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CHL.a FLUORESCENCE RELATED TO PHYTOPLANKTON SPECIES SUCCESSION AND DAYLIGHT

by

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Abstract:
The fluorescence data were collected during 1o cruises in Western Kiel Bight. Additional results are presented about phytoplankton species and biomass analysis, POC and PON measurements, available light and primary productivity.The investigation period covers three stages of the annual shallow water pelagic ecosystem: late winter, spring bloom and development of the summer pelagic food web. Phytoplankton species composition changed from µ-flagellates over large diatom chains to small, unarmoured dinoflagellates.
Despite different environmental and biological backgrounds, fluorescence profiles showed rather the same depth depending patterns: independent of actual Chl.a concentration fluorescence increases with depth approx. in the upper 1o meters. This pattern showed daytime dependency.The fluorescence/Chl.a (Fy) ratios were roughly 3times lower during diatom spring bloom than in flagellate dominated stages. These differences in fluorescence yield are probably due to reactions of the light harvesting compartments in the phytoplankton chloroplasts. The in situ fluorescence method is recommended to obtain vertical profiles of relative Chl.a distribution in the sea whereas the determination of Chl.a concentrations remains problematic.

Introduction

The Chl.a - fluorescence, discovered by BREWSTER in 1834, occurs whenever plants -terrestric or marine- are exposed to light. LORENZEN (1966) introduced the continous detection of Chl.a fluorescence into marine biology. His method to measure on board pumped samples is prevelant until now. But the conversion from fluorescence into Chl.a concentration appeared to be difficult (UNESCO 1980). The factors influencing the obtainable fluorescence are distributed over the whole range of biological and physical parametes influencing phytoplankton physiology: for genus specific differences in Fluorescence/Chl.a ratios (Fy) see CULLEN + RENGER (1979) and YENTSCH + YENTSCH (1979); for temperature dependency YENTSCH + MENZEL (1963) and for light history dependent Fy KAUTSKY + HIRSCH (1931) and KIEFER (1973 a). Likewise variations in Fy occur due to changes in nutrient availability (KIEFER, 1973 b and SAKSHAUG + HOLM-HANSEN, 1977) and due to an intrinsic clock which regulates the photosynthetic activity within a daily rythm (PRÈZELIN + SWEENEY, 1977; PRÈZELIN et al., 1977; ROY + LEGENDRE, 1979; SWEENEY et al., 1979 and PRÈZELIN + LEY, 1980). Hence Chl.a fluorescence in every case is an expression of physiological state of phytoplankton especially in regard to ambient and past light conditions and therefore fluorescence measurements can give some additional information for the investigation of phytoplankton ecology. For immediate conversion, however, of fluorescence into Chl.a one needs a lot of biological and physical background data not available in the same quickness. Nevertheless the in situ fluorometry, just when submersible fluorescence probes are used, can give more detailed information about small scale vertical distribution of Chl.a.

Materials and Methods:

Between February 21 and June 9 1980 a fixed station in western Kiel Bight (54° 32' N, 10° 03' E) was visited ten times in 3 to 34 day intervals. Higher sampling frequency (3 to 7 days) was carried out during phytoplankton spring bloom.

The Chl.a profiles were obtained with a fluorescence probe from Electronic Optics Suarez, Germany, which was slacked downwards with o.5 m s^{-1}. This probe consists of an excitation and a detection part whose optical axes are mounted in right angles to each other. The excitation flashes have a 10/sec frequency with a duration of less than 10 µsec and an energy of more than 466 µ E $m^{-2} sec^{-1}$. Excitation light ranges between 38o and 5oo nm, the measuring part detects Chl.a fluorescence at 685 ± 15 nm. The incoming signal is integrated over a given time interval which starts synchronously with each flash (synchronous detector). The measured volume is approx.1 ml.

Water samples were taken with 5 l Niskin water samplers and sieved through 3oo µ nets to remove greater particles (i.e. zooplankton). The Chl a measurements were carried out according to the UNESCO recommendations (UNESCO 1966) with modifications according to DERENBACH

(1969). The calculations were done according to EDLER (1979). The carbon and nitrogen analyses were carried out with a Hewlett Packard CHN analyzer, model 185 B. Primary production was determined from subsamples with the ^{14}C method according to STEEMANN-NIELSEN (1952). The samples were incubated for 3 to 4 hours over local noon in standard depths (0.5 m, 2.5 m; 5 m, 7.5 m, 10 m, 15 m and 20 m). The counting was done by the ^{14}C agency at Hørsholm, Denmark. The daily irradiation was measured with a Kipp and Zonen solarimeter within a range of 2oo nm to 3 µm. Phytoplankton cells were counted with an inverted microscope according to UTERMÖHL (1931 and 1958); the biomasses were calculated using the factors given by SMETACEK (1975) and EDLER (1979).

The measurement of extracted Chl.a was done with spinach Chl.a delivered from SIGMA; FRG and carried out in 100 % aceton because of the strong decrease of Chl.a fluorescence due to aceton-water mixtures (GIBBS 1979).

Results:

I The Environmental Background

The investigation period comprises three different stages of the pelagic ecosystem: 1. winter, 2. spring bloom, 3. maturation of pelagic food web. The spring bloom occured between March 3 and April 9 and can be divided into two substages: the increase of phytoplankton biomass until March 28 and the following ageing and sedimentation of the cells. The maturation of the system took place during the end of the investigation period (June 9), and was characterized by the development of a stable stratification, low Chl.a concentration and the formation of a remineralization cycle within the mixed layer. This was indicated by increasing biomasses of proto- and metazooplankton. For further information see PEINERT et al.(1982) and STEGMANN and PEINERT (in press).

II Depth and Daytime Depending Fluorescence Yield (Fy)

As shown in figs. 1 a,b there was a striking increase of the fluorescence with increasing depth within the upper approx. 10 m of the watercolumn which did not appear in the Chl.a values. This phenomenon was detectable throughout the entire investigation period and independent of the total Chl. a content (compare Febr. 21 and March 28). Additionally this increase of fluorescence seemed well- defined for nearly the whole daylight period as shown on April 1o (fig. 1b).

On this day first and last measurements were done 3 h 15 min after and before sunrise and sunset respectively. Only when the measurements were done closer to the beginning and the end of the daylight period increasing fluorescence seemed to be less marked. This pattern occurred also independent of the photosynthetic activity (fig. 2 ; March 28 , April 23 and May 27). While on the former day the primary production rate decreased from 0 m to 7.5 m, a strong increase on April 23 and May 27 is obvious and appeared without a significant influence in the Fy values . This increase in the assimilation number (an) could be due to photoinhibition because of the much greater light intensity on April 23 and on May 27 (table 1) compared to March 28. Likewise the depth depending increase in Fy values occured independently of an on Febr. 21 and april 23.

III Phytoplankton species succession

At the beginning of the investigation period the quite low standing stock of phytoplankton was dominated by small unidentified flagellates of 2 - 7 µ diameter, which contributed to 63 % of total phytoplankton carbon (PPC). The dinoflagellates, responsible for one third of the biomass, consisted mainly of Ceratium tripos. The following spring bloom peak was dominated by Detonula confervacea and total diatom biomass contributed to 74 % of total PPC. Towards the end of the bloom the diatom biomass decreased to 49 % of the total biomass (April 3) and the dominating genus changed to Achnanthes taeniata. This species accounted for 28 % of the total phytoplankton biomass. The mixed diatom population persisted at the "Hausgarten"- area until April 9. At the beginning of April 1980 the development of naked dinoflagellates of 7 - 3o µ diameter took place. They contributed up to 67 % of total PPC on April 23. On this day as well as on the end of the investigation period diatoms were nearly absent. On June 9 98% of the PPC were dinoflagellates (79% of PPC) and µ-flagellates (19%).

IV Species dependent fluorescence yield (Fy)

The Fy values also exhibited great variations, dependent on the phytoplankton species succession. During the domination of µ-flagellates in the winter the value reached its maximum while the minimum occurred at the end of the spring bloom. The development of the dinoflagellate population later on led again to an increase of the fluorescence yield. The fluorescence/PPC ratio showed almost the same pattern(fig.3). It reached its minimum at March 28 during the spring bloom. The C/N ratios with two maxima showed that Fy should not only be a reflection of the physiological state of the phytoplankton population (table 1).

To determine whether a given Chl.a value showed a relatively high or low fluorescence compared to the other data, a regression curve was calculated (fig. 4). This curve was obtained from 99 pairs of data of all ten days of the investigation period with exception of those of the upper 10 m. These data were excluded because of their species independent low Fy values as shown above (Results II and figs. 1, 2). So that they fit in well with the intrinsic characteristc curve of the fluorescence probe, two types of calculation were used. A linear regression suits the probe's baseline best in the lower range of fluorescence while the curve for the upper part was obtained from a polynom of the third degree which fits more exact to the probes baseline within the higher fluorescence values. The graph in fig. 4 consists of these two calculation results and could therefore be used to differentiate between relatively low (i.e. April 3) and relatively high (i.e. April 23, Febr. 21) fluorescence yields.

Fig. 4 gives some detailed information about the Fy of different phytoplankton genera. On April 3 the mixed diatom - dinoflagellate population was responsible for the same amount of fluorescence as a dinoflagellate - µ-flagellate population which developed three weeks later. But the Chl.a content on that day (April 23) was roughly only one third compared to the content on April 3. Likewise the fluorescence

of Febr. 21 was higher than expected from the Chl.a concentration. Data from other days did not exhibit this species dependency of Fy as there was no distinct dominance of one species or genus compared to the specified days.

V Scattering of fluorescence profiles

During the investigation period fluorescence profiles showed characteristic oscillation patterns (fig. 5). The larger the Chl.a containing unity the greater the short time oscillations. Winter phytoplankton standing stock, dominated by small µ-flagellates was responsible for a very smooth profile with scarcely discernable scattering. Somewhat greater was this towards the end of the investigation (April 23 and June 9), when phytoplankton consisted mainly of dinoflagellates, naturally larger than winter population cells. Most pronounced scattering appeared just after the peak of the spring bloom, when large diatom chains contributed up to 74 % of total PPC (April 23). Although the cells of the bloom forming species are not greater than the unarmoured dinoflagellates or Prorocentrum balticum which was responsible for the fluorescence peak on June 9 in 1o m depth, diatoms form large chains and contains twice as much Chl.a as dinoflagellates (KREY 1958). To validate that this scattering is not due to the absolute Chl.a concentration a measurement with extracted Chl.a was carried out. Chl.a concentrations up to 7.9 µg/l showed no significant scattering (fig. 5 b). Therefore it seems possible to get a first broad impression of the size of the Chl.a containing unity (i.e. cells or chains) from the scattering of continous fluorescence profiles.

Discussion:

As the presented data show there is a broad range of variations in Chl.a fluorescence. To keep this discussion easy to survey the different influencing factors identified in this investigation shall be discussed successively. This differentiation does not mean that only one factor is due to the received variations in Fy. The measured actual fluorescence is always the result of different environmental as well as intrinsic factors and therefore must be understood as the sum of all influencing parameters.

In the upper meters of the water column the increase of Fy is a regular phenomenon. In Kiel Bight this has been observed during the whole daylight period although the effect seems to be less intensive both just after and just before sunrise ad sunset respectively (fig. 1 b). Increasing Fy-values in relation to light regime are discussed by several authors (with freshwater samples by HEANEY 1978, with unialgal cultures by KIEFER 1973 a, with pumped samples by KIEFER 1973 b, with in situ data by LOFTUS & SELIGER 1975). PRÉZELIN & LEY (1980) showed an increase of the relative Chl.a fluorescence between 9.oo and 15.oo hrs. in surface near layers in the Santa Barbara Channel. At their station this increase of Fy was observed down to some 20 m, whereas in this investigation it did not appear beneath the 1o m depth line, probably due to the greater attenuation of Kiel Bight waters.

This lower Fy is not explainable by photoinhibition, as it is not concomittant with changes in assimilation numbers (fig. 2). On May 27, when primary production exhibited great variations with depth and photoinhibition seems to occur between 0 m and 2.5 m , the Fy values remains uneffected. Likewise on April 23 primary production rate reached a maximum in 5 m depth while Fy values increased continously. On the other hand a strong decrease of primary production occured on March 10 while Fy values remains more or less constant throughout the water column.

One probable explanation is that the thylakoid membrane in the cells chloroplasts contracts in greater light intensities and thus the photosystems I and II (PS I, PS II) are located closer to each other (MURAKAMI & PACKER 1970). This reversible contraction is obviously independent of species composition and nutritious state of the cells (VINCENT 1979). According to KIEFER(1973 a) this change in chloroplast morphology is a fast reaction of the cells - within seconds to minutes - to changes in incident light and occurs without degredation of Chl.a. This reversable reaction, even quicker to be recognized by in situ fluorometry, is not detectable by ^{14}C primary production measurements as the assimilation numbers show. The flattening of the thylakoid membrane does not lead to an increase of fluorescence because of a "spill- over" of energy between the mainly fluorescent PS II Chl.a molecules and the PS I without releasing oxygen i.e. avoiding the centre of PS II, the P 680 (VINCENT 1979, MOHANTY 1972). This "spill-over" leads to the phenomenon that less Fy not necessarily is accompanied by an increase in photosynthetic activity. The light energy which is transferred to the PS I is available to the cell's energy consuming reactions (i.e. reduction of NADP or building of ATP).

Hence an increase of Fy in the upper water layers probably is a result of a fast response of the thylakoid membrane within the chloroplasts to sunlight. It starts with a contraction of chloroplasts and leads finally to a piling up of chloroplasts within the cells. Photoinhibition, as detectable by primary production measurements, becomes evident at a greater time scale.

This increase of Fy in surface near layers during the daylight period has to be taken into consideration whenever submersible fluorometer data are to be interpreted or one attempts to convert fluorescence data into actual Chl.a concentration.

Besides this obviously common and species independent differences in Fy, data were obtained during this investigation which exhibited a species dependent Fy.

Although the literature about the species dependent Fy is numerous, there is no agreement about the respective Fy of the two major constituents of marine phytoplankton, both diatoms and dinoflagellates. At latest since HOLM-HANSEN et al. (1965) differences of Fy were explained - among others - by differences in species composition (FLEMER 1969, BERMAN 1972, SLOVACEK & HANNAN 1977). The differences in Fy which STRICKLAND (1968) explained by changes in species composition were due to a malfunctioning instrument (THOMAS 1974). Nevertheless there are species

dependent differences in Fy. Higher Fy values due to diatoms rather than to dinoflagellates are reported by several authors (KIEFER 1973 b, HEANEY 1978 and YENTSCH & YENTSCH 1979). FLEMER (1969) found a less Fy during a Prorocentrum and Peridinium dominated bloom compared to the time before this bloom. KIEFER (1973 b) reported a much higher Fy (by a factor of 10) associated with a Thalassiosira subtilis population compared to a Ceratium dens dominated population.

The results of this investigation however are in contrast to the above mentioned (fig. 3). While Fy values associated with diatoms were the lowest recorded; µ-flagellates and naked dinoflagellates of 7-30 µ-diameter showed an increase in Fy by a factor of 3 . Although the biomass ratio between µ-flagellates and dinoflagellates changed between Febr. 21 and April 23 from 2:1 to approx. 1:3 the Fy values seems to be uneffected. This occured while the Chl.a amount increased from 10.0 mg/m^2 to 33.0 mg/m^2 on the latter day. Therefore it seems that different Fy values are due to species or even genus composition rather than to total Chl.a concentration in the water column. Additionally this could be supported by the fact that the highest Chl.a amounts in the water column do not lead to the lowest Fy values (table 1). On the other hand the lowest Fy on April 3 did not coincide with the highest portion of diatoms on PPC. On that day diatoms were only responsible for half the biomass of the phytoplankton.

Hence there are some indications for a lower Fy during diatoms dominated stages in the investigated area but these results need further confirmation to associate Fy with phytoplankton species distribution.

The obtained scatterings in the fluorescence profiles are not due to environmental or physiological factors but are the result of interactions between the size of the Chl.a containing unity, their patchy distribution and the relatively small measured volume of the used fluorescence probe.

From theoretical considerations it is obvious that a given amount of Chl.a distributed in a lot of small cells should lead to a fluorescence profile which is more even than a profile obtained from fewer great cells containing the same quantity of Chl.a. The fluorescence profiles from Febr. 21 and March 28 confirm this consideration.

The relatively small measured volume of the probe is additionally responsible for the distinctness of fluorescence profiles. The smaller the volume the greater are the fluctuations of Chl.a through this volume, because of patchy distribution especially of greater cells or chains. Enlarging this volume would lead to a decrease of the observed scattering but likewise to a decrease of resolution power. LORENZEN (1966) recommended a measured volume of approx. 2o ml to avoid scattering due to the size of Chl.a containing unities. On the other hand this small volume is responsible for the probes suitability to obtain an immediate impression of the patchiness of the Chl.a concentration in the water column in relation to the measured volume.

Conclusions:

1. Fluorescence increasing with depth within the upper meters of the water column did not necessarily indicate increasing Chl.a concentration within the same depth. This pattern of increasing fluorescence was observed almost throughout the whole daylight period. The Fluorescence/Chl.a ratios (Fy) were found to vary within one day by a factor of three.

2. Mean Fy ratios obtained from one day could not be used as converting factors on other days because of differences of a factor of three between different days (i.e. perhaps stages of the ecosystem) in this investigation. In contrast to other observations diatoms exhibited a pronounced lower Fy than dinoflagellates and µ-flagellates.

3. Scattering of fluorescence profiles could probably serve to decide whether phytoplankton standing stock consists mainly of relatively great or small Chl.a containing unities.

4. To get useful factors for converting fluorescence into Chl.a concentration one needs more in situ data. Especially in regard to remote-sensing the world ocean's surface we need much more investigations about the possible reactions of phytoplankton to ambient environmental conditions expressed as Chl.a fluorescence. And on the way to the explanation of sun light induced fluorescence data the artificially excited fluorescence method used in this investigation can give some help.

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Table 1

Date	Chl. a mg m^{-2}	% of PPC Diat.	Dinofl.	µ-Flag.	Light intensity during incubation time KWs m^{-2}	Primary production mg C	mg Chl. a $^{-1}h^{-1}$	C/N	Fy	Fl/ PPC	PPC/ Chl. a
21.2.	10.3	4	32	63	4500	1.19	2.5 m	8.5:1	194	6.7:1	30:1
						0.78	5 m				
						0.72					
						0.37	10 m				
						0.56					
						0.03	20 m				
28.3.	122.0	74	9	16	2100	2.12	0 m	7.1:1	94	2.4:1	43:1
						1.21					
						0.43	5 m				
						0.21					
						0.15	10 m				
						0.08	20 m				
3.4.	91.2	49	26	19	3800	0.8	0 m	7.8:1	63	3.0:1	21:1
						0.9	2.5 m				
						0.7	5 m				
						0.5	7.5 m				
						0.2	10 m				
						0.1	15 m				
						0.1	20 m				
23.4.	32.9	0	67	26	9500	0.68	0 m	5.8:1	181	5.8:1	31:1
						2.07					
						2.17	5 m				
						1.94					
						1.80	10 m				
						0.44					
						0.21	20 m				
9.6.	40.1	1	79	19	-	-	-	5.2:1	137	6.0:1	27:1

Table 1 The development of different parameters during the investigation period. On March 28 the diatom population consists mainly of Detonula confervacea and Achnanthes spec.. On June 9 a Prorocentrum balticum population occured concentrated in 10 m depth.

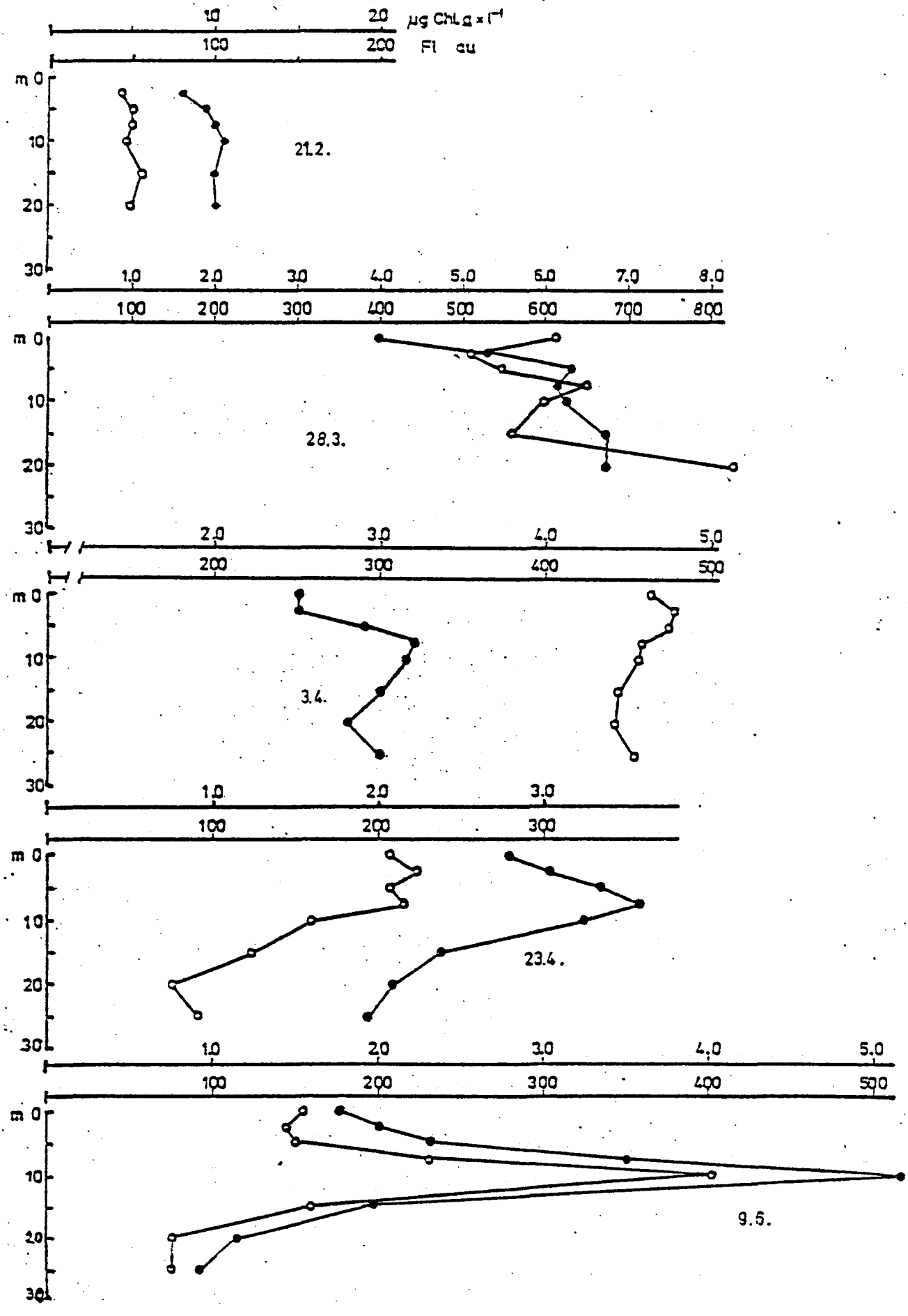

fig. 1 a Fluorescence (● , arbitrary units) and Chl.a (o , µg/l) curves which show the increase of fluorescence within in the upper 10 m of the water column while the Chl.a seems to be more evenly distributed or even decreases (28.3.).

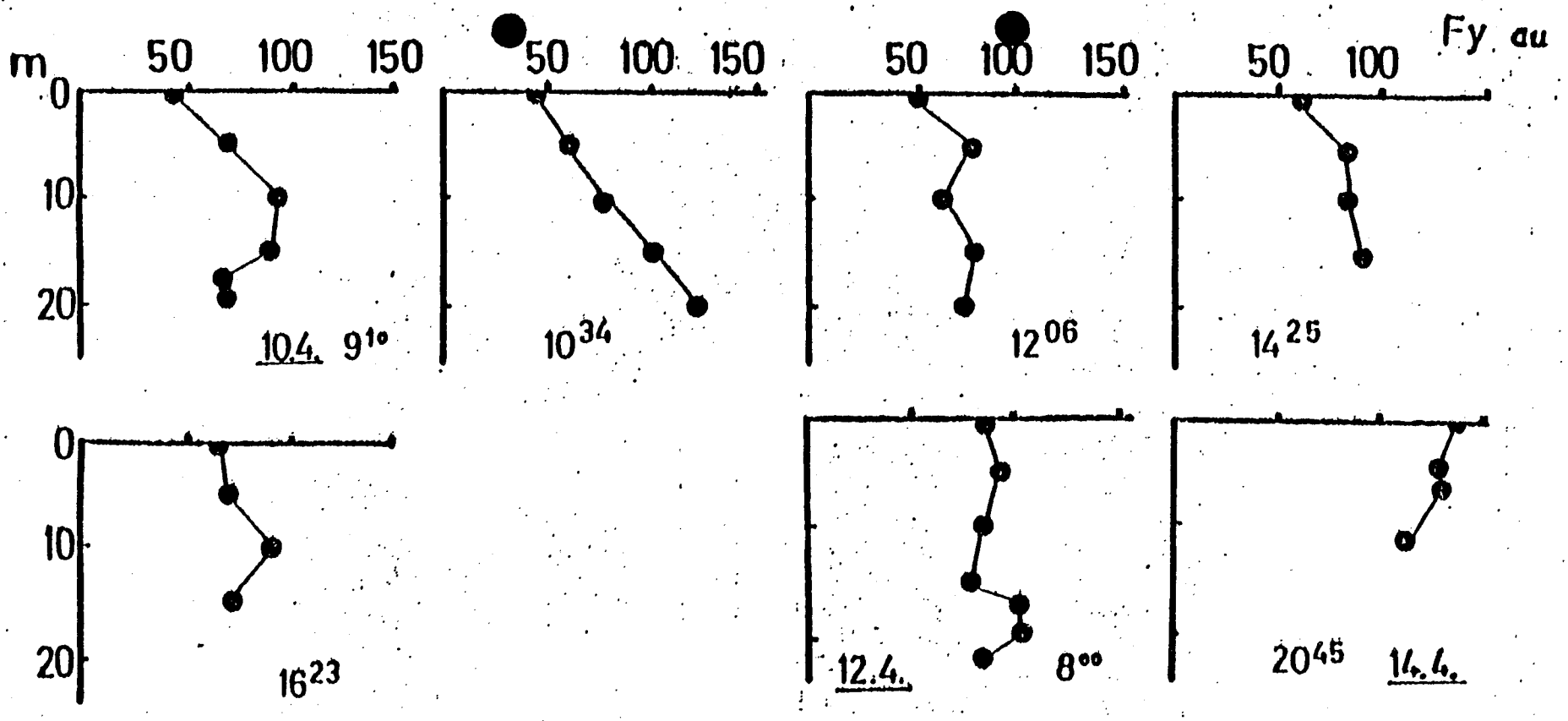

fig. 1 b Fy (Fl./Chl.a) curves obtained on April 10 during the daylight period showing the same depth dependent increase in Fy within the surface near water layers as in fig. 1 a. On April 12 at 8.00 hrs and on April 14 at 20.45 hrs this increase seems to be absent.

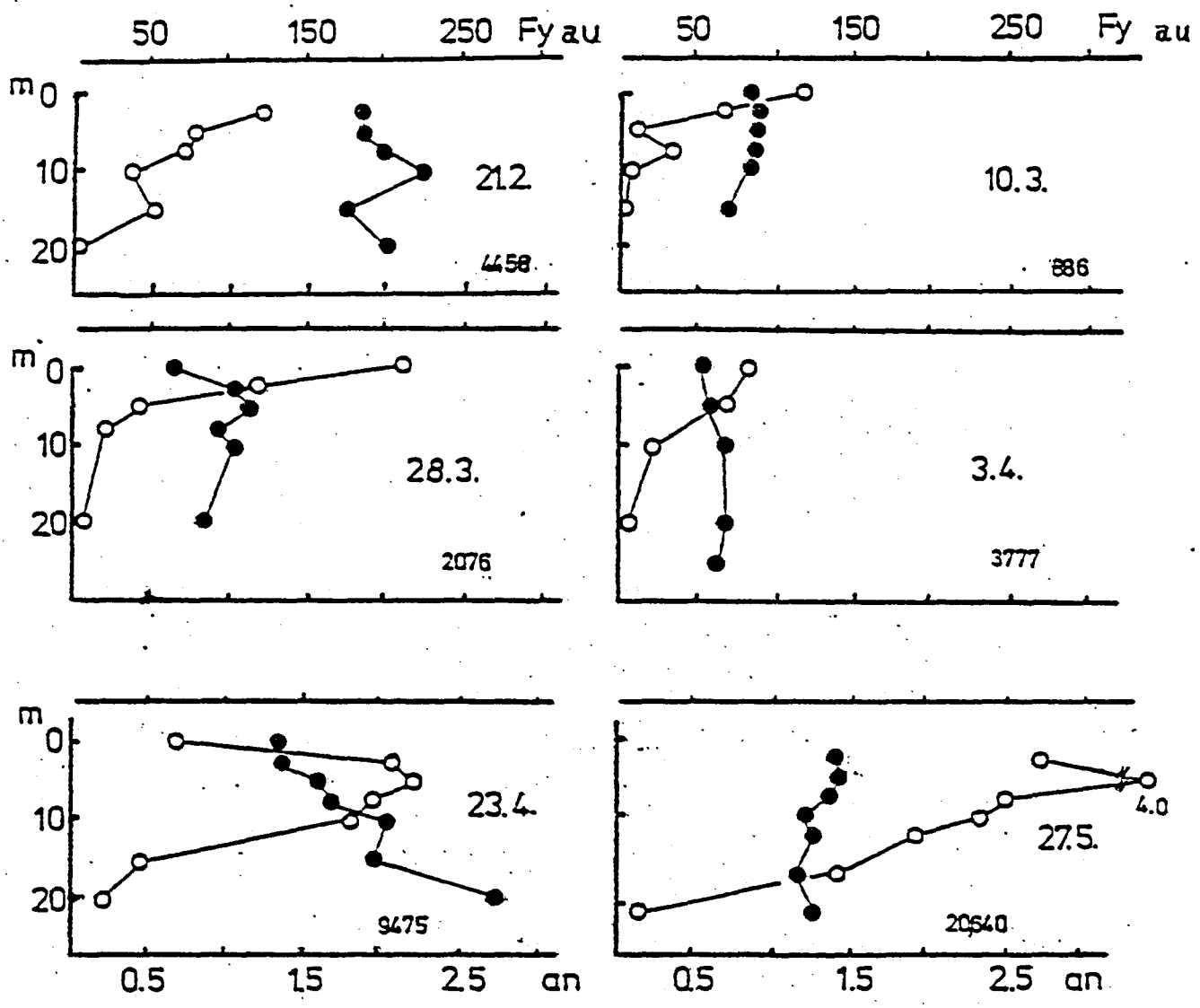

fig. 2 Fy (● , arbitrary units) and primary production given as assimilation numbers (o , an, mg C mg Chl.a^{-1} h^{-1}) from 6 different days. The numbers show the light intensity integrated over the incubation time in KWs m^{-2} . On all days the variations in Fy showed more or less the same pattern while the primary production rates seems to be related to the ambient light quantity.

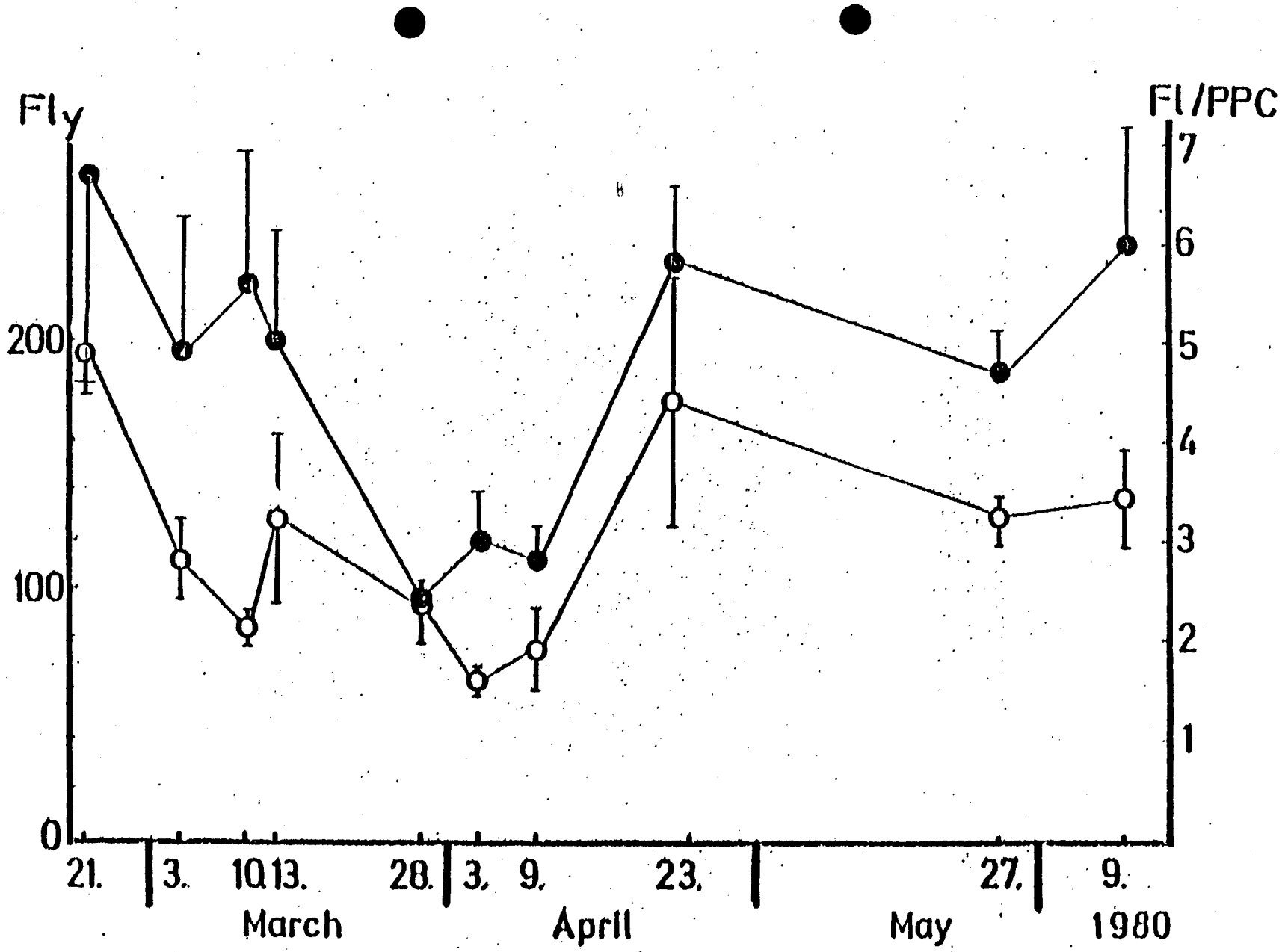

fig. 3 The Fy (o) and the Fl/PPC ratios (●) during the whole investigation period given as means of the water column. Bars indicate standard deviation.

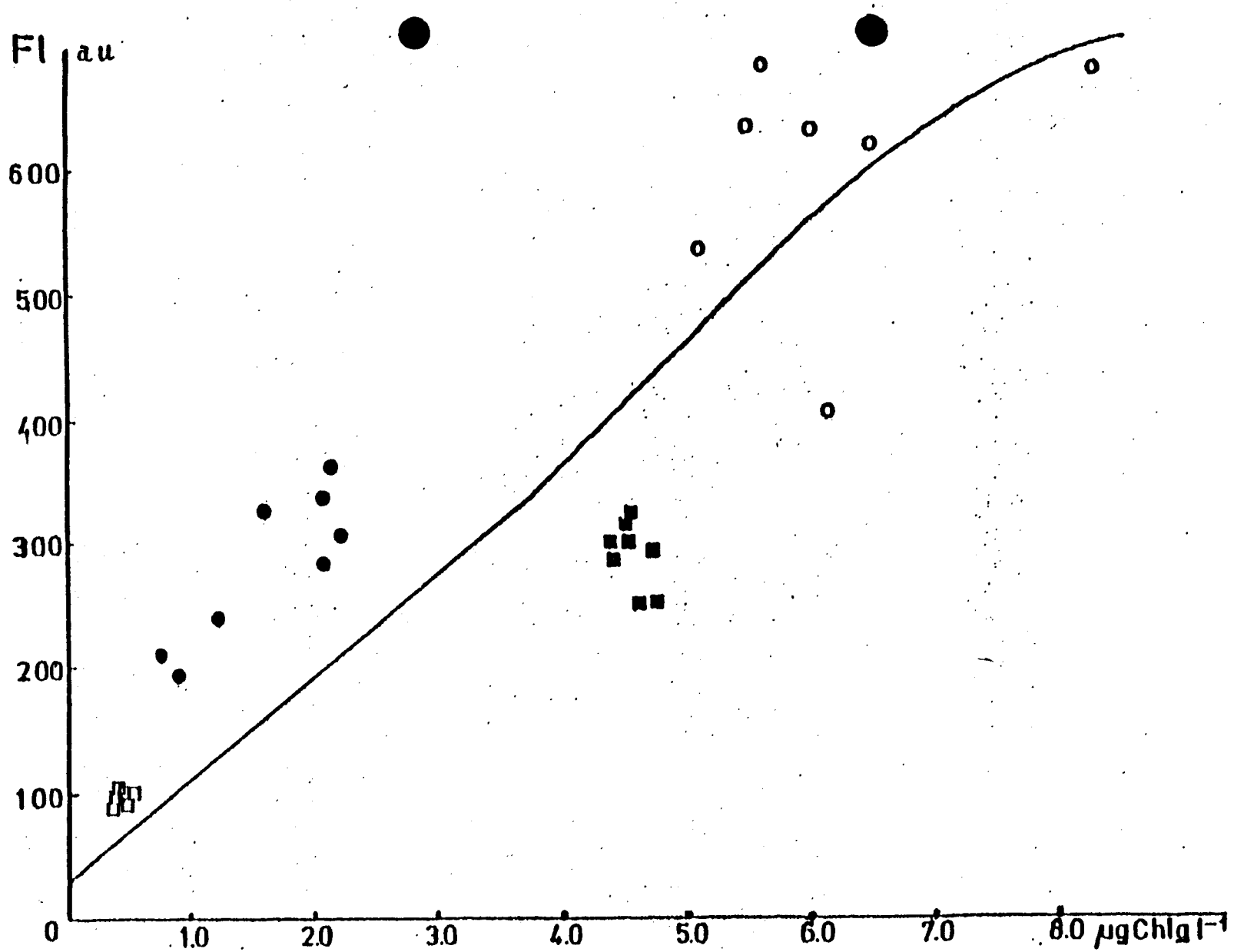

fig. 4 Fluorescence (Fl , arbitrary units) to Chl.a (µg/l) relation on 21.2., □ ; 28.3., o ;3.4., ■ and 23.4, ● . The regression curve consists of two different graphs: in the lower part it follows y = 30.2 + 80.5 x, r = o.886 and in the upper part it follows y = 96.3 + 3.73 x + 22.0 x2 - 1.66 x3, r = o.896; both calculations are done with n = 99 and reaches P = 0.001.

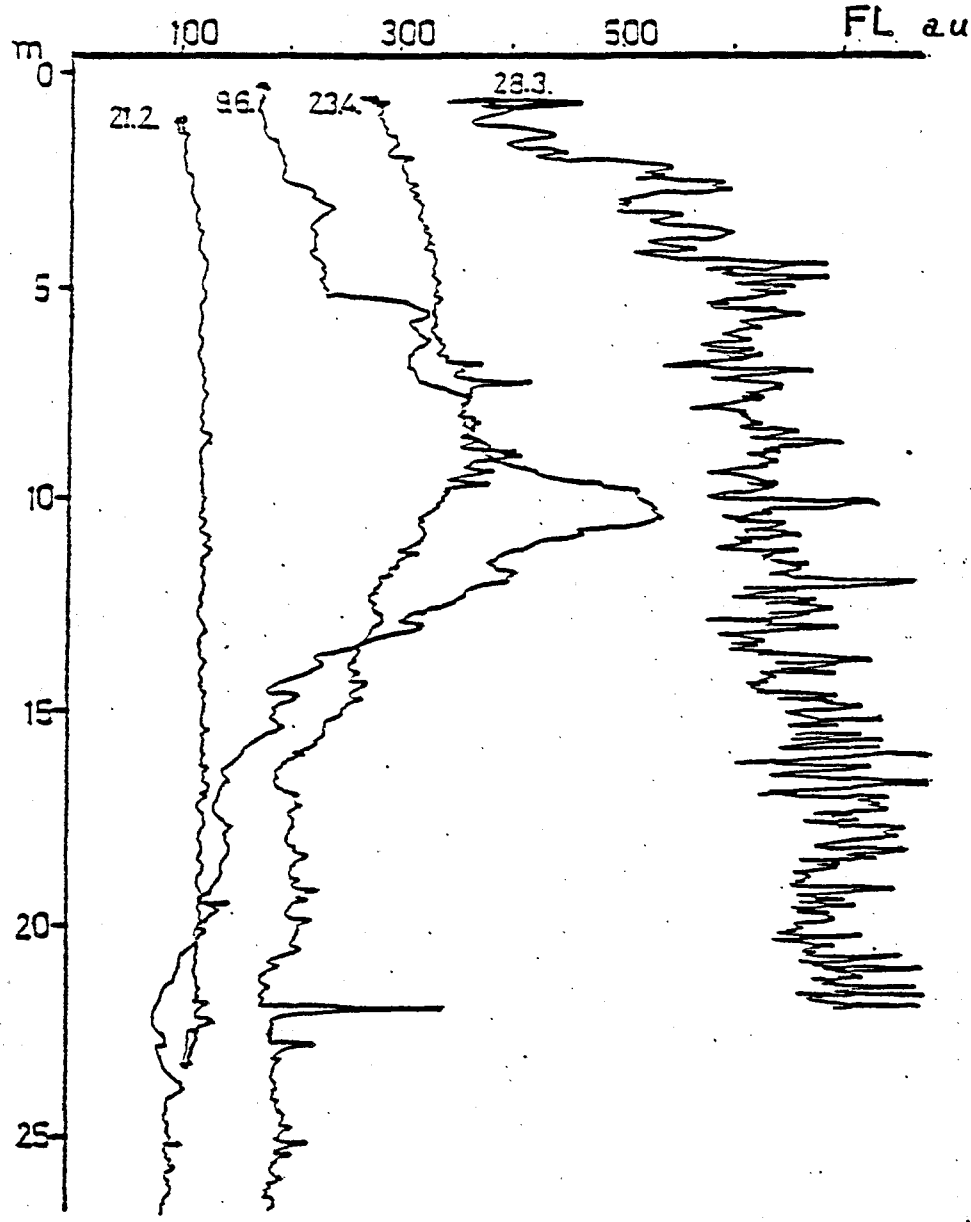

fig. 5 a Fluorescence profiles (arbitrary units) from 4 different days. The peak is due to a Prorocentrum balticum population in 1o m depth. The diatom chains on 28.3. are great in relation to the probes measured volume and therefore probably responsible for the greater scattering on that day.

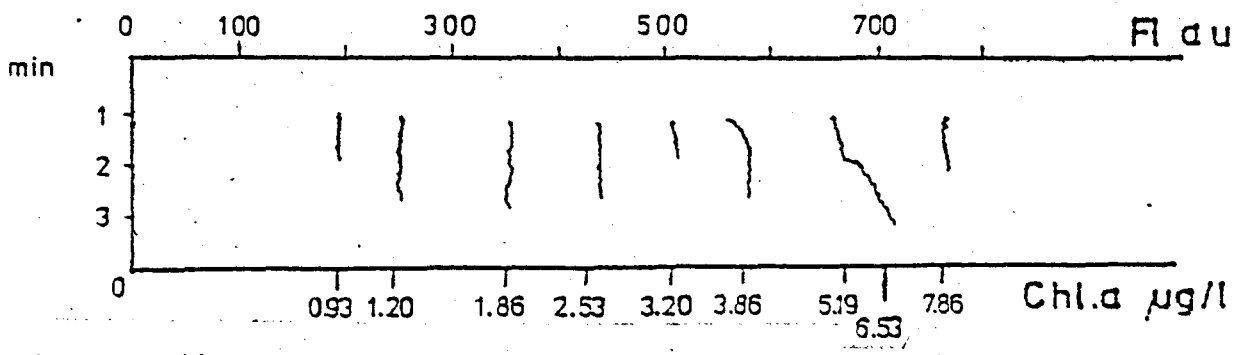

fig. 5 b Fluorescence profiles (arbitrary units) obtained from extracted Chl.a. The scattering is very small due to the much more evenly distributed Chl.a molecules compared with Chl.a linked to chloroplasts and cells. Hence the scattering seems to be independent from total Chl.a concentration.