that this model arises when there is a fluctuation in the growth rate from time to time.

Time autocorrelation describes the average change of sample-to-sample resemblance in a series of successive samples collected during a certain period of time. This analysis has been used by Steven, Globitza (1972) to interpret the oscillatory variation in time of the species Trichodesmium thiebaudii.

In this investigation an attempt has been made to use the frequency distribution for abundance and the autocorrelation functions for explaining intraspecific and interspecific differences in growth and distribution patterns of phytoplanktonic species. It might be argued that the monthly sampling schedule followed in this work provided incomplete information regarding certain population maxima or minima which could go unsampled. A more meaningful way of looking at this problem is by considering the length of the sampling period (5 years) and the number of samples (60) which are large enough to include most of the seasonal variations and assure statistically significant interpretations.

(0.05)

On the basis of between-station comparisons of hydrographic data (Fig. 1, Tab. 1), it is apparent that temperature and salinity fluctuated similarly at both stations and therefore these parameters could not be directly associated with the observed intraspecific and interspecific differences in growth and distribution patterns of the examined phytoplanktonic species. On the other hand, the range, mean and annual fluctuations of the $P-PO_4$ and $N-NO_3$ (Fig. 1, Tab. 1) nutrients demonstrated clearly the eutrophic character of station S_1 in relation to S_3 and the question arose how the differences in the trophic regime affected the ecological behaviour of the different phytoplanktonic species.

The results of this work show that the eutrophic environment (station S_1) promoted the growth of the species Sk. costatum, Ch. didymum and Ch. affine but did not affect quantitatively the growth of the species Ch.

curvisetum, Rh. fragilissima and Rh. stolterfothii which attained similar abundance levels at both stations. Previous studies on the association between eutrophication and species abundance (Ignatiades, 1984) have also shown that an increase in nutrient enrichment does not always lead to an increase in the abundance of all species of a phytoplankton community. Furthermore, the eutrophic environment (station S_1) provided the conditions for regular annual oscillatory behaviour of the species Sk. costatum, Ch. didymum and Rh. fragilissima whereas the oligotrophic environment (station S_3) favoured the oscillatory behaviour of the species Ch. affine and Ch. curvisetum. The pattern of annual fluctuations of Rh. fragilissima was similar at both stations. It is obvious that the level of abundance of a species and the regularity of its annual fluctuations are parameters which are not necessarily in direct association.

It has been shown (Tab. 3) that all the examined species have been derived from the same log-normal parent population. Therefore, the observed intraspecific differences in abundance levels and annual fluctuations might be attributed to the existence of physiological races of the same species which might be adapted to high or low nutrient concentrations (Carpenter, Guillard, 1971). Other factors associated with the abundance and periodicity patterns of a species at a certain environment could be interspecific competition (Hooper, 1969), the requirement for a specific nutrient or vitamin (Curl, McLeod, 1961), sensitivity to changes of nitrogen:phosphorus ratio (Ryther, Dunstan, 1971), selective grazing (Frost, 1980), the requirement of a certain substrate if it forms a sedentary stage (McIntire, and current transport (Walsby, Moore, 1977) Reynolds, 1980).

According to Emlen (1972) any species displays a range or a collection of areas in which it lives. Individuals of a species inhabiting large areas (central populations) are living in an environment to which they are well adapted whereas individuals inhabiting peripheral areas, near the limits of the range (marginal populations) are adapted to a narrower range of living conditions than their centre-range relatives. Emlen's theory might provide some synoptic view of the observed differences in the growth and distribution of the examined species. The stations S_1 (eutrophic) and S_3 (oligotrophic) are located in an area (range) which is inhabited by all six species. On the basis of abundance levels and regularity in periodicity of the species Sk. costatum, Rh. fragilissima and Ch. didymum in the eutrophic habitat, it is obvious that this environment favours certain physiological and behavioural adaptations of these species. For this reason, the above species could be characterized as central populations of the eutrophic environment and marginal populations of the oligotrophic environment where either their abundance levels have been reduced or their annual fluctuations are aperiodic. On the other hand, the species Ch. curvisetum and Ch. affine showed a better adaptation in the oligotrophic environment because they displayed there good growth and regular annual periodicity. Therefore, these species could be characterized as central populations of the oligotrophic habitat and marginal populations of the eutrophic environment where they grew efficiently but with irregular annual periodicity. The population of Rh. stolterfothii with low abundance and similar annual fluctuations at both stations does not seem to have any behavioural adjustment to the above described ecological gradient and it could be characterized as an opportunistic species (Ricklefs, 1973) proliferating only when certain favourable environmental conditions prevail.

This investigation provides evidence that the eutrophic environment, although it is a good substrate for certain species (*Sk. costatum, Ch. didymum, Rh. fragilissima*) it may induce some physiological stresses to other (*Ch. curvisetum, Ch. affine*). Topping (1976) has drawn the same conclusion, emphasizing that the species with poor adaptation may eventually fall to very low numbers and be excluded from the community.

This work also supports the view (Kilham, Kilham, 1980) that concepts related to phytoplankton ecology can be better understood when considering phytoplankton as individual species rather than some collective group.

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