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I. SUMMARY

The effect of nutrient enrichment from the Rhine on some major characteristics of the phytoplankton ecosystem of dutch coastal waters was studied with ^{14}C, liquid scintillation and Coulter Counter techniques. The magnitude of primary production in the most eutrophic waters closest to shore and the Rhine mouth was found to be affected by turbidity, rather than by concentration of nutrients only. That the annual production cycle starts later in onshore waters than in the clear offshore water mass is probably also due to turbidity. Primary production of dissolved organic matter was at times up to 20 % of the total carbon fixed per square meter. It is suggested that filtrate radio-activity is to a large, though unknown, extent derived from labeled organic compounds of the mucus of colony-forming species like *Phaeocystis globosa* and *Chaetoceros socialis*.

The nutrient regime and degree of eutrophication, but also other factors like stratification, turbulence, and light conditions seem to control the community structure and species composition of the populations, and therewith the amount of primary productivity. Diatom productivity in the dutch coastal water mass can be high even in summer, in spite of a near-depletion of silicate already early in spring. This can be so because silicate concentrations may periodically rise, e.g. in stratified water due to the dominance of dinoflagellates in the primary producer populations, or after periods with certain climatic-hydrographic conditions when diatoms may sink out of the euphotic zone. *After* such periods, "silicate demand" may become high again (diatom growth is enhanced by eutrophication), up to a level where this nutrient becomes

near-depleted and possibly even limiting.

Chlorophyll a can serve as a rough index for algal biomass, the latter expressed in μ^3 and calculated with a Coulter Counter technique. Chlorophyll a concentration at the surface is also linearly related with surface primary productivity - although the rate of production per unit chlorophyll fluctuates considerably with the season, if only because of seasonal fluctuations in the phytoplankton community structure.

It can be surmised from ^{14}C dark fixation experiments that bacterial activity is high especially close to the coast and the river Rhine outflow.

It may be tentatively suggested that during late fall and in winter, in the virtual absence of phytoplankton, the shape of the size spectrum of suspended particles (in the size range 2 - 120 μ) is predictable for various regions in the Southern Bight of the North Sea.

II. INTRODUCTION

That the discharge of the river Rhine into the Southern Bight of the North Sea causes eutrophication and high fertility of dutch coastal waters is hardly being questioned these days. However, to what extent this increase in nutrients gives rise to enhanced phytoplankton growth, and how nutrients and primary productivity interact in these waters had until now hardly been analyzed. Due to this lack of knowledge, a theoretical framework is still missing around which to build our ability to predict undesirably heavy phytoplankton blooms, to forecast the occurrence of the occasional summer blooms of toxic dinoflagellates, and to control and direct the eutrophication process to a point where a beneficial effect on the marine ecosystem would result. Two recent studies on primary production in coastal waters of the Netherlands, one by Postma and Rommets (1970), one by de Kroon (1971), fill up part of the gap in our knowledge.

The purpose of the present study was to acquire an understanding of the effect of nutrient enrichment from the Rhine on some major characteristics of the phytoplanktonic ecosystem of dutch coastal waters. At a number of stations the seasonal variations in chlorophyll concentration and productivity were analyzed; the biomass of the various population components (μ-flagellates and nanoplankton, the larger diatoms, and the larger dinoflagellates) was measured, and its distribution in size classes established in order to characterize the community; and the most important species were identified. Assessment of the abiotic factors assumed to have most influence on the dynamics of the phytoplankton community in the various seasons included measurements of hydrographical and chemical nature, and the drawing of particle size spectra of suspended particles.

One goal of the present investigations is to find out which factors that can be monitored automatically (for example, with a Turner Fluorometer (Strickland & Parsons, 1968), or an Auto Analyzer (Andersen, 1970) can account for most of the temporal and spatial variations in the magnitude of primary production in dutch coastal waters.

III. MATERIAL AND METHODS

Four one-week cruises were made in 1971 in the eastern section of the Southern Bight of the North Sea: one in late winter (1-5 March), one in spring (26-29 April), one in summer (30 August - 3 September), and one in the fall (1-5 November). The stations that were occupied are shown in Fig. 1.

Surface samples were taken with a plastic bucket, sub-surface samples with 5 liter HydroBios samplers with a non-metallic inner lining, at depths that correspond to 100, 70, 50, 10 and 5% of surface light intensity. The depth of the euphotic zone was computed from Secchi disc observations with the simple formula $Z_{0.01} = 3 \times$ Secchi (Visser, 1970); the assumption being that the euphotic depth is that depth where incoming radiation is attenuated to 1% of its value at the surface. The other depths were calculated from extinction curves derived from the same Secchi values using Poole and Atkins' formula (Anderson, 1964); an underwater irradiance photometer was used only very occasionally, because readings were quite erratic due to wave - induced ship movements and passing clouds.

Primary production was measured with the carbon - 14 method of Steemann Nielsen (1952), using a simulated in situ technique. This method was at one occasion checked with an <u>in situ</u> series. Good agreement between the two methods was found. Samples in light and dark 100cc glass bottles (and in some experiments quartz bottles) were inoculated with 4 μCi ampules obtained from the International Agency for ^{14}C Determination (Charlottenlund, Denmark), and incubated from sunrise to noon, or from noon to sunset, in a deck-mounted incubator described by Jitts (1963). The side walls and bottom of the incubator compartments were blackened in order to simulate conditions at depth as good as possible (Cushing, 1957). The compartments were covered with gray neutral-density filters that transmitted the same fraction of surface light intensity as was present at the depths that were sampled. Surface water was continuously pumped through the incubator. The samples were agitated gently by the ship's movements (cf. Holmes, 1968).

After incubation, samples were filtered with 0.45 μ membrane filters. These were not fumed with HCl, since acidification can remove a large fraction of previously incorporated carbon (Allen, 1971). The filters were directly put into 20 ml . Packard vials containing 15 ml of a scintillation solution with the same composition as described by Anderson and Zeutschel (1970), and stored at room temperature for later counting at 5° C on a Nuclear-Chicago Liquid Scintillation Counter. Quench correction for the establishment of counting efficiency (which proved to be around 80 to 85%) was done with the Channels Ratio method. In order to measure production of dissolved organic carbon, 2 ml aliquots of the air-bubbled and acidified (pH=2.8) filtrates were also added to 15 ml scintillation solution in 20 ml vials that were later counted at 5° C in the laboratory. Duration of the air bubbling was no more than 15 minutes, because longer periods of "gas washing" hardly reduce the background (Thomas, 1971). Calculations of the amount of primary productivity of organic matter were done following Doty and Oguri (1957), but with a correction for isotope discrimination (Strickland, 1960) and for the ampule activity, which was found not to be 4 μCi as stated by the International Agency for ^{14}C Determination, but 3.5 μCi (cf. Lloyd, 1971). Chlorophyll a was determined according to methods described by Strickland and Parsons (1968).

The pigment ratio D_{430}/D_{665}, which according to Margalef (1963, 1965) and Castellví (1964) is a rough measure for the ratio "yellows/greens", was also estimated. D_{430} and D_{665} stand for spectrophotometric extinction at wavelengths 430 and 665 nanometer.

Biomass of phytoplankton (expressed in μ^3) was measured with a Coulter Counter model B. Particle size spectra (Sheldon and Parsons, 1967a) of all particles between 3 and 120 μ equivalent diameter (i.e. the diameter of a sphere with the same volume as the particle) were obtained with a two-tube technique (Sheldon and Parsons, 1967b). For each size class, the ratio of non-living to living particles was then estimated with a Zeiss inverted microscope on counts taken on sedimented samples in lugol's solution with glacial acetic acid (Utermöhl, 1958). Diameters of phytoplankton species were checked with diameter and equivalent diameter data in the literature (e.g. Saunders & Glenn, 1969; Reid Fuglister & Jordan, 1970).

Salinity was measured with an inductivily coupled salinometer; silicate and phosphate according to Strickland & Parsons (1968); total P according to Menzel & Corwin (1965); and the dissolved organic P concentration was obtained by subtracting the phosphate phosphorus value from the total P value. Ammonia was determined according to Koroleff (1970) and Solórzano (1969), nitrate according to Shinn (1941), and nitrate following Wood, Armstrong & Richards (1967).

IV. HYDROGRAPHY OF THE AREA

1. Water masses, salinity, turbidity

High-salinity Atlantic water (35 ‰) enters the southern North Sea through the Straits of Dover, and water of low salinity is found along the continental and British coasts due to run-off from the land. In the area studied (the eastern section of the Southern Bight) two water types can thus be distinguished: Channel Water, with an oceanic origin and found in the central Southern Bight; and continental coastal water (Laevastu, 1963). The latter is a mixture of Channel Water and Rhine, Meuse and Scheldt river water, the largest supply of freshwater coming from the Rhine. Because the residual current flows along the dutch coast in a north-easterly direction, the river water is deflected to the right upon entering the North Sea; the isohalines characteristically run parallel to the dutch coast, salinity increasing seawards (see, e.g., Tijssen, 1969). The salinity values for surface water found for 1971 (Table I) also show this increase with increasing distance from shore (for location of stations, see Fig. 1).

Secchi disc readings are given in Table I. In general, turbidity increased towards the coast. However, a general correlation between salinity and transmittance was not found, if only because of the spatial and seasonal variability in biomass and in concentration of other suspended particles (see section V).

Notice that the salinity is not the same in all seasons at any of the stations. Most interesting is the value found (at high tide) at station 7 in late winter, when the freshwater discharge from the Rhine was apparently quite high. The comparatively high salinity found (at high tide) in the fall of 1971 at coastal stations 6, 7 and (most strikingly) 8 (located very close to the Rhine mouth) are due to the fact that during the preceding weeks very little water, but containing relatively much chloride flowed through the Rhine. Apparently, and not surprisingly, the salinity at stations close to the dutch coast depends to a large extent upon the magnitude of the Rhine discharge. In contrast, seasonal changes in salinity were quite small at stations 4 and 1, farthest from shore and least under the influence of the dutch coastal water mass.

As a rule, the water of the Southern Bight is homohaline and homothermal the whole year round (Laevastu, 1963; Tomczak and Goedecke, 1964), except for the seasonal haline stratification in summer in the region near the island of Texel, Vlieland and Therschelling (Dietrich, 1950). Very close to the dutch coast a stratification gradient, due to fresh water discharge from the rivers (Visser, 1970), may sometimes occur.

2. Nutrients

Bimonthly distribution charts with isopleths for inorganic phosphate, nitrate and silicate in the North Sea can be found in the Serial Atlas of the Marine Environment, folio no. 11 (Johnston & Jones, 1965). Values found for these nutrients on the four cruises made in 1971 for the present study agree with the levels plotted in the above mentioned Atlas and those found by Tijssen (1969).

a. Phosphate and dissolved organic P.

In Table II all phosphate measurements are recorded; values for dissolved organic phosphorus are placed between brackets. A marked seasonal variation was found at all stations, the lowest PO_4-P values being generally found in spring. Dissolved organic phosphorus values were generally higher in summer than in spring, and decreased seawards, the exception being station 1 during cruise II. The variation in dissolved organic phosphorus from station to station was very much smaller than the spatial variation in inorganic phosphorus.

b. Silicate

Table III gives the distribution of the silicate concentration (in μgrat/l) in 1971. The high concentrations found in the beginning of March (cruise I) had disappeared hardly two months later (spring cruise) at all stations. Low silicate concentrations persisted in summer, but values were increasing again in the fall. The very high value found at station 7 (in the eutrophic water close to the Rhine mouth) in late winter probably reflects the fact that river water supplies most of the silicate in dutch coastal waters. Interesting is the finding of a rather high value at station 1 (a far-offshore station in oligotrophic water, S = 34.4 ‰) in summer. This silicate had been depleted again in the fall, when values at all stations were on the increase.

c. Nitrate, nitrite, ammonia

Table IV summarizes the distributions of nitrate, ammonia and nitrite, all expressed in μgrat/l. In all seasons, values for all three decreased seawards with increasing salinity, except that the ammonia values in summer at stations 2 and 5 were found to be slightly higher than at the more coastward stations of their sections (resp. station 3 and 6).

Nitrite concentrations remained most constant from season to season, with the most pronounced spring-summer minimum at the farthest offshore, oligotrophic stations 1, 4 and 5, and with a remarkable constancy at stations in the eutrophic waters close to the dutch coast (stations 6, 7 and 3).

The nitrate/ammonia ratio showed large seasonal variations at all stations. Generally speaking, lower concentrations of both ammonia and nitrate were encountered in spring and summer, than in late winter and in the fall. However, the nitrate concentration had a more outspoken seasonal variation than the ammonia concentration. Depletion of nitrate proceeded more rapidly than ammonia depletion in spring and at all stations; but in the fall ammonia levels had increased since the foregoing summer cruise to a greater extent than had nitrate concentrations at the most coastal stations (6, 7 and 8); while at stations farther offshore, in more saline oligotrophic waters, nitrate concentrations had risen more rapidly than ammonia in the period between cruises III and IV.

V. PARTICLE SIZE SPECTRA

Particle size spectra of suspended particles in surface water samples taken at the various stations are given in Figures 2 to 5 inclusive. The spectra were obtained by sizing and counting particles in subsamples with a Coulter Counter, equipped with a 100µ and a 280µ orifice tube. The most informative way of presenting the data has been found by Sheldon & Parsons (1967) to be when particle counts are given (on the ordinate) as volume, not numbers, in each size class, while particle diameter is measured on the abscissa on a log scale.

1. Total particle volume and phytoplankton volume

In Table V all particle volume data are given; biomass data are calculated only for groups of algae: Bacillariophyceae (= diatoms), µ - flagellates (incl. naked dinoflagellates), and Dinophyaeae (= the larger, armed dinoflagellates like *Ceratium*, *Peridinium*, and *Dinophysis*). Because the two-tube technique used did not allow particles larger than 120µ to be sized and enumerated, only those organisms smaller than 120µ (equivalent) diameter have been counted. This is a very good approximation of the total biomass, because organisms with a diameter over 120µ (e.g. *Biddulphia regia*, *B. sinensis*, *Coscinodiscus* spp.) made up only a minor fraction of the total algal volume.

In all seasons, the total volume of suspended particles increased towards shore - a finding that could have been anticipated from the Secchi disc data reported in Table I, where we saw a coastward increase in turbidity.

The particle size spectra and biomass data show that seasonal variations both in total particle volume and in phytoplankton biomass (volume) are considerable at all stations. This is probably the main reason why the correlation coefficient between salinity and secchi disc readings was found to be rather low. The most important factor influencing the large season - to - season variations in total particle volume was the seasonally varying phytoplankton standing stock, both in offshore waters and at the coastal stations; although it cannot be generalized that seasonal variations in total suspended matter closely followed quantitative variations in phytoplankton standing stock. The seasonal variation in the content of non-living particles was stronger in eutrophic coastal water than in the oligotrophic area of the central Southern Bight (see Table III).

The ratio living/non-living suspended particles varied greatly with the seasons at all stations. Very low ratios were generally found in spring and fall, especially at stations close to shore (stations 3, 7, 8), where the value was as low as 1:70. In both spring and summer, however, values were generally much higher, up to between roughly 1:2 and 1:1. The exceptions are the oligotrophic offshore Central Southern Bight stations, where phytoplankton biomass decreased in the period between late winter and spring, while in the same period the volume of non-living particles increased. But also here, the summer ratio non-living/living particles was high: about 1:1.

Finally, it is interesting to notice how little difference there was between the particle size spectra and the total particle volumes in late winter and in the fall at some stations. These two seasons resemble each other in that there is very little phytoplankton present in the water in these periods. The particle size spectrum of the water closest to the river Rhine outflow (station 7 of cruise I, station 8 of cruise IV) was nearly the same in late winter and in the fall, with a peak around 8 to 10µ. The same phenomenon was found in the saline Channel Water mass of the central Southern Bight, where the particle volume of non-living particles found in late winter (cruise I) hardly differed from the one found in the fall, 9 months later.

It may be concluded that it seems to be possible to use the particle size spectrum as a water mass tracer, but only in those seasons when phytoplankton is absent.

2. Seasonal variations in algal biomass in oligtrophic and eutrophic areas

In spring, summer and fall, a biomass increase towards shore was found on both sections (see Fig. 1 for location of sections). However, biomass levels were comparatively low at the most eutrophic stations 7 and 8, located closest to the river Rhine outflow. At stations 2 and 3, much less directly under the influence of polluted freshwater discharge, biomasses were amongst the highest found in spring and summer. A linear increase in biomass with increasing eutrophication was thus not found.

During the late winter cruise, in contrast, the algal biomass in the oligotrophic offshore water (stations 1 and 4) was found to be 6 to 10 times higher than at the most coastal stations of the corresponding sections. Apparently, in the Southern Bight of the North Sea the "spring bloom" starts later in the turbid water close to the dutch coast, than in the clear saline Channel Water mass of the Southern Bight, where it is already underway even before spring has come.

As already mentioned before, phytoplankton biomass varied with the seasons at all stations. Two patterns can be seen. In the oligotrophic Channel Water (central Southern Bight) there was a late winter maximum ("spring bloom"), a rapid decrease during early spring, another peak in summer, and a decrease towards the fall. In contrast, in the coastal water mass very little biomass was encountered in late winter, but a rapid increase took place in early spring to a biomass level that was roughly the same in spring and summer. Biomass decreased rapidly in the fall.

3. Particle size spectra of major phytoplankton groups

In the spring, only two major algal groups were found: µ-flagellates and diatoms. In this season, the µ-flagellates had a larger biomass than diatoms at all stations except those closest to the Rhine outflow, where diatoms outweighted the nanoplankton.

In summer, however, the diatom biomass greatly exceeded the biomass of the other algal groups (µ-flagellates and dinoflagellates) at all stations, except at station 1 (located relatively far offshore, in the stratified water mass off Texel). Here the bulk of the summer biomass consisted of large dinoflagellates of the genus *Ceratium* (mainly *C. fusus*), with an equivalent diameter between 25 and 35 µ.

If we group all phytoplankton organisms with a diameter under 20µ as "nanoplankton" (Sheldon & Parsons, 1967), and all algae larger than this under the term "netplankton", we see that, generally speaking, nanoplankton (= μ-flagellates plus the smallest diatoms) were the most important primary producers in spring at all stations.

In summer, however, netplankton formed the bulk of the primary producer biomass, and increasingly so in a coastward direction towards areas where the freshwater discharge has more influence. In the dutch coastal water mass there was an increasing preponderance of large diatoms towards the coast in summer. The biomass of large dinoflagellates (*Ceratium*, *Peridinium*, *Dinophysis*) decreased in the same direction in this season, to a total absence at those stations closest to the Rhine mouth.

Summarizing the above we may state that there was an offshore-inshore trend in the ratio nanoplankton-netplankton, with the netplankton increasing in importance towards the coast.

4. Species composition of spring and summer communities

The species composition showed a marked temporal and spatial variation. Some major features of this variation are:

a. the large amounts in spring of *Phaeocystis globosa* (= *P. pouchetii*; Boney, 1970) a colony-forming μ-flagellate (individuals 7 to 10 μ diameter),

b. the occurrence in the plankton of small (< 10μ) benthic pennate diatoms, a.o. of the genera *Navicula*, *Rhaphoneis*, *Gyrosigma*, *Pleurosigma*, at the stations very close to shore,

c. the finding at station 8 (very close to the Rhine outflow) of freshwater and estuarine indicators like *Scenedesmus* and *Melosira borreri*,

d. the fact that species assumed in the literature to be spring species (certain species of *Thalassiosira* and *Coscinodiscus*) occur along the dutch coast also in summer,

e. the fact that the coastal diatom community in summer has a species composition quite different from that in spring,

f. the correlation between species composition and distance from the coast, or rather: the relationship between species composition of the community and degree of eutrophication.

These latter, most important points will receive more attention here. It was already noticed during the spring cruise that certain phytoplankton species occurred predominantly at coastal stations, while other species were more typical for the more offshore stations. Of course, some species found in spring were common both in oligotrophic offshore and in eutrophic inshore waters: *Chaetoceros spp.*, *Phaeocystis globosa*. However, *Eucampia zoodiacus*, *Cerataulina bergoni* and *Skeletonema costatum* were found to be much more abundant at coastal stations than at offshore station 1 and 4. On the other hand *Rhizosolenia stolterfothii* and *Nitzschia "delicatissima"* were much more abundant in offshore waters. *Noctiluca miliaris*, a large flagellate that because of its size (diameter 500-700 µ) could not be counted with the Coulter Counter technique used and is therefore not represented in the particle size spectra, was much more abundant inshore than offshore.

A difference in species composition between offshore and inshore stations was even more pronounced in summer with stations 2, 5 and 6 again having a position in-between, as in spring. During the summer cruise the characteristic phytoplankters at coastal stations were chain-forming diatom species of *Lauderia* and *Thalassiosira*, with relatively large cells; whereas at the offshore station 4 (located in the (non-stratified) water of the central Southern Bight) a bloom of the very small diatom *Nitzschia "delicatissima"* was typical. The situation at station 1 (offshore, located in the stratified water mass off Texel) was remarkable in that the comminuty here was dominated by *Ceratium fusus* and some other large armed dinoflagellates (*C. lineatum*, *C. furca*, *C. macroceros*, *Peridinium spp.*). A diatom characteristic for both offshore stations was *Bacteriastrum sp.* Diatom species like *sterionella japonica*, *Coscinodiscus spp.*, *Ditylum brightwelli*, *Skeletonema costatum*, *Nitzschia seriata* and *Biddulphia mobiliensis* were all indicative for the coastal stations. Two diatom species were predominantly found at stations 2, 5 and 6, located between the oligotrophic offshore and the eutrophic inshore waters: *Chaetoceros socialis* and *Rhizosolenia hebetata*.

A case in itself was the summer distribution of two closely related species of *Biddulphia*: *B. regia*. *Biddulphia regia* was much more abundant then *B. sinensis* at stations 1 and 4, in oligotrophic offshore waters, but *Biddulphia sinenis* greatly outnumbered *B. regia* at the more coastal stations (ratio 8.5 : 1), with a large predominance of *B. sinensis* (ratio over 15 : 1) at the most onshore stations (3 and 8).

VI. PRIMARY PRODUCTIVITY OF TOTAL ORGANIC MATTER

The ^{14}C method normally used for the estimation of primary productivity only accounts for the particulate organic matter produced. However, recent studies have made clear that from 1 up to 50% of the carbon assimilated during phytoplanktonic photosynthesis can be excreted in the water again in soluble form (Fogg, Nalewajko & Watt, 1965; Hellebust, 1967; Horne, Fogg & Eagle, 1969; Anderson & Zeutschel, 1970; Thomas, 1971; Watt, 1971). Release of ^{14}C-tagged compounds ("excretion") could thus lead to a serious under - estimation of organic productivity by the ^{14}C - technique of

Steemann Nielsen (1952). It was therefore decided to estimate primary production of both the particulate and the dissolved organic fraction on a routine basis. A liquid scintillation method outlined by Anderson & Zeutschel (1970) was used.

Figures 6 to 9 inclusive show the primary production - depth profiles for all stations during the early winter, spring, summer and fall cruises. The amount of carbon fixed per square meter per day is also indicated. Amounts of carbon fixed per cubic meter per day at the various depths were calculated by simply multiplying by 2 the production values obtained in half-day incubations that lasted either from sunrise to noon, or from noon to sunset. It is realized that by calculating daily productivity in this way, we will sometimes overestimate, sometimes underestimate the latter slightly; photosynthetic activity is not always the same in the morning and in the afternoon. Diurnal variations in productivity may occur (e.g. McAllister, 1963). Newhouse, Doty & Tsuda (1967) observed that neritic phytoplankton tends to reach maximal photosynthetic rates in the afternoon, oceanic plankton in the morning. Malone (1971) pointed out that these diurnal rhythms may be related to the nutrient regime, photosynthetic rates tending to peak earlier in the day where nutrient concentrations are low. It seems to depend upon the ratio nanoplankton: netplankton in the population whether the maximum in photosynthetic rate will be found in the morning or in the afternoon. The best estimate of daily production would have been obtained from a series of short incubations, covering the whole day, of samples taken in the same body of water.

1. Main aspects

a. The high percentage of dissolved organic matter production relative to production (= dissolved plus particulate) organic production was striking. In spring, up to 55% of the ^{14}C was found incorporated in the dissolved fraction of organic matter produced in surface samples at stations 6 and 7. Addition of antibiotics to the samples before incubation did not appear to have any influence. In summer percentages were lower ($<$20%), except at stations 2 and 5, where in surface samples they were up to 40%. Less production of dissolved relative to total organic matter was generally found at greater depth. Whenever radioactivity in the filtrate did not rise significantly above the background level, "excretion" was not measured, and production of dissolved organic matter was then assumed to be low. When measured as column productivity (= carbon fixation per square meter, per day), the percentage of recently assimilated carbon going into dissolved organic matter was 20% at most, with a mean in summer of no more than 10%.

b. The "spring bloom" started earlier (as a matter of fact, as early as in late winter) in offshore than in inshore waters. This had already been concluded from the patterns of seasonal variation in biomass at the various stations (see section V. 2).

c. The production per unit biomass (and per unit chlorophyll a) was higher in spring than in summer. The verylarge proportion of nanoplankton in the spring phytoplankton community (see Fig. 3) probably accounts for this finding. Contribution to the primary production by nanoplankton is usually much greater than would be expected from the magnitude of its biomass (e.g. Saijo, 1964; Watt, 1971), nanoplankton having a higher carbon assimilation rate per unit biomass than large diatoms (Findenegg, 1965). Also the column productivity (carbon fixed per square meter per day) was much higher, roughly 2 to 3 times in spring than in summer (except at the offshore stations 1 and 4), although the phytoplankton biomass was approximately the same in spring and in summer.

d. Both in spring and in summer (the most productive seasons) and also in the fall there was an offshore - inshore trend of increasing productivity at the surface (with the exception of station 1). This is not totally unexpected: in section V (2) we saw that there was also a trend of increasing phytoplankton biomass towards the coast in surface samples.

However, productivity per square meter (the productivity of the total water column) decreased towards shore in all seasons (excepting stations 1 and 4, located in the oligotrophic waters of the central Southern Bight). Apparently, increasing eutrophication does not necessarily imply a greater productivity. Since the productivity-depth profiles (Figs. 6 to 9) clearly show a decrease in depth of the euphotic zone towards shore, parallel with an increase in the volume of suspended particles (see Table V), the productivity limiting factor is probably turbidity, or ultimately light.

2. Relationship of chlorophyll with biomass and production

a. Regression lines for the chlorophyll-biomass relationship are shown in Fig. 10. A close correlation between total phytoplankton volume and chlorophyll a cannot be expected, if only because of the variability in species conposition and size spectrum of the phytoplankton community (see Figs. 2 to 5) and in environmental conditions. For example, the ratio chlorophyll *a*/cell volume is generally much higher for nanoplankton and small diatoms than for large netplankton species (Parsons, 1969). Factors that influence the amount of pigments in the same species are the physiological condition of the cells, and light intensity (Hellebust, 1970).

From the regression lines (Fig. 10) it may be concluded that the chlorophyll *a* concentration of a sample taken in the Southern Bight of the North Sea can serve as a rough index for its biomass (or total algal volume) contents (r = 0.9). However, when a large dinoflagellate like *Ceratium* dominates the biomass (station 1 in summer; see Fig. 4), a large phytoplankton volume can apparently be expected at low chlorophyll *a* concentrations. The presence of such a bloom can be suspected from a higher pigment ratio (i.e., the ratio "yellows/greens"): over 3.3. However, pigment ratios (D430/D665) over 3.3 were also found when there was much non-living suspended particulate matter relative to living present in the water. When plankton is scarce relative to tripton, the pigment ratio is merely indicative for the pigment diversity of the non-living suspended particulate matter.

b. Regression lines for the chlorophyll *a* - primary production relationship are drawn in Fig. 11. It can be seen that generally speaking a linear relationship seems to hold. However, the slope of the lines is variable, probably because in spring such a high proportion of the primary producer biomass consisted of µ-flagellates, which resulted in a high production per unit chlorophyll; while in summer larger diatoms dominated, with a much lower production per unit chlorophyll. An exception is station 2 during cruise II, where due to the predominance of μ-flagellates a very high production took place at a relatively low chlorophyll concentration. A second exception is station 1 during the summer cruise, where the dominance of *Ceratium fusus*, a large dinoflagellate, resulted in a high rate of photosynthesis at a rather low chlorophyll *a* concentration.

In summary we can say that the photosynthetic capacity (rate of photosynthesis per unit weight of chlorophyll *a*) in dutch coastal waters has a considerable seasonal variation; its value strongly depends upon the phytoplankton community structure.

3. Dark fixation

When primary productivity is measured with the ^{14}C-technique of Steemann Nielsen (1952), a "dark" bottle is routinely incubated parallel to a "light" bottle; the "dark" value is then substracted from the "light" value in order to obtain a good approximation of the amount of carbon fixed in the process of photosynthesis. The origin of the radio-activity of organic material in the *dark* bottles cannot be photosynthetic fixation of ^{14}C, but seems to be mainly the non-photosynthetic biochemical processes (e.g. the Wood-Werkman reaction) going on both in the algae and in heterophs.

The hypothesis that non-photosynthetic assimilation of $^{14}CO_2$ is indeed to a large extent due to the activity of marine micro-organisms would be supported if a positive correlation were found to exist between dark fixation and water temperature: higher temperature generally results in a greater bacterial activity (cf. Takahashi & Ichimura, 1971). I found that dark fixation was lowest in late winter (water temperature 4° C), higher in spring (temperature 8° C), and still higher in summer. Fall values (cruise IV) were even higher (though not significantly) than the summer values, although the water temperature had dropped to 13° C. This finding supports the assumption that micro-organisms contribute materially to fixation of ^{14}C in the dark, because the seasonal variation in bacterial population size does not follow closely the seasonal variation in temperature: Sieburth (1967) showed that the bacterial curve lagged behind the temperature curve by two months (which suggests that a selection of thermal and taxonomic types is continuously taking place).

A positive correlation between dark fixation and the amount of suspended matter might be expected: it is fairly well known that suspended particles are significant for bacteria in that they provide the necessary substrate on which to grow. However, a significant position correlation was not found. There was no correlation between amount of primary production and dark fixation.

VII. DISCUSSION AND CONCLUSIONS

An important conclusion is that the primary production measured with the conventional ^{14}C technique can lead to a serious underestimation of total (=particulate plus dissolved) organic productivity: the method of Steemann Nielsen (1952) only accounts for the particulate fraction. In the present study it was found that the percentage of recently assimilated carbon going into dissolved organic matter can be up to 20% of the total amount of carbon fixed per square meter. Percentages were always highest when colony-forming phytoplankton species like Phaeocystis globosa and Chaetoceros socialis were important constituents of the populations. I suspect therefore that the radio-activity in the filtrates is not merely due to excretion of organic compounds by the phytoplankton: it is probably to a large, though unknown, extent derived from labeled polysaccharides and other organic compounds of the gelatinous material in which the colony is imbedded. This mucus is no doubt easily pressed through 0.45 $/u$ membrane filters. Secretion of gelatinous sheaths may thus greatly contribute to filtrate activity. Extracellular "release" of dissolved organic matter may further be caused by physical breakage of delicate algal cells upon filtration (cf. Schindler & Holmgren, 1971).

Primary production of organic matter per square meter (i.e., productivity of the water colum) was found to be lower at stations closest to shore, than at more seaward stations. Apparently, eutrophication does not necessarily lead to a greater productivity. The decrease in depth of the euphotic zone towards shore parallel with the increase in amount of both living and non-living suspended particulate material at the surface (see Figs. 2 to 5, inclusive) makes it reasonable to suggest that productivity in dutch coastal waters is negatively affected by "shading", resulting from turbidity. Nutrient concentrations not being in short supply in the waters closest to shore and the Rhine outflow, primary production here is more likely to be ultimately controlled by light than by nutrients. The great load of suspended particles in the coastal water mass, resulting in a decreased transparency, probably also causes the phenomenon that here the production cycle starts later than in the clear waters of the central Southern Bight (at stations 1 and 4, located far offshore). That radiation (not temperature) is a major factor causing the spring outburst of phytoplankton growth was also pointed out by Pechlaner (1970).

Where depth of light penetration is an important factor controlling production rates,nutrient concentrations are governed by phytoplankton growth, rather than the opposite. This may explain the surprising fact that phosphate concentrations at the most onshore stations 8, 7 and 3 were higher in summer than in spring. An increase in the supply of phosphate from land drainage can not be expected to increase primary productivity in the waters closest to shore.

That phosphate concentrations are found to be low in spring and summer does not necessarily mean that this nutrient is limiting photosynthetic rates: excretion by zooplankton (Beers, 1964) and bacterial mineralization (Duursma, 1961) are factors that enrich the water with phosphorus - which, however, is continuously being utilized by the phytoplankton, and taken away by sorption reactions with suspended particles (Jaworski et al., 1972). As to mineralization by bacteria: the observations on dark fixation (section VI. 3) suggest, that bacterial activity was highest in summer and early fall, and especially so in areas where the amount of suspended particulate material in the water was greatest. Dissolved organic phosphorus values were generally higher in summer than in spring, concentrations being highest onshore. Bacterial decomposition of detritus and other organic materials seems to proceed at a faster rate at higher temperatures, fastest in areas where large quantities of particulate matter support large bacterial populations. However, excretion by zooplankton (Butler et al., 1970) and phytoplankton (Kuenzler, 1970) may also be responsible for part of the D.O.P. present. The suggestion that there is a zone of intensive mineralization of organic matter along the dutch coast is supported by the finding, that after the phytoplankton growing season was over the increase in ammonia concentration was more rapid than for nitrate, especially near the Rhine mouth (stations 7 and 8).

Levels of both ammonia and nitrate were sharply reduced at all stations during the phytoplankton growing season (spring and summer). However, it would seem that there is a large spatial and temporal variability in relative importance of these two nutrients as a nitrogen source. From the present work it is not clear whether preference for either nitrogen source occurred in the natural populations of the southern North Sea, although nitrogen uptake based on nitrate seems to be the most important both offshore and inshore. It should be noticed that the seasonal fluctuation in ammonia and nitrate uptake is complicated by interaction between these two nitrogen sources (Dugdale & Goering, 1971), and between light and inorganic nitrogen (McIsaac & Dugdale, 1972).

In view of the abundance of diatoms in dutch coastal waters (see Figs. 3 and 4) silicate should be regarded as one of the primary nutrient salts required by the phytoplankton. It is therefore surprising to find a high diatom productivity not only in spring, but also in summer, in spite of a near-depletion of silicates already early in the growing season. Apparently, silicate did not limit primary productivity all of the time during the vegetative part of the year. Findings of 1972 suggest, that silicate concentrations may rise periodically, e.g. after calm-weather periods, when diatoms tend to sink out of the euphotic zone, while the Rhine and other run-off goes on with supplying silicate to the coastal waters; also after periods of flagellate dominance silicate is again found in the water, since flagellates hardly require any silicate. After such periods the "Silicate Demand" (Kilham, 1971) may become high again through diatom growth, up to near-total depletion of this nutrient, because nitrogen and phosphorus are supplied by the Rhine in such large quantities that silicate may become limiting - a situation similar to the one found in Lake Michigan (Schelske & Stoermer, 1971, 1972).

Support for the theory that phytoplankton succession may be related to nutrient concentrations, rather than merely to temperature (Braarud, 1961), is lend by recent studies on the dynamics of nutrient limitation in the sea (Dugdale, 1967; Dugdale & Goering, 1971). These new insights in the kinetics of nutrient uptake may explain the finding in summer of an inshore - offshore trend of decreasing importance of the larger diatoms, over 25 µ equivalent diameter (cf. Eppley & Thomas, 1969), and possibly also the increase in abundance of the larger dinoflagellates (*Ceratium*, *Dinophysis*, etc.) towards the increasingly oligotrophic regions offshore. This latter group will never be of great importance relative to diatom biomass in the Southern North Sea, where the water column is, as a rule, never stratified. Summer stratification, however, van be expected to result in an algal biomass dominated by motile dinoflagellates; in stratified water, diatoms sediment and disappear. At station 1, located in the area off Texel where a haline stratification tends to occur in summer (Dietrich, 1950; Tomczak & Goedecke, 1964) the phytoplankton biomass was indeed dominated by *Ceratium fusus* and other large Dinophyceae in summer. The low nutrient concentrations did not seem to hamper a vigorous productivity. Margalef (1967) has pointed out that motility is important in a stabilized water column not only as a means to avoid sedimentation, but also because it increases nutrient absorption. Since dinoflagellates do not require silicate for their growth, this nutrient can be expected to increase in concentration in an area where the bulk of primary producers consists of species of this group. At station 1, a comparatively high concentration of silicate was found in summer. In this case, the concentration of this nutrient was governed not by the magnitude of primary production, but by the species composition of the primary producer population.

When certain precautions are taken (section VI. 2), chlorophyll a can serve as a rough index for phytoplankton biomass off the dutch coast. The roughly linear relationship found to exist between surface production and chlorophyll will make it possible to obtain reliable primary production surface isopleths by continuous measurement of this pigment with a Turner fluorometer. Some *in situ* productivity estimates remain necessary because of the seasonal variation in assimilation ratio (productivity per unit chlorophyll a): see Fig. 11. The latter can be expected to be high where μ-flagellates or dinoflagellates are the major primary producers (section VI. 2).

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Table I

Salinities (in S ‰) and (between brackets) Secchi values (in m).

Number of stations		Late winter	Spring	Summer	Fall
Section I, station	1	34.0	35.3 (10.0)	34.4 (7.5)	35.4 (6.0)
	2	31.7 (3.5)	33.1 (2.0)	31.4 (3.0)	32.8 (4.5)
	3	31.1 (2.5)	33.1 (2.0)	29.6 (1.7)	- -
Section II, station	4	34.9	35.2 (8.0)	34.7 (5.0)	35.1 (5.5)
	5	33.8 (7.0)	-	33.2 (3.5)	33.0 (5.0)
	6	30.8 (3.0)	31.8 (2.5)	31.5 (2.5)	32.5 (3.0)
	7	26.4 (2.5)	30.7 (2.0)	30.6	30.9 (3.0)
	8	-	-	25.1 (1.5)	30.1 (2.0)
		1-5 III	26-29 IV	30 VIII - 3 IX	1-5 XI

Table II

Phosphate and (between brackets) dissolved organic P; μ grat/1.

Number of stations		Late winter	Spring	Summer	Fall
Section I, station	1	1.20	0.05 (0.31)	0.11 (0.11)	-
	2	1.32	0.11 (0.14)	0.53 (0.43)	-
	3	1.60	0.09 (0.18)	1.02 (0.48)	-
Section II, station	4	0.29	0.10 (0.14)	0.08 (0.23)	0.2
	5	1.16	-	0.15 (0.30)	0.2
	6	1.92	0.24 (0.22)	0.18 (0.30)	0.7
	7	2.68	0.65 (0.23)	0.78 (0.50	1.5
	8	-	-	2.65 (0.70)	3.0

Table III

Silicate (in μ grat/1) in 1971

		1-5 maart	26/29 april	[illegible]	1-5 nov.
Number of stations		Late winter	Spring	Summer	Fall
Section I, station	1	8.2	0.2	2.7	0.9
	2	17.7	0.6	0.3	1.86
	3	20.6	0.2	0.6	-
Section II, station	4	1.5	0.9	0.2	1.50
	5	8.0	-	0.3	3.93
	6	23.8	0.7	0.3	4.90
	7	38.0	0.8	0.5	8.14
	8	-	-	7.1	11.10

Table IV

Nitrate, ammonia and nitrite in 1971 (µ grat/l)

Number of stations	Late winter	Spring	Summer	Fall
Section I,				
Station 1	24.1- 5.2-0.88	0.2- 0.5-0.1	0.29- 3.0-0.06	0.6- 2.3-0.18
2	31.0-14.8-1.20		0.56- 9.7-0.12	7.2- 7.9-1.12
3	34.6-17.3-1.43	8.4- 3.2-1.6	7.71- 6.5-1.60	
Section II,				
Station 4	6.3- 1.1-0.45	0.4- 1.7-0.1	0.30- 2.8-0.08	0.6- 2.3-0.22
5	18.5- 6.9-0.92		0.31- 5.9-0.26	6.3-17.1-0.84
6	38.2-24.6-1.43	8.4-15.0-1.3	3.58- 3.9-1.28	9.1-16.6-1.34
7	54.9-49.8-2.05	11.4-21.7-1.8	5.45- 9.5-1.64	16.0-31.2-2.04
8			18.56-22.4-2.67	18.2-55.2-2.34

Table V

Particle volumes and biomass ($\mu^3/0.5$ ml)

	Stat. 1	Stat. 2	Stat. 3	Stat. 4	Stat. 5	Stat. 6	Stat. 7	Stat. 8
Late winter cruise								
Total particles	985,000		1,890,000	950,000			2,905,000	
Non-living particles	825,000		1,865,000	550,000			2,860,000	
Total phytoplankton	160,000		25,000	400,000			40,000	
Diatoms	60,000		15,000	240,000			25,000	
μ-flagellates	100,000		10,000	160,000			20,000	
larger dinoflagellates								
Spring cruise								
Total particles	1,440,000	4,695,000	5,830,000	1,185,000		3,200,000	4,435,000	
Non-living particles	1,395,000	3,135,000	3,410,000	1,150,000		1,495,000	2,360,000	
Total phytoplankton	45,000	1,560,000	2,420,000	35,000		1,705,000	2,075,000	
Diatoms	20,000	400,000	765,000	10,000		1,125,000	1,125,000	
μ-flagellates	25,000	1,160,000	1,625,000	25,000		480,000	890,000	
larger dinoflagellates			30,000			100,000	60,000	
Summer cruise								
Total particles	1,972,000	6,674,000	9,789,000	1,735,000	2,900,000	4,792,000	5,505,000	8,305,000
Non-living particles	900,000	3,997,000	6,315,000	865,000	1,475,000	3,170,000	3,570,000	6,305,000
Total phytoplankton	1,072,000	2,677,000	3,465,000	870,000	1,425,000	1,622,000	1,935,000	2,000,000
Diatoms	280,000	2,400,000	3,260,000	810,000	1,340,000	1,530,000	1,780,000	1,970,000
μ-flagellates	7,000	250,000	200,000	30,000	45,000	80,000	155,000	30,000
Larger dinoflagellates	785,000	27,000	5,000	30,000	40,000	12,000		

Table V. (continued)

Particle volumes and biomass (μ^3/0.5 ml)

	Stat. 1	Stat. 2	Stat. 3	Stat. 4	Stat. 5	Stat. 6	Stat. 7	Stat. 8
Fall cruise								
Total particles	650,000	970,000		545,000	839,000	1,485,000	1,625,000	2,532,000
Non-living particles	635,000	950,000		525,000	817,000	1,465,000	1,590,000	2,495,000
Total phytoplankton	15,000	20,000		20,000	22,000	20,000	35,000	37,000
Diatoms	10,000	15,000		10,000	5,000	3,000	15,000	20,000
μ-flagellates	5,000	5,000		10,000	17,000	17,000	20,000	17,000
Larger dinoflagellates								

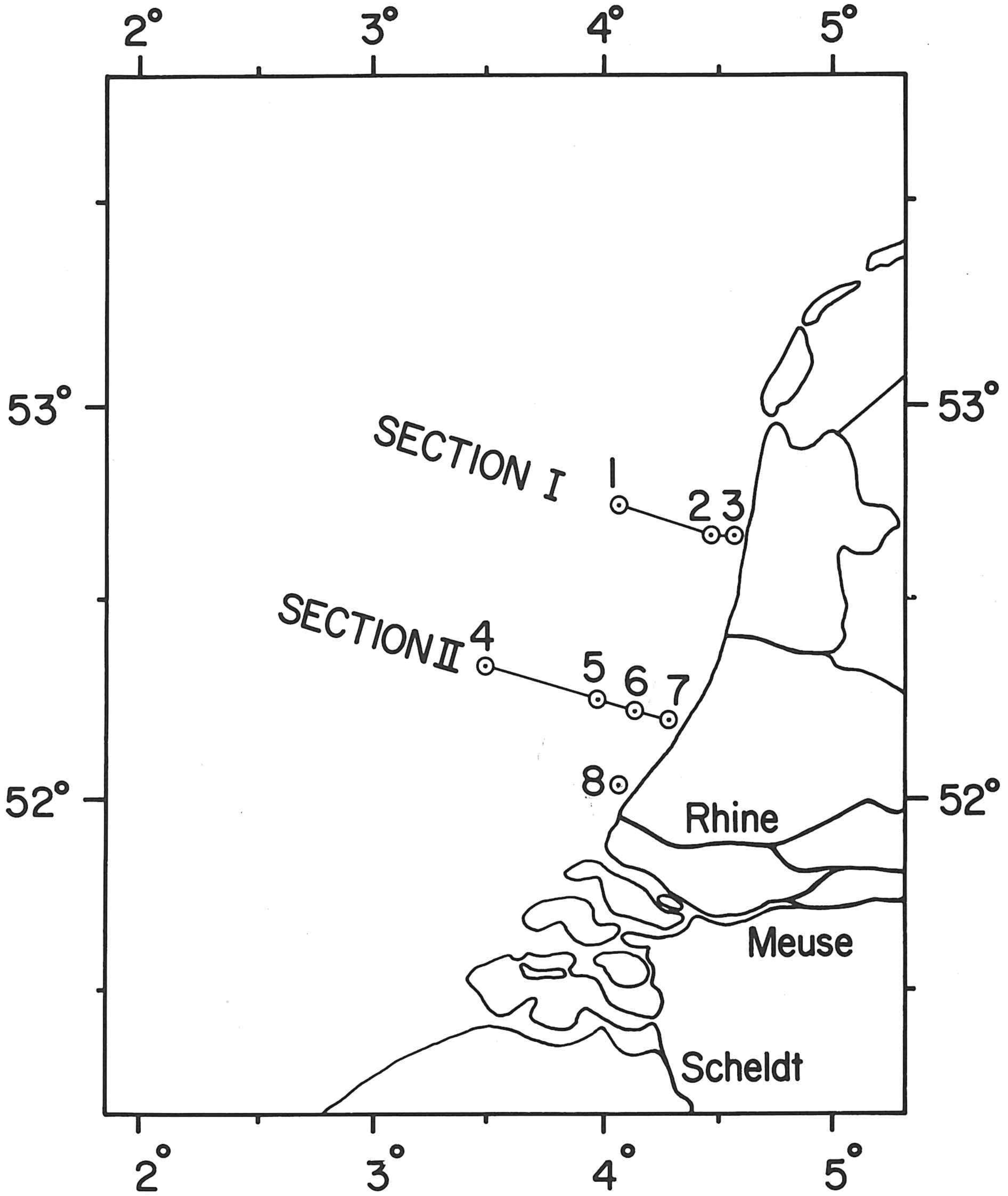


Fig. 1. Position of stations and sections.

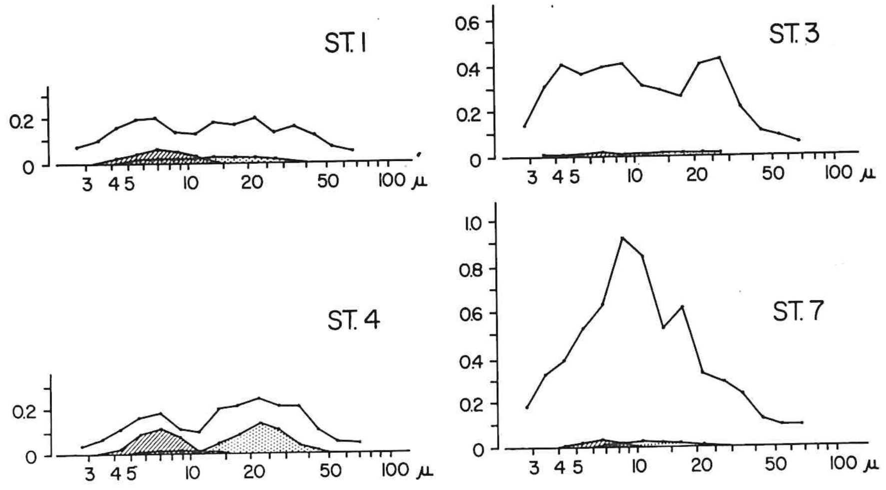


Fig. 2. Size spectra of suspended particles (surface samples) in the beginning of March 1971. For position of stations see Fig. 1. Abscissa: particle diameter ("equivalent" diam; see text, Methods section), log scale. Ordinate: volume of particles, expressed in ppm (by volume; ppm stands for parts per million). Upper line in each diagram: all suspended particles (both living and non-living). Hatched: µ-flagellates only. Dotted: diatoms only.

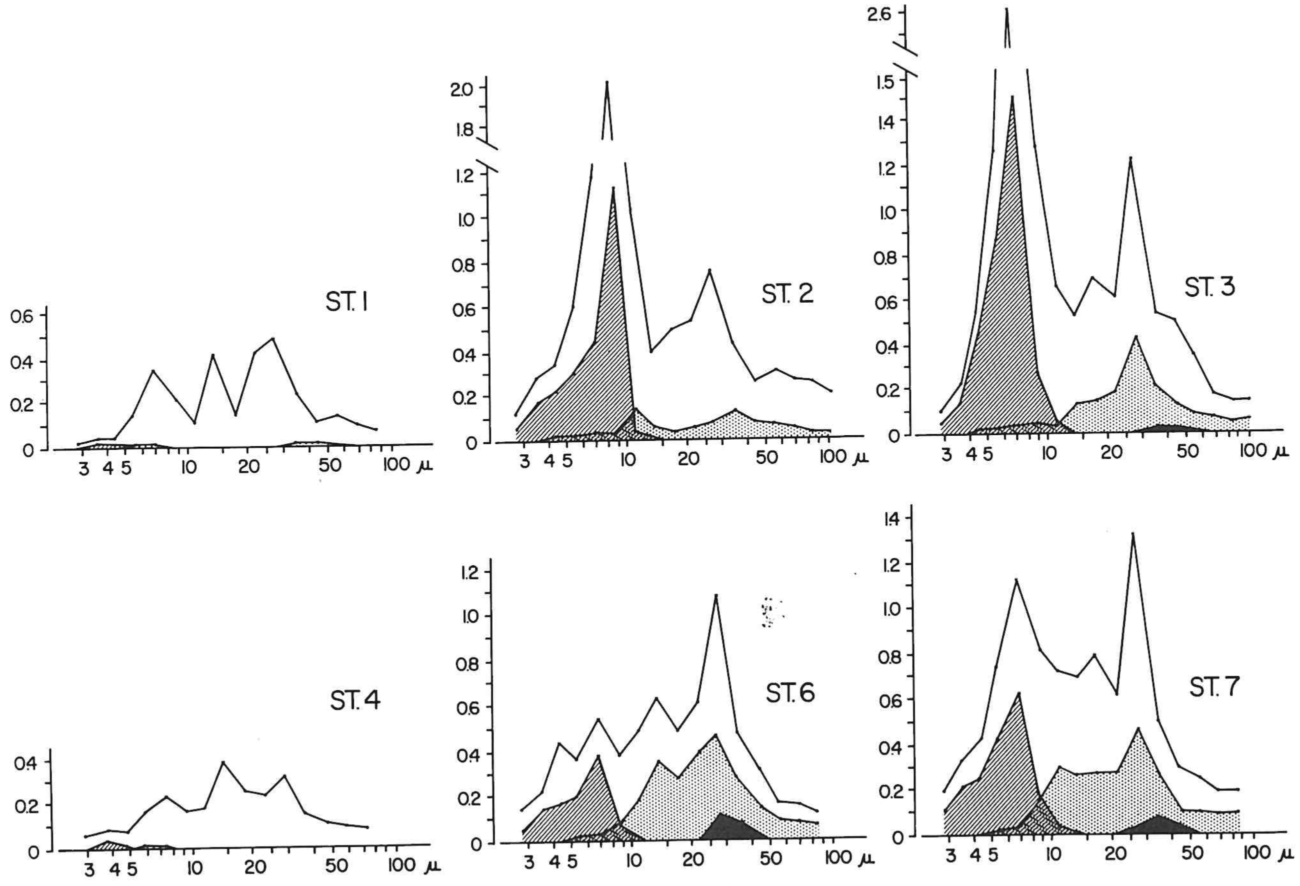
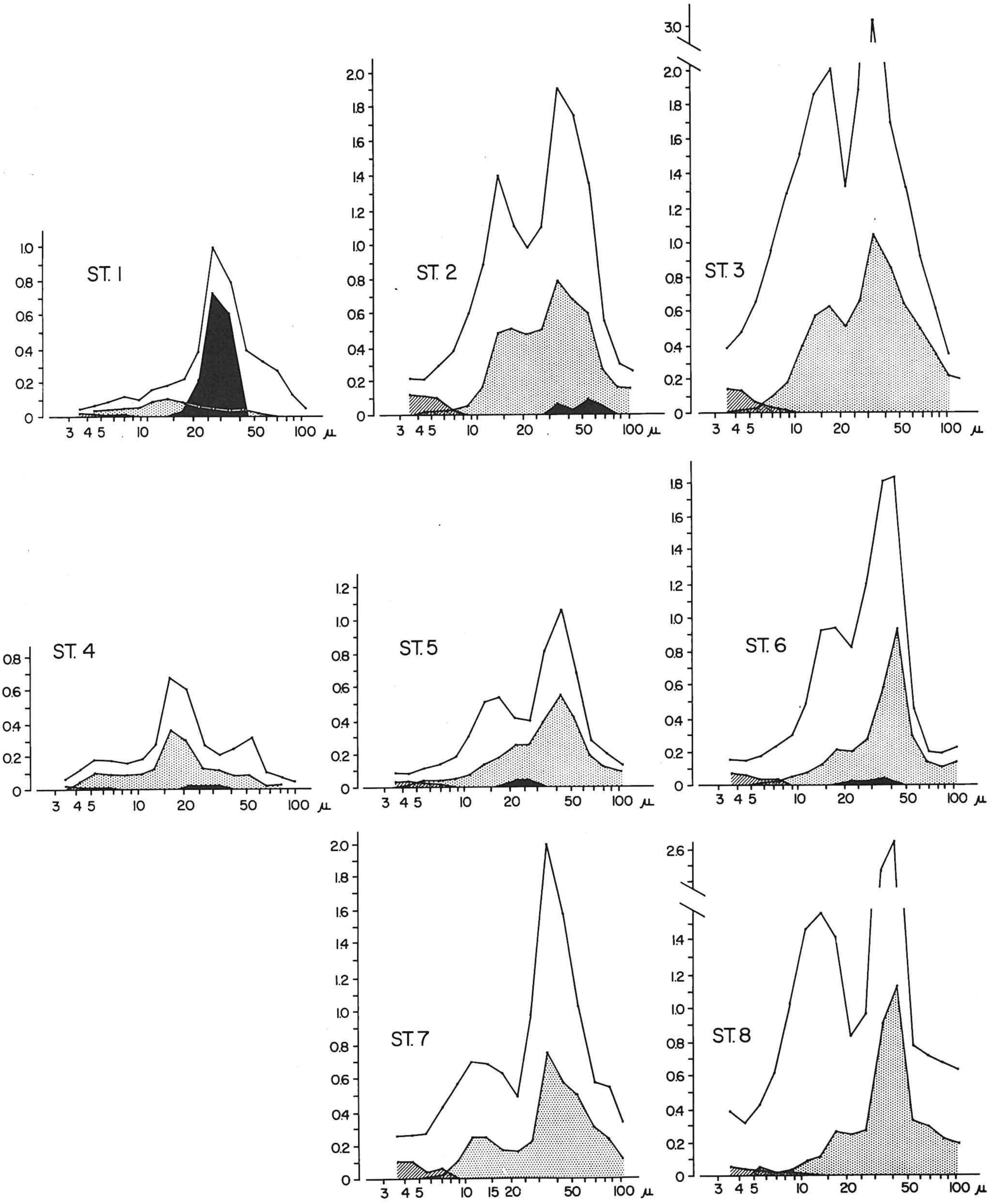


Fig. 3. Size spectra of suspended particles (surface samples), end of April 1971. Location of stations: Fig. 1. Abscissa: particle diameter ("equivalent" diam; see text, Methods section), log scale. Ordinate: volume of particles, expressed in ppm (by volume; ppm stands for parts per million). Upper line in each diagram: all suspended particles, both living and non-living. Hatched: µ-flagellates only. Dotted: diatoms only. Black: armoured dinoflagellates (Ceratium spp., Peridinids, e.a.) only.



g. 4. Size spectra of suspended particles (surface samples), latesummer cruise 1971. For location of stations, see Fig. 1. Abscissa: particle diameter ("equivalent" diam; see text, Methods section), log scale. Ordinate: volume of particles, expressed in ppm (by volume; ppm stands for parts per million). Upper line in each diagram: all suspended particles, both living and non-living. Hatched: μ-flagellates only. Dotted: diatoms only. Black: armoured dinoflagellates (Ceratium spp:, Peridinids, e.a.) only.

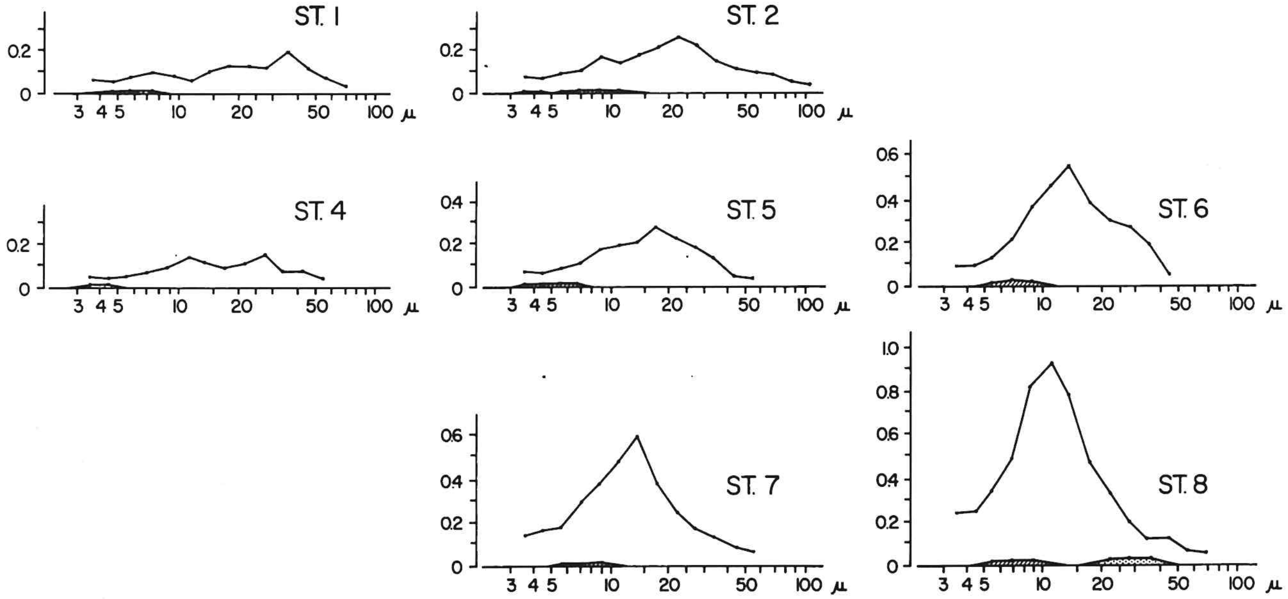
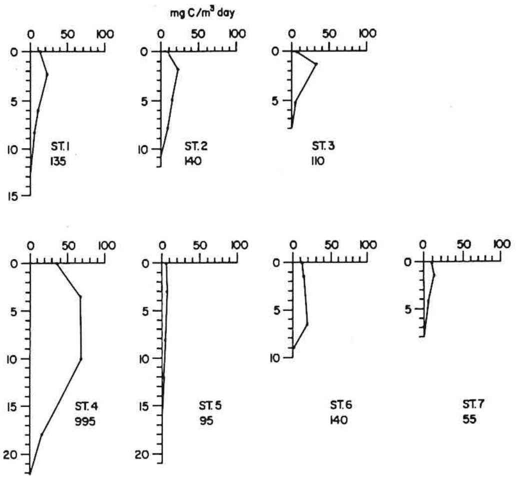


Fig. 5. Size spectra of suspended particles (surface samples), beginning of November 1971. For location of stations, see Fig. 1. Abscissa: particle diameter ("equivalent" diam; see text, Methods section), log scale. Ordinate: volume of particles, expressed in ppm (by volume; ppm stands for parts for million). Upper line in each diagram: all suspended particles, both living and non-living. Hatched: µ-flagellates only. Dotted: diatoms only.



ig. 6. Primary productivity - depth profiles, first week of March 1971. Depth in meters. Amounts of carbon fixed include the dissolved organic fraction. Numbers below station nr. indicate amount of carbon fixed per square meter.

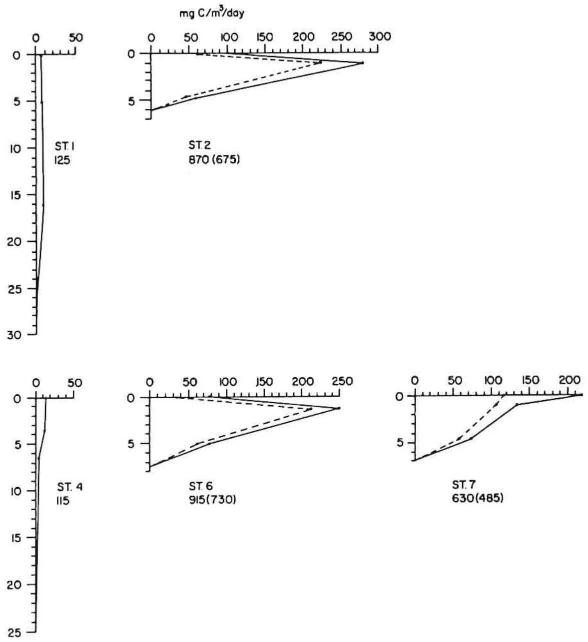


Fig. 7. Primary productivity - depth profiles, end of April 1971. Depth in meters. Dotted line: primary production of particulate organic matter. Unbroken line: primary production of particulate plus dissolved organic matter. Numbers below Station nr. indicate amount of carbon fixed per square meter (numbers between brackets: amount of the particulate fraction only).

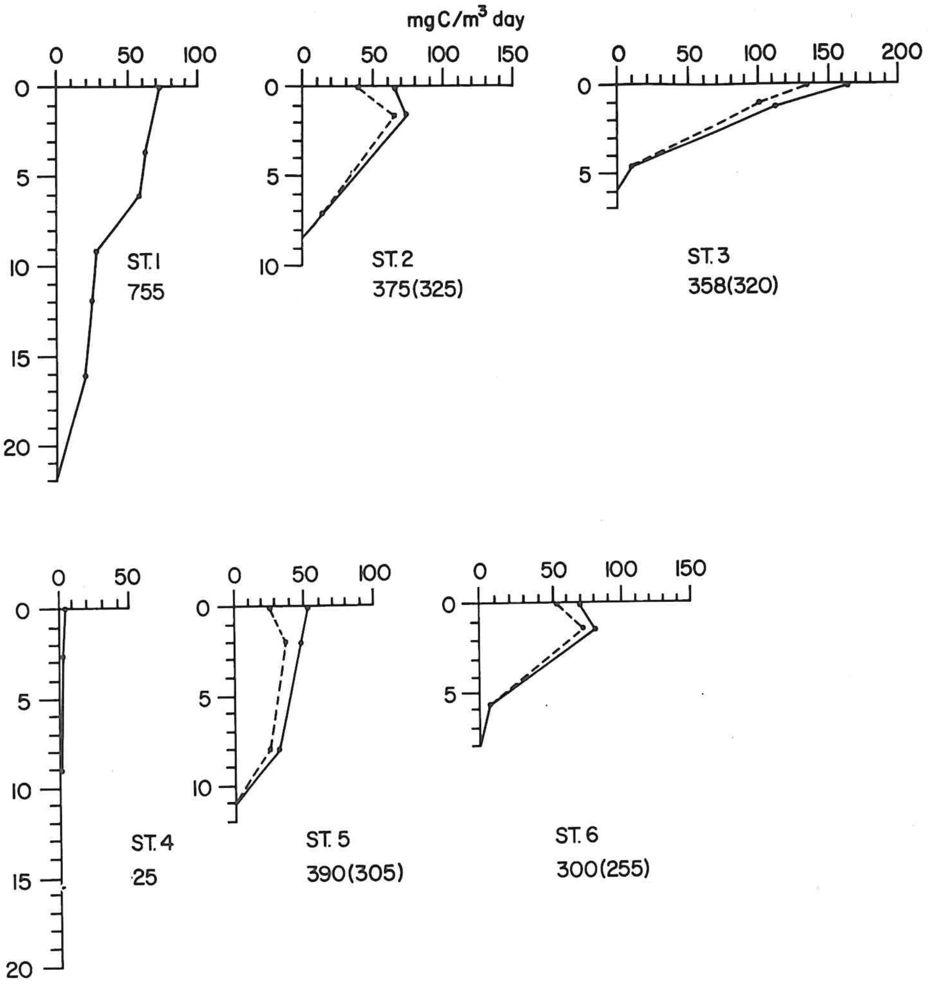


Fig. 8. Primary productivity - depth profiles, latesummer cruise 1971. Depth in meters. Dotted line: primary production of particulate organic matter. Unbroken line: primary production of particulate plus dissolved organic matter. Numbers below station nr. indicate amount of carbon fixed per square meter (numbers between brackets: amount of the particulate fraction only).

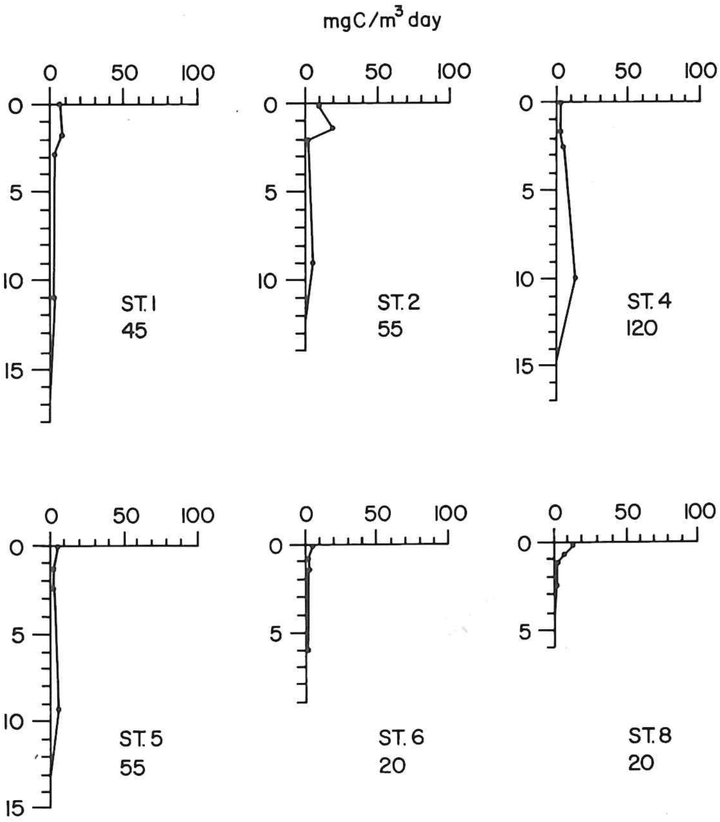
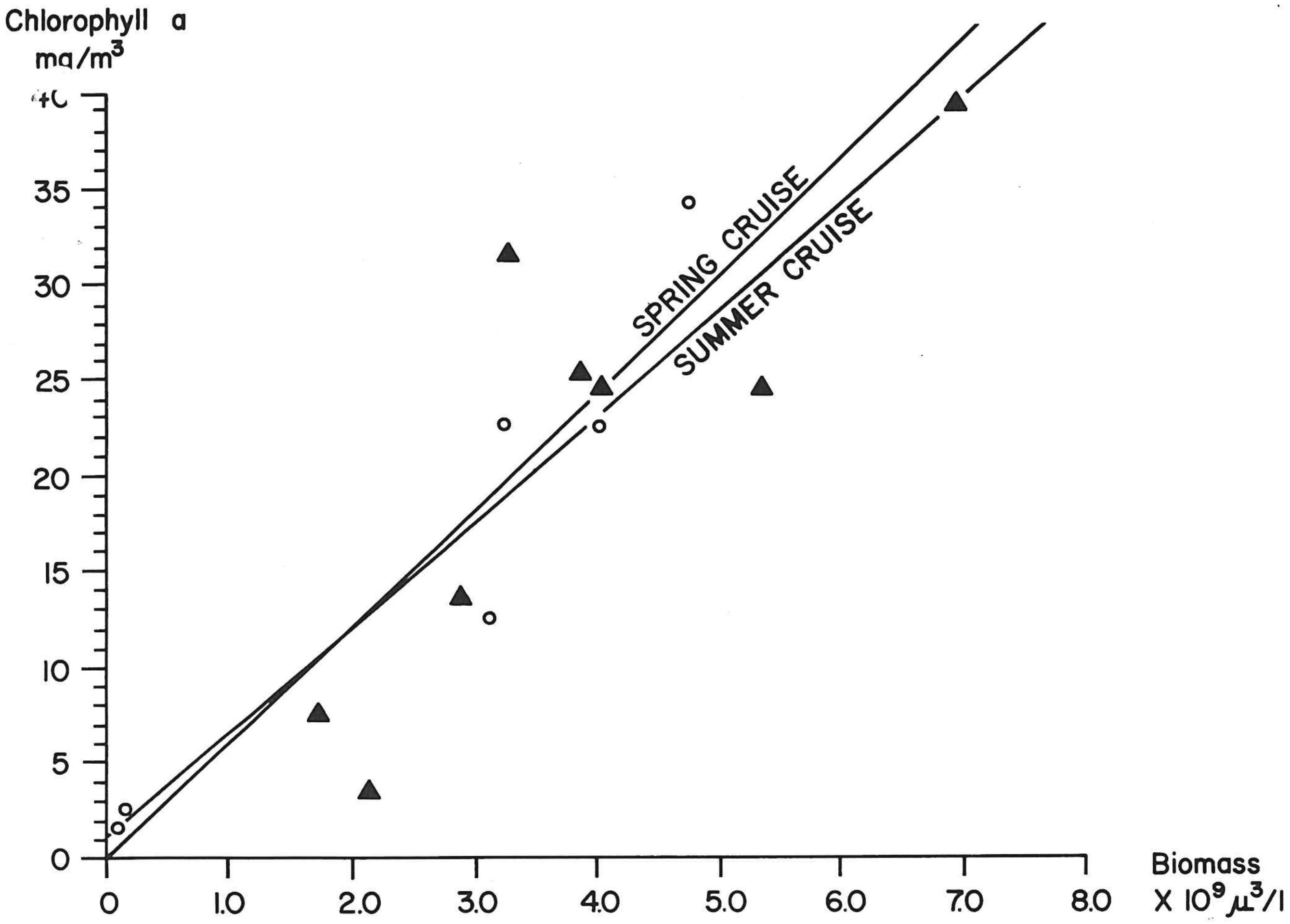


Fig. 9. Primary productivity - depth profiles, first week of November 1971. Depth in meters. Amounts of carbon fixed include the dissolved organic fraction. Numbers below station nr. indicate of carbon fixed per square meter.



.g. 10. Chlorophyll - biomass relationship; r = 0.9. Biomass calculated from the Coulter Counter data presented in Figs. 3 and 4 (and see Table V).

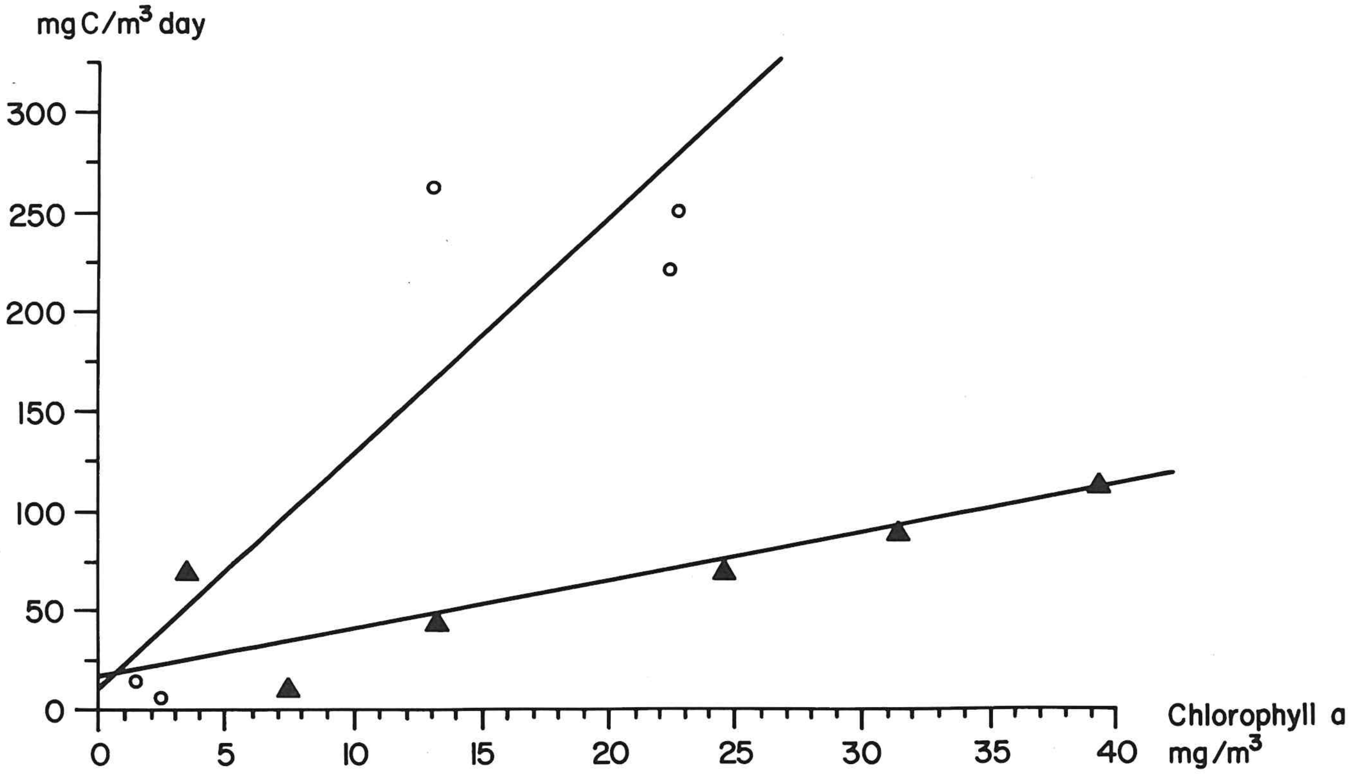


Fig. 11. Primary productivity of the upper meter of the water column versus chlorophyll. Circles: spring cruise. Triangles: summer cruise.