THE COMPOSITION OF PARTICULATE ORGANIC MATTER IN THE EUPHOTIC ZONE OF LAKE SUPERIOR

by

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Running Head
Particulate organic matter in Lake Superior

EXECUTIVE OVERVIEW

The distribution of particulate material between biological living material and either decaying organic or inorganic material in a lake has an important influence on the relationships between the nutrient contents and biological production levels. This paper examines observational data collected during the intensive studies of Lake Superior under the International Joint Commission, Upper Lakes Reference.

It is shown that living seston comprise the greatest portion of the particulate material with an increase of detrital material to about thirty nine percent by autumn. Thus the chlorophyll a values correlate well with the particulate organic carbon. This relationship would indicate that the available phosphorus is being rapidly recycled during the production season and not significantly bound in detrital material. This is indicated by lack of correlation between the phosphorus and organic carbon.

RÉSUMÉ POUR LA DIRECTION

La répartition de la matière particulaire entre la matière biologique vivante et la matière en voie de décomposition ou inorganique d'un lac influe considérablement sur les relations entre les teneurs en matières nutritives et les niveaux de production biologique. On traite, dans le présent document, de données recueillies lors d'études exhaustives portant sur le lac Supérieur et effectuées dans le cadre de l'étude de la pollution des lacs Supérieur et Huron de la Commission mixte internationale.

On y montre que le seston vivant représente la plus grande partie de la matière particulaire, la fraction de détritus augmentant jusqu'à une valeur d'environ 39 % à l'automne. Il y a donc une bonne corrélation entre les teneurs en chlorophylle$_{a}$ et en carbone organique particulaire. Cette relation porte à penser que le phosphore disponible est rapidement recyclé pendant la saison productive et qu'il n'est pas lié, de façon appréciable, aux détritus. Ce phénomène se manifeste par l'absence de corrélation entre les teneurs en phosphore et en carbone organique.

ABSTRACT

The composition of particulate organic matter (POM) as living and dead material was derived by the regression method in the euphotic zone of Lake Superior, May to November 1973. The regression method used in the literature was modified because it had a conceptual bias and overestimated detritus. Living seston was the major component of POM during the year. Detritus was minimal during the year and increased to 39% of POM by fall. Most detritus was autochthonous. POM composition expressed as chlorophyll, particulate organic carbon, particulate organic nitrogen, and particulate organic phosphorus was also analyzed.

La répartition en composantes vivante et non vivante de la matière organique particulaire (MOP) de la zone euphotique du lac Supérieur a été déterminée par régression pour la période de mai à novembre 1973. La méthode de régression utilisée dans la littérature a été modifiée, car elle comportait une erreur de conception et surestimait les teneurs en détritus. Le seston vivant a été la principale composante de la MOP au cours de l'année. La teneur en détritus a été très faible, mais augmentait jusqu'à 39 % de la MOP en automne. La plupart des détritus étaient autochtones. On analyse aussi la composition de la MOP en termes de chlorophylle ainsi que de carbone, d'azote et de phosphore organiques particulaires.

INTRODUCTION

The importance of organic detritus in the metabolism of aquatic ecosystems has been clearly stated (Melchiorri-Santolini and Hopton, 1972); however, the relationships between detritus, phytoplankton, zooplankton and bacteria are complex and the contribution of each to the total carbon flow in different waters is variable (Leach, 1975). The composition of detritus depends primarily upon its age and the resulting stage of its decomposition or mineralization (Menzel and Ryther, 1964). A working definition of detritus was introduced by Odum and de la Cruz (1963) as dead particulate organic matter inhabited by decomposer micro-organisms.

Lake Superior is one of the largest lakes in the world and is situated at the southern edge of the Canadian Shield. Because of the geology of the drainage area and lack of large anthropogenic loading, the lake does not receive large nutrients loading and has remained fairly oligotrophic to this day (Matheson and Munawar, 1978). Lake Superior is a large source of clean water and it is frequently surveyed by ships of the Canadian and American governments to maintain a knowledge of the state of the lake. During these surveys, about 40 physical, chemical and biological parameters are regularly sampled. In 1973, a more complete effort was made to study the lake. Several scientists participated in six monthly surveys from May to November to perform a wide range of experiments. Several

reports have since been published (Watson et al., 1975; Cook, 1975; Munawar, 1978a, b; Munawar and Munawar, 1975). Out of 221 sampled stations in each cruise, a comprehensive sampling of particulate organic matter (POM) as POC, PON, POP, and chlorophyll a was made in 27 stations, 12 offshore and 15 inshore. Their location is shown in Figure 1.

METHODS

Water samples for carbon, phosphorus and nitrogen determination were taken at 1, 5, 10, 25, 50, and 100 meters with a submersible centrifugal pump (pumping rate of about 16 litres per minute) that was fitted with an electronic bathythermograph (EBT). Water samples were taken with Van Dorn bottle casts every 50 meters thereafter as far as the bottom. Data were integrated by the trapezium rule over the depths where chlorophyll was sampled. POM for pigment, carbon, phosphorus and nitrogen determinations were collected on 55 mm diameter Whatman GF/C glass fibre filters at a vacuum not exceeding 177 mm Hg. On four cruises, chlorophyll samples were obtained from the top 20 meters by a 0-20 m integrator (Schroder, 1969). In shallow water ($<$ 22 m), the integrator was used down to two meters from the bottom. On the May cruise, samples were taken by a 0-50 m integrator but because of the very slow lowering rate, it was replaced on future cruises by the 0-20 m size. In October, the integrator was lost in rough weather and part of the cruise determinations were made from a

mixed sample from 5 and 15 meters with Van Dorn bottles. The validity of the integrator values was checked by comparing them with vertical profiles of chlorophyll a from samples taken at 1, 5, 10, and 25 meters (Watson et al., 1975).

The method of Strickland and Parsons (1968) was used for chlorophyll extraction. Chlorophyll a was corrected for phaeopigments by the acidification method of Lorenzen (1967). Fluctuations of chlorophyll a and primary production are presented and discussed by Watson et al. (1975). All chemical analysis were performed by the Analytical Services Section of the Canada Centre for Inland Waters according to the methodologies described by Philbert and Traversy (1973).

REGRESSION METHOD IN PRESENCE OF RANDOM VARIATION

Methods used to collection POM, such as microfiltration, do not allow separation of living and dead fractions. One efficient and convenient method for routine analysis to estimate the detritus percentage in POM is the regression method (Menzel and Ryther, 1964; Stoermer, 1968; Sutcliff et al., 1970; Robertson et al., 1971; Stadelman and Munawar, 1974). Leach (1975) discussed in detail its advantages and disadvantages and concluded that the method gave satisfactory results. When applied to Lake Erie data over a three year

period, the method produced fairly uniform estimates of detritus on a seasonal basis.

The method allows computation of the percentage of detrital POC in seston. When a linear relationship is found between POC and chlorophyll, the assumption is made that the amount of POC identified by the intercept of the regression line at zero chlorophyll is not associated with living material and, therefore, it is detrital. Eppley (1968) analyzed several alternative methods and concluded that a rapid and precise method for the estimation of phytoplankton was still badly needed.

The regression method as used in the literature has two pitfalls: users assume that one variable is measured with error while the other is fixed and that one variable must depend on the other. As a matter of fact, biological variables, such as POC and chlorophyll, are always measured with errors and they do not depend on each other's presence. Statistically, they must be considered random variables and if a linear relationship is hypothesized, the regression analysis must be done accordingly. Therefore, in this study, the slope of the regression line was computed by the geometric mean (GM) functional regression (Ricker, 1973):

$$b = \sqrt{\frac{\sum y^2}{\sum x^2}} \qquad (1)$$

where x and y represent the deviations from their means, i.e. $x = X - \overline{X}$; $y = Y - \overline{Y}$. Since both variables are independently subject to natural variation and measurement error, Dent (1935) and Ricker (1973) recommended the GM regression as the most appropriate. This functional regression minimizes the sum of the products of the vertical and horizontal distance of each point from the line.

Figure 2 shows the regression line determined by this method together with the two least-squares regression lines Y on X and X on Y for chlorophyll a and POC in Lake Superior. The other figures (Figures 3 and 4) show only the regression line computed through Equation 1. Numerical values are presented in Table 3.

RESULTS

Chlorophyll Relations

Pigment concentrations (Table 1) were low compared with reported values for the other Great Lakes. A range of individual station values from 0.3 to 6.6 μg/L was found in 1973 (Watson *et al.*, 1975). The percentage of phaeopigments varied widely with the largest proportion occurring in late summer. Correlation between POC and chlorophyll a (corrected and uncorrected for phaeopigments) was highly significant during the studied period (Table 2). This correlation, however, varied during the year with high values in May and June and

lower ones in late summer and autumn (Table 3). The significant correlation between chlorophyll a and POC indicates that changes in the amounts of these variables are related to changes in living plankton. These related behaviours suggest that living seston was the major component of POM. This similar behaviour is also visually described in Figure 2. Most data can be included into an ellipse, and this indicates that they have a joint bivariate normal distribution. In this instance, the functional regression line is quite close to the major axis of the ellipse.

The slope of the regression line indicates a ratio POC/chlorophyll a of 114:1. When individual stations are analyzed, the ratio varies widely; a range of values between 54-190:1 (by weight in stations where the correlation is significant) is observed. On a monthly lake-wide basis, these ratios range between 176-247:1 in summer to 63-70:1 in autumn. The intercept of the regression line on the carbon axis indicates formation of detrital carbon in considerable amounts only since September (Table 3). In this month, the maximum production is observed (El-Shaarawi and Munawar, 1978).

Chlorophyll and POP were not often correlated (Table 2) and no regression line could be fit to the data, thus indicating liability of phosphorus compounds. Also, the ratios between nitrogen and chlorophyll changed significantly from station to station (6-24:1 by weight) and in different months (4-9:1). Yentsch and Vaccaro (1958)

and Menzel and Ryther (1964) suggested that the large variability of such ratios in living cells may be induced by nitrogen limitation. This conclusion is not supported by the continuous observations in Lake Superior which show that nitrogen is always present in nonlimiting amounts in the lake waters.

Carbon Nitrogen Relations

Carbon in POM is, on the average, less than an order of magnitude (C/N-7:1) greater in quantity than nitrogen. POC and PON were correlated significantly in 1973 (Table 2). Their ratio was fairly constant until September (8-9:1). Later in the year, this ratio was reduced to 4-6:1. Since the seasonal mixing also took place since October, this decreased ratio is likely due to mixing of epilimnetic and hypolimnetic waters. These ratios may also reflect detritus composition, even if the C/N ratio is suspiciously low.

Phosphorus Correlation with Other Elements

On an average lake-wide basis, phosphorus was correlated with both POC and PON at a much lower level of significance than all other correlations (Table 2). When the data were analyzed by stations and by months, these correlations are no more significant. Thus, it can be concluded that the correlation with 8 months data is significant only because a large number of data is available, but probably

the POP behaviour is independent from the other two elements. POP is also not correlated with chlorophyll a and thus it may be concluded that phosphorus has a very fast turnover rate in both detrital matter and living seston.

Productivity and Detritus Composition

The ratio POC-Chlorophyll a varied during the year. In spring, the ratio was high and then it decreased regularly (Table 3). Steele and Baird (1961, 1962, 1965) and Robertson et al. (1971) interpreted their samples with low ratios as coming from periods of high plankton productivity. Likewise, they interpreted high ratios, i.e., low relative amounts of chlorophyll, as indicative of times of relatively low productivity caused by environmental limitations. If this hypothesis is valid, the present results indicate a low productivity in spring and early summer and an increase in productivity as the season progressed until a maximum in October.

This pattern was similar to the observed behaviour of primary production (Watson et al., 1975; El-Shaarawi and Munawar, 1978). In spring, nutrients were high and light was at its maximum. Water temeprature was low and this was the limiting factor (Halfon and Lam, 1978; Lam and Halfon, 1978). The formation of a thermal gradient between the shallow coastal zones and the deep part of the lake caused an increase of production in coastal zones. By July, however, the

differences were not significant. Production was of the same order of magnitude all over the lake. Also, POM composition was not statistically different in coastal and offshore zones, and therefore, the data from all stations were analyzed together. Maximum production was observed in September when it became limited by nutrient depletion in epilimnetic waters. In November, production was at a much lower level than indicated by the POC-Chlorophyll a ratio (El-Shaarawi and Munawar, 1978). Autumn is also the period when one may expect the greatest amount of detritus of autochthonous origin. Therefore, a great increase of detritus in this period may mean that allochthonous detritus is relatively low.

Detrital carbon was estimated by the regression method (Leach, 1975 and pers. comm.) and modified as indicated above. In spring and early summer, detrital carbon was not present and then increased to high levels (up to 39% of POC in October). This detritus was formed autochthonousally as the plankton population grew and died. By autumn, the percentage of detritus was approxiamtely one third of living seston. The mean percentages of living seston during the year 1973 are estimated as 100% in spring, 95% in summer and 72% in autumn. These estimates depend upon the assumption that chlorophyll a is a good indicator of phytoplankton biomass. In fact, El-Shaarawi and Munawar (1978) computed a very strong linear relationship between chlorophyll a and phytoplankton biomass. This linear relationship was not observed in the lower Great Lakes (Munawar et al., 1974).

DISCUSSION

In a large spatially heterogeneous environment a linear relationship was found between POC, PON and chlorophyll a. Detritus in a lake has two main origins, autochthonous and allochthonous. The latter seems not be an important source of POM in Lake Superior (Thomas and Dell, 1978). Inputs to the lake do not significantly influence the lake behaviour (Halfon and Lam, 1978). Coastal production by epiphytes and periphyton is locally important (Stokes et al., 1970) but is a minimal percentage of total production (Munawar, pers. comm.; Munawar et al., 1978). Detritus increased until October. Later it decreased possibly because of biological degradation and mixing of epi- and hypolimnetic waters.

Primary production in 1973 began in May, reached a peak in September and decreased to minimal levels in November (El-Shaarawi and Munawar, 1978). A mathematical model of the lake (Halfon and Lam, 1978; Lam and Halfon, 1978) identified temperature as a major controller of primary production. Light and nutrients, mainly phosphorus, were limiting beginning in September. The POC - chlorophyll ratio closely described this behaviour of production (Table 3).

Golterman (1972) stated that mineralization is quite an efficient process, which means that little detritus is formed from

algal tissues (10-20%). This may explain the observation that detritus was only a small fraction of seston and that the maximum amount was found in October, shortly after the peak of primary production. Therefore, most detritus should be of algal origin. Also, detritus is not abundant since algae are readily decomposed. These results are different from those of Paerl et al. (1976) in another oligotrophic lake, Lake Tahoe, Nevada. They observed that the detritus peak was not related to the production peak and occurred several months later. They explained their results with the microbial transformation of DOC into POC. This phenomenon seems to be not important in Lake Superior where detrital carbon is present in the lake only after an algal bloom. However, an analysis of the C/N/P ratio indicates that POM composition is quite similar in both lakes. The C/N/P ratios are 100: 17.7: 2.5 and 100: 16.2: 1.4 in Lake Superior and Lake Tahoe (Holm-Hansen, 1972), respectively.

Since detritus has mostly an autochthonous origin, it should not be produced in great amounts during the winter months, when primary production is at low levels and microbial activity is reduced. Low levels of observed detritus in spring confirms the idea that allochthonous POM is not an important source of detritus. Wetzel (1975) stated that a high DOC/DON ratio would indicate presence of allochthonous dissolved material, since nitrogen compounds are more readily utilized. Unfortunately, no simultaneous measure of DOC and

DON was done at any station since observations begain in 1968. Thus, the influence of DOM inputs can not be assessed.

In conclusion, this study indicates that the mean percentage of living seston during the year was quite high. When the regression line method was used, living seston was estimated to be an average 98% of POM. These results agree with the correlation analysis (Tables 1-3) which showed that chlorophyll a and POC had quite similar patterns of behaviour. Thus, living phytoplankton made up a major fraction of POM. Assumptions confirmed by Munawar et al. (1978) and also taken by Bukata et al. (1978) in their analysis of optical properties of Lake Superior. These conclusions are different from results obtained by Robertson et al. (1971) and Leach (1975) in Lake Michigan and Lake Erie, respectively, and by Paerl et al. (1975) in the oligotrophic Lake Tahoe. These researchers found that up to 50% of POM was detrital.

One final remark regarding the regression formula is also appropriate. The geometric mean functional regression does not overestimate detrital matter as usually happens when the standard regression analysis is used. This is because both variables are considered independent and subject to measurement error and intrinsic variation. This remark should be taken into account when this study is compared with others because their estimate of living seston may be in defect.

In conclusion several statements can be made regarding the Lake Superior ecosystem: Most organic seston was produced in the lake. Inputs of sediments are very low because of the rocky nature of most of the shoreline and the absence of highly erodable bluffs (Thomas and Dell, 1978). Indeed, it is possible that much of the sediments now being deposited represents reworked material derived from subaqueous erosion.

Lake Superior water closely resembles the composition of the rain falling on the watershed, since the rocks are chemically resistent. The soil cover contributes little to the dissolved solids content of lake water (Matheson and Munawar, 1978).

Concentration of organic matter was similar in coastal and offshore zones. Production in these areas was different only in spring when water temperature increased more rapidly in shallow water. This statement is confirmed by a statistical classification of Lake Superior of El-Shaarawi and Munawar (1978). They showed (see their Figure 1) that most of the lake is fairly uniform in terms of primary production but for a very small area in the northwest shore from Silver Bay, Minnesota to Thunder Bay, Ontario.

Between 60 and 100% of seston was alive. These estimates depend on the assumption that chlorophyll a is a good indicator of

phytoplankton biomass. El-Shaarawi and Munawar (1978) confirmed that, contrary to what happens in other lakes, this assumption is valid.

The POC/chlorophyll ratio followed the behaviour of primary production from June to October.

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Tables legends

Table 1: Composition of particulate organic matter at each cruise. Values shown represent the mean ±1 SD.

Table 2: Correlation between seston components, POC, POP and PON, May to November, 1973.

Table 3: Seasonal regressions of chlorophyll *a* (corrected) and POC, chlorophyll *a* (corrected) and PON, POC and PON, May to November, 1973.

Table 1

Date (1973)	number of stations	Chl *a* (μg l^{-1})	Chl *a* (corr.) (μg l^{-1})	POC (μg l^{-1})	POP (μg l^{-1})	PON (μg l^{-1})
May 17-22	27	.89±.25	.75±.23	103±52	2.27±1.90	15.6±5.7
June 15-28	20	.88±.11	.75±.11	91±28	1.27± .51	12.7±3.1
July 27-Aug. 7	19	1.19±.26	1.07±.27	150±47	1.41± .76	18.1±5.6
Sept. 6-16	17	1.47±.40	1.31±.39	148±30	1.91± .97	20.0±3.2
Oct. 14-25	18	1.67±.63	1.53±.54	157±34	1.95±1.05	25.3±8.3
Nov. 14-26	19	.98±.16	.89±.17	80±13	1.34± .82	11.0±2.3

Table 2

Relationship	n	r	P
Chlorophyll *a* - Chlorophyll *a* (cor.)	120	.98	<< .001
Chlorophyll *a* - POC	120	.60	<< .001
Chlorophyll *a* - POP	117	.16	N.S.
Chlorophyll *a* - PON	120	.66	<< .001
Chlorophyll *a* (cor.) - POC	120	.60	<< .001
Chlorophyll *a* (cor.) - PON	120	.64	<< .001
Chlorophyll *a* (cor.) - POP	117	.13	N.S.
POC - POP	117	.24	< .01
POC - PON	120	.75	<< .001
POP - PON	117	.19	< .05

Table 3

Date (1973)	Regression Equations (y = bx + a)	n	r	P
May - November	POC = 113.75 Chl *a* + 2.39	120	.60	<<.001
	PON = 16.3 Chl *a* + 0.11	120	.64	<<.001
	POC = 6.97 PON + 1.62	120	.76	<<.001
May 17 - 22	POC = 220.74 Chl *a* - 62.40	27	.64	<.001
	PON = 24.18 Chl *a* - 2.48	27	.57	<.01
	POC = 9.12 PON - 39.68	27	.49	<.01
June 15 - 28	POC = 247.11 Chl *a* - 97.43	20	.47	<.05
	PON = 28.05 Chl *a* - 8.73	20	.51	<.05
	POC = 8.80 PON - 20.54	20	.85	<<.001
July 27 - Aug. 7	POC = 176.18 Chl *a* - 38.87	19	.34	N.S.
	PON = 20.92 Chl *a* - 4.35	19	.64	<.01
	POC = 8.42 PON - 2.22	19	.83	<<.001
Sept. 6 - 16	POC = 75.22 Chl *a* + 46.67	17	.45	N.S.
	PON = 7.96 Chl *a* + 9.45	17	.38	N.S.
	POC = 9.45 PON - 42.59	17	.60	<.01
Oct. 14 - 25	POC = 62.99 Chl *a* + 60.55	18	.44	N.S.
	PON = 15.44 Chl *a* + 1.66	18	.33	N.S.
	POC = 4.07 PON + 53.78	18	.73	<.001
Nov. 14 - 26	POC = 77.70 Chl *a* + 10.74	19	.55	<.05
	PON = 13.18 Chl *a* - .81	19	.47	<.05
	POC = 5.90 PON + 15.62	19	.83	<<.001

Figure legends

Figure 1. Location and number of sampling stations in 1973.

Figure 2. The relation between chlorophyll *a* (corrected) and POC in the euphotic zone of Lake Superior, 1973. The solid line is obtained by the geometric mean functional regression. The dotted lines are the standard linear regression relations between chlorophyll *a* and POC, and POC and chlorophyll *a*, respectively.

Figure 3. The relation between chlorophyll *a* (corrected). Euphotic zone of Lake Superior.

Figure 4. The relation between POC and PON. Euphotic zone of Lake Superior.

Figure 1

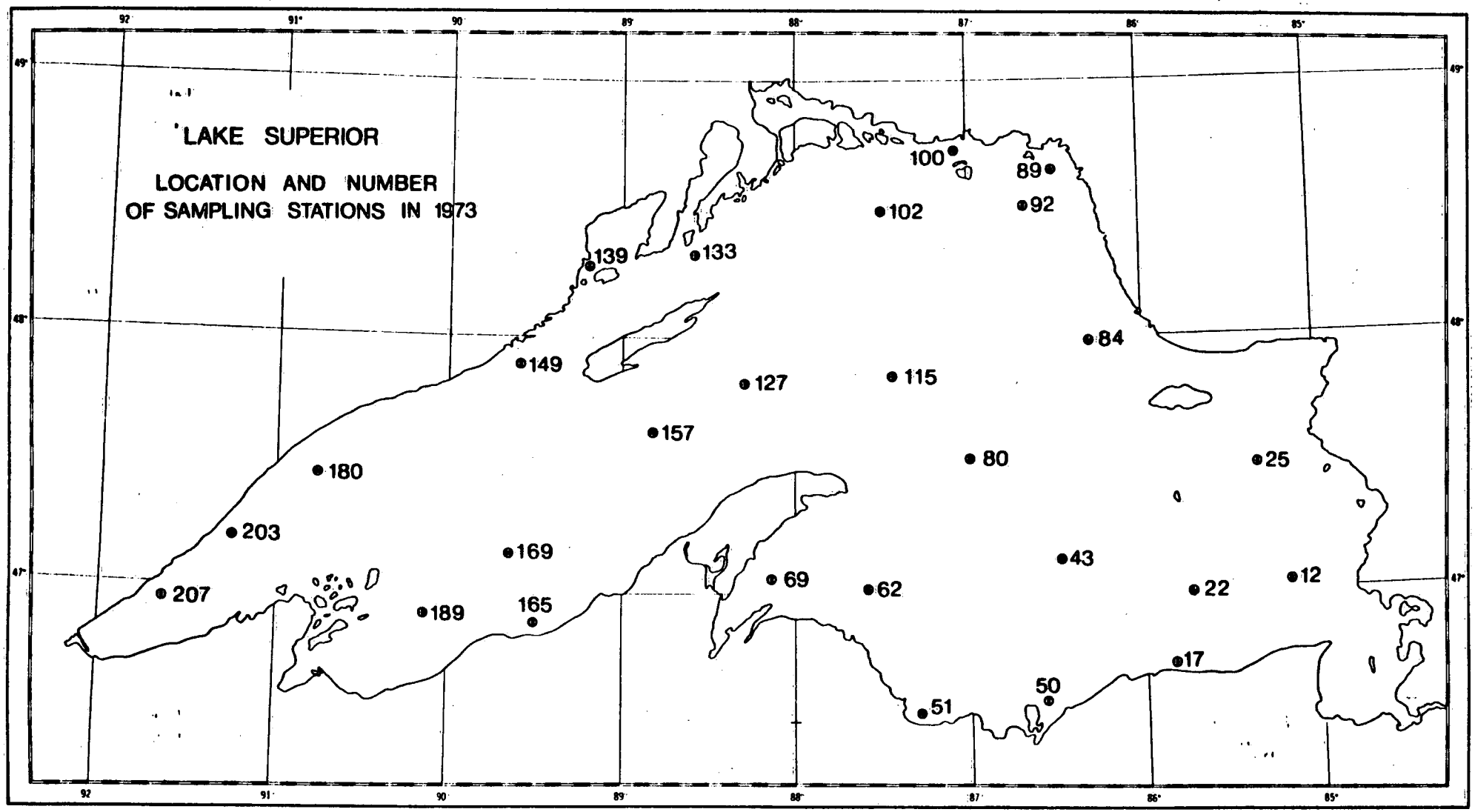

LAKE SUPERIOR
LOCATION AND NUMBER
OF SAMPLING STATIONS IN 1973
92
91
90
89
88
87
86
85
49
48
47
100
89
92
102
139
133
84
149
127
115
157
80
25
180
203
169
43
69
62
12
22
207
189
165
17
50
51

Figure 2

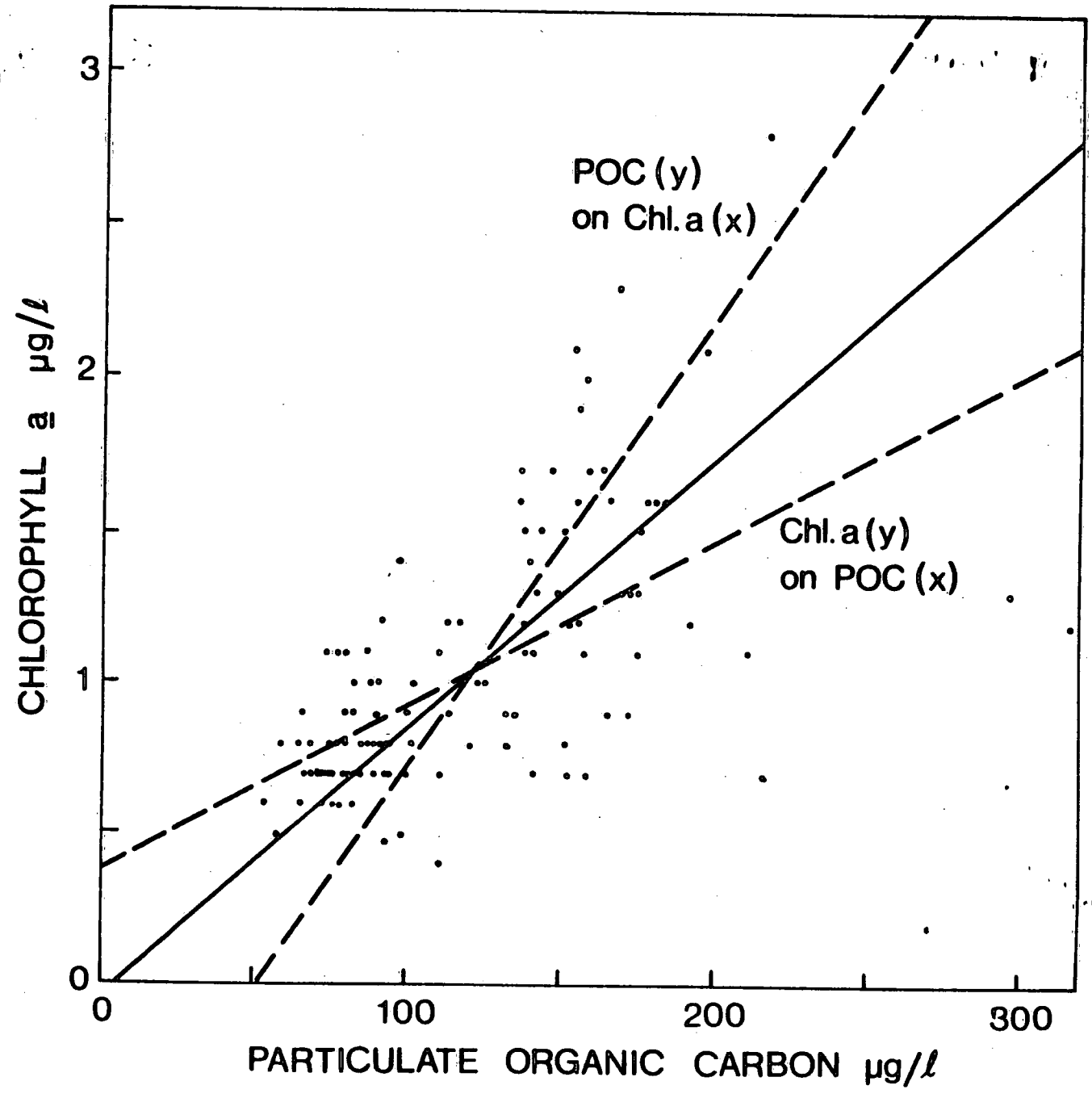

POC (y)
on Chl. a (x)
Chl. a (y)
on POC (x)
CHLOROPHYLL a µg/ℓ
PARTICULATE ORGANIC CARBON µg/ℓ
0
1
2
3
0
100
200
300

Figure 3

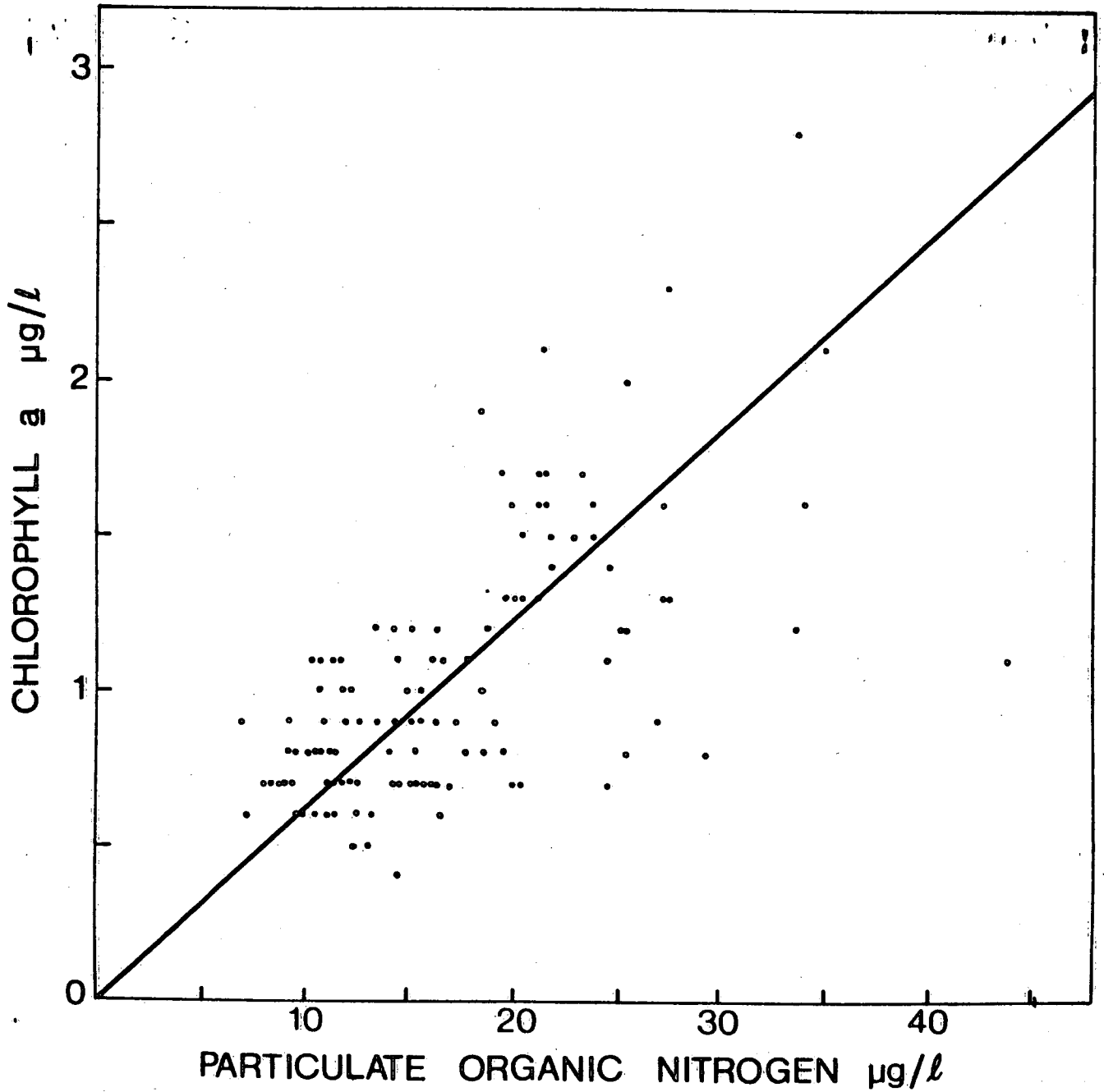
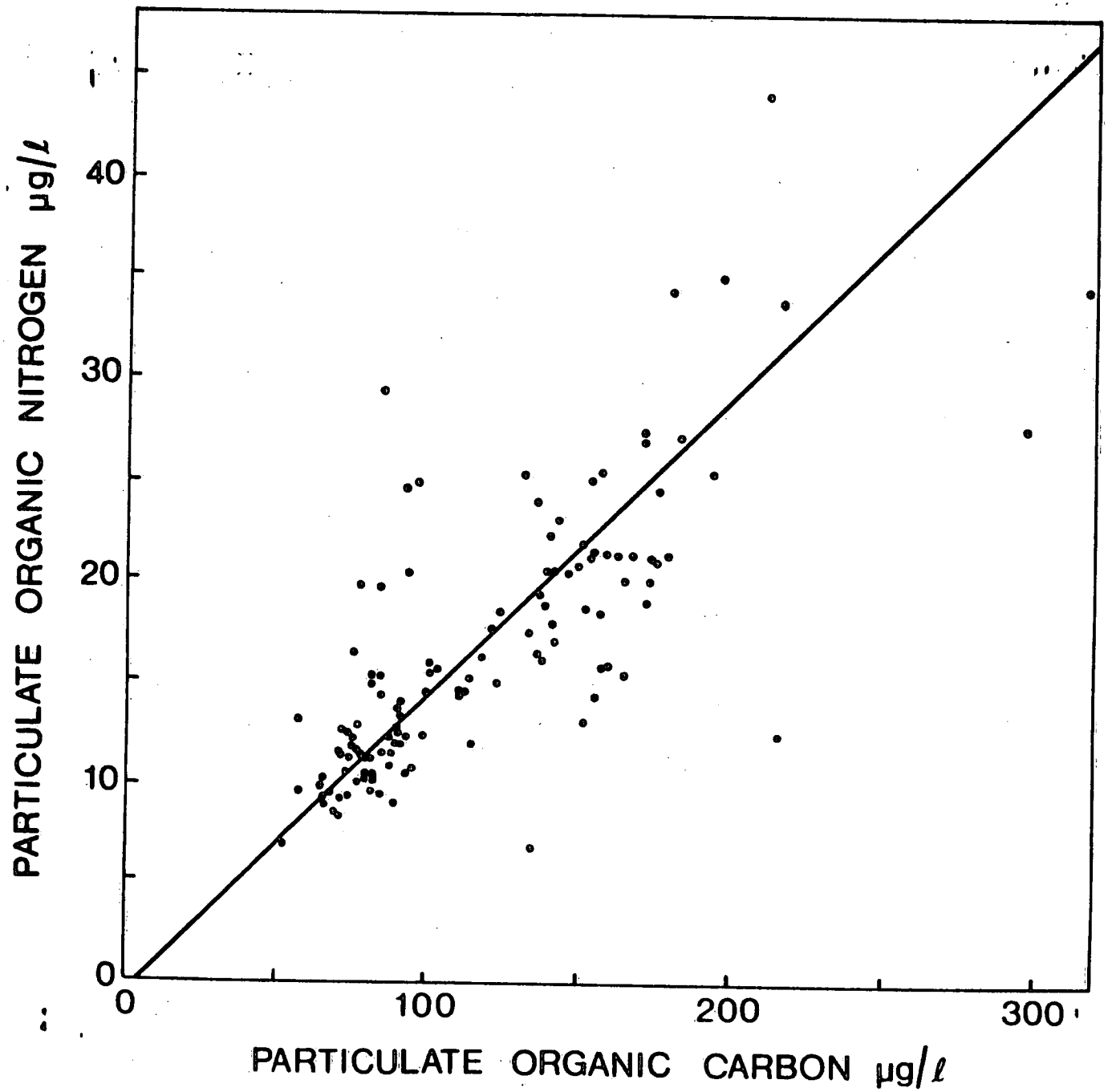

CHLOROPHYLL a µg/ℓ
0
1
2
3
10
20
30
40
PARTICULATE ORGANIC NITROGEN µg/ℓ

Figure 4


PARTICULATE ORGANIC NITROGEN µg/ℓ
0
10
20
30
40
0
100
200
300
PARTICULATE ORGANIC CARBON µg/ℓ

9794