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1.

The primary production cycle in the Southern Bight of the North Sea

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Two main approaches were considered in our previous synthesis of the phytoplanktonic production studies (Jo Podamo , 1974) .

1) The first one has long been the major topic . It deals with the adequate quantification of primary production in the sampled area . Today , one may conclude that the phytoplankton is usually homogeneously distributed in the water column . Along a transect perpendicular to the coast , the phytoplancton abundance decreases within the first 50 km (zone 1) and then is relatively stable (zone 2). At the two extremes of the transect , average potential production figures are 25 mg C/m^3/h and 3 mg C/m^3/h . In both zones , the integrated daily rate is however comparable , the lower water transparency counterbalancing the higher potential production in zone 1 , and inversely in zone 2 . Fractionated ~~fxx~~ samples proofs showed that the total activity of larger phytoplankton cells (> 25 µ ; e.g. diatoms) was relatively more important than that of smaller cells (nannoplankton) in zone 1 during the spring and fall outbursts .Conversely , nannoplanktonic activity prevailed in zone 2 during all the year and in both zones in winter and summer .

The most difficult problems encountered were relevant to the assessment of the vertical photosynthesis profile and its integration , followed by the computation of the daily production rate . This latter aspect has been further developed in this report .

2) The second approach is the dynamic one . The possibilities of a correct interpretation of the transformations observed and of a good

prediction of the production cycle depend on our knowledge of the ecophysiological processes involved in the functionning of the ecosystem (e.g. nutrients-growth relationships , uptake rates ,respiration rates , mortality rates , nutrients regeneration rates ,excretion rates,etc.) . One is presently striving towards a simulation model of phytoplankton fluctuations .

In our previous studies , the nannoplankton was showed to exhibit higher production-to-chlorophyll ratios than netplankton . This was presumably correlated to different nutrient saturation kinetics . Some results on the phytoplankton-nutrient relationship are presented in the second section of our report on primary production .

I . The assessment of daily rates and the computation of an annual primary production figure .

Since the 1972 and 1973 in situ work , the parameters of the light-photosynthesis relationships have been determined for the phytoplankton in our area of investigation . Hence the use of an analytical model (Vollenweider ,1965) . The recalculation of all our results and some comments on the model have been published in a technical report (Mommaerts , 1974)

1. Review of some steps involved in the calculation of production rates.

1.1. Potential production

The first problem is a problem of conversion of in vitro figures to true gross p_{opt} figures (p_{opt} = production with optimal light). Indeed , only gross figures can be used in the Vollenweider model .

Dark fixation :fractionated filtrations have revealed that the dark fixation of the prefiltered samples (i.e. nannoplankton + bacteria) was equal to that of the total samples . Therefrom , the dark fixation by pure phytoplankton (netplankton) was zero or not measurable . This and other indications make us believe that dark fixation figures are mostly relevant to bacterial anaplerotic fixation of CO_2 and should thus be subtracted from light assimilation figures .

Respiration : measured CO_2 fixation rates are neither net nor gross. We have considered a 60% figure for the reassimilation of intracellular respiratory CO_2 (according to Steemann Nielsen ,1955) and temporarily taken the respiration rate as 10% of gross p_{opt} .

Excretory losses : excretory losses (e.g. glycollate) have been known for some time . An average figure seems to be 15% of the assimilated carbon . Many indications in the literature allow us to inversely relate the % excretion to the growth rate (taken as an indication of the physiological status of the phytoplankton) and to consider the excretion rate in the water column being proportionnal to the gross photosynthesis rate (thus exhibiting a sub-surface maximum) . Excretory losses have not been considered in the above mentionned technical report but well in this synthesis report where all figures have been reevaluated by 15 % .

1.2. Integrated production : daily rates

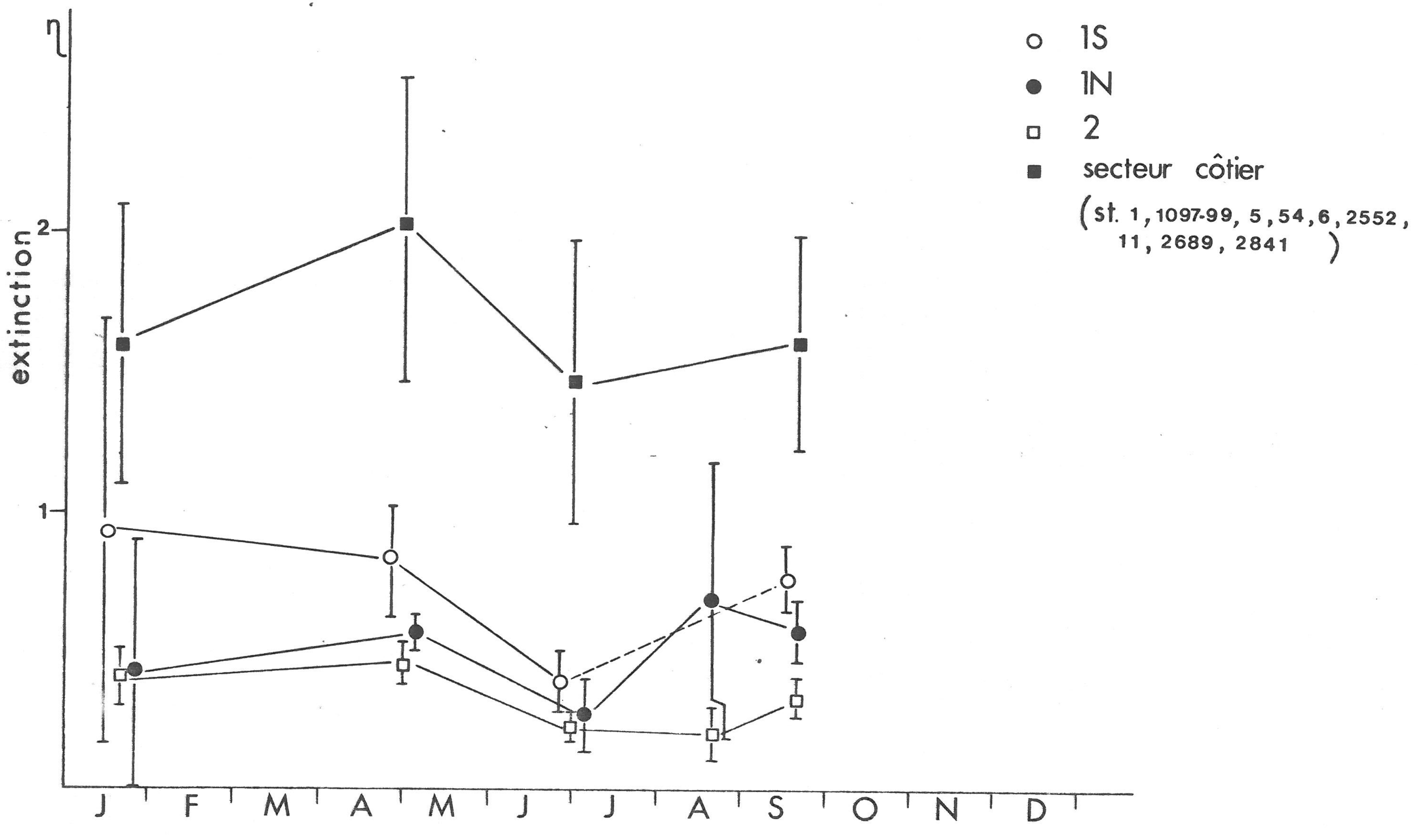
The integration on depth and the calculation of gross rates were made according to the Vollenweider model and the assumption of a sinusoidal variation of surface irradiance . The parameters used are those of the photosynthesis-light relationship , the average extinction coefficient of water (400-700 nm) , daylength and hourly maximal surface irradiance (400-700 nm) .

The problems arise mostly with the estimation of net production. Indeed , the assumption of a respiration rate constant with depth and time is crude . Another point concerns the choice of the depth . Net production rates have been computed for the euphotic depth . Accordingly , the net rates represent about 50 % of the gross rates. This kind of proportion was already mentionned before by Steemann Nielsen . However , in the Southern Bight , the phytoplankton distribution in the water column is nearly homogeneous , this extending to the bottom as a consequence of a good mixing . Thus respiration figures are to be computed for depths exceeding the euphotic depth by about 1-2 times (open sea) to 2-5 times (coastal area). Consequently , the actual net production figures would still be lower , being null or even negative in the coastal zone . This is not always the case since phytoplankton growth is observed . Hence the strong need for an improved evaluation of phytoplankton respiratory rates .

2. Results

The usual range of gross production/day lies between 50 and 800 mg C/m^2/day in the costal area (zone 1) and between 50 and 500 mg C/m^2/day in the open sea (zone 2) . These results agree with the few available data (the last FAO Atlas of biological ressources of the Seas indicates a range of 200-500 mg C/m^2/day , apparently ignoring the low winter figures and the blooms) .

On the basis of potential production figures and extinction coefficients (fig. 1) , a coastal fringe has been distinguished . The limits are often clear-cut . In some instances , one has seen a sampling station belong in an alternate way to a coastal bloom and an open sea water mass (e.g. station 16 , 8 May 73) as a result of tidal streams . This distinction was necessary for a better weighing of results ,as most sampling stations of zone 1 were located in this fringe . The variability is


η
extinction
2
1
J
F
M
A
M
J
J
A
S
O
N
D
1S
1N
2
secteur côtier
(st. 1, 1097-99, 5, 54, 6, 2552,
11, 2689, 2841)

also much higher in the fringe than in the remain of zone 1 (see 95 % confidence limits from fig . 1)

Annual production figures (gross rates)

Four years of observations make it possible to picture a relatively consistent pattern of seasonal variation .In figs. 2,3,4,5, 6 the results of each cruise have been averaged and the 95% confidence limits figured . The spring bloom (April-May) and a less conspicuous autumnal outburst (September) are seen in about all zones .

The integration is difficult : usually three figures have been computed : a minimal one (lower limit of the 95% confidence belt)

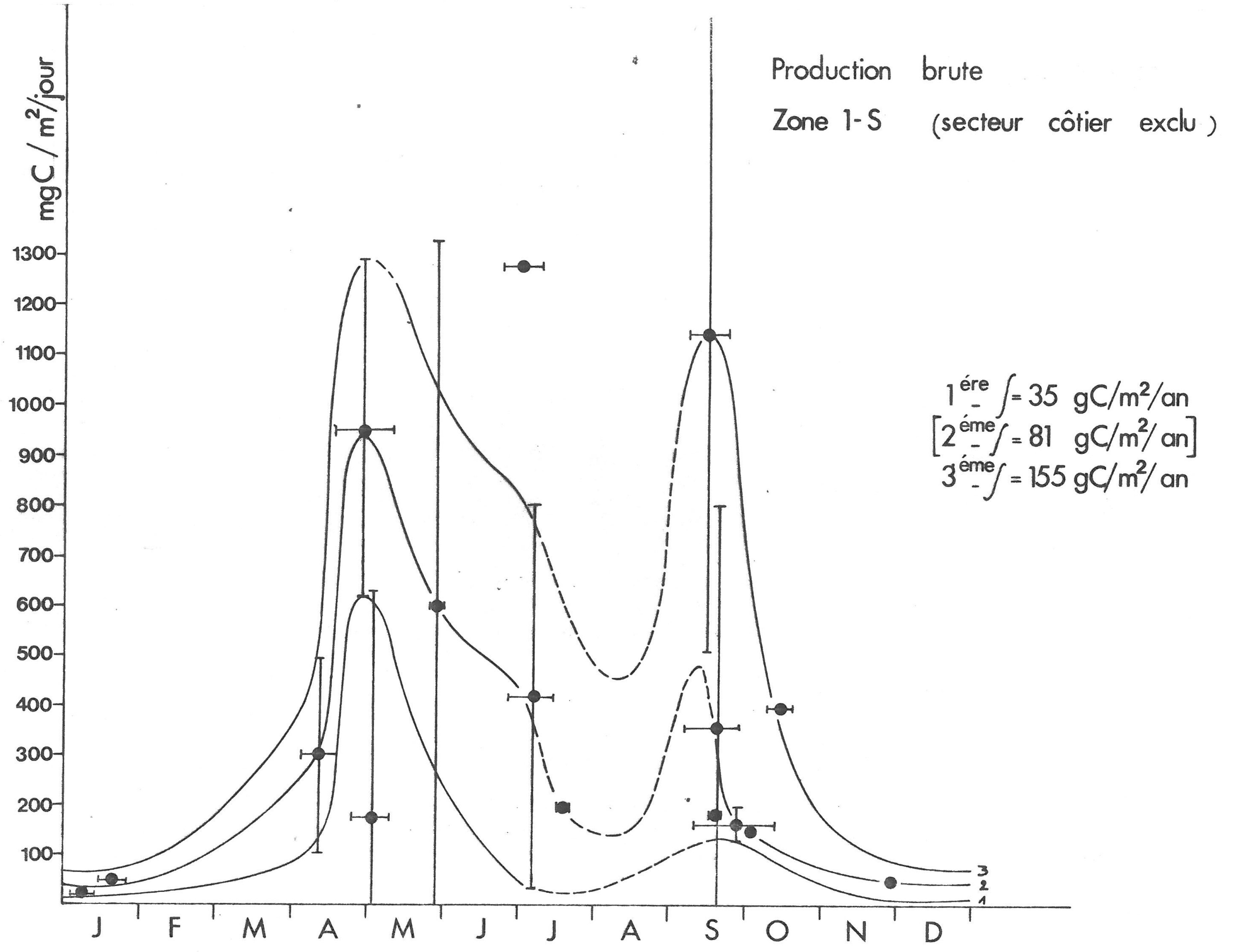
an averaged one

an maximal one (upper limit of the 95 % confidence belt)

The average figures are :

zone 1-S (coastal finge)	60 g C/m^2/year	
zone 1-S (beyond fringe)	81 g "	"
zone 1-N (coastal fringe)	85 g "	"
zone 1-N (beyond fringe)	58 g "	"
zone 2	78 g "	"

Thus 80 ± 40 g C/m^2/year would be a typical figure for the Southern Bight . Year-to-year variations may (however) sometimes bring a remarkable episode as in 1971 when gross production might have been twice the average .
As a matter of comparison ,we may mention Steele (1974) who gives a gross primary production figure of 70 g C/m^2/year in the Northern North Sea (~~and~~ 90 g C/m^2/year for the coastal waters of the same area).



Production brute
Zone 1-S (secteur côtier exclu)
1ére ∫ = 35 gC/m²/an
[2éme ∫ = 81 gC/m²/an]
3éme ∫ = 155 gC/m²/an
mgC / m²/jour
1300
1200
1100
1000
900
800
700
600
500
400
300
200
100
J
F
M
A
M
J
J
A
S
O
N
D
3
2
1

Fig 2

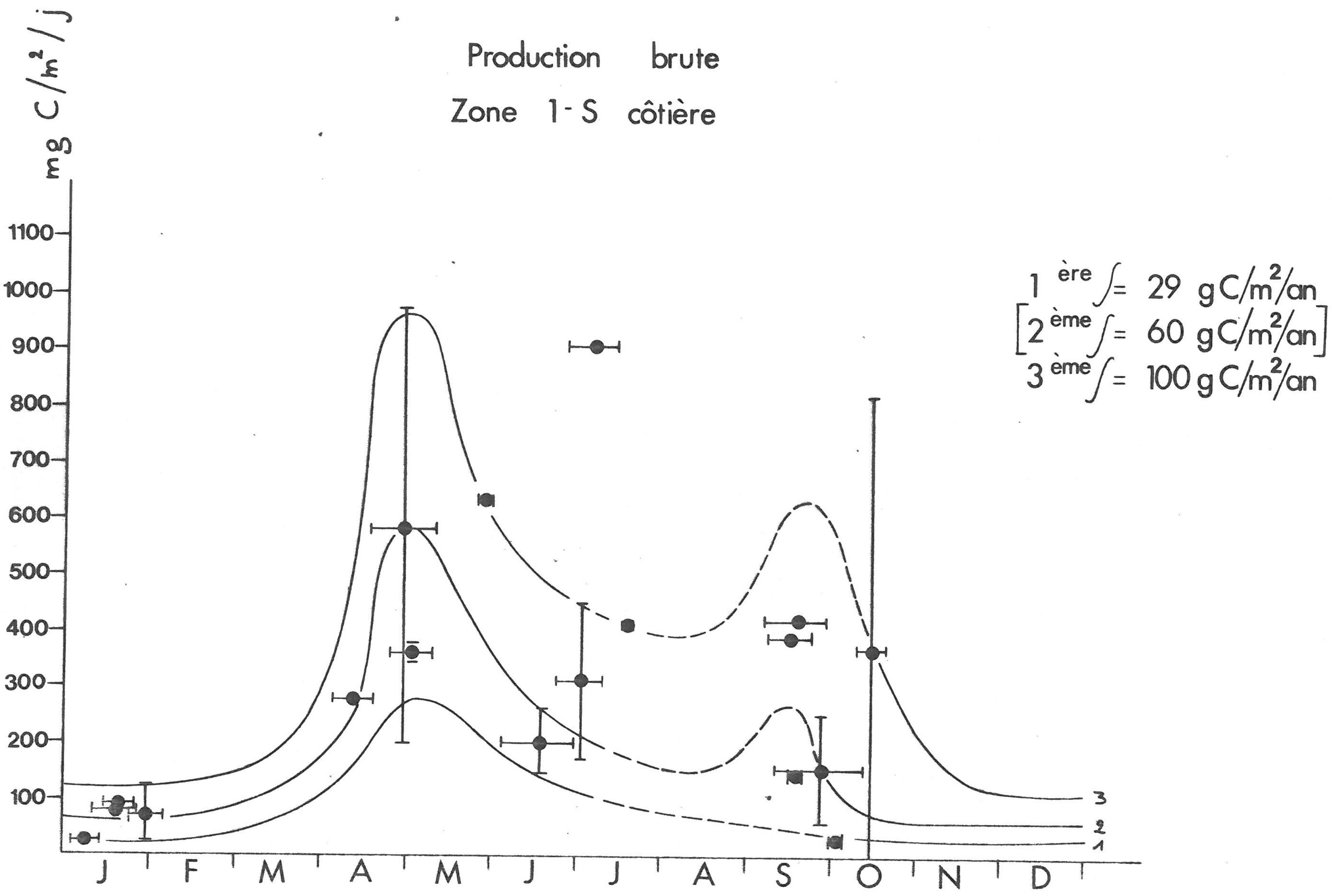

Production brute
Zone 1-S côtière
mg C/m²/j
1100
1000
900
800
700
600
500
400
300
200
100
J
F
M
A
M
J
J
A
S
O
N
D
3
2
1
1ère ∫ = 29 gC/m²/an
[2ème ∫ = 60 gC/m²/an]
3ème ∫ = 100 gC/m²/an

Fig 3

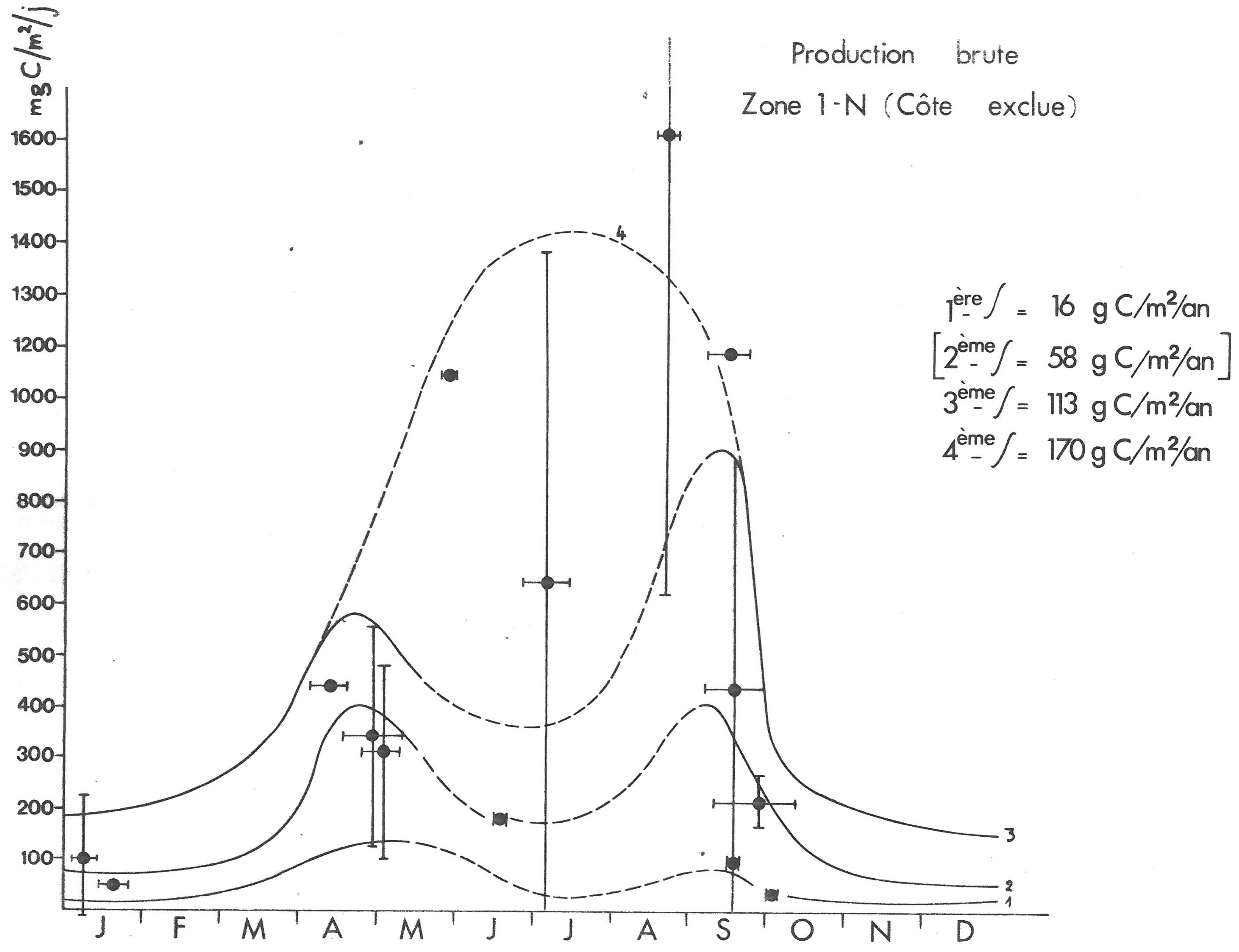
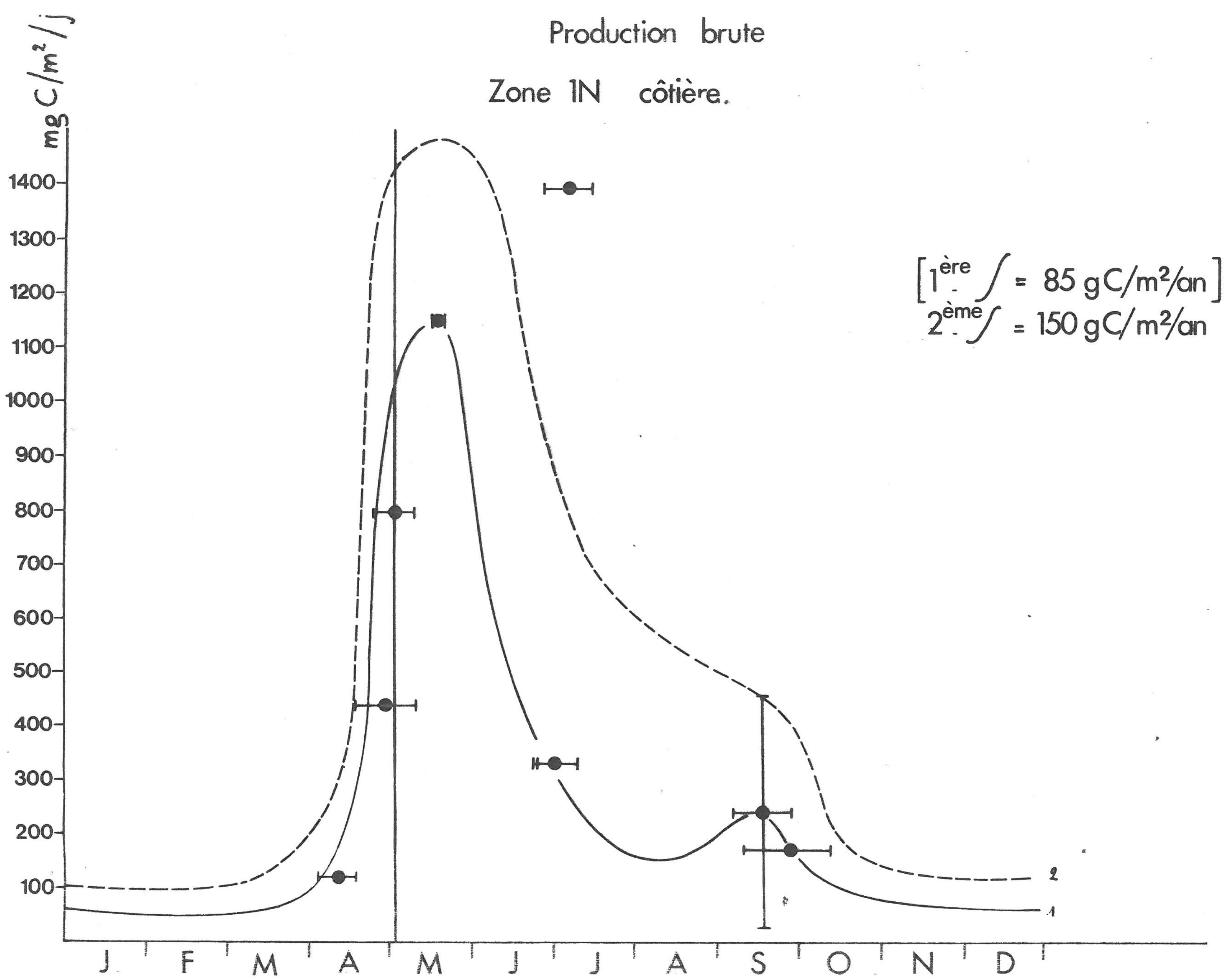

Production brute
Zone 1-N (Côte exclue)
mg C/m²/j
1600
1500
1400
1300
1200
1000
900
800
700
600
500
400
300
200
100
J F M A M J J A S O N D
1ère ∫ = 16 g C/m²/an
[2ème ∫ = 58 g C/m²/an]
3ème ∫ = 113 g C/m²/an
4ème ∫ = 170 g C/m²/an
4
3
2
1

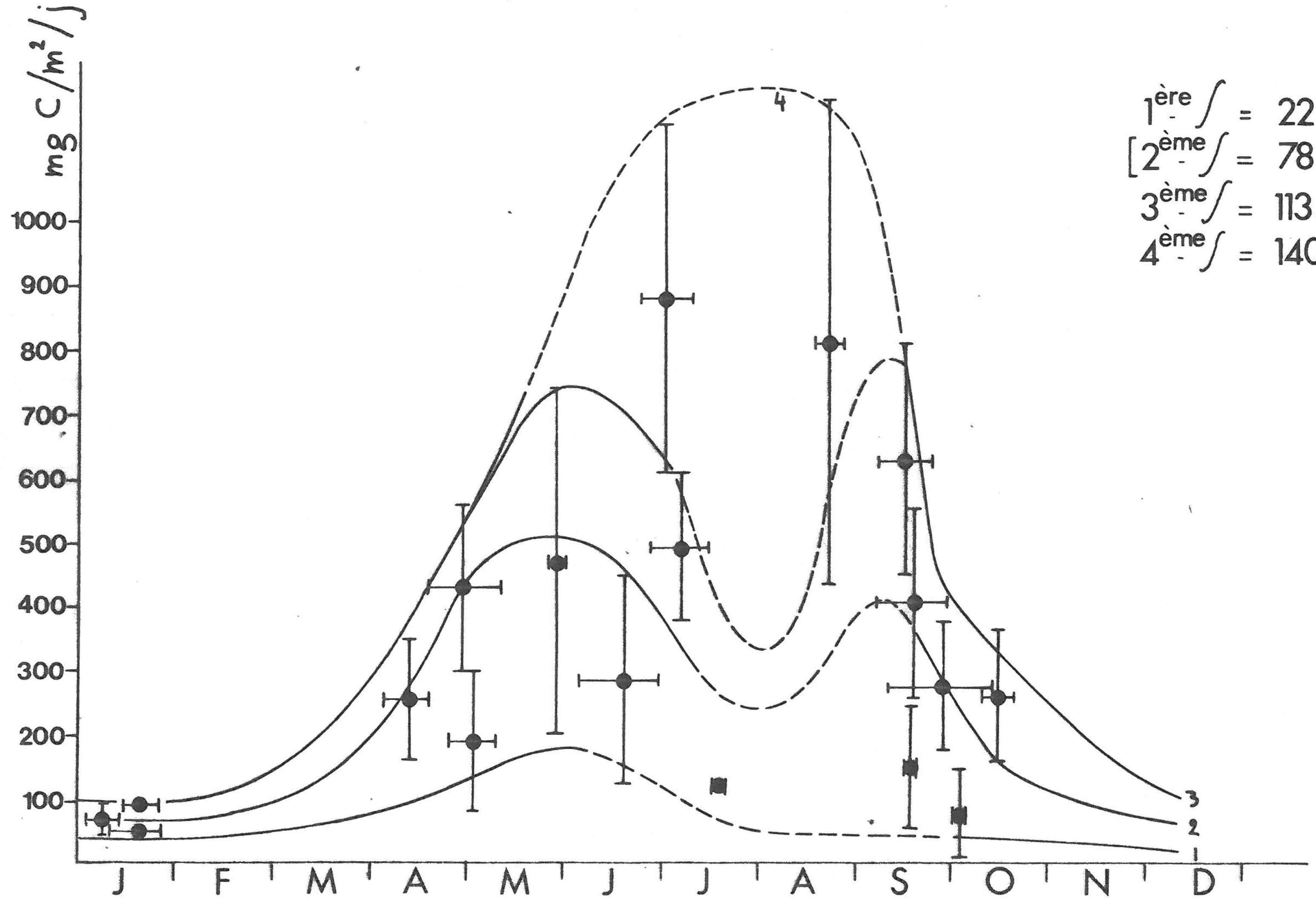
Fig 4



mg C/m²/j
1400
1300
1200
1100
1000
900
800
700
600
500
400
300
200
100
J
F
M
A
M
J
J
A
S
O
N
D
2
1
Production brute
Zone 1N côtière.
[1ère ∫ = 85 gC/m²/an]
2ème ∫ = 150 gC/m²/an

Fig 5

Production brute Zone 2



$1^{\text{ère}} \int = 22$ g C/m²/an

$[2^{\text{ème}} \int = 78$ g C/m²/an$]$

$3^{\text{ème}} \int = 113$ g C/m²/an

$4^{\text{ème}} \int = 140$g C/m²/an

Fig 6

II. Interpretation of the seasonal variation and nutrient dependency problems .

1. The spring bloom of 1974

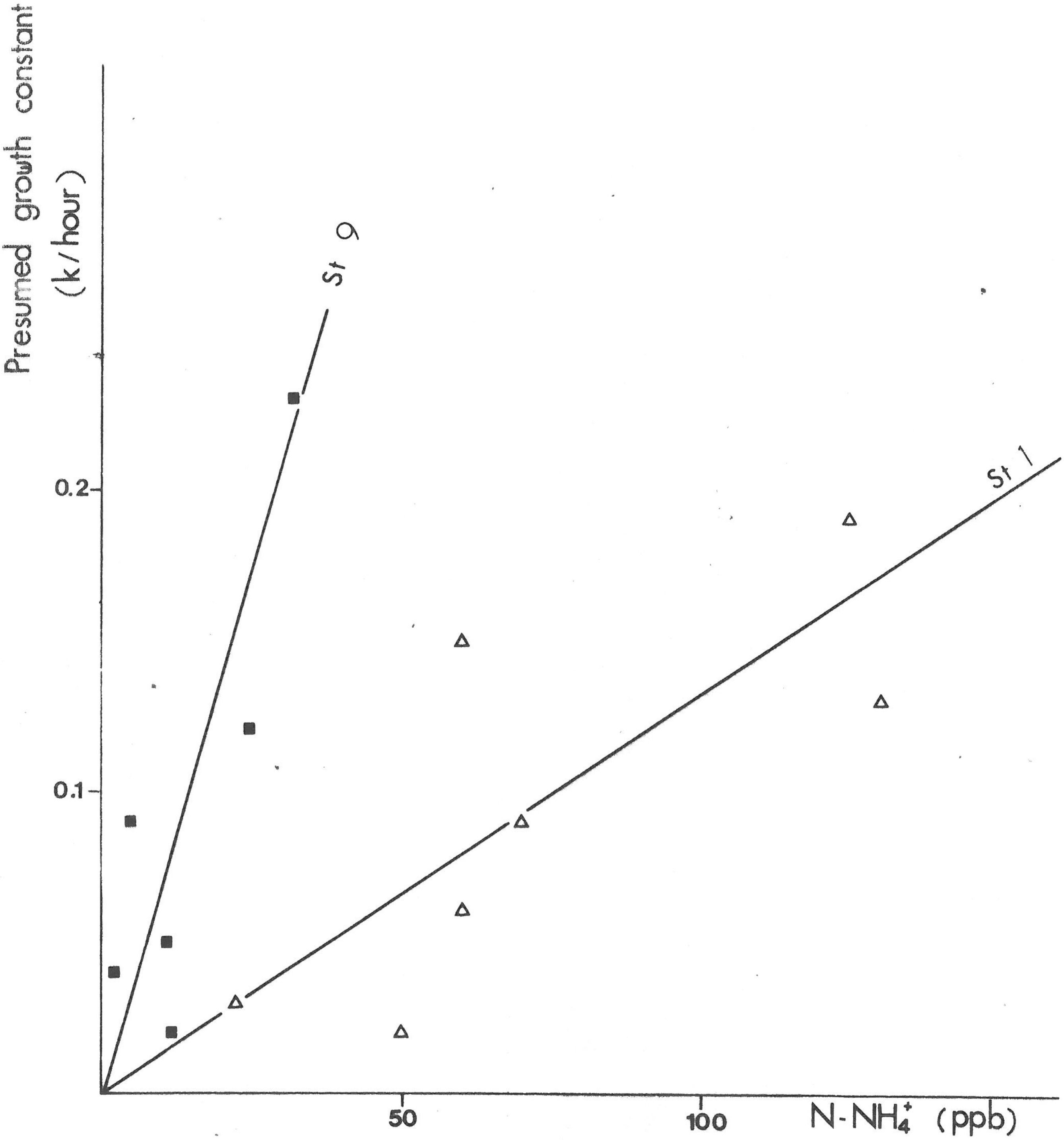
As mentionned in the introduction , an effort is made to interpret the seasonal variation observed . The measurements made at some sampling stations during the spring bloom should allow us such a work . The results however were so confusing that they are discussed in an apart section (see chap. 7 a) .

2. Ammonium control of growth and of nitrate uptake

At the time of the spring bloom , the physiological state of the phytoplankton , given by the ratio P_{opt}/chlor. a has been seen to be rather well correlated with the NH_4^+ concentration in water and not with the NO_3^- or the total inorganic nitrogen concentration (fig. 7) . P_{opt}/chlor.a ratios have the same dimensions as specific growth constants. Provided the relation chlor.a-carbon in phytoplankton cells is ascertained ,one can express the hourly optimal growth rate as a function of limiting nutrient substrate (Michaëlis-Menten kinetics) . From fig. 7 , it appears that the phytoplankton of station 1 (zone 1-S) would exhibit a higher half-saturation constant than that of station 9 (zone2) , presumably due to the differences in taxonomic composition . In neither station , k_{max} seems to be reached . For modelling purposes , a linear relationship could thus replace the usual hyperbola .

The question arises whether NO_3^- is consumated at all . On the 19th April , the NO_3^- and NH_4^+ concentrations in water at station 1 were respectively 53 and 10 μM/l . Thus a ratio of about 5 . Strickland and others (1969) have shown that for ratios below 7.5 , NH_4^+ was

Fig. 7



preferentially used . This is due to the repression of nitrate reductase synthesis by NH_4^+ (Eppley and others ,1969) . Thus there would be no significative uptake of NO_3^- before the 30th April (ratio = 8) .Such observations are also supported by the work of Helder (1974) on the Wadden Sea where the NO_3^- variations in time seem not to be correlated with the biological activity . In our area ,such a demonstration is made difficult by the spatial heterogeneity problems (see chap. 7 a).

The particular topic of nutrient dependency will be further investigated on the field by the means of enrichment proofs that should allow us to indicate which are the limiting nutrients and the corresponding saturating concentrations .

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