INTRODUCTION

In 1978 a project was initiated aiming at elucidating the factors governing growth of cultivated Mytilus edulis L. on the Swedish west coast. Growth of M. edulis is largely a function of the amount of available food (Winter & Langton 1976). It is a filter feeder, which with its gills collects particles of down to a few µm size, i.e. within the size range of most phytoplankton ~~algae~~. One part of the project therefore was engaged in quantifying the phytoplankton biomass and primary production in the area. In addition to these measurements, Particulate carbohydrates and proteins were quantitatively analysed as a direct measure of the amount of potential food.

Since, to my knowledge, no previous investigation has been carried out combining those aspects on the quality and quality of phytoplankton production, the present paper ~~has been prepared presenting the results separately~~ will deal with the latter, while later, a joint publication, with the emphasis on dynamics of the M. edulis population, will be published ~~later.~~

MATERIAL AND METHODS

Description of the area.

Samples were collected at three stations in a narrow entrance sound between two islands in the archipelago south of Strömstad on the Swedish west coast (Fig. 1). The sound is about 30 - 300 m wide, and 3 km long from the narrow point where Stn 3 was situated to the western end where it connects with the open sea. The depth gradually decreases from 25 m in the western end to 7 m at Stn 3. The freshwater influence is moderate; annual precipitation is about 650 mm and there are no river mouths in the vicinity of the studied area. Tide amplitudes are on the average 30 cm.

In winter the inner part of the archipelago normally is covered with ice. At Stn 1 the sound was frozen from the end of January to early April both years. At Stn 3 the current keeps the water open throughout winter.

Sampling.

In 1979 samples were collected with a plastic-rubber Van Dorn sampler or with an aluminium-plexiglass Ruttner sampler at depths of 0, 1, 2, 3, 5, 7, 9, and 12 m ~~depths~~ at Stn 1 and at ~~from~~ 1, 3, and 5 m ~~depths~~ at Stn 2. Water from 0 m was collected with the sampler held horizontally at about 10 cm depth to avoid contamination of ~~from~~ the surface water. During the spring bloom 1980 samples were collected at 2 and 4 m depths at Stn 3 and from May onwards 1980 at Stn 1 at 1, 3, and 5 m ~~depths of~~.

Secchi-disc depth, temperature, salinity, and pH.

Secchi-disc depths were measured with a disc of 25 cm diameter from the shadowed side of the boat. Temperature was measured with a thermometer fixed inside the sampler. Salinity was measured at the laboratory with a Yellow Springs Instruments model 33 S-C-T meter, and pH with a Metrohm E 516 pH meter.

Carbon assimilation.

In situ carbon assimilation was measured by the ^{14}C method at all depths at Stn 1. 1 ml $NaH^{14}CO_3$ solution (3 uCi ml^{-1}, prepared from concentrate as recommended by Strickland & Parsons (1972)) was added to sample water in 117 ml clear Pyrex bottles. They were incubated for about 4 h around noon at the sampled depths after which the bottles were transported in a light-tight box to the laboratory. 40 ml were filtered directly onto 0.45 um Sartorius membrane filters and 40 ml were prefiltered through 5 um nylon mesh. The filters were dried over silica gel, treated with fumes of HCl and counted with liquid scintillation. Counting efficiency was determined by external standard ratio calibrated against quenched standards.

Carbon assimilation of samples from 1, 3, and 5 m at Stn 1 and 2, and from 2 and 4 m depths at Stn 3 ~~was~~ were also? measured at a fixed light intensity in an incubator cooled with running surface water from the bay outside the laboratory. Light was provided by three fluorescent tubes (Philips TL 40/57) delivering a total energy of 150 uE $m^{-2}sec^{-1}$ at the distance where the bottles were placed. Incubation was started as soon as possible after arrival at the laboratory, usually 30 minutes after the beginning of the in situ incubations. After about 4 h the samples were fractionated and treated as described above.

~~described above.~~

Radiation values for calculation of daily assimilation rates were obtained with a Fuess Actinograph outside the laboratory. Daily rates were computed by multiplying incubation rates by the factor (total daily radiation)/(radiation during incubation). Total inorganic carbon was calculated from temperature, salinity, and pH according to Öström (1977).

Chlorophyll a.

Particulate material for chlorophyll a and phaeopigment analyses was collected on $MgCO_3$-covered 47 mm Ø Whatman GF/C filters. From each sample one subsample of 150 - 200 ml was prefiltered through 200 um nylon mesh and one subsample was prefiltered through 5 um nylon mesh. The filters were dried over night over silica gel in the dark. They were kept dry and frozen until analysis. After 1 min. homogenization with 3 ml 90 % acetone in a Thomas teflon grinder the pigments were extracted with a total of 10 ml 90 % acetone for 5 h at 10°C in the dark. The content of chlorophyll a and phaeopigment was measured with a Turner 111 fluorometer; phaeopigments after addition of HCl. Since a precise acid factor for calculating phaeopigments is difficult to obtain, the chlorophyll concentrations are given without subtraction of phaeopigments.

Carbohydrate and protein.

All glass-ware which was used for carbohydrate and protein analyses was washed with chromosulphuric acid and well rinsed with tap water and distilled water. Filters were cleaned by heating to 500°C and all equipment was protected from dust.

Particulate carbohydrate and protein in volumes of 100 - 250 ml were separated into fractions <200 um and <5 um in the same manner as the chlorophyll samples. Samples were collected on 12 mm Ø Whatman GF/C filters. They were dried at room temperature for a few hours and stored frozen in capped glass test tubes.

Carbohydrates were quantitatively determined by the L-tryptophan method originally described for dissolved carbohydrates by Josefsson et al. (1972). After hydrolyzation with 0.8 ml 80 % H_2SO_4 for about 20 h (Myklestad & Haug 1972) the tubes were placed in an ice-bath and 1.5 ml of distilled water and 1.5 ml of tryptophan reagent (5 g L-tryptophan + 25 g boric acid dissolved in 1000 ml conc. H_2SO_4) were added to the hydrolysate. The tubeswere capped, the content

was well mixed and the tubes were heated in a boiling water bath for 15 min. after which they again were cooled in an ice bath. They were centrifuged for 10 min. at about 2000 G and the absorbance at 540 nm was measured in 1-cm cuvettes with a Hitachi 101 spectrophotometer. Three glucose standards and three blanks, with filters only, were included in each batch of analyses.

Quantitaive analysis of protein was carried out as described by Dorsey et al. (1977), with the difference that the reagent volumes were reduced to a final volume of 3.3 ml against 5.5 ml. Standards were made of bovine serum albumine (Sigma) dissolved in distilled water.

Histochemical staining.

Particulate material was collected by very slowly pouring water through a 5 um nylon mesh. The material was either fixed with neutralized formalin or treated further immediately. For staining a subsample was transferred to an 8 mm Ø glass tube with one end covered with 5 um mesh. All reagents were slowly added and removed through the mesh, thus no foreign particles could contaminate the samples. Proteins were stained with the mercuric bromphenol blue method (Mazia et al. 1953) and carbohydrates with the aqueous PAS technique. Both procedures were taken from Humason (1972).

Protein and carbohydrate containing particles <200 um were identified as phytoplankton, zooplankton, or detritus. They were measured and counted on glass slides at 125 or 250 X magnification. Since thickness could not be measured or estimated the measurements refer to area only.

RESULTS

Stn 1 0 - 12 m, 1979.

Temperature, salinity, and Secchi-disc depth.

Up to the middle of March water temperatures were below 0°C (Fig. 2 A). Summer temperatures were in the range 14 - 17°C near the surface and somewhat lower at 5 - 12 m. After August temperatures decreased to 3 - 4°C in December. Salinity ranged from 12 to 33 °/oo. In April - July salinities were below 20 °/oo in the upper part of the water column (Fig. 2B). Salinities above 30 °/oo were found in November and December.

Secchi-disc depths were not measured under the ice. In the period April - August they were 4.5 - 7 m and from the end of September onwards 7 - 15 m. On 28 August was obtained a depth of 11.5 m and on 15 September one of 4 m.

Phytoplankton composition.

Until April phytoplankton were dominated by diatoms. Thalassiosira spp., Thalassionema nitzschoides Grunow, and Rhizosolenia hebetata Bailey f. semispina made up the main part of the spring bloom in February, together with Skeletonema costatum (Grev.) Cleve and Chaetoceros spp.. Dinoflagellates - Peridinium spp., Peridinium trochoideum (Stein) Lemmermann, Dinophysis spp., Prorocentrum micans Ehrenberg - were frequent from April to September. In the middle of September a large bloom of Ceratium spp. had developed in cold and saline water which was present in the area already at the end of August - from 16 to 28 August salinity increased from 20 - 22 °/oo to 27 - 28 °/oo and temperature decreased from 15 - 16°C to 11 - 13°C. From September onwards the population was dominated by Ceratium spp, foremost C. tripos (O.F. Müller) Nitzsch, C. furca (Ehrenb.) Clap. u. Lachm., and C. fusus (Ehrenb.) Dujard..

Chlorophyll a, carbohydrate, and protein 0 - 12 m.

The annual variations of the integrated content at 0 - 12 m of chlorophyll a, carbohydrate, and protein in the two size fractions <200 um and <5 um are shown in Fig. 3. Chlorophyll a and carbohydrate <200 um differed in details but followed the same general pattern with pronounced peak values in February and September. The protein content <200 um was proportionally higher in the period between the blooms, when it frequently approached the spring bloom value.

As the blooms were caused by algae larger than 5 um, the variations of the <5 um fractions differed from those of the <200 um fractions. The content remained rather low during the blooms, and the highest concentrations were instead obtained in the period April - August, when 52 - 89 % of the particulate material <200 um were recovered in the <5 um fractions (Fig. 4). The percentages of chlorophyll a, carbohydrate, and protein <5 um were similar in April - August, but during the blooms the percentages of chlorophyll a were consistently lower, some 5 - 10 % against 20 - 40 % of carbohydrate and protein. The ratio chlorophyll a/phaeopigment was always higher in the <200 than in the <5 um fraction

Particulate matter in the <200 um fraction on the average contained 2.7 times more protein than carbohydrate, with ratios ranging from 0.8 in the middle of September to 4.6 on 11 April. (Fig 5) The ratios were generally low during the blooms in spring and autumn. The fraction <5 um had a somewhat higher average of 2.9. The annual cycle on the whole showed the same variations as the <200 um fraction, but the range was smaller, 1.2 - 4.2, and particularly during the Ceratium bloom in autumn did not deviate as much from the average as the larger fraction.

Average carbohydrate/chlorophyll a ratios were 52 of particles <200 um and 91 of particles <5 um, with ranges of 15 - 132 and 30 - 181, respectively (Fig. 5) Since carbohydrate concentrations changed less than chlorophyll a (Figs 3 A and B) the ratio generally increased with decreasing chlorophyll content, except that rather high ratios were found in both fractions at the time of the Ceratium bloom.

Due to the relatively small fluctuations of the protein/carbohydrate ratio, the ratio protein/chlorophyll a rather well followed the changes of the ratio carbohydrate/chlorophyll a. (Fig. 5) The average ratio of the fraction <200 um was 128, range 43 - 282, and that of the <5 um fraction 239, range 100 - 535.

Carbon assimilation 0 - 12 m.

The total integrated in situ carbon assimilation at 0 - 12 m ranged from 0.03 g m^{-2} day^{-1} in December to 2.7 g m^{-2} day^{-1} in July. (Fig. 6) The rates during the blooms were comparatively low, in February about 0.4 g m^{-2} day and in September 1.4 g m^{-2} day^{-1}. Carbon assimilation thus showed an annual variation which differed much from those of the particulate matter, specially carbohydrate. The calculated annual assimilation was 222 g m^{-2}, of which the fraction <5 um contributed 117 g m^{-2}, or 53 %. In Fig. 5 the period March - November has been divided into three equal parts, roughly corresponding to spring, summer, and autumn. In spring 17 % took place of the total assimilation ~~in the period~~, in summer 65 %, and in autumn 18 %. Carbon assimilation in the fraction <5 um was most active in summer, when it contributed 76 % of the assimilation of the fraction <200 um. In spring it contributed 54 % and in autumn 23 %. The spring bloom, which actually occurred in February, added only 16 g m^{-2}, or 7 %, to the total annual carbon assimilation.

Vertical distribution.

There was no consistent differences between the vertical distribution of chlorophyll a, carbohydrate, and protein, nor between the fractions <200 um and <5 um. (Fig. 7) As indicated by the large spread in Fig. 7, the values from 0 m were occasionally very variable, e.g. under the ice on 20 March the highest chlorophyll a and protein concentrations ever, 35 and over 4000 mg m^{-3} respectively, were found at 0 m against about 2 and about 200 mg m^{-3} respectively in the 0 - 12 m samples.

Only the 9 and 12 m samples contained significantly smaller amounts than the other samples, but, as exemplified by the chlorophyll a profile in Fig. 8, large concentrations of particulate matter could occur below 12 m. In the interval 0 - 15 m the integrated content was 55 mg m^{-2} and in the interval 15 - 200 m 100 mg m^{-2}. Thus only 1/3 of the content of the entire water column on that occasion occurred in the interval routinely sampled at Stn 1.

Average carbon assimilation rates were highest at 0 m, where the variations were as large as those of the particulate material. It decreased to 50 % of the 0 m rates at about 4 m depth and 10 % at 10 m depth. On the average 1.7 % of the total carbon assimilation took place at 12 m depth. Carbon assimilation below the sampled interval therefore was insignificant.

(Fig. 9)

Stn 1; 1, 3, and 5 m, 1979-80, and Stn 3; 2 and 4 m, 1980.
Sampling at 1, 3, and 5 m depths at Stn 1 was continued in May - December 1980. February - April 1980 samples were collected at Stn 3 at 2 and 4 m depths. The change of locality was caused by the ice conditions; at Stn 3 the current was strong enough to keep the water open throughout winter when samples were taken from a bridge 15 m above.

Fig. 10 shows the average concentrations of chlorophyll, protein, and carbohydrate at 1, 3, and 5 m (2 and 4 m) depths from January 1979 to December 1980. Although the main features of the annual cycles were the same in both years, 1980 in some respects differed from 1979. Possibly due to more frequent sampling the spring bloom appeared to have been more intense in 1980, particularly with respect to chlorophyll a. During summer the concentrations of particulate matter were low in 1980 compared to 1979 (Table 1). In both years the autumn blooms were caused by Ceratium spp. but in 1980 the bloom was brief with high concentrations on one occasion only.

In other respects the years were remarkably similar. In Fig. 11 the com-

parison has been restricted to the period May - December, which both years was covered by sampling at 1, 3, and 5 m at Stn 1. In both years the ratio protein/carbohydrate was on the average 2.4, and the seasonal variations agreed well. Carbohydrate/chlorophyll a and protein/chlorophyll a variations were also very similar, but average ratios were about 20 % higher in 1980. The average percentages of the <200 um fraction recovered in the <5 um fraction differed little between the two years, and the seasonal variations in 1979 resembled those in 1980.

Integrated over the periods/ 7 May - 4 December 1979 and 7 May - 7 December 1980 3.17 and 3.41 g carbon, respectively, were assimilated per m^{-3} at the fixed light intensity in the incubator (Fig. 12). Since the concentrations of particulate material was lower in 1980 than in 1979, the assimilation rates relative to chlorophyll a, carbohydrate, and protein were higher the former year ~ 1980.

Stn 1 and 2; 1, 3, and 5 m, 1979.

Although the average carbon assimilation rates and concentrations of particulate matter at Stns 1 and 2 differed with 10 % or less in the period 11 April - 18 December, the differences on individual dates occasionally were large (Fig. 13). As the magnitude or direction of the differences sometimes disagreed for carbon assimilation rates, chlorophyll a, protein and carbohydrate, the resulting ratios at Stn 2 sometimes deviated from those at Stn 1, indicating that the uneven distribution of seston was not only quantitative but also qualitative.

Histochemical identification of protein and carbohydrate.

~~Seston contains a mixture of inorganic and organic particles. The organic particles include phytoplankton, zooplankton, and organic detritus, mainly fragments of dead organisms~~. The proportion of protein and carbohydrate in the ~~three~~ the organic fractions (phytoplankton, zooplankton, and detritus) was estimated for particles 5 - 200 um in samples

collected in the period June 1979 - August 1980.

During the vegetation period protein was mostly bound to phytoplankton, making up 50 - 98 % of the particulate protein. Zooplankton, mainly Tintinnoinea, occasionally contained up to 40 % of the protein, and the same percentage was occasionally bound to detritus (Fig. 14). In November - December very little protein occurred as phytoplankton, while detritus contained over 90 % of the particulate protein. During the vegetation periods detritus contained a larger proportion of the particulate carbohydrate than of the protein (Fig. 14), mainly due to what appeared to be carbohydrate rich fragments of terrestial plants. Therefore in the vegetation periods the proportion of carbohydrate bound to phytoplankton was smaller than that of protein, while similar percentages were found in November - December.

The identification of protein and carbohydrate containing particles only included the size range 5 - 200 um. Frequently the major portion of the particulate matter passed a 5 um mesh and was consequently not included in the identification.

The spring bloom 1980.

In temperate waters the spring bloom offers good oppurtunities to study large scale changes within a comparatively homogenous phytoplankton population which is little grazed by zooplankton. Therefore frequent sampling was carried out 13 February - 10 April 1980, covering the period before the onset of the bloom, the bloom, and the period after the bloom. Samples were collected at 2 and 4 m depths. Carbon assimilation was measured in incubator only. The other analyses were performed as described above.

The archipelago around Tjärnö was covered by ice up to early April. Temperature was -1.1 - -0.7°C up to 5 March, 5 - 31 March +0.6 - +1.5°C, and on 10 April 10 +2.1°C. There was thus a sudden temperature increase from 3 to 5 March, from -0.9 to 1.5°C. Salinity in the whole period ranged from 19.7 to 27.3°/oo. The temperature increase at 3 - 5 March was accompanied by an increase of the salinity from

21 to 24°/oo.

All parameters, chlorophyll a, protein, carbohydrate, and carbon assimilation, showed that the bloom was essentially restricted to particulate matter >5 um. Already in the middle of February the phytoplankton population was entirely composed of diatoms, mainly Skeletonema costatum, Thalassiosira spp., and Chaetoceros spp.. Thalassionema nitzschoides appeared in late February and from that date on the species composition, dominated by Thalassiosira spp. and S. costatum, remained unaltered throughout the bloom. On 10 April diatoms were few, much detritus and some dinoflagellates were then found in the samples.

The chlorophyll content (Fig. 15A) slowly increased from the middle of February (0.5 mg m^{-3}) to 7 March (3 mg m^{-3}). The bloom culminated on 17 March (16 mg m^{-3}). On 28 March (2 mg m^{-3}) the bloom was ended. Protein (Fig 15B) and, especially, carbohydrate (Fig 15C) showed larger variations than chlorophyll a between the depths and less pronounced variations over the period, most evidently after the bloom when the decrease of the chlorophyll content was much more rapid than that of protein and carbohydrate.

The average content at 2 and 4 m depths of protein ranged from 70 to 610 mg m^{-3} and of carbohydrate from 40 to 360 mg m^{-3}. The highest concentrations were in both cases obtained on 19 March, two days after the culmination as judged by chlorophyll a. Chlorophyll a, on the one hand, and protein and carbohydrate, on the other, differed with respect to the percentages recovered in the <5 um fraction (Fig. 16). The percentages of protein and carbohydrate ranged from 30 in the middle of March to 70 - 80 before and after the bloom, while the percentages of chlorophyll a in the <5 um fraction were generally below 50 and in the middle of March below 10.

The ratio protein/carbohydrate was on the average 2.1 for both size fractions with ranges from 1.3 to about 3.7 (Fig. 17). There was no obvious correlation with the development of the bloom. The ratios of protein and carbohydrate versus chlorophyll a progressively decreased towards the chlorophyll a maximum in the middle of March and then again increased (Fig. 17). The ratios of the <5 um fractions were consistently higher then those of the <200 um fractions, particularly at the end of

the bloom. The average ratio protein/chlorophyll a was 122 of the <200 um fraction and 342 of the <5 um fraction. The carbohydrate/chlorophyll a ratios were 44 and 125, respectively.

Carbon assimilation ranged from 0.6 mg m^{-3} in the middle of February to 54 - 55 mg m^{-3} in the middle of March. (Fig. 18) Although the amplitude of the variations was larger, they followed those of the particulate matter, most closely the chlorophyll a variations. One exception to the general agreement occurred on 19 March, immediately after the culmination of the bloom, when unexpectidly low rates were obtained. Temperature and salinity did not indicate a change of the water mass, but the phytoplankton composition on 19 March differed from that on both 17 and 21 March. On the latter dates were present Thalassiosira spp., and Skeletonema costatum, together with Chaetoceros spp. and Thalassionema nitzschoides, while on 19 March, besides Thalassiosira spp. and S. costatum, were found only a few unidentified pennate diatoms.

In accordance with the small variations of the protein/carbohydrate ratio the ratios carbon assimilation/protein and carbon assimilation/carbohydrate followed almost identical courses, (Fig. 19) save one exceptional ratio of carbon assimilation/carbohydrate <200 um of 33.9. Otherwise that ratio ranged from 0.3 to 20 and the ratio carbon assimilation/protein from 0.2 - 8.5. The ratios of the fractions <5 um were lower, 0.5 - 6 and 0.2 - 3 for carbon assimilation versus carbohydrate and protein, respectively. Carbon assimilation/chlorophyll a ratios in both fractions changed in the same manner as the other ratios, but due to the low chlorophyll a concentrations <200 um before the bloom, the range of the <200 um ratio was comparatively narrow, 0.5 - 4, against 0.5 - 8 for the <5 um fraction. The ratios of the <200 um fractions increased rapidly from 5 to 10 March and remained about constant up to and including 17 March. The increase of the <5 um ratios began about two days later, but after that followed the same course as the <200 um ratios.

Bag experiment.

In order to follow the processes in a defined body of water an experiment was performed 15 - 20 July 1980 in the bay outside the laboratory. 2 polythene bags, holding about 100 litres each, were filled with surface water and anchored floating at the surface. $NaNO_3$, Na_2SiO_3, and Na_2HPO_4 were added in amounts corresponding to final concentrations of 200 ug N and Si l^{-1} and 40 ug P l^{-1}. Samples for chlorophyll *a*, protein, carbohydrate, and carbon assimilation measurements were collected daily at about 10 a.m. for 5 days. Carbon assimilation was measured both in situ at the average depth of the bags and in the incubator used for the measurements above. Before samples were taken, the content of the bags was well mixed for about 1 minute. One bag collapsed during sampling on day 4, the other appeared to have been tight; it wsa still filled with water several weeks after the experiment, until it was finally run over by a speed-boat.

When the experiments began salinity was 18.3°/oo and temperature was 18.4°C. Temperature increased to 19.7°C on the last day, and pH ranged from 8.2 to 8.3.

Changes of the chlorophyll *a*, carbohydrate, and, initially, the protein content were mainly due to the <5 um fraction. (Fig. 20) The nutrient additions caused a rapid increase of the chlorophyll *a* concentrations <5 um, which more than doubled from day to day 2. Carbohydrate behaved differently; the concentrations remained about constant from day 1 to day 2, after which the <5 um fraction increased more than 3 times from day 2 to day 3. Protein in the <5 um fraction followed the same course as chlorophyll *a*, but in contrast to both chlorophyll *a* and carbohydrate the content in the 5 - 200 um fraction remained high until the end of the experiment.

In situ and incubator carbon assimilation rates differed little and showed about the same variations as the chlorophyll *a* content, although with a still more marked dominance of the <5 um fraction. (Fig. 21) Ratios carbon assimilation/chlorophyll *a* fluctuated less in the <200 um fraction, from 4.4 to 8.8, than in the

(Fig.22)
<5 um fraction, where the range was 5.5 - 14.1. Carbon assimilation/carbohydrate showed the widest ranges, <200 um 2.5 - 25.5 and <5 um 2.4 - 34, against 1.4 - 8 for carbon assimilation/protein <200 um and 3 - 8.2 for the fraction <5 um.

Since the carbohydrate concentrations changed little from day 1 to day 2, the ratios protein/carbohydrate initially increased in both fractions, <200 um from 2.5 to 3.4 and <5 um from 2.1 to 4.3. (Fig.22) Day 3 - 6 they were of the magnitude 1 - 2. Protein/chlorophyll a in both fractions ranged from 90 to 320 - 340, with the highest ratios on days 4 - 5. At the beginning of the experiment the carbohydrate/chlorophyll a ratios were 60, on day 2 only about 25. The highest ratios were found on day 4, 180 in the <200 um fraction and 318 in the <5 um fraction.

The accumulated in situ carbon assimilation over the 5 days the experiment lasted amounted to 1411 mg m^{-3} in the <200 um fraction. On day 6 the protein content was 150 mg m^{-3} higher than on day 1 and the carbohydrate content was 181 mg higher. Calculating with about 40 % of carbon both in proteins and carbohydrates, the increase of protein and carbohydrate corresponded to about 120 mg carbon m^{-3}, i.e. less than 10 % of the assimilated amount. A few percentages were probably incorporated as lipids, but the remainder, some 90 %, was lost from the analysed particulate material.

DUSCUSSION

In the present study particulate chlorophyll *a*, protein, and carbohydrate were studied in the size fractions <200 and <5 um. Few plankton algae >200 um were found. *Ceratium* spp., of which some are about 200 um between the tips, passed the 200 um screen, but *Rhizosolenia hebetata*, f. *semispina*, which occurred during the spring blooms, may be up to 800 um long and was probably retained to some extent, partly depending on their orientation in relation to the mesh. Most microzooplankters, mainly ciliates and rotatorians, were smaller than 200 um. *Helicostomella subulata* was the only common microzooplankter >200 um. As its diameter is less than 200 um an unknown portion was included for the same reason as *R. hebetata*.

The 5 um mesh for separating net- and nanoplankton had smaller mesh size than usual for that purpose, but from microscopical observations on phytoplankton it appears to be a suitable size for obtaining one fraction containing what is often termed unidentified naked flagellates, i.e. a fraction including most phytoplankton species too small for accurate identification and - because of their fragility - ennumeration. The fractionation appeared to have worked well since a good separation, with no obvious clogging or contamination by chlorophyll *a* or incorporated ^{14}C from the >5 um fraction, was obtained even when diatom and dinoflagellate blooms were large.

The samples were collected on Whatman GF/C filters with an effective pore size of about 0.7 um (Sheldon 1972). Gordon (1969) found no significant differences between amounts of particulate organic carbon when using filters with 0.45 and 1.2 um pore size. Therefore comparisons between ^{14}C assimilation and concentrations of particulate matter could be made without introducing a methodical error. Much organic carbon in the sea is present as "dissolved" compounds, i.e. matter passing common filters. E.g. Holm-Hansen et al. (1966) found 450 - 600 mg m^{-3} of organic carbon passing glass-fibre filters, against 30 - 100 mg m^{-3} retained. The dissolved fraction was of little interest in

the present context and has not been analysed.

The concentrations of particulate matter at Stn 1 was rather evenly distributed with depth in the interval 0 - 12 m. The average summer concentrations at 1 - 5 m of 60 - 200 mg m^{-3} (Table) of carbohydrate agreed well with those reported by Marshall & Orr (1964) of 50 - 200 mg m^{-3} from Loch Striven and the concentrations of 84 - 450 mg m^{-3} found by Mayzaud & Taguchi (1979) in June - October in Bedford Basin. In the open sea concentrations normally are in the range 10 - 30 mg m^{-3} (Handa & Yanagi 1969, Hobson and/1967), concentrations of 30 - 120 mg m^{-3} have been reported from an upwelling area (Hitchcock 1977).

Protein concentrations in open sea surface waters have been reported in ranges 20 - 30 mg m^{-3} off the African Atlantic coast (Hagmeier 1964) and 30 - 115 mg m^{-3} in the N. Atlantic Ocean (Hagmeier 1964). Mayzaud & Taguchi (1979) obtained concentrations of 185 - 600 mg m^{-3} in Bedford Basin, values similar to the summer values of 200 - 800 mg m^{-3} found in the present study. The annual range, 110 - 970 mg m^{-3}, was lower than the range observed in Lynher Estuary, SE. England, of about 300 - 1300 mg m^{-3} (Widdows et al. 1979).

Published protein/carbohydrate ratios are very variable. Parsons et al. (1961) found ratios ranging from 0.8 for two species of dinoflagellates to 3.4 for Tetraselmis maculata, Prasinophyceae. Low ratios of dinoflagellates are due to their cellulose-like wall material, and thus largely indedependent of environmental factors. Diatoms in the stationary phase accumulate carbohydrate in the form of glucan (Myklestad & Haug 1972). In contrast to dinoflagellates the protein/carbohydrate ratio of diatoms would therefore decrease during unfavourable conditions. Accordingly, Barlow (1979) recorded ratios <1 at the early stage of a bloom in the Benguela upwelling region and ratios >1 at the late stages, Haug et al. (1973) found a rapid decrease of the ratio during the development of diatom spring blooms in the Trondheimsfjord, and Antia et al. (1963) on the basis of experimental data from natural populations

suggested a raito of 10 for vigorously growing diatoms and 1.7 in NO_3-depleted water (ratios computed from their Table 2). In cultures similar variations have been obtained by Myklestad & Haug (1972). Conflicting results have been published by Pugh (1975), who obtained ratios ranging from 1.6 in young cultures of Coscinodiscus excentricus to 8.1 in the stationary phase (ratios computed from his Table 1). Since nitrogen usually is the limiting element in marine environments, a decrease of the protein/carbohydrate ratio towards the end of a bloom is not so surprising, and e.g. Hobson & Pariser (1971) have shown that the composition of algae change during nitrogen deficiency. However, during other nutrient regimes the composition may change differently, which possibly explains the results of Pugh (1975).

During the diatom spring bloom 1980 the protein/carbohydrate ratio was rather constant and there was no obvious decrease with time. Nutrient analyses on 18 March, one day after the culmination, yielded concentrations of 21 ug NO_3-N, 15 ug Si, and 5 ug PO_4-P l^{-1}, indicating silicate rather than nitrogen limitation as the cause for the termination of the bloom. Indications of silicate limitation of diatom spring blooms have been obtained also from coastal waters in W. Norway (Lännergren & Skjoldal 1976, Lännergren 1980). In the plastic bag experiment, on the other hand, the protein/carbohydrate ratio fluctuated widely, particularly in the <5 um fraction where the main growth occurred. From day 1 to day 2 carbohydrate remained at the same level, and increased from day 2 to day 3, while carbon assimilation, chlorophyll a, and protein increased from day 1 to day 2 and then decreased. It thus appeared that the build-up of biomass during the period of intense growth day 1 - 2 was restricted to protein only, and that storage of carbohydrates began after that period. The resulting ratios of protein/carbohydrate consequently varied in agreement with the observations quoted above, except that of Pugh (1975); on day 1 the ratio was 2, on day 2 it was 4, and on days 3 and 4 less than 1.

It was noted by Mayzaud & Taguchi (1979) that low protein/carbohydrate ratios followed high levels of carbon assimilation, which they explained by correlation between carbohydrate content and phytoplankton volume. In the present study, supporting their observations, the ratio was low during both diatom and dinoflagellate blooms, and high ratios were found in the period April - August, coinciding with comparatively low chlorophyll *a* concentrations and large percentages of particles <5 um. The value of the ratio was frequently above 3, and occasionally above 4, which was somewhat higher than earlier reported from natural, unperturbed waters. Parsons & Strickland (1962) obtained a ratio of 3.0 at 15 - 35 m depth in the E. Pacific, Smetacek & Hendriksen (1979) 1.8 at 10 m depth in the period August - April in Kiel Bight, and Mayzaud & Taguchi (1979) 1.3 - 2.7 at 5 m in June - October in Bedford Basin. As mentioned earlier, Antia et al. (1963) found ratios of up to 10.9 during experiments with a natural population. Nutrients were added and the high ratios were found in the first phase of growth. Comparatively low ratios, 0.5 - 1.8, were obtained by Haug et al. (1973), but their sampling was restricted to particles >25 um, and sampling was terminated when zooplankton became abundant. Although high ratios in the present investigation coincided with large percentages of particles <5 um, during the spring blooms the <5 um fraction did not deviate from the <200 um fraction, in spite of the fact that most of the particulate matter then was in the size range 5 - 200 um, and the only period when the two fractions consistently differed was during the autumn blooms, when dinoflagellates of 5 - 200 um size caused higher ratios of the <200 um fraction than of the <5 um fraction.

The ratios carbohydrate/chlorophyll *a* of 10 - 21 of diatoms in the log phase and 13 - 57 of seven other species, including dinoflagellates, given by Parsons et al. (1961), were frequently exceeded in the present study, where average annual ratios for the <200 um fraction were 90 - 100, in the bag experiment 150, and during the spring bloom 1980 181. Antia et al. (1963) suggested ratios of 6 for healthy and 60 for NO_3-limited algae, and suggested corresponding

protein/chlorophyll a ratios of 60 and 100, also being considerably lower than found here. Smetacek & Hendriksen (1979) stressed the "basic similarity in gross chemical composition between phytoplankton and particulate detritus". This similarity did not include pigments as they found only negligable amounts associated with detritus. The histochemical identification of protein and carbohydrate revealed large percentages bound in detritus and zooplankton on most occasions, but during spring and autumn blooms most particulate matter occurred as phytoplankton. As an effect of the dominance of phytoplankton in the particulate matter, and possibly also because of the physiological state of the algae, low ratios were found when the spring bloom 1980 culminated. Carbohydrate/chlorophyll was then 12 - 25 and protein/chlorophyll 37 - 59, i.e. not far from the ratios suggested for healthy algae by Antia et al. (1963). Also during the less frequently sampled spring bloom 1979 and autumn blooms protein/chlorophyll ratios were lower than at other times, while carbohydrate/chlorophyll showed more irregular seasonal variations. The average values of the two ratios involving chlorophyll were consistently higher in the <5 um fraction than in the <200 um fraction. The differences were mainly due to high <5 um ratios in spring and autumn, which in autumn 1979 could not be unconditionally attributed to the bloom since a high ratio occurred already in August, a few weeks before the Ceratium bloom in September. However, the August ratio may be excused with the saline, cold, and particle poor water which entered the area between 16 and 28 August, while high ratios <5 um in general occurred during blooms and probably were caused by protein and carbohydrate fragments from the algae and/or by bacteria associated with the blooms. The artificial bloom of the <5 um fraction in the bag experiments showed that the ratios of that fraction followed the same course as has been demonstrated for larger species; when growth increased from day 1 to day 2 the ratios decreased to 22 of carbohydrate/chlorophyll and 91 of protein/chlorophyll. Both ratios were higher than those obtained during the spring bloom 1980. After day 2 they rapidly increased to over 300 on days 4 and 5, respectively. Thus in the short time of 3 - 4 days there was a 14 fold in-

crease of the carbohydrate/chlorophyll ratio and an almost 4-fold increase of the protein/chlorophyll ratio.

The annual primary production in 1979, 222 mg C m^{-2}, was remarkably close to the value of 220 mg m^{-2} obtained in the same year in the outer part of the Gullmarsfjord about 75 km south of Tjärnö (O. Lindahl, pers. commn). 53 % of the total annual production was contributed by the <5 um fraction, which agreed well with observations from the Oslofjord, where Throndsen (1978) found that organisms <5 um contributed on the average about half of the primary production capacity with extremes of 15 and 89 %, a range very similar to that of 9 - 90 % obtained here, and he observed a similar annual variation with the highest percentages in the period May - November.

Carbon assimilation per unit chlorophyll a (mg C assimilated (mg Chl a)$^{-1}h^{-1}$, Assimilation number or Productivity index) is widely used as an indication of the conditions for growth. In coastal waters average productivity indexes usually are around 5 (e.g. Durbin et al. 1975, Platt & Jassby 1976, Malone 1977). The average in situ index of the integrated rates and concentrations <200 um 0 - 12 m 1979 was only 1.5. As it included samples well below light optimum, the 1, 3, and 5 m samples had a higher average of 2.0. In 1980, when samples were collected at Stn 1 only in May - December, an average of 5.2 was obtained. The incubator measurements yielded somewhat higher indexes, 2.3 in 1979 and 6.3 in 1980. The indexes of the <5 um fraction were in all cases higher, in accordance with results presented by e.g. Malone (1971, 1977), while McCarthy et al. (1974) and Durbin et al. (1975) could demonstrate no significant difference between indexes of different size fractions.

Average incubator carbon assimilation rates <200 um per unit protein (mg C ass (mg Prot x 10^{-2})$^{-1}h^{-1}$) were in 1979 2.2 and in 1980 4.5, and the rates per unit carbohydrate (mg C ass (mg COH x 10^{-2})$^{-1}h^{-1}$) 5.6 and 10.0, respectively. In contrast to the productivity indexes the average ratios involving protein were lower in the <5 um than in the <200 um fraction, and those involving carbohydrate

only slightly higher. However, during the spring bloom 1980 and in the bag experiment the relationship between the fractions was different; the spring bloom was caused by algae 5 - 200 um and both ratios were highest in the <200 um fraction,, while the artificial bloom in the bag experiment was caused by algae <5 um and the highest ratios were then found in that fraction.

There was a positive correlation between carbon assimilation rates and the content of particulate matter. (Table 2) The coefficients of linear regressions were about equally good for carbon assimilation versus chlorophyll a and protein. The coefficients versus carbohydrate were generally somewhat lower, and lower coefficients were obtained for the <5 um fraction[s/] than for the <200 um fraction.[s/]

The variations of the productivity index and the ratios carbon assimilation/protein and carbon assimilation/carbohydrate were partly due to temperature. High values were obtained during spring blooms and in summer. Spring blooms in many respects are unique events; the high summer values, on the other hand, indicated a positive correlation with temperature, as has been shown by Eppley (1972). Excluding the spring bloom values, coefficients for productivity indexes and ratios versus temperature/ were generally around 0.7 (Table 3). Except for the coefficient of 0.57 for the productivity index <5 um, no large/ differences were found between the analysed constituents of the particulate matter.

The fact that the coefficients of the correlations were similar, wether calculated for carbon assimilation rates versus chlorophyll a, protein, or carbohydrate concentrations, does not imply that protein and carbohydrate was associated with photosynthetic organisms to the same extent as chlorophyll a, but similar fluctuations of the concentrations. When comparing annual or seasonal fluctuations the similarities were rather large. Quite different results were obtained from the spring bloom 1980 and, particularly, the bag experiment. The ensuing correlations indicated in both cases a high degree of correlation with

crease of the carbohydrate/chlorophyll ratio and an almost 4-fold increase of the protein/chlorophyll ratio.

The annual primary production in 1979, 222 g C m^{-2}, was remarkably close to the value of 220 g m^{-2} obtained in the same year in the outer part of the Gullmarsfjord about 75 km south of Tjärnö (O. Lindahl, pers. commn). 53 % of the total annual production was contributed by the <5 um fraction, which agreed well with observations from the Oslofjord, where Throndsen (1978) found that organisms <5 um contributed on the average about half of the primary production capacity with extremes of 15 and 89 %, a range very similar to that of 9 - 90 % obtained here, and he observed a similar annual variation with the highest percentages in the period May - November.

Carbon assimilation per unit chlorophyll a (mg C assimilated (mg Chl a)$^{-1}h^{-1}$, Assimilation number or Productivity index) is widely used as an indication of the conditions for growth. In coastal waters average productivity indexes usually are around 5 (e.g. Durbin et al. 1975, Platt & Jassby 1976, Malone 1977). The average in situ index of the integrated rates and concentrations <200 um 0 - 12 m 1979 was only 1.5. As it included samples well below light optimum, the 1, 3, and 5 m samples had a higher average of 2.0. In 1980, when samples were collected at Stn 1 only in May - December, an average of 5.2 was obtained. The incubator measurements yielded somewhat higher indexes, 2.3 in 1979 and 6.3 in 1980. The indexes of the <5 um fraction were in all cases higher, in accordance with results presented by e.g. Malone (1971, 1977), while McCarthy et al. (1974) and Durbin et al. (1975) could demonstrate no significant difference between indexes of different size fractions.

Average incubator carbon assimilation rates <200 um per unit protein (mg C ass (mg Prot x 10^{-2})$^{-1}h^{-1}$) were in 1979 2.2 and in 1980 4.5, and the rates per unit carbohydrate (mg C ass (mg COH x 10^{-2})$^{-1}h^{-1}$) 5.6 and 10.0, respectively. In contrast to the productivity indexes the average ratios involving protein were lower in the <5 um than in the <200 um fraction, and those involving carbohydrate

chlorophyll a, during the spring bloom only in the <200 um fraction, and in the bag experiment also with protein, <5 um/ while the coefficients for carbohydrate were low and in the bag experiment even negative (Table). Obviously in unperturbed samples the relative amounts of protein and carbohydrate associated with active photosynthetic organisms were lower in the <5 um fraction than in the <200 um fraction: compared to the ratios carbon assimilation/chlorophyll a <5 um the ratios versus protein and carbohydrate were lower in the <5 um fraction relative to the ratios <200 um, and a larger proportion of detritus in the <5 um fraction was indicated by lower chlorophyll a/phaeopigment ratios there than in particulate matter <200 um.

The histochemical determination of the proportions of carbohydrate and protein in phytoplankotn, zooplankton, and detritus was restricted to particles 5 - 200 um. It was an attractive method because of its simplicity and directness, but suffered from being tedious and inexact. Since only the area and not the volume of particles was measured the percentages can not be entirely trusted. Further, the sample preparation may have destroyed fragile particles in spite of careful handling, and the quantification, particularly of protein, was problematic due to varying colour/ intensity. As suggested by Gordon (1970) the intensity and the quality of the colour, sometimes being violet rather than blue, may be due to the composition of the proteins and not to the quantity. The resulting percentages may nevertheless be trusted to indicate magnitudes with at least the same precision as more indirect methods, e.g. by applying fixed ratios for calculating phytoplankton carbon from chlorophyll a or separating dead and live matter by fixed ATP/carbon ratios. From a large set of data Hobson et al. (1973) concluded that the proportion of phytoplankton to the total particulate organic carbon content increased with increasing concentrations of particulate organic carbon. In the present study, where the large seasonal variations of the content of particulate matter were caused by phytoplankton blooms, that conclusion very obviously was true. During blooms over 95 % of both protein and carbohydrate were bound in phytoplankton, while over 90 % were bound in detritus

in the winter months. Estimates from other areas fall within the wide range and indicate the same differences between low- and high-productive waters as was found here between low- and high-productive periods. McAllister et al. (1960) calculated that about 15 % of the particulate organic carbon in the NE. Pacific occurred as phytoplankton, and Hobson et al. (1973) obtained percentages of 20 - 55 for the open sea in general and some 70 - 90 % in the upwelling zone off Peru. They reported values below 10 % in oligotrophic regions, as did Mullin (1965) from the W. Indian Ocean. Lenz (1977) estimated the average annual percentages of organic carbon attributable to phytoplankton, heterotrophs, and detritus in the Kiel Bight to 27, 33, and 41, respectively, and Smetacek & Hendrikson (1979) in the same area calculated the contribution of detritus carbon to total carbon to be above 75 % in winter and frequently below 25 % in April-October. In spite of the similar gross chemical composition of phytoplankton and detritus, which they proposed, the relative amount of detritus probably decides the degree of digestibility of the particulate matter as it seems reasonable that the proportion of refractory organic compounds is larger in detritus than in phytoplankton. The large seasonal variations found in the present study therefore indicate corresponding variations of the quality of food for, above all, the filter feeders.

The degree to which filter feeders can utilize detritus is disputed. In the following calculation of the energy content of the suspended particulate matter the proportion of detritus has therefore not been considered. Since lipids were not analysed, an estimated percentage has to be added to the protein and carbohydrate content. Reported percentages of lipids are somewhat variable; Haug at al. (1973) found at most 8 % in netplankton >25 um, in contrast Nival et al. (1976) got 18 % in late spring, Mayzaud & Taguchi (1979) 8 - 12 % (calculated from their Table 4), and Widdows et al. (1979) 4 - 18 % with the highest percentages in summer. In the following 12 % of the organic matter is assumed to have been in the form of lipids, and the energy content of the particulate

matter is calculated by applying average energy equivalents of lipids, 39.65 J mg^{-1}, carbohydrates, 17.16 J mg^{-1}, and proteins, 23.65 J mg^{-1} (Winberg).

The energy content, naturally, showed the same variations with time as the organic content. At, 1,3, and 5 m depths the average content ranged from 3 to 6 KJ m^{-3} in winter to about 45 KJ m^{-3} during the autumn blooms. The <5 um fraction represented about 70 % of the energy content in summer and some 15 - 30 % during the blooms. In summer 1979 the content was 19 - 28 KJ m^{-3}, considerably higher than in summer 1980, when it was between 11 and 16 KJ m^{-3}.

FIGURE TEXTS

Fig. 1. Station locations in the investigated area. TMBL = Tjärnö Marine Biological Laboratory.

Fig. 2. (A) Temperatures (^{o}C) and (B) salinities (^{o}/oo) at 0 - 12 m depths, Stn 1, January - December 1979.

Fig. 3. Integrated chlorophyll a (A), carbohydrate (B), and protein (C) concentrations (g m^{-2}) at 0 - 12 m depths, Stn 1, January - December 1971. Continuous line: fraction <200 um, broken line: fraction <5 um.

Fig. 4. Percentages of concentrations <200 um recovered in the <5 um fraction. Calculated from the integrated concentrations in Fig. 3.

Fig. 5. Ratios of protein/carbohydrate (P/CHO), protein/chlorophyll a (P/Chl), and carbohydrate/chlorophyll a (CHO/Chl). Calculated from the integrated values in Fig. 3. Continuous line: fraction <200 um, broken line: fraction <5 um.

Fig. 6. In situ carbon assimilation (g C $m^{-2}d^{-1}$) at 0 - 12 m depths, Stn 1, 1979. Continuous line: total assimilation, broken line: assimilation of fraction <5 um, dotted line: in situ rates calculated from incubator values.

Fig. 7. Average vertical distribution of chlorophyll a (Chl), carbohydrate (CHO), and protein (P) at Stn 1, January - December 1979, calculated as percentages of total content 0 - 12 m depths. Horizontal bars denote standard deviation.

Fig. 8. Vertical distribution of chlorophyll a 0 - 200 m in the open sea, 4 km SW of Stn 1, 11 July 1979.

Fig. 9. Vertical distribution of in situ carbon assimilation rates. Otherwise as Fig. 7.

Fig. 10. Average concentrations (mg m^{-3}) of chlorophyll a, protein, and carbohydrate at 1, 3, and 5 m depths at Stn 1 January - December 1979 and May - December 1980. Also showing average concentrations at 2 and 4 m depths at Stn 3, February - April 1980. Continuous line: fraction <200

um, broken line: fraction <5 um.

Fig. 11. (A) Ratios of protein/carbohydrate (P/CHO), carbohydrate/chlorophyll a (CHO/Chl), and protein/chlorophyll a (P/CHO) of average concentrations at 1, 3, and 5 m depths, Stn 1, May - December. Continuous line: 1979, broken line: 1980.

Fig. 12. Average incubator carbon assimilation rates (mg C $m^{-3}h^{-1}$) of samples from 1, 3, and 5 m depths, Stn 1, February - December 1979 and May - December 1980. Also showing average rates of samples from 2 and 4 m depths, Stn 3, 1980. Continuous line: total rates, broken line: rates of fraction <5 um.

Fig. 13. Comparance between average carbon assimilation rates (C ass), chlorophyll a (Chl), protein (P), and carbohydrate (CHO) concentrations at 1, 3, and 5 m depths at Stns 1 and 2, 1979. Upward bar indicates higher value at Stn 1. Differences calculated as percentages of values at Stn 1

Fig. 14. Percentages of carbohydrate and protein bound in detritus, zooplankton (close-dotted area), and phytoplankton (thin-dotted area), estimated by histochemical staining of particles 5 - 200 um.

Fig. 15. Spring bloom 1980. Concentrations (mg m^{-3}) of (A) chlorophyll a, (B) protein, and (C) carbohydrate in size fractions <200 and <5 um. Continuous line: 2 m depth, broken line: 4 m depth.

Fig. 16. Spring bloom 1980. Percentages of concentrations <200 um recovered in the <5 um fraction. Calculated from average concentrations at 2 and 4 m depths. Dotted line: chlorophyll a, continuous line: protein, broken line: carbohydrate.

Fig. 17. Spring bloom 1980. Ratios of protein/carbohydrate (P/CHO), protein/chlorophyll a (P/Chl), and carbohydrate/chlorophyll a (CHO/Chl). Calculated from average concentrations at 2 and 4 m depths. Continuous line: fraction <200 um, broken line: fraction < 5 um.

Fig. 18. Spring bloom 1980. Incubator carbon assimilation rates of total and of fraction <5 um. Continuous line: 2 m depth, broken line: 4 m depth.

Fig. 19. Spring bloom 1980. Ratios of carbon assimilation/chlorophyll a (C ass/Chl), carbon assimilation/protein (C ass/P), and carbon assimilation/carbohydrate (C ass/CHO). Calculated from average concentrations at 2 and 4 m depths for size fractions <200 and <5 um.

Fig. 20. Bag experiment 1980. Concentrations (mg m^{-3}) of chlorophyll a (Chl), protein (PROT), and carbohydrate (CHO) in Bag II on days 1 to 6. Also showing concentrations in Bag I (thin lines and no dots) on days 1 to 4. Continuous lines: fraction <200 um, broken lines: fraction <5 um.

Fig. 21. Bag experiment 1980. In situ and incubator carbon assimilation rates (mg C $m^{-3}h^{-1}$) of samples from Bag II on days 1 to 6.

Fig. 22. Bag experiment 1980. (A) Ratios of carbon assimilation/chlorophyll a (C as Chl), carbon assimilation/protein (C ass/P), and carbon assimilation/carbohydrate (C ass/CHO) of samples from Bag II on days 1 to 6, in fractions <200 and <5 um.

(B) Ratios of protein/carbohydrate (P/CHO), protein/chlorophyll a (P/Chl), and carbohydrate/chlorophyll a (CHO/Chl) of the same samples.

Fig. 23. Average energy content in particulate matter at 1, 3, and 5 m depths at Stn 1, February 1979 - December 1980. Continuous line: fraction <200 um, broken line: fraction <5 um.

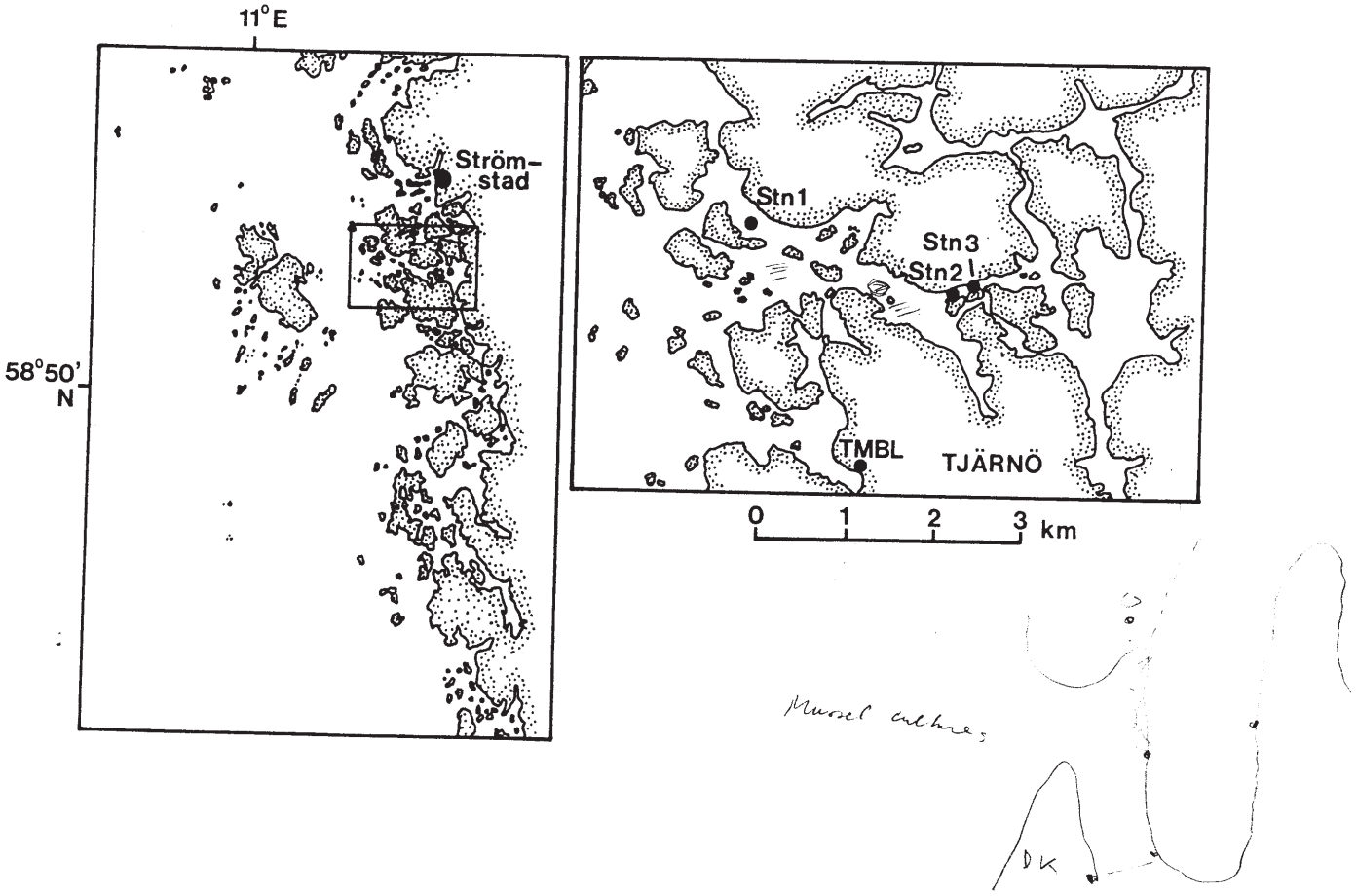
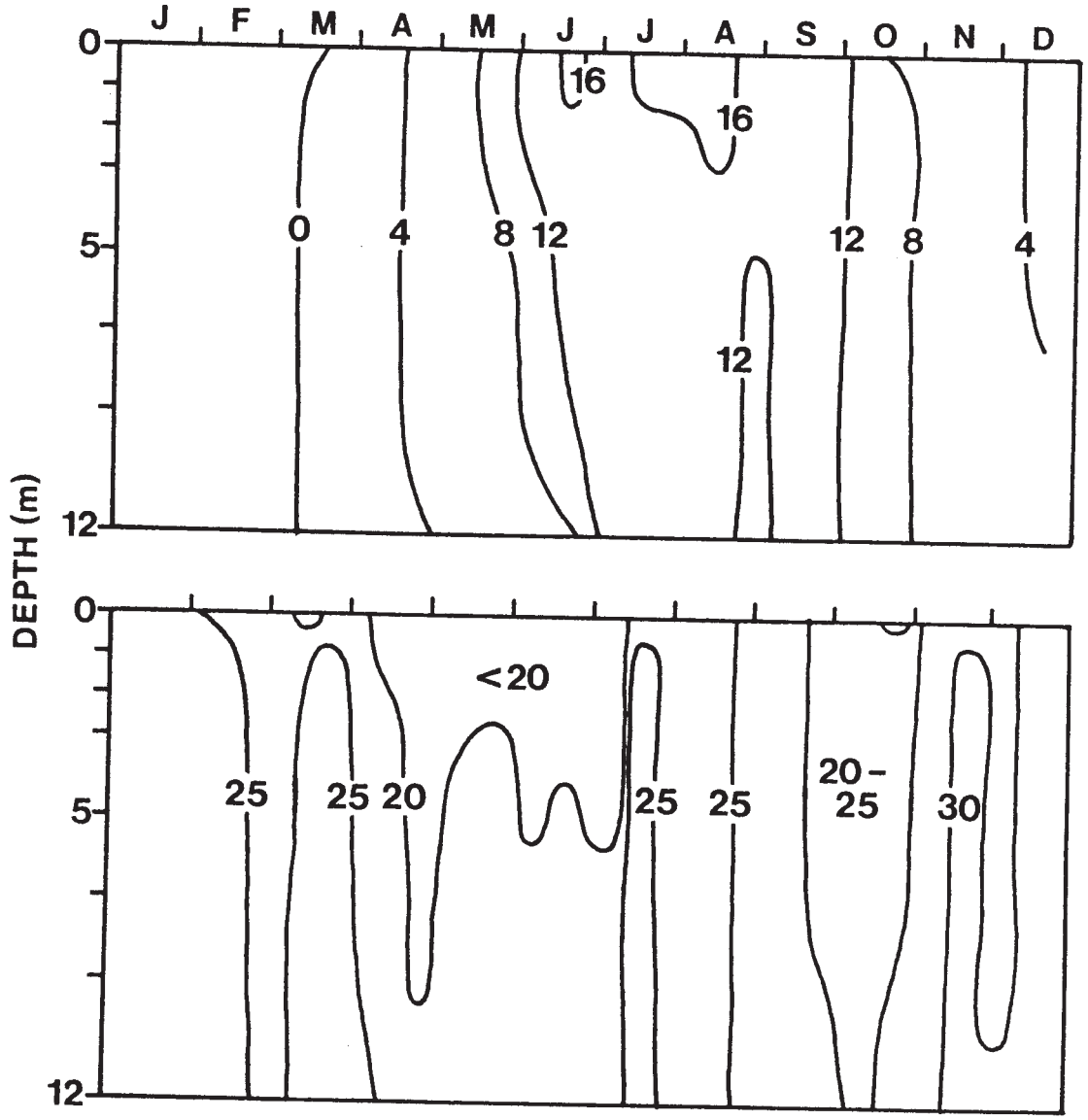


Fig. 1. Station locations in the investigated area. TMBL = Tjärnö Marine Biological Laboratory.



(A) (B)

Fig. 2. Temperatures (°C) and salinities (°/oo) at 0 - 12 m depths, Stn 1, January - December 1979.

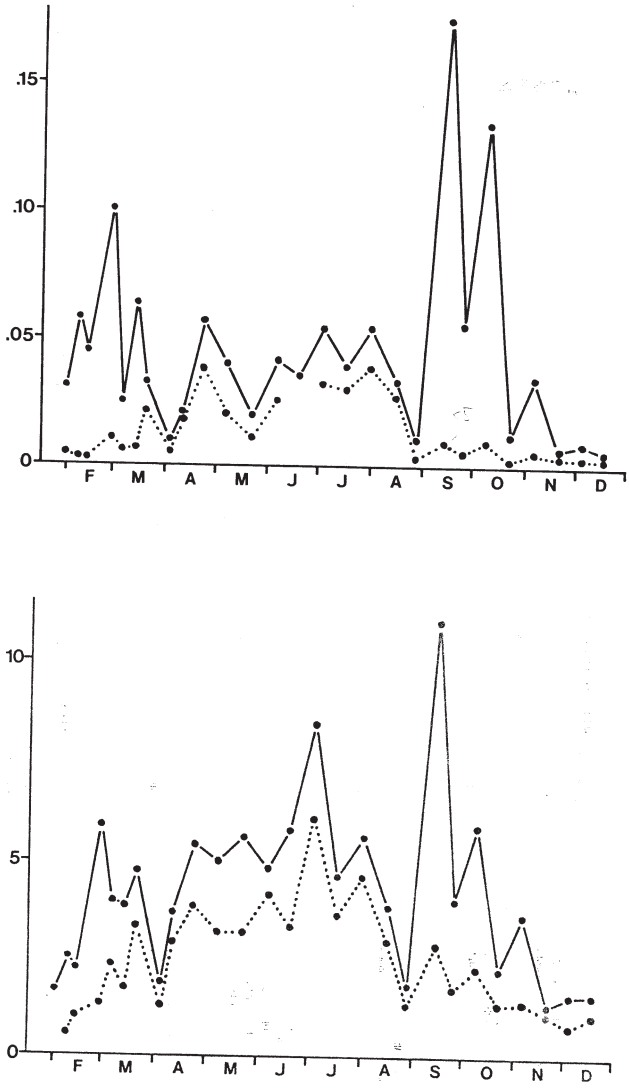


Fig. 3. Integrated chlorophyll a (A), carbohydrate (B), and protein (C) concentrations (g m^{-2}) at 0 - 12 m depths, Stn 1, January - December 1971. Continuous line: fraction <200 um, broken line: fraction <5 um.

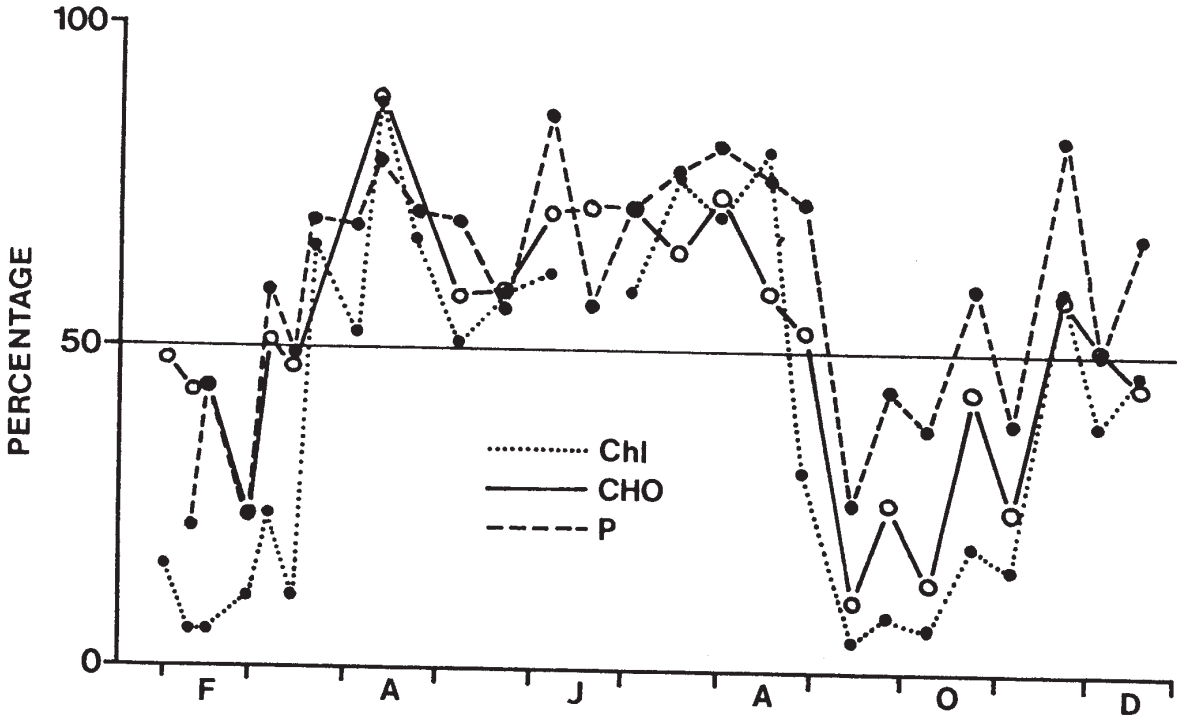


Fig. 4. Percentages of concentrations <200 um recovered in the <5 um fraction. Calculated from the integrated concentrations in Fig. 3.

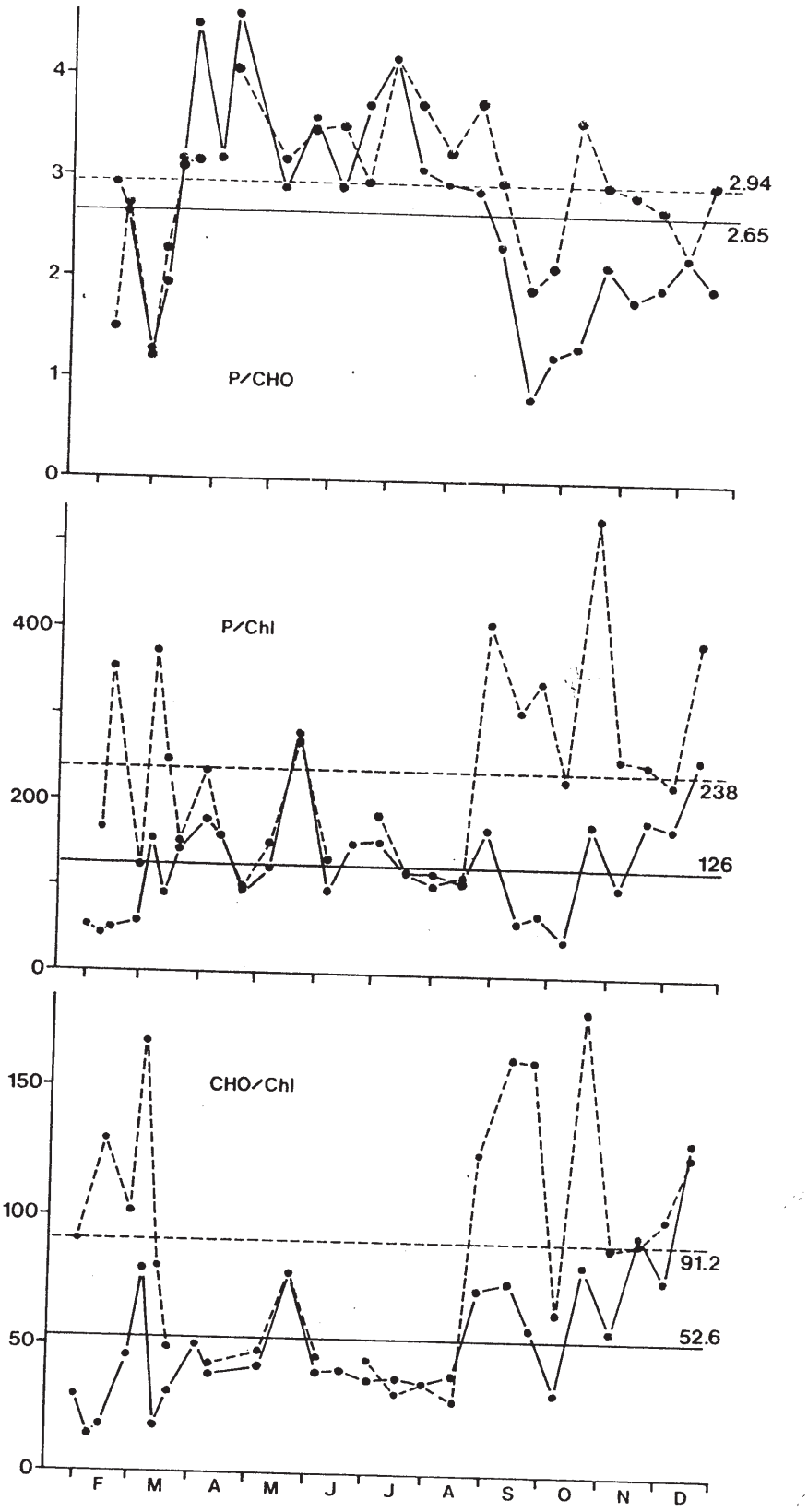


Fig. 5. Ratios of protein/carbohydrate (P/CHO), protein/chlorophyll a (P/Chl), and carbohydrate/chlorophyll a (CHO/Chl). Calculated from the integrated values in Fig. 3. Continuous line: fraction <200 um, broken line: fraction <5 um.

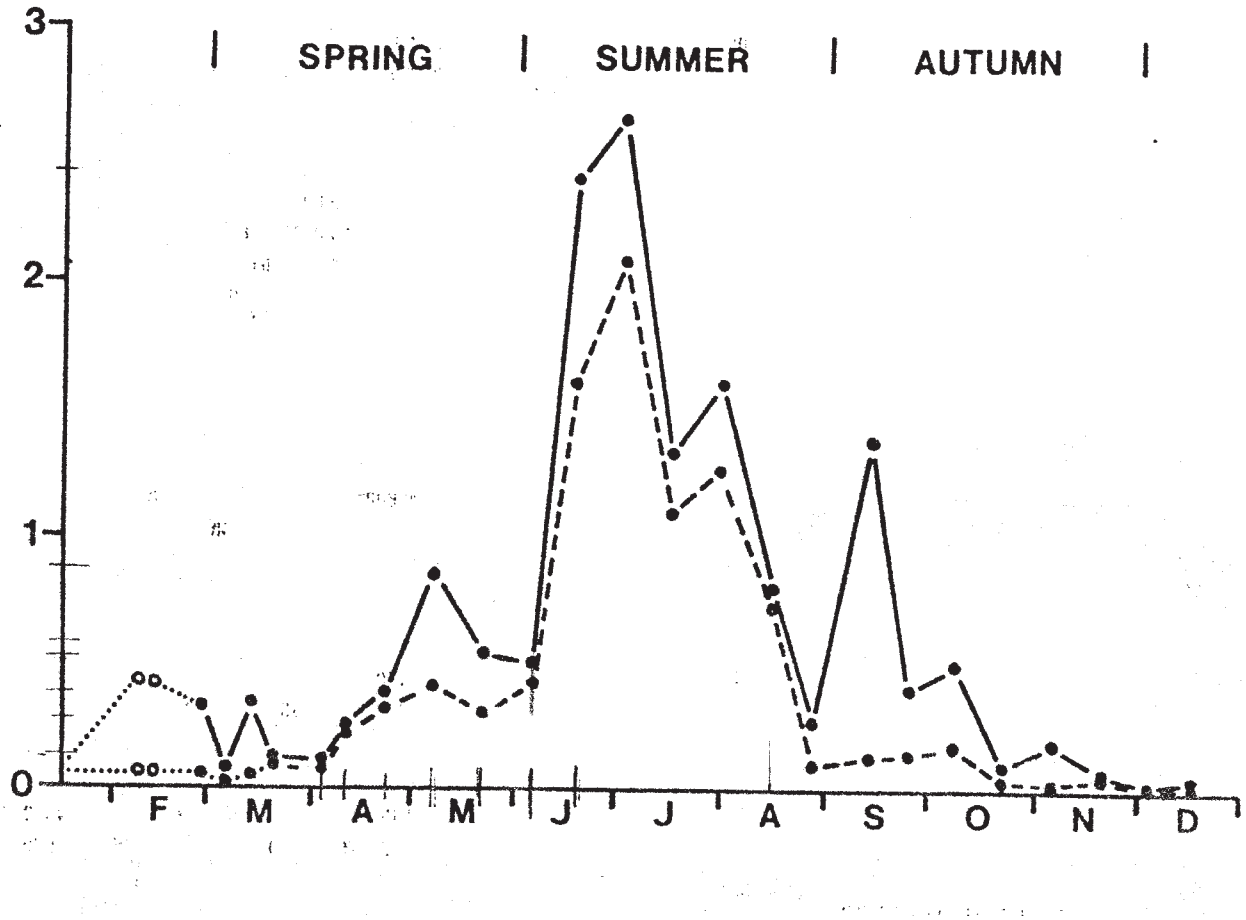


Fig. 6. In situ carbon assimilation (g C $m^{-2}d^{-1}$) at 0 - 12 m depths, Stn 1, 1979. Continuous line: total assimilation, broken line: assimilation of fraction <5 um, dotted line: in situ rates calculated from incubator values.

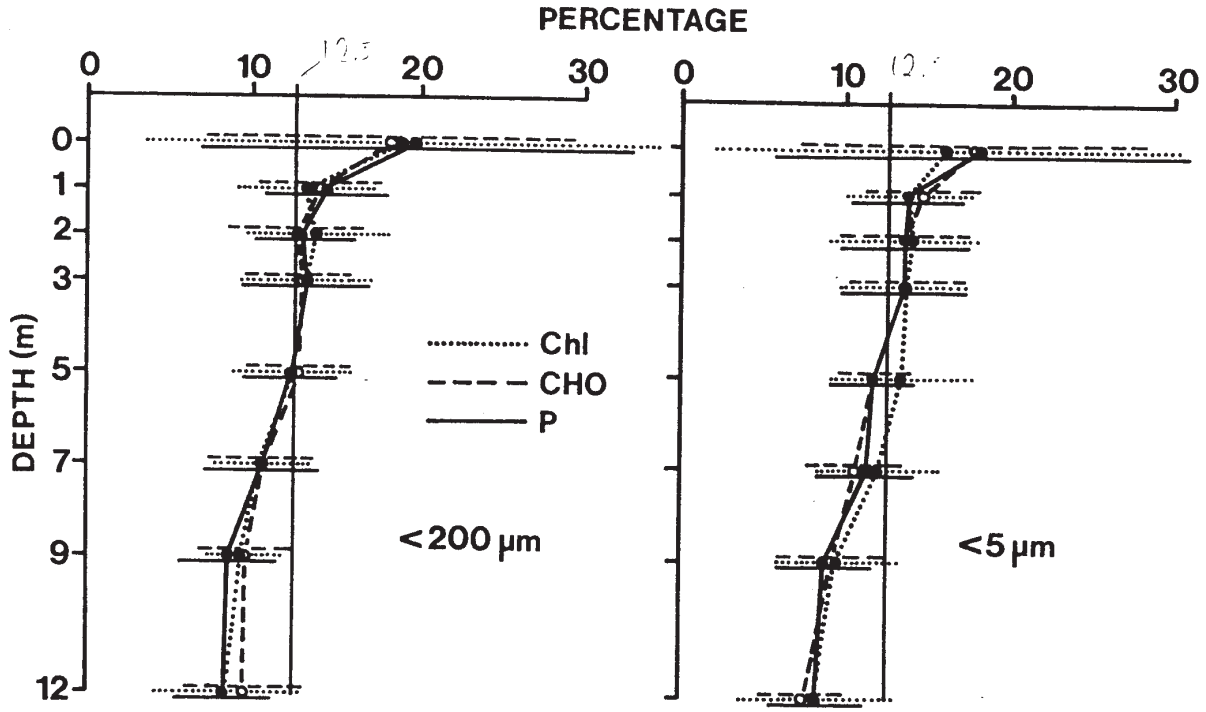


Fig. 7. Average vertical distribution of chlorophyll a (Chl), carbohydrate (CHO), and protein (P) at Stn 1, January - December 1979, calculated as percentages of total content 0 - 12 m depths. Horizontal bars denote standard deviation.

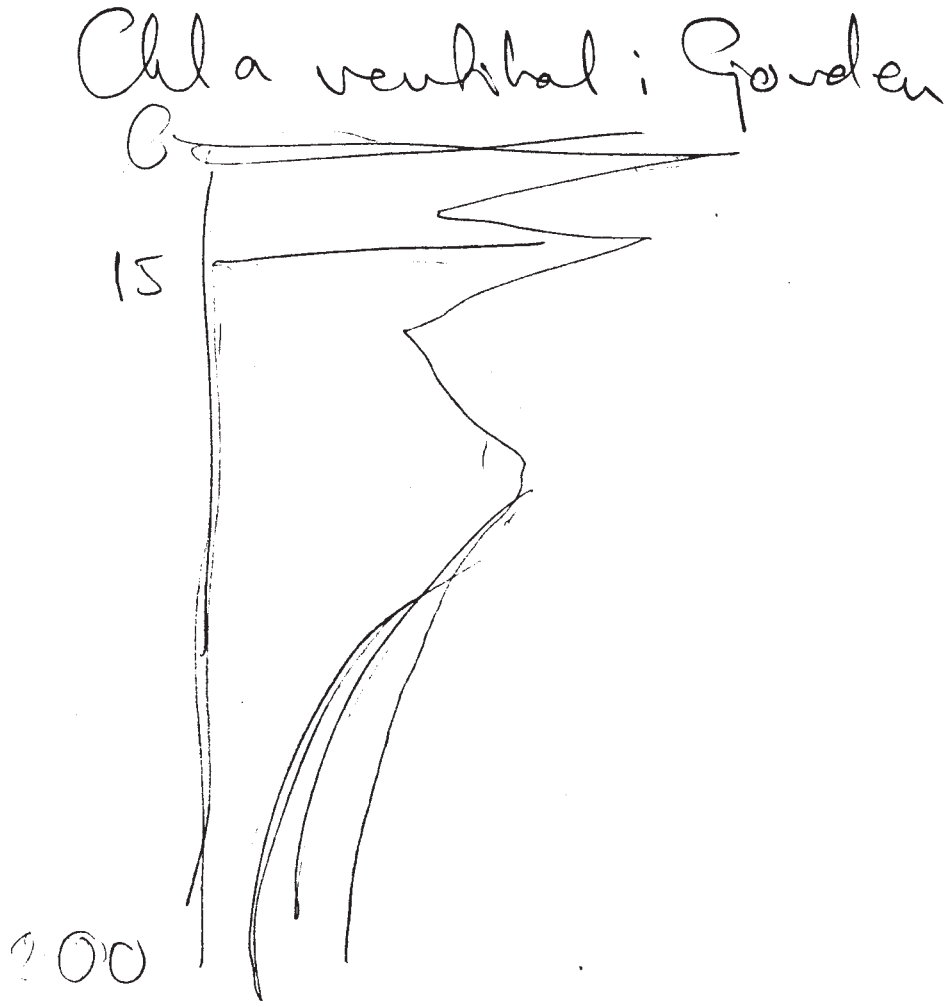


Fig. 8. Vertical distribution of chlorophyll a 0 - 200 m in the open sea, 4 km SW of Stn 1, 11 July 1979.

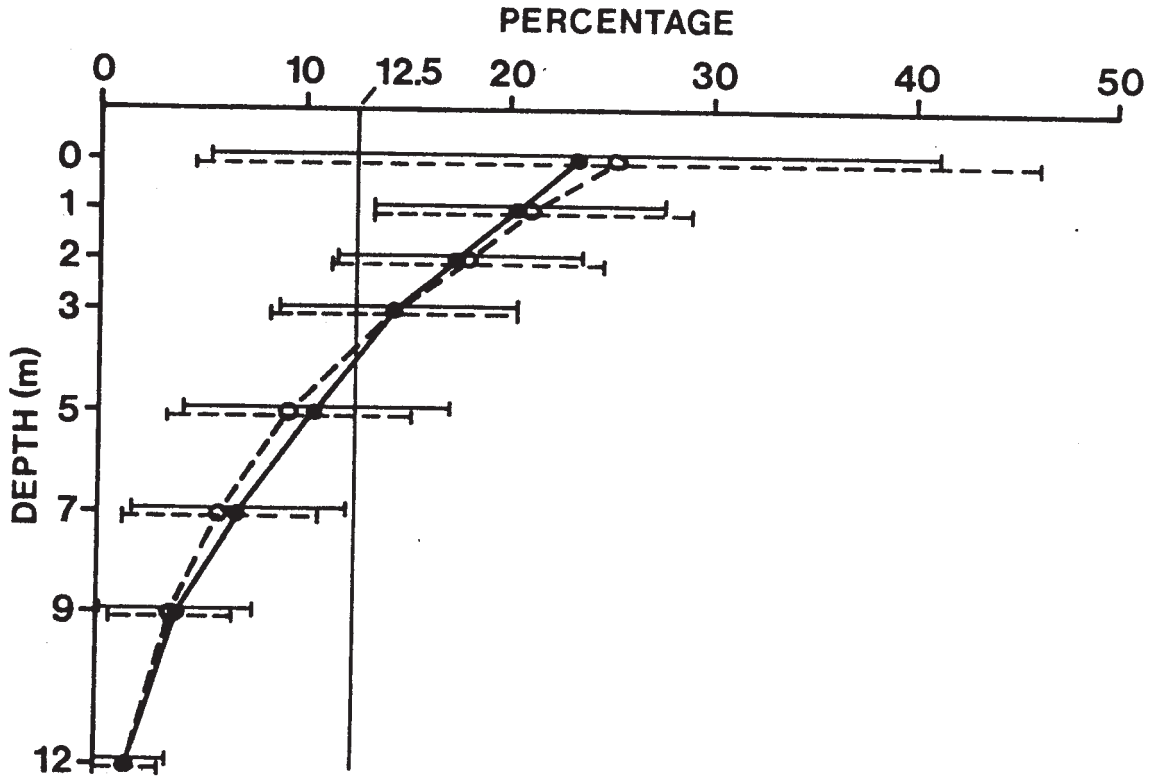


Fig. 9. Vertical distribution of in situ carbon assimilation rates. Otherwise as Fig. 7.

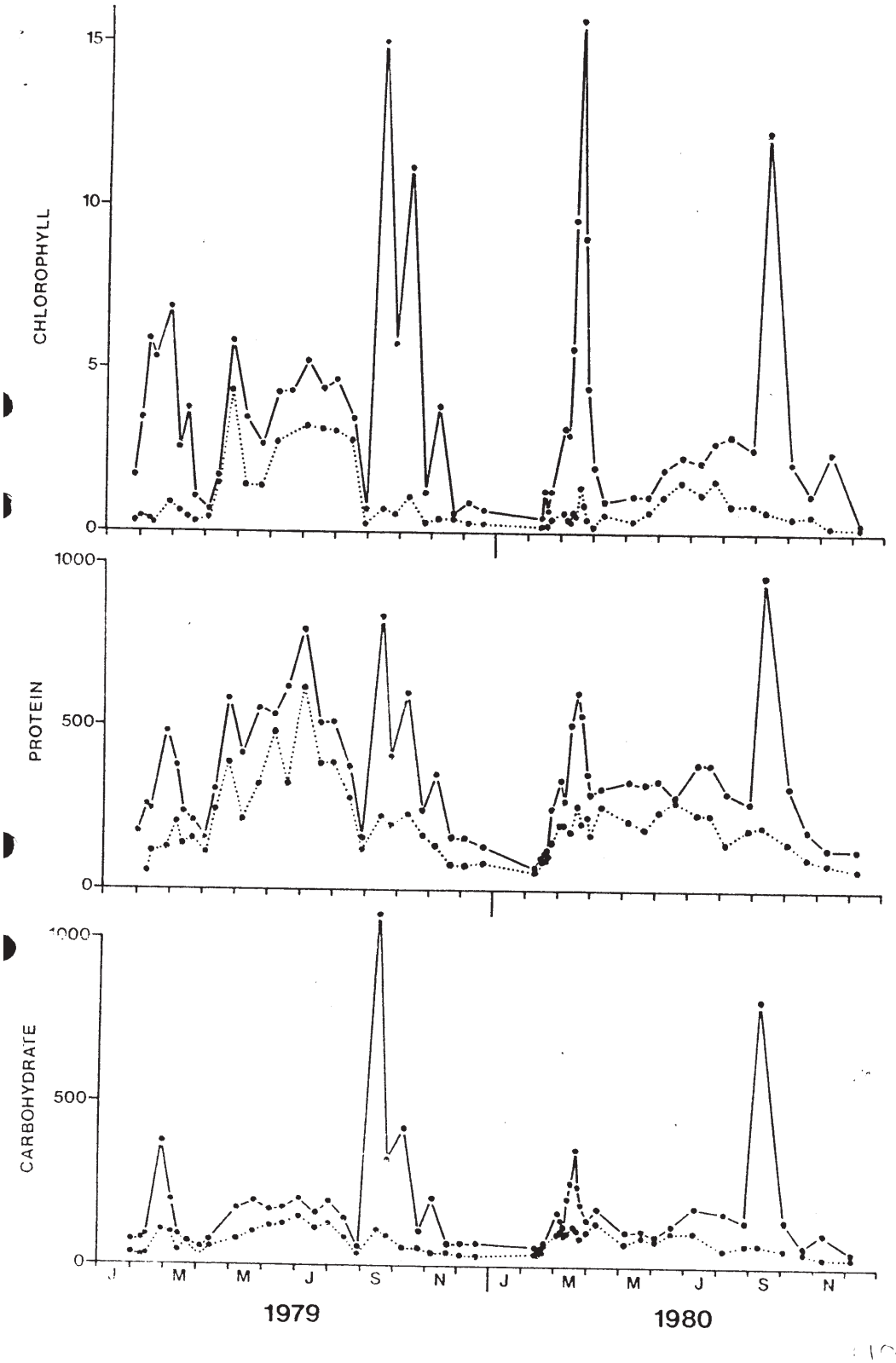


Fig. 10. Average concentrations (mg m^{-3}) of chlorophyll a, protein, and carbohydrate at 1, 3, and 5 m depths at Stn 1 January - December 1979 and May - December 1980. Also showing average concentrations at 2 and 4 m depths at Stn 3, February - April 1980. Continuous line: fraction <200 um, broken line: fraction <5 um.

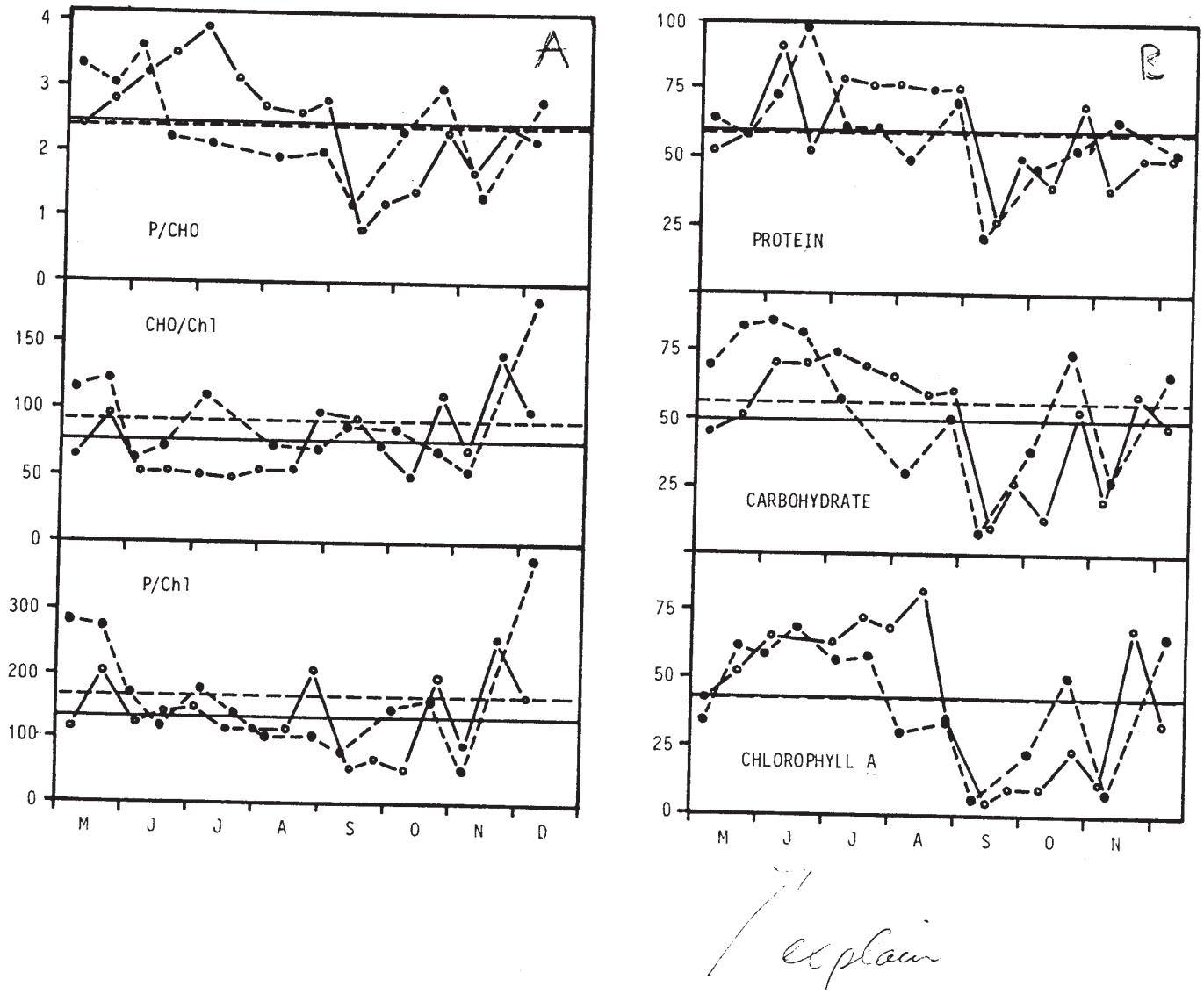


Fig. 11. (A) Ratios of protein/carbohydrate (P/CHO), carbohydrate/chlorophyll a (CHO/Chl), and protein/chlorophyll a (P/CHO) of average concentrations at 1, 3, and 5 m depths, Stn 1, May - December. Continuous line: 1979, broken line: 1980.

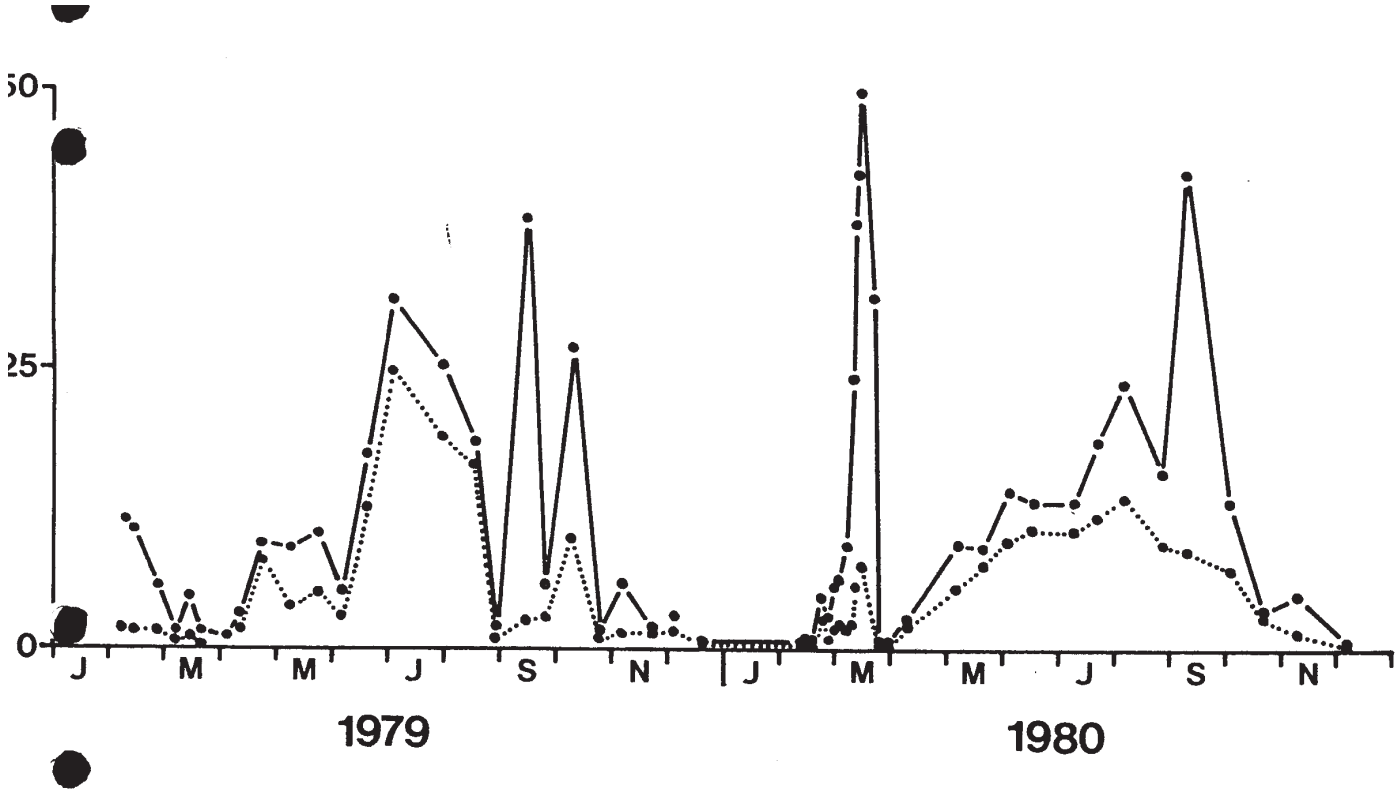


Fig. 12. Average incubator carbon assimilation rates (mg C $m^{-3} h^{-1}$) of samples from 1, 3, and 5 m depths, Stn 1, February - December 1979 and May - December 1980. Also showing average rates of samples from 2 and 4 m depths, Stn 3, 1980. Continuous line: total rates, broken line: rates of fraction <5 um.

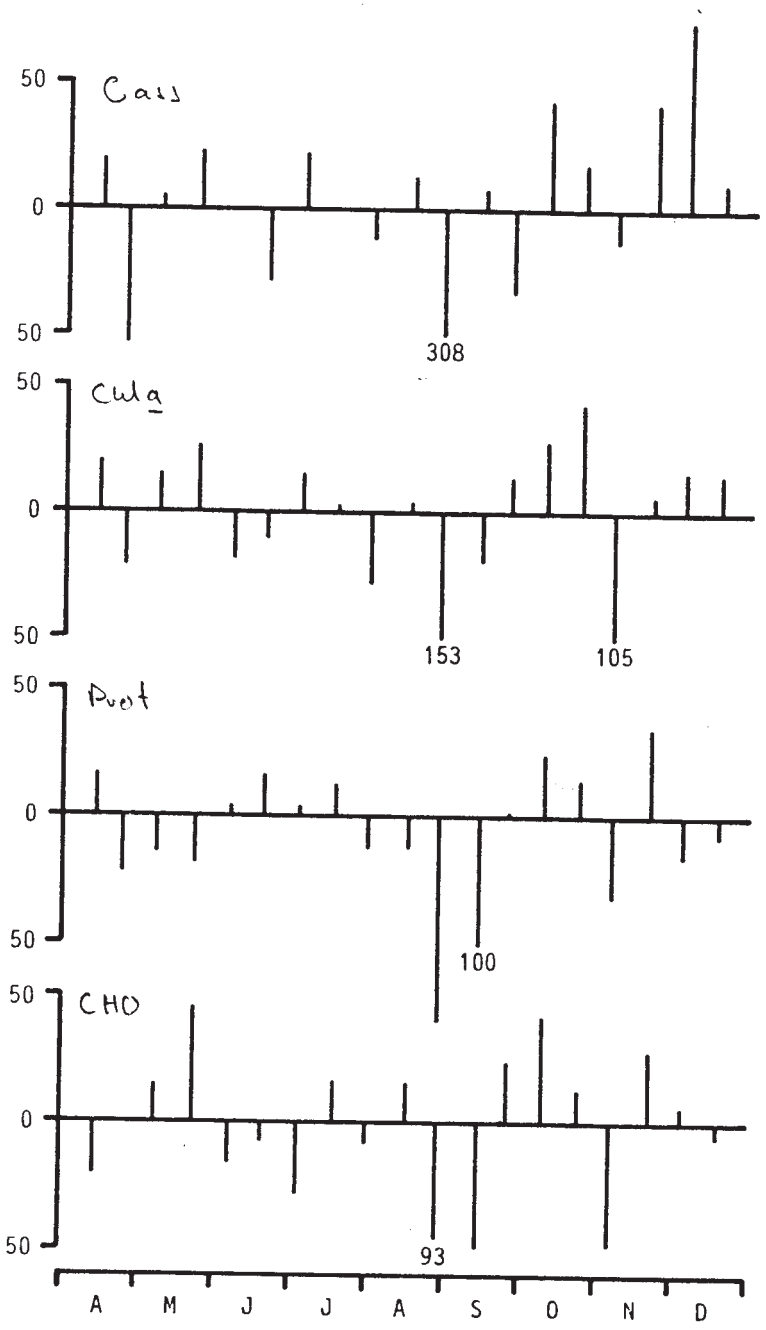


Fig. 13. Comparance between average carbon assimilation rates (C ass), chlorophyll a (Chl), protein (P), and carbohydrate (CHO) concentrations at 1, 3, and 5 m depths at Stns 1 and 2, 1979. Upward bar indicates higher value at Stn 1. Differences calculated as percentages of values at Stn 1

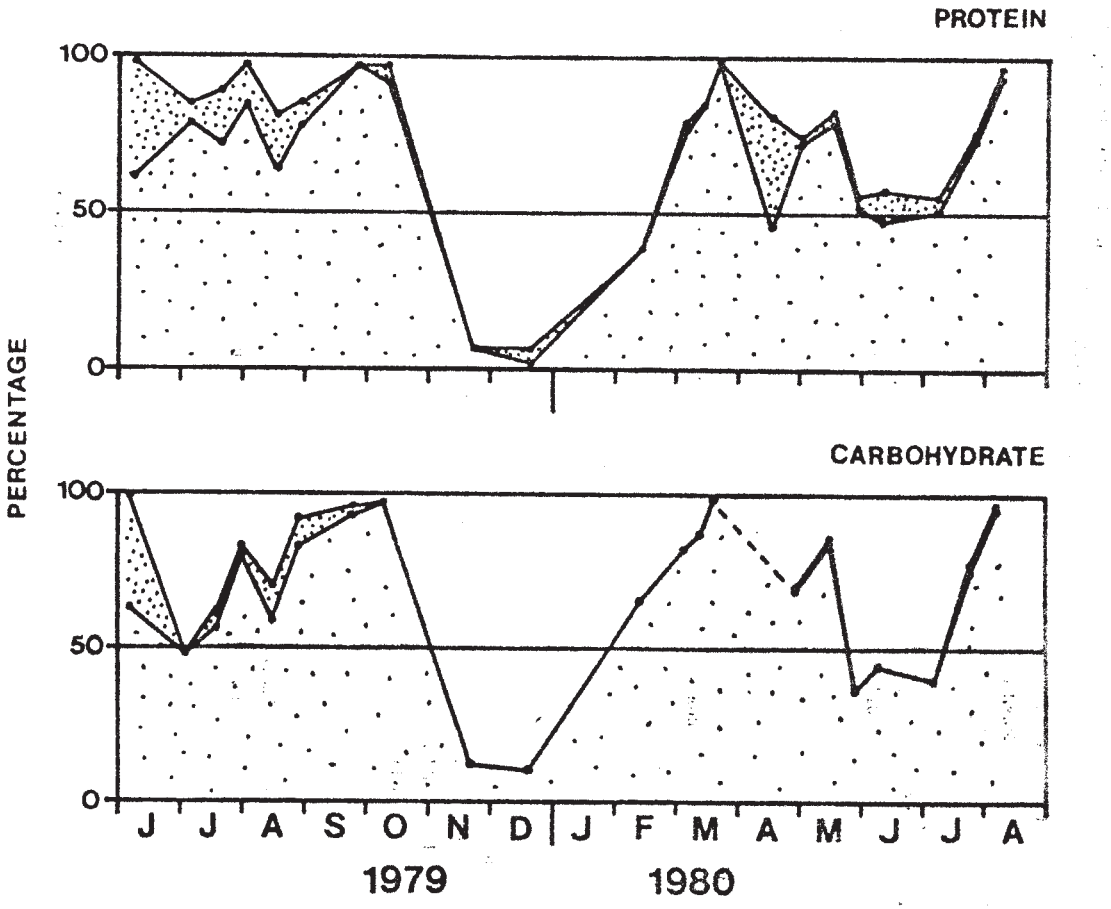


Fig. 14. Percentages of carbohydrate and protein bound in detritus, zooplankton (close-dotted area), and phytoplankton (thin-dotted area), estimated by histochemical staining of particles 5 - 200 um.

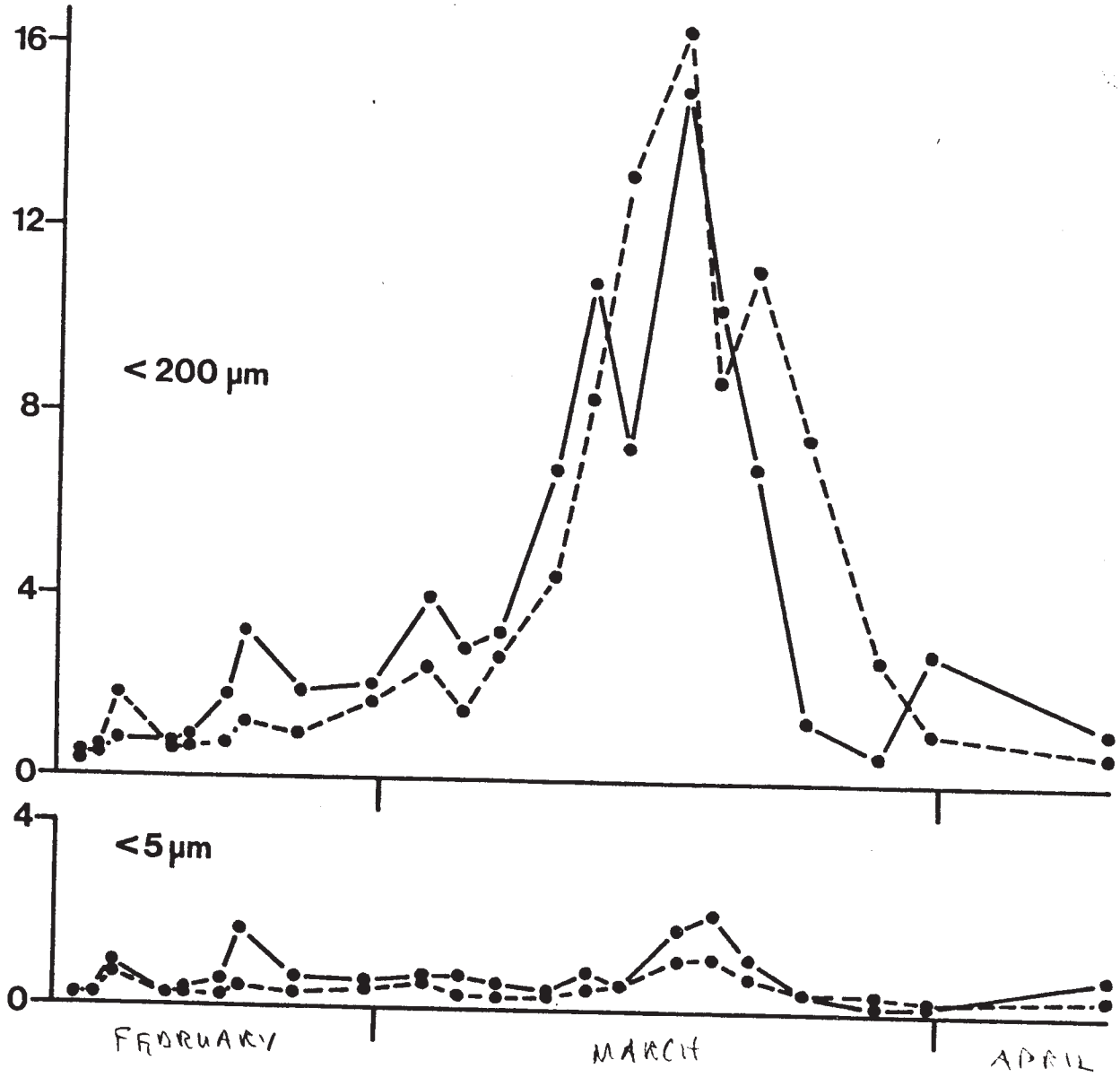


Fig. 15. Spring bloom 1980. Concentrations (mg m^{-3}) of (A) chlorophyll a, (B) protein, and (C) carbohydrate in size fractions <200 and <5 um. Continuous line: 2 m depth, broken line: 4 m depth.

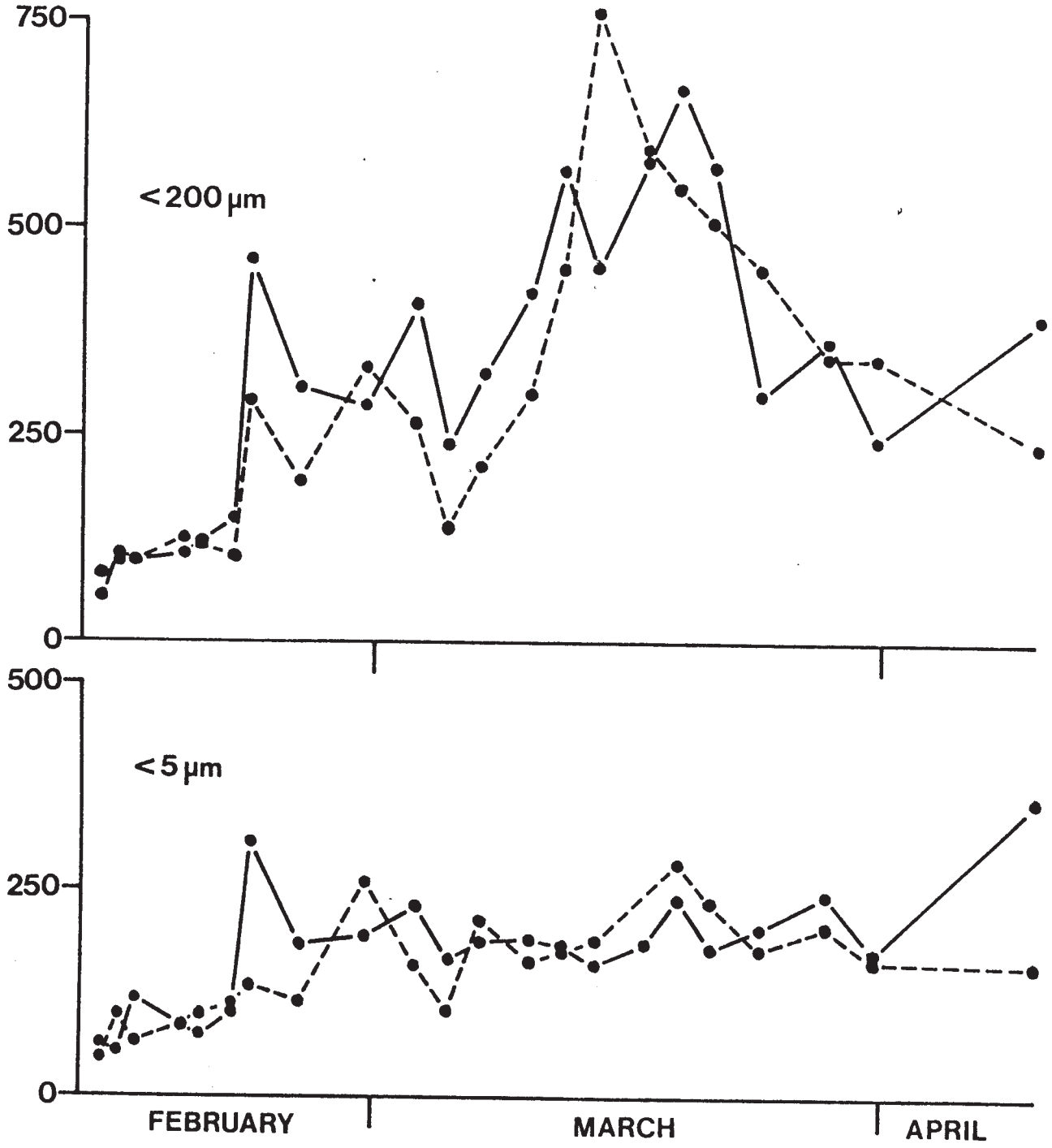


Fig. 15. Spring bloom 1980. Concentrations (mg m^{-3}) of (A) chlorophyll a, (B) protein, and (C) carbohydrate in size fractions <200 and <5 um. Continuous line: 2 m depth, broken line: 4 m depth.

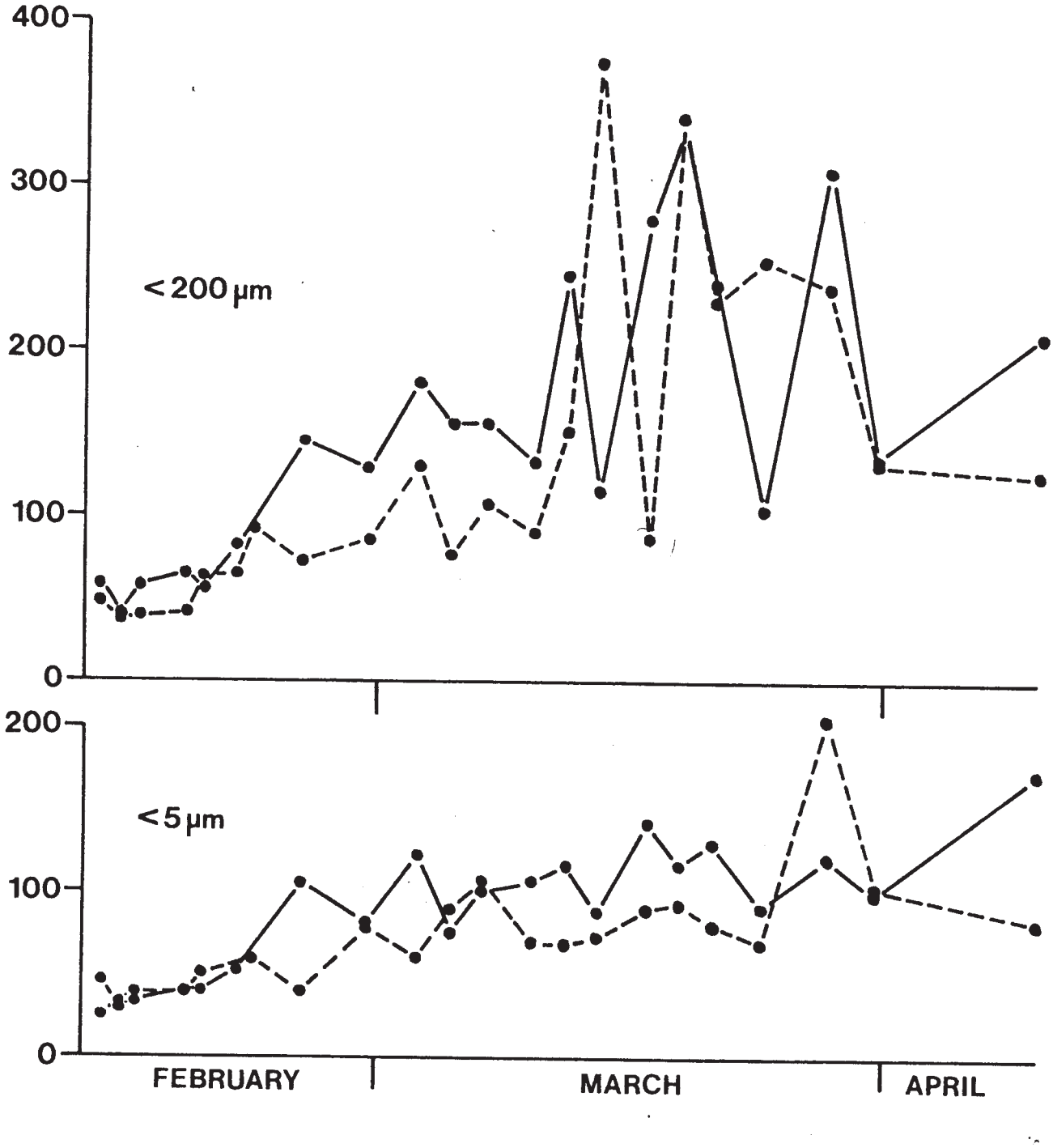


Fig. 15. Spring bloom 1980. Concentrations (mg m^{-3}) of (A) chlorophyll a, (B) protein, and (C) carbohydrate in size fractions <200 and <5 um. Continuous line: 2 m depth, broken line: 4 m depth.

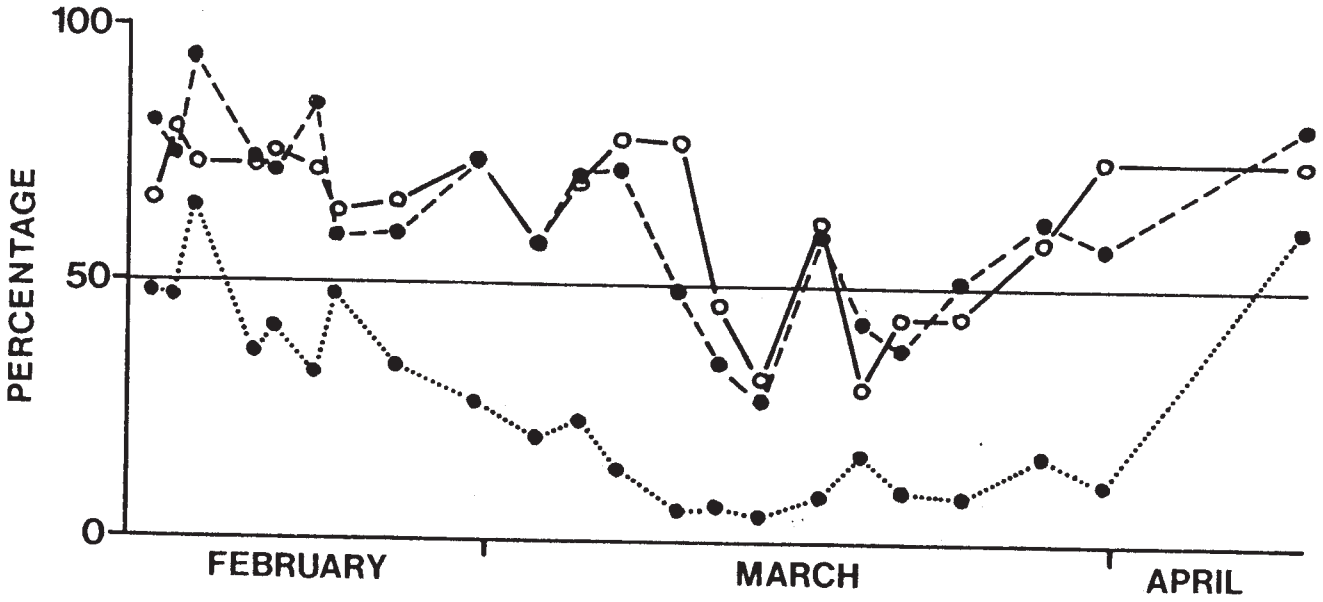


Fig. 16. Spring bloom 1980. Percentages of concentrations <200 um recovered in the <5 um fraction. Calculated from average concentrations at 2 and 4 m depths. Dotted line: chlorophyll a, continuous line: protein, broken line: carbohydrate.

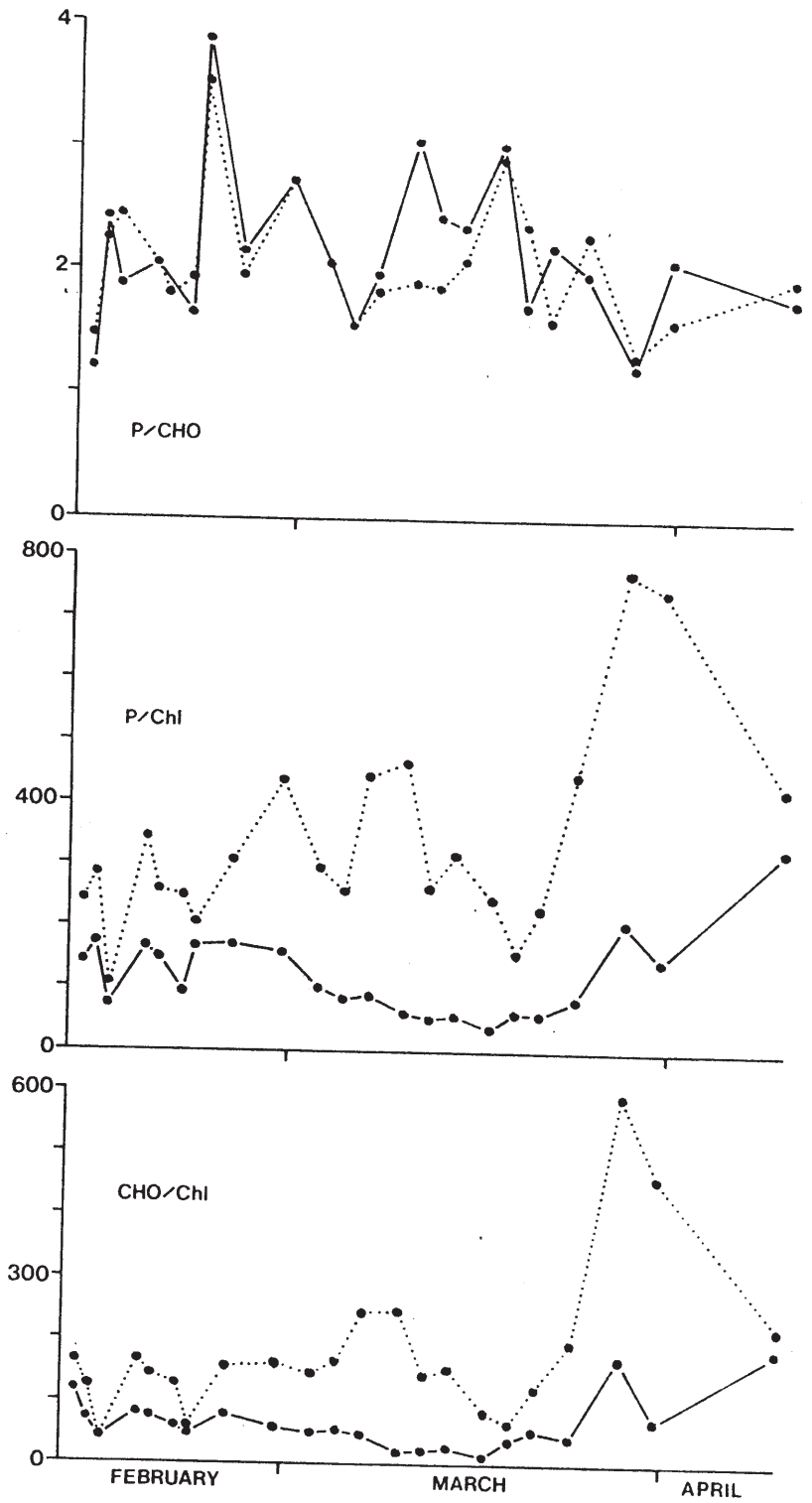


Fig. 17. Spring bloom 1980. Ratios of protein/carbohydrate (P/CHO), protein/chlorophyll a (P/Chl), and carbohydrate/chlorophyll a (CHO/Chl). Calculated from average concentrations at 2 and 4 m depths. Continuous line: fraction <200 um, broken line: fraction < 5 um.

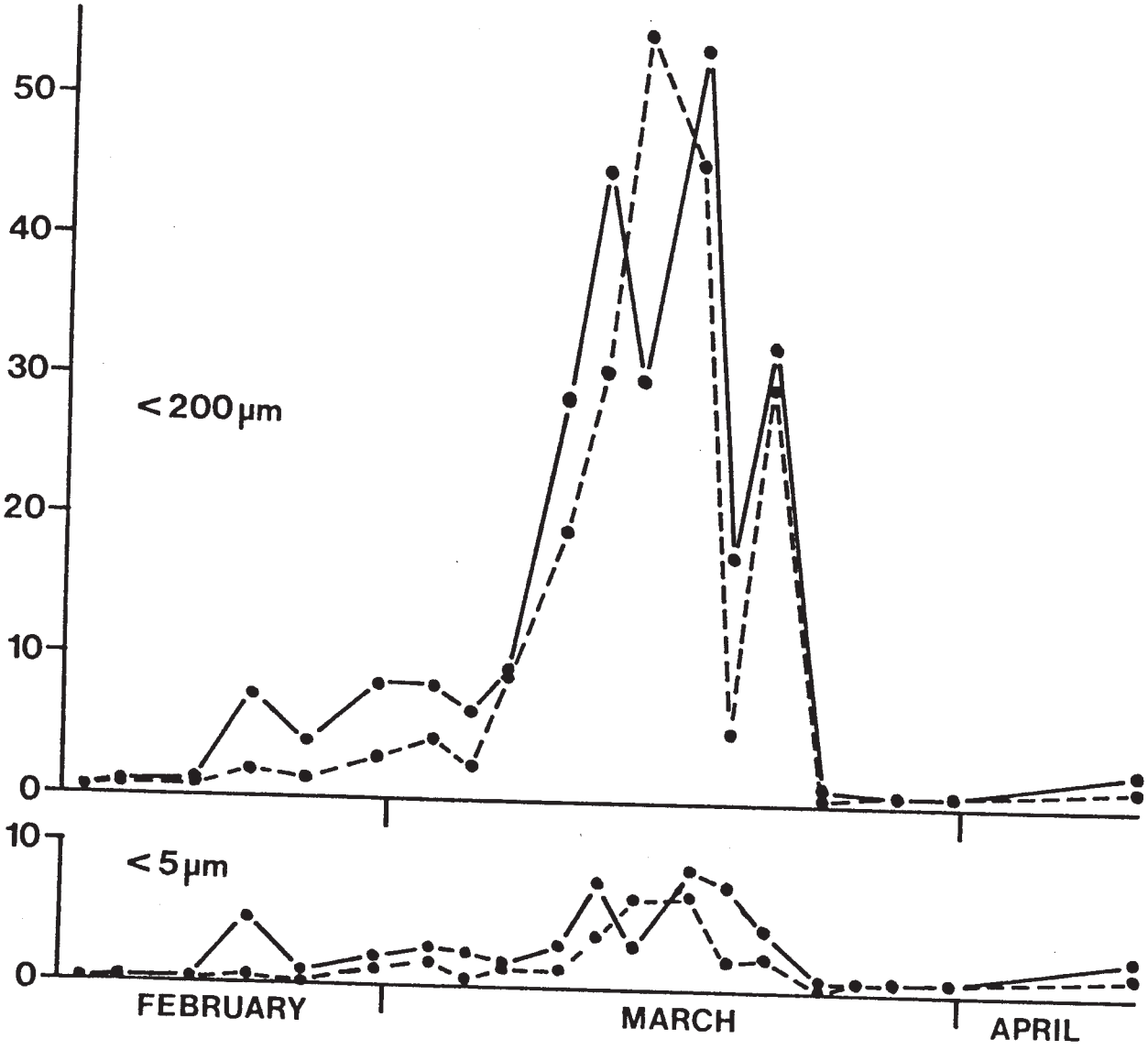


Fig. 18. Spring bloom 1980. Incubator carbon assimilation rates of total and of fraction <5 um. Continuous line: 2 m depth, broken line: 4 m depth.

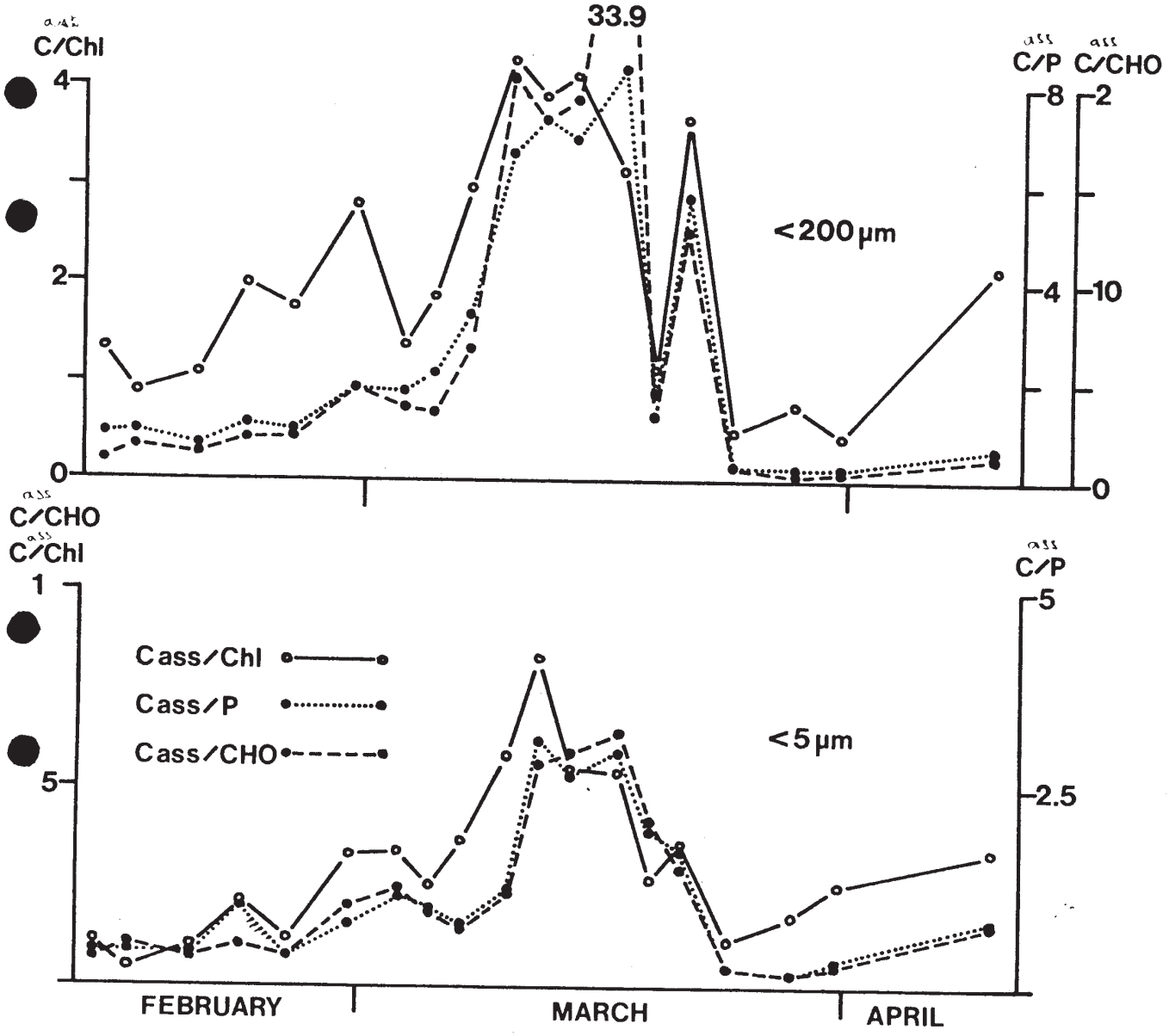


Fig. 19. Spring bloom 1980. Ratios of carbon assimilation/chlorophyll a (C ass/Chl), carbon assimilation/protein (C ass/P), and carbon assimilation/carbohydrate (C ass/CHO). Calculated from average concentrations at 2 and 4 m depths for size fractions <200 and <5 um.

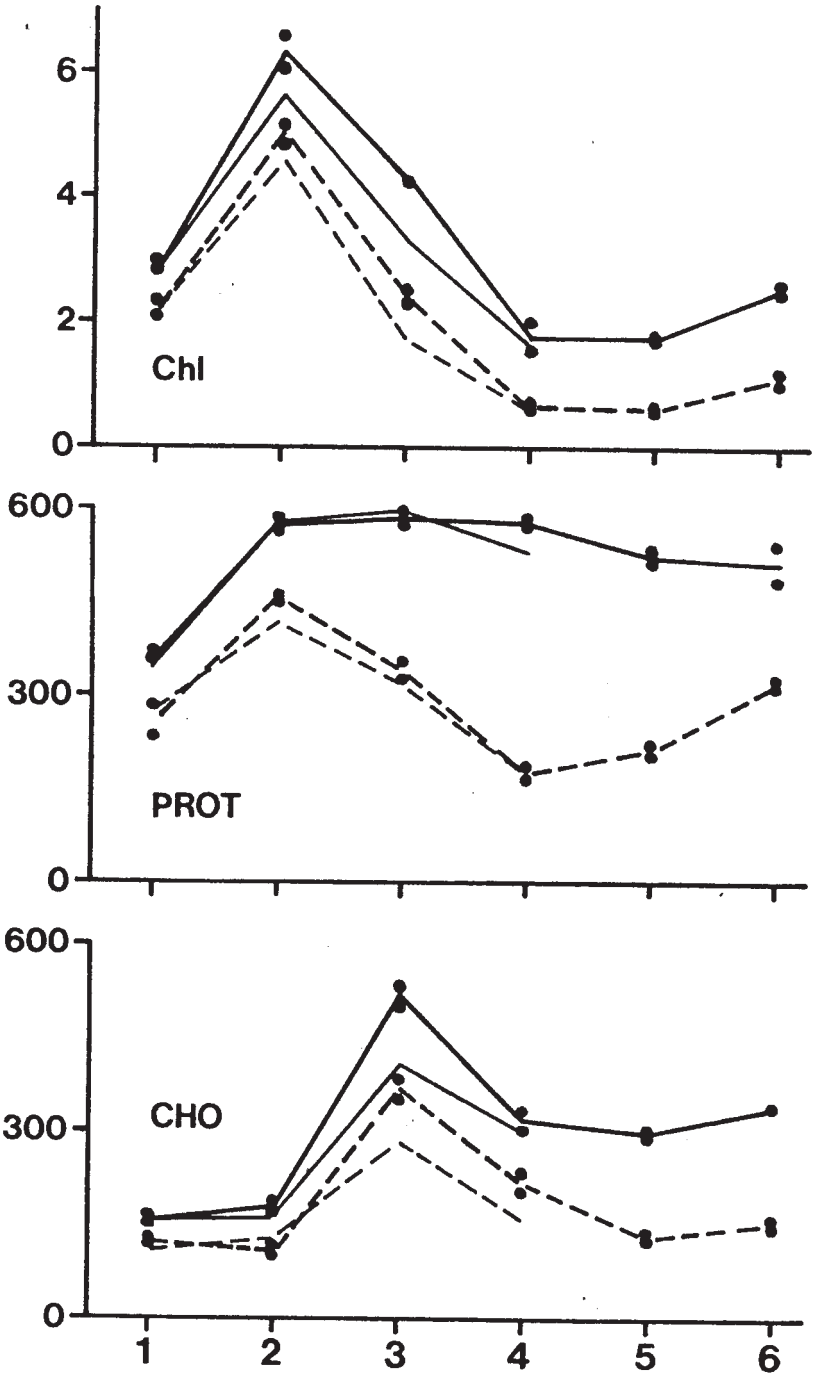


Fig. 20. Bag experiment 1980. Concentrations (mg m^{-3}) of chlorophyll a (Chl), protein (PROT), and carbohydrate (CHO) in Bag II on days 1 to 6. Also showing concentrations in Bag I (thin lines and no dots) on days 1 to 4. Continuous lines: fraction <200 um, broken lines: fraction <5 um.

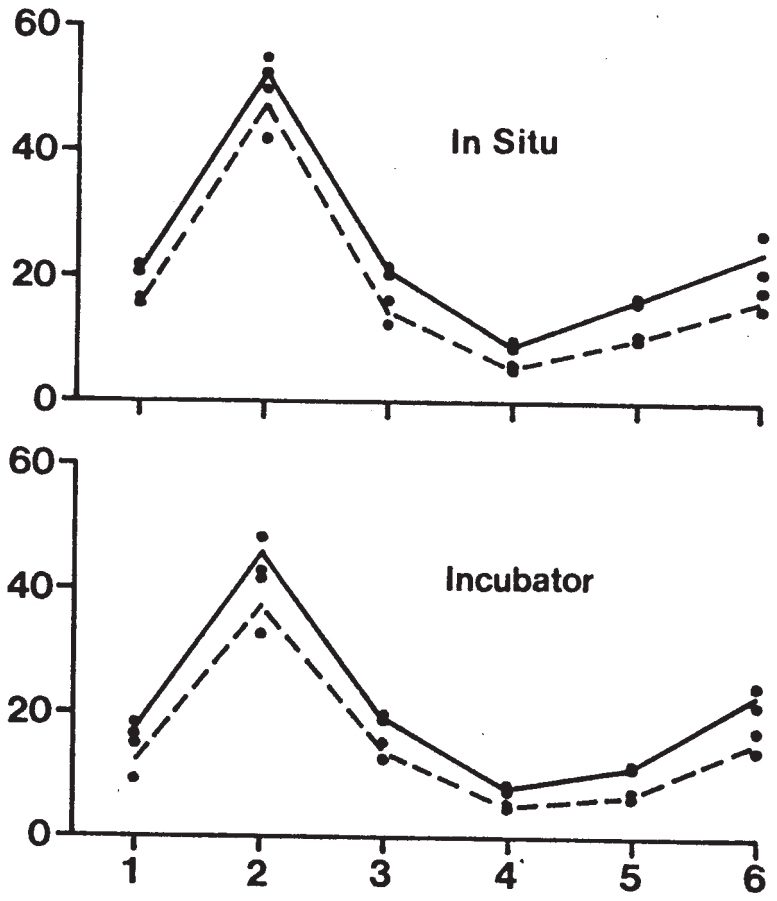


Fig. 21. Bag experiment 1980. In situ and incubator carbon assimilation rates (mg C $m^{-3}h^{-1}$) of samples from Bag II on days 1 to 6.

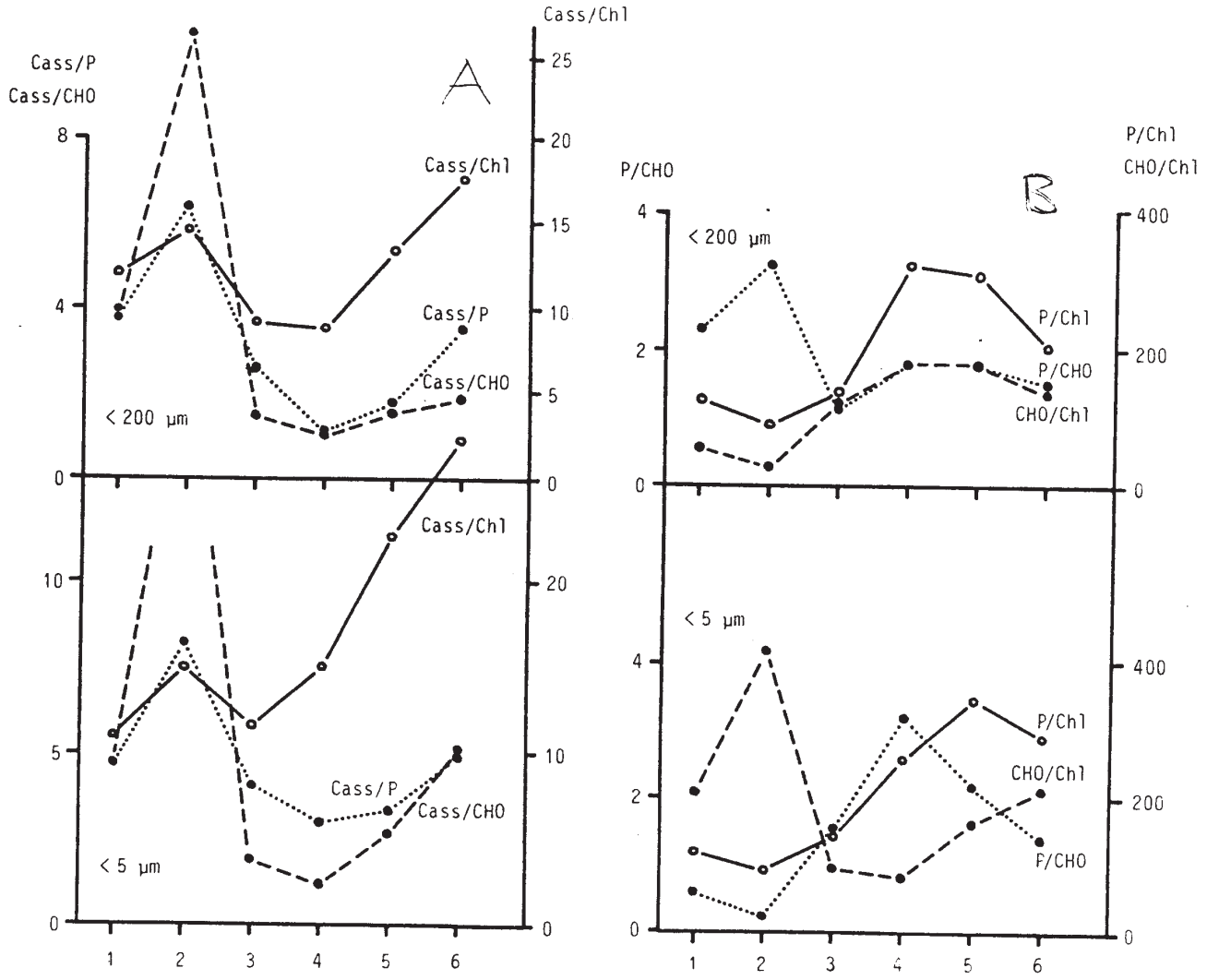


Fig. 22. Bag experiment 1980. (A) Ratios of carbon assimilation/chlorophyll a (C as Chl), carbon assimilation/protein (C ass/P), and carbon assimilation/carbohydrate (C ass/CHO) of samples from Bag II on days 1 to 6, in fractions <200 and <5 um.

(B) Ratios of protein/carbohydrate (P/CHO), protein/chlorophyll a (P/Chl), and carbohydrate/chlorophyll a (CHO/Chl) of the same samples.

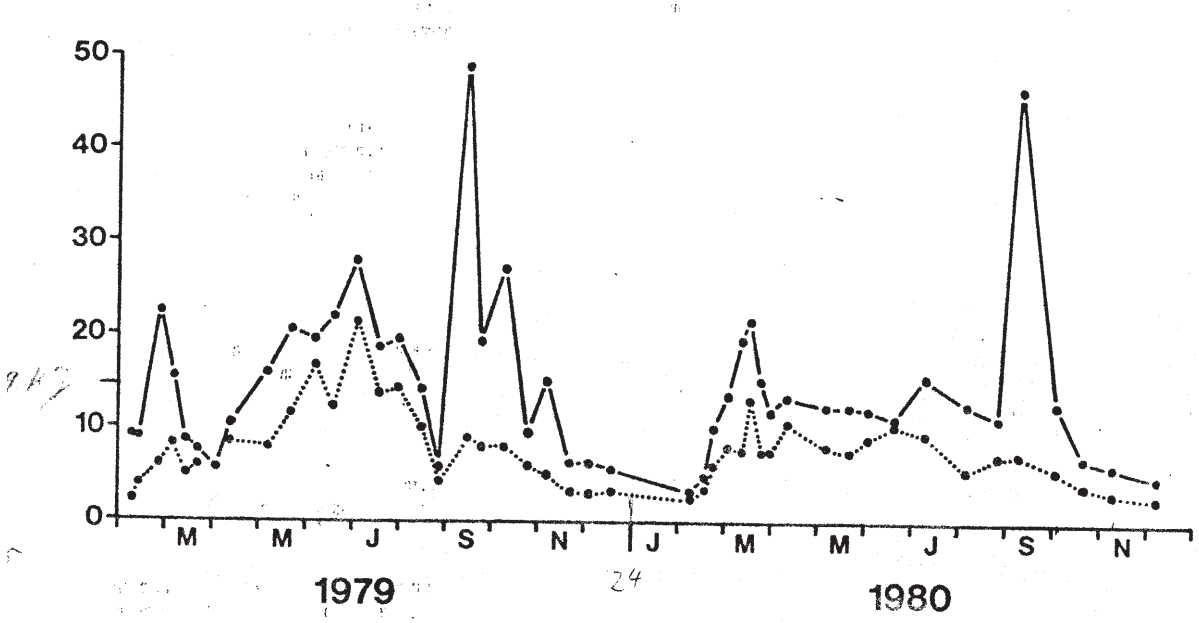


Fig. 23. Average energy content in particulate matter at 1, 3, and 5 m depths at Stn 1, February 1979 - December 1980. Continuous line: fraction <200 um, broken line: fraction <5 um.

Table 1. Average concentrations (mg m^{-3}) and ranges of chlorophyll a (Chl), protein (Prot.), and carbohydrate (CHO) in size fractions <200 and <5 um at 1, 3, and 5 m depths at Stn 1 in spring (March-May), summer (June-August), and autumn (September-November) 1979, and in summer and autumn 1980.

		1979						1980			
		Spring		Summer		Autumn		Summer		Autumn	
	Fraction	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Chl a	<200 um	2.8	0.7-5.9	3.9	0.8-5.3	6.3	0.6-15.1	2.5	2.0-3.0	4.6	1.2-12.4
	<5 um	1.3	0.3-4.4	2.6	0.3-3.3	0.6	0.3-1.2	1.2	0.9-1.6	0.5	0.2-0.7
Prot.	<200 um	355	156-588	503	158-799	436	163-846	330	272-392	403	132-973
	<5 um	221	111-388	372	118-622	174	81-234	220	146-273	132	85-198
CHO	<200 um	123	56-198	159	57-206	367	68-1074	141	93-182	279	61-814
	<5 um	76	46-101	108	35-152	65	40-111	80	50-104	49	28-69

Table 3. Coefficients of linear correlation for ratios carbon assimilation/chlorophyll a (C ass/Chl), carbon assimilation/protein (C ass/Prot.), and carbon assimilation/carbohydrate (C ass/CHO) versus temperature, size fractions <200 um and <5 um, for periods February 1979 - December 1980, using average concentrations and incubator rates from 1, 3, and 5 m depths at Stn 1 and 2 and 4 m depths at Stn 3.

	Fraction	r
Temperature - C ass/Chl	<200 um	.69
	<5 um	.57
Temperature - C ass/Prot.	<200 um	.72
	<5 um	.73
Temperature - C ass/CHO	<200 um	.73
	<5 um	.71

FIGURE TEXTS

Fig. 1. Station locations in the investigated area. TMBL = Tjärnö Marine Biological Laboratory.

Fig. 2. (A) Temperatures (^{o}C) and (B) salinities (^{o}/oo) at 0 - 12 m depths, Stn 1, January - December 1979.

Fig. 3. Integrated chlorophyll a (A), carbohydrate (B), and protein (C) concentrations (g m^{-2}) at 0 - 12 m depths, Stn 1, January - December 1971. Continuous line: fraction <200 um, broken line: fraction <5 um.

Fig. 4. Percentages of concentrations <200 um recovered in the <5 um fraction. Calculated from the integrated concentrations in Fig. 3.

Fig. 5. Ratios of protein/carbohydrate (P/CHO), protein/chlorophyll a (P/Chl), and carbohydrate/chlorophyll a (CHO/Chl). Calculated from the integratec values in Fig. 3. Continuous line: fraction <200 um, broken line: fraction <5 um.

Fig. 6. In situ carbon assimilation (g C $m^{-2}d^{-1}$) at 0 - 12 m depths, Stn 1, 197 Continuous line: total assimilation, broken line: assimilation of fraction <5 um, dotted line: in situ rates calculated from incubator values.

Fig. 7. Average vertical distribution of chlorophyll a (Chl), carbohydrate (CHO and protein (P) at Stn 1, January - December 1979, calculated as percentages of total content 0 - 12 m depths. Horizontal bars denote standard deviation.

Fig. 8. Vertical distribution of chlorophyll a 0 - 200 m in the open sea, 4 km SW of Stn 1, 11 July 1979.

Fig. 9. Vertical distribution of in situ carbon assimilation rates. Otherwise a Fig. 7.

Fig. 10. Average concentrations (mg m^{-3}) of chlorophyll a, protein, and carbohydrate at 1, 3, and 5 m depths at Stn 1 January - December 1979 and May - December 1980. Also showing average concentrations at 2 and 4 m depths at Stn 3, February - April 1980. Continuous line: fraction <200

um, broken line: fraction <5 um.

Fig. 11. (A) Ratios of protein/carbohydrate (P/CHO), carbohydrate/chlorophyll a (CHO/Chl), and protein/chlorophyll a (P/CHO) of average concentrations at 1, 3, and 5 m depths, Stn 1, May - December. Continuous line: 1979, broken line: 1980.

Fig. 12. Average incubator carbon assimilation rates (mg C $m^{-3} h^{-1}$) of samples from 1, 3, and 5 m depths, Stn 1, February - December 1979 and May - December 1980. Also showing average rates of samples from 2 and 4 m depths, Stn 3, 1980. Continuous line: total rates, broken line: rates of fraction <5 um.

Fig. 13. Comparance between average carbon assimilation rates (C ass), chlorophyll a (Chl), protein (P), and carbohydrate (CHO) concentrations at 1, 3, and 5 m depths at Stns 1 and 2, 1979. Upward bar indicates higher value at Stn 1. Differences calculated as percentages of values at Stn 1.

Fig. 14. Percentages of carbohydrate and protein bound in detritus, zooplankton (close-dotted area), and phytoplankton (thin-dotted area), estimated by histochemical staining of particles 5 - 200 um.

Fig. 15. Spring bloom 1980. Concentrations (mg m^{-3}) of (A) chlorophyll a, (B) protein, and (C) carbohydrate in size fractions <200 and <5 um. Continuous line: 2 m depth, broken line: 4 m depth.

Fig. 16. Spring bloom 1980. Percentages of concentrations <200 um recovered in the <5 um fraction. Calculated from average concentrations at 2 and 4 m depths. Dotted line: chlorophyll a, continuous line: protein, broken line: carbohydrate.

Fig. 17. Spring bloom 1980. Ratios of protein/carbohydrate (P/CHO), protein/chlorophyll a (P/Chl), and carbohydrate/chlorophyll a (CHO/Chl). Calculated from average concentrations at 2 and 4 m depths. Continuous line: fraction <200 um, broken line: fraction < 5 um.

Fig. 18. Spring bloom 1980. Incubator carbon assimilation rates of total and of fraction <5 um. Continuous line: 2 m depth, broken line: 4 m depth.

Fig. 19. Spring bloom 1980. Ratios of carbon assimilation/chlorophyll a (C ass/Chl), carbon assimilation/protein (C ass/P), and carbon assimilation/carbohydrate (C ass/CHO). Calculated from average concentrations at 2 and 4 m depths for size fractions <200 and <5 um.

Fig. 20. Bag experiment 1980. Concentrations (mg m^{-3}) of chlorophyll a (Chl), protein (PROT), and carbohydrate (CHO) in Bag II on days 1 to 6. Also showing concentrations in Bag I (thin lines and no dots) on days 1 to 4. Continuous lines: fraction <200 um, broken lines: fraction <5 um.

Fig. 21. Bag experiment 1980. In situ and incubator carbon assimilation rates (mg C $m^{-3}h^{-1}$) of samples from Bag II on days 1 to 6.

Fig. 22. Bag experiment 1980. (A) Ratios of carbon assimilation/chlorophyll a (C a Chl), carbon assimilation/protein (C ass/P), and carbon assimilation/carbohydrate (C ass/CHO) of samples from Bag II on days 1 to 6, in fractions <200 and <5 um.

(B) Ratios of protein/carbohydrate (P/CHO), protein/chlorophyll a (P/Chl), and carbohydrate/chlorophyll a (CHO/Chl) of the same samples.

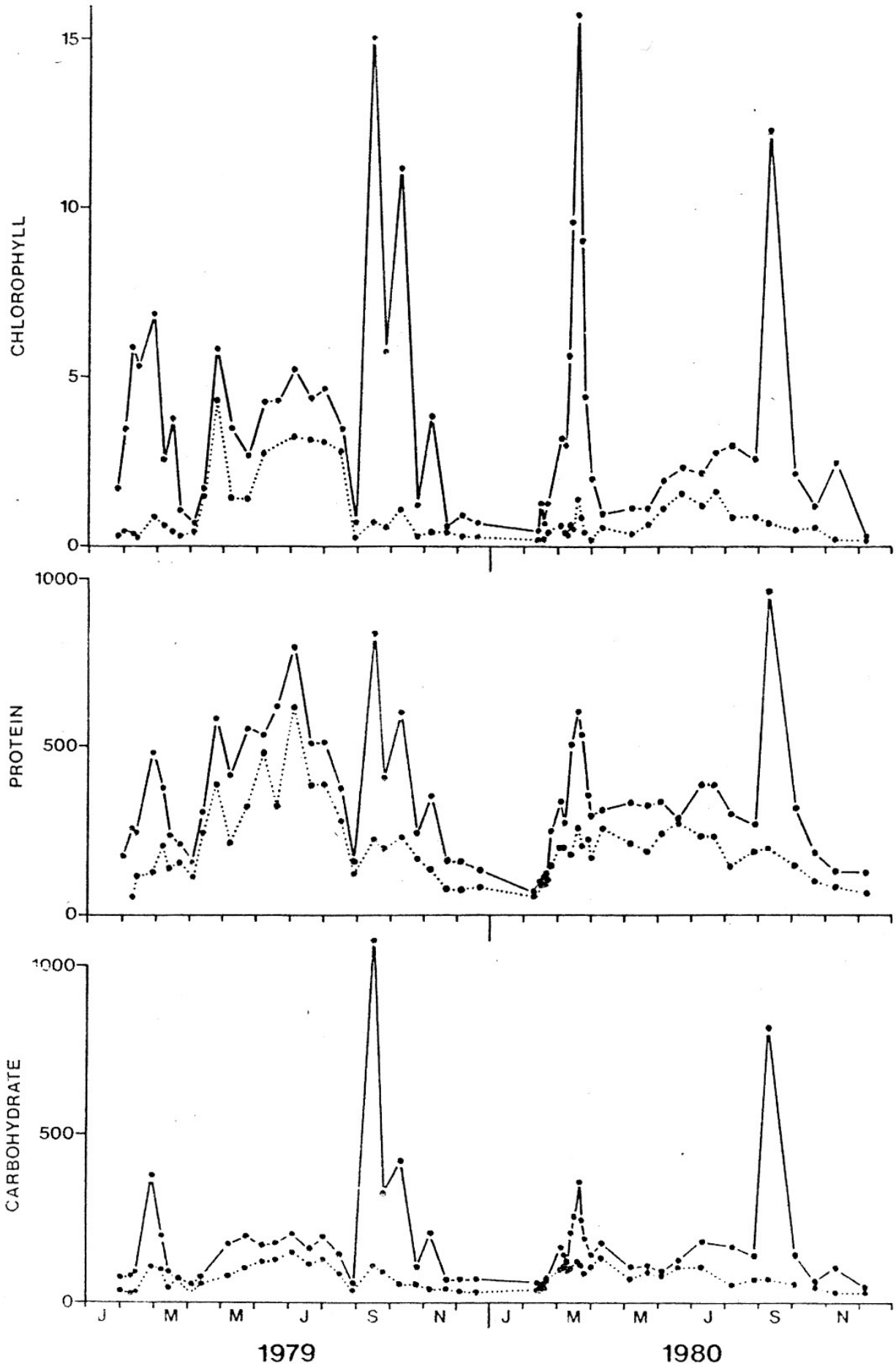
Fig. 23. Average energy content in particulate matter at 1, 3, and 5 m depths at Stn 1, February 1979 - December 1980. Continuous line: fraction <200 um, broken line: fraction <5 um.

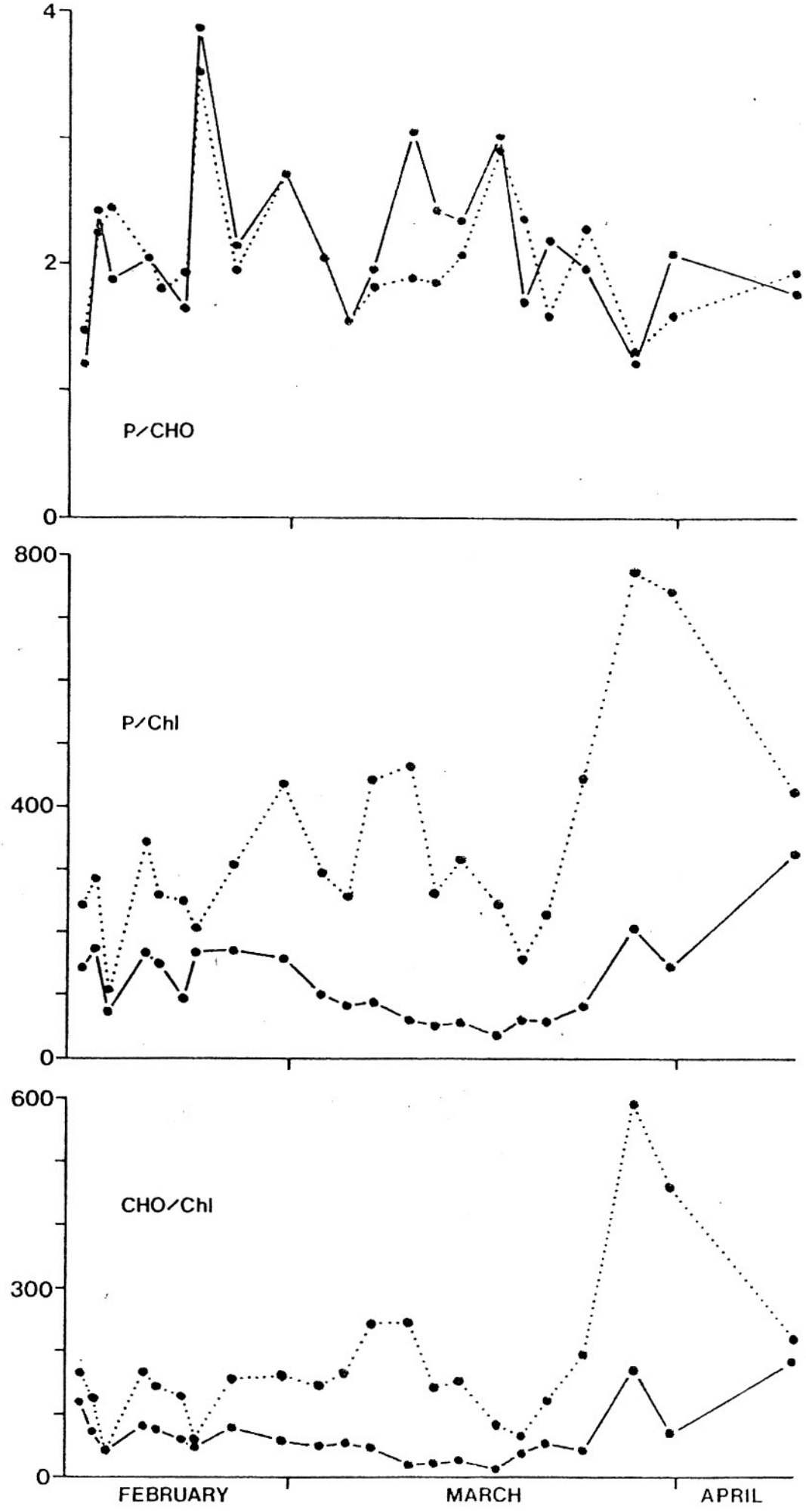
Table 1. Average concentrations (mg m^{-3}) and ranges of chlorophyll a (Chl), protein (Prot.), and carbohydrate (CHO) in size fractions <200 and <5 um at 1, 3, and 5 m depths at Stn 1 in spring (March-May), summer (June-August), and autumn (September-November) 1979, and in summer and autumn 1980.

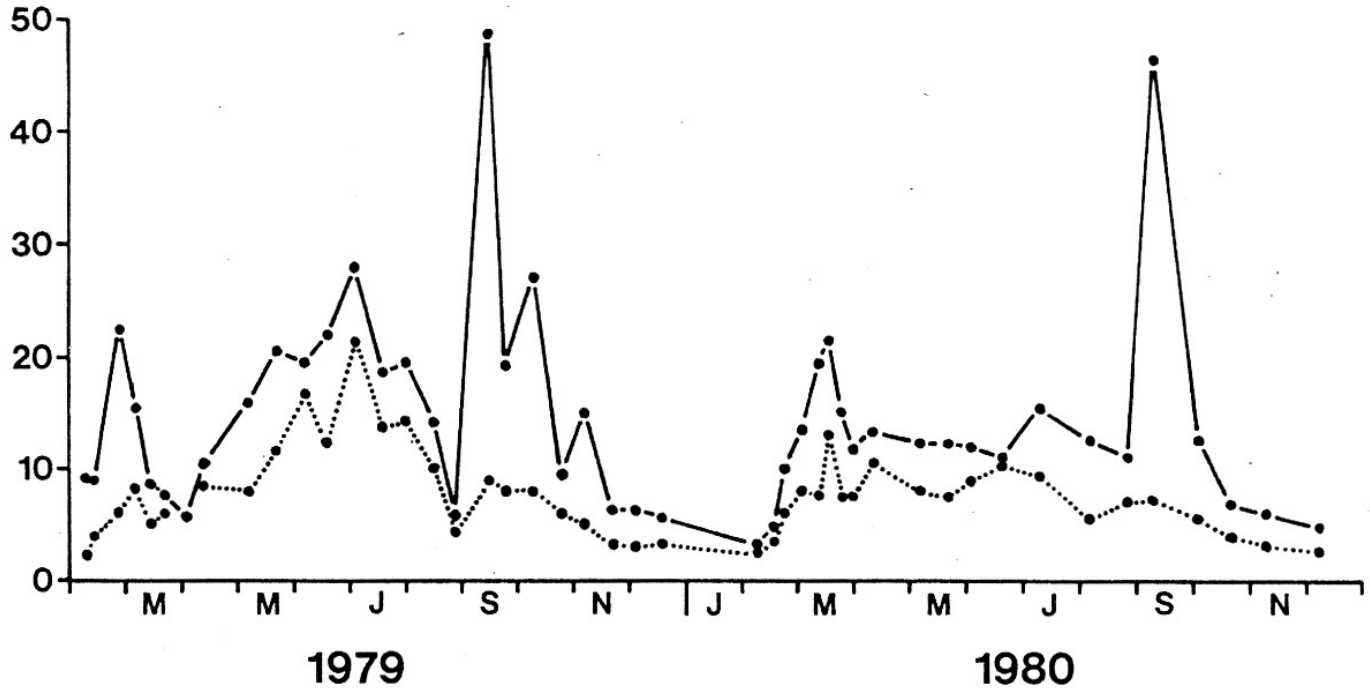
		1979						1980			
		Spring		Summer		Autumn		Summer		Autumn	
	Fraction	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Chl a	<200 um	2.8	0.7-5.9	3.9	0.8-5.3	6.3	0.6-15.1	2.5	2.0-3.0	4.6	1.2-12.4
	<5 um	1.3	0.3-4.4	2.6	0.3-3.3	0.6	0.3-1.2	1.2	0.9-1.6	0.5	0.2-0.7
Prot.	<200 um	355	156-588	503	158-799	436	163-846	330	272-392	403	132-973
	<5 um	221	111-388	372	118-622	174	81-234	220	146-273	132	85-198
CHO	<200 um	123	56-198	159	57-206	367	68-1074	141	93-182	279	61-814
	<5 um	76	46-101	108	35-152	65	40-111	80	50-104	49	28-69

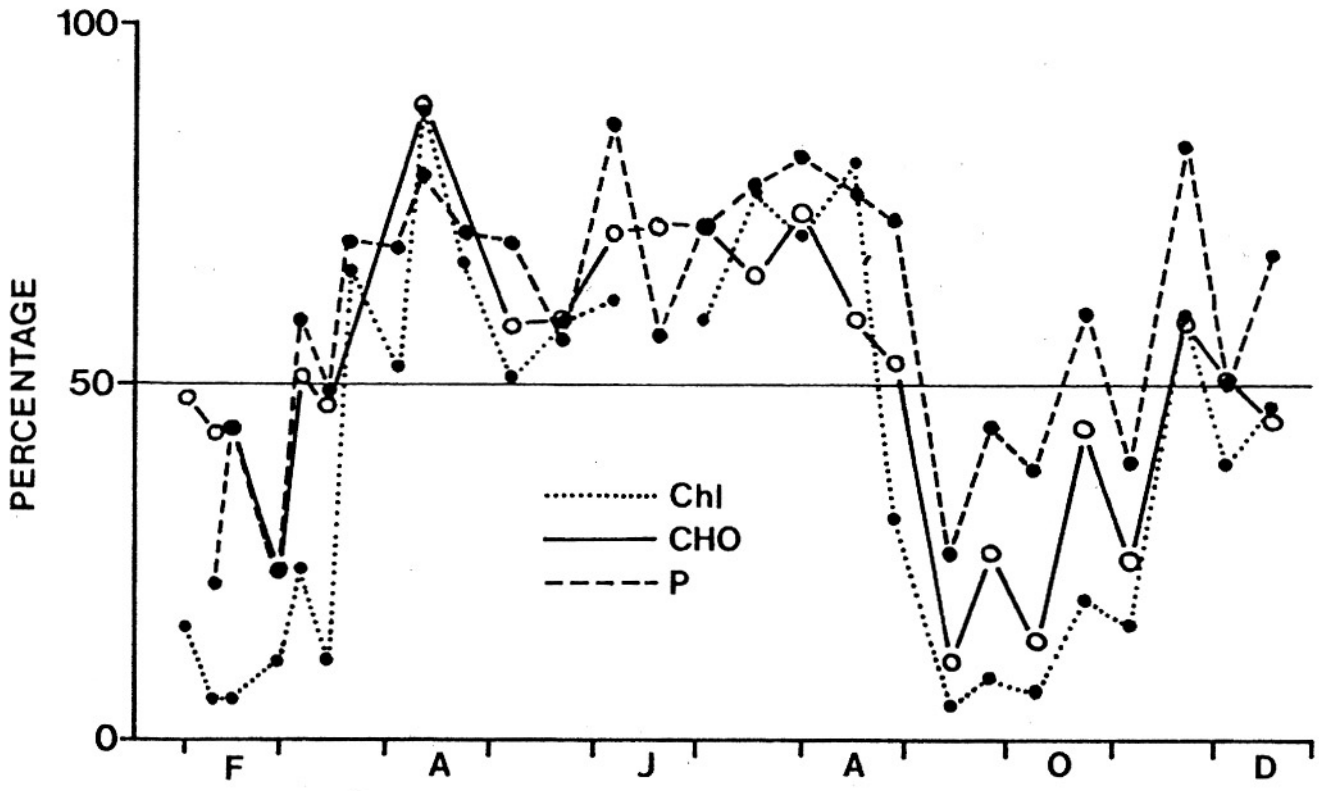
Appendix table. Compiled ranges, averages ($\bar{X}$), standard deviations (SD), and coefficients of variation (CV) of ratios mentioned in the text.

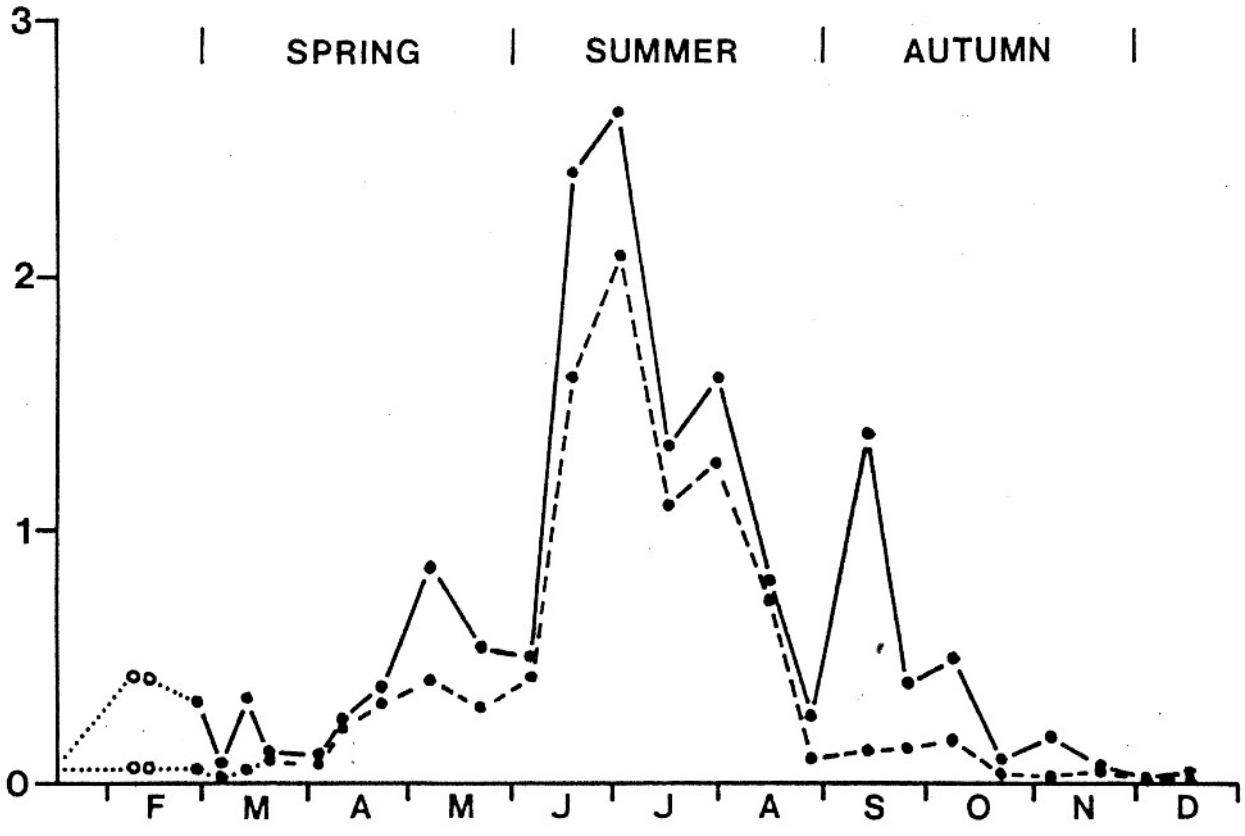
	0-12 m, Stn 1, 1979 8(27)Feb.-18 Dec				1,3,5 m, Stn 1, 1979 8(27)Feb.-18 Dec.				1,3,5 m, Stn 1, 1980 7 May-7 Dec.				Spring bloom, 1980 13 Feb.-10 April				Bag experiment, 1980 15-20 July			
Ratio	Range	$\bar{X}$	SD	CV	Range	$\bar{X}$	SD	CV	Range	$\bar{X}$	SD	CV	Range	$\bar{X}$	SD	CV	Range	$\bar{X}$	SD	CV
P/C																				
<200 um	0.8-4.9	2.8	1.1	40	0.8-4.1	2.5	0.8	32	1.2-3.6	2.4	0.8	32	1.2-3.9	2.2	0.6	29	1.1-3.2	2.0	0.7	37
<5 um	1.2-4.2	2.9	0.8	26	1.2-4.3	2.9	0.8	28	2.1-3.1	2.7	0.4	14	1.3-3.5	2.1	0.5	24	0.8-4.2	1.9	1.2	63
P/Chl																				
<200 um	43-282	128	62	48	43-259	128	62	48	52-382	169	94	56	37-325	122	68	56	91-321	198	97	49
<5 um	100-535	239	112	47	45-579	248	134	54	143-543	257	113	44	107-776	342	166	49	91-343	206	103	50
C/Chl																				
<200 um	15-132	52	28	54	13-108	55	25	45	40-138	69	27	40	12-184	63	44	70	28-177	115	61	53
<5 um	30-181	91	48	53	30-240	97	55	57	56-178	101	37	37	44-590	181	125	69	22-318	150	107	72
In situ																				
Cass/Chl																				
<200 um	0.2-4.2	1.5	1.0	68	0.6-5.7	2.0	1.4	67	1.2-7.8	5.2	2.1	41					5.0-9.5	7.5	2.0	27
<5 um	0.5-5.0	1.9	1.1	59	0.6-7.3	2.7	1.6	59	1.0-15.3	9.1	4.0	44					6.2-17.0	10.7	4.4	41
Cass/P																				
<200 um	0.2-2.7	1.2	0.7	59	0.4-3.9	1.7	1.1	65	0.3-7.8	3.8	1.8	48					1.6-9.1	4.7	2.6	56
<5 um	0.1-3.2	1.0	0.8	74	0.1-4.6	1.5	1.2	78	0.3-9.0	4.0	2.3	55					3.3-10.6	5.8	2.5	44
Cass/C																				
<200 um	0.6-10.1	3.3	2.7	81	0.8-14.6	4.2	3.7	87	0.9-14.6	8.1	4.2	52					3.0-29.3	10.3	9.9	96
<5 um	0.3-11.1	3.4	3.0	87	0.3-15.9	4.7	4.2	90	0.7-26.9	10.5	6.8	64					2.6-44.0	13.8	15.3	111
Incubator																				
Cass/Chl																				
<200 um					0.8-5.9	2.3	1.3	58	3.0-9.4	6.3	2.0	31	0.4-4.3	2.1	1.3	60	4.4-8.8	6.3	1.7	27
<5 um					1.0-8.7	3.3	2.1	63	1.6-20.9	10.3	5.2	50	0.5-8.2	3.1	2.0	64	5.5-14.1	8.6	3.4	39
Cass/P																				
<200 um					0.4-4.9	2.2	1.6	71	0.8-7.4	4.5	1.8	41	0.2-8.5	2.8	2.8	100	1.4-8.0	4.0	2.3	58
<5 um					1.0-6.2	1.9	1.6	82	0.5-7.9	4.2	1.9	46	0.2-3.1	1.1	0.9	80	3.0-8.2	4.7	1.9	40
Cass/C																				
<200 um					0.8-15.3	5.6	4.7	84	2.3-15.1	10.0	3.8	38	0.3-33.9	7.3	9.3	129	2.5-25.5	8.8	8.7	99
<5 um					0.5-20.8	6.0	6.0	100	1.1-23.3	11.2	6.3	56	0.3-6.4	2.2	1.9	86	2.4-34.0	10.9	11.8	108


CHLOROPHYLL
15
10
5
0
PROTEIN
1000
500
0
CARBOHYDRATE
1000
500
0
J
M
M
J
S
N
J
M
M
J
S
N
1979
1980


4
2
0
P/CHO
800
400
0
P/Chl
600
300
0
CHO/Chl
FEBRUARY
MARCH
APRIL


50
40
30
20
10
0
M
M
J
S
N
J
M
M
J
S
N
1979
1980


100
50
0
PERCENTAGE
Chl
CHO
P
F
A
J
A
O
D


SPRING
SUMMER
AUTUMN
3
2
1
0
F
M
A
M
J
J
A
S
O
N
D