THE EFFECT OF ENVIRONMENTAL FACTORS ON THE CHEMICAL CONSTITUTION OF A NATURALLY-OCCURRING PHYTOPLANKTON POPULATION PRIOR TO AND DURING THE SPRING DIATOM INCREASE IN SAANICH INLET

by

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ABSTRACT

Certain environmental factors controlling the initiation and development of the spring diatom maximum in Saanich Inlet, B.C. were investigated in detail between March 22 and May 30, 1971. Changes in the selected physical and chemical characteristics of the water column to 50 m were measured at two-day intervals and were correlated with changes in phytoplankton biomass and biochemical composition.

During this period two peaks in phytoplankton biomass occurred. A minor increase in algal standing stock began to develop in mid-April under the influence of a calm, sunny period. This was interrupted in early May by the recurrence of changeable weather and unstable water conditions. A brief period of nutrient regeneration followed. Through early and mid-May, phytoplankton levels remained low, while weather continued unstable. The observations indicate that sub-optimal weather, water column instability and heavy grazing pressure combined to suppress an early diatom maximum.

In late May weather stabilized and a strong density stratification pattern was set up in the upper 30 m of the water column. Initiation of the second and larger peak in diatom biomass coincided with the penetration of the 8.5°C. isotherm into deeper water. Light conditions in the same period increased from 400 ly/day to 600 ly/day.

In situ conditions during this period were near optimal for the growth of the bloom-forming diatom *Thalassiosira rotula* Meunier, which at the peak of its growth in late May reached a doubling time of 10

hours, very close to the minimum doubling time observed by Schöne (1972) in culture under similar conditions of light and temperature.

The progress of this diatom increase was marked by a number of changes in the relative amounts of chemical constitutents in the filtered material. These changes were consistent with the progress of a phytoplankton population from active log-phase growth through steady-state and into senescence, and could be related to increased self-shading and to nutrient deficiency. In the progress of the bloom carotenoid to chlorophyll-a ratios rose, as did protein to carbohydrate ratios. At the same time carbohydrate to chlorophyll-a ratios, protein to chlorophyll-a ratios and protein to carbohydrate ratios all dropped. Observations of these phenomena in culture experiments by other workers have been associated with nitrogen limitation.

A strong inverse relationship exists between the daily incident radiation budget and the ambient nitrate level in surface waters for the first part of the study, March 22 to April 22. This effect was not observed after daily light budgets surpassed 500 ly/day in the latter part of May, instead a strong inverse relationship was formed between water column temperature and the nitrate levels found at specific depths. These two relationships show similar slopes but are complementary in nature. The shift from one effect to the other occurs at light levels between 500 and 600 ly/day, water temperatures between 9 and 16°C. and at nitrate-nitrogen levels of 12 to 16 μg-at NO_3 N m^{-3}.

The warming of the water column that brought about the second, temperature-related, diatom increase was the result of more prolonged weather stability towards the end of May and the resultant increase in water stability.

From this it can therefore be seen that light and temperature were the two factors which most markedly affected the induction of the spring diatom increases in Saanich Inlet, while stability of weather and the water column played a secondary role in this process.

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INTRODUCTION

Saanich Inlet has been of special interest to oceanographers for many years both from physical and biological points of view. The combined factors of a deep glacial basin, a shallow entrance sill, and low annual runoff has produced a highly stable deep water mass with little exchange with surrounding waters. A permanent oxygen minimum layer is present below sill depth (Herlinveaux, 1962). Standing stocks of zooplankton (Hoos, 1970) and fish (Bary, 1967) are exceptionally high and a vertically-migrating deep scattering layer is continuously present (Bary, 1967). The waters above sill depth show physical characteristics similar to those of nearby Georgia Strait in fall and winter (Herlinveaux, 1962) but in the spring and summer months runoff to Saanich Inlet is so low that surface waters become strongly stratified and very little net outward movement occurs (Herlinveaux, 1972). Average net water outflow at a depth of two meters was estimated by Herlinveaux, (1972) for the period of May to July 1968 and considered to move 0.3 to 0.6 nautical miles per day out of the inlet. The combination of high stability, low surface exchange and strong summer stratification make Saanich Inlet an extremely interesting locale for the study of phytoplankton ecology.

The simplest combination of ecological factors occurs prior to and during the exponential phase of the spring diatom increase (Riley and Chester, 1971). It was therefore decided to examine phytoplankton dynamics throughout the spring and early summer in the central (deepest) part of Saanich Inlet. It is only during this period that the various environmental factors may be considered optimal for phytoplankton growth (Riley and Chester, 1971). These factors include high and fairly uniform production, low levels of predation and optimal light, combined with low temperature and increasing stability of the water column.

Parameters selected for investigation in this study fall into two general categories; physicochemical and biochemical. The first of these includes light penetration, water temperature, salinity, density and nutrients, to form the physicochemical environment to which a phytoplankton population responds. This response is particularly strong in the spring when biotic factors seem to have a minimal effect and phytoplankton growth is limited by light, temperature and water column stability but is stimulated by high nutrient levels.

The many laboratory experiments undertaken in the last ten years in microplankton physiology have produced relatively consistent values for light and temperature optima for many marine algae and in particular for bloom component phytoplankton under laboratory conditions, (Brown and Richardson, 1968; Davey, 1970; Eppley, Holmes and Paasche, 1967; Eppley and Sloan, 1966; Hulburt and Guillard, 1968; Ignatiades and Smayda, 1970; Jitts et al, 1964; Jorgensen, 1968; etc.). But evidence provided by Carpenter and Guillard, 1971; Hulburt and Guillard, 1968 and Steemann-Nielson, 1968b indicate that environmental conditions may operate to modify these optima in nature in a form of physiological adaptation.

The mechanism actually involved in this physiological adaptation is not clear but recent work by Morris and Glover (1974) and by Wallen and Geen, (1971a,b,c) has opened up some promising leads. Morris and Glover (1974) have found that photosynthetic rates decrease at higher temperatures because of a decrease in the ability of the organism to assimilate CO_2 which results in enhanced dry weight to chlorophyll-a ratios at lower temperatures (7°C). The controlling element may be a supression of enzyme function at higher temperatures rather than the result of increased photosynthetic enzyme production at lower temperatures as has been generally considered (Steeman Nielson and Hansen, 1959). Wallen and Geen (1971a,b,c), working in the laboratory and later in Saanich Inlet, investigated the effect of light quality on micro-constituent ratios in phytoplankton. They reported an increased incorporation of ^{14}C in the ethanol insoluble fraction (high m.w. carbohydrates) in blue-green light (equivalent to the light quality in deeper water) as opposed to white light. Later field observations confirmed that a similar phenomenon occurred in the field with increasing depth in the photic zone (Wallen and Geen 1971c).

Quite apart from the physiological effect of physical parameters on algal production are the purely physical effects due to buoyancy, stability and density of the water column. These factors act to control the distribution of phytoplankton in the photic zone, thus affecting the amount of light available and the rate at which nutrients are supplied for uptake.

One of the earliest works discussing the effect of water column stability on production in a phytoplankton population is that of Gran and Braarud (1935), which introduces the concept of critical depth. This is the depth above which the total photosynthesis for the water column is equal to the total respiration of primary producers. This concept was developed into a mathematical model by Sverdrup (1953). When the mixing zone is shallower than the critical depth the standing stock of phytoplankton increases if factors other than light are not limiting. In the spring this must occur before the spring bloom can be initiated. Once the water has stabilized and stratifies into a density and/or temperature discontinuous system other phenomena can be observed. For example the physical effect of density discontinuity is to vary the rate of particle sinking as different density layers are encountered. This has the effect of causing particles to collect in regions of rapid density change such as the bottom of the thermocline or halocline.

Lorenzen, (1967) reports that chlorophyll maxima occur near the base of the euphotic zone in the thermocline. Phaeopigment maxima either coincide with chlorophyll maxima or occur slightly deeper at a depth where nutrient levels begin to increase. Lorenzen speculates that the high levels of phaeopigments result from leaching of the faecal pellets of herbivorous zooplankton. Hobson and Lorenzen, (1972) were able to correlate chlorophyll maxima in the Atlantic Ocean and the Gulf of Mexico with density structures. Biggs and Wetzel (1968) report a similar distribution pattern for carbohydrate concentrations. High concentrations of carbohydrates occur at the surface and at, or near, the thermocline, but no correlation was found between chlorophyll-a and carbohydrate.

Chemical phenomena also have major important effects on phytoplankton physiology and ecology, chiefly in the role of macro- and micro-nutrients. Although both nitrogen and phosphorus are of major importance as metabolites in phytoplankton nutrition there is some evidence that nitrogen is the most commonly limiting micronutrient in a system with heavy zooplankton grazing pressure. Observations by Pomeroy *et al.* (1963), Johannes (1965) and Martin (1968) show that grazing zooplankton and marine protozoa return large amounts of phosphorus to the environment during grazing. Butler *et al.* (1970) goes further. Working with grazing *Calanus finmarchicus* during an April bloom in the Clyde Sea, they show that over 80% of ingested phosphorus is returned to the environment both as faecal and soluble compounds. Most forms of organic phosphorus are readily mineralized, either spontaneously, at the alkaline pH of seawater, or by the action of hydrolytic phosphatase present in many marine bacteria and on the surface of some phytoplankton (Parsons and Takahashi, 1973). Further to this Antia *et al.* (1963) indicate that even in the absence of zooplankton grazing, half of phytoplankton phosphorus is mineralized in approximately 14 days, although in the same experiment no mineralization of organic nitrogen was observed in over 75 days. The rate of turnover of phosphorus, especially in the presence of zooplankton indicates that phosphorus is generally available for phytoplankton metabolism, even during bloom conditions, and that nitrogen is far more likely to exert a limiting effect on phytoplankton growth. The latter conclusion is supported by Cushing's observations in the North Sea (1964), where he found that during the ten weeks of the spring phytoplankton bloom inorganic phosphorus did not decrease below 0.6 μg-at/l.

In the oceans, nitrogen exists chiefly as organic molecules and as the inorganic salts; ammonia, nitrite and nitrate. Of these, ammonia is preferentially assimilated by those plankton algae that have been investigated, (Morris and Syrett, 1963; Dugdale and Goering, 1967; and Eppley et al, 1969b). It is utilized directly for amino acid synthesis through transamination without any energy consuming intermediate step such as a requirement involving the induction or synthesis of uptake or reductive enzymes. Both nitrite and nitrate assimilation require such steps. Reduction of nitrite appears to require light (Eppley and Coatsworth, 1968) and photosynthetically-reduced ferredoxin is used to reduce nitrite to ammonia (Hattori and Myers, 1966).

Nitrate is reduced by the action of the enzyme nitrate reductase, independently of light but dependent on levels of nitrate in the environment (Hattori, 1962). Its induction is inhibited by significant levels of ammonia in the environment. In some areas the nitrogen source may differ with depth with deeper phytoplankton (closer to the bottom of the discontinuity layer) utilizing the more readily available nitrate, and shallower phytoplankton (in nitrate-improverished waters) subsisting on ammonia derived from zooplankton grazing by-products (Goering et al, 1970).

The requirement of a minimum environmental nitrate level for nitrate reductase induction may have further significance in species succession during the spring bloom. The high nitrate content of early spring water allows the full response of eutrophic species of phytoplankton, which have high half-saturation constants and correspondingly high growth rates on higher background levels of nitrates (Eppley and Thomas, 1969; McIsaac and Dugdale, 1969; Carpenter and Guillard, 1971). Such species require relatively high levels of nitrate in the growth medium to induce nitrate reductase systems (Eppley _et al_, 1969a). What is more, they exhibit an increasing inefficiency in production as environmental nutrient levels drop, losing in the process, any competitive advantage they may have had over species with lower half-saturation constants and relatively more efficient nutrient scavenging abilities.

In this way spring phytoplankton communities which are initially dominated by a comparatively small number of opportunistic species, with short doubling times, high growth rates and high half-saturation constants, become increasingly diverse. As in-situ nutrient and light levels drop below optimum for the bloom dominants, other more oligotrophic species take over and a highly diverse, low standing-stock summer population forms, controlled chiefly by low nutrient levels zooplankton grazing pressure and the rate of remineralization of limiting nutrients from zooplankton excretory products (Hulburt, 1970).

Temporal and spatial variations in light, temperature and nutrient levels have strong effects on the morphology and chemical composition of the algal unicells comprising a bloom population.

Parsons and Takahashi, (1973) describe four stages in a phytoplankton spring bloom in stratified temperate waters. In the earliest stage, immediately after a period of vertical mixing, the algal population is homogeneously distributed throughout the water column to the bottom of the mixed layer. _In-situ_ photosynthesis per unit of biomass (mg C/mg chl-a/day) is actively inhibited at the surface through a suppression or deactivation of dark reaction photosynthetic enzymes by high light levels (Steeman-Nielson and Jorgenson, 1968). Biomass decreases from a subsurface maximum as light is attenuated.

As the bloom progresses biomass levels increase, the average extinction coefficient of light increases and self-shading will occur (Aruga, 1964). Throughout this phase the ratio of chlorophyll-a to auxiliary pigments is high in all subsurface portions of the population. At the same time the surface component begins to exhibit an increased carotenoid to chlorophyll-a ratio. This is due to a high-light-triggered degradation of chlorophyll-a accompanied by an increase in carotenoids and auxiliary pigments such as chlorophyll-c. These pigments are thought to perform a protective function by absorbing excess light and thus shading chlorophyll-a from high light deactivation (Fujita, 1970).

The shape and arrangement of chloroplasts in the surface population of diatoms may also differ from that of the deeper population. In high light, phytoplankton chloroplasts are aggregated into clumps at the centre of the cell surrounded by the bulk of the protoplast, while in the dark the reverse occurs; chloroplasts are arranged in a thin layer all around the periphery of the cell in positions most advantageous for light absorption (Brown and Richardson, 1968).

In this early phase of the bloom nutrients are not yet limiting to growth. Population growth proceeds at near logarithmic rates, deviating from this pattern only at the surface where it is suppressed somewhat by high light levels as already described. The doubling times of the subsurface algal population are short and protein to carbohydrate ratios are high. Population levels quickly increase to the point where self-shading may occur. When this happens the distribution of biomass changes and becomes highest at the surface. Biomass decreases steadily with depth, the growth rate in the deeper segment of the population being light-limited. Like the light-suppressed surface populations earlier in the bloom these phytoplankters show an increased carotenoid and auxiliary pigment level. It is thought that in this case auxiliary pigments such as chlorophyll-c may absorb light at wavelengths unavailable to chlorophyll-a and transfer part of that energy to chlorophyll-a for use in the photosynthetic light reaction (Fujita, 1970).

As cell populations rise, however, nutrient levels drop rapidly and nutrient limitations begin to have an effect on the population. Since phytoplankton growth rates in the surface waters are highest, nutrient limitation first makes itself felt in these shallow populations. Biomass distribution changes again and a subsurface maximum at or near the top of the thermocline becomes established. This population is maintained by diffusion of nutrients across the discontinuity layer. Its maximum development is controlled by the rate of such diffusion. The shallower population may be maintained by nutrients reintroduced by grazing zooplankton through remineralization from faeces, as already described.

Such a nutrient-limited population exhibits several biochemical responses to this stress. If the limiting nutrient is nitrogen, as often is the case, protein synthesis may slow down. Carbon fixation proceeds at the same rate but insufficient N is available for proportional protein synthesis. The response to such a situation varies from one algal species to another. Some incorporate the carbon as lipid storage products (Fogg, 1956). Others store high m.w. carbohydrates, in particular B 1,3-linked glucans like laminarin or chrysolaminarin, which may increase even after all other syntheses have been brought to a halt (Mykelstad and Haug, 1972). If such products accumulate in large amounts, plastid and other cell membranes may be seriously disrupted and general cell metabolism interferred with. Such cells cannot maintain their position in the water column and tend to settle out of the population (Smayda, 1970).

Some phytoplankton, particularly oligotrophs, overcome this problem by excreting part of their carbon-fixation products in the form of low m.w. carbohydrates such as glucose (Nalewajko, 1966; Berman and Holm-Hansen, 1974). Fogg, (1966) records that in some cases up to 50% of daily fixed carbon may be released as soluble organic compounds. However, in general cases Eppley and Sloan (1965) and Hellebust (1965) found that 15% or less was excreted. Three factors which affect the release of soluble organics are light intensity, age, and nutritional history of the cells. Hellebust (1965) suggests that excretion is high during periods of intense illumination when carbon-fixation is at a peak. Anderson and Zeutschel (1965) report that high rates of organic excretion occur in cells collected at the end of a bloom, while Eppley and Sloan, (1965) have observed that the same is true of cells reared under conditions of nitrogen deficiency. All of these observations are consistent with a theory that low m.w. carbon compounds are excreted from cells to conserve a balance between protein and carbohydrates. Conversely, low light, low temperature and decreasing degrees of nitrogen limitation all markedly increase the relative rate of protein synthesis by surface phytoplankton, generally at the expense of stored polysaccharides (Morris et al, 1974b).

In this thesis selected environmental parameters and algal cell constituents will be examined throughout the period preceding and including the spring diatom increase, on the assumption that this is the period most easily duplicated in batch culture. It is during this period that various factors important to diatom growth may be considered optimal. Production is high, cells are young and healthy, grazing pressure is minimal and because light levels are high and temperatures are relatively low, the most favourable respiratory quotients are obtainable.

It should be possible, therefore, to watch the transition of an algal population from a simple system operating under optimal conditions to one successively under stress by one or more limiting factors and to follow, in the process, the changes in cell chemistry and metabolic functions usually only observed in culture. Such a large body of laboratory experimental data is available, some of it specifically applicable to Saanich Inlet (Wallen and Geen, 1971c), that it should be possible, by following changes in physicochemical parameters, biochemical plankton constituents and species composition, to gain some insight into the factors controlling productivity and population dynamics in the early spring phytoplankton community in Saanich Inlet.

MATERIALS AND METHODS

A single station (Fig. 1) in Saanich Inlet (Lat. 48°40' N, Long. 123°29' W) was occupied every other day from March 22, 1971 to May 30, 1971, insofar as ship time was available. Sample dates are given in Table 1. The study was terminated because of the unavailability of further ship time although the bloom under study had not yet ended.

Samples were collected from the oceanographic launch Vancouver II made available to the University of Victoria Biology Department by the Canadian Department of Transport.

Weather conditions were noted (Table 1) including cloud cover, wind speed and wind direction. Bathythermograph temperature profiles were made using a 100 m and a 60 m bathythermograph on loan from DREP (Defense Research Establishment Pacific) calibrated by bucket surface temperature measurements.

Light readings were taken at five meter intervals to 30 m using a flat plate irradiance meter with deck and subcell components (G.M. Mfg. and Inst. Co. N.Y.). The deck cell was calibrated with a solar radiometer, data being recorded in Langley-hrs (gram-cal. $cm^{-2}\ hr^{-1}$ = joules $m^{-2}\ hr^{-1}$). Light and temperature data were taken as close as possible to PST 1400 h. The sample time varied less than plus or minus one hour throughout the period.

Water samples were collected with a 20 litre Niskin-type bottle from depths of 1, 5, 10, 15, 25, 40, and 50 meters. The sampling bottle was routinely lowered to just below the depth to be sampled and raised slowly to the required depth to allow a representative sample to be

Fig. 1 Sampling site, Station 'E',
Saanich Inlet

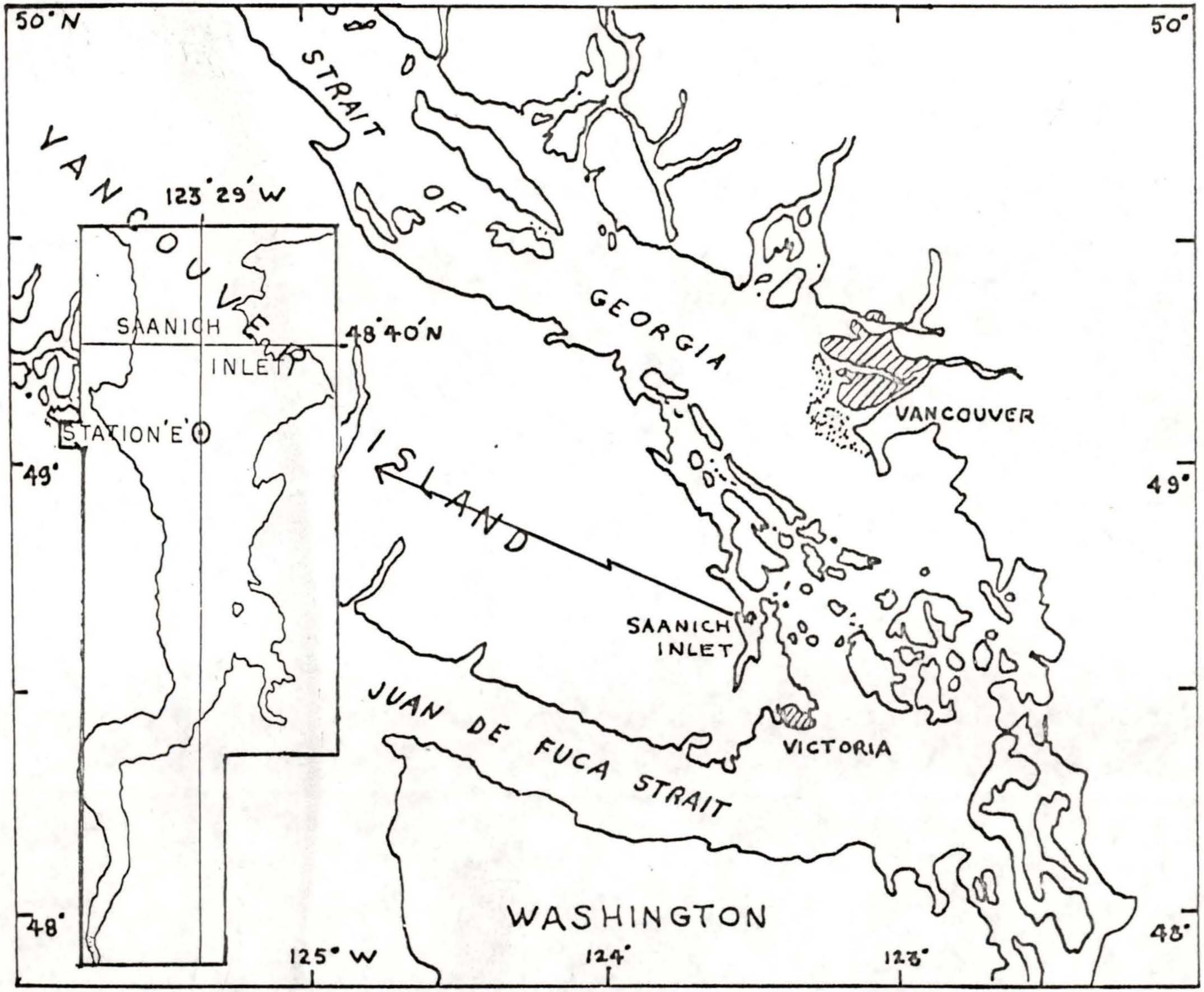

50°N
50°
STRAIT OF GEORGIA
VANCOUVER ISLAND
123°29'W
SAANICH INLET
48°40'N
STATION 'E'
VANCOUVER
49°
49°
SAANICH INLET
VICTORIA
JUAN DE FUCA STRAIT
WASHINGTON
48°
48°
125° W
124°
123°

Figure 1

Table 1. Weather at station 'E', Saanich Inlet
March 22 to May 30, 1971

TABLE 1

WEATHER

Sample Date 1971		Radiation * langleys/day	Cloud cover	wind speed and direction	Time of arrival Stn. E
March	22	72(400)**	full sun	light airs	1425 hrs PST
	23	246	mixed cloud	light airs	1340
	24	343	sun w cloud	S.W. 10-20 km	1400
	25	407	sun w cloud	S.W. 10 km	1345
	27	235	rain w sun	S.W. 10-15 km	1520
	28	165	rain, cloud	S.W. 5-10 km	1320
April	14	261 (500)	cloud w sun	S.W. 25 km	1500
	16	312	full cloud	S.W. 10	1430
	19	469	sun w cloud	calm	1440
	21	521	sun w cloud	S. 15 km	1400
	23	530	sun w cloud	calm	1400
	25	587	sun	N. 5-8 km	1400
	27	260 (580)	sun	calm	1500
May	3	624	sun	calm	1330
	4	380	cloud w sun	S.E. 5 km	1340
	6	636	sun	light airs	1340
	8	644	sun	S.E. 3-5 km	1430
	13	340	cloud, rain	S.W. 10 km	1430
	15	119 (600)	cloud, rain, sun	calm	1400
	17	581	sun	W. 5 km	1415
	19	622	sun, cloud	S.W. 15 km	1530
	21	533	sun, hazy	E. 4 km	1300
	26	680	sun	E. 7-8 km	1520
	27	714	sun	light airs	1450
	28	573	sun, hazy	S.E. 5-6 km	1530
	30	594	sun, hazy	S.E. 2-5 km	1430

* Radiation data from Nanaimo, Departure Bay, Eppley Model 2 Pyranometer

** estimates of field conditions

taken, before the closure was triggered. Once on deck the water was emptied into 20 litre polyethylene carboys each marked and retained specifically for that depth.

Duplicate one-litre aliquots were immediately withdrawn and filtered through 47 mm diameter 0.45μ porosity membrane Millipore ™ filters for later photosynthetic pigment and lipid determinations. Gridded membrane filters of the same porosity were used to filter 100 ml aliquots for later species identification and counting. Glass-fiber Gelman ™ filters, 47 mm diameter, 0.5μ porosity previously heated to 500°C. to volatilize contaminants were used, at reduced pressure (-5 p.s.i.) to filter 1-liter aliquots for particulate nitrogen and carbohydrate determinations. All filters and contents were folded between marked pieces of thick qualitative Whatman ™ filter papers. These were immediately sealed in Twirl-pak ™ plastic bags with a small quantity of silica gel dessicant and placed on dry ice in an insulated container.

One-litre aliquots were withdrawn into polyethylene containers for salinity, nitrate, nitrite and ammonia determinations. Samples were kept cool and in the dark while on board, and upon return to the laboratory were stored at -2°C. until analysis. Additional 200 ml aliquots, preserved with 5% buffer formalin were retained for later counting and identification of the phytoplankton species.

Salinity determinations were completed on aliquots retained for nutrient analysis, using a Model 6221 Hytech Laboratory Salinometer ($\frac{\text{Bissett}}{\text{Berman}}$ Corporation, San Diego, Calif.) calibrated with Copenhagen standard sea water. Sigma-t and stability coefficients were calculated based on salinity and temperature data using the U.S. Naval Hydrographic Tables and the equation for stability employed by Hobson and Lorenzen, (1972):

$$E' = 10^{-3} d6_t/dz$$

E' = Stability coef.
$d6_t$ = change sigma-t
dz = depth interval

Reactive nitrate was analysed using the cadmium/copper reduction method reported in Strickland and Parsons (1968).

Ammonia was determined using Solorzano's (1969) modification of the phenol-hypochlorite method originally described by Berthelot. Difficulty was experienced in getting and maintaining water sufficiently low in ammonia for use in blank determinations. A composite blank was derived from the lowest modal value for ammonia obtainable during the process of the late May bloom. This blank was applied in all calculations for ammonia.

Particulate nitrogen was determined using the method detailed in Strickland and Parsons (1968), a Kjeldahl-type digestion with a ninhydrin-hydrindantin finish.

Particulate carbohydrate was analysed using the phenol-sulphuric acid method of Dubois et al (1956) as described in Strickland and Parsons, (1968). This method was selected over the anthrone or N-ethylcarbazole method because of its relative non-specificity for any particular sugar (see Handa, 1966). Glass fibre filters holding the particulate material were trimmed and dispersed in 2.0 ml of phenol reagent, added from a burette. In quick succession 10 ml of sulphuric acid-hydrazine sulphate reagent were added. This material was mixed using a tube homogenator until the glass fibres had been dispersed thoroughly. The mixture was allowed to cool for an hour before a portion of the supernatant was withdrawn. The extinction of this hydrolysate was then measured at 490 nm in a 1 cm cell and calibrated against a glucose standard.

Lipids were isolated and purified using a method described by Folch _et al_ (1957) whereby membrane filters containing the particulate material were ground with 2:1 chloroform-methanol. This extract was shaken with 1/5 of its volume of 0.02% $CaCl_2$ then left to stand until the phases separated. As much as possible of the upper phase was then removed. Final removal of upper phase solutes were accomplished by rinsing the interface with pure upper phase solvents for which purpose the upper phase of a mixture of clean 2:1 chloroform methanol and 0.02% $CaCl_2$ was retained. The clean lower phase containing most of the lipid was then dried in an oven equiped with flowing nitrogen at approximately 40°C. The dried lipid material was taken up in a small quantity of anhydrous ethyl ether and placed in pre-weighed 1 ml vials, evaporated to dryness as before and weighed. The dried material was thus available for further characterization by thin-layer chromatography, (Walsh _et al_, 1965).

Chlorophyll-a was measured following the recommendations of SCOR-UNESCO, reported in Strickland and Parsons, (1968).

Carotenoids were also measured applying the equation for Chrysophyta/ Pyrrophyta (Strickland and Parsons, 1968).

Phaeopigments were measured as per Strickland and Parsons, 1968, and chlorophyll-a values were corrected to true chlorophyll-a by subtracting values for phaeopigments.

Phytoplankton species were counted and identified using a membrane-clearing method (A.P.H.A., 1976). By this method 100 ml volumes of formalin-preserved sample were filtered through gridded Millipore (TM) membrane filters. Before the sample completely passed through the filter, the plankton was partially dehydrated by adding gradually increasing amounts of ethanol until a final rinse through the filter with a portion of absolute ethanol completed the process. Following this rinse 10 to 20 ml of xylene were passed through the filter to clear it optically. Without allowing the filter to dry it was placed on a few drops of permount diluted with xylene, on a large slide. When the permount had diffused through the filter a few more drops were added and a cover slip pressed firmly down excluding all air bubbles in the process. This preparation was dried in a low temperature over and made air-tight with a final ring of permount around the edge of the cover slip. Slides were labelled with a diamond pencil. Phase-contrast microscopy was employed for counts and identifications. Calibration of the visual field was achieved using a 2 mm stage micrometer. Ten whole-fields of 1 mm^2 were counted and the phytoplankton assorted in species and numbers using the equation provided by the Millipore company with their filtration apparatus:

$$N = \frac{C \times 255}{V \times 10}$$

Where N = Number of organisms
C = count in 10 fields of 1 mm^2 ea.
255 = filtering area in mm^2
V = volume of sample filtered
10 = number of fields examined

RESULTS

Weather

Daily incident radiation, extracted from Canadian meteorological records for the Nanaimo, Departure Bay station was combined with estimations of cloud cover and wind direction and speed made on-station throughout the sample period. This information is summarised in Table 1. Inspection of the available meteorological records indicate that weather during spring, 1971, was typical for lower Vancouver Island. Throughout March and for most of April, weather was unsettled. Winds were variable, daily incident solar radiation averaged less than 450 ly-day^{-1} and few days of full sun without rain were experienced. Near the end of April the weather began to stabilize and longer periods of calm, sunny weather ensued.

The rapid establishment of the summer thermocline (Fig. 2) was the most notable event of this period. A brief, five day period of stormy, rainy weather interrupted this process in the middle of May but stability had been reestablished by May 19. The advent of a long, calm sunny spell averaging 614 ly-day^{-1} of incident radiation and less than 10 km winds set up conditions for the thermal and saline stratification of the upper 50 m of Saanich Inlet.

Irradiance

The temporal distribution of isolumes for the period of intensive study, April 14 to May 30, 1971, based on <u>in-situ</u> light measurements and expressed as a percentage of total light penetrating the water surface (measured at 0.1 m) is shown in Fig. 3.

Fig. 2 Isotherms (^{o}C)

0 to 50 m, April 14 to May 30

FIGURE 2

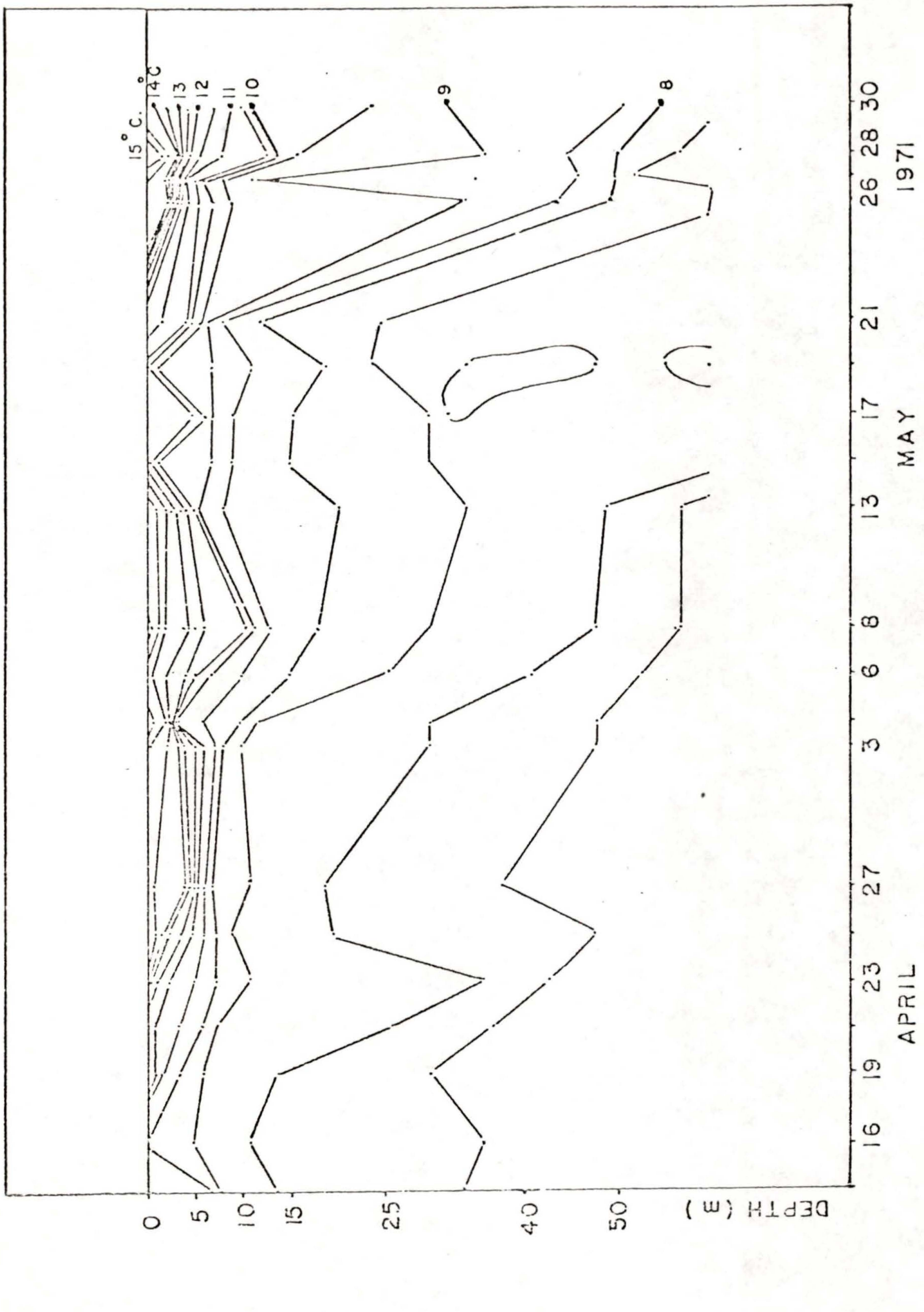
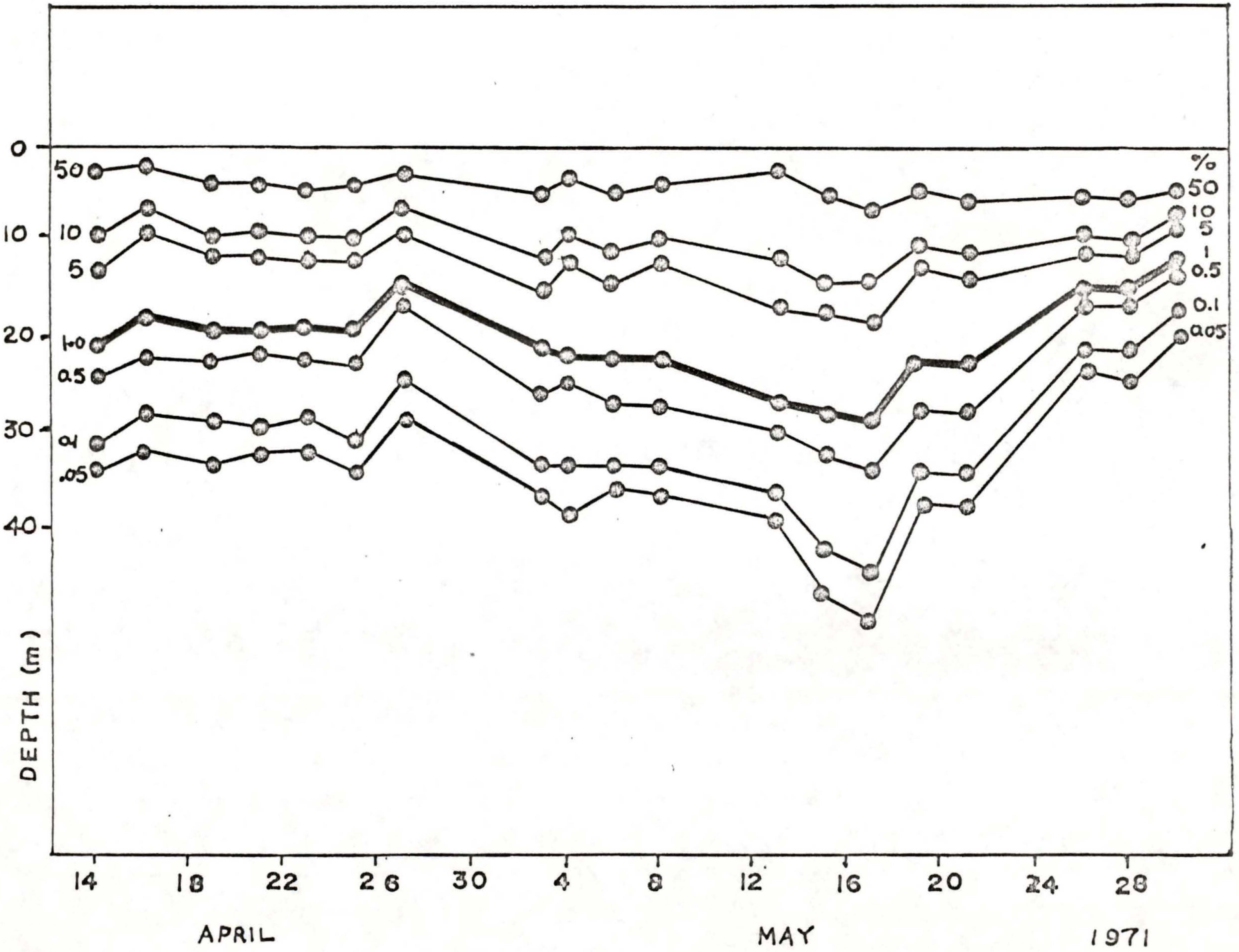

15°C.
14°C
13
12
11
10
9
8
0
5
10
15
25
40
50
DEPTH (m)
16
19
23
27
3
6
8
13
17
21
26
28
30
APRIL
MAY
1971

Fig. 3 Percent surface light isolumes

0 to 40 m, April 14 to May 30


0
10
20
30
40
DEPTH (m)
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10
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1·0
0.5
0.1
.05
%
50
10
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1
0.5
0.1
0.05
14
18
22
26
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4
8
12
16
20
24
28
APRIL
MAY
1971

FIGURE 3

The depth to which one percent of the surface light penetrates is commonly considered to be the compensation point or the lower limit of net phytoplankton photosynthesis. In the present study the depth to which one percent of the light passing the air/water interface penetrates is shown by the heavy line in Fig. 3. This isolume maintains a constant depth between 16 and 18 m during the first ten days of April. It then gradually deepens to a maximum depth of 26 m on May 17. From this point it rises sharply and steadily to a minimum depth of 8 m on May 30.

The depth of the 0.0015 ly/min. isolume, measured *in-situ* with a submersible photocell, is illustrated in Fig. 4. It follows the pattern of the one percent isolume but occurs about 6 m shallower than the latter. This measured value is considered by some to be a more accurate indicator of the depth of the compensation depth and has been included herein for comparison purposes.

Since both of these estimates of compensation intensity are at best instantaneous measurements and cannot be applied to the 24-hr light regime that a phytoplankton population actually experiences, several authors (McAllister *et al*, 1964: Hobson, 1966) have recommended the use of a 24-hr compensation intensity for temperate seas with a value between 0.002 and 0.009 ly/min. Both of these have been calculated from daily irradiance figures reported in the Canadian meteorological records for 1971, at Departure Bay, Nanaimo, and are illustrated in Fig. 5. In general these two isolumes bracket the one percent isolume except on May 15 when they are 5 and 15 m respectively above the one percent level.

Fig. 4 Observed compensation depths

0.0015 ly/min. and 1% surface light.

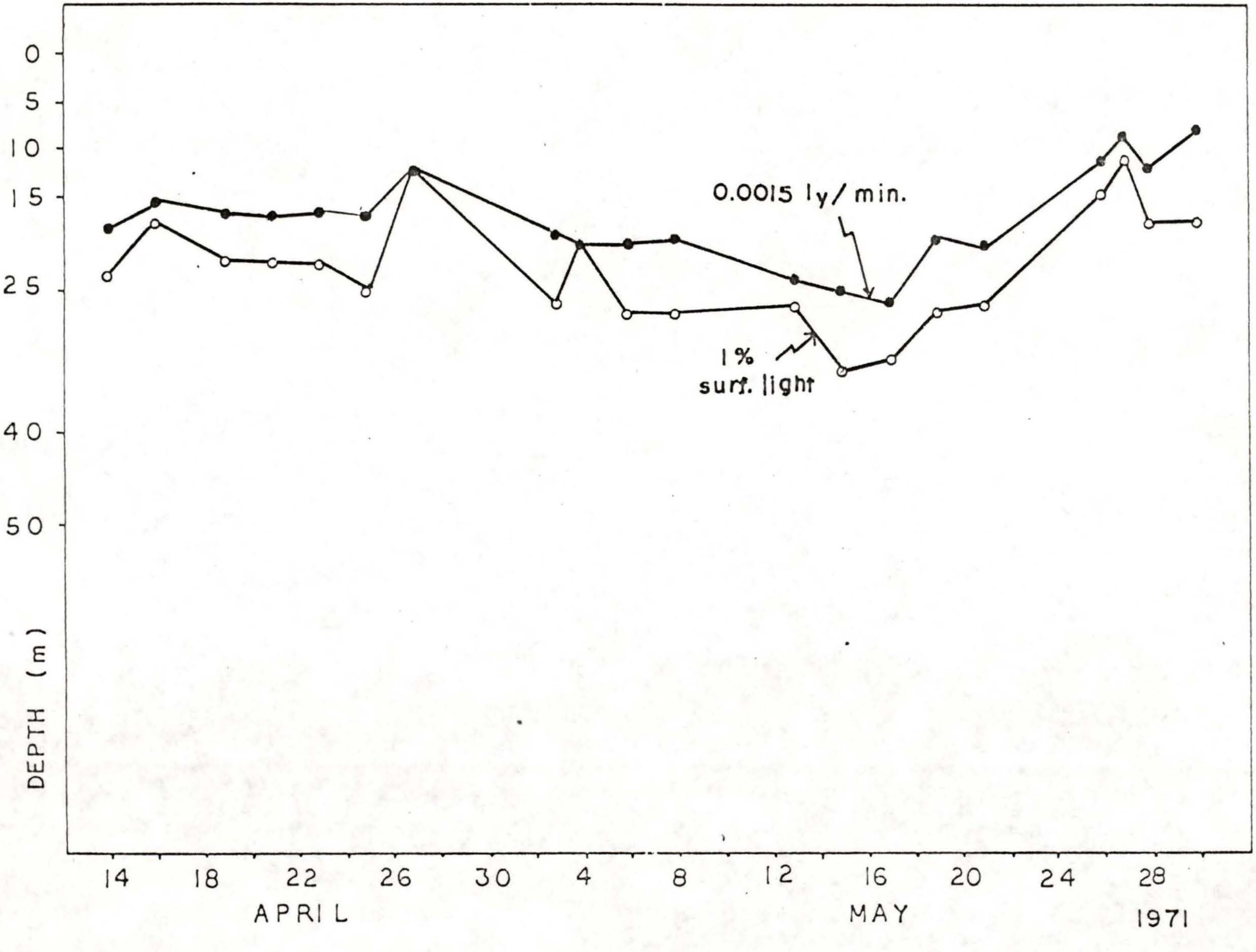
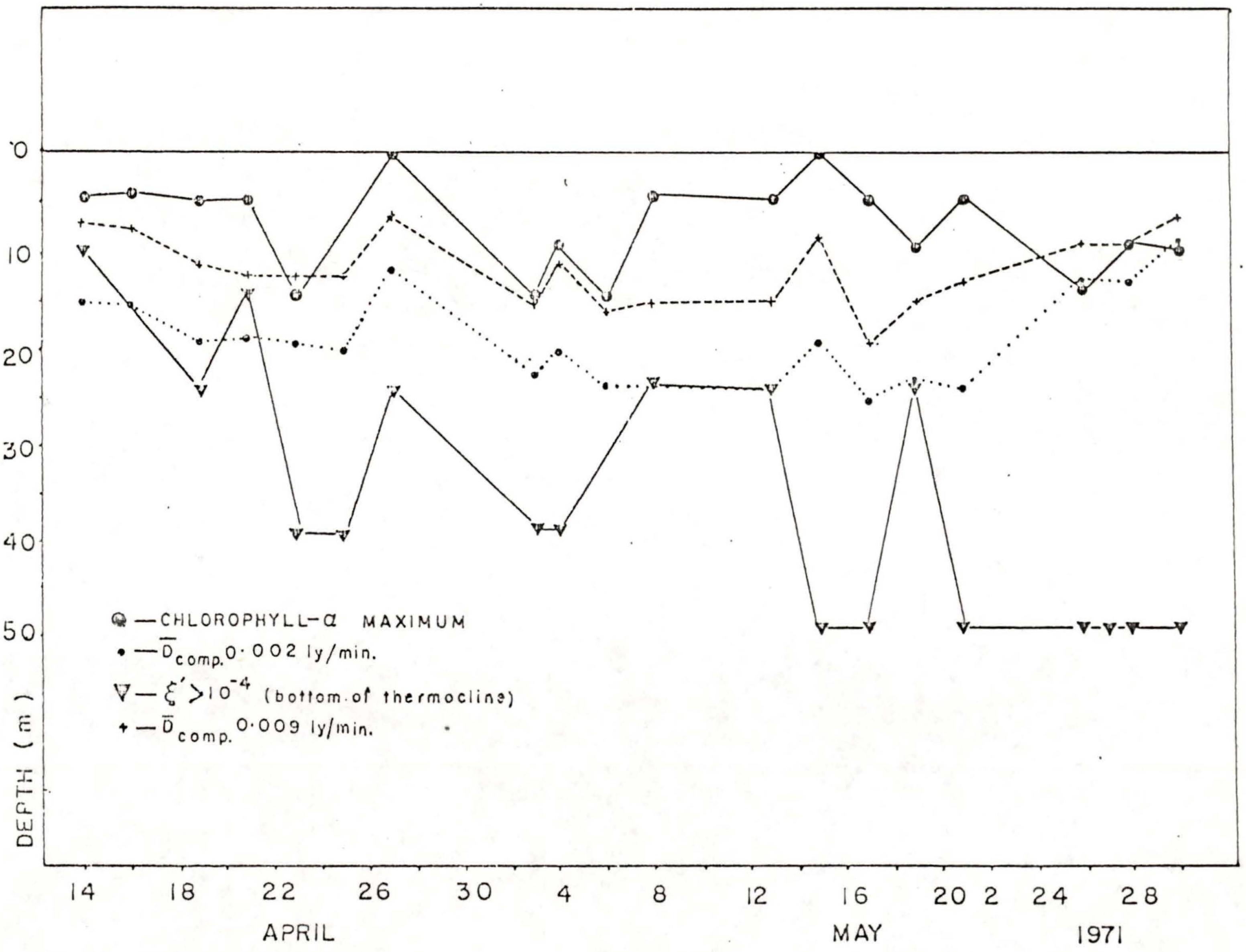

0
5
10
15
25
40
50
DEPTH (m)
0.0015 ly/min.
1%
surf. light
14
18
22
26
30
4
8
12
16
20
24
28
APRIL
MAY
1971

FIGURE 4

Fig. 5 Temporal variation in chlorophyll-a maxima, theoretical compensation depth (0.002 and 0.009 ly/min.) and stability maxima ($E' > 10^{-4}$), April 14 to May 30


0
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DEPTH (m)
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26
30
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20 2
24
28
APRIL
MAY
1971
— CHLOROPHYLL-a MAXIMUM
• — $\overline{D}_{comp.}$ 0·002 ly/min.
▽ — $\xi' > 10^{-4}$ (bottom of thermocline)
+ — $\overline{D}_{comp.}$ 0·009 ly/min.

FIGURE 5

The average extinction coefficient (k), defined as the reduction of radiation energy per unit of depth was calculated from the equation:

$$k = \frac{\ln I_i - \ln I_j}{d_j - d_i}$$

where k = extinction coefficient
I_j,i = intensities at depths 'i' and 'j'
d_j,i = distance (meters) between the two depths 'i' and 'j'.

This coefficient follows a pattern similar to, but steadier than that of the compensation isolumes. For the period April 14 to 25 it varied little from 0.32, but then went into oscillations from April 27 onward, gradually decreasing from May 3 to 17 and rising slowly to a maximum on May 30 (see Table 2).

Hydrography

Temperature data taken between April 14 and May 30 are shown in Table 3. The water at Station E above 60 m underwent a warming trend as the spring progressed. Thermal stratification in the upper water was minimal in the early part of April but increased steadily from April 19 to May 13. During the week of May 13 to 19 the upper component of the temperature profile broke down possibly as a result of wind mixing. From May 21 to May 30 thermal stratification was strongly re-established and the warming trend was extended into 60 m water. Temperature increased 2.0°C. at 50 m between May 1 and May 30 while the 8.5°C. isotherm deepened from 0 m on May 14 to 50 m on May 30. Temperature at 50 m increased from less than 6.5°C. in April to 8.5°C. by the end of May and by this time surface warming had extended down to 50 m.

Table 2. Light Data: Extinction coefficients for submarine light.

TABLE 2

Date		DEPTH (m)							
1971		k(0-3)	k(3-5)	k(5-10)	k(1015)	k(15-20)	k(20-25)	k(25-30)	k(ave.)
April	14	0.155	0.372	0.202	0.154	0.408	0.291	0.200	0.254
	16	0.350	0.407	0.227	0.157	0.338	0.183	0.285	0.278
	19	0.314	0.202	0.324	0.223	0.405	0.183	0.306	0.279
	21	0.301	0.284	0.316	0.169	0.402	0.308	0.183	0.280
	23	0.231	0.312	0.311	0.237	0.411	0.168	0.269	0.277
	25	0.291	0.238	0.310	0.220	0.441	0.296	0.225	0.289
	27	0.485	0.301	0.295	0.425	0.259	0.277	0.322	0.338
May	3	0.210	0.172	0.234	0.248	0.640	0.307	0.231	0.291
	4	0.396	0.190	0.245	0.154	0.154	0.183	0.313	0.234
	6	0.196	0.208	0.283	0.175	0.220	0.309	0.203	0.228
	8	0.294	0.269	0.266	0.129	0.625	0.324	0.214	0.303
	13	0.135	0.275	0.147	0.134	0.193	0.545	0.206	0.234
	15	0.248	0.110	0.162	0.228	0.127	0.188	0.315	0.197
	17	0.238	0.169	0.243	0.147	0.184	0.134	0.398	0.216
	19	0.287	0.210	0.322	0.130	0.635	0.326	0.224	0.305
	21	0.234	0.291	0.285	0.223	0.137	0.354	0.225	0.250
	26	0.264	0.651	0.357	0.331	0.573	0.263	0.261	0.386
	27	0.322	0.575	0.192	0.697	0.287	0.283	0.118	0.353
	28	0.201	0.247	0.442	0.677	0.134	0.287	0.264	0.363
	30	0.441	0.748	0.639	0.493	0.241	0.250	0.393	0.458

Table 3. Temperature (^{o}C) *in-situ*
March 22 to May 30, 1971.

TABLE 3

DATE	DEPTH (m)						
1971	0	5	10	15	25	40	50
March 22	6.8	7.5	7.5	7.3	7.2	7.5	7.5
23	7.0	6.5	6.4	6.5	6.5	6.5	6.5
24	7.5	7.4	7.1	7.0	7.0	7.0	7.0
25	7.5	7.3	7.2	7.1	7.0	7.0	6.7
27	7.4	7.3	7.2	7.1	7.0	6.9	7.0
28	7.4	7.3	7.2	7.1	7.0	7.0	7.0
April 14	8.8	8.8	7.4	7.0	6.8	6.5	6.5
16	7.8	7.6	7.0	6.9	6.7	6.5	6.5
19	10.1	7.8	7.3	6.9	6.6	6.5	6.5
21	9.5	8.0	7.3	7.0	7.0	6.5	6.5
23	11.6	8.5	7.5	7.3	7.0	6.6	6.5
25	11.9	9.0	7.3	7.0	7.0	6.6	6.5
27	11.7	10.0	7.5	7.3	7.0	6.5	6.5
May 3	14.1	9.5	7.5	7.4	7.3	6.8	6.5
4	13.2	8.7	8.0	7.5	7.3	6.8	6.5
6	12.9	9.5	8.5	8.0	7.5	7.2	6.8
8	13.2	10.8	9.5	8.3	7.8	7.3	6.9
13	12.9	9.0	8.5	8.0	7.8	7.5	7.5
15	10.4	9.3	8.5	8.0	7.8	7.5	7.5
17	10.7	9.8	8.5	8.0	7.7	7.5	7.4
19	10.0	10.0	9.0	8.5	7.5	8.0	7.8
21	11.3	10.0	8.3	8.0	7.5	7.5	7.5
26	14.9	10.8	9.5	9.3	9.3	8.8	8.0
27	14.7	11.0	9.0	9.0	9.0	9.0	8.0
28	16.7	11.5	11.0	9.5	9.3	8.5	8.0
30	13.8	12.0	10.5	9.7	9.5	9.0	8.5

Salinity values for the period of study are shown in Table 4. Surface salinity varied between 24.4 o/oo and 28.8 o/oo with an average value of 26.7 o/ooo. Salinity values at 50 m varied from 29.3 o/oo to 30.0 o/oo. The average salinity during April was 28.9 o/oo for all depths, 0 to 50 m. This value dropped to 27.8 o/oo in early May and then rose to 28.8 o/oo from May 13 to May 30.

Isopleths of salinity are shown in Fig. 6. The general trend was a decrease in salinity throughout the water column for the period of study. The 29.5 o/oo isohaline extended its depth from 25 m to 50 m in the process. The salinity stratification was strong throughout the major part of April and May but two periods of turnover in the surface waters (0 to 15 m) were discernable. The first of these, between April 27 and May 6 was not extensive, penetrating no deeper than 5 m, but the second extended well into the 15 m depth and had a strong effect on the deeper isohalines, raising them 10 to 20 m shallower in the water column.

Density (sigma-t) was calculated for all depths 0 to 50 m for the duration of the study.

$$\text{Sigma-t: } (\text{density}-1) \times 10^3.$$

The isopycnals for the study period are shown in Fig. 7. Density stratification was greatest in the period between May 3 and May 8, but equally strong stratification occurred late in April and in late May. The interval between May 13 and May 17, however, was one of extreme instability, with low density water overlaid with higher density water. Isopycnals are all sharply sloped, with maximum slopes on May 15. With the onset of

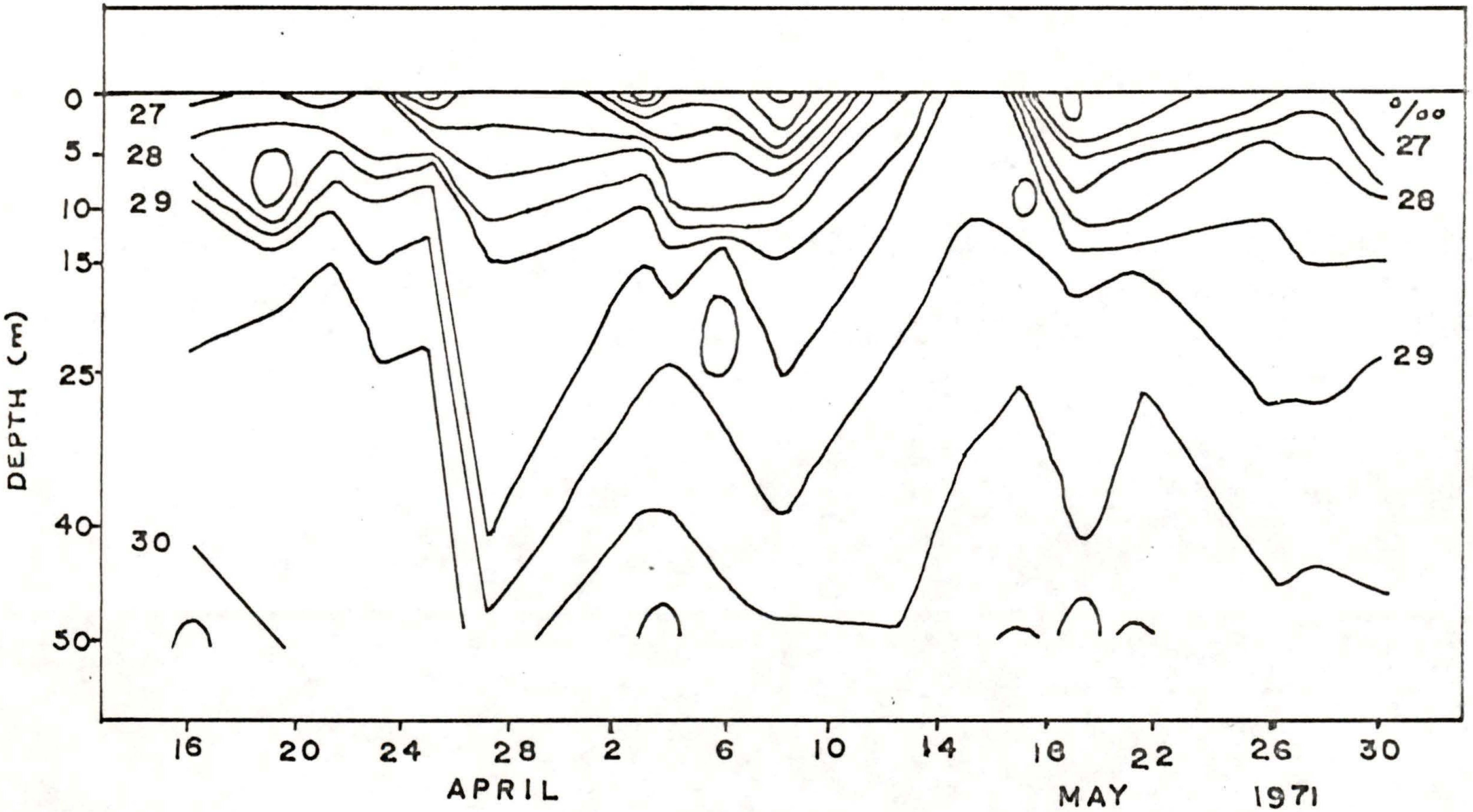
Table 4. Salinity (o/oo), April 14 to May 30, 1971.

TABLE 4

DATE 1971		DEPTH (m) 0	5	10	15	25	40	50
April	14							
	16	26.98	27.66	29.18	29.08	29.65	29.93	29.72
	19	27.29	27.88	27.23	29.28	29,73	29.88	29.98
	21	26.87	28.28	28.99	29.63	29.66	29.75	29.81
	23	27.12	27.45	28.61	29.08	29.59	29.73	29.81
	25	25.04	27.95	28.78	29.22	29.63	29.76	29.86
	27	26.71	26.15	27.42	28.06	28.33	28.40	29.33
May	3	24.37	27.19	28.11	28.73	28.90	29.64	29.46
	4	25.43	26.32	26.97	28,32	29,18	29.67	29.26
	6	25.41	26.63	27.03	29.12	28.71	29.40	29.69
	8	24.31	25.24	27.23	28.15	28.31	29.31	29.69
	13	27.74	28.08	28.55	28.74	29.26	29.39	29.60
	15	28.78	28.83	29.00	29.10	29.46	29.69	29.91
	17	28.15	28.65	27.69	29.12	29.40	29.75	30.00
	19	28.39	26.82	27.62	28.78	29.42	29.42	28.06
	21	26.30	27.54	27.27	29.10	29.47	29.77	30.01
	26	27.09	28.20	28.46	28.89	28.91	29.42	29.71
	27	27.42	27.95	28.16	28.52	29.27	29.64	29.69
	28	27.28	27.45	28.14	28.78	29.25	29.55	29.67
	30	26.69	27.00	28.10	28.54	29.10	29.35	29.62

Fig. 6 Salinity isopleths, 0 to 50 m

April 14 to May 30



0
5
10
15
25
40
50
DEPTH (m)
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28
29
30
°/oo
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2
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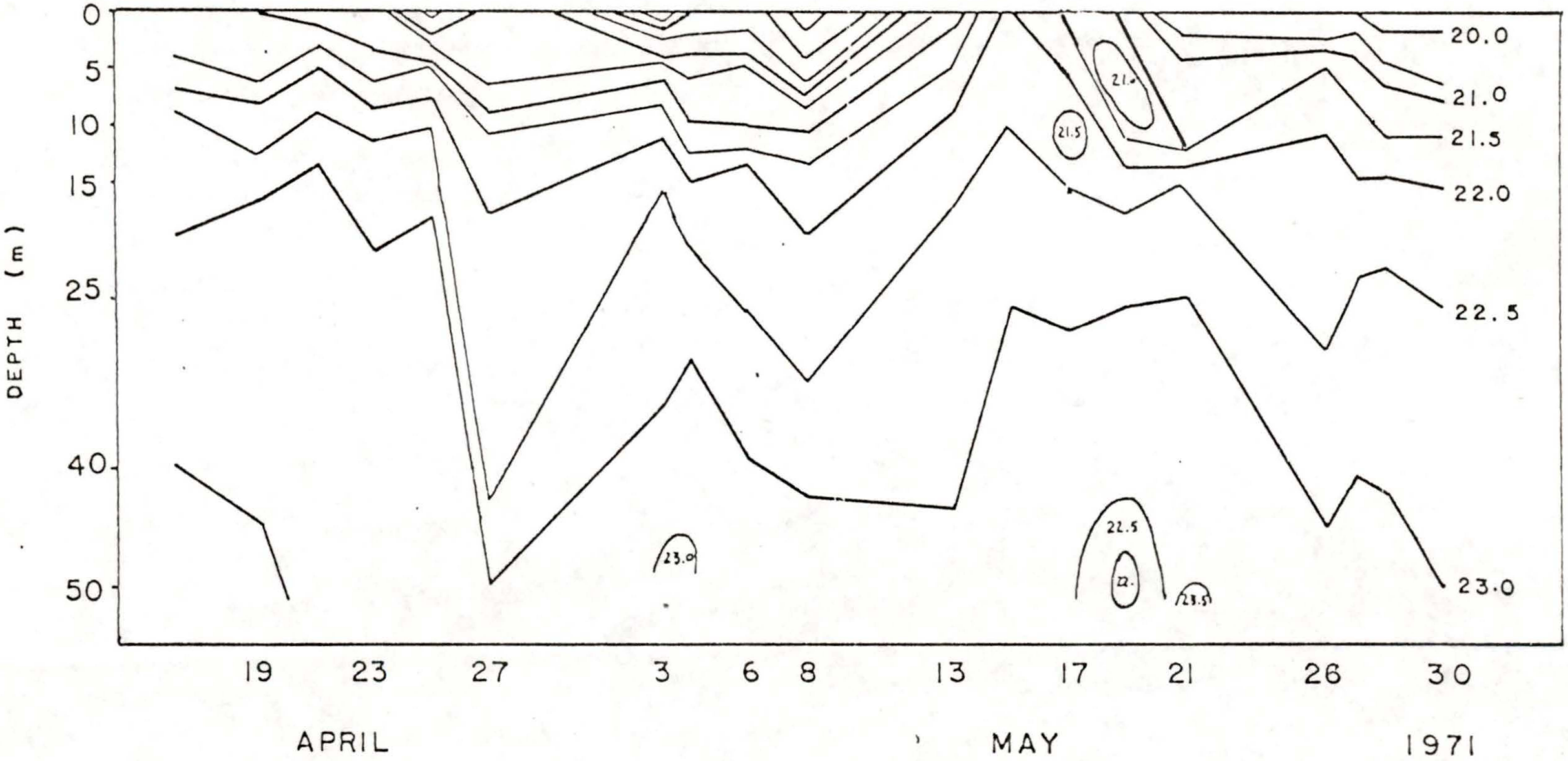
22
26
30
APRIL
MAY
1971

FIGURE 6

Fig. 7 Isopycnals, (sigma-t)
0 to 50 m, April 14 to May 30


DEPTH (m)
0
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10
15
25
40
50
20.0
21.0
21.5
22.0
22.5
23.0
21.0
21.5
23.0
22.5
22.
23.5
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26
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APRIL
MAY
1971

FIGURE 7

warm, calm weather on May 17, stratification gradually was re-established until a highly stable water column was set up during the last week of May.

Stability coefficients for the period April 16 to May 30 are shown in Table 5. Negative values indicate unstable water masses. These are particularly common in the surface waters between May 15 and May 19. Unstable units of water appear in the 40-50 m depth occasionally and are probably associated with tidal movements. The body of water above 50 m is above sill depth in Saanich Inlet and seems to move independently of deeper water, causing temporary instabilities in shear eddies between the two water masses.

Chemistry

Nitrate-N, integrated under a meter square down to 50 m and to the compensation depth (calculated as the one percent light level and as the 0.0015 ly/min. level) is shown in Fig. 8, as it varies over the period of study. The amount of nitrate-N above 50 m decreases from a high of 1,200 mg-at NO_3-N, in April (a value which is similar to the winter values for nitrate in February and November), to less than 30 mg-at NO_3-N in late May. In this text the term mg-at N will be used throughout. 1 mg-at N is equivalent to 14 mg N which equals 1 millimole of N.

The pattern of nitrate depletion is similar at both calculated compensation depths although the 0.0015 ly/min. D_{comp} levels are consistently higher, reflecting its deeper position in the water column. An initial high level of around 400 mg-at NO_3-N drops to 100 mg-at NO_3-N m^{-2} in late April but then rises to its original value in the middle of May

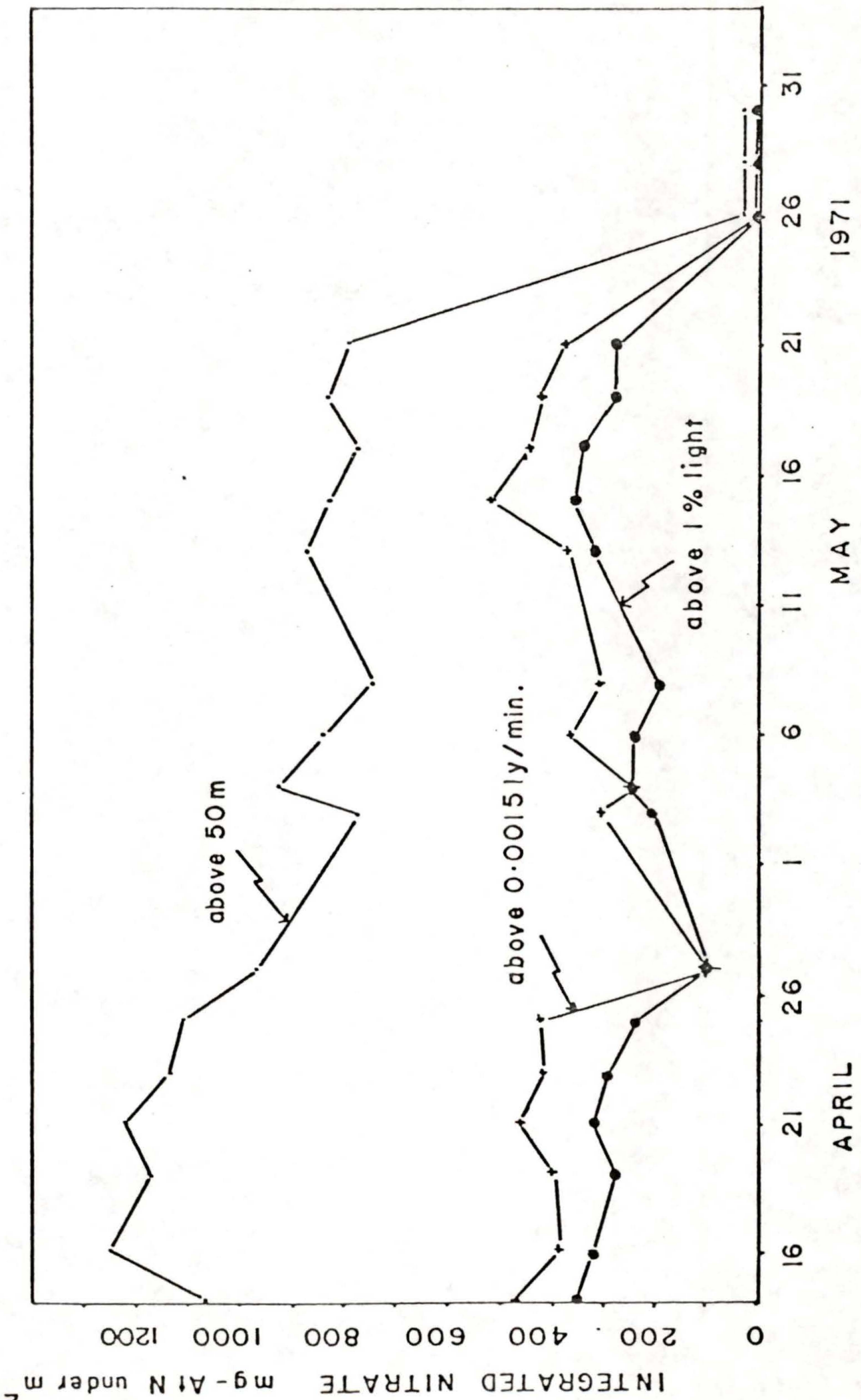
Table 5. Stability coefficients ($E' \times 10^6$ m^{-1})
April 14 to May 30.

TABLE 5

DATE		DEPTH (m)					
1971		0-5	5-10	10-15	15-25	25-40	40-50
April	14	+128.0	+ 48.0	- 6.0	+ 4.5	+ 16.7	- 16.0
	19	+168.0	+ 60.0	+170.0	+ 41.0	+ 6.7	+ 9.0
	21	+270.0	+130.0	+104.0	+ 4.0	+ 9.3	+ 70.0
	23	+155.0	+218.0	+ 70.0	+ 43.0	+ 11.3	+ 6.0
	25	+540.0	+176.0	+ 78.0	+ 33.0	+ 10.0	+ 8.0
	27	- 26.0	+270.0	+104.0	+ 25.0	+ 8.7	+ 70.0
May	3	+590.0	+204.0	+106.0	+ 12.0	+ 42.7	- 8.0
	4	+270.0	+128.0	+226.0	+ 68.0	+ 31.3	- 30.0
	6	+290.0	+100.0	+140.0	- 20.0	+ 36.7	+ 25.0
	8	+236.0	+340.0	+180.0	+ 25.0	+ 53.3	+ 35.0
	13	+186.0	+ 90.0	+ 50.0	+ 15.2	+ 8.0	+ 25.0
	15	+ 42.0	+ 48.0	+ 28.0	+ 29.0	+ 16.0	+ 18.0
	17	+114.0	-130.0	+275.0	+ 28.0	+ 20.0	+ 13.0
	19	-252.0	+164.0	+200.0	+ 62.0	- 67.0	-100.0
	21	+240.0	0.0	+300.0	+ 70.0	+ 50.0	+ 34.0
	26	+322.0	+ 86.0	+ 74.0	+ 3.0	+ 30.0	+ 35.0
	27	+222.0	+ 92.0	+ 60.0	+ 57.0	+ 20.0	+ 19.0
	28	+236.0	+116.0	+150.0	+ 40.0	+ 23.3	+ 17.0
	30	+120.0	+216.0	+100.0	+ 50.0	+ 21.3	+ 10.0

Fig. 8. Integrated nitrate above 50 m, 0.0015 ly/min. and 1 percent surface light, April 14 to May 30.

FIGURE 8


INTEGRATED NITRATE mg-At N under m²
0
200
400
600
800
1000
1200
16
21
26
1
6
11
16
21
26
31
APRIL
MAY
1971
above 50m
above 0·0015 ly/min.
above 1% light

in correspondance to a temporary breakdown in the stability of the water column. When stability was reestablished nitrate-nitrogen was quickly depleted until levels of less than 10 mg-at NO_3-N m^{-2} were recorded in the last week of May. Nitrate isopleths from April 14 to May 30 are shown in Fig. 9. From these it may be seen that depletion proceeded at a faster rate above the compensation depth than below it. This rate accelerated in the deeper water late in May to such an extent that levels dropped from 15 ug-at NO_3-N m^{-3} to zero in five days.

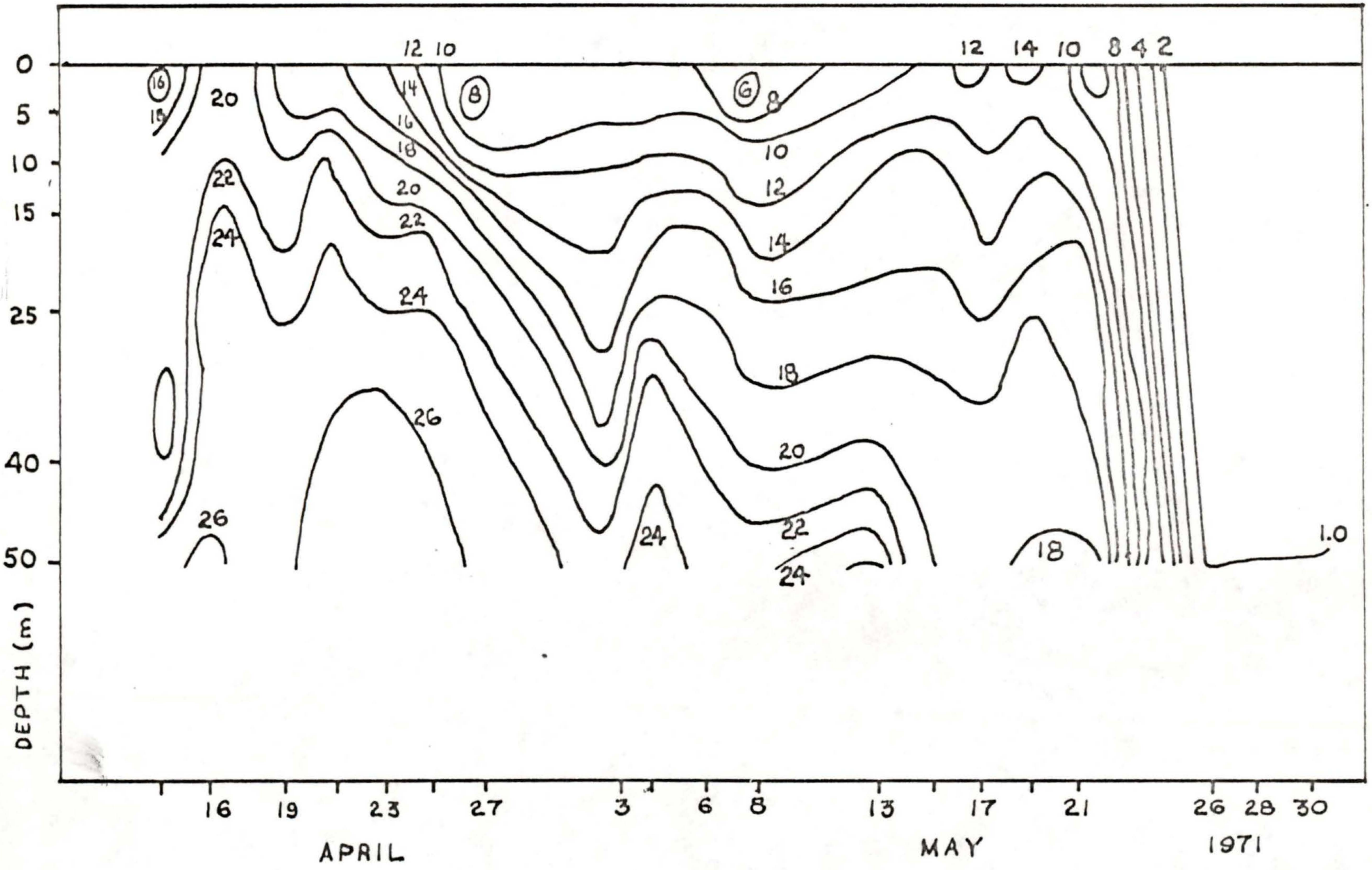
Nitrite-nitrogen values integrated under a square meter (Fig. 10) for the period April 14 to May 30, fluctuate around an average of 9 mg-at NO_2-N m^{-2} above 50 m, showing no distinct or significant trend. For a short period between April 14 and April 25 nitrite values fell in a smooth curve from 13 mg-at NO_2-N m^{-2} to 7 mg-at NO_2-N m^{-2}.

After this period, values oscillate between 5 and 12 mg-at NO_2-N m^{-2} without any obvious correlation with chemical or physical events.

Integrated values of nitrite above the compensation depth seem to follow the general pattern that nitrate-nitrogen follows, falling from around 6 mg-at NO_2-N m^{-2} on April 14 to approximately 1 mg-at NO_2-N m^{-2} on May 30, with a strong increase to 7 mg-at NO_2-N m^{-2} on May 15 coinciding with a period of water column instability (Table 5). Isopleths illustrating the seasonal variation in nitrite nitrogen at the various depths sampled are presented in Fig. 11.

Integrated ammonia levels above 50 m as shown in Fig. 12 vary from 200 mg-at NH_3-N m^{-2} to less than 50 mg-at NH_3-N m^{-2}. But as with nitrite, wide variations in the values tend to obscure any pattern that might be present.

Fig. 9. Isopleths of Nitrate (μg-At N m^{-3})
0 to 50 m, April 14 to May 30



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DEPTH (m)
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26 28 30
APRIL
MAY
1971

FIGURE 9

Fig. 10. Integrated nitrite above 50 m, above $D_{comp.}$ 0.0015 ly/min. and above 1 percent surface light.

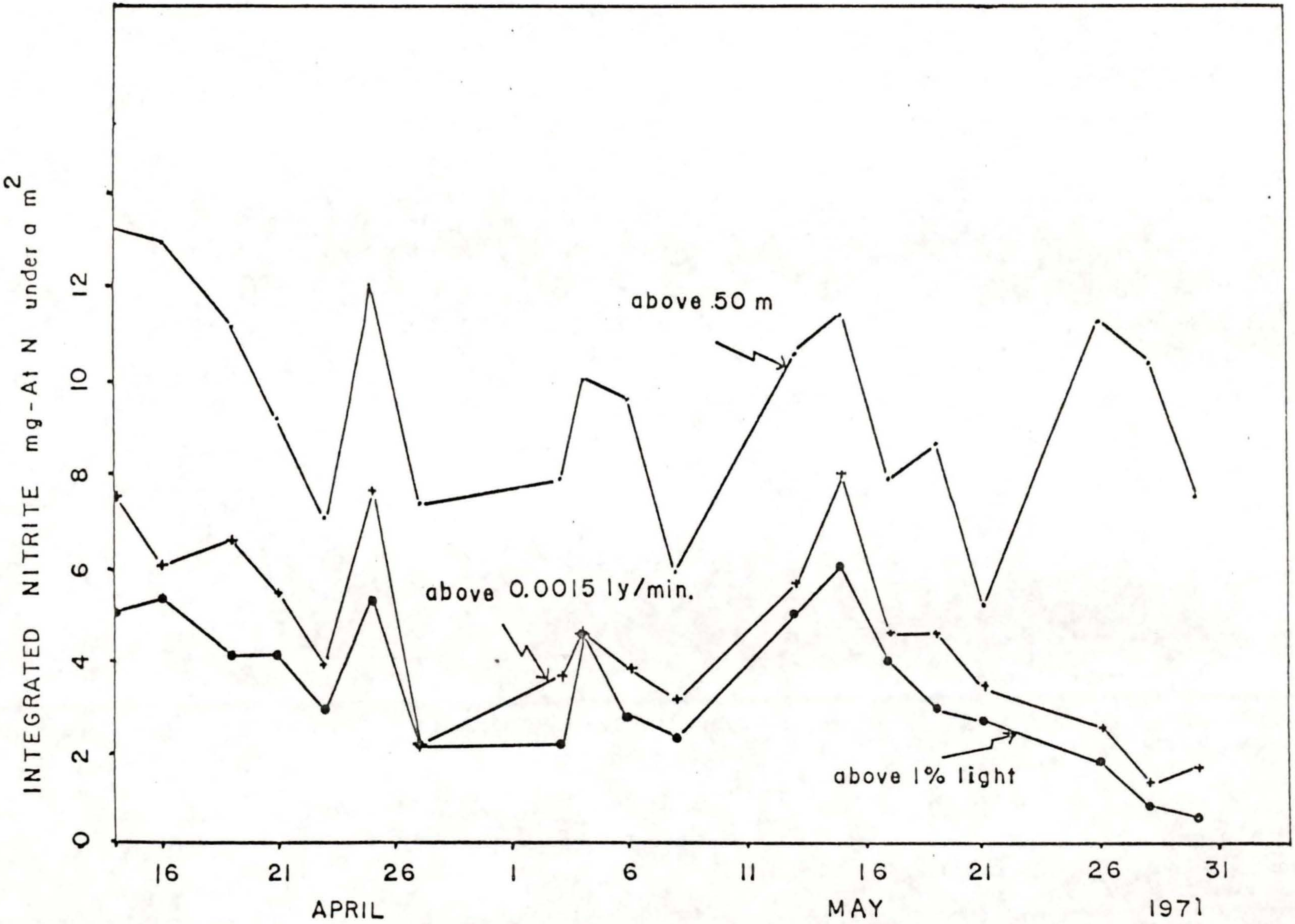
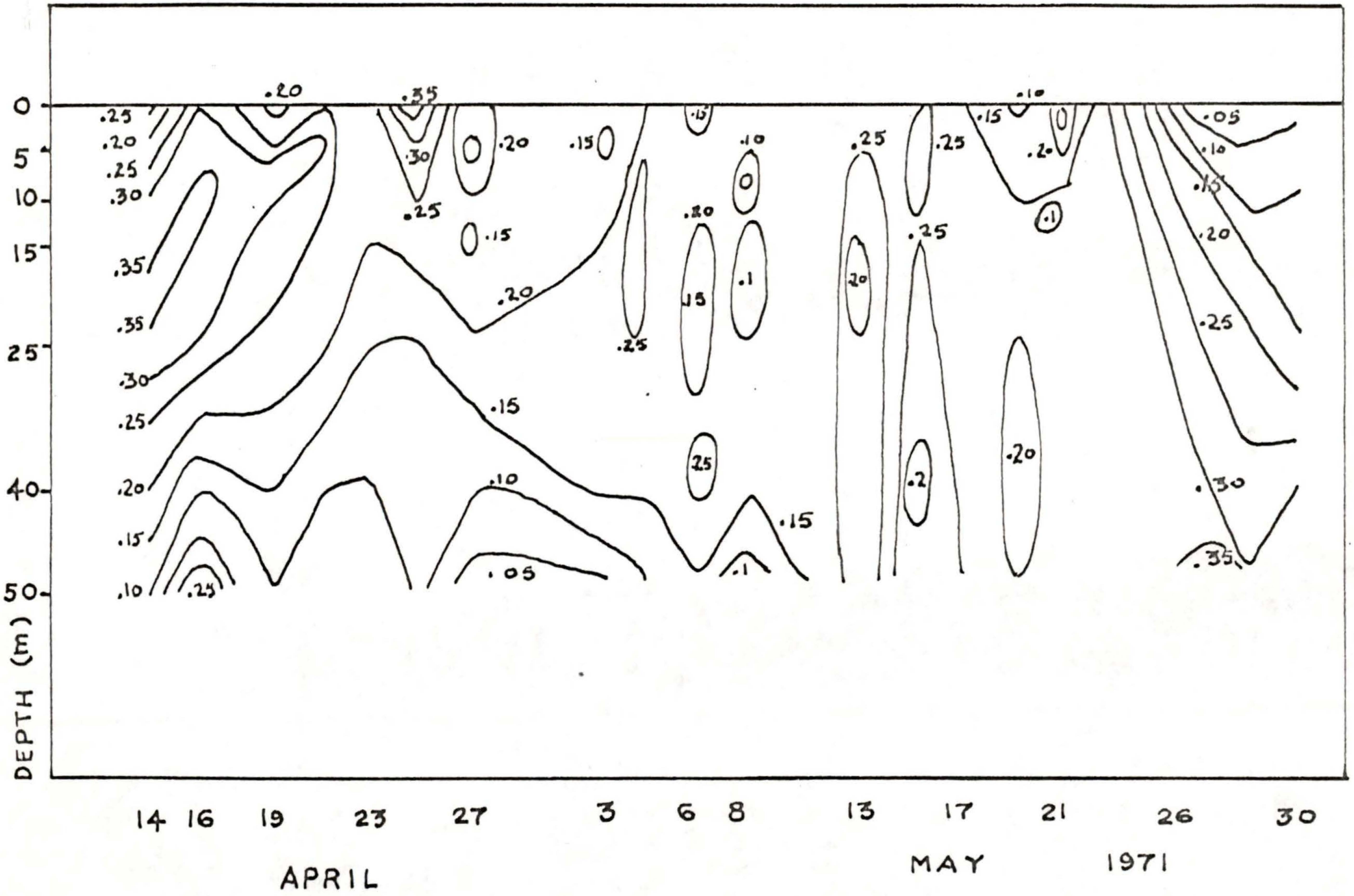

INTEGRATED NITRITE mg-At N under a m^2
0
2
4
6
8
10
12
16
21
26
1
6
11
16
21
26
31
APRIL
MAY
1971
above 50 m
above 0.0015 ly/min.
above 1% light

FIGURE 10

Fig. 11. Isopleths of nitrite, 0 to 50 m
April 14 to May 30, µg-at N-m^{-3}



0
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40
50
DEPTH (m)
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.30
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APRIL
MAY
1971

FIGURE 11

Fig. 12. Integrated ammonia above 50 m, above 0.0015 ly/min. and above 1 percent light.

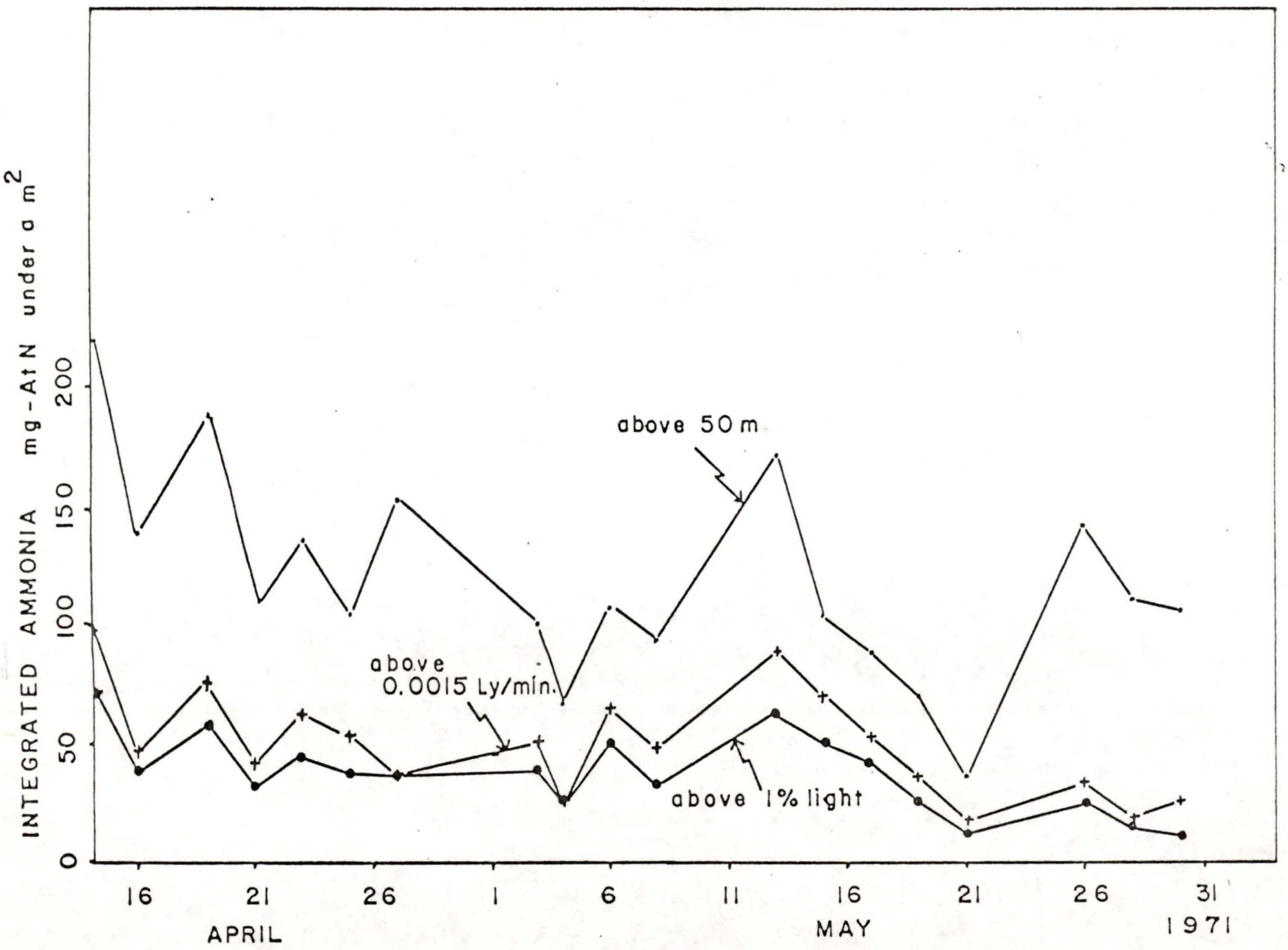

INTEGRATED AMMONIA mg-At N under a m²
0
50
100
150
200
16
21
26
1
6
11
16
21
26
31
APRIL
MAY
1971
above 50 m
above 0.0015 Ly/min.
above 1% light

FIGURE 12

The ammonia levels above the compensation depth oscillated slightly around 50 mg-at NH_3-N m^{-2} during the latter part of April and the early part of May. A sharp rise to about 80 mg-at NH_3-N m^{-2} occurred around May 13 and then dropped in a linear fashion from May 13 to May 21, the lower level varying around 20 mg-at NH_3-N m^{-2} from May 21 to May 30. Isopleths of the seasonal changes in ammonia at the different depths sampled are shown in Fig. 13.

Temporal changes in the integrated values for total nitrate, nitrite and ammonia under a square meter have been summed in Fig. 14. Above 50 m, total inorganic nitrogen dropped smoothly from approximately 1400 mg-at N m^{-2} to 950 mg-at N m^{-2} between April 16 and May 3. The level remained relatively constant at this value between May 3 and May 21, then continued to drop at an even faster rate from May 19 to 21, until a low value of 150 mg-at N m^{-2} was reached and maintained between May 26 and May 30.

Levels of total inorganic nitrogen above the compensation depth exhibit the two distinct phases also shown in each of the forms of inorganic-nitrogen analysed; the first, in late April began with nitrogen levels steady around 400 mg-at N m^{-2} for the period April 16 to 25. This was followed by a sharp drop to 100 mg-at N m^{-2} on April 27 then rose slowly to a peak near 500 mg-at N m^{-2}. In a second phase, this level dropped sharply again in the period May 21 to May 26 until a constant low level around 30 mg-at N m^{-2} was reached between May 27 and May 30.

Chemical Constitution of the Phytoplankton

Particulate organic nitrogen values, integrated under a square

Fig. 13. Isopleths of ammonia (μg-At N m^{-3})

0 to 50 m, April 14 to May 30

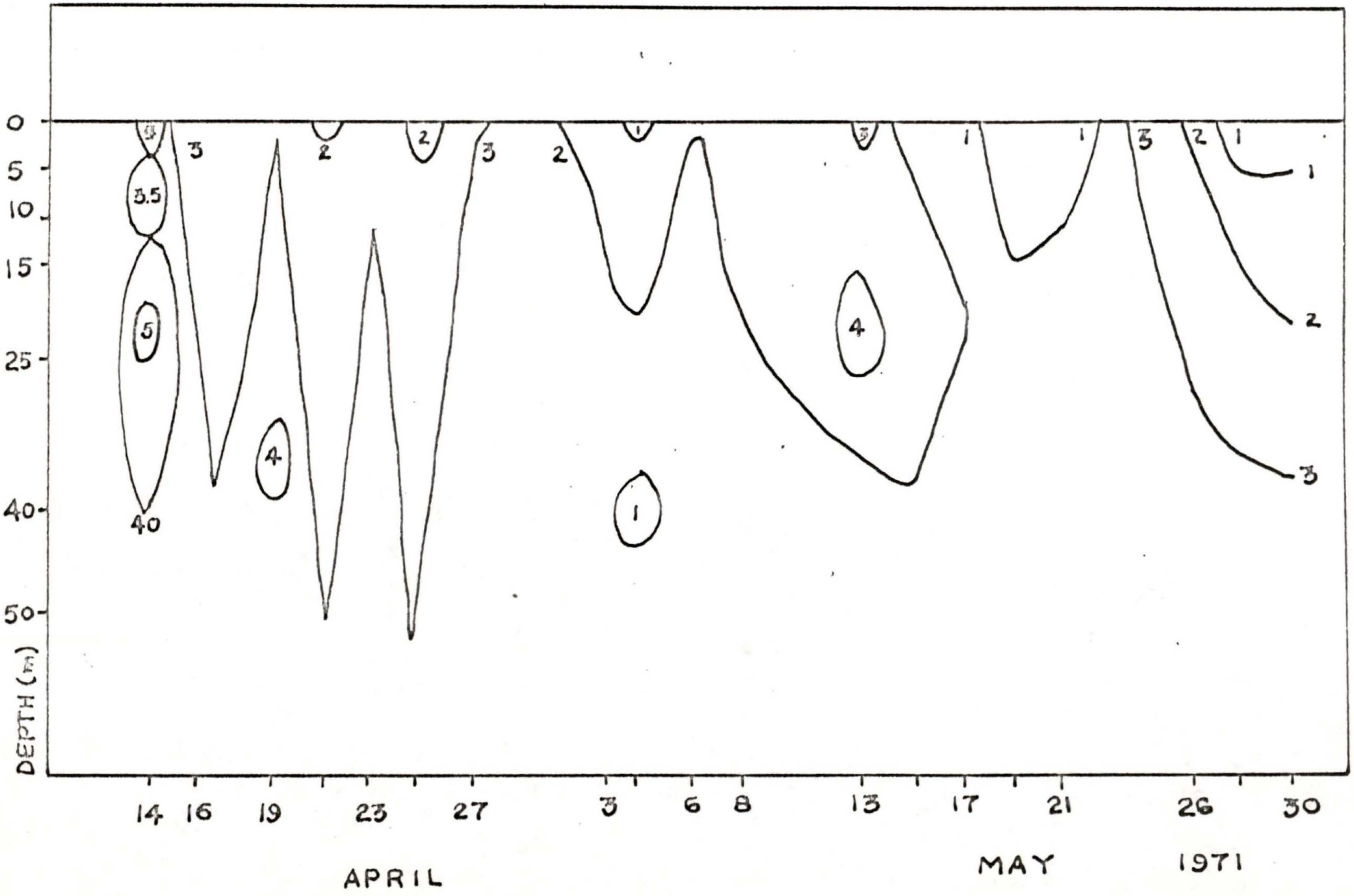

0
5
10
15
25
40
50
DEPTH (m)
14
16
19
23
27
3
6
8
13
17
21
26
30
APRIL
MAY
1971
3.5
5
40
3
4
2
2
3
2
1
1
4
3
1
1
3
2
1
1
2
3

FIGURE 41

Fig. 14. Integrated total of inorganic nitrogen sources, above 50 m, 0.0015 ly/min. and one percent light.

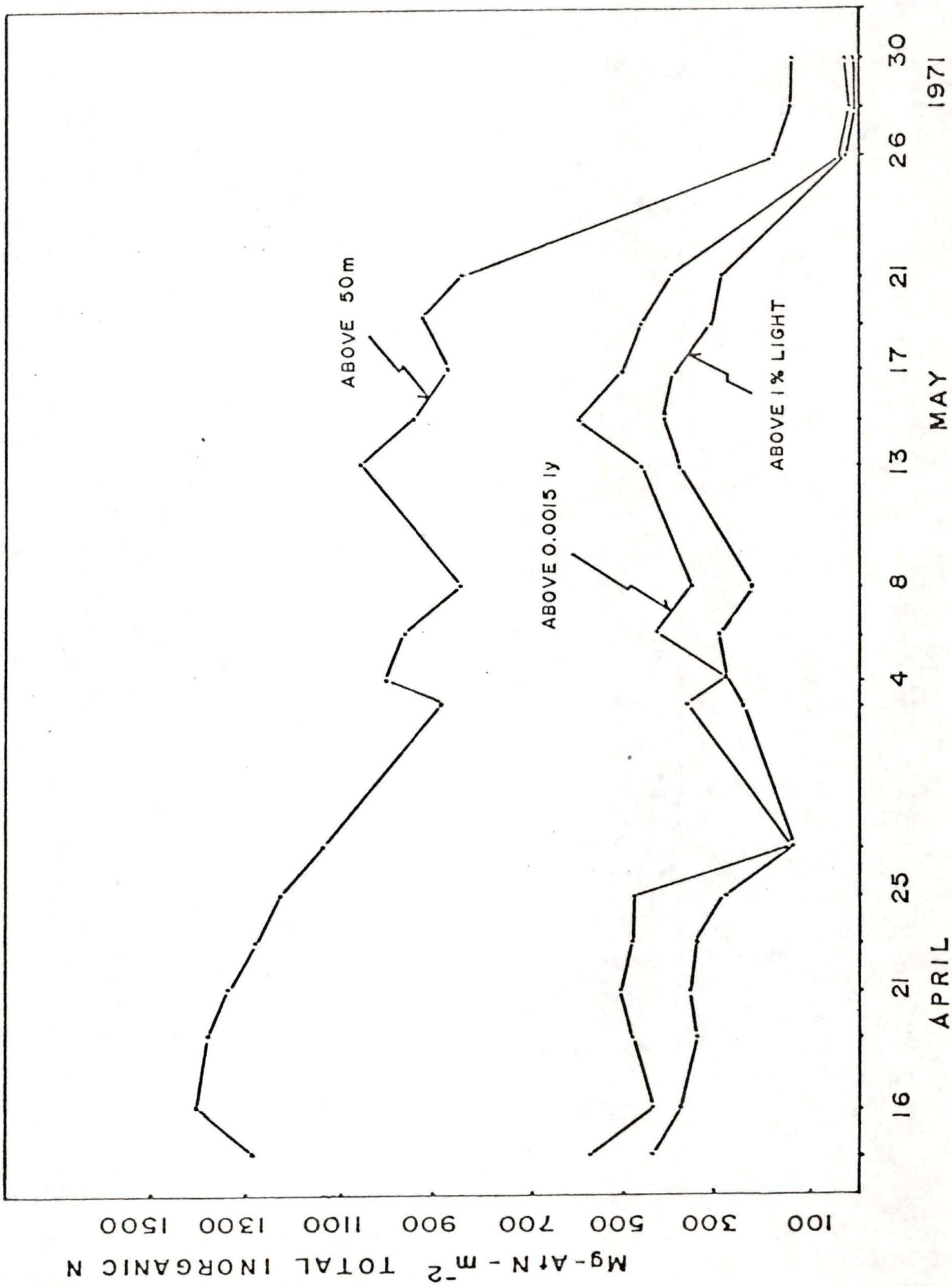


FIGURE 14

Mg-At N - m^-2 TOTAL INORGANIC N
100
300
500
700
900
1100
1300
1500
16
21
25
APRIL
4
8
13
17
21
MAY
26
30
1971
ABOVE 50m
ABOVE 0.0015 ly
ABOVE 1% LIGHT

meter between April 14 and May 30, are shown in Fig. 15. The level of particulate nitrogen observed down to the compensation depth showed the same pattern regardless of which compensation intensity was employed. Values based on 0.0015 ly/min. were generally higher, reflecting the deeper position of this compensation intensity in the water column.

Levels of particulate nitrogen rose gradually from around 60 g-at N m^{-2} on April 16 to 150 g-at N m^{-2} on April 27, coincident with a period of water column instability, already discussed, and with the termination of the April diatom increase.

Except for a single high value on May 8, particulate nitrogen levels dropped continuously from April 27 to May 19. By this date water column stability had been re-established. Levels of particulate nitrogen down to 50 m rose steadily from May 17 to May 30. Values near 460 g-at N m^{-2} were recorded on May 30.

The level of particulate nitrogen above the compensation depth showed a much less pronounced increase from May 17 to May 28. However, on May 30, in a space of two days, levels rose from 110 g-at N m^{-2} to nearly 300 g-at N m^{-2}.

Fig. 16 shows isopleths of seasonal changes in particulate nitrogen, for each of the depths sampled. From this figure it can be seen that most changes in particulate nitrogen occurred between 0 and 15 m.

The temporal pattern of particulate nitrogen levels is similar for 0, 5, 10, and 15 m. but there is some indication of a time displacement of peak levels. High levels in late April and early May occurred first at the surface between April 27 and May 3, with lower levels occurring

Fig. 15. Integrated particulate nitrogen above 50 m, 0.0015 ly/min. and one percent light.

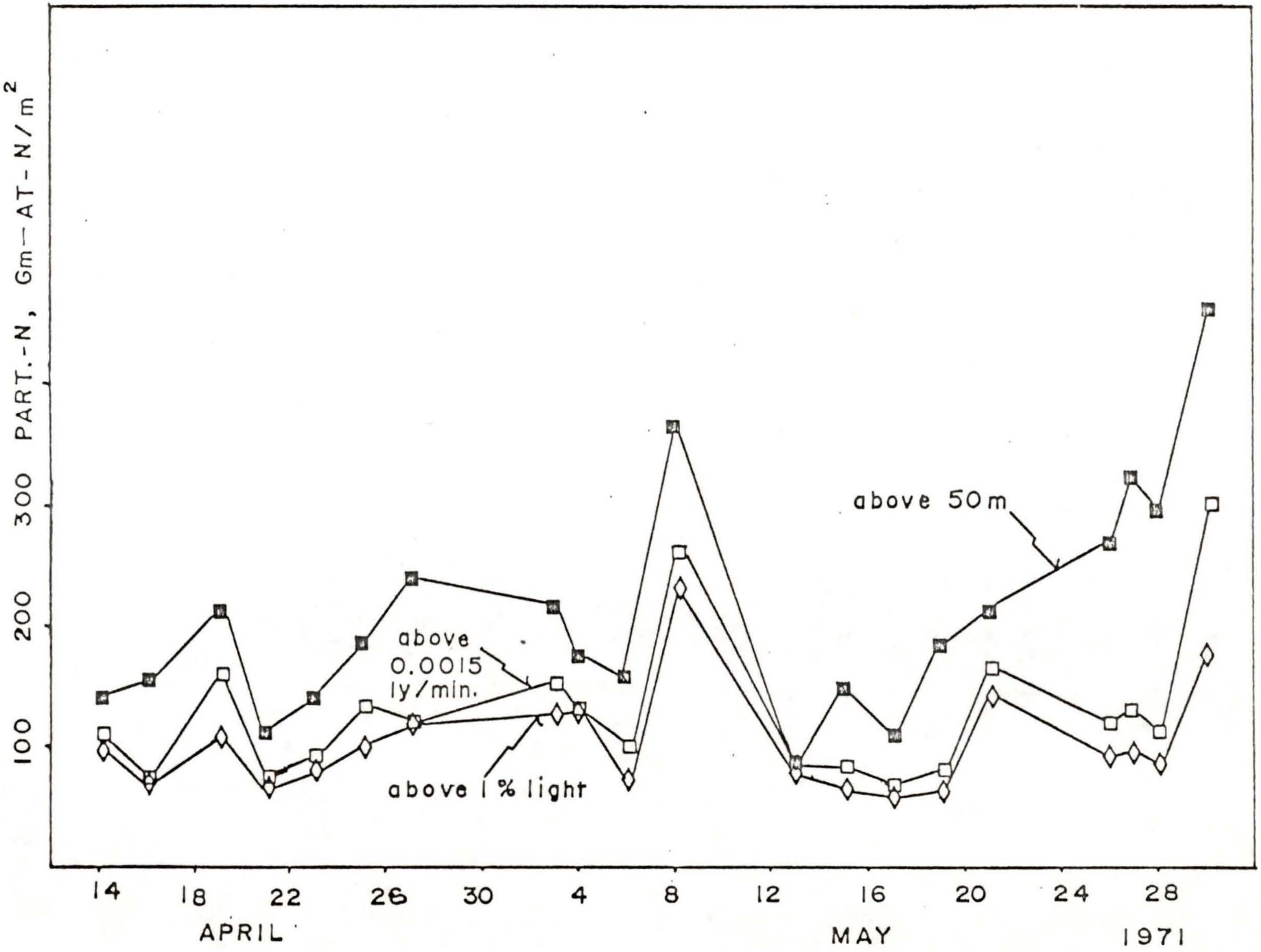

PART.-N, Gm-AT-N/m^2
100
200
300
14
18
22
26
30
4
8
12
16
20
24
28
APRIL
MAY
1971
above 50m
above 0.0015 ly/min.
above 1% light

FIGURE 15

Fig. 16. Isopleths of Particulate Nitrogen (mg/l N)
0 to 50 m, April 14 to May 30, 1971

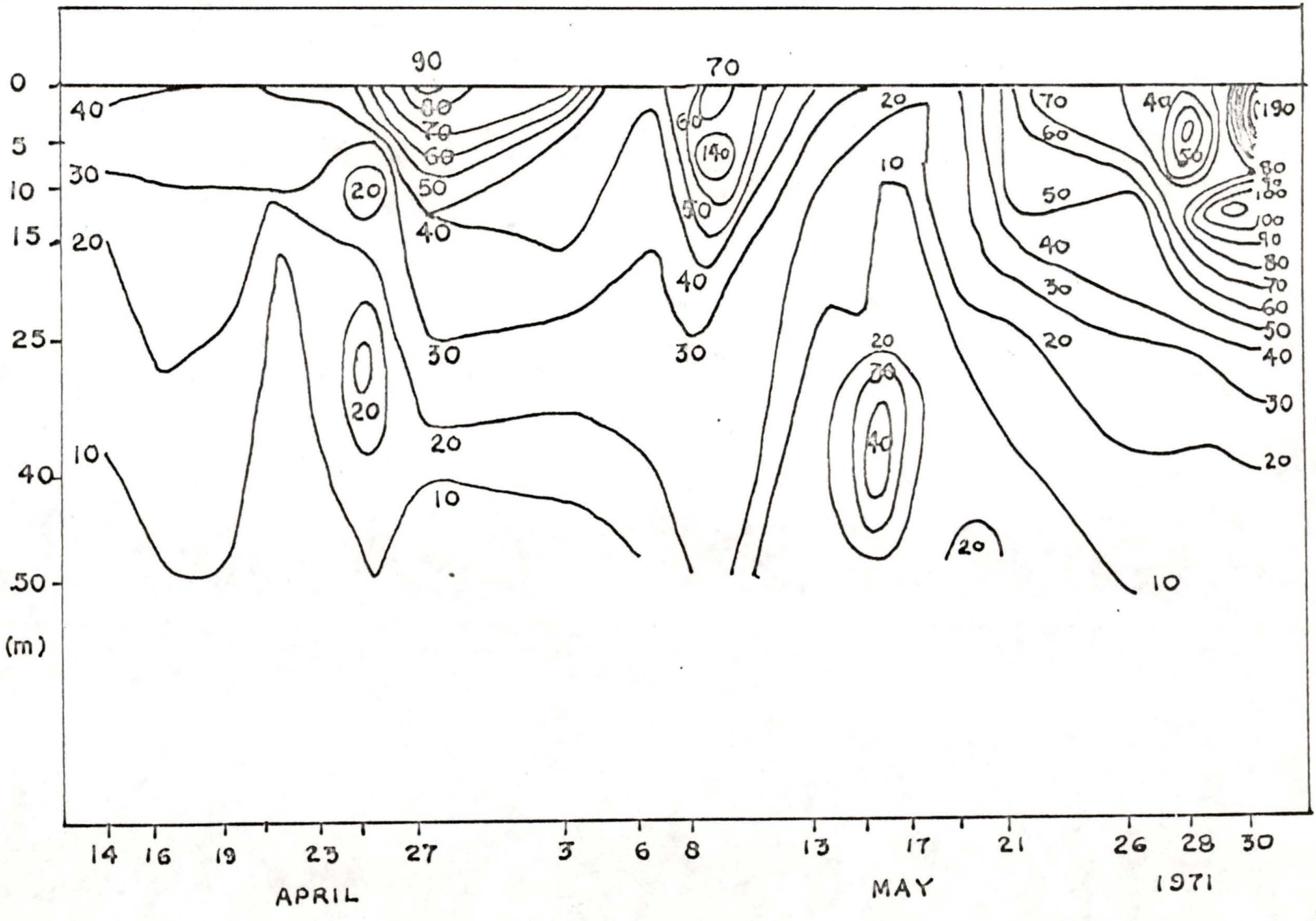

0
5
10
15
25
40
50
(m)
90
80
70
60
50
40
30
20
10
140
190
100
14
16
19
23
27
3
6
8
13
17
21
26
28
30
APRIL
MAY
1971

FIGURE 16

at 10 m and 15 m. From May 4 to 8 the particulate nitrogen maximum occurred at 10 m, the bottom of the discontinuity layer for that date. Values for particulate nitrogen subsequently dropped to a uniform low level at all depths between May 13 and May 21.

In the process of the bloom (May 19 to 30) peak values of particulate nitrogen occurred initially at 10 to 15 m, but were subsequently recorded from shallower water, at 0 and 5 m. Levels were never very high in surface waters and did not even double over the period of study.

Particulate carbohydrate levels under a square meter down to the compensation depth show only minor fluctuations (Fig. 17). A basal value of 2,000 mg m^{-2} rose to nearly 4,000 mg m^{-2} in late April and again in late May, coinciding in both cases with increases in phytoplankton standing stock. These are relatively small increases when compared to the large increase in integrated carbohydrate values observed during the period May 13 to May 19, when levels of particulate carbohydrate rose from 2,000 mg m^{-2} to 6,000 mg m^{-2}.

Isopleths of seasonal change of carbohydrates at seven depths 0 to 50 m are shown in Fig. 18. Carbohydrate maxima occur first at the surface (May 19 and 19) then deeper (5 m on May 26, 27, 28 and 30) with the higher levels of carbohydrate spreading widely through the water column. Carbohydrate minima occur primarily at 25 m. The quantity of carbohydrate at this depth was consistently about 100 mg m^{-3}. High levels of carbohydrate are experienced at this depth only in late April, a function of the non-stratified water column below 15 m. The very high levels of carbohydrate observed in the period between May 15 and May 21

Fig. 17. Integrated carbohydrate above 50 m.
0.0015 ly/min. and above one percent light.

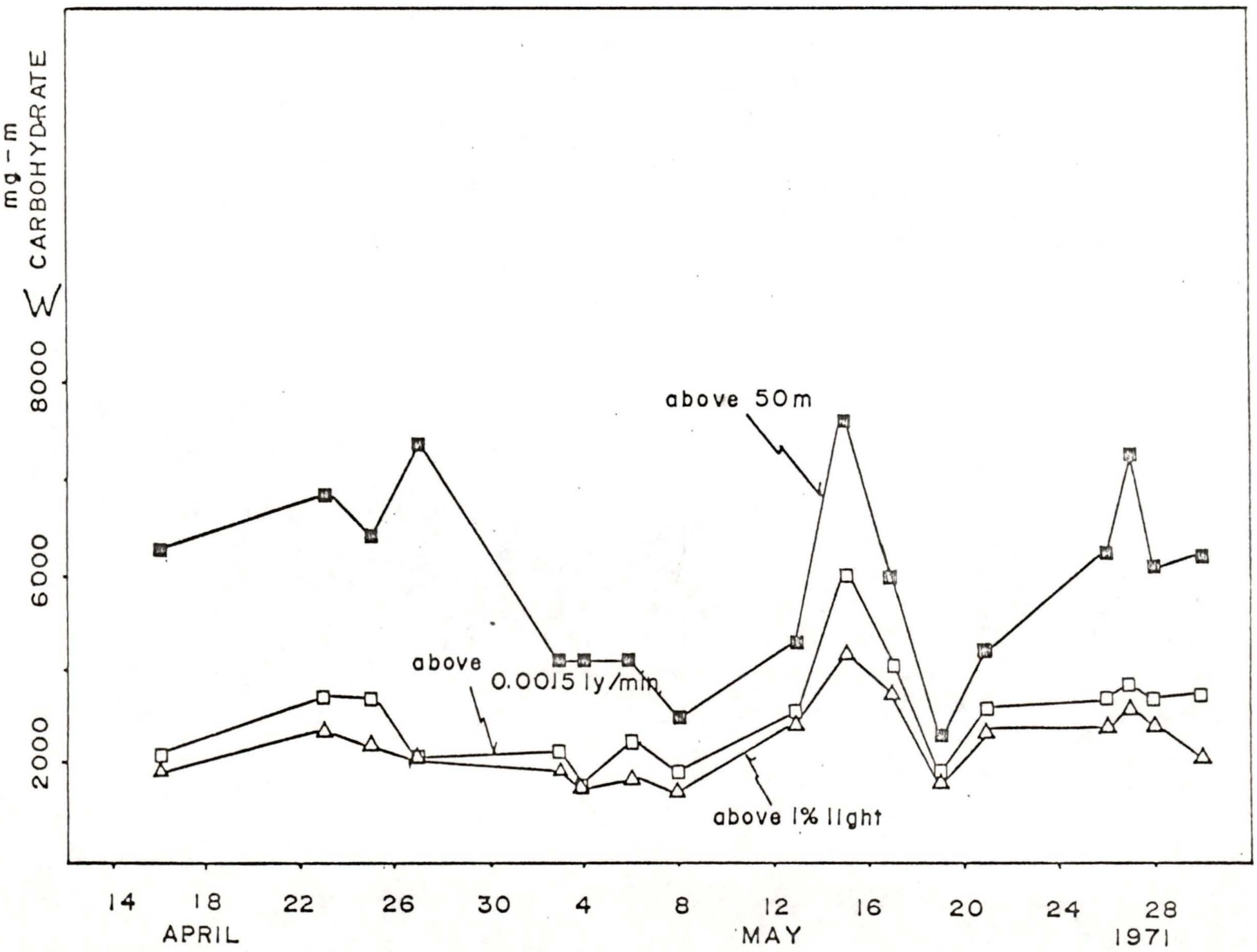

Σ mg - m^{-2} CARBOHYDRATE
8000
6000
2000
above 50m
above 0.0015 ly/min
above 1% light
14
18
22
26
30
4
8
12
16
20
24
28
APRIL
MAY
1971

FIGURE 17

Fig. 18. Isopleths of particulate carbohydrate (mg glucose m^{-3}), 0 to 50 m, April 14 to 30.

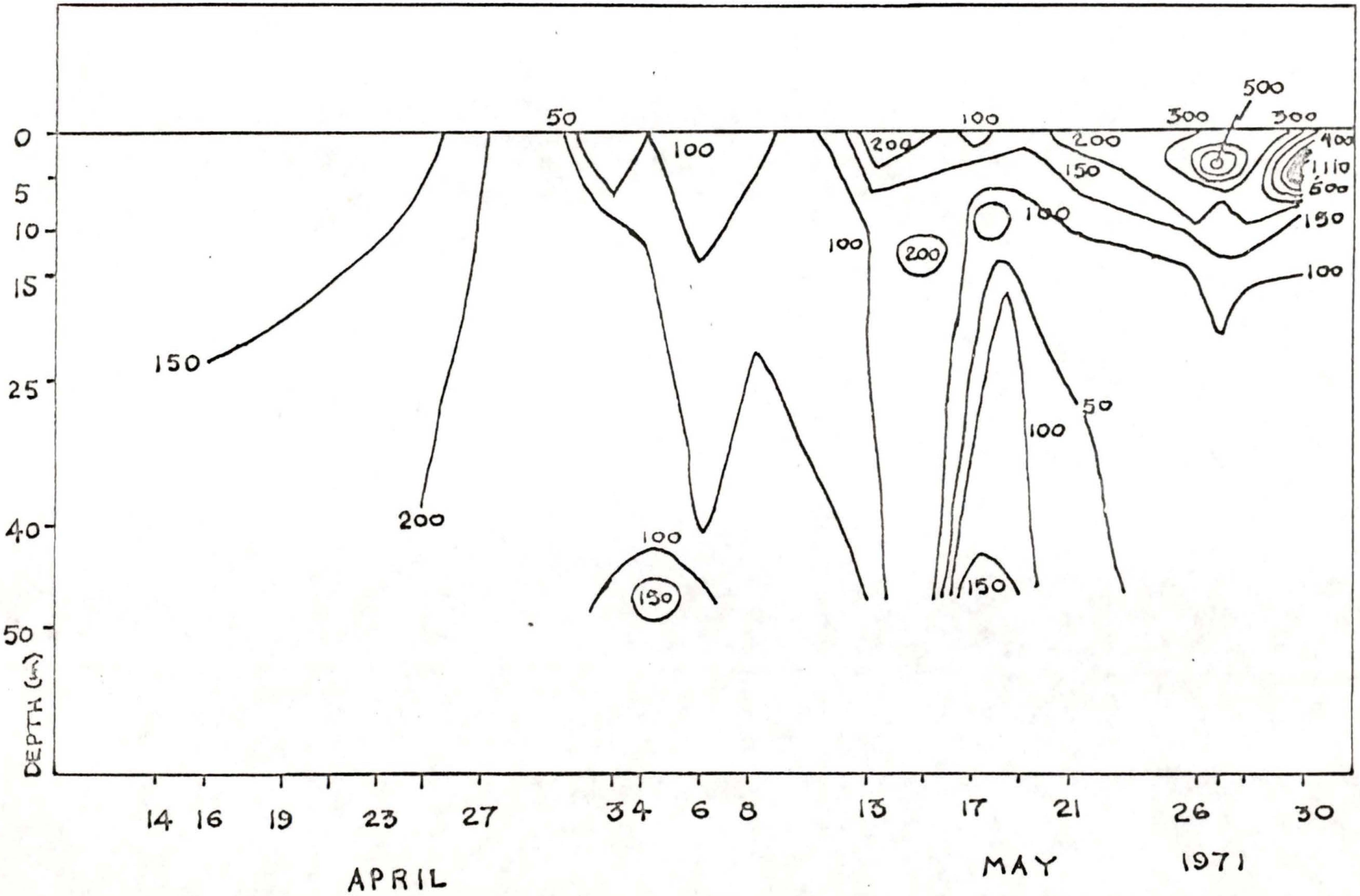

0
5
10
15
25
40
50
DEPTH (m)
14 16 19 23 27 3 4 6 8 13 17 21 26 30
APRIL
MAY
1971
150
200
50
100
100
150
100
200
200
100
100
50
100
150
100
200
300
500
300
400
1110
600
200
150
150
150
100
100

FIGURE 18

show no maxima in their depth distribution but are uniformly high throughout the water column to 50 m.

Phytoplankton Pigments

Chlorophyll-a levels were measured for all seven depths during the study period. These readings were corrected for phaeopigments and both values were recorded. Chlorophyll-a levels are recorded as isopleths in Fig. 19, while isopleths of phaeopigment are illustrated in Fig. 20.

Integrated values of chlorophyll-a below a square meter to 0.0015 ly/min., to one percent surface light, and to 50 m depth are shown in Figs. 21 to 23. From these figures it can be seen that chlorophyll-a increased in two separate pulses during the period of study. These two increases, the first in late April and the second in late May, were separated by a long period when little or no chlorophyll-a could be detected in the filtered material collected.

Phaeopigment levels (Figs. 24 to 26) rose markedly during this period of depressed chlorophyll-a. Phaeopigment to chlorophyll-a ratios (Fig. 27) increased by a factor of 5 during this period reaching their highest levels between May 4 and 6. Values for this ratio are also much higher below the compensation depth than above it.

Despite the greatly increased value of phaeopigment to chlorophyll-a ratios, actual levels of phaeopigments show little variation with depth through early and mid-May, remaining in the region of 0.4 to 0.6 mg m^{-3}. Chlorophyll-a levels, however, drop to non-detectable amounts resulting in an increased phaeopigment to chlorophyll-a ratio.

Low chlorophyll-a levels continued until May 19 when values began to rise to the spring bloom quantities. Phaeopigment levels began to

Fig. 19.. Isopleths of Chlorophyll-a

0 to 50 m, April 14 to May 30

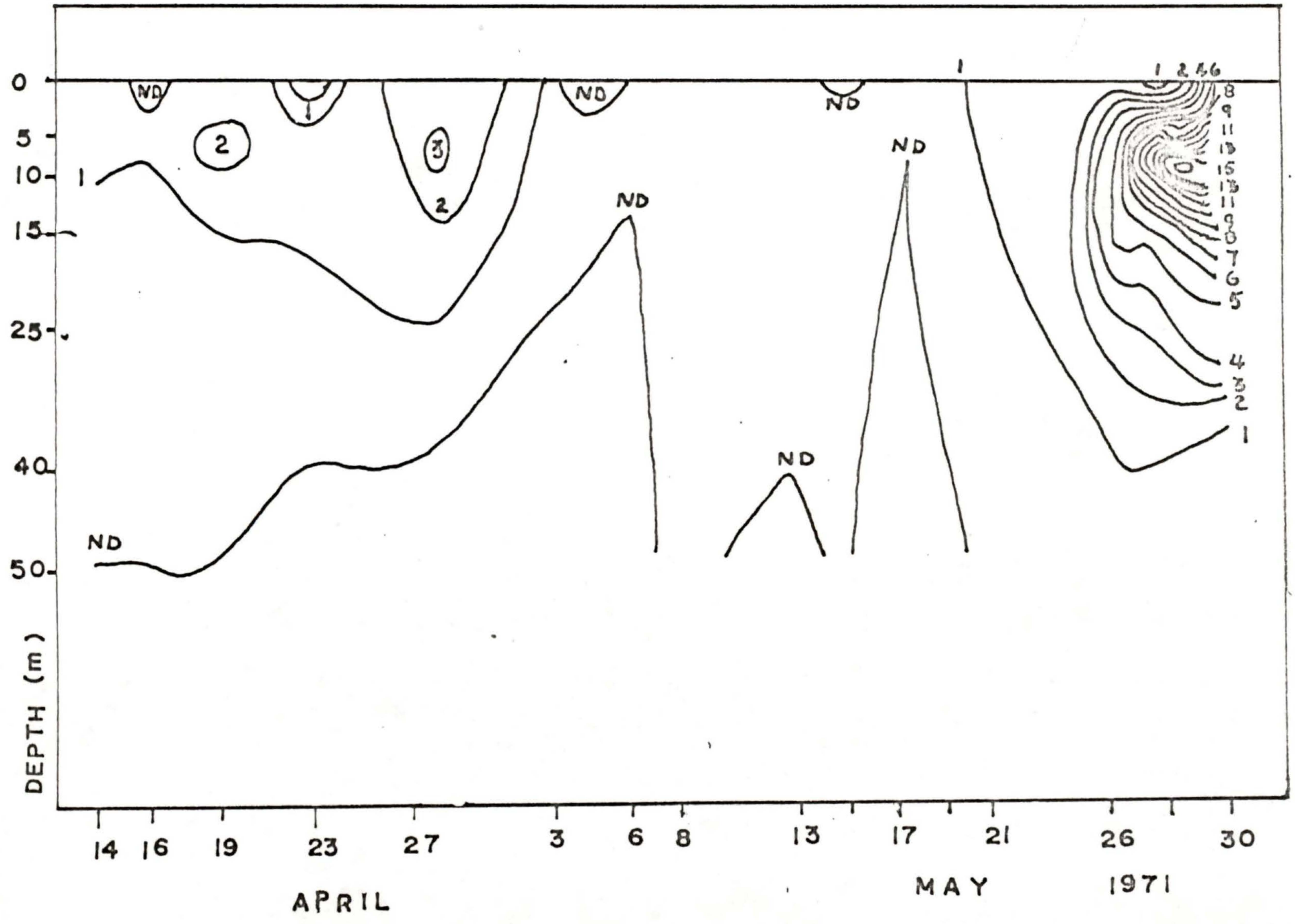

0
5
10
15
25
40
50
DEPTH (m)
ND
2
3
2
1
ND
ND
ND
ND
ND
ND
1
1 2 4 6
8
9
11
13
15
13
11
9
8
7
6
5
4
3
2
1
14
16
19
23
27
3
6
8
13
17
21
26
30
APRIL
MAY
1971

FIGURE 19

Fig. 20. Isopleths of phaeopigments, 0 to 50 m, April 14 to May 30.

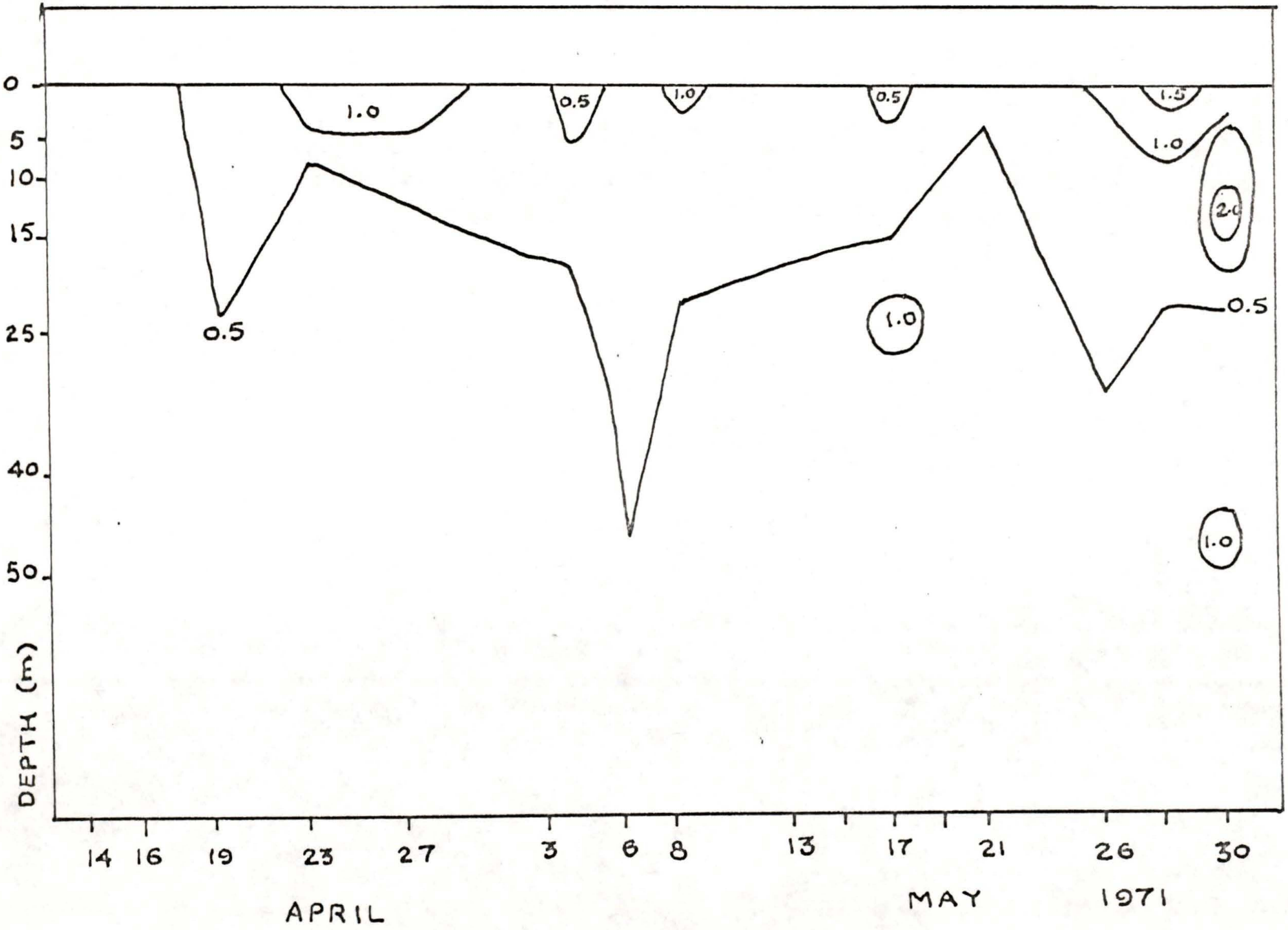

0
5
10
15
25
40
50
DEPTH (m)
0.5
1.0
0.5
1.0
0.5
1.0
1.5
1.0
2.0
0.5
1.0
14
16
19
23
27
3
6
8
13
17
21
26
30
APRIL
MAY
1971

FIGURE 20

Fig. 21. Integrated chlorophyll-a, carotenoids, and phaeopigments down to 50m.

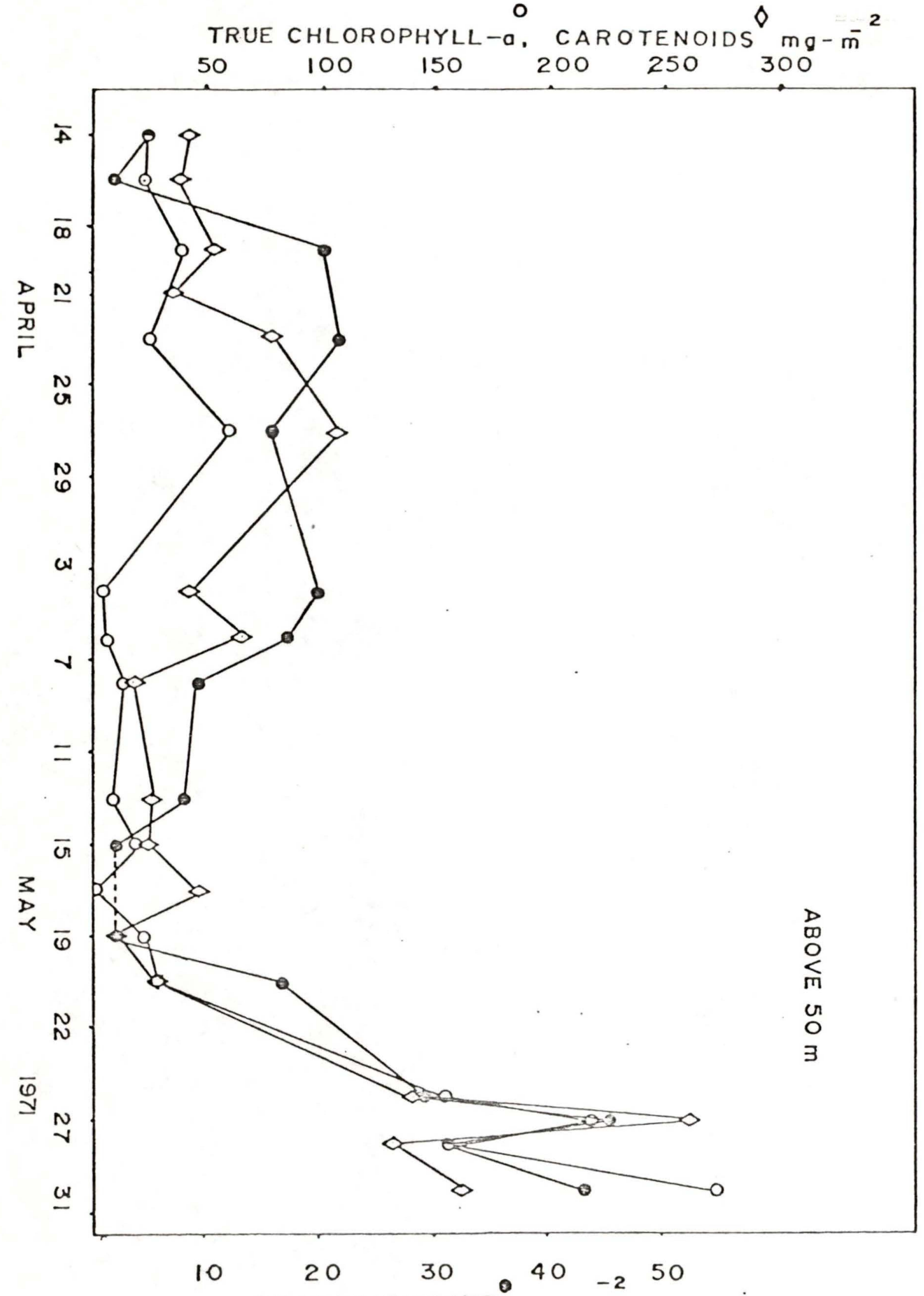

TRUE CHLOROPHYLL-a, CARBOTENOIDS mg-m⁻²
50
100
150
200
250
300
14
18
21
25
29
3
7
11
15
19
22
27
31
APRIL
MAY
1971
ABOVE 50 m
10
20
30
40
50
PHAEOPIGMENTS mg-m⁻²

FIGURE 21

Fig. 22. Integrated chlorophyll-a, carotenoids and phaeopigment above 0.0015 ly/min.

FIGURE 22

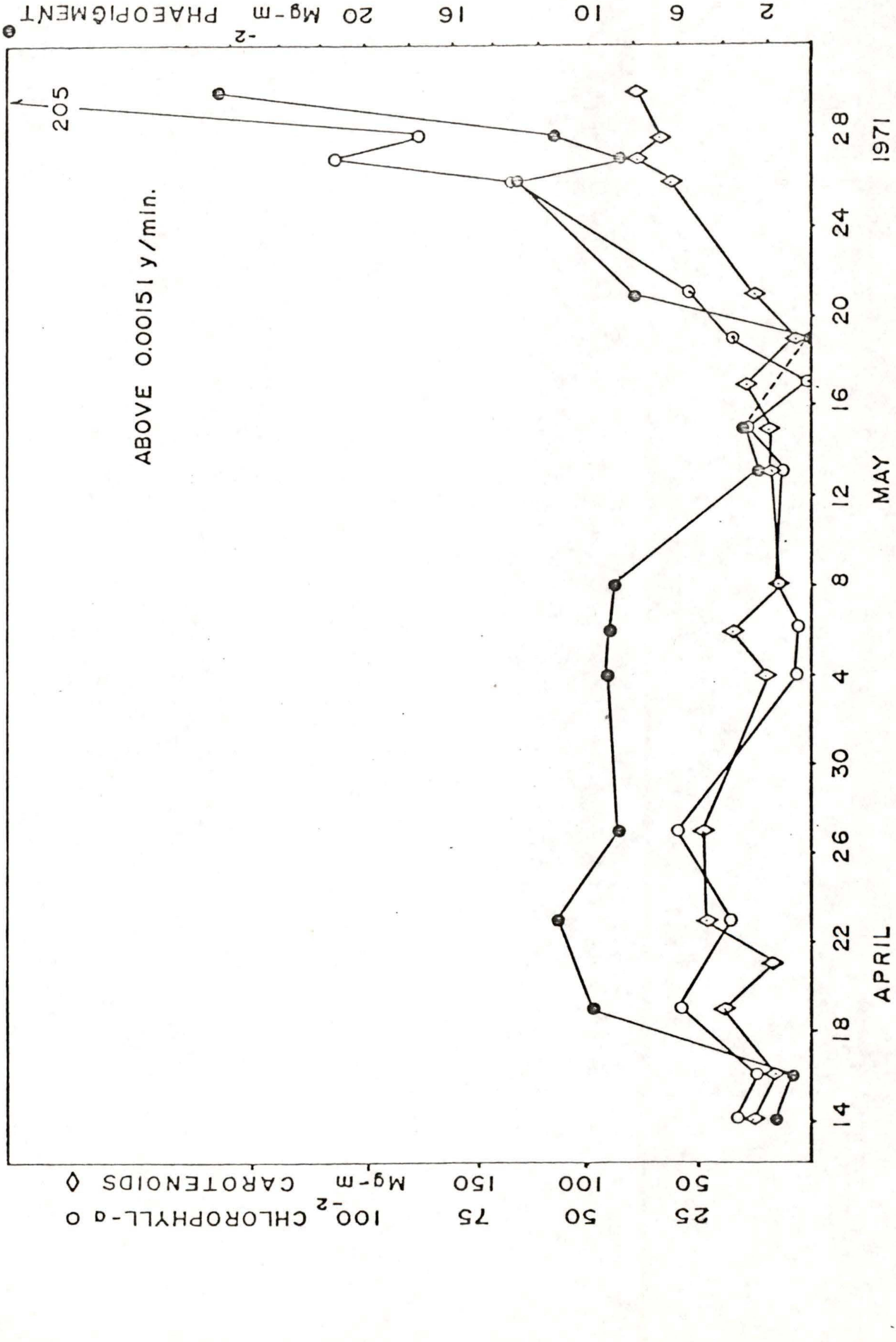

ABOVE 0.00151 y/min.
205
14
18
22
26
30
4
8
12
16
20
24
28
APRIL
MAY
1971
25
50
75
100 Mg-m⁻² CHLOROPHYLL-a ○
50
100
150
Mg-m⁻² CAROTENOIDS ◊
2
6
10
16
20 Mg-m⁻² PHAEOPIGMENT ●

Fig. 23. Integrated chlorophyll-a, carotenoids and phaeopigment above one percent light.

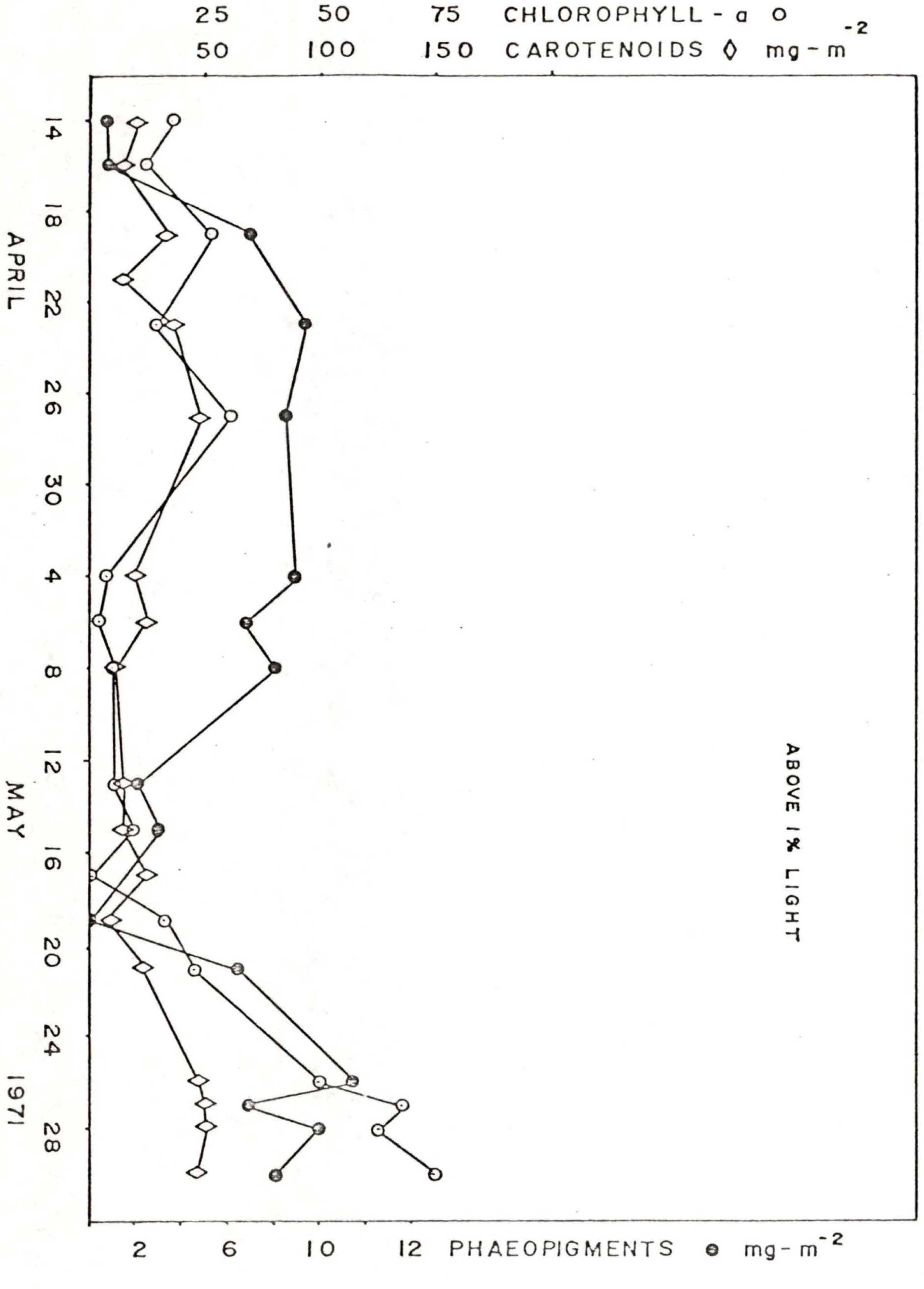

25 50 75 CHLOROPHYLL - a ○
50 100 150 CAROTENOIDS ◊ mg - m^{-2}
14
18
22
26
30
4
8
12
16
20
24
28
APRIL
MAY
1971
ABOVE 1% LIGHT
2 6 10 12 PHAEOPIGMENTS ● mg - m^{-2}

Fig. 24. Regression of chlorophyll-a against particulate nitrogen, above 50 m.

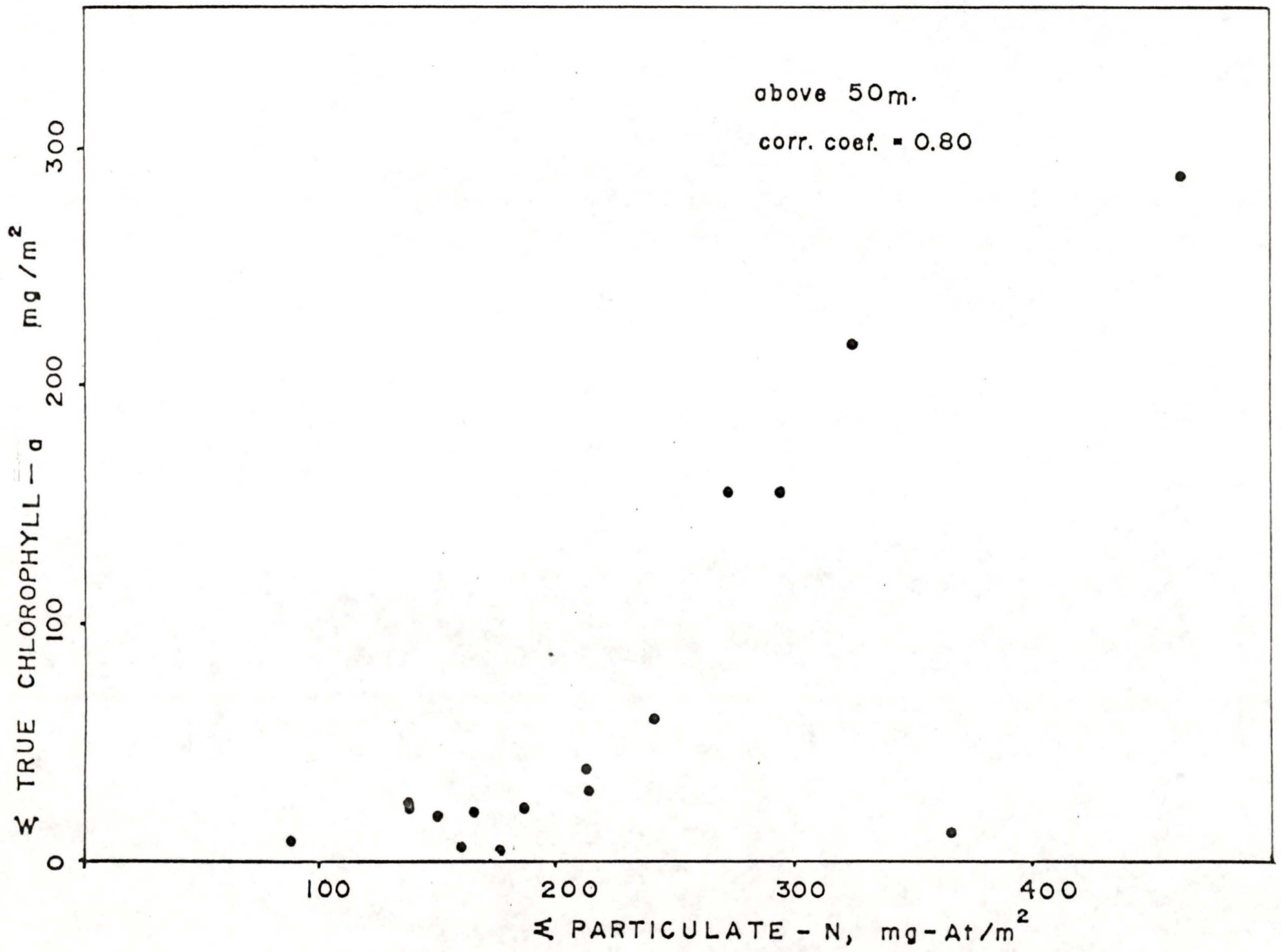
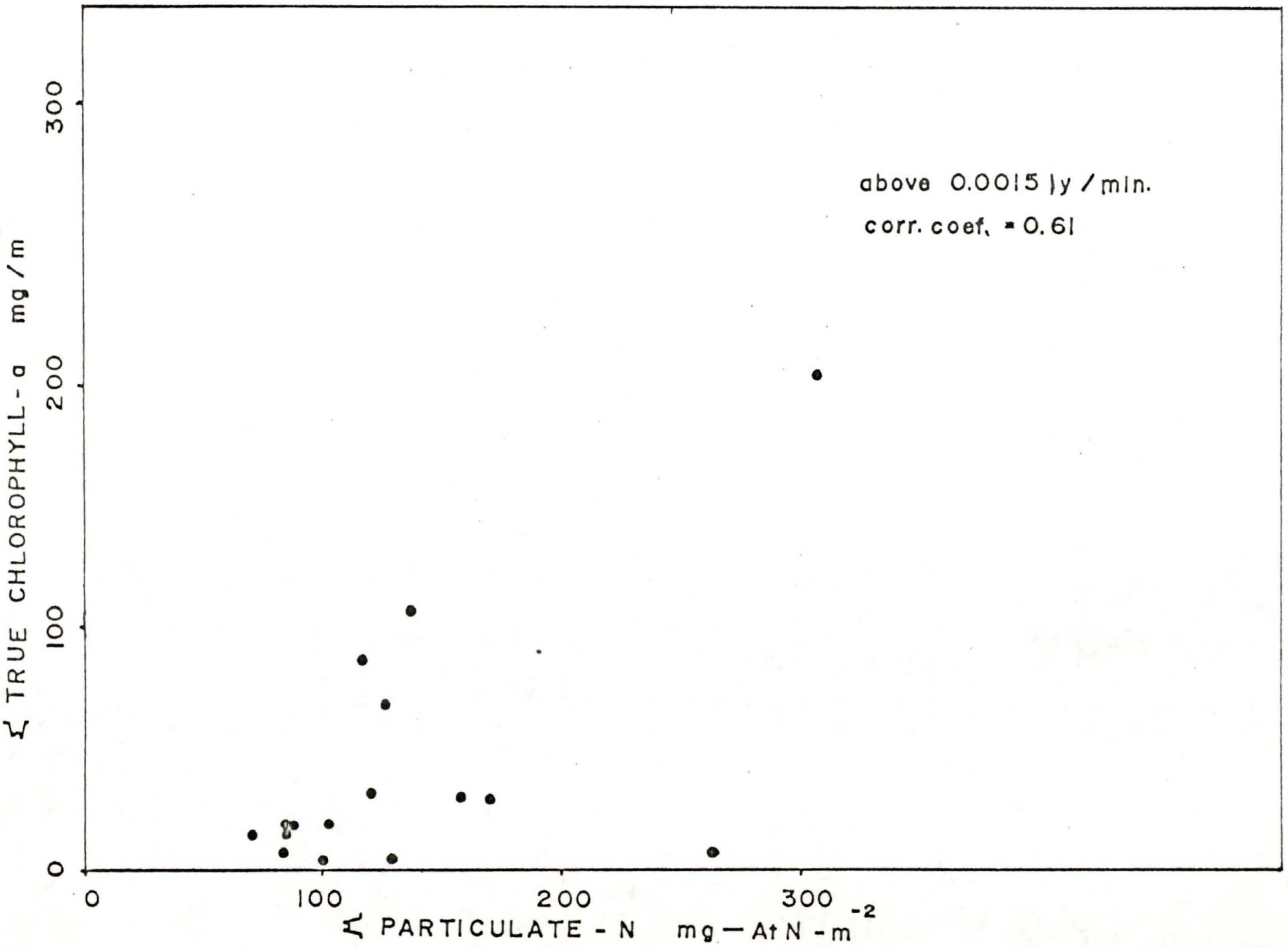

above 50m.
corr. coef. = 0.80
Σ TRUE CHLOROPHYLL — a mg/m²
0
100
200
300
Σ PARTICULATE – N, mg-At/m²
100
200
300
400

FIGURE 24

Fig. 25. Regression of chlorophyll-a against particulate nitrogen, above 0.0015 ly/min.



above 0.0015 ly / min.
corr. coef. = 0.61
Σ TRUE CHLOROPHYLL - a mg / m²
Σ PARTICULATE - N mg — At N - m⁻²
0
100
200
300
0
100
200
300

FIGURE 25

Fig. 26. Regression of chlorophyll-a against particulate nitrogen, above one percent light.

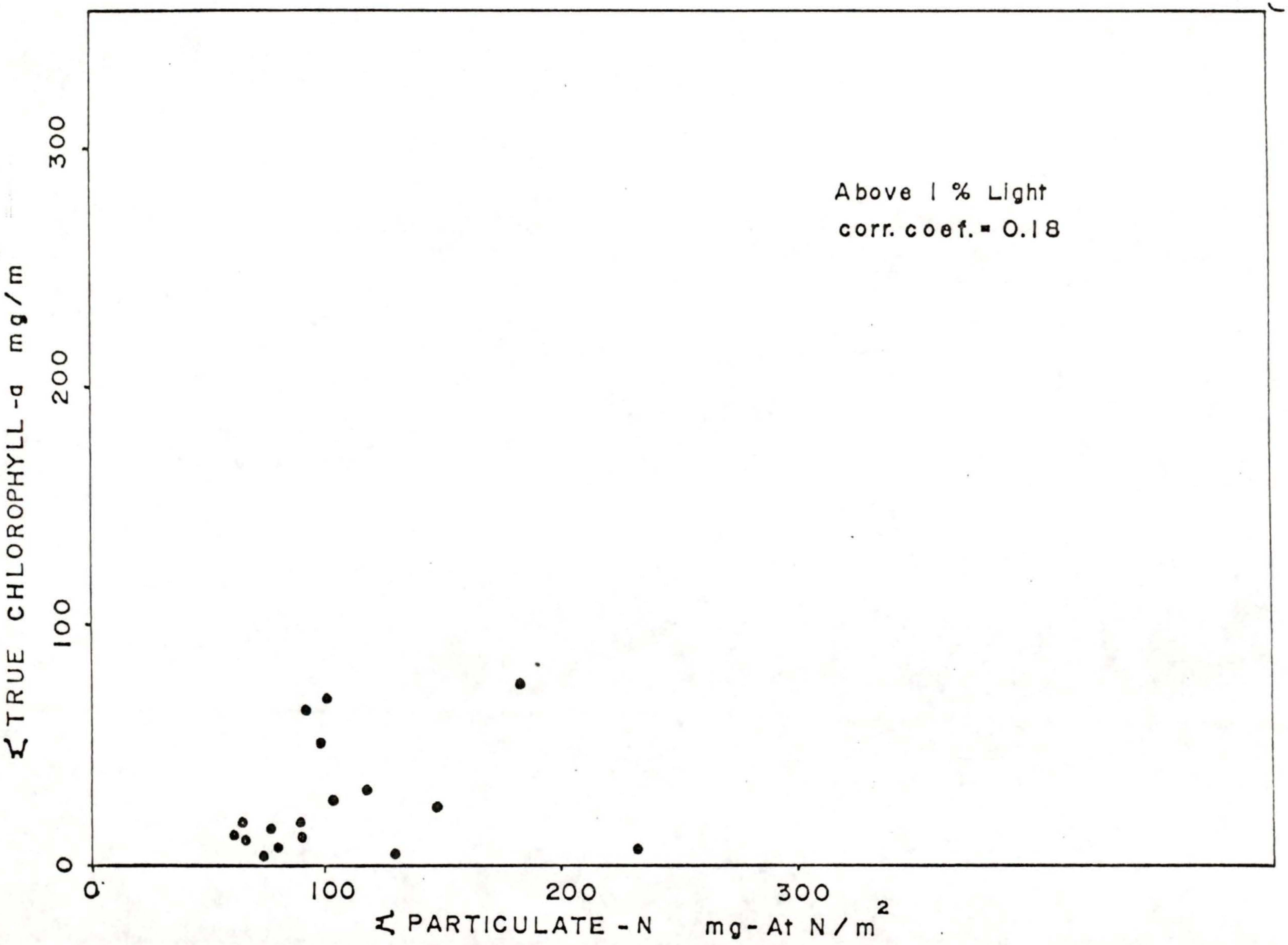

Above 1 % Light
corr. coef. = 0.18
Σ TRUE CHLOROPHYLL -a mg/m^2
0
100
200
300
Σ PARTICULATE - N mg-At N/m^2
0
100
200
300

FIGURE 26

Fig. 27. Temporal change in the ratio of integrated phaeopigments to integrated Chlorophyll-a, April 14 to May 30.

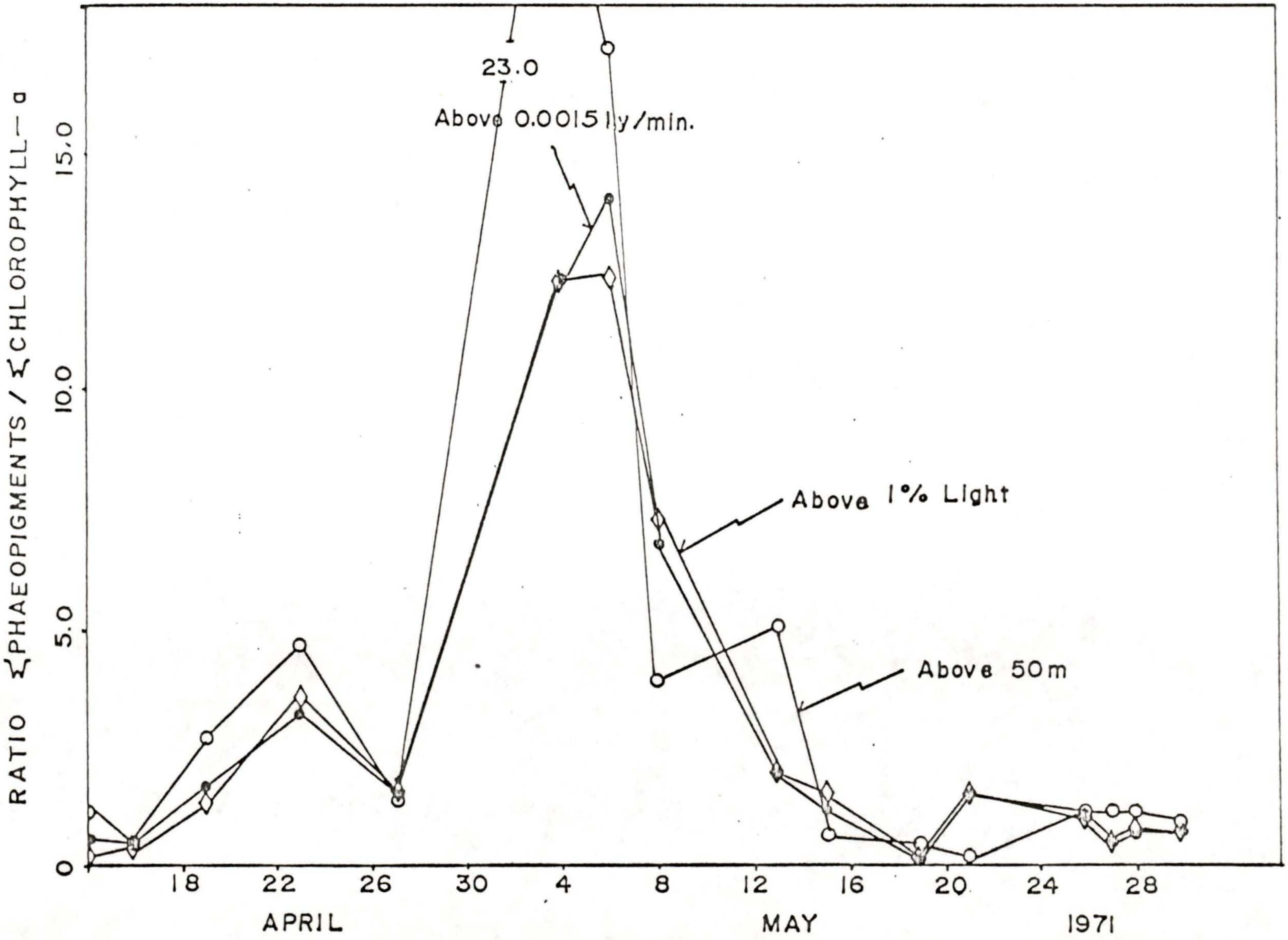

RATIO ΣPHAEOPIGMENTS / ΣCHLOROPHYLL— a
0
5.0
10.0
15.0
23.0
Above 0.0015 ly/min.
Above 1% Light
Above 50m
18
22
26
30
4
8
12
16
20
24
28
APRIL
MAY
1971

FIGURE 27

rise at this stage as well but not as strongly as chlorophyll-a. As a result, the ratio of phaeopigment to chlorophyll-a drops to its lowest level (around 0.05 as opposed to a maximum of 23.0) through the final part of May. During this final period, phaeopigment levels were about ten percent of chlorophyll-a and range from nondetectable to 1.5 mg m^{-3}, with higher levels occurring in the period April 25 to May 26. Phaeopigment levels began to rise earlier than chlorophyll-a as the bloom was initiated, with noticeable increases in phaeopigment starting on May 26.

The depth of the chlorophyll-a maximum (Fig. 5) varied throughout the study period although it never fell below 15 m. In the beginning of April, during the first upsurge in phytoplankton crop, the depth of the chlorophyll-a maximum was constant at 5 m. It descended to 15 m on April 23 when the highest chlorophyll-a levels for the period were recorded. During the latter period, levels of chlorophyll-a approached zero and no real maxima were observable. However, when chlorophyll-a levels began to rise again in the middle of May the depth of the chlorophyll-a maximum returned to 5 m. The depth of this maximum subsequently increased to 12 m as phytoplankton levels rose in the bloom conditions of late May.

Carotenoid maxima generally coincided with chlorophyll-a maxima but carotenoids were more often high throughout a larger part of the water column, especially in deeper water. Integrated carotenoid levels remained between 25 and 50 mg m^{-2} above the compensation depth, following a pattern similar to that of chlorophyll-a but not increasing as quickly nor rising so high as the latter when the bloom was initiated.

Integrated carotenoid levels above 50 m were as high or higher than chlorophyll-a and show a pronounced bimodal pattern throughout the study period. The two peaks coincided with the mid to late April and the late May chlorophyll-a increases.

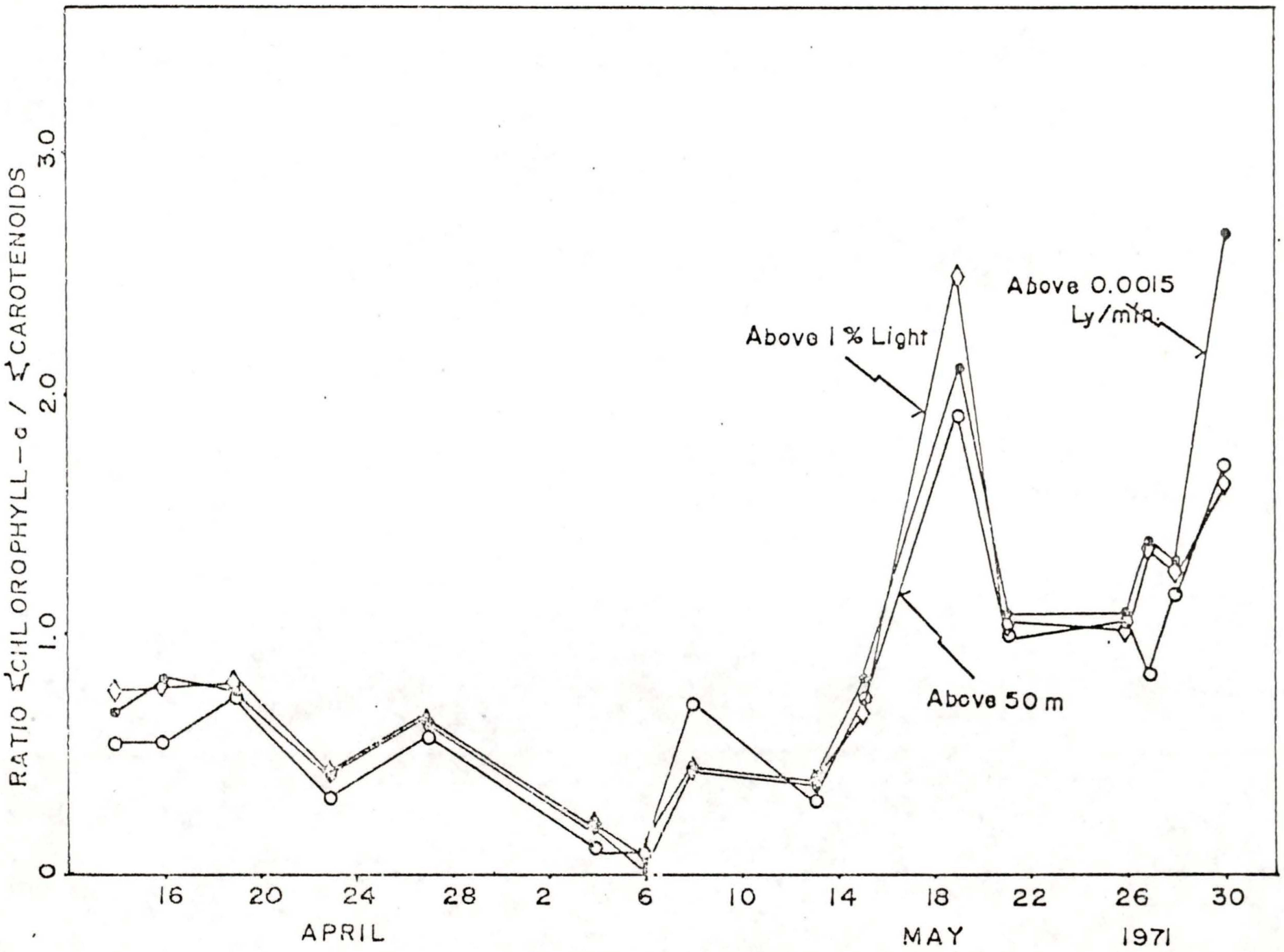
Temporal changes in the integrated chlorophyll-a to carotenoid ratios (Fig. 28) followed a similar bimodal curve and were almost the same magnitude above the compensation depth as above 50 m. This ratio was between 0.6 and 0.8 in mid-April but dropped steadily thereafter to a low value of 0.05 on May 6. It began to rise again on May 15 in response to a prolonged sunny period in the weather, dropped to 1.0 between May 19 and May 26 as the final bloom was initiated, and finally rose sharply in the last part of May to levels near 2.8.

The Process of the Bloom

As chlorophyll-a levels begin to rise towards the end of May, a closer look at species composition and abundance became necessary. Cleared and mounted Millipore ™ filter preparations were employed for all identifications and counts. While this method damages small flagellates beyond identification, it is ideal for the routine identification and counting of planktonic diatoms, and is acceptable for other heavy-walled phytoplankton.

The diatom population was very sparse on May 19, the first day of noticable chlorophyll-a increases. It was composed chiefly of *Coscinodiscus* spp, *C. excentricus* Ehren. *Tabellaria* spp. and *Melosira* spp.. However, on May 21 the species composition began to change and very few of the

Fig. 28. Temporal change in the ratio of integrated chlorophyll-a to integrated carotenoids.



RATIO Σ CHLOROPHYLL – a / Σ CAROTENOIDS
3.0
2.0
1.0
0
16
20
24
28
2
6
10
14
18
22
26
30
APRIL
MAY
1971
Above 1 % Light
Above 0.0015 Ly/min.
Above 50 m

FIGURE 28

earlier components were to be found. *Thalassiosira rotula* Meunier, *Chaetoceros radicans* Schutt and *C. didymus* Ehren., were the three obvious co-dominants although in terms of volume, *T. rotula* far exceeded the other two species. The number of *T. rotula* cells increased from nil on May 19 to 5.3 x 10^6 cells per meter^3 on May 30. The bloom seems to have begun at 0 m (May 26) but later maxima occur between 10 and 15 m. (See Table 10).

The integrated values of *T. rotula* biomass are expressed in terms of carbon calculated from volume measured using the equation from Antia *et al.* (1968):

$$\log C = 0.758 \log V - 0.422$$

C = carbon/cell picograms

V = cell vol. in μ^3

There were 75.6 g C m^{-2} on May 26, 468.5 on May 27, 25.2 on May 28 and 362.2 on May 30 (Table 10). The depth distribution of *T. rotula* cell carbon approximates a semi-logarithmic distribution (Fig. 29), the highest value occurring at the surface. The population showed signs of sinking on May 27, with low values at the surface, increasing steadily to 10 m and then decreasing to 25 m. Levels were constant to 50 m. By May 28 the population maximum has sunk to 15 m, but levels near the surface had begun to increase due in part to increased wind mixing in the surface waters down to 10 m and a subsequent more homogeneous distribution of cells through to this depth.

Several other species phytoplankton began to appear around the 28 May, notably *Ditylum brightwellii* (West) Gran, *Coscinodiscus excentricus*

Table 10. Cell counts and estimated cell carbon for the dominant diatoms of the May diatom increase, May 26 to May 30.

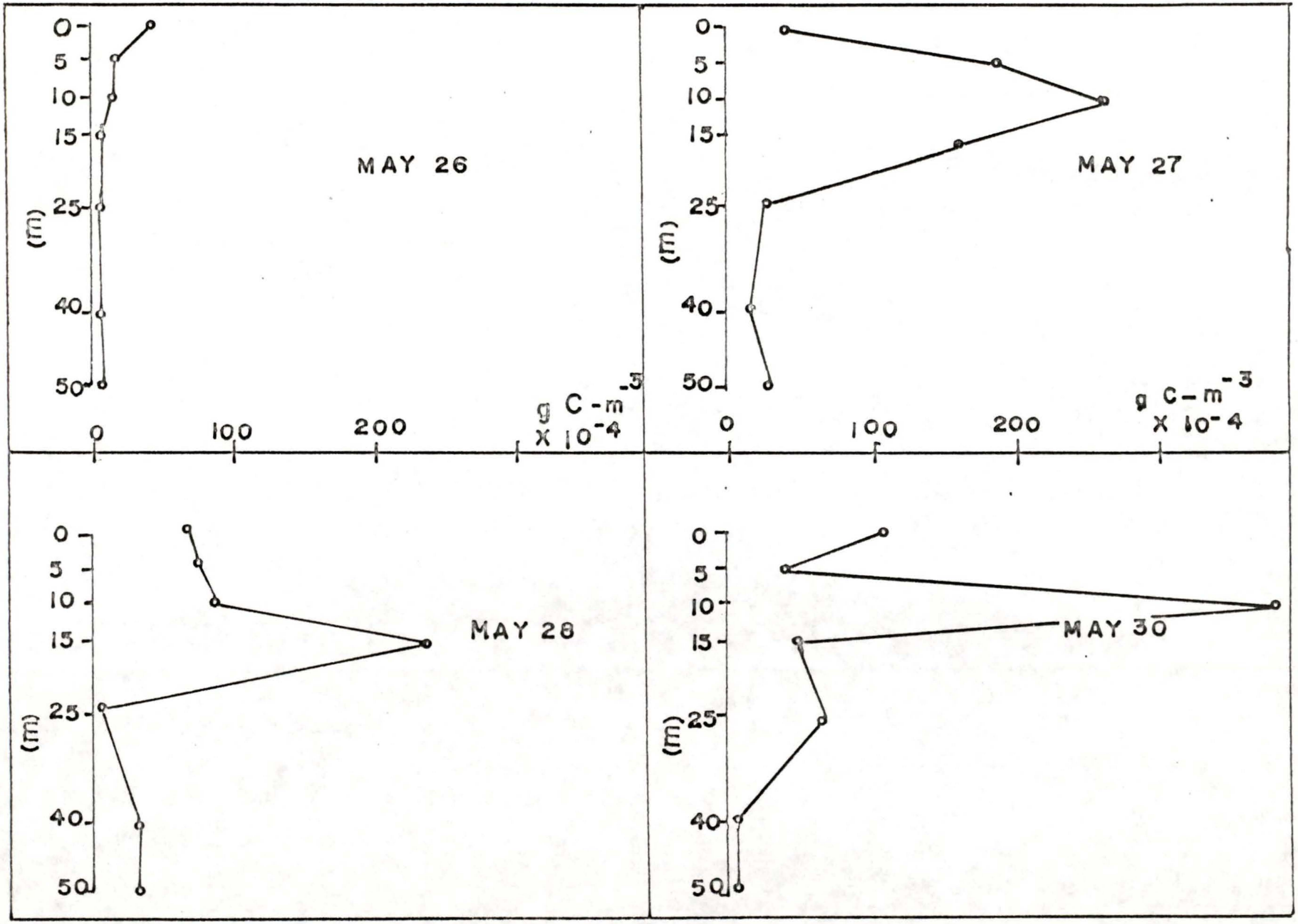
TABLE 6

May 26, 1971			May 27, 1971			
Depth (m)	cell counts x 10^3	estimated Carbon x 10^{-4}	Depth (m)	cell counts x 10^3	estimated Carbon x 10^{-4}	
0	1,848 /m^3	13.91 g/m^3	0	528/m^3	3.80 g/m^3	
5	616	1.30	5	2,640	18.98	
10	616	1.30	10	3,608	25.93	Thalassiosira rotula
15	264	.56	15	2,112	15.18	
25	88	.19	25	352	2.53	
40	88	.19	40	176	1.27	
50	176	.37	50	352	2.53	
0	968	1.1	0	352	0.4	
5	704	0.8	5	2,288	2.6	Chaetoceros radicans
10	264	0.3	10	2,816	3.2	
15	440	0.5	15	616	0.7	
25	440	0.5	25	1,232	1.4	
40	264	0.3	40	88	0.1	
50	88	0.1	50	88	0.1	
0	264	0.3	0	-	-	
5	-	-	5	1,408	1.6	
10	-	-	10	616	0.7	Chaetoceros didymus
15	88	0.1	15	-	-	
25	-	-	25	88	0.1	
40	-	-	40	-	-	
50	-	-	50	176	0.2	

May 28, 1971			May 30, 1971			
0	880	6.33	0	1,430	10.31	
5	968	6.96	5	501	3.61	Thalassiosira rotula
10	1,144	8.22	10	5,280	37.95	
15	3,256	23.40	15	660	4.74	
25	88	0.63	25	880	6.33	
40	440	3.16	40	-	-	
50	440	3.16	50	-	-	
0	-	-	0	774	0.88	
5	1,936	2.2	5	12,575	14.29	
10	1,320	1.5	10	2,728	3.10	Chaetoceros radicans
15	1,760	2.0	15	3,194	3.63	
25	176	0.2	25	2,314	2.63	
40	88	0.1	40	1,214	1.68	
50	-	-	50	554	0.63	

Fig. 29. Depth distribution of estimated cell carbon for <u>Thalassiosira rotula</u> (mg C $m^{-3} \times 10^{-4}$)

FIGURE 29



Thalassiosira rotula Meunier

Ehren. *Melosira* spp, *Fragilaria* spp. *Asterionella japonica*, Cleve; and *Skeletonema* spp.. The bulk of *Chaetoceros radicans* was found in the form of hypnospores. *Thalassiosira rotula* chains were found with cell diameters half the size of the original bloom organism in log-phase growth.

Through the inital stage of the bloom (May 10 to 27) the minimum doubling time observed for *Thalassiosira rotula* was 10 hours half the time observed by Antia *et al*, (1968). The maximum cell population occurred between 5 and 10 m where the light and temperature were near the optimal range for maximum *T. rotula* growth, of 12°C and 0.33 ly/min., as reported by Schöne (1972). By May 30 the population had decreased at all depths except at 10 m where a large population still persisted.

An increase in the detrital fraction of the material collected on the membrane filters was also observed at this time. In the early part of the bloom very little detritus had been observed above 25 m and no zooplankton faecal pellets were found. Below 25 m *Chaetoceros radicans* were represented chiefly by resting hypnospores but small numbers of live cells from the shallower population were also present. As the bloom progressed, larger amounts of detritus were observed, especially broken phytoplankton cells and faecal material. Bacterial clumps were observed, both free and on portions of zooplankton test and on diatom fragments. These were observed in relatively large numbers on the surface to 10 m filters, fewer on the 25 m to 40 m filters and by far the largest quantity on the 50 m samples.

Several chemical changes were observed in the phytoplankton during this period. The ratio of phaeopigment to chlorophyll-a, integrated throughout the water column (Fig. 27) rose from 0.03 on May 21 to 0.21 on May 27.

Chlorophyll-a to carotenoid ratios (Fig. 28) rose from 0.4 On May 14 to 2.5 on May 19. They dropped to 1.0 as the bloom was initiated, remained at or near this value for the first eight days of the bloom, only to rise sharply on May 30 to nearly 3.0.

Carbohydrate to chlorophyll-a ratios dropped from 384 to less than 12 (Table 7) between May 19 and May 29, but then began to rise again on May 30. These values reflect an increase in the relative amount of chlorophyll-a as the bloom progressed. Protein to chlorophyll-a ratios (Table 8) dropped from 740 On May 19 to 150 on May 30. The inverse ratio is presented in Fig. 30. Protein to carbohydrate ratios (Table 9) remained near 3.5 in the early part of the bloom but increased slightly to 6.4 on May 30, the reverse of expectation.

Table 7. Ratio of carbohydrate to chlorophyll-a (uncorrected), March 22 to May 30.

TABLE 7

DATE	DEPTH (m)						
1971	0	5	10	15	25	40	50
March 22	302	—	59	300	294	400	294
23	268	199	110	208	430	274	1173
24	185	144	85	125	144	353	214
25	171	101	81	72	166	226	154
27	150	82	126	254	331	81	676
28	263	281	245	193	251	258	696
April 14	—	—	—	—	—	—	—
16	141	115	131	243	297	648	907
19	—	—	—	—	—	—	—
21	—	—	—	—	—	—	—
23	117	—	70	55	121	330	287
25	—	—	—	—	—	—	—
27	51	43	43	54	89	181	378
May 3	321	182	104	101	78	74	452
4	135	111	86	56	116	80	355
6	137	107	86	104	116	78	125
8	177	113	154	188	307	400	215
13	349	841	462	257	300	406	
15	430	361	403	645	494	1278	839
17	135	259	159	355	291	349	468
19	386	280	152	146	213	246	320
21	206	104	96	107	371	210	286
26	178	57	23	17	27	73	179
27	148	61	12	—	27	96	107
28	363	54	23	—	31	58	189
30	48	111	10	14	15	77	83

Table 8. Ratio of protein to chlorophyll-a (uncorrected) March 22 to May 30.

TABLE 8

DATE 1971		DEPTH (m) 0	5	10	15	25	40	50
March	22	429	296	104	243	239	258	150
	23	776	543	288	379	73	247	1949
	24	294	383	204	78	278	87	520
	25	134	135	144	209	204	20	13
	27	164	129	121	251	280	106	629
	28	202	132	62	128	67	603	256
April	14	183	179	219	178	232	135	533
	16	211	148	194	310	382	511	551
	19	127	73	59	629	49	14	331
	21	—	—	—	—	—	—	—
	23	164	116	76	50	81	114	213
	25	—	—	—	—	—	—	—
	27	140	106	75	69	96	81	329
May	3							
	4	343	267	473	136	96	90	116
	6	394	196	156	190	178	125	136
	8	869	504	2323	713	1349	1611	618
	13	719	581	482	434	154	328	
	15	358	306	329	427	192	1314	403
	17	187	236	119	244	222	273	298
	19	280	307	248	438	631	1693	1263
	21	353	223	251	418	511	379	99
	26	209	76	57	66	61	84	152
	27	416	64	32	49	52	96	234
	28	338	94	24	77	71	173	230
	30	108	118	34	59	49	87	146

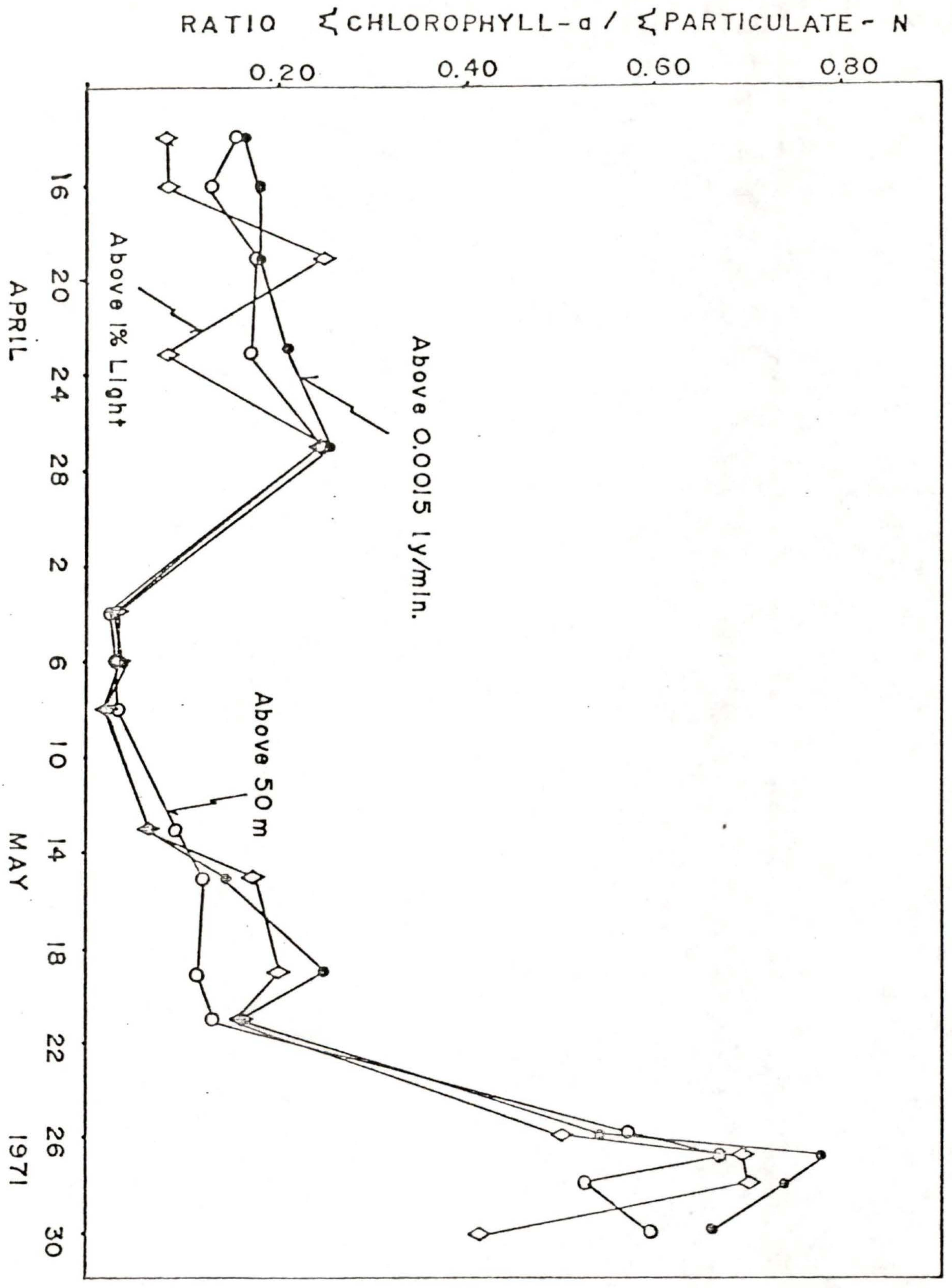
Table 9. Ratio of protein to carbohydrate,
March 22 to May 30, 1971.

TABLE 9

DATE	DEPTH (m)						
1971	0	5	10	15	25	40	50
March 22	1.60		1.76	0.79	0.86	0.59	0.51
23	2.86	2.67	2.60	1.81	0.18	0.56	2.11
24	1.58	2.63	2.38	0.60	1.93	0.22	2.43
25	0.77	1.31	1.94	2.96	1.21	0.09	1.12
27	1.07	1.59	0.98	0.97	0.97	0.82	1.35
28	0.79	0.47	0.21	0.67	0.26	2.33	0.31
April 14	—	—	—	—	—	—	—
16	1.49	1.33	1.51	1.26	0.98	0.88	0.60
19	—	—	—	—	—	—	—
21	—	—	—	—	—	—	—
23	1.42	—	1.12	0.92	0.67	0.36	0.76
25	3.01	0.94	2.57	0.86	1.63	0.46	0.45
27	2.73	2.47	1.77	1.28	1.07	0.46	0.90
May 3	3.28	1.92	3.22	3.05	2.63	1.57	1.26
4	2.56	2.46	7.02	2.51	0.87	1.10	0.30
6	2.93	1.69	1.64	1.80	1.51	1.60	1.10
8	4.51	4.51	15.11	3.86	4.42	4.04	2.94
13	2.05	0.69	1.04	1.63	0.56	0.72	
15	0.84	0.84	0.79	0.66	0.36	1.02	0.49
17	1.35	0.94	0.74	0.69	0.81	0.77	0.64
19	0.74	1.13	1.58	3.03	3.00	6.84	3.91
21	1.73	2.18	2.60	3.81	1.40	1.86	0.26
26	1.17	1.33	2.47	3.91	2.20	1.21	0.92
27	2.59	1.07	2.59	—	1.82	0.96	2.16
28	0.93	1.75	1.07	—	2.25	3.01	1.23
30	2.24	—	3.36	4.33	3.33	1.11	1.82

Fig. 30. Temporal change in the ratio of integrated chlorophyll-a to particulate nitrogen April 14 to May 30.

FIGURE 30


RATIO ΣCHLOROPHYLL-a / ΣPARTICULATE - N
0.20
0.40
0.60
0.80
16
20
24
28
2
6
10
14
18
22
26
30
APRIL
MAY
1971
Above 1% Light
Above 0.0015 ly/min.
Above 50 m

DISCUSSION

Three of the physical parameters measured in the process of this study; stability, light and temperature, have had the most marked effect on phytoplankton growth and nutrient uptake.

The water column at the sampling station in Saanich Inlet generally increased in stability as spring progressed under the influence of increasing density stratification (a function of thermal and salinity stratification).

Thermal stratification increased as the value of the 24-hr light budget increased from 350 to 700 ly/day.

Salinity stratification increased as less saline water flowed into Saanich Inlet from an increased Fraser River output in the middle of May (Herlinveaux, 1962).

The process of density stratification was interrupted on two occasions by periods of unstable weather, once in mid-April and once in mid-May (Fig. 7). These periods of cool, rainy, windy weather allowed the surface to cool and the action of wind-mixing turned over the surface waters destroying any stratification which had been established.

The inflow of high nutrient, low salinity water from the Fraser River plume, between May 15 and 19 coincided with the beginning of an extended period of sunny, calm weather and marked the beginning of the first major spring bloom.

The 24-hr light budget increased from 350 to 700 ly/day over the period of study. This increase showed its most marked effect on the rate of depletion of nitrate from surface waters (Fig. 31). A strong

Fig. 31. Regression of the daily light budget (ly/day) against nitrate concentration at 0 m.

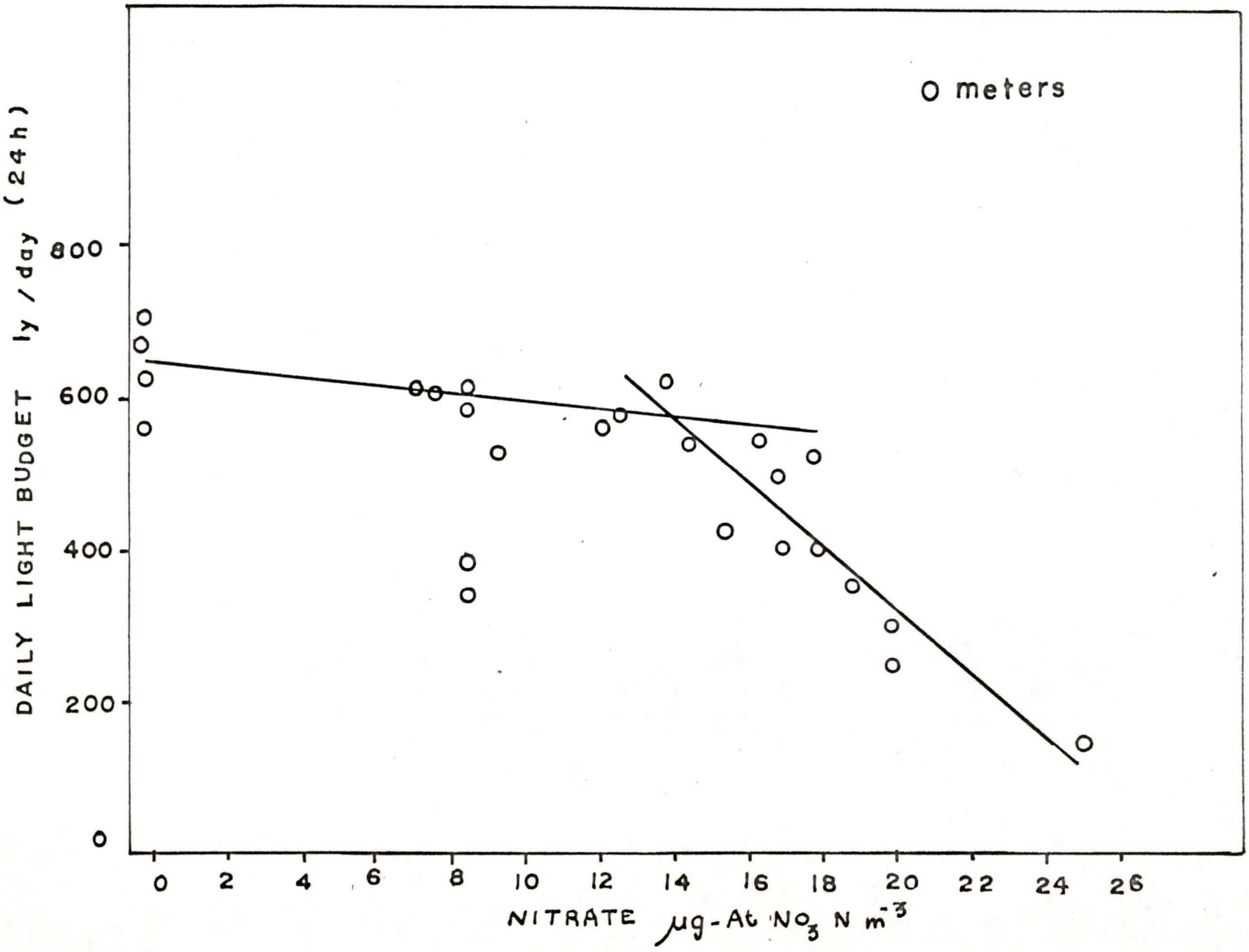
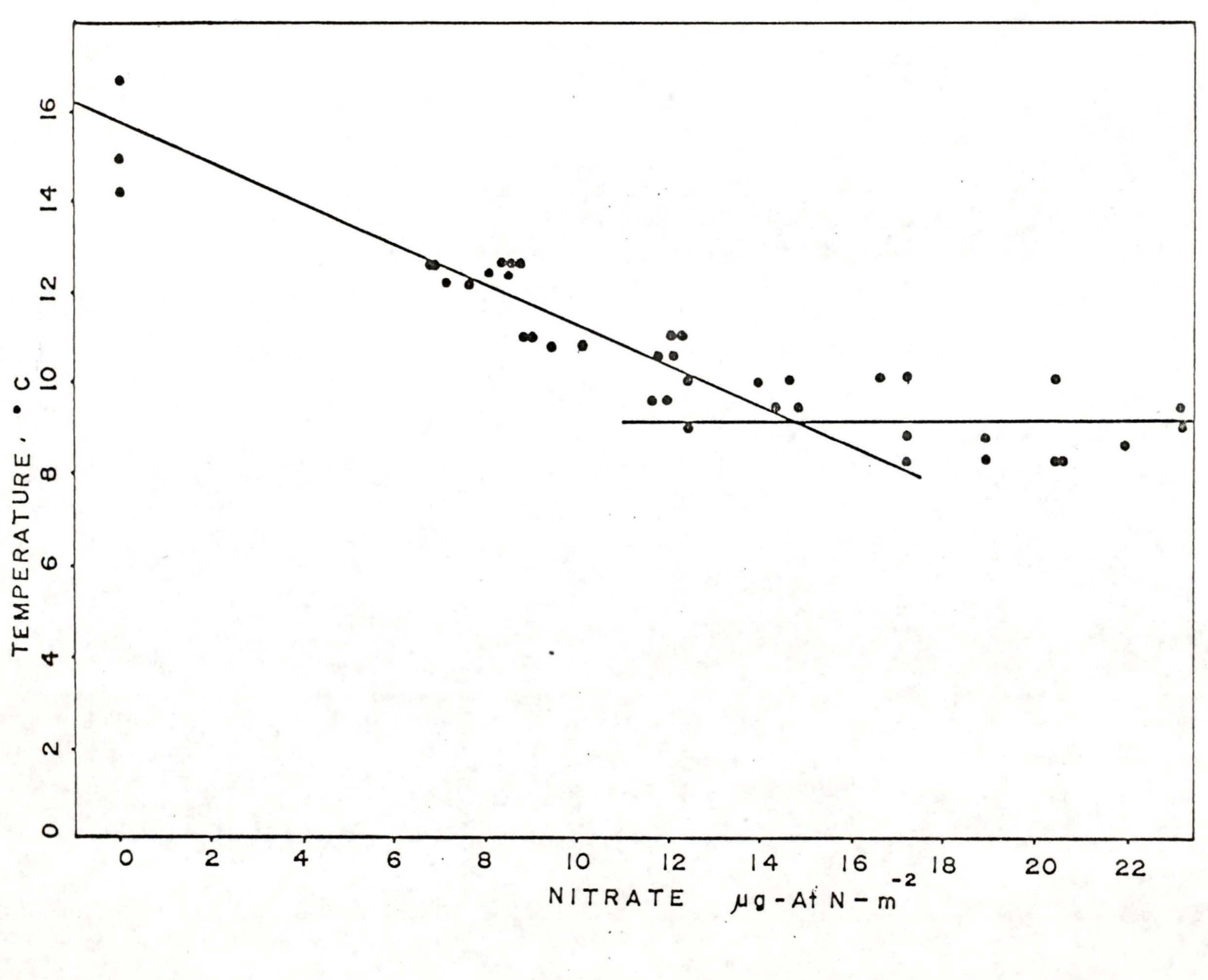

O meters
DAILY LIGHT BUDGET ly / day (24h)
0
200
400
600
800
0
2
4
6
8
10
12
14
16
18
20
22
24
26
NITRATE μg-At NO3 N m-3

FIGURE 31

Fig. 32. Regression of temperature against nitrate
at 0 m, March 22 to May 30


TEMPERATURE, °C
0
2
4
6
8
10
12
14
16
NITRATE μg-At N-m^{-2}
0
2
4
6
8
10
12
14
16
18
20
22

32 FIGURE 32

correlation exists between the incident radiation and the ambient nitrate levels in surface waters for the first part the study, March 22 to April 25. Throughout this period nitrate levels dropped steadily in a linear fashion as the daily light budget increased. However, when nitrate levels between 12 and 15 µg-at NO_3N m^{-3}, and light levels around 600 ly/day, were reached this correlation disappeared. All further decreases in nitrate from 12 to 0 µg-at NO_3N m^{-3} occurred in a narrow light regime between 600 and 700 ly/day, incident radiation (Fig.31).

It seems that the rate of nutrient consumption in the first part of the study (March 22 to April 25) was limited by light but that light saturation occurred at a daily light budget near 600 ly/day. A similar condition involving the light-limitation of a winter population of phytoplankton has been discussed in detail by Hitchcock and Smayda, 1977.

The relationship between temperature and nutrient depletion exhibits a similar but complementary relationship. In Fig. 32 it can be seen that temperature cannot be correlated with the rate of nitrate depletion in the surface waters down to levels of nitrate between 12 and 16 µg-at NO_3N m^{-3}. Below this nutrient level, however, and at temperatures between 9 and 16°C a strong linear correlation exists between water temperature and ambient nitrate concentration, so that as temperature increases, environmental levels of nitrate decrease. This phenomenon has been observed off La Jolla Calif. by Strickland (ed.) (1970).

Two stages exist, therefore, in the nutrient uptake dynamics of the spring diatom population of Saanich Inlet. In the first stage light is the limiting factor with nitrate uptake proceeding in a linear fashion as the daily light budget increases.

Fig. 33. Regression of integrated inorganic nitrogen against particulate nitrogen above 50 m.

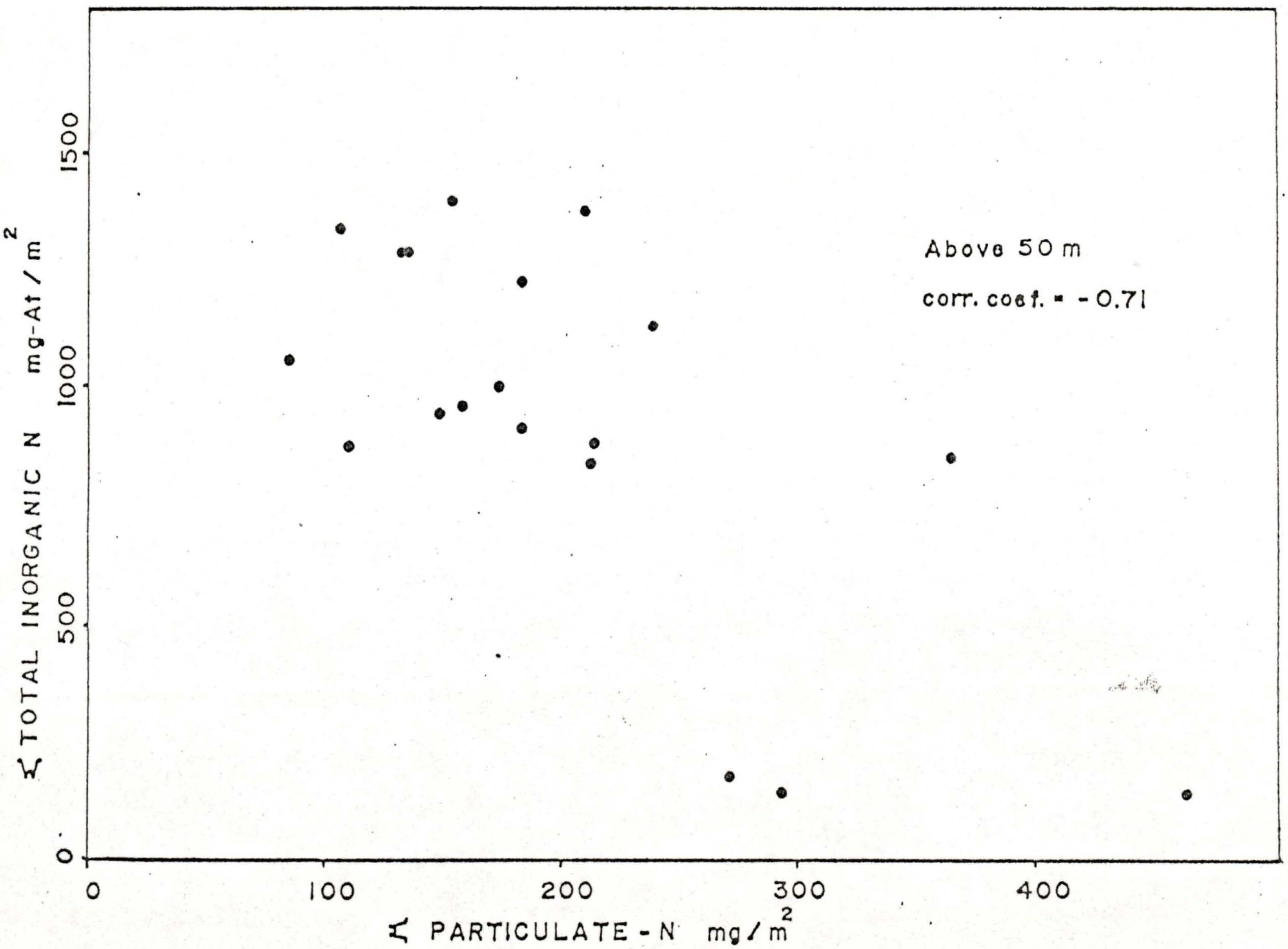
Σ TOTAL INORGANIC N mg-At / m²
0
500
1000
1500
Σ PARTICULATE - N mg / m²
0
100
200
300
400
Above 50 m
corr. coef. = - 0.71

FIGURE 33

Fig. 34. Regression of integrated total inorganic nitrogen against particulate nitrogen above 0.0015 ly/min.

FIGURE 34

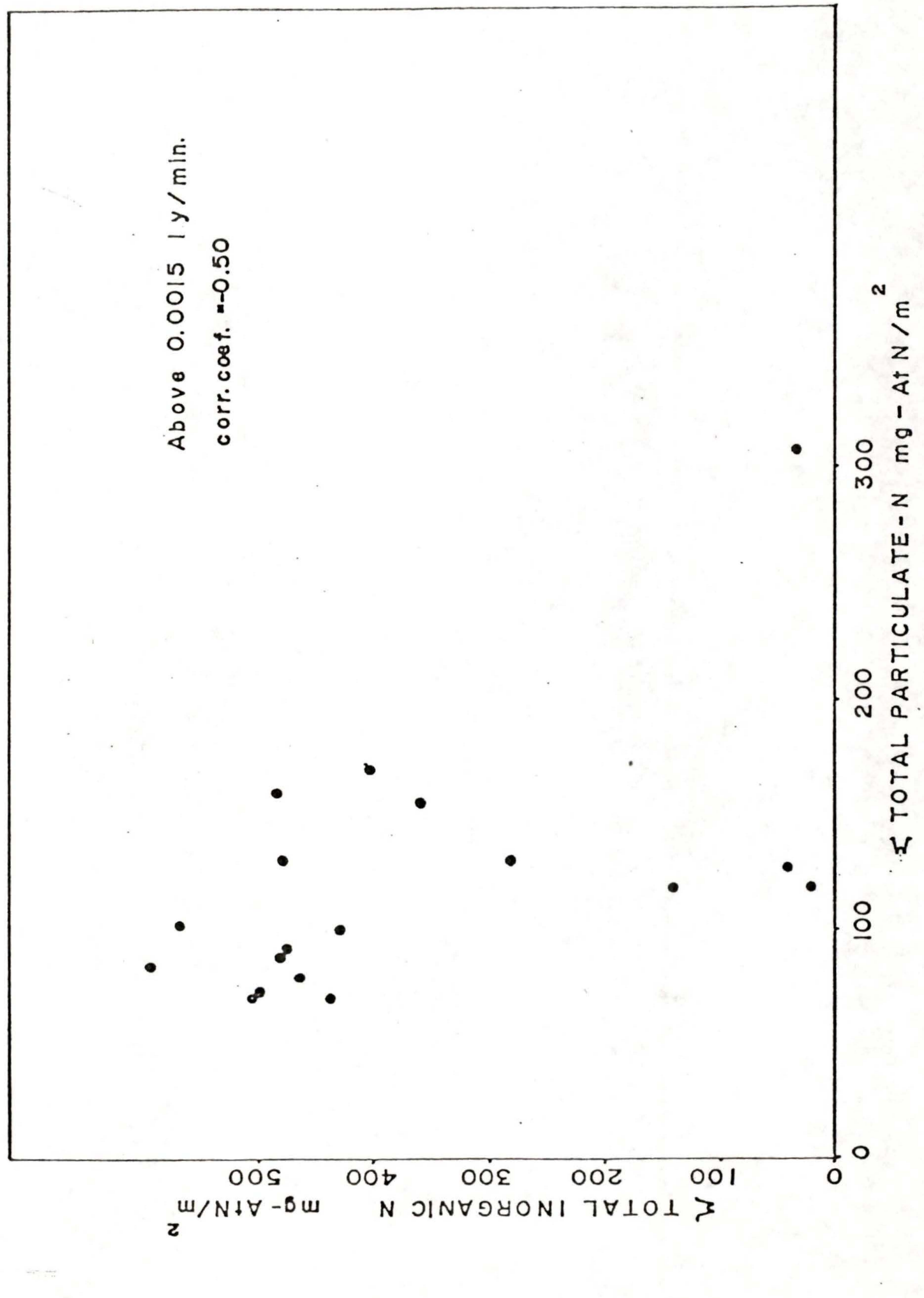

Above 0.0015 ly/min.
corr.coef. =-0.50
Σ TOTAL PARTICULATE-N mg-AtN/m²
0
100
200
300
Σ TOTAL INORGANIC N mg-AtN/m²
0
100
200
300
400
500

Fig. 35. Regression of integrated total inorganic nitrogen against integrated particulate nitrogen above one percent light.

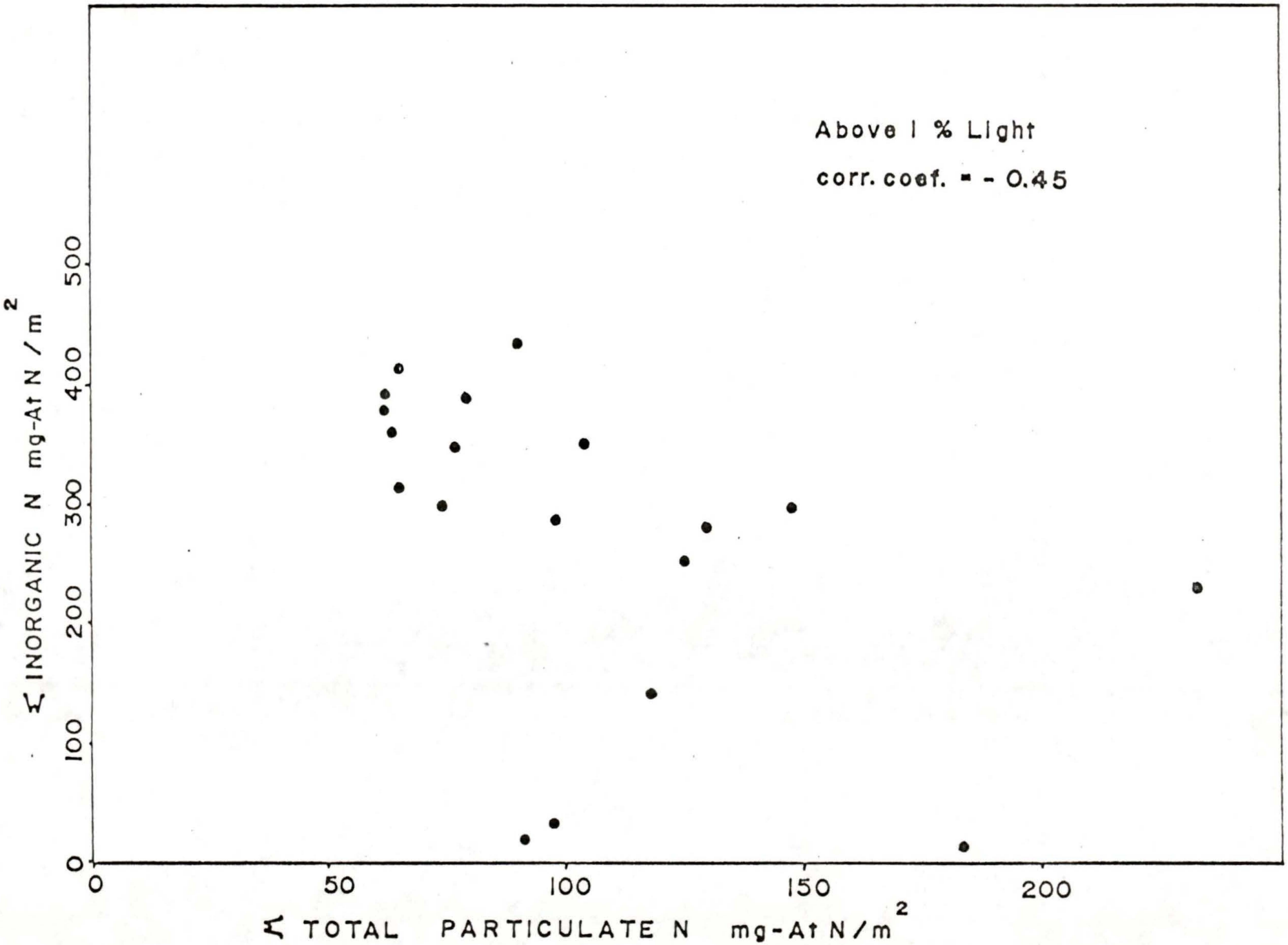

Above 1 % Light
corr. coef. = - 0.45
Σ INORGANIC N mg-At N / m²
0
100
200
300
400
500
Σ TOTAL PARTICULATE N mg-At N / m²
0
50
100
150
200

FIGURE 35

Fig. 36. Regression of uncorrected chlorophyll-a against particulate nitrogen above 50 m.

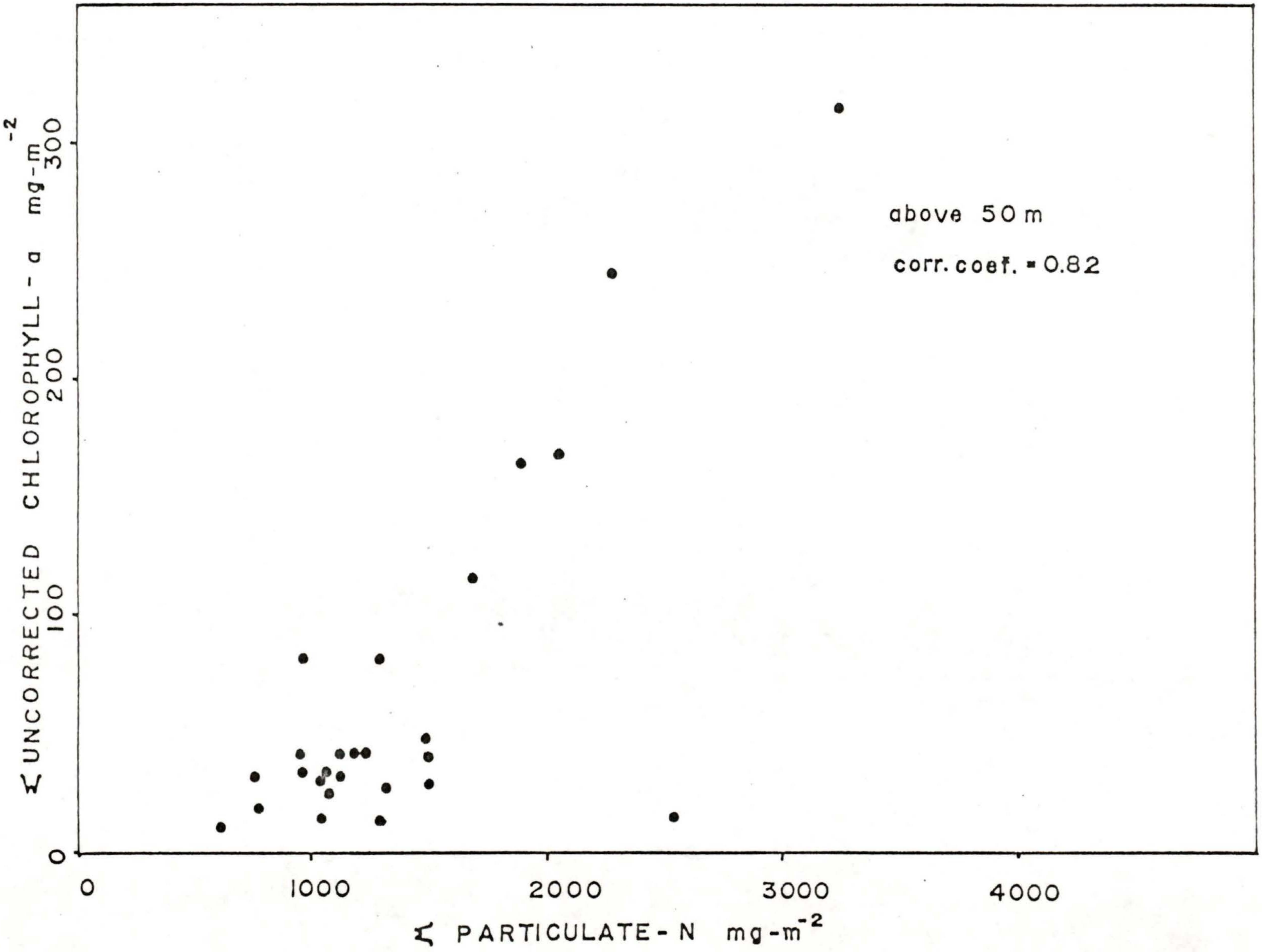

above 50 m
corr. coef. = 0.82
Σ UNCORRECTED CHLOROPHYLL - a mg-m^{-2}
0
100
200
300
0
1000
2000
3000
4000
Σ PARTICULATE - N mg-m^{-2}

FIGURE 36

Fig. 37. Regression of nitrate against chlorophyll-a above 50 m.

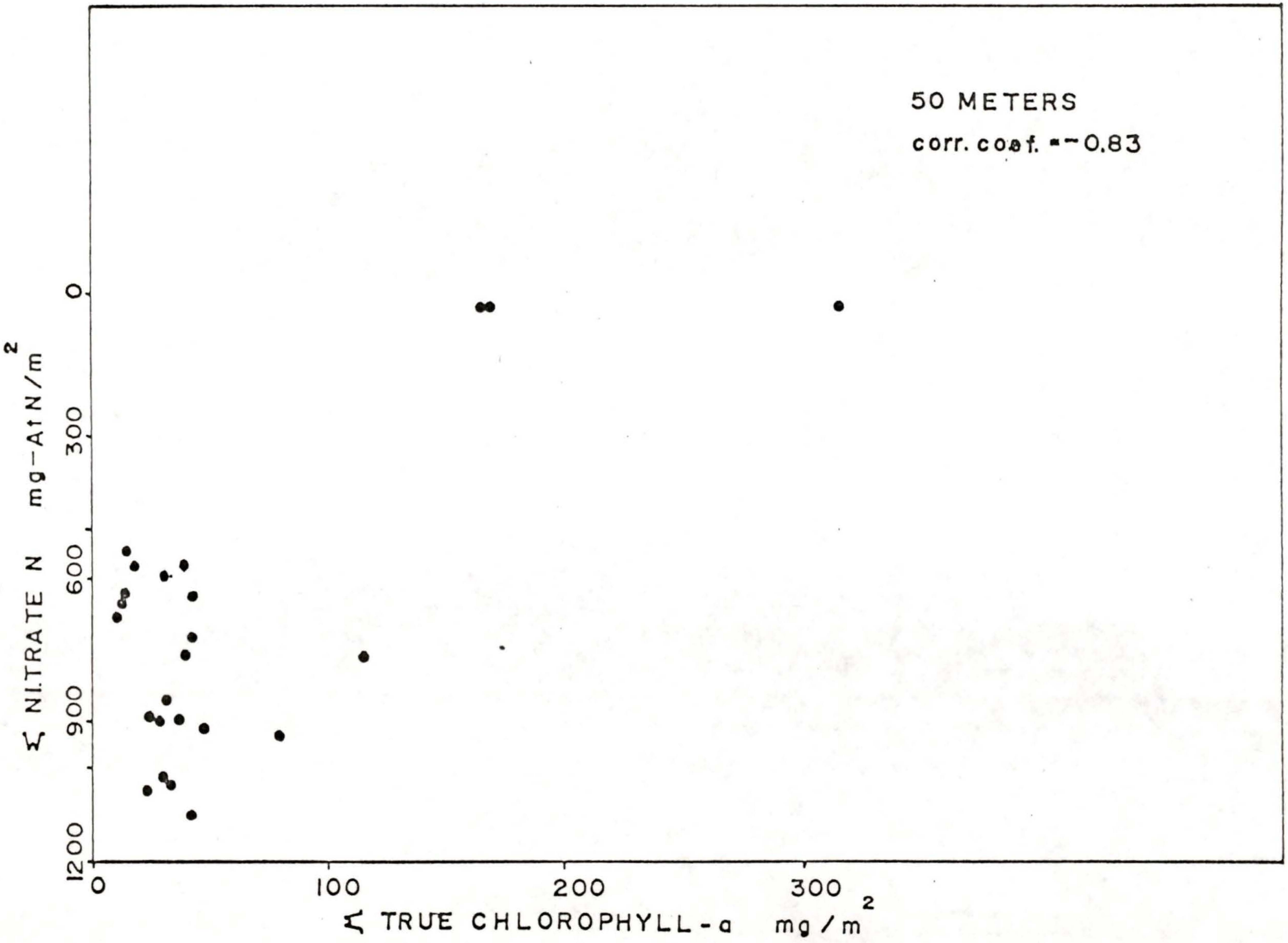

50 METERS
corr. coef. = −0.83
Σ NITRATE N mg-At N/m²
0
300
600
900
1200
0
100
200
300
Σ TRUE CHLOROPHYLL-a mg/m²

FIGURE 37

In the second stage the light budget has reached a saturation level and, a second factor, temperature, becomes limiting. In Saanich Inlet temperature remains the factor controlling nitrate uptake until nitrate levels approach non-detectability. This changeover in limiting environmental factors occurs at a nitrate level of 14 μg-at NO_3N m^{-3} and a temperature of 9°C. whether nitrate is regressed against light or against temperature. Whether this is purely fortuitous or whether it reflects a change in species composition of the diatom population is not clear.

Such a change did occur. Two separate increases in diatom populations were observed. The first of these increases occurred in the light-limited stage of nitrate depletion. Its progress was brought to an abrupt halt at the onset of a period of windy, cloudy weather and a daily light budget between 200 and 400 ly/day.

Fig.14, in which changes in integrated total inorganic nitrogen are shown, illustrates this point. The most active period of the April increase coincides with sunny weather (450 to 580 ly/day). During this period a rapid, smooth decrease in ambient nitrate level occurs simultaneously with a swift, though short-term, rise in the chlorophyll-a content of the seston.

On May 4 the weather changed, chlorophyll-a levels dropped and ambient nitrate levels ceased to fall. Several days of alternating cloudy and sunny weather ensued, with nitrate levels rising and falling as light levels did. Over the period May 4 to May 21 no net loss of nitrate occurred in the water column down to 50 m (Fig.9). This may have been due in part to contributions of nutrients from intrusive Fraser River plume water but it seems likely that a major factor was decreased uptake by a light-limited phytoplankton population.

This period ended with the onset on May 19 of stable, sunny weather. Ambient inorganic nitrogen levels exhibited a second major decline which proceeded at a much faster rate than the April decline.

A major feature of this second period was the penetration of the 8.5°C isotherm into 25 m water. It is this period of nitrate uptake that is temperature controlled. Light is no longer limiting and nitrate levels decrease at an accelerating rate as water column temperature increases.

Although nutrient uptake curves show two obvious peaks in phytoplankton activity this pattern is not so clear in the temporal variation of particulate materials such as protein, carbohydrate and pigments.

The April increase (16 to 28 April) showed maximum development at 0 m as measured both by particulate nitrogen and by carbohydrate levels. The May bloom (May 19 to 30) had its maximum development at 5 m in both particulate nitrogen and carbohydrate. Both diatom increases resulted in elevated levels of carbohydrate and particulate nitrogen down to 15 m.

Integrated particulate nitrogen (Fig. 15) increased strongly between April 21 and May 3. Minimal levels (except on May 8) occurred between May 6 and 19. A second marked increase in integrated particulate nitrogen started on May 19 and continued until May 30 but the bulk of this last increase appears to have formed below the euphotic zone.

Good correlations (Corr. Coeff. $\geq +0.80$) exist between particulate nitrogen and chlorophyll-a during the peak of the late May bloom, although, on the whole, these correlations were not good for the entire bloom period (between 0.45 and 0.61) (see Table 9).

The ratio of integrated chlorophyll-a to integrated particulate nitrogen shows a very strong bimodal pattern with high levels between 16 and 28 April and between May 15 and 30, the periods of the two diatom increases.

A strong correlation (0.99) exists between integrated values of carotenoid pigments and particulate nitrogen when normalized against chlorophyll-a, evidence that the greater portion of both particulate nitrogen and carotenoid is of an algal origin (Table10). This correlation drops to less than 0.7 when a single particulate nitrogen value, taken from May 8, is included in the general calculation. This very high single value may be the result of a peak in bacterial and detrital particulate nitrogen following a bloom of the herbivorous zooplankter, *Oikopleura*.

From May 4 to 8 the particulate nitrogen maximum occurred at 10 m, the bottom of the discontinuity layer for that date (Fig.9). This maximum may be related to the accumulation of detritus and moribund phytoplankton cells in the pycnocline, as a result of slower sinking rates through this zone.

The pattern of particulate nitrogen distribution is not perfectly clear. While it is evident (because of the correlation between particulate nitrogen and chlorophyll-a) that most of the particulate nitrogen present above 15 m during the two phases of the spring bloom was of phytoplankton origin, it also seems likely that large amounts were of bacterial and zooplankton origin. This is especially clear during the inter-bloom period. The presence of a high proportion of bacterial and faecal material on the filters during this period coincides with random peaks in particulate nitrogen. Such peaks (eg. May 8) follow periods of high zooplankton grazing and are probably due to high bacterial levels in decomposing herbivore faeces.

The temporal distribution of carbohydrate follows a pattern similar to that of particulate nitrogen. And, like particulate nitrogen, the bimodal peak pattern is somewhat obscured by stray peaks in periods of low phytoplankton biomass. As with particulate-nitrogen, such stray peaks in carbohydrate can be correlated with increases in the bacterial population involved in the breakdown of zooplankton faecal material and phytoplankton detritus. Bacteria isolated from samples taken during the May 13 to May 16 inter-bloom period included the marine actinomycete Nocardia marina Waksman, 1947 (Hooper, 1972). This organism produces large quantities of cell wall and sheath polysaccharides which would be included in the particulate carbohydrate fraction. Carbohydrate levels down to 50 m exhibit a strong tendency to peak during population increases in phytoplankton and bacterial levels.

As it can be seen in Fig. 18 carbohydrate maxima occur around 40 m in late April. This is the bottom of the pycnocline and is likely the depth of greatest bacterial activity. Increased levels of carbohydrate recorded during the two diatom blooms presumably represent a combination of bacterial and phytoplankton carbohydrate.

Table 10. Simple correlation coefficients between particulate constituents and environmental factors.

TABLE 10

Test Situation	Corr. Coeff.	Slope
Temperature vs nitrate, 0 m	- .95	- 2.61
5 m	- .93	- 4.90
10 m	- .87	- 5.59
15 m	- .95	- 8.29
25 m	- .97	- 9.12
40 m	- .92	- 9.64
50 m	- .85	-11.47
Inorg. N vs tot. part. N		
to 50 m	-.71	-.169
to 0.0015 ly/min.	-.50	-.144
to 1% surf. light	-.45	-.150
Tot. chl-a vs tot part. N		
to 50 m	+.80	+.95
to 0.0015 ly/min.	+.60	+.75
to 1% surf. light	+.18	+.35
Chl-a vs protein to 50 m	+.75	+88.1
$\frac{\text{protein}}{\text{chl-a}}$ vs $\frac{\text{carotenoids}}{\text{chl-a}}$		
to 50 m	+.79	+.239
to 0.0015 ly/min.	+.66	+.138
to 1% surf. light	+.98	+.218

The temporal variation in chlorophyll-a showed a strong clearly bimodal distribution with peaks in late April and late May, separated by a long period when little or no chlorophyll-a could be detected in the seston fraction.

The elevated levels of chlorophyll-a in mid-April (April 14 to 27) strongly indicate an incipient bloom. However, the steady increase in chlorophyll-a levels stops abruptly between April 27 and May 3, apparently halted by a long period of changeable weather, dark days (119 to 380 ly/day) and unstable, ($\acute{E}$ = -232) water conditions. This period also coincides with an increase in herbivorous zooplankton, especially small copepods, and was followed by a massive bloom of the herbivorous larvacean urochordate, *Oikopleura sp*. Water instability, poor weather conditions and heavy zooplankton grazing pressure apparently combine to bring phytoplankton standing stock to non-detectable levels.

Phaeopigment levels rise sharply during the period of depressed chlorophyll-a levels, resulting in very high phaeopigment to chlorophyll-a ratios (Fig. 27). This ratio is much higher when pigments are integrated to 50 m, rather than to the compensation depth, suggesting that detritus, either from dead and moribund cells or from zooplankton faecal pellets forms the larger part of the suspended particulate matter.

Chlorophyll-a and phaeopigments show a tendency to vary inversely, rises in phaeopigment levels coinciding with drops in chlorophyll-a. This is especially obvious during the period May 4 to May 21 and is possibly related to zooplankton grazing effects. This relationship between chlorophyll-a and phaeopigment has been observed by Glooshenko

(1972) in the Great Lakes and by Lorenzen (1967) off Baja, Calif. in the Pacific. Both correlated levels of phaeopigment to zooplankton abundance. Spence and Steven, (1974) working in the Gulf of St. Lawrence, disagree. They found that the chlorophyll-a to phaeopigment ratio was determined chiefly by the rate of growth of phytoplankton and was due mainly to variation in chlorophyll-a. They found no relationship between phaeopigment and zooplankton biomass.

Neither of these theories can be verified in the present study. Both conditions prevail, poor conditions for algal growth and high grazing pressure. The actual case probably lies between the two and both non-optimum growth conditions and high grazing pressure contribute to increases in phaeopigment relative to chlorophyll-a.

The depth of the chlorophyll-a maximum (Fig. 5) varied throughout the study period although it never fell below 15 m. In the beginning of April, during the first upsurge in phytoplankton crop, the depth of the chlorophyll maximum was constant at 5 m. It descended to 15 m on April 23 when the highest chlorophyll-a levels for the period were recorded. During the period of cold windy weather beginning on April 27 the chlorophyll-a maximum was found at the surface but dropped again to 12 m early in May. During the latter period, levels of chlorophyll-a approach zero and no real maximum was observable. When chlorophyll-a levels began to rise again in the middle of May the depth of the chlorophyll-a maximum returned to 5 m, dropping thereafter to a depth of 12 m as phytoplankton levels increased to bloom levels in late May.

The modal depth for the actively growing log-phase diatom population appears to be about 5 m (Fig. 29), suggesting that conditions are optimal in this part of the water column. Light in the region is about ten percent of surface light and the temperature is between 9.0 and 10.0°C. close to the optimum reported for the diatom, Thalassiosira rotula Meunier, the dominant diatom found in the late May population, (Schöne, 1972).

Carotenoid maxima generally coincided with chlorophyll-a maxima but carotenoids were more often high throughout a larger part of the water column, especially in deeper water. This may be due in part to the presence of small herbivorous zooplankton on the filters, which often contain carotenoids among stored lipids.

Integrated carotenoid levels (Figs. 21 to 23) follow a pattern similar to that of chlorophyll-a but did not increase as quickly nor did theyrise so high as the latter when the bloom was initiated, (Fig.31).

Integrated carotenoid levels above 50 m were as high or higher than chlorophyll-a and showed a pronounced bimodal pattern throughout the study period. The two peaks coincided with the mid to late April and the late May chlorophyll-a increases.

Temporal changes in the integrated chlorophyll-a to carotenoid ratios (Fig. 28) follow a similar bimodal curve almost the same magnitude above the compensation depth as above 50 m.

It seems that low chlorophyll-a to carotenoid ratios may be a feature of the death phase of a bloom, an observation made by Antia et al. (1963) in their work on mixed phytoplankton populations grown in-situ in a large volume plastic sphere. As populations reach maximum standing stock the high particle content of the water often acts to shade

Fig. 38. Isopleths of carotenoids (mg m^{-3})
0 to 50 m, April 14 to May 30

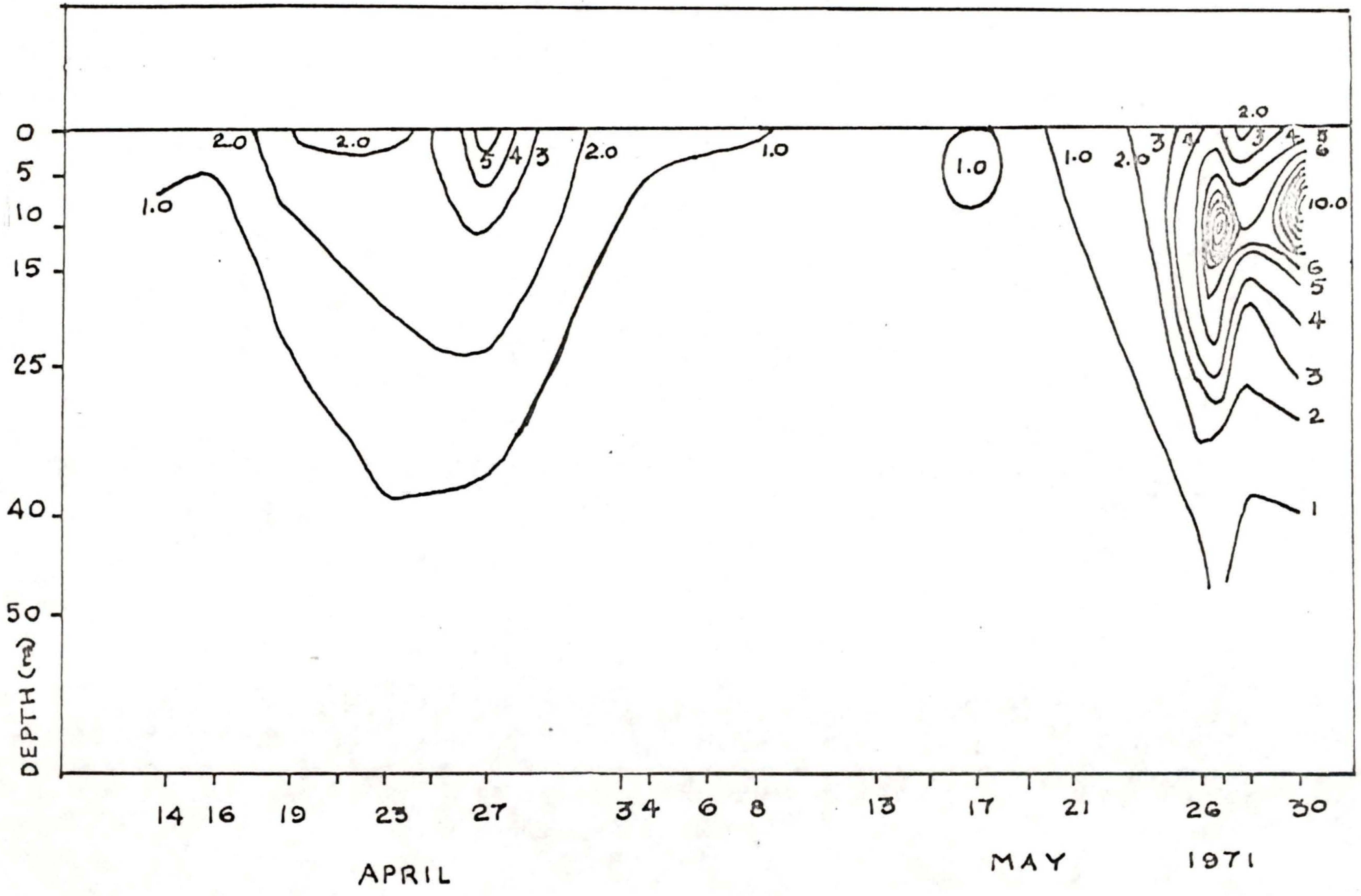

0
5
10
15
25
40
50
DEPTH (m)
2.0
1.0
2.0
5
4
3
2.0
1.0
1.0
1.0
2.0
3
4
3
4
5
6
10.0
6
5
4
3
2
1
14
16
19
23
27
3
4
6
8
13
17
21
26
30
APRIL
MAY
1971

FIGURE 38

the deeper portion of the population. A typical reaction of the deeper population to self-shading is to increase amounts of auxiliary pigments in the plastids, where they act to absorb light at wavelengths not normally available to chlorophyll-a. This light energy is then passed to chlorophyll-a to act in the light reactions of the cells. As a result available light is utilized more efficiently. The end result is an increased level of carotenoids and xanthophylls relative to chlorophyll-a, (Haxo and Blinks, 1950).

The Spring Diatom Increase

Nitrogen depletion dynamics and algal biomass measurements (as chlorophyll-a, particulate nitrogen and carbohydrate) both exhibit a bimodal pattern, with a peak in late April and another in late May. Inspection of species composition during both these blooms revealed that diatoms were the dominant algae.

The minor April increase, initiated in response to a brief period of sunny weather, was composed chiefly of the larger phytoplankton. Such diatoms as *Coscinodiscus excentricus* Ehren., *C. curvatulus* Grunow, and *Thalassiosira decipiens* (Grunow) formed the bulk of the population but substantial numbers of other large diatoms were present as well. *Chaetoceros curvatulus* Castracone, *Ditylum brightwellii* (West), *Thalassiothrix nitzschioides* (Grunow), *Asterionella japonica* Cleve and *Skeletonema costatum* (Greville) the last with many resting spores, were present in large numbers.

This diatom increase has been shown, through its strong correlation with the daily light budget, to have been light limited. Its termination appears to have been related to unstable weather and to grazing pressure.

Steeman-Nielson (1962) suggests that grazing pressure acts to suppress blooming when the onset of favourable conditions is gradual. Unsettled weather in the period of increasing daily light budgets would have such an effect.

The second diatom increase during which ambient inorganic nitrogen dropped below detectability above 50 m, was dominated by the large diatom, *Thalassiosira rotula* Meunier. The co-dominants of this organism *Chaetoceros didymus* Ehren. and *C. radicans* Schutt are considerably smaller. As this bloom aged the relative abundance of *Chaetoceros* spp. increased, (Table 6).

The difference in cell size of the bloom dominants for the two bloom periods and the decrease in the proportion of large cells to smaller cells in the second bloom is one of the symptoms of nutrient depletion or other such limiting conditions.

It has been suggested (Dugdale, 1967), that the size of the components of an phytoplankton community has a great deal to do with the nutrient uptake efficiency of the population and may determine the temporal sequence of species in relationship to the decreasing nutrient levels in communities isolated by the thermocline as is the case in late May.

Specifically, large diatoms grown at high nutrient concentrations have a competitive advantage over small diatoms in that they grow faster at high nutrient levels, (Dugdale, 1967) (Eppley and Thomas, 1969). However, as nutrient levels drop this advantage is reversed. Because small phytoplankton are more efficient at scavenging nutrients at low levels (Dugdale, 1967) they compete successfully with larger phytoplankton when nutrient levels drop in the process of a bloom. The decreasing size of Thalassiosira rotula over the period of the late May increase and the increasing dominance of smaller phytoplankters as nutrient levels dropped is a function of such interspecific competition.

The late May increase in numbers of Thalassiosira rotula seems to have been initiated with the penetration of the 8.5°C. isotherm into 25 m water. It has already been demonstrated that the rate of loss of nitrate from the water column during this period was strongly correlated with temperature at all depths (Table10), in contrast to the late April bloom for which the rate of nitrate depletion was correlated with daily light budget. This indicates that light, which was limiting during the April diatom increase no longer was limiting in the May increase and that in the last instance temperature controlled the level of response of the bloom organisms.

Work with Thalassiosira rotula by Schöne (1972) has shown that a minimum doubling time of 9 hours can be obtained with temperature and light regimes of 12°C. and 0.33 ly/min. These conditions occurred between 5 and 9 m over the period of the May bloom. A minimum doubling time of 10 hours was observed between May 26 and May 27, the first two days of the bloom. During this early bloom period growth rates approached the logarithmic rate obtainable in culture.

Major cell populations of T. rotula occurred first at the surface, with cell carbon (based on cell volume to carbon conversion) decreasing in a steady curve with increasing depth (Fig. 29). The first sign of surface light inhibition was observable on May 27, the day of maximum

Thalassiosira rotula numbers. From May 27 to May 30 the depth range of maximum cell carbon narrowed. On May 27, high numbers of *T. rotula* occurred in an 18 m band between 2 and 20 m. On May 28 the band had shrunk to a 10 m width between 10 and 20 m. By May 30 this band had narrowed further to about 5 m wide at a depth between 7 and 12 m. At this point cell numbers began to increase at the surface again.

The progressive narrowing of the band of maximum growth is strongly indicative of self-shading in the phytoplankton population. The depth of the maximum corresponds to the compensation depth and is located at the bottom of the thermocline. Sinking cells slow down as they pass through the thermocline and tend to accumulate at the bottom of this zone. The increase in biomass at the surface coincides with an increase in ammonia at the surface on May 30. By this time nitrate had been almost completely removed from the water column above 50 m and nutrient limitation was probably a factor in slowing down algal growth towards the end of the bloom. The remineralization of ammonia and other nitrogen solubles from zooplankton waste products is the main source of nitrogen during the summer (Herlinveaux, 1962).

By May 30, the number of species comprising the diatom population had increased and the average cell size had decreased both in response to the aging of the bloom and the decrease in nutrient uptake efficiency of *Thalassiosira rotula*.

All indications were that the bloom initiated around May 18 had begun to age and was on the decline by May 30 although it had by no means terminated. It is likely that a combination of nutrient deficiency, severe self-shading and grazing pressure acted to bring about this situation. The weather, uniformly clear, sunny and calm throughout the period of the bloom, did not seem to play a part in the decline of the bloom. Some grazing was noticable with the presence of faecal material on the cleared filters, but the continued high population levels indicate that grazing was not severe.

Several chemical changes were observed in the phytoplankton during this period which further suggests that the population was declining. The ratio of phaeopigment to chlorophyll-a, integrated through the water column (Fig. 27) rose from 0.03 to 0.21 between May 21 to May 27. Such an increase in the degradation products of chlorophyll-a may also indicate that the population was suffering from stress, or was no longer in healthy log-phase growth. It may also indicate that the proportion of detrital phytoplankton cells was high because of the presence of faecal material from herbivorous zooplankton.

Chlorophyll-a to carotenoid ratios (Fig. 28) rose from 0.4 on May 14 to 2.5 on May 19. They drop to 1.0 as the bloom is initiated, remain at or near this value for the first 8 days of the bloom, only to rise sharply on May 30 to near 3.0. The low value of this ratio in the period immediately preceding the bloom may reflect a relative rise in carotenoid masking pigments. This period was one of maximum water clarity (Fig. 3) and high daily incident radiation (Table 1). Under such conditions chlorophyll-a in a lag-phase phytoplankton population may be de-activated by high light intensities (Fujita, 1970). Carotenoids are synthesized in large quantities and act as protective filters, perhaps by being photo-oxidized themselves (Salisbury and Ross, 1969).

The increase in chlorophyll-a to carotenoid ratio on May 19 indicates log-phase conditions. Cells are not suffering undue stress and growth rates are maximal. But as the bloom progresses and biomass increases, self-shading may limit the light penetrating to the deeper population. The relative carotenoid content may increase in response to light limitation. Carotenoid pigments, particularly, xanthophylls, have an active role in light-limited photosynthesis. They are able to transfer excitation energy directly to chlorophyll-a when illuminated. And since they absorb light at wavelengths unavailable to chlorophyll-a, they allow a much more efficient utilization of the light penetrating the deeper part of the euphotic zone, (Haxo and Blinks, 1960).

Carbohydrate to chlorophyll-a ratios dropped from 384 to 0, (Table 7) between May 19 and May 29, but then began to rise again on May 30. These values reflect an increase in the relative amount of chlorophyll-a as the bloom progresses. The increase in this ratio on May 30 may be a sign of increased nitrogen limitation as the result of a relative increase in the storage of carbon products as long-chain carbohydrates (Mykelstad and Haug, 1972).

Protein to chlorophyll-a ratios (Table 8) dropped from 740 on May 19 to 150 on May 30. High ratios are strongly indicative of a population actively dividing in healthy log-phase. Relative protein levels tend to drop as the population ages and no longer is producing nuclear proteins at a high rate. It is also likely that nitrogen limitation is affecting this ratio. As already discussed, under conditions of nitrogen limitation protein synthesis may be effectively halted long before other processes are affected. In the bloom population under observation, chlorophyll-a increased steadily between May 19 and May 30 at a pace which protein synthesis could not match.

These changes in phytoplankton chemical consitution compare in several instances with those obtained by Antia *et al* (1963) in Departure Bay. In the present situation carbohydrate to chlorophyll-a ratios, protein to chlorophyll-a ratios and protein to carbohydrate ratios disagree with Antia *et al*'s findings. These disagreements may be due in part to the presence of large quantities of non-plytoplankton carbohydrates, such as the cell- wall carbohydrates of the marine bacterium *Nocardia marina* found in significant amounts as clumps and on detritus in the water column at station 'E' during this study.

SUMMARY

The various environmental factors controlling the initiation and development of the spring diatom maximum in Saanich Inlet, B.C. were investigated in detail between March 22 and May 30, 1971. Changes in diatom biomass and the biochemical constituents of filtered material were measured at 2-day intervals at depth intervals to 50 m and correlated with changes in the physical and chemical environment, in particular; light, temperature, stability and the components of the nitrogen cycle. Changes in the physical and chemical characteristics of the water column to 50 m were measured at two-day intervals and were compared with changes in ambient nutrient and biochemical composition phytoplankton biomass.

In this period two peaks occurred in phytoplankton biomass. A first minor peak, represented by an increased level of chlorophyll-a and carbohydrates, occurred between April 14 and 27.

The steady drop in ambient nitrate levels accompanying this rise in phytoplankton biomass was strongly correlated with the increasing 24 h light budget. A steady increase in these two parameters was halted in early May by a recurrence of changeable weather, marked by dark days and unstable water conditions continuing throughout the middle of May. Through early and mid-May, chlorophyll-a levels remain low while the weather continued unstable. During this period filters cleared for microscopic examination contained few whole cells. Faecal pellets and broken diatom frustules were common and chlorophyll-a breakdown products in the form of phaeopigment were in high proportion to

chlorophyll-a. Water clarity was highest during this same period. At the same time, large numbers of the herbivorous larvacean, *Oikopleura* sp. were observed in surface waters. It is presumed that sub-optimal weather, water column instability and heavy grazing pressure combined to suppress an early diatom maximum.

In late May the weather stabilized into a long sunny, calm period, setting up a strong density stratification pattern in the water column. At the same time the Fraser River plune invaded the waters of the Inlet bringing increased nutrients to surface waters. Initiation of the second and largest peak of diatom biomass coincided with the penetration of the 8.5°C. isotherm into deeper water. This isotherm, at 0 m on May 14, had extended into 50 m on May 30. Simultaneously light conditions increased from less than 400 ly/day to more than 600 ly/day. During this period ambient levels of nitrate dropped steadily, in strong correlation with the increasing temperature of the water column. As *in situ* conditions became optimal for its growth, the bloom-forming diatom, *Thalassiosira rotula* Meunier began to increase in number along with two co-dominant species of *Chaetoceros*. At the peak of its growth, the doubling time of *T. rotula* approached 10 hours. This is very close to the minimum doubling time of 9 hours observed by Schöne (1972) in batch cultures of the same organism under light and temperature conditions similar to those found at the depth of maximum biomass.

After ten days the bloom began to sink, although cell numbers did not immediately drop. The biomass maximum was observed to sink from near the surface to approximately 10 m, the depth of strongest density discontinuity. Increased numbers of faecal pellets and Chaetoceros hypnospores were observed on the cleared filters towards the end of May, by which time nutrient levels had dropped to non-detectable levels.

The progress of this diatom increase was marked by a number of changes in the relative amounts of biochemical constituents of the filtered material. These changes were consistent with the progress of a phytoplankton population from active log-phase growth through steady-state and into senescence, and could be related to increased self-shading and to nutrient deficiency. Ratios of phaeopigment to true chlorophyll-a, integrated under a square meter to 50 m rose from 0.03 on May 21 to 0.21 on May 27. Carotenoid to true chlorophyll-a ratios rose from 0.2 to 1.2 between May 19 and May 27. Carbohydrate to chlorophyll-a ratios dropped from 151 to 23 in the same period. At the same time, protein to chlorophyll-a ratios drops from 740 on May 19 to 150 on May 30. Protein to carbohydrate ratios remained around 3.5 through most of the period but increased to 6.4 on May 30. Lipid to chlorophyll-a ratios showed a strong inverse relationship with cell carbon, being low when the latter was high and vice versa. Observations of these phenomena in culture experiments by other workers indicate that nitrogen limitation may be the factor most likely to effect such changes in biochemical constituents of the population.

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Table 1.

Sigma-t

TABLE 1

DATE		DEPTH (m)						
1971		0	5	10	15	25	40	50
April	14	—	—	—	—	—	—	—
	16	21.00	21.64	22.88	22.85	23.30	23.55	23.39
	19	20.98	21.83	22.12	22.97	23.38	23.48	23.57
	21	20.70	22.05	22.70	23.22	23.24	23.38	23.45
	23	20.55	21.33	22.42	22.77	23.20	23.37	23.43
	25	18.95	21.65	22.53	22.92	23.25	23.40	23.48
	27	20.23	20.10	21.45	21.97	22.22	22.35	23.05
May	3	18.00	20.95	21.97	22.50	22.62	23.26	23.18
	4	19.03	20.38	21.02	22.15	22.83	23.30	23.00
	6	19.05	20.50	21.00	22.70	22.50	23.05	23.30
	8	18.12	19.30	21.00	21.90	22.15	22.95	23.30
	13	20.82	21.75	22.20	22.45	22.83	22.95	23.30
	15	22.10	22.31	22.55	22.69	22.98	23.22	23.40
	17	21.53	22.10	21.45	22.70	22.98	23.22	23.40
	19	21.84	20.58	21.40	22.40	23.02	22.92	21.92
	21	20.00	21.20	21.20	22.70	23.05	23.30	23.47
	26	19.94	21.55	21.98	22.35	22.38	22.83	23.18
	27	20.24	21.35	21.81	22.11	22.68	22.98	23.17
	28	19.72	20.90	21.48	22.23	22.63	22.98	23.15
	30	19.82	20.42	21.50	22.00	22.50	22.82	23.02

Table 2.

Nitrate (μg-at m^{-3})

TABLE 2

DATE	DEPTH (m)						
1971	0	5	10	15	25	40	50
March 22	18.5	21.2	21.7	21.6	23.0	21.0	24.7
23	16.4	20.7	21.6	23.5	21.4	23.1	24.8
24	19.2	19.5	19.8	24.5	22.0	22.4	23.0
25	16.0	16.2	18.1	19.6		20.3	19.4
27	19.8	21.3	22.8	21.5	21.8	22.2	21.9
28	24.8	24.0	24.8	24.4	25.3	24.5	24.0
April 14	18.2	16.0	20.4	22.0	21.8	21.1	25.4
16	20.5	20.7	23.7	25.1	26.0	24.8	26.3
19	16.9	17.3	19.4	21.3	23.7	24.6	25.3
21	16.7	20.2	22.5	24.2	25.6	26.4	26.9
23	14.6	15.9	19.0	21.2	24.8	26.7	24.8
25	12.2	13.1	17.8	21.7	24.2	25.8	26.6
27	9.0	7.2	9.3	18.0	22.4	25.0	26.1
May 3	8.6	9.2	12.5	13.0	14.9	19.1	23.1
4	8.7	9.2	12.1	15.9	19.8	23.7	24.8
6	7.5	10.0	12.2	15.8	16.4	21.7	23.6
8	6.9	6.0	10.2	11.8	16.0	19.6	23.7
13	8.3	11.6	14.7	15.0	17.5	21.1	26.5
15	11.9	12.0	14.4	14.8	17.3	19.3	20.3
17	11.9	12.1	11.4	13.3	15.6	19.1	19.0
19	14.3	12.6	13.8	15.0	18.9	18.7	18.3
21	9.8	11.5	12.5	15.8	16.3	19.3	18.6
26	0.02	0.02	0.3	0.52	0.7	0.84	0.92
27							
28	0.07	0.00	0.00	0.43	0.79	0.84	1.0
30	0.06	0.18	0.25	0.50	0.78	0.86	1.0

Table 3

Nitrite (μg-at m^{-3})

TABLE 3

DATE 1971	DEPTH (m) 0	5	10	15	25	40	50
March 22	0.26	0.25	0.25	0.18	0.26	0.18	0.13
23	0.22	0.24	0.25	0.23	0.20	0.21	0.12
24	0.38	0.22	0.18	0.22	0.20	0.17	0.12
25	0.19	0.39	0.19	0.17		0.22	0.16
27	0.23	0.33	0.12	0.27	0.23	0.38	0.20
28	0.31	0.21	0.19	0.24	0.17	0.23	0.15
April 14	0.26	0.19	0.30	0.30	0.39	0.19	0.11
16	0.30	0.32	0.37	0.32	0.30	0.12	0.25
19	0.18	0.26	0.29	0.28	0.28	0.15	0.10
21	0.26	0.29	0.25	0.27	0.20	0.09	0.08
23	0.10	0.17	0.18	0.20	0.18	0.08	0.06
25	0.34	0.29	0.29	0.29	0.31	0.12	0.12
27	0.18	0.16	0.20	0.13	0.23	0.10	0.01
May 3	0.13	0.17	0.14	0.19	0.18	0.15	0.06
4	0.20	0.24	0.24	0.22	0.25	0.16	0.08
6	0.14	0.18	0.19	0.20	0.15	0.25	0.16
8	0.09	0.10	0.17	0.08	0.11	0.14	0.09
13	0.22	0.25	0.21	0.17	0.20	0.22	0.21
15	0.25	0.23	0.23	0.25	0.24	0.20	0.22
17	0.14	0.13	0.13	0.16	0.18	0.15	0.19
19	0.08	0.13	0.14	0.18	0.20	0.17	0.19
21	0.12	0.20	0.14	0.10	0.10	0.07	0.05
26	0.06	0.19	0.18	0.23	0.22	0.23	0.35
27							
28	0.02	0.06	0.08	0.18	0.21	0.28	0.32
30	0.03	0.07	0.09	0.14	0.15	0.29	0.32

Table 4

Ammonia, µg-at N m^{-3}.

TABLE 4

DATE		DEPTH (m)						
1971		0	5	10	15	25	40	50
April	14	3.20	4.20	3.50	4.85	5.42	4.00	4.10
	16	2.55	2.45	2.45	2.55	2.70	2.95	3.50
	19	3.86	3.26	3.37	3.66	3.80	4.12	3.94
	21	2.15	1.65	2.32	1.75	2.03	2.27	2.86
	23	2.61	2.42	2.55	3.42	2.65	2.74	2.62
	25	2.37	2.05	2.39	2.06	1.98	2.14	2.34
	27	2.44	3.48	2.75	2.95	3.18	3.06	3.26
May	3	1.67	1.71	2.04	2.12	2.14	2.13	2.24
	4	1.27	0.74	0.74	1.92	2.19	1.06	1.04
	6	1.36	2.17	2.28	2.64	2.46	1.99	1.70
	8	1.69	1.59	1.74	1.71	2.00	1.98	2.09
	13	2.50	3.32	3.53	2.66	4.10	3.88	2.34
	15	1.80	1.89	2.46	1.76	2.26	2.06	2.31
	17	1.25	1.33	1.68	1.80	2.06	1.94	1.82
	19	1.37	1.63	1.16	1.14	1.57	1.51	1.43
	21	0.16	0.57	0.43	1.11	0.66	0.94	0.61
	26	1.55	2.19	2.41	2.83	2.56	3.50	3.35
	27	0.06	0.00	0.00	0.12	0.72	0.76	0.78
	28	0.94	0.96	1.68	1.80	2.71	3.08	2.36
	30	1.73	1.11	1.55	1.53	1.99	3.10	3.05

Table 5.

Uncorrected chlorophyll-a
$mg\ m^{-3}$

TABLE 5

DATE 1971		DEPTH (m) 0	5	10	15	25	40	50
March	22	0.60	0.72	6.00	0.56	0.34	0.28	0.34
	23	0.50	0.73	1.55	0.53	0.30	0.27	0.11
	24	0.88	0.70	1.20	0.53	0.59	0.40	0.42
	25	1.43	1.18	1.72	0.95	0.74	0.38	0.41
	27	0.78	1.20	1.21	0.57	0.55	1.00	0.38
	28	0.72	0.74	0.85	0.67	0.72	0.52	0.29
April	14	1.30	1.50	0.81	0.69	0.42	0.45	0.18
	16	0.95	1.10	0.95	0.51	0.38	0.21	0.15
	19	1.65	2.16	2.10	1.25	0.63	0.28	0.20
	21	1.17		1.02	0.80	0.77	0.31	0.21
	23	1.45	2.32	2.40	2.46	1.15	0.53	0.45
	25							
	27	4.30	4.00	4.25	3.23	2.14	0.90	0.46
May	3	0.43	0.65	0.82	0.86	0.81	0.88	0.33
	4	0.75	0.80	1.32	1.00	0.85	0.80	0.44
	6	0.70	0.69	0.88	1.00	0.80	1.00	0.77
	8	0.48	0.93	0.39	0.41	0.15	0.15	0.26
	13	0.35	0.27	0.26	0.28	0.28	0.16	0.19
	15	0.50	0.44	0.32	0.33	0.35	0.18	0.23
	17	0.60	0.74	0.66	0.38	0.33	0.35	0.34
	19	0.49	0.45	0.52	0.45	0.16	0.13	0.15
	21	1.27	1.70	1.13	0.75	0.21	0.20	0.21
	26	1.69	5.86	5.75	5.88	3.50	1.15	0.62
	27	1.00	9.15	17.30	7.25	3.80	1.19	0.88
	28	0.67	4.80	9.34	7.42	2.77	0.89	0.47
	30	7.20	10.00	15.70	10.90	5.10	1.28	0.88

Table 6

Chlorophyll-a (mg $\bar{m}^3$)

(corrected for phaeopigments)

TABLE 6

DATE 1971		DEPTH (m) 0	5	10	15	25	40	50
March	22	0.54	0.54	3.74	0.60	0.00	0.60	0.54
	23	0.27	0.54	1.14	0.47	0.20	0.00	0.13
	24	0.26	0.20	0.80	0.67	0.67	0.47	0.60
	25	1.20	0.07	1.27	0.93	0.53	0.40	0.20
	27	0.00	0.06	0.39	0.00	0.00	0.00	0.00
	28	0.00	0.20	0.00	0.00	0.00	0.00	0.00
April	14	1.20	1.60	1.07	0.27	0.00	0.40	0.00
	16	0.27	0.67	1.20	0.40	0.29	0.27	0.00
	19	1.47	1.87	1.87	1.07	0.27		0.40
	21							
	23	0.00	0.07	1.61	1.41	0.40	0.00	0.00
	25							
	27	2.74	2.34	2.47	2.20	1.00	0.00	0.00
May	3							
	4	0.00	0.00	0.46	0.20	0.00	0.00	
	6	0.00	0.07	0.40	0.00	0.07	0.14	0.00
	8	0.40	0.27	0.40	0.27	0.13	0.27	0.27
	13	0.40	0.27	0.13	0.27	0.27	0.00	0.00
	15	0.53	0.27	0.13	0.40	0.80	0.13	0.13
	17	0.13	0.00	0.00	0.00	0.00	0.00	0.00
	19	0.53	0.67	0.67	0.80	0.13	0.13	0.40
	21	1.47	1.47	0.67	0.94	0.27	0.13	0.40
	26	1.20	5.07	5.34	5.74	3.20	—	0.40
	27	0.94	8.54	16.69	6.41	3.34	0.67	0.40
	28	0.00	4.54	8.68	6.94	2.40	0.67	0.00
	30	6.81	9.21	14.82	9.75	4.54	0.80	0.27

Table 7.

Phaeopigments (mg m^{-3})

TABLE 7

DATE	DEPTH (m)						
1971	0	5	10	15	25	40	50
March 22	0.18	2.37	3.79	0.08	0.84	1.31	0.00
23	0.39	0.36	1.74	0.10	0.52	0.70	0.00
24	1.09	1.11	0.70	0.02	0.15	0.22	0.06
25	0.44	2.13	0.79	0.05	0.36	0.00	0.45
27	3.56	5.07	1.42	1.87	2.73	5.12	5.58
28	5.89	1.13	2.48	6.14	3.54	2.03	2.20
April 14	0.02	0.00	0.00	0.08	0.28	0.00	0.03
16	0.11	0.14	0.00	0.03	0.02	0.00	0.04
19	0.30	0.38	0.37	0.43	0.66	—	0.00
21	—	—	—	—	—	—	—
23	0.66	0.90	0.30	0.44	0.28	0.42	0.36
25	—	—	—	—	—	—	—
27	0.54	0.90	0.63	0.33	0.41	0.00	0.00
May 3	—	—	—	—	—	—	—
4	0.66	0.60	0.32	0.36	0.55	0.51	
6	0.47	0.32	0.18	0.46	0.28	0.34	0.51
8	0.16	1.13	0.06	0.29	0.60	0.00	0.01
13	0.00	0.11	0.24	0.01	0.11	0.28	0.37
15	0.00	0.29	0.33	0.00	0.00	0.02	0.00
17	0.19	0.77	0.61	0.52	1.31	0.62	0.40
19	0.00	0.00	0.00	0.00	0.06	0.05	0.15
21	0.00	0.50	0.82	0.00	0.00	0.15	0.00
26	0.86	1.27	0.73	0.24	0.53	—	0.08
27	1.46	0.42	1.04	0.44	0.68	0.45	0.75
28	1.46	0.42	1.04	0.44	0.68	0.45	0.75
30	0.66	1.34	1.35	2.00	0.68	0.88	1.01

Table 8

Carotenoids, (mg/ m^{-3})

TABLE 8

DATE	DEPTH (m)						
1971	0	5	10	15	25	40	50
March 22	289.4	219.0	625.0	132.8	85.9	66.4	50.8
23	383.1	386.9	445.6	199.0	23.4	62.5	210.9
24	258.1	265.6	242.5	39.4	164.4	31.3	218.9
25	187.5	156.3	250.0	196.3	148.4	7.8	70.3
27	125.0	156.3	148.4	140.6	148.4	109.4	242.2
28	148.4	97.5	46.9	85.9	46.9	312.5	62.5
April 14	242.2	273.4	175.8	125.0	93.8	59.0	93.8
16	199.2	168.0	187.5	156.3	148.4	109.4	82.0
19	203.1	156.3	125.0	781.3	27.5	8.1	66.3
21	281.3	226.9	74.4	74.4	90.0	55.0	46.9
23	242.2	265.5	187.5	125.0	93.8	62.5	97.7
25	460.9	128.9	343.8	125.0	218.8	93.8	66.4
27	601.6	421.9	320.3	222.7	203.1	74.2	156.3
May 3	453.1	226.9	273.8	265.6	165.6	101.9	187.5
4	258.1	218.8	625.0	140.6	86.3	70.6	46.9
6	281.3	125.0	125.0	187.5	140.6	125.0	105,6
8	383.1	468.8	906.3	296.9	203.1	242.5	164.4
13	250.0	156.3	125.0	117.5	46.9	46.9	—
15	180.0	133.1	101.9	140.6	62.5	234.4	93.8
17	109.4	180.0	78.1	93.8	78.1	93.8	101.9
19	140.6	140.6	125.0	203.1	101.9	218.8	187.5
21	453.1	383.1	281.3	305.0	109.4	78.1	15.6
26	351.9	445.6	320.6	390.6	211.3	101.9	101.9
27	383.1	593.9	555.0	359.4	187.5	109.4	203.1
28	226.9	453.1	226.9	578.1	195.6	156.3	109.4
30	781.3	1187.5	523.8	640.6	250.0	109.4	133.1

Table 9. Carbohydrate

mg glucose m^{-3}

TABLE 9

DATE		DEPTH (m)						
1971		0	5	10	15	25	40	50
March	22	0.58	0.73	4.53	0.83	0.73	0.95	0.63
	23	0.63	0.88	1.53	0.60	0.40	0.23	0.05
	24	1.60	1.18	1.55	1.66	1.68	1.08	0.55
	25	2.13	1.65	1.90	1.49	1.08	0.65	0.68
	27	0.85	0.88	1.19	0.55	0.30	0.53	0.40
	28	1.03	1.15	1.08	0.85	1.10	1.00	0.83
April	14	1.65	1.78	0.90	0.85	0.60	0.70	0,50
	16	0.88	1.13	0.90	0.43	0.78	0.35	0.23
	19	1.55	2.63	2.40	1.38	0.75	0.40	0.40
	21	0.75	—	0.85	0.75	0.65	0.45	0.55
	23	1.48	2.60	2.33	2.38	1.45	0.70	0.53
	25	—	—	—	—	—	—	—
	27	4.25	4.40	3.63	2.65	2.00	0.85	0.78
May	3							
	4	0.85	0.93	1.18	1.03	0.70	0.95	0.83
	6	1.38	1.05	1.65	1.33	1.13	1.58	1.18
	8	0.65	1.23	0.55	0.48	0.23	0.13	0.18
	13	0.55	0.58	0.60	0.50	0.53	0.55	0.40
	15	0.63	0.63	0.58	0.70	0.40	0.38	0.55
	17	1.18	1.40	1.05	0.68	0.85	0.80	1.08
	19	0.40	0.50	0.35	0.25	0.12	0.12	0.33
	21	1.20	1.65	1.03	0.88	0.15	0.25	0.30
	26	2.20	4.88	4.18	4.80	3.18	1.15	0.85
	27	1.25	6.35	11.95	11.40	5.35	1.33	1.30
	28	1.03	3.63	1.55	5.15	2.50	1.13	0.58
	30	4.43	6.00	9.88	7.20	4.15	1.28	0.83

Table 10.

Protein (mg m^{-3})

(Protein = N x 6.25)

TABLE 10

DATE 1971		DEPTH (m) 0	5	10	15	25	40	50
March	22	181		356	168	100	112	100
	23	134	145	171	110	129	74	129
	24	163	101	102	66	85	141	90
	25	245	119	139	68	123	86	63
	27	117	98	152	145	182	81	257
	28	189	208	225	129	181	134	202
April	14	—	—	—	—	—	—	—
	16	134	126	124	124	151	124	136
	19	—	—	—	—	—	—	—
	21	—	—	—	—	—	—	—
	23	170		168	136	139	175	129
	25	153	137	134	146	134	206	147
	27	220	171	181	174	190	163	174
May	3	138	118	85	87	63	65	149
	4	101	89	113	56	99	64	156
	6	96	74	76	104	93	78	96
	8	85	104	60	77	46	60	56
	13	122	227	120	72	84	65	—
	15	215	159	129	213	173	230	193
	17	81	192	105	135	96	122	159
	19	189	126	79	67	34	32	48
	21	262	176	108	80	78	42	60
	26	300	335	130	100	96	84	111
	27	148	556	214	—	103	114	94
	28	243	259	212	—	87	52	89
	30	349	1112	156	148	75	99	73

Table 11.

Particulate nitrogen (mg m^{-3})

TABLE 11

DATE		DEPTH (m)						
1971		0	5	10	15	25	40	50
March	22	46.3	35.0	100.0	21.3	13.8	10.6	8.1
	23	61.3	61.9	71.3	31.9	3.8	10.0	33.8
	24	41.3	42.5	38.8	6.3	26.3	5.0	35.0
	25	30.0	25.0	40.0	31.3	23.8	1.3	11.3
	27	20.0	25.0	23.8	22.5	23.8	17.5	38.8
	28	23.8	15.6	7.5	13.8	7.5	50.0	10.0
April	14	38.8	43.8	28.1	20.0	15.0	9.4	15.0
	16	31.9	26.9	30.0	25.0	23.8	17.5	13.1
	19	32.5	25.0	20.0	125.0	4.4	1.3	10.6
	21	45.0	36.3	11.9	11.9	14.4	8.8	7.5
	23	38.8	42.5	30.0	20.0	15.0	10.0	15.6
	25	73.8	20.6	55.0	20.0	35.0	15.0	10.6
	27	96.3	67.5	51.3	35.6	32.5	11.9	25.0
May	3	72.5	36.3	43.8	42.5	26.4	16.3	30.0
	4	41.3	35.0	100.0	22.5	13.8	11.3	7.5
	6	45.0	20.0	20.0	30.0	22.5	20.0	16.9
	8	61.3	75.0	145.0	47.5	32.5	38.8	26.3
	13	40.0	25.0	20.0	18.8	7.5	7.5	—
	15	28.8	21.3	16.3	22.5	10.0	37.5	15.0
	17	17.5	28.8	12.5	15.0	12.5	15.0	16.3
	19	22.5	22.5	20.0	32.5	16.3	35.0	30.0
	21	72.5	61.3	45.0	48.8	17.5	12.5	2.5
	26	56.3	71.3	51.3	62.5	33.8	16.3	16.3
	27	61.3	95.0	88.8	57.5	30.0	17.5	32.5
	28	36.3	72.5	36.3	92.5	31.3	25.0	17.5
	30	125.0	190.0	83.8	102.5	40.0	17.5	21.3

Table 12

Ratio of carotenoids to

chlorophyll-a (uncorrected)

TABLE 12

DATE		DEPTH (m)						
1971		0	5	10	15	25	40	50
March	22	0.96	1.00	0.76	1.40	2.10	3.30	1.80
	23	1.25	1.20	1.00	1.10	1.60	0.85	0.44
	24	1.81	1.70	1.30	3.10	2.60	2.60	1.30
	25	1.48	1.39	1.08	1.55	1.50	1.70	1.70
	27	1.09	0.79	0.95	0.93	0.54	0.50	1.10
	28	1.43	1.50	1.10	1.30	1.50	1.90	2.80
April	14	1.29	1.10	1.10	1.20	1.40	1.90	3.00
	16	0.97	0.94	0.93	0.83	2.00	3.20	1.60
	19	0.93	1.20	1.20	1.08	1.19	1.36	1.99
	21	—	—	—	—	—	—	—
	23	0.99	2.24	0.97	0.96	1.25	1.30	1.16
	25	—	—	—	—	—	—	—
	27	0.99	1.10	0.87	0.82	0.93	0.96	1.71
May	3	—	—	—	—	—	—	—
	4	1.05	1.22	0.89	1.01	0.86	1.26	1.84
	6	1.98	1.53	1.86	1.36	1.41	1.58	1.54
	8	1.32	1.32	1.41	1.14	1.45	0.81	0.62
	13	1.60	2.07	2.35	1.94	1.76	3.45	2.35
	15	1.24	1.47	1.92	2.07	1.22	2.09	2.44
	17	2.05	1.88	1.62	1.79	2.61	2.26	3.12
	19	0.82	1.07	1.24	0.53	1.13	1.11	1.68
	21	0.94	0.99	0.91	1.17	0.78	1.26	1.46
	26	1.30	0.83	0.72	0.82	0.91	1.00	1.36
	27	1.28	0.69	0.69	1.57	1.40	1.11	1.50
	28	1.53	1.76	0.71	0.69	0.91	1.26	1.23
	30	0.62	0.60	0.64	0.66	0.81	1.00	0.94

Table 13

Ratio of particulate nitrogen
to chlorophyll-a

TABLE 13

DATE 1971		DEPTH (m) 0	5	10	15	25	40	50
March	22	68.7	47.4	16.7	38.9	38.3	41.2	24.0
	23	124.2	86.8	46.1	60.6	11.6	39.5	311.9
	24	47.1	61.2	32.7	12.5	44.5	13.9	83.2
	25	21.4	21.6	23.1	33.4	32.7	3.2	2.1
	27	26.3	20.7	19.4	40.1	44.8	17.0	100.6
	28	32.3	21.1	9.9	20.5	10.7	96.4	40.9
April	14	29.3	28.7	35.0	28.4	35.6	21.6	40.9
	16	33.8	23.6	31.1	49.6	61.1	81.7	88.2
	19	20.3	11.6	9.4	100.6	7.8	2.3	52.9
	21	—	—	—	—	—	—	—
	23	26.3	18.6	12.1	8.0	13.0	18.3	34.0
	25	—	—	—	—	—	—	—
	27	22.4	16.9	12.0	11.1	15.3	12.9	52.6
May	3	—	—	—	—	—	—	—
	4	54.9	42.7	75.7	21.8	15.3	14.4	18.5
	6	63.1	31.0	25.0	30.4	28.4	20.0	21.7
	8	138.6	80.7	371.6	114.0	215.9	257.7	98.9
	13	114.9	92.9	77.1	69.4	24.7	52.4	—
	15	57.3	48.9	52.3	68.3	30.7	210.2	64.4
	17	29.9	37.8	19.0	39.0	35.6	43.6	47.7
	19	44.8	49.1	39.6	70.1	100.9	269.3	202.1
	21	56.4	35.7	40.1	66.8	81.8	60.7	15.9
	26	33.4	12.1	9.1	10.6	9.7	13.4	24.3
	27	66.6	10.3	5.1	7.9	8.3	15.3	37.5
	28	54.1	15.1	3.8	12.3	11.3	27.6	36.8
	30	17.3	18.9	5.4	9.4	7.8	13.9	23.3

Table 14.

Ratio of chlorophyll-a

to total carotenoids

TABLE 14

DATE 1971		DEPTH (m) 0	5	10	15	25	40	50
April	14	0.73	0.90	1.19	0.31	0.00	0.57	0.00
	16	0.30	0.59	1.34	0.93	0.38	0.76	0.00
	19	0.95	0.71	0.78	0.77	0.36	—	1.00
	21	—	—	—	—	—	—	—
	23	0.00	0.03	0.69	0.59	0.28	0.00	0.00
	25	—	—	—	—	—	—	—
	27	0.65	0.53	0.68	0.83	0.50	0.00	0.00
May	3	—	—	—	—	—	—	—
	4	0.00	0.00	0.39	0.19	0.00	0.00	
	6	0.00	0.06	0.24	0.00	0.06	0.09	0.00
	8	0.62	0.22	0.73	0.56	0.58	2.05	1.48
	13	0.73	0.46	0.22	0.53	0.50	0.00	0.00
	15	0.85	0.42	0.23	0.58	2.00	0.35	0.79
	17	0.11	0.00	0.00	0.00	0.00	0.00	0.00
	19	1.34	1.34	1.91	3.20	1.12	1.12	0.41
	21	1.22	0.89	0.65	1.06	1.78	0.54	1.34
	26	0.55	1.04	1.28	1.20	1.01	—	0.47
	27	0.75	1.35	1.40	0.56	0.62	0.50	0.31
	28	0.00	1.25	1.32	1.35	0.96	0.59	0.00
	30	1.54	1.54	1.50	1.35	1.09	0.63	0.32

Table 15

Nitrogen sources mg-at m^{-3} integrated below a m^2 to 50 m.

TABLE 15

DATE 1971		NITROGEN SOURCES Nitrate-N	Nitrite-N	Ammonia-N	Part.-N	Total N
April	14	1055	13.13	217.5	138.4	1423
	16	1250	12.88	137.5	156.3	1556
	19	1175	11.05	187.5	212.0	1586
	21	1220	9.08	105.0	109.4	1443
	23	1135	7.00	135.0	138.4	1412
	25	1110	11.95	104.0	185.3	1411
	27	970	7.25	152.5	241.0	1371
May	3	775	7.75	100.0	216.6	1100
	4	925	9.88	67.5	176.3	1178
	6	840	9.50	107.5	160.7	1118
	8	745	5.85	92.5	366.1	1209
	13	875	10.43	170.0	87.0	1142
	15	830	11.25	104.0	149.6	1096
	17	775	7.75	88.1	111.6	988
	19	835	8.50	70.0	185.3	1099
	21	795	5.08	36.9	214.3	1051
	26	30	11.13	140.0	272.4	453
	27	—	—	21.9	325.9	—
	28	30	10.25	110.6	294.6	445
	30	32	7.38	106.3	464.3	610

Table 16

Nitrogen sources mg m^{-2}
(Integrated under a m^{2} to 0.0015 ly/min.)

TABLE 16

DATE		NITROGEN SOURCES				
1971		Nitrate-N	Nitrite-N	Ammonia-N	Part. -N	Total N
April	14	467	7.45	97.6	102.7	675
	16	387	5.95	45.0	69.2	507
	19	399	6.50	76.1	158.4	640
	21	459	5.40	41.5	70.5	576
	23	415	3.85	62.5	87.5	569
	25	420	7.50	53.1	129.5	610
	27	101	2.13	36.3	118.3	257
May	3	312	3.58	50.0	154.5	520
	4	248	4.55	25.0	129.4	407
	6	365	3.75	63.8	100.5	533
	8	308	3.10	47.5	263.0	622
	13	370	5.58	89.4	83.0	548
	15	518	7.90	70.0	84.8	681
	17	445	4.53	52.5	72.3	574
	19	423	4.50	36.3	84.8	548
	21	380	3.38	18.1	170.5	571
	26	3.1	2.50	33.8	126.8	166
	27	—	—	10.0	137.1	—
	28	1.2	1.28	19.4	118.3	140
	30	5.0	1.65	26.3	308.0	341

Table 17

Nitrogen sources mg m^{-2}

(integrated under a m^2 down to 1% surf. light)

TABLE 17

DATE 1971	NITROGEN SOURCES Nitrate-N	 Nitrite-N	 Ammonia-N	 Part.-N	 Total N
April 14	357	4.98	72.6	89.3	517
16	335	5.25	38.8	62.1	483
19	287	4.05	58.0	104.0	412
21	323	4.10	32.5	62.5	437
23	298	2.88	44.6	76.8	443
25	242	5.25	38.1	98.2	403
27	101	2.13	36.3	118.3	257
May 3	312	2.15	38.8	125.0	378
4	248	4.55	25.0	129.5	407
6	245	2.75	50.0	73.7	372
8	193	2.30	33.1	232.1	832
13	322	5.03	61.9	80.4	469
15	360	5.98	50.1	64.7	481
17	346	4.00	42.5	62.5	455
19	285	3.00	25.6	64.7	379
21	278	2.75	13.1	147.3	441
26	1.45	1.80	26.3	98.2	128
27	—	—	0.08	99.6	—
28	0.25	0.78	15.0	91.5	108
30	1.45	0.53	11.3	183.0	196

Table 18.

Particulate Analyses

(integrated under a m^2 down to 50 m)

TABLE 18

PARTICULATE ANALYSIS

DATE 1971		True Chl a mg/m^2	Phaeopigment mg/m^2	Carotenoids mg/m^2	Carbohydrate mg/m^2	Protein mg/m^2
April	14	22.00	4.30	41.75	—	12,112
	16	20.75	1.45	38.50	6,500	13,675
	19	38.75	20.25	52.50	—	18,550
	21	—	—	34.25	—	9,575
	23	23.75	21.46	77.75	7,688	12,113
	25	—	—	—	6,813	16,213
	27	60.05	15.50	106.50	8,750	21,088
May	3	—	—	—	4,250	18,950
	4	4.25	19.55	43.00	4,250	15,425
	6	5.00	17.06	65.00	4,250	14,063
	8	12.00	9.01	17.00	3,000	32,038
	13	8.00	8.00	26.75	4,563	7,613
	15	18.50	3.10	25.25	9,250	13,088
	17	0.30	36.90	45.25	6,000	9,769
	19	21.80	1.80	11.50	2,625	16,213
	21	29.00	8.70	29.25	4,375	18,750
	26	155.00	29.00	142.50	6,500	23,831
	27	217.50	45.50	261.50	8,500	28,519
	28	155.00	31.00	132.50	6,250	40,625
	30	275.00	43.50	161.75	6,375	40,625

Table 19

Particulate analyses

(integrated under a m^2 to 0.0015 ly/min.)

TABLE 19

DATE			PARTICULATE ANALYSIS				
1971		D. comp. .0015 ly min.	True Chl a mg/m^2	Phaeopig. mg/m^2	Carotenoid mg/m^2	Carbohyd. mg/m^2	Protein mg/m^2
April	14	23.5	17.50	1.65	26.25	—	8,981
	16	17.7	12.75	0.90	15.75	2,188	6,056
	19	21.8	29.50	9.80	38.75	—	13,863
	21	21.8	—	—	17.00	—	6,175
	23	22.2	18.50	11.36	36.75	3,363	7,656
	25	25.0	—	—	—	3,375	11,331
	27	12.0	30.50	8.65	48.50	2,188	10,350
May	3	26.5	—	—	—	2,313	13,519
	4	20.0	3.75	9.15	20.00	1,625	11,331
	6	27.5	3.25	9.10	33.75	2,500	8,788
	8	27.5	6.60	8.92	14.50	1,875	23,050
	13	26.7	6.25	2.45	16.25	3,125	7,269
	15	33.7	15.00	3.02	18.50	6,063	7,425
	17	32.6	0.30	25.65	29.25	4,125	6,325
	19	27.4	17.50	0.23	8.00	1,938	7,425
	21	26.7	26.75	7.76	24.75	3,188	14,925
	26	15.0	68.50	13.05	62.50	3,375	11,094
	27	11.4	106.00	9.10	76.75	3,688	11,994
	28	15.3	86.75	11.50	67.00	3,375	10,350
	30	18.0	204.00	26.50	76.75	3,500	26,956

Table 20

Particulate analyses

(integrated under a m^2 down to 1% surf. light)

TABLE 20

PARTICULATE ANALYSIS

DATE 1971		D. comp.	True Chl a mg/m^2	Phaeopig. mg/m^2	Carotenoids mg/m^2	Carbohyd. mg/m^2	Protein mg/m^2
April	14	18.5m	17.25	0.70	22.75	—	7,813
	16	15.7	11.75	0.83	15.00	1,938	5,421
	19	16.8	26.25	7.10	34.00	—	9,100
	21	17.2	—	—	14.00	—	5,469
	23	16.7	14.25	9.56	36.75	2,688	6,719
	25	17.3	—	—	—	2,375	10,350
May	3	19.3					10,938
	4	20.0	3.75	9.15	20.00	1,625	11,331
	6	20.0	2.75	6.76	25.25	1,750	6,444
	8	19.7	5.80	8.32	12.50	1,500	20,313
	13	24.0	5.70	2.18	14.75	2,875	7,031
	15	25.0	10.00	2.95	15.00	4,313	5,663
	17	26.4	0.30	19.30	24.45	3,500	5,469
	19	19.7	16.25	0.18	6.50	1,688	12,894
	21	20.5	23.75	6.58	22.75	2,688	12,894
	26	11.6	49.00	11.60	47.00	2,813	8,594
	27	8.7	68.50	7.05	50.25	3,188	8,713
	28	12.3	64.25	10.00	51.00	2,875	8,006
	30	8.5	75.00	8.20	46.00	2,188	16,019

Table. 21. Lipid in seston, 0 to 50 m
March 28 to May 30.

TABLE 21

LIPID mg/m^3

Depth (m)	0	5	10	15	25	40	50
March 28	1430	1170	1520	1480	1080	1260	1240
April 14	1085	1360	1930	1500	1370	1460	1590
May 21	730	560	990	720	515	640	600
May 26	1160	960	800	1200	250	320	350
May 27	640	1010	900	630	600	1000	930
May 28	540	450	490	——	480	410	470
May 30	480	650	1000	1060	810	410	510

Table 22.

BASIC program for linear regression analysis

TABLE 22

BASIC Program for

Linear Regression Analysis

$$R = \frac{(x_1 - \bar{x})^2 + (X_2 - \bar{x})^2 + \;.\;.\;.\;.\;.(x_n - \bar{x})^2}{n}$$

```
Linreg  23:32                            29-Sep-75

10  Print "Linear Regression Analysis"
20  Dim X(20), Y(20)
30  Input "Number of Data Points =";  N
40  For I = 1 to N
50  Print "X("I;") =";: Input X(I)
60  Print "Y("I;") =";: Input Y(I)
70  X(I) = FNX(X(I))
80  Y(I) = FNY(Y(I))
90  Next I
100 Input "Number of Data Changes Desired = "; N1
110 If N1 = 0 Then 190
120 For I1 = 1 to N1
130 Input "Case Number ="; 12
140 Print "X(";12;") = ";: Input X(12)
150 Print "Y(";12;") = ";: Input Y(12)
160 X(L@) = FNX(X(12))
170 Y(12) = FNY(Y(12))
180 Next I1
190 S1,S2,S3,S4,S5 = 0
200 For I = 1 to N
210 S1 = S1 + X(I)
220 S2 = S2 + X(I)12
230 S3 = S3 + Y(I)
240 S4 = S4 + Y(I)12
250 S5 = S5 + X(I)*Y(I)
260 Next I
270 D = N*S2-S1 2
280 M = (N*S5-S1*S3)/D
290 B = (S3*S2-S1*S5)/D
300 S8 = SOR((N/(N-2))*(S4-M*S5-B*S3)/D)
310 S9 = S8*SQR(S2/N)
320 R = (N*S5-S1*S3)?SQR(D*(N*S4-S3 2)
330 Print "Slope = " M; "+-" S8
340 Print "Y-Intercep = " B;  "+-" S9
350 Print "Correlation Coefficient = " R
360 Def FNX(X) = X
370 Def (FNY(Y) = Y
380 END
```

Table 23.

Growth rate:

Equation for crop doubling per day

TABLE 23

Growth rate = crop doublings per day

μ = doublings per day

$$= \frac{3.32}{t} \log_{10} \left[\frac{P_o + \delta P}{P_o}\right]$$

t = days

$3.32 = \log_2 10$

P_o = initial crop size in g C/m^2

δP = daily increment in crop size
net carbon assimilation g C/m^2/day

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IN SAANICH INLET

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