SEASONALITY, SINKING AND THE CHLOROPHYLL MAXIMUM OF AN OLIGOTROPHIC BRITISH COLUMBIA LAKE

by

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ABSTRACT

A field investigation was carried out over two seasonal periods on an oligotrophic coastal British Columbia lake to determine the role of sinking in the formation of the chlorophyll maximum as well as some aspects of phytoplankton seasonality.

Sinking rates of two diatoms were measured and found to be highest in the epilimnion and lowest at the depth of the chlorophyll maximum. Light affected sinking rate as well as the position of the chlorophyll maximum. The chlorophyll maximum formed at 10-12 m following the onset of seasonal thermal stratification and descended to ca. 22 m for the summer. A major factor in the formation of the chlorophyll maximum is the decrease of phytoplankton sinking rate at depth.

Rhizosolenia eriensis is one of the first phytoplankters to bloom in the spring. Small flagellates (3-15 um) and occasionally Dinobryon sp. were also important numerically. In the summer Cyclotella spp. displaced R. eriensis as the dominant diatom in the epilimnion. The relative timing of seasonal maxima of blooms of various species remained similar during the two years investigated.

Lake fertilization affected the phytoplankton standing stock. R. eriensis did not greatly benefit from fertilization since it

sank out of the epilimnion and became a major constituent of the chlorophyll maximum before fertilization. Because of its large size and low C : cell volume ratio due to a large vacuole, R. eriensis is probably not a good food source for zooplankton.

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Introduction

Lake Enrichment Programme

The federal government of Canada and provincial government of British Columbia jointly run the Salmonid Enhancement Programme (SEP) which has as its goal, the enhancement of declining sockeye salmon (Oncorhynchus nerka) stocks. Krokhin (1967) suggested that the comercial salmon fishery may cause a nutrient deficit in lakes by decreasing the number of salmon carcasses available for decay and release of nutrients. Therefore, fertilization of such lakes may replace this potential nutrient deficit.

One of three major sections of SEP is the Lake Enrichment Programme (LEP). Through addition of inorganic nitrogen and phosphorus (in the form of agricultural grade fertilizer) to selected ultra-oligotrophic lakes in which sockeye salmon spawn, LEP has increased primary production, which has in turn increased secondary production and resulted in more food being available to juvenile sockeye (Barraclough and Robinson, 1972; LeBrasseur and Kennedy, 1972; Parsons et. al., 1972; Stockner and Shortreed, 1985).

Larger juvenile sockeye result from an increase in available food (zooplankton) in LEP's study lakes. Ricker (1962) noted that larger juvenile sockeye salmon have a higher "in-lake" survival and those migrating to sea have a higher "at-sea" survival rate

than smaller counterparts. Additionally, Hyatt and Stockner (1985) suggest that larger sockeye smolts may decrease their age-at-return as adults.

It is desirable to have an enrichment regime which ultimately results in enhancement of sockeye salmon populations only. The cost-effectiveness of LEP's programme can be maximized if nutrient added to lakes is incorporated into the sockeye salmon food chain. The efficiency of this process will be high if there are only two steps in the resulting food chain (ie., phytoplankton ---> zooplankton ---> juvenile sockeye salmon). A decreaease in cost-effectiveness may occur if there are more than two steps in the resulting food chain or if predators other than juvenile sockeye consume the enhanced zooplankton stock.

A common and abundant pelagic diatom, Rhizosolenia eriensis has increased notably in some lakes following nutrient enrichment (Parsons et al., 1967; J.G. Stockner, pers. comm.). Following bloom conditions in the spring this diatom sinks and becomes a major constituent (both in terms of numbers and biovolume) of a hypolimnetic chlorophyll maximum (Stockner and Hyatt, 1984) which typically persists through the summer until fall overturn.

Incorporation of R. eriensis into the chlorophyll maximum typically occurs at the bottom of the euphotic zone (defined as 1% surface irradiance or greater) concurrent with the nitracline (J.G. Stockner, pers comm.). Prevailing light and nutrient

conditions at depth may play a role in chlorophyll maximum formation by altering cellular buoyancy of R. eriensis as it encounters different environmental conditions while sinking through the mixed layer and thermocline.

Rhizosolenia eriensis is a large centric diatom with a length of of 100-150 um. Filter feeding zooplankton may not be capable of efficiently grazing this alga due to its relatively large size (Parsons et al., 1967). Hence, blooms and subsequent incorporation into the chlorophyll maximum may represent an energy loss (as nutrients) or carbon sink through diversion from food chains leading to juvenile sockeye in fertilized lakes. To understand the potential impact of R. eriensis in relation to the cost-effectiveness of the Lake Enrichment Programme, an understanding of the biology of this diatom is required. A useful starting point is an investigation of the physiological ecology of R. eriensis, concentrating on the effect(s) of various environmental parameters on sinking rate and chlorophyll maximum formation and maintenance.

Chlorophyll maxima

Phytoplankton physiologists studying pelagic communities are often interested in obtaining a convenient, semi-quantitative measurement of phytoplankton biomass. In vivo chlorophyll fluorescence (Lorenzen, 1966) has become a standard measurement used to estimate the concentration of chlorophyll a, which serves

as a rough index of photosynthetically active biomass. One disadvantage of using an in vivo fluorescence technique is that it does not include heterotrophic phytoplankton. A feature characteristic of many vertical in vivo fluorescence profiles is a subsurface fluorescence maximum (Cullen, 1982). This feature exists in oceans (Anderson, 1969; Venrick et al., 1973), large lakes (Kiefer et al., 1973; Moll et al., 1984) and small lakes (Fee, 1978). Despite the fact that chlorophyll maxima are frequent features observed in vertical fluorescence profiles, their contribution to net areal primary production is poorly understood.

The subsurface chlorophyll maximum is often found associated with low light levels. This layer typically occurs at about the 1% surface irradiance level (Fee, 1976) but it may occur at levels up to 5% surface irradiance (Moll et al., 1984). In addition to low light levels, subsurface chlorophyll maxima often occupy (vertically) relatively thin layers (ca. 5-20 m; Postel, 1975) in close proximity to strong vertical gradients. Such gradients vary and may include the nutricline (Kiefer et al., 1975), thermocline (Cullen, 1982) or pycnocline (Postel, 1975).

Cullen (1982) has classified four types of chlorophyll maxima based on the method of formation in each case. This classification is briefly outlined below:

I. Chlorophyll maximum and primary production maximum near the nitracline: typical tropical structure (TTS). This classification follows from Dugdale's (1967) concept of the euphotic zone as a two-layered system where phytoplankton growth is nutrient-limited in the upper layer and light-limited in the lower layer. The chlorophyll and primary production maxima occur in the transition zone where phytoplankton switch from light-limited to nutrient-limited growth. One can visualize such a chlorophyll maximum in the tropics or temperate zone during summer stratification. It is necessary for the euphotic zone depth to exceed the depth of the thermocline so light is present below the mixed layer. This assumes the nitracline is coincident with the thermocline and that nitrogen is the nutrient which limits phytoplankton growth.

II. Physiological adaptation of C : Chl a. One physiological adaptation to low light intensities by phytoplankton is an increase in Chl a per cell (Beardall and Morris, 1976; Banse, 1977; Prezelin and Matlick, 1980). An observed chlorophyll maximum may simply be an adaptation to the low light intensities present at the stratum where the chlorophyll maximum is located and may not necessarily be a biomass (= carbon) maximum.

III. Behavioral aggregation. While any type of aggregation

might broadly be considered a behavioral response, the present context equates behavior to motility. Therefore, behavioral aggregation would be almost exclusively exhibited by flagellated cells. Exceptions may be envisioned such as with the ciliate Mesodinium rubrum, which is known to contain algal pigments (Holm-Hansen et al., 1970). M. rubrum may contribute significantly to organic production in some regions (Smith and Barber, 1979) and may therefore have a significant impact on chlorophyll maximum dynamics. Many dinoflagellates exhibit phototactic diurnal vertical migration. Such cells are typically found in surface waters during daylight hours and deeper during the night. Movement of whole populations on a diurnal basis results in movement of the chlorophyll maximum, as demonstrated for Gymnodinium splendens in the Southern California bight (Lasker, 1975; Fielder, 1982). Generally, motile phytoplankton are capable of vertical movement and of forming thin layers (Harris et al., 1979; Falkowski et al., 1980).

IV. Decrease in sinking rate. Steele and Yentsch (1960) demonstrated that nutrient-limited diatoms sink and accumulate at a subsurface nitracline. Sinking rate of Thalassiosira pseudonana is significantly lower at light intensities characteristic of the subtropical chlorophyll maximum than at light intensities characteristic of the overlying mixed layer (Bienfang et al., 1983). Such a response suggests that growth at low irradiances may create physiological changes which are

manifested, in part, by alteration of cell buoyancy. Bienfang et al., 1983, also found a step function in the response of T. pseudonana to changes in irradiance; cells at high light (> 64 uE$\cdot m^{-2} \cdot s^{-1}$) exhibited one sinking rate while cells at low light (< 27.4 uE$\cdot m^{-2} \cdot s^{-1}$) exhibited a significantly lower sinking rate.

Cullen's (1982) classification scheme is useful because it allows an understanding of important dynamic processes, although it does not attempt to quantify such processes. If a chlorophyll maximum is formed as a result of physiological adaptation to low light by phytoplankton then the direct importance to production in the euphotic zone may be small. However, if in situ primary production is occurring, the chlorophyll maximum may be extremely important as a food source for higher trophic levels. A good example is first-feeding anchovy larvae feeding on Gymnodinium splendens off the coast of California (Lasker, 1975). If cells sink and aggregate at a nitricline (Steele and Yentsch, 1960) they may not be lost from the euphotic zone and may be recirculated into the epilimnion during storm activity. In this situation the chlorophyll maximum may be an important seed population leading to phytoplankton blooms subsequent to intense mixing events.

It is of interest to know whether a chlorophyll maximum also represents a carbon maximum. Carbon is a useful common

denominator to use when considering transfer of energy through food chains. If a chlorophyll maximum is formed as a result of physiological adaptation by phytoplankton cells manifested as an increase in Chl a per cell then one would expect a decrease in the C : Chl a levels. Normalizing particulate carbon measurements to chlorophyll will eliminate problems of increased carbon values due to increases in chlorophyll.

Sinking

Phytoplankton sinking has received much attention in oceanographic, and to a lesser extent, freshwater literature because sinking affects the vertical distribution of phytoplankton and, as a result, the carbon budget of the euphotic zone. The standing crop of phytoplankton in the euphotic zone is a static measure of a number of dynamic processes. Such processes include increases due to growth and losses due to cell mortality, grazing and sinking. Thus, understanding the importance of standing stock necessarily requires understanding growth, mortality, grazing and sinking functions which combine to result in the observed standing stock. The importance of sinking has been realized and many mathematical models for primary production (Steele, 1956, 1961, 1962; Ryther and Yentsch, 1957; Anderson, 1974; Bannister, 1974; and many more) include a term for phytoplankton sinking.

Buoyancy regulation may play an important role in determining the

vertical distribution of phytoplankton. A variety of mechanisms may be used to alter cellular buoyancy. Physiological processes have the most dramatic effect on sinking rate (Bienfang et al., 1982, 1983) while other processes, such as altering cellular lipid component (Anderson and Sweeney, 1977) or production of spines or ridges (Lannergren, 1979) play a smaller role. Mediation of turgor pressure on gas vacuole membranes is an important buoyancy regulation mechanism in some cyanobacteria; however, this mechanism would tend to be more important in freshwater rather than marine systems because lakes typically contain more filamentous cyanobacteria.

Study Objectives

There are two main objectives of this study: 1. The first is to determine whether Rhizosolenia eriensis is a sink for nutrients added to the fertilized arm of Sproat Lake; and 2. To determine if low light and high nutrient concentrations act together to significantly decrease sinking rate of R. eriensis until it becomes neutrally buoyant and forms a layer at depth. These findings will be related to the cost effectiveness of the Lake Enrichment Program.

Materials and Methods

Study Area

Sproat Lake (49°14'N, 125°06'W; Fig. 1) is located on central Vancouver Island, British Columbia. The lake is approximately 22.5 km long and varies between 1 and 1.5 km wide. The surface area is 41 km^2 and elevation of the lake is 26 m above sea level. The mean depth is 56 m, with maximum depth of about 260 m. River flow into the lake is primarily via the Taylor River but numerous streams and creeks are present during spring melt. Most of the shoreline slopes very abruptly into deep water.

Sproat Lake is a warm monomictic coastal lake. Water residence time is ca. 8 y. Sproat Lake has a small littoral zone, low inorganic nutrient levels and low phytoplankton and zooplankton biomass (Stockner and Shortreed, 1985).

The specific dates of sampling various parameters are outlined in Appendix I. Two stations were sampled: Stn 1 in Taylor Arm which received nutrient enrichment in 1986 but not in 1987 and Stn 2, the control station in Two Rivers Arm which received no nutrient enrichment (Fig. 2). Two seasonal periods are considered in this study: 1 April to 9 August 1986 and 7 March to 1 June 1987.

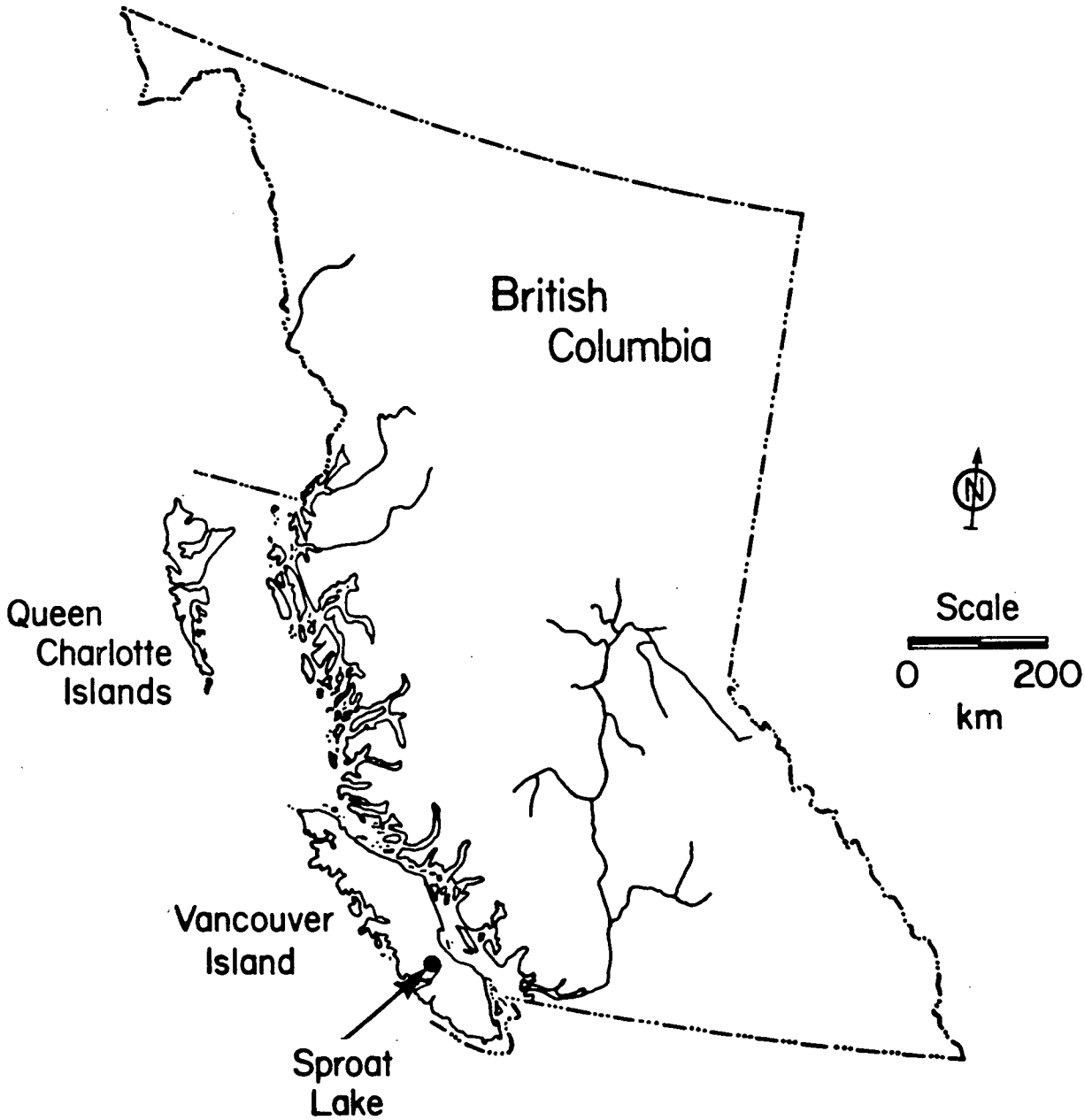


Figure 1. Map of British Columbia, Canada, indicating the location of Sproat Lake.

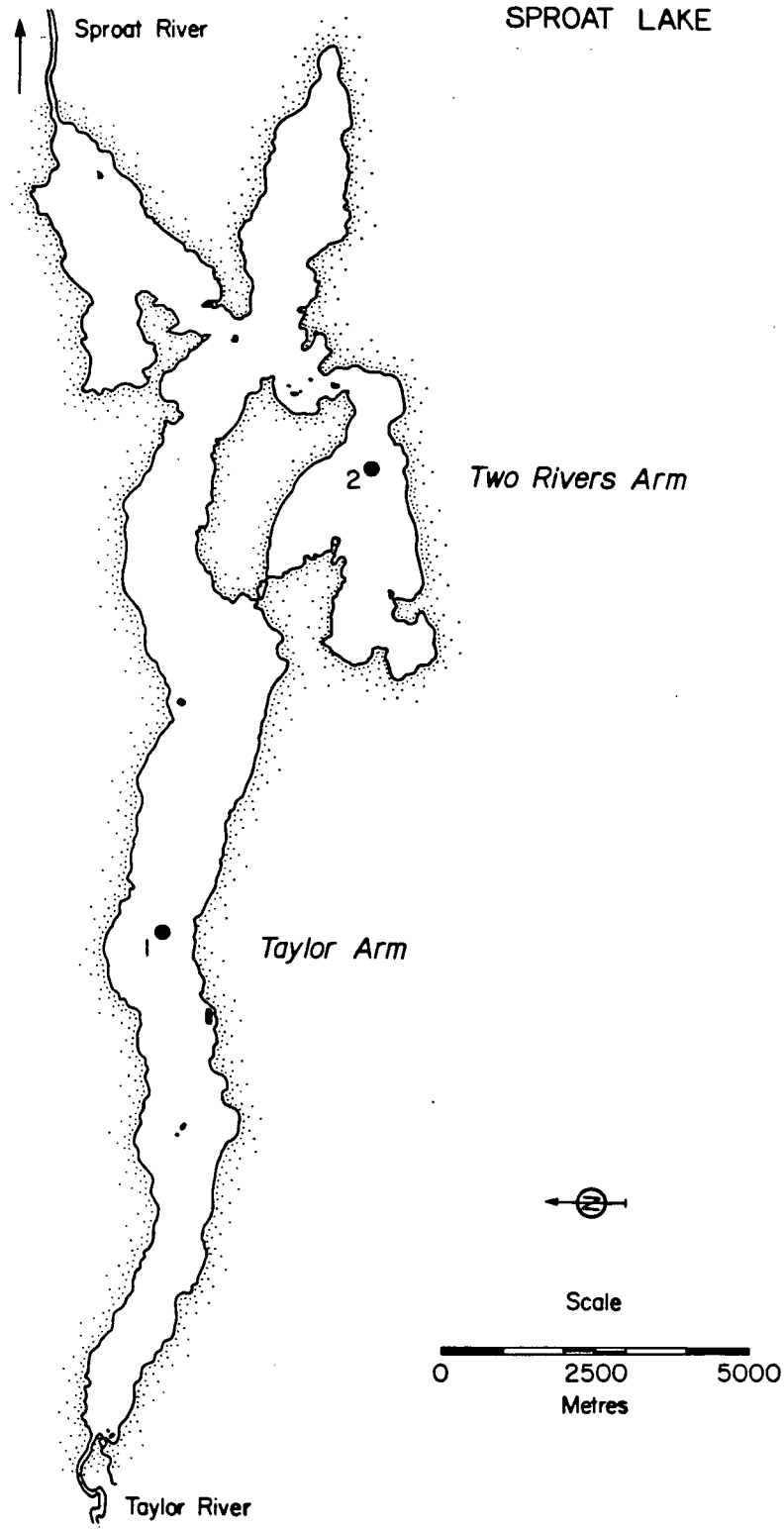


Figure 2. Map of Sproat Lake, indicating the sampling locations in Two Rivers (control) and Taylor (experimental) arms.

Samples for chlorophyll, nutrients and phytoplankton were obtained from 5 or 6 discrete depths while samples for temperature were obtained from up to 17 discrete depths using either a 3 L or 6 L van Dorn PVC water sampler.

Chlorophyll

During the 1986 season LEP staff measured chlorophyll, light intensity and nutrient concentrations in Sproat Lake as part of their complete programme. In 1987, I measured chlorophyll and light intensity and took samples for nitrate and total phosphate. The nutrient analysis for 1987 was performed by LEP staff. An effort was made to sample and measure chlorophyll, light intensity and nutrients so the data from both years could be pooled and differences in values would reflect true *in situ* differences and not differences in experimental design or technique.

Samples were filtered onto 47 mm cellulose acetate/cellulose nitrate mixed ester membrane filters (Millipore Corp.). Following filtration, filters were folded in half, placed into labelled glassine envelopes and stored frozen in a sealed glass container containing dessicant until extraction and analysis (maximum storage time ca. 14 weeks).

At the time of analysis, filters were ground in a tissue homogenizer with 90 % chilled acetone, extracted for 20 h and read on a fluorometer following the method of Parsons *et al.*,

1984 (duplicate samples indicated 6.5 % variability). LEP staff used a 2 h extraction and analysed the chlorophyll extracts with a Turner Designs fluorometer (model 111), factory-fitted with a red sensitive phototube (R136), equipped with an F4T5 blue fluorescent lamp, a Corning CS5-60 primary filter and a Corning CS2-64 secondary filter. The equations used to calculate chlorophyll and phaeophytin concentrations for 1986 are outlined in Stephens and Brandstaetter (1983). My chlorophyll methodology differed from LEP's since I used a 20 h extraction and followed the equations of Parsons et al., 1984, to determine pigment concentrations.

Light Intensity

Light intensity was measured with a Li-Cor quantum light meter (model 185A) equipped with an underwater cosine collector. Measurements were made just below the surface (representing the surface value) and at every metre to approximately 20 m. Values of light intensity profiles were used to measure the 1 % light depth as well as the light attenuation coefficient, k_e.

Nutrients

Samples were placed in acid washed (a 10% acid wash followed by three rinses with deionized distilled water) 1 L polyethylene bottles (Nalgene Corp.) for transport (storage time up to ca. 2 h) to the laboratory. Water samples were filtered through preashed and prewashed 47 mm glass fibre filters (Whatman GF/F; average pore size 0.7 um) and stored in acid washed glass bottles

with foil-lined screw-top caps at 2°C for 8 to 20 weeks.

Nitrate was analysed by a modified seawater technique (Stephens and Brandstaetter, 1983) of Brewer and Riley (1975). Buffered samples containing nitrate were passed through a cadmium column reducing nitrate to nitrite. The reduced sample reacted with sulphanilamide and N(1-napthyl) ethylene diamine (NNED) forming a coloured azo dye. The azo dye was quantified colourmetrically using a Technicon Autoanalyzer II system equipped with a 540 nm filter. The limit of detection was 1 ug NO_3-N$\cdot L^{-1}$.

Total filtered phosphorus was analysed by a modified method (Stephens and Brandstaetter, 1983) of Traversy (1971). Samples were digested with a persulphate-sulphuric acid solution, converting particulate phosphorus, polyphosphates and organically bound phosphorus to orthophosphate. Orthophosphate then reacted with ammonium molybdate and stannous chloride to form a blue phospho-molybdenum complex. This complex was quantified colourmetrically using a Technicon Autoanalyser II system equipped with a 660 nm filter. The limit of detection was 1 ug P$\cdot L^{-1}$.

Temperature

Early in the field season, before thermal stratification occurred, temperature was measured at 0.5, 5, 10 ..., 45 and 50 m. After the surface water had begun to warm, temperature was measured at 0.5, 2.5, 5, 7.5 ..., 30, 35, 40, 45 and 50 m.

Temperature values were plotted and the resulting curves were used to define the epilimnion, thermocline and hypolimnion depths.

In vivo fluorescence

In vivo fluorescence was measured on a relative scale and since it was not standardized and converted to known values, eg., chlorophyll a, it was reported without units. In vivo fluorescence profiles were measured with a Turner Designs fluorometer (Model 10) equipped with filters to measure chlorophyll a and modified for flow through operation. A diaphragm pump (Jabsco electric bilge pump, model 34600-0000) was run for a minimum of 60 s prior to reading a sample to flush the hose of the previous sample. When the pump was shut off, 30 s was allowed to elapse to ensure the same time had passed for each reading and to allow the fluorometer signal to stabilize. Depths sampled were 0.5, 2.5, 5 ..., 27.5, 30, 35, 40, 45 and 50 m. The time between successive sample dates varied between 3 and 5 days (Appendix I). In vivo fluorescence profiles were obtained in the morning and Two Rivers arm was sampled first.

Phytoplankton

Depths chosen depended on the vertical distribution of chlorophyll as estimated by the in vivo fluorescence profile on each sample date. Nalgene bottles (1 l) were filled and stored cool and in the dark. Upon return to the laboratory, subsamples were taken for immediate enumeration (the volume depended on the

amount required for enumeration) and for long term storage (25 ml). These samples were fixed and preserved with Rhodes Lugol's solution plus acetic acid (Sournia, 1978). The following groups were enumerated: Rhizosolenia eriensis, Cyclotella spp. (3 species) Asterionalla formosa, Fragilaria sp., Synedra sp., Melosira sp., Dinobryon sp., ciliates, cysts, large flagellates (15 um and larger), small flagellates (3-15 um) and others (up to four groups in some samples and primarily diatoms). Phytoplankton cell density profiles generally corresponded to specific in vivo fluorescence profiles although phytoplankton samples were not taken for every fluorescence profile. Identification and enumeration of phytoplankton was by Utermöhl technique (Utermöhl, 1948) using a Wild M40 inverted microscope equipped with phase contrast optics at either 200X or 600X magnification.

During the 1987 field season two comparisons of phytoplankton cell density (variability between duplicate counts was 8.5 %) and in vivo fluorescence profiles were performed for both the control and experimental arms. Phytoplankton samples were taken every 3 m from 0.5-30 m. This comparison was performed before and after the establishment of the fluorescence maximum at both Stn 1 and 2. The first comparison was performed on 9 April while the second was performed on 20 May.

Sinking rates

A SETCOL apparatus (Bienfang, 1981) was used to determine the sinking rates of the phytoplankton sampled from various depths before and after the chlorophyll maximum formation during the 1987 field season. Depths chosen were 5, 10, 17.5 and 22.5 m. Sinking rate measurements were performed in duplicate. A cooling water bath and water jackets around the SETCOL apparatus ensured that temperature was constant during the experiments. Natural light was used and varied by using cheesecloth as screening. Temperature and light conditions used during the sinking rate experiments were chosen to approximate values found at the depths from which water samples for the experiment were obtained.

Samples were obtained early in the morning and kept cool and in the dark until they were transported to the laboratory (60 min maximum elapsed time). The experiments were run for 4 h following which subsamples from the columns were taken, preserved in Rhodes acidic Lugol's solution and enumerated following the procedure outlined for phytoplankton enumeration. Cell density was used as the measure of biomass required in calculating sinking rate when using a SETCOL apparatus (Bienfang, 1981); hence, it was possible to calculate a sinking rate for each diatom species typically enumerated in the bottle samples.

Sediment traps

The sediment traps (Fig. 3) were 51 cm high with a mouth diameter of 12.5 cm. These traps were constructed of PVC plastic. Both

the baffles and the collection cup were made of plastic. Once material sedimented past the column mouth, the column baffles prevented removal by currents outside the sediment traps. Similarly, while the column was draining the collection cup baffles prevent loss of material that had sedimented into the collection cup. The rubber O-ring provided a tight seal between the collection cup and column so water did not leak out of the traps while the traps were out of the water but still full. The top of the collection cup was beveled so sedimenting material would fall into the cup.

Pairs of sediment traps were deployed at 7 and 15 m (Fig. 4) at both Stn 1 and Stn 2. The collection cup (Fig. 3) contained a brine solution of 1.5 % NaCl to kill grazers and to maintain a high density solution in the collection cup. At sampling time (7 d periods during 1986 and 4 d periods during 1987) the traps were brought to the surface and the upper portion drained (Fig. 3). The contents of the collection cup were transferred to a 1 L Nalgene bottle (with the aid of a funnel to avoid spilling) and stored in a cool, dark styrofoam chest until they were returned to the laboratory. In the laboratory, each sample was mixed and 100 mL was transferred to a glass bottle before fixing and preserving with Lugol's solution. Samples were enumerated at 200X magnification following the procedure outlined for phytoplankton.

Rhizosolenia eriensis was enumerated as whole cells and frustule

pieces containing a spine; the latter was counted as half a cell. Cell flux determinations are based on R. eriensis cell counts including both whole cells and frustule pieces. Additional groups enumerated were Cyclotella spp., Asterionella formosa, Fragilaria/Synedra, and others.

Fertilization regime

During 1985 and 1986 Taylor arm was fertilized while Two Rivers arm was not fertilized. Neither arm was fertilized during 1987. Fertilizer was purchased as granular NH_4NO_3 and $(NH_4)_2PO_4$ and dissolved in water before it was sprayed on the lake by a DC-6B water bomber. Details of the fertilization regime are outlined in Table 1. The area of Taylor arm which received nutrient enrichment is illustrated in Figure 5.

Nutrient addition was weekly. The aircraft flew at a low altitude and made a number of passes, on different paths, to help maximize fertilizer areal distribution. Mixing in the epilimnion and variable flight patterns helped ensure an even nutrient distribution in the top portion of the epilimnion in the treatment area.

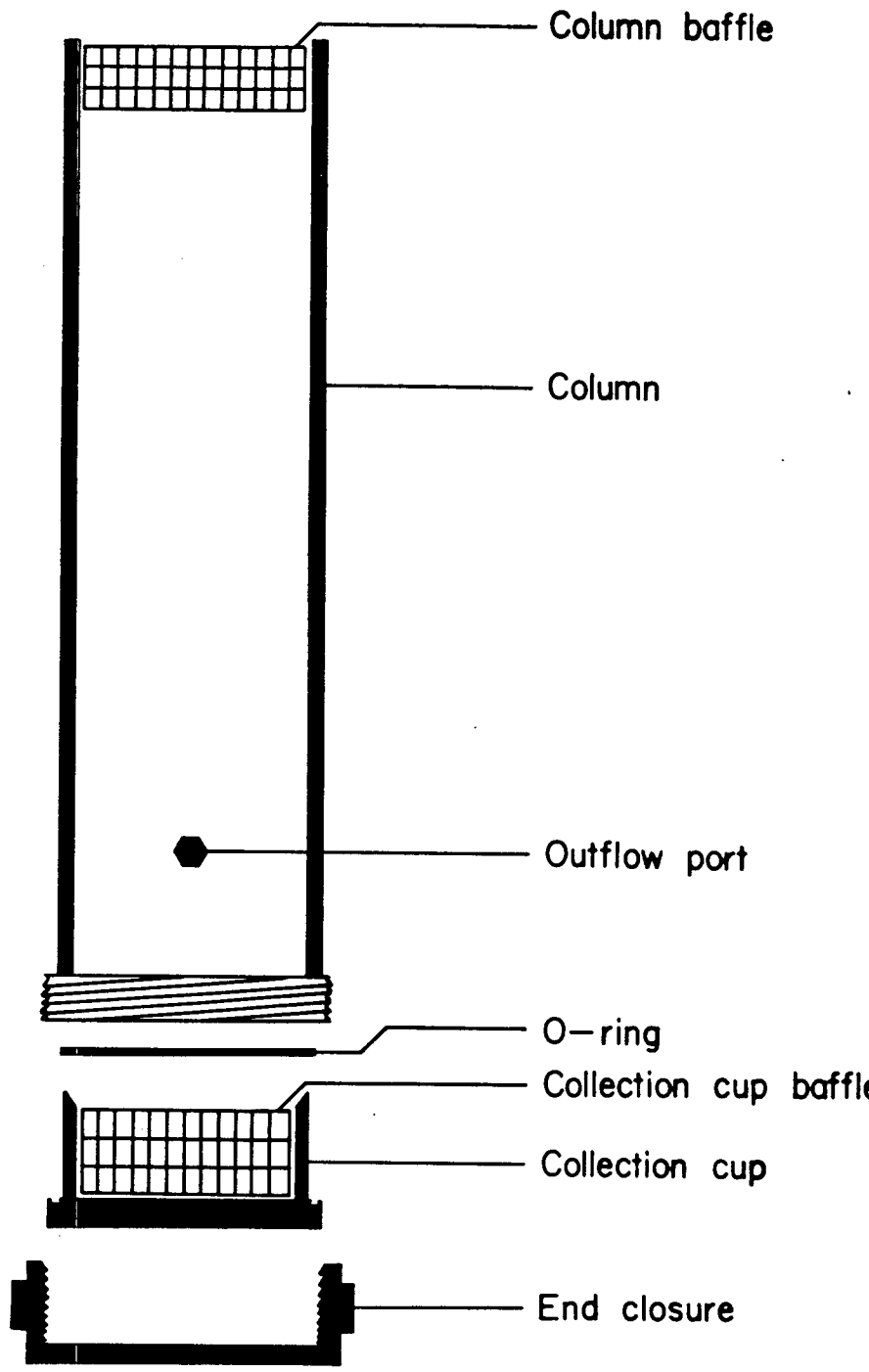


Figure 3. Cross section of a sediment trap used to collect sedimenting phytoplankton.

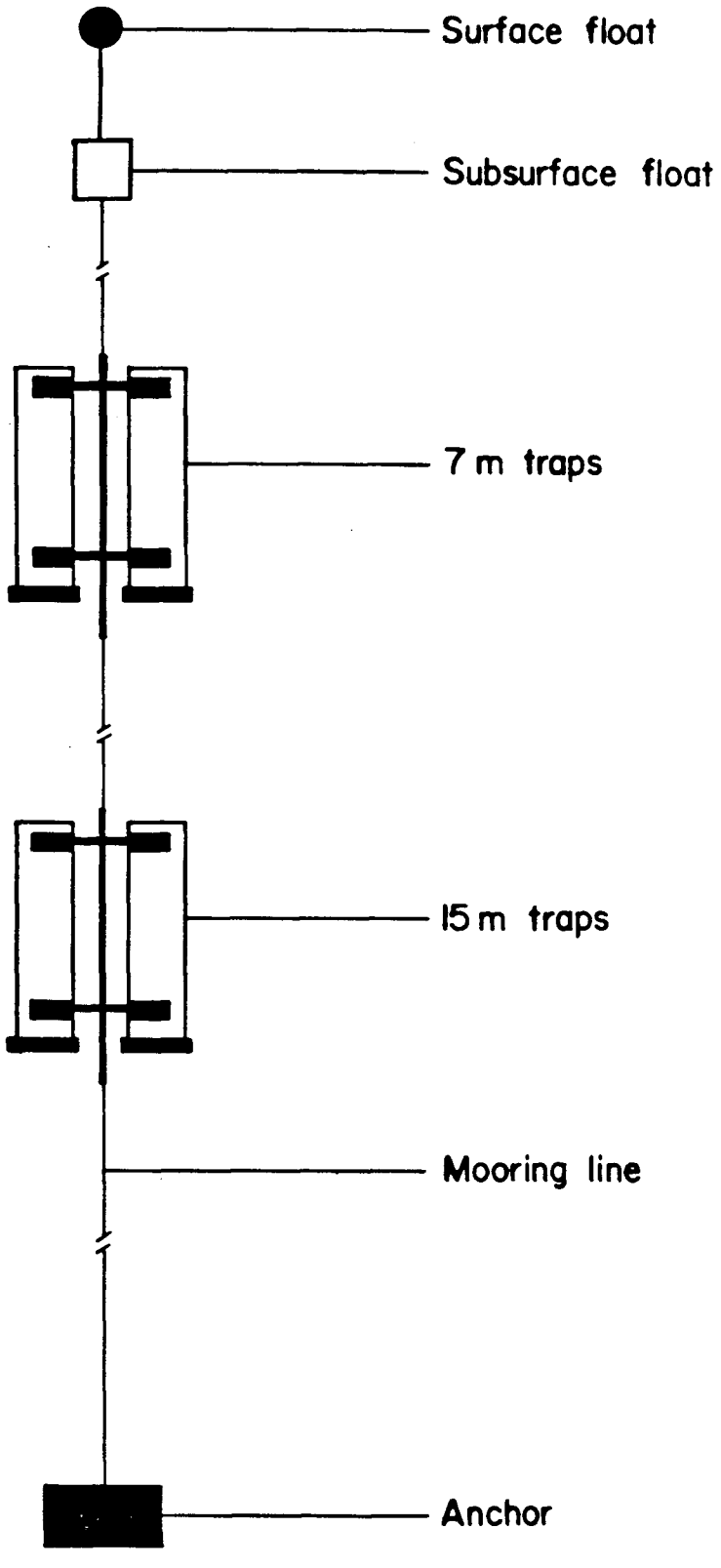


Figure 4. Schematic representation of the arrangement of sediment traps and components of the mooring line.

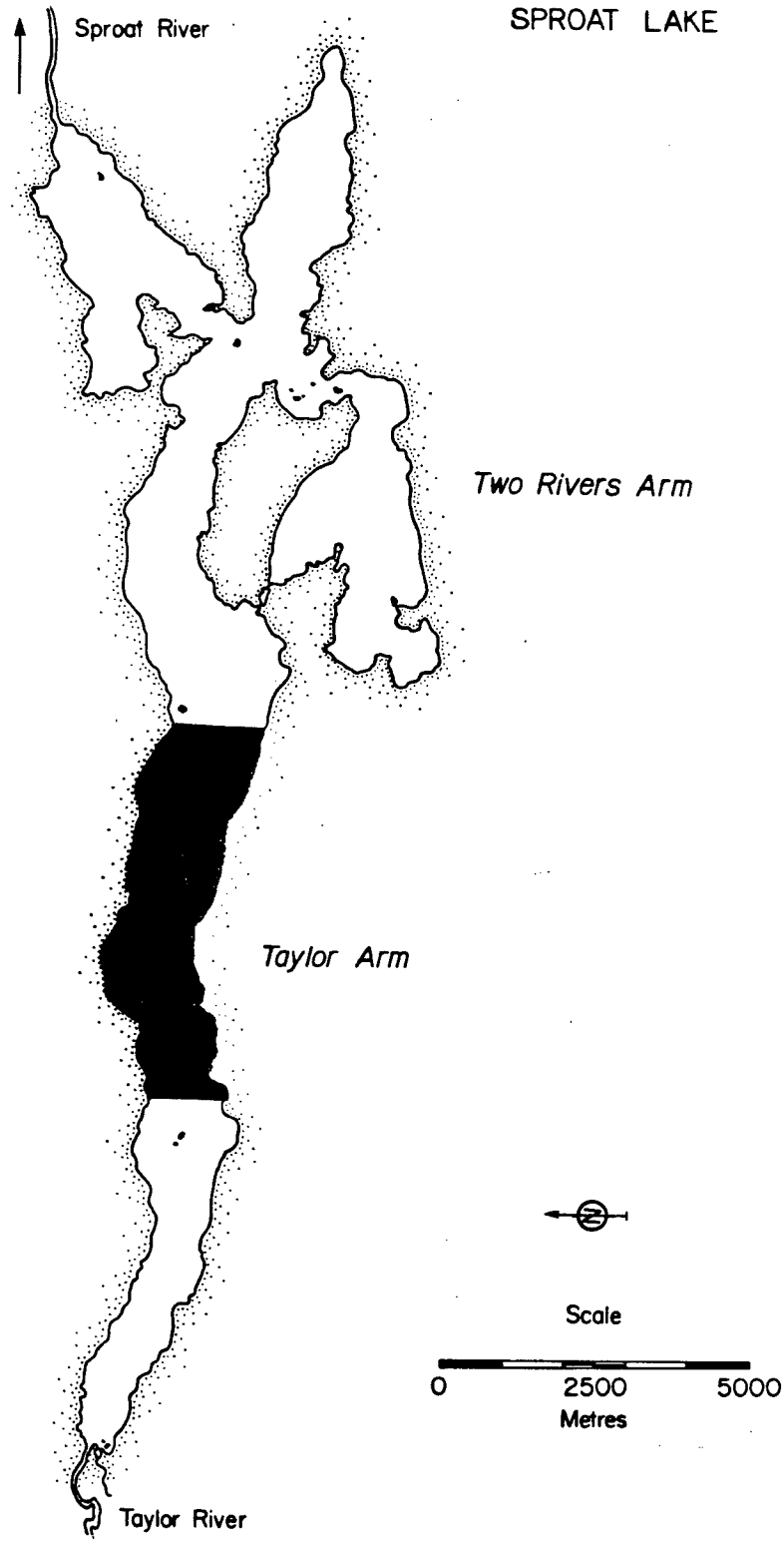


Figure 5. Map of Sproat Lake, indicating (black section) the area of Taylor arm receiving nutrient enrichment.

Table 1. Details of the Sproat Lake fertilization regime during 1985 and 1986 (N:P ratio by atoms).

Year	fertilization	duration	P-load	N:P
1985	weekly	18 weeks	3.0 mg $P \cdot m^{-2} \cdot wk^{-1}$	50:1
1986	weekly	8 weeks	5.6 mg $P \cdot m^{-2} \cdot wk^{-1}$	50:1

Results

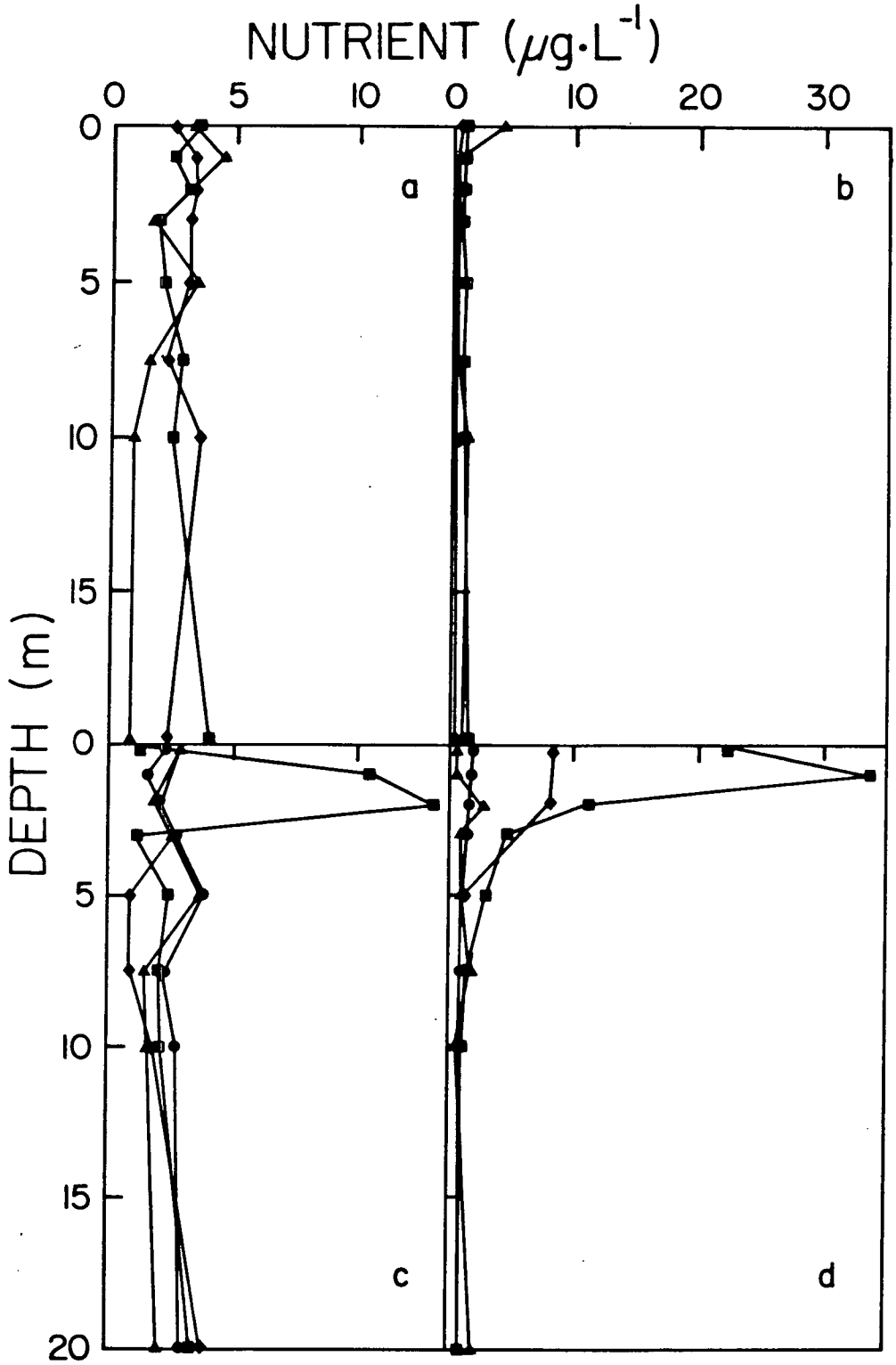
The fate of nitrogen and phosphorus following fertilization in Great Central Lake is illustrated in Figure 6 (from Stockner et al., 1980). Great Central Lake shares many similar physical, chemical and biological characteristics with Sproat Lake and is therefore useful for comparison. Figure 6 illustrates that soluble reactive phosphorus (SRP) returned to pre-fertilization levels after one day and nitrate after two days following fertilization. The exact time for all fertilizer to be consumed will depend on the phytoplankton biomass, the nutrient demand of the phytoplankton and phytoplankton nutrient uptake capabilities.

Vertical Profile Replication

On 5 April 1987, the variability in in vivo fluorescence within and between Two Rivers and Taylor arms was assessed. Figure 7 illustrates the profile sites. In Taylor arm the stations were all within the boundaries of that portion of the area receiving nutrient enrichment during 1986.

Generally, profiles in each arm were similar while those between arms were not (Fig. 8). The Two Rivers arm profiles all peaked at 15 m and all surface fluorescence values were similar, indicating that the within site variability was low. The Taylor arm profiles had more variability than the Two Rivers arm profiles but they were all generally similar.

Figure 6. Soluble reactive phosphorus (a,c) and nitrate (b,d) concentrations in unfertilized (a,b) and fertilized (c,d) areas of Great Central Lake, British Columbia on the day before fertilization (▲), day of fertilization (■), and one (◆) and two (●) days following fertilization (from Stockner et al., 1980).


NUTRIENT ($\mu g \cdot L^{-1}$)
0
5
10
0
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20
30
DEPTH (m)
0
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10
15
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5
10
15
20
a
b
c
d

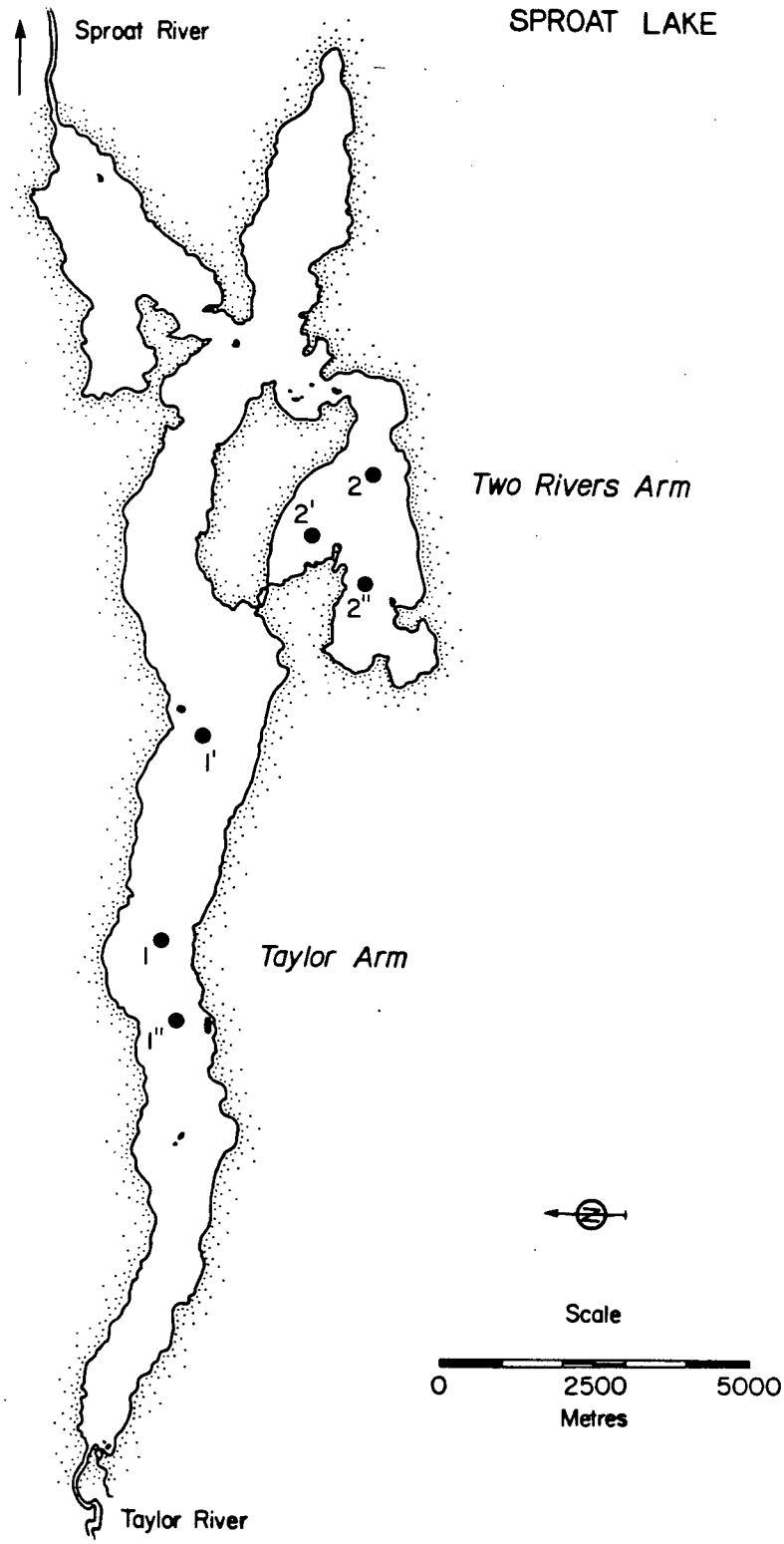

Figure 7. Map of Sproat Lake, indicating profile stations for <u>in vivo</u> fluorescence comparison of 5 May 1987.

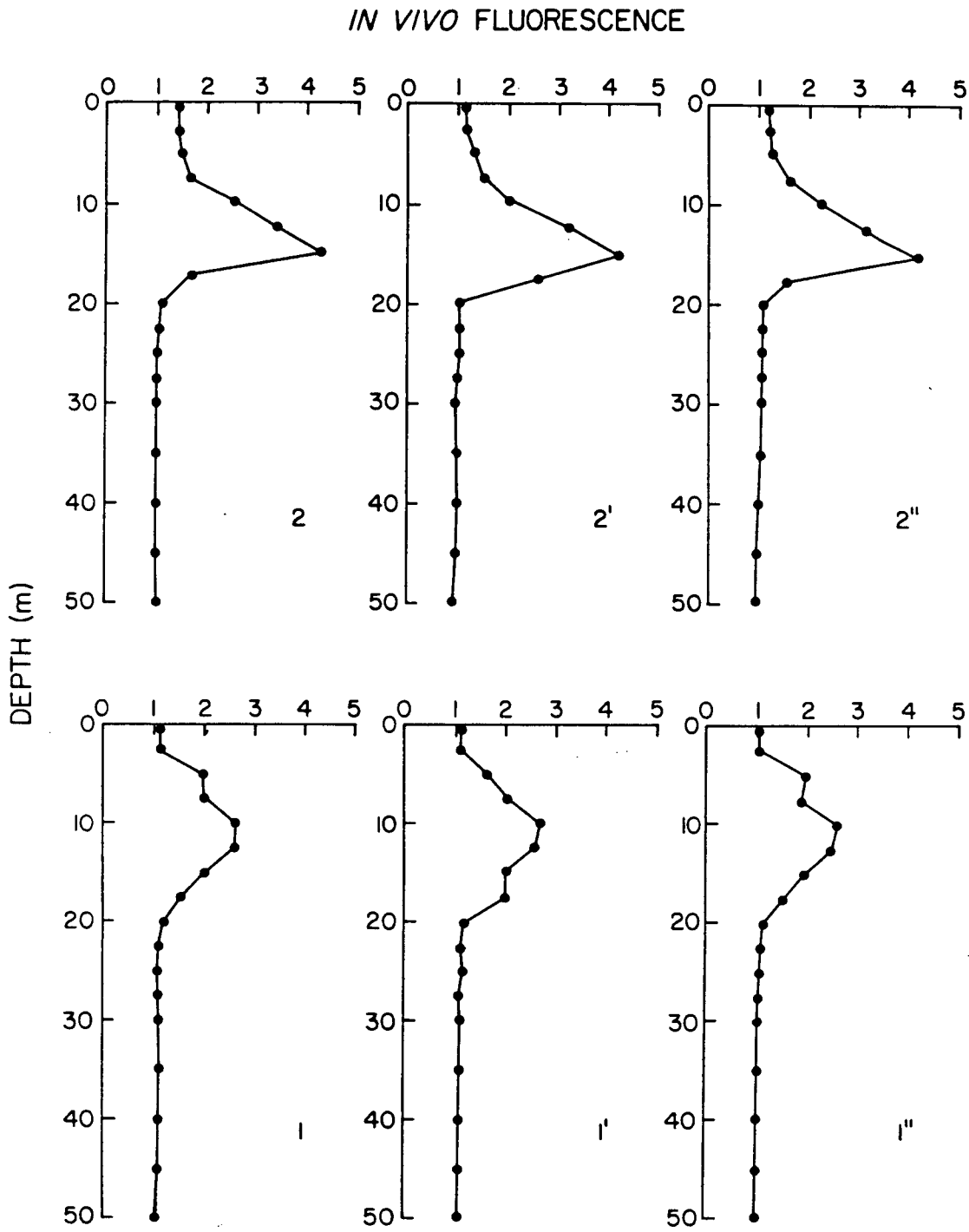

Figure 8. In vivo fluorescence profiles at six stations on 5 May 1987. Numbers in the bottom right corner correspond to station numbers of Figure 7.

Comparisons between sites revealed that the Two Rivers arm profiles had a sharper peak than the profiles in Taylor arm. The maximum value of the fluorescence profiles of Taylor arm was only 64 % that of Two Rivers arm. Both sets of profiles had similar fluorescence profiles in the surface waters as well as similar fluorescence values from 20-50 m.

Two seasonal periods are considered in this thesis. Results for the 1986 field season (23 April to 6 August) will be presented followed by the results for the 1987 field season (7 March to 1 June). Where possible, an attempt will be made to consider the data for both field seasons together. Since the 1986 field season started late and the 1987 was terminated early, the period of overlap between the two years was from 23 April to 1 June.

Physical observations

Temperature

1986

On 27 May, the beginning of the first seasonal period, the temperature profile was not isothermal (Fig. 9). Surface temperature was approximately 8.0^{o}C with a near constant decrease of temperature with depth to 5.4^{o}C at 17.5 m in both arms. Through the sampling period stratification intensified. The maximum surface temperature was ca. 23.1^{o}C in Taylor arm on 11 August. From the temperature profiles the epilimnion was

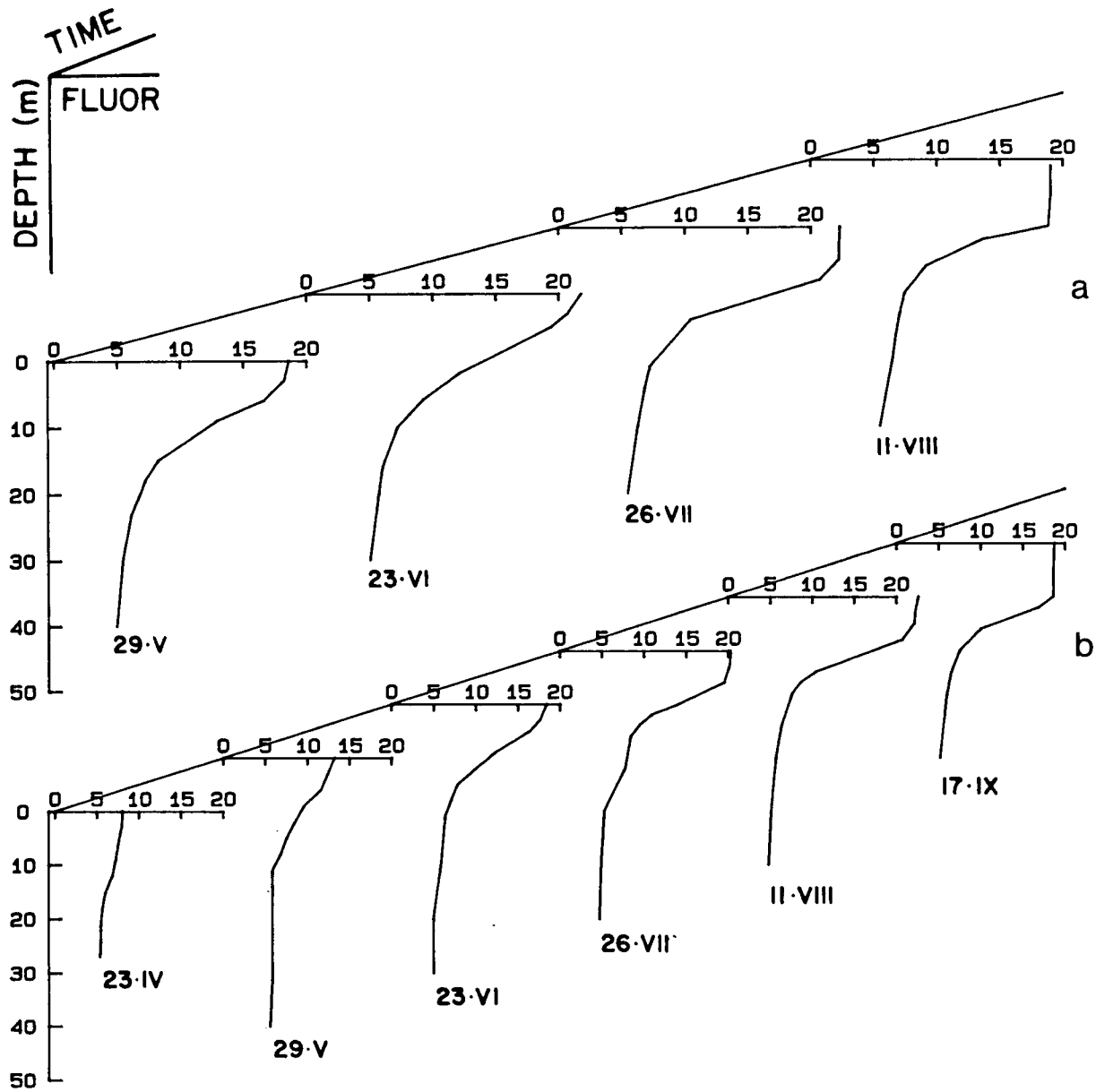

Figure 9. Temperature profiles for Two Rivers (a) and Taylor (b) arms, 1986.

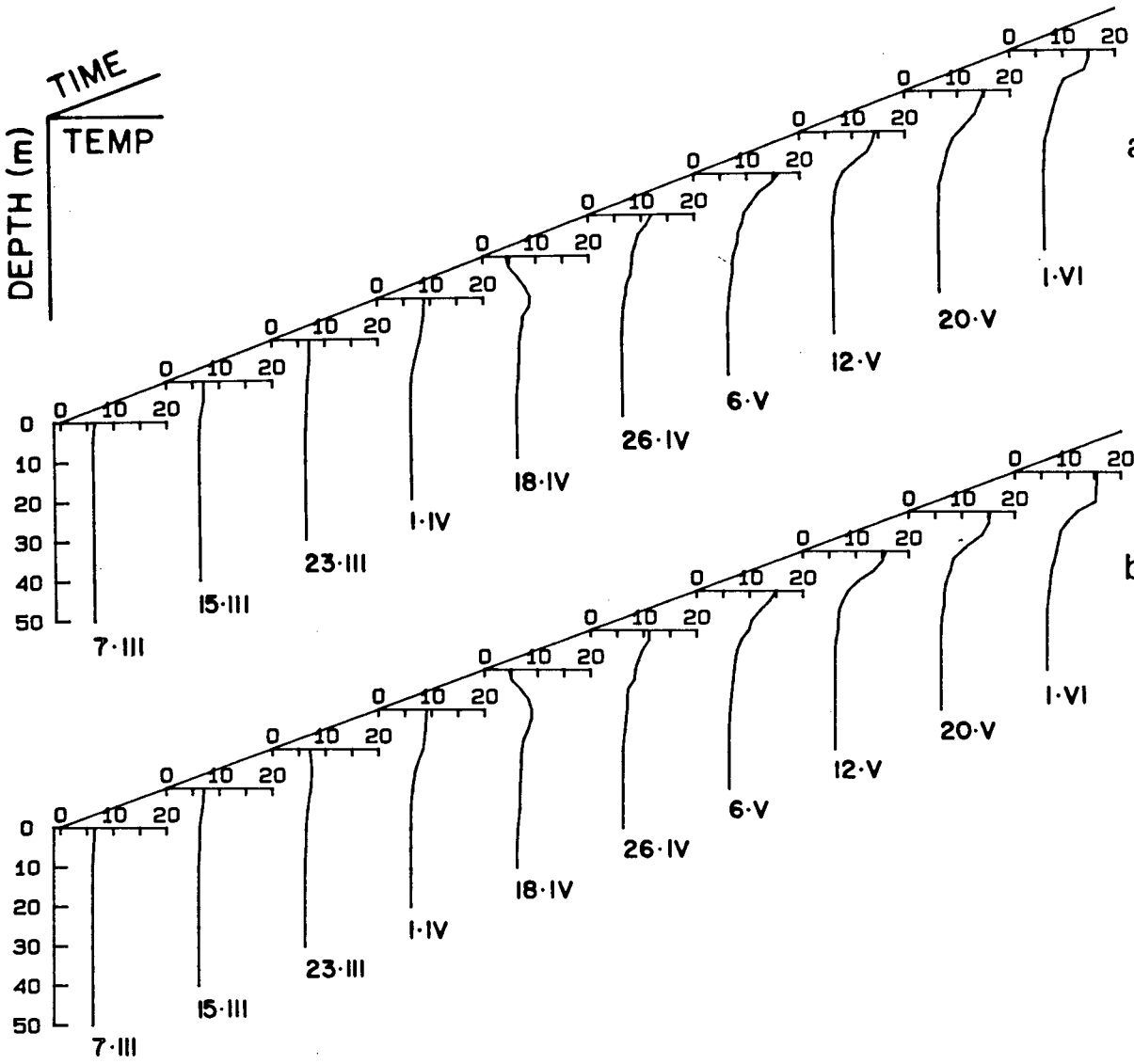

Figure 10. Temperature profiles for Two Rivers (a) and Taylor (b) arms, 1987.

estimated to be 0-10 m, the thermocline 10-17.5 m, and the hypolimnion 17.5-bottom in both Two Rivers and Taylor arms.

1987

The first profile (Fig. 10), of 7 March, shows isothermal conditions from 0-50 m of ca. 6.0°C. By 1 April thermal stratification had commenced. There was a temperature inversion in the surface water on 18 April; this followed three nights of sub-zero temperatures and no apparent wind during either the night or day. Stratification continued to intensify through 1 June, at which time surface temperatures were ca. 15°C. The epilimnion was slightly shallower in Taylor arm, possibly due to more mixing early in the spring delaying the onset of permanent seasonal stratification. In general, the temperature profiles for both arms were similar. Depths of the epilimnion, thermocline and hypolimnion were estimated to be 0-7.5 m, 7.5-12.5 m and 12.5-bottom respectively, in Two Rivers arm and 0-5 m, 5-7.5 m and 7.5-bottom respectively, in Taylor arm on 1 June.

Light

1986

The 1 % light depth was generally deeper in Two Rivers than Taylor arm (except for late summer) in 1986 (Fig. 11). Values increased from 20.5 m and 18.3 m in the spring to 22.5 m and 19.2 m in the fall in Two Rivers and Taylor arms respectively.

The Two Rivers arm extinction coefficient varied between 0.26 m^{-1} on 23 April to 0.21 m^{-1} on 17 September (Fig. 11). The extinction coefficient values for Taylor arm were generally lower than those of Two Rivers arm.

1987

In Two Rivers arm the 1 % light depth decreased from 20.4 m on 15 March to 14.4 m on 23 April and increased to 22.3 m on 1 June (Fig. 12). The light compensation depth was not as deep in Taylor arm as in Two Rivers arm.

The extinction coefficient in Two Rivers arm increased from 0.21 m^{-1} on 15 March to 0.33 m^{-1} on 23 March and then decreased to 0.21 m^{-1} by 1 June (Fig. 12). In Taylor arm k_e increased from 0.24 m^{-1} on 15 March to ca. 0.32 m^{-1} on 1 April, then decreased to 0.25 m^{-1} by 1 June.

Water chemistry

Nitrate

1986

In Two Rivers arm nitrate was below detection from 0 to 15 m by 28 May and remained low to undetectable throughout the field season (Fig. 13 a). Nitrate was not sampled on 23 April. The nitracline began at ca. 15 m and continued through 40 m, the lowest depth sampled during 1986. Nitrate concentration ranged from ca. 30-40 ug $N \cdot L^{-1}$ at 40 m.

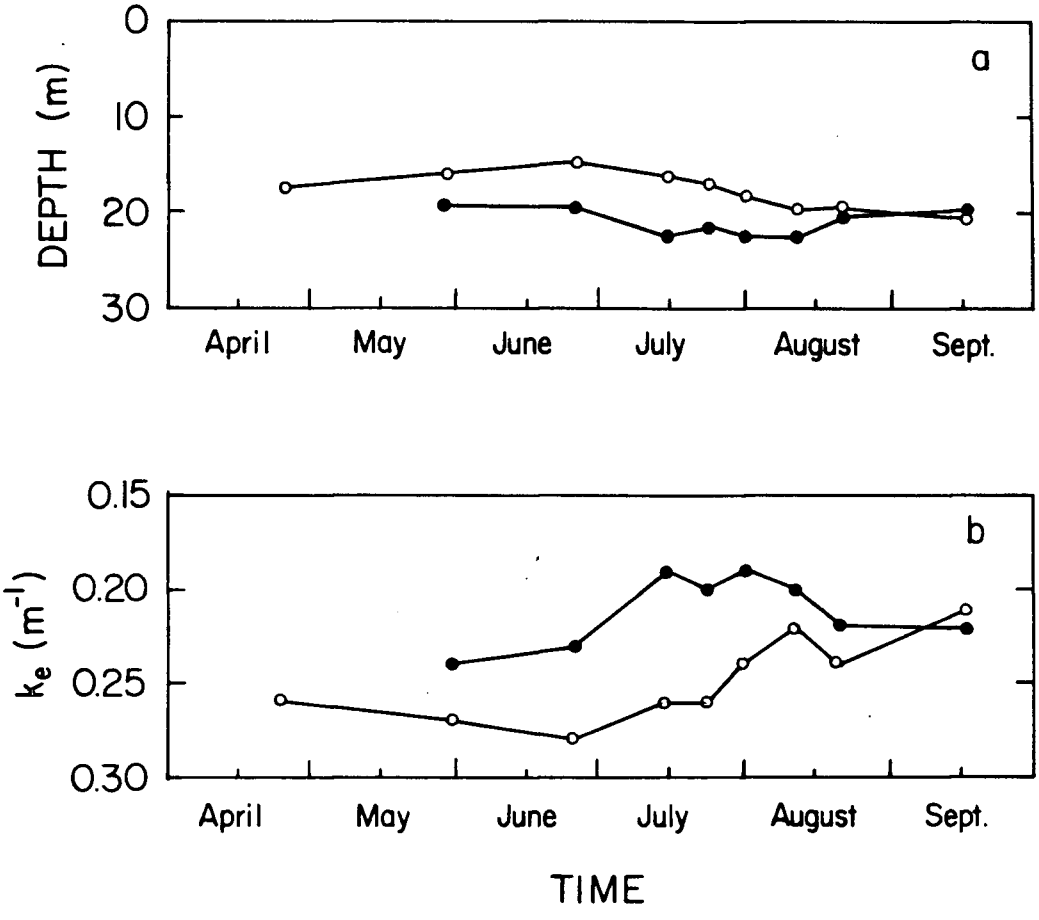

Figure 11. 1 % light depth (a) and extinction coefficient (b) in Two Rivers (●) and Taylor (O) arms, 1986.

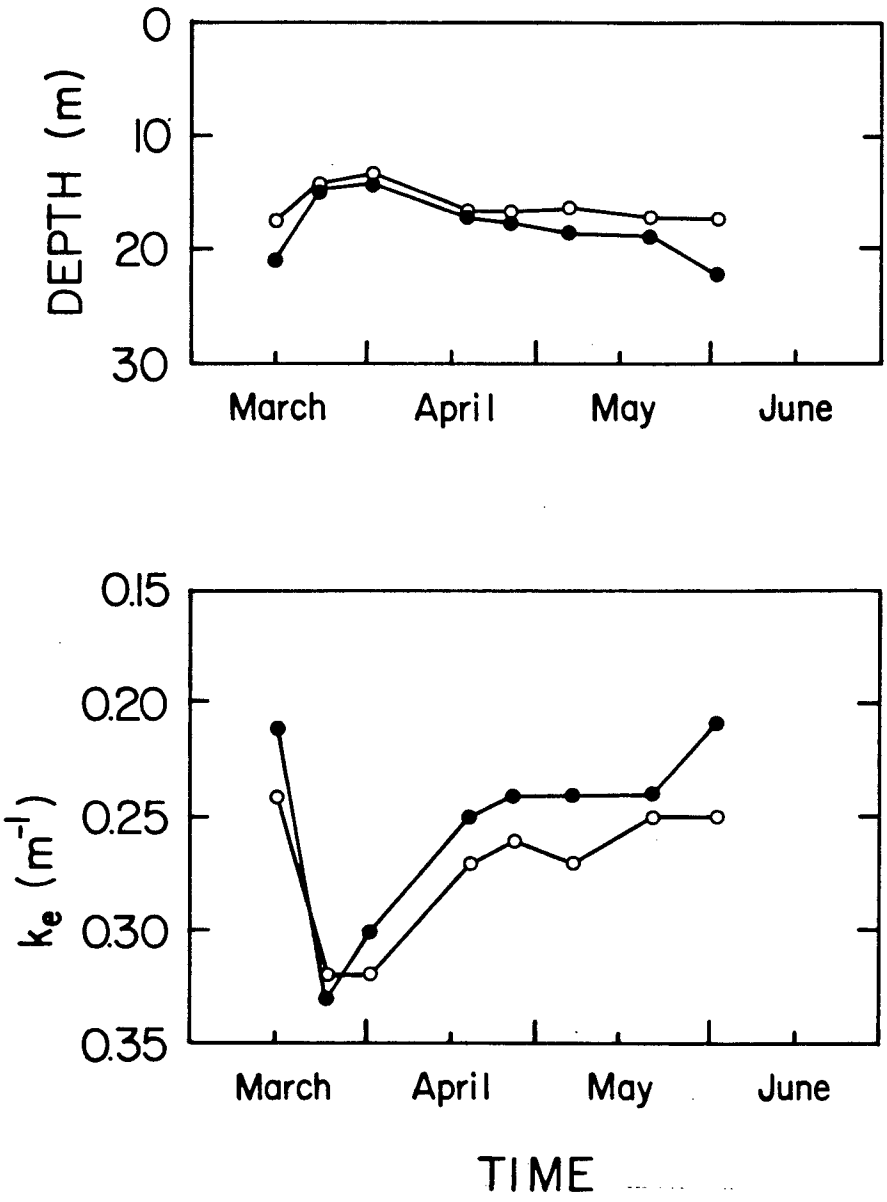

Figure 12. 1 % light depth (a) and extinction coefficient (b) in Two Rivers (●) and Taylor (O) arms, 1987.

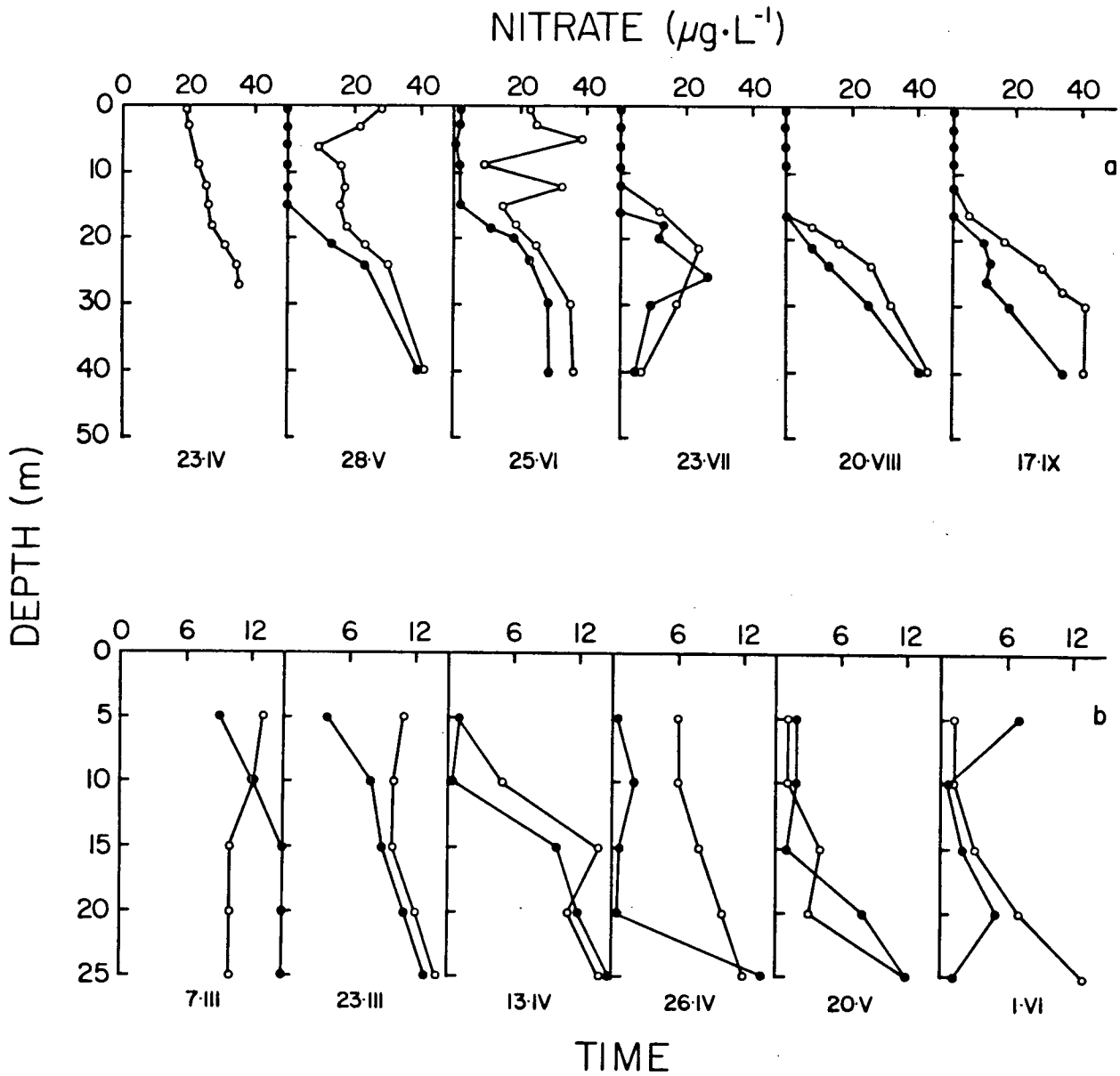

figure 13. Nitrate concentration during 1986 (a) and 1987 (b) in Two Rivers (●) and Taylor (o) arms.

In Taylor arm nitrate was present in the epilimnion until sometime between 25 June and 23 July. Epilimnetic nitrate concentrations ranged between 10-40 ug $N \cdot L^{-1}$. The nitrate profile in Taylor arm was similar to that of Two Rivers arm once nitrate concentrations had become undetectable in surface waters by 23 July. On 23 July there appeared to be a nitrate maximum at 22.5-25 m in both arms. Considering the 25 June and 20 August profiles, an error in the 30-40 m samples on July 23 resulting in low nitrate values at these depths may have caused such an apparent maximum.

1987

In Two Rivers arm nitrate showed little variability with depth on 7 March, with the concentration ranging from 9-12 ug $N \cdot L^{-1}$ (Fig. 13 b). Generally, nitrate decreased over time but never became undetectable as it did during 1986. The same trend occurred in Taylor arm; however, there was still ca. 13 ug $N \cdot L^{-1}$ at 25 m on 1 June.

Total Filtered Phosphorus (TFP)

1986

The maximum TFP measured was 6 ug $P \cdot L^{-1}$ in Two Rivers arm on 28 May (Fig. 14 a). The maximum TFP in Taylor arm was 4 ug $P \cdot L^{-1}$ (measured on both 25 June and 23 July). Generally, TFP was extremely low throughout the 1986 field season.

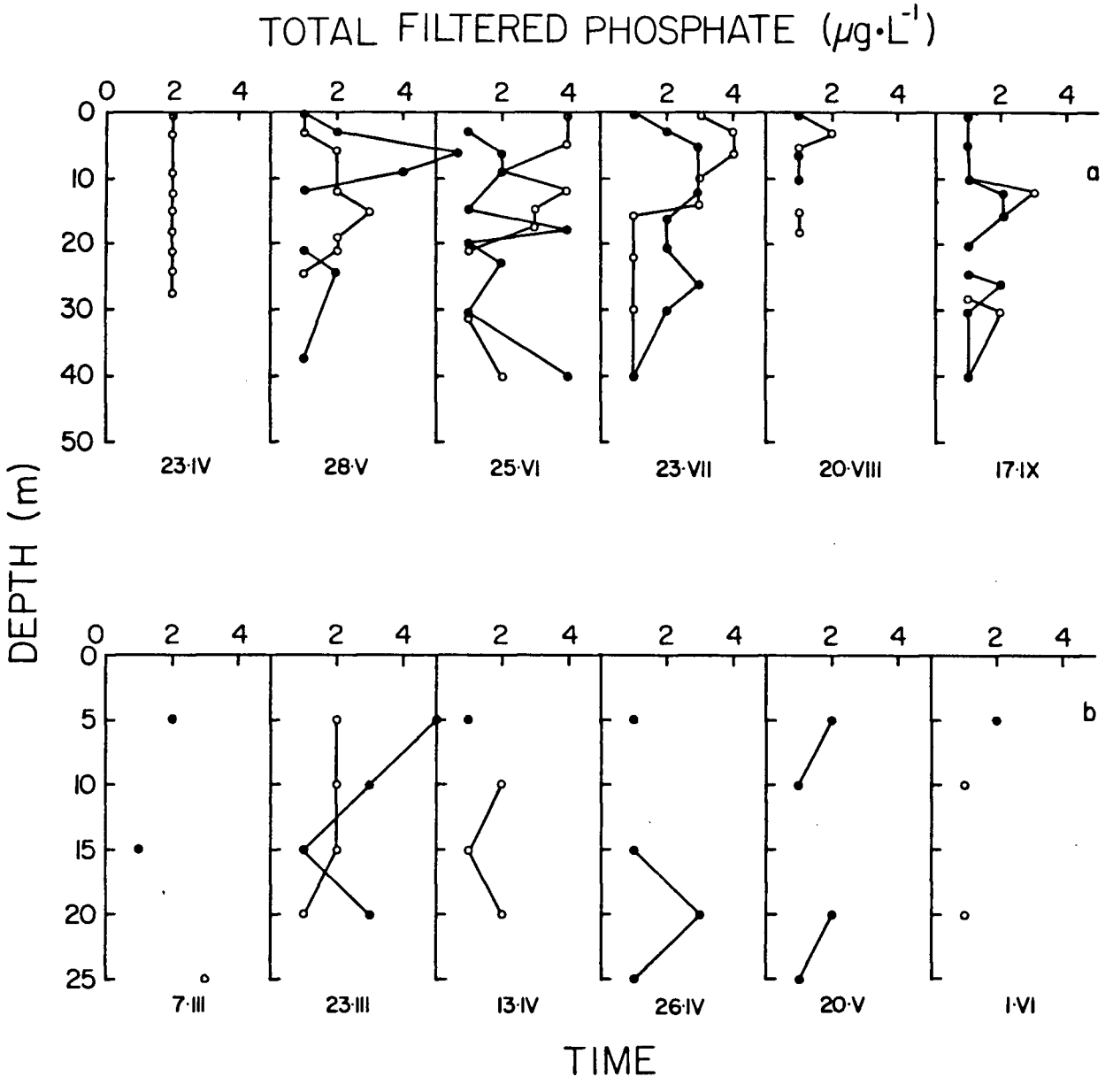

Figure 14. Total filtered phosphorus concentration during 1986 (a) and 1987 (b) in Two Rivers (●) and Taylor (O) arms.

1987

The maximum TFP measured in Two Rivers arm was 6 ug $P \cdot L^{-1}$ (at 5 m on 23 March), the same as in 1986 (Fig. 14 b). In contrast, maximum TFP was 3 ug $P \cdot L^{-1}$ at 25 m on 7 March in Taylor arm. At other times during the 1987 sampling period TP < 2 ug $P \cdot L^{-1}$, with the exception of 20 m on 13 April in Two Rivers arm.

Biological Observations

In vivo fluorescence

1986

The 8 May profile (Fig. 15) illustrates that a fluorescence maximum was already present at the beginning of the 1986 sampling period in both Two Rivers and Taylor arms. The value of the fluorescence maximum increased in Two Rivers arm until 12 June, where it reached a value of 0.410 at 22.5 m. The fluorescence maximum varied spatially and temporally but was typically at 20-25 m. The maximum fluorescence value slowly decreased through the sampling period subsequent to 12 June.

In Taylor arm the fluorescence profile initially formed slower than in Two Rivers arm (compare profiles of 8 May). A maximum value of 0.490 occurs on 12 June at 22.5 m. On 3 July there was a second peak of fluorescence at 10 m in addition to the seasonal fluorescence maximum at 22.5 m. The occurrence of this second fluorescence peak coincided with an epilimnetic bloom of algal picoplankton. By 26 July the value of both fluorescence maxima

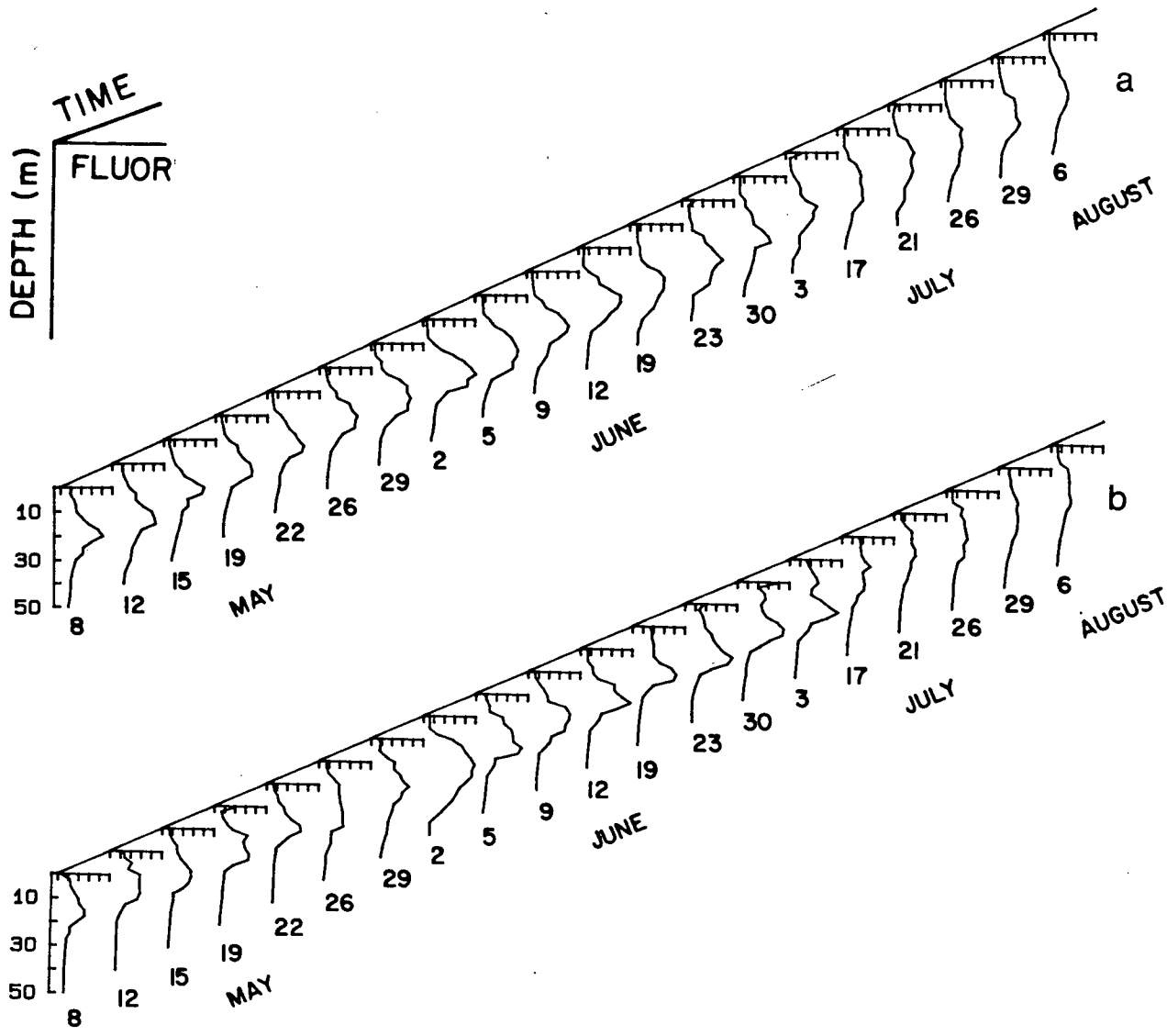

Figure 15. In vivo fluorescence profiles for Two Rivers (a) and Taylor (b) arms, 1986.

had dropped to 0.160 for the 10 m maximum and 0.212 for the 22.5 m maximum. By 6 August there was relatively little change with depth in the Taylor arm profile.

1987

The first Two Rivers arm profile (Fig. 16, 11 March) illustrates that there was very little change in _in vivo_ fluorescence with depth. From the 15 March profile onward there was a fluorescence profile characteristic of a subsurface chlorophyll maximum. The fluorescence profile became thicker with the maximum value for each profile increasing until 13 April when it reached a value of 0.550. The fluorescence maximum was situated at 12.5-15 m until 13 April, after which it descended until it reached 20 m by 1 June. The profile changed shape after 13 April with proportionally more fluorescence below the peak than above it.

In Taylor arm the same series of events occurred but later in time. A fluorescence peak did not really start to form until 1 April. This was approximately 2 weeks later than in Two Rivers arm. The fluorescence maximum continued to increase in intensity through June. The fluorescence maximum formed at 10-12.5 m (e.g., 22-30 April) and sank deeper to 20 m by 1 June, similar to Two Rivers arm.

In all fluorescence profiles there was a baseline of fluorescence ranging from ca. 0.070-0.090.

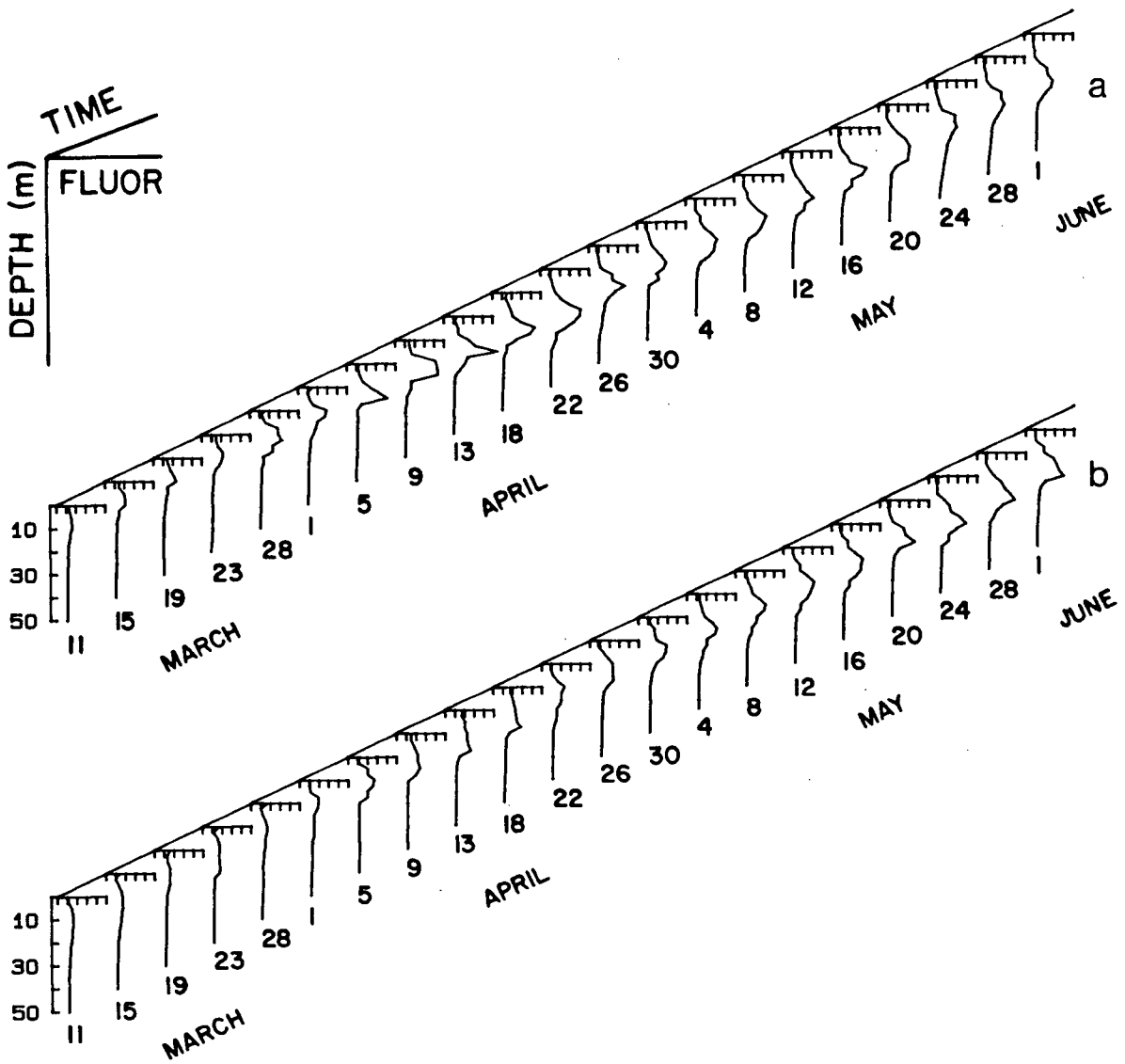

Figure 16. In vivo fluorescence profiles for Two Rivers (a) and Taylor (b) arms, 1987.

Chlorophyll

1986

On 23 April in Two Rivers arm there were greater chlorophyll concentrations in the epilimnion compared to deeper values (Fig. 17). By 28 May, a subsurface chlorophyll maximum was beginning to form at 15-20 m and by 25 June a well-defined chlorophyll maximum (ca. 2.40 ug Chl $\underline{a} \cdot L^{-1}$ and the highest value during 1986) was situated at ca. 18 m. The chlorophyll maximum remained at ca. 16 m throughout July and August with a value ranging from 1.57-1.97 ug Chl $\underline{a} \cdot L^{-1}$. By 17 September the chlorophyll maximum was located at ca. 22.5 m and had a value of 1.75 ug Chl $\underline{a} \cdot L^{-1}$.

Epilimnetic chlorophyll was variable in Two Rivers arm throughout the 1986 seasonal sampling period. Generally, epilimnetic chlorophyll increased until 14 July and then decreased through the remainder of the sampling period.

Trends in Taylor arm were similar to those of Two Rivers arm. Following formation at ca. 22.5 m the subsurface chlorophyll maximum remained slightly deeper than in Two Rivers arm. The first date of sampling (28 May) illustrates a broad subsurface chlorophyll maximum, which appeared to have two small peaks at 18 and 24 m. The maximum subsurface chlorophyll value was 2.63 ug Chl $\underline{a} \cdot L^{-1}$ on 20 August. At other times the maximum value was similar in both Taylor and Two Rivers arm.

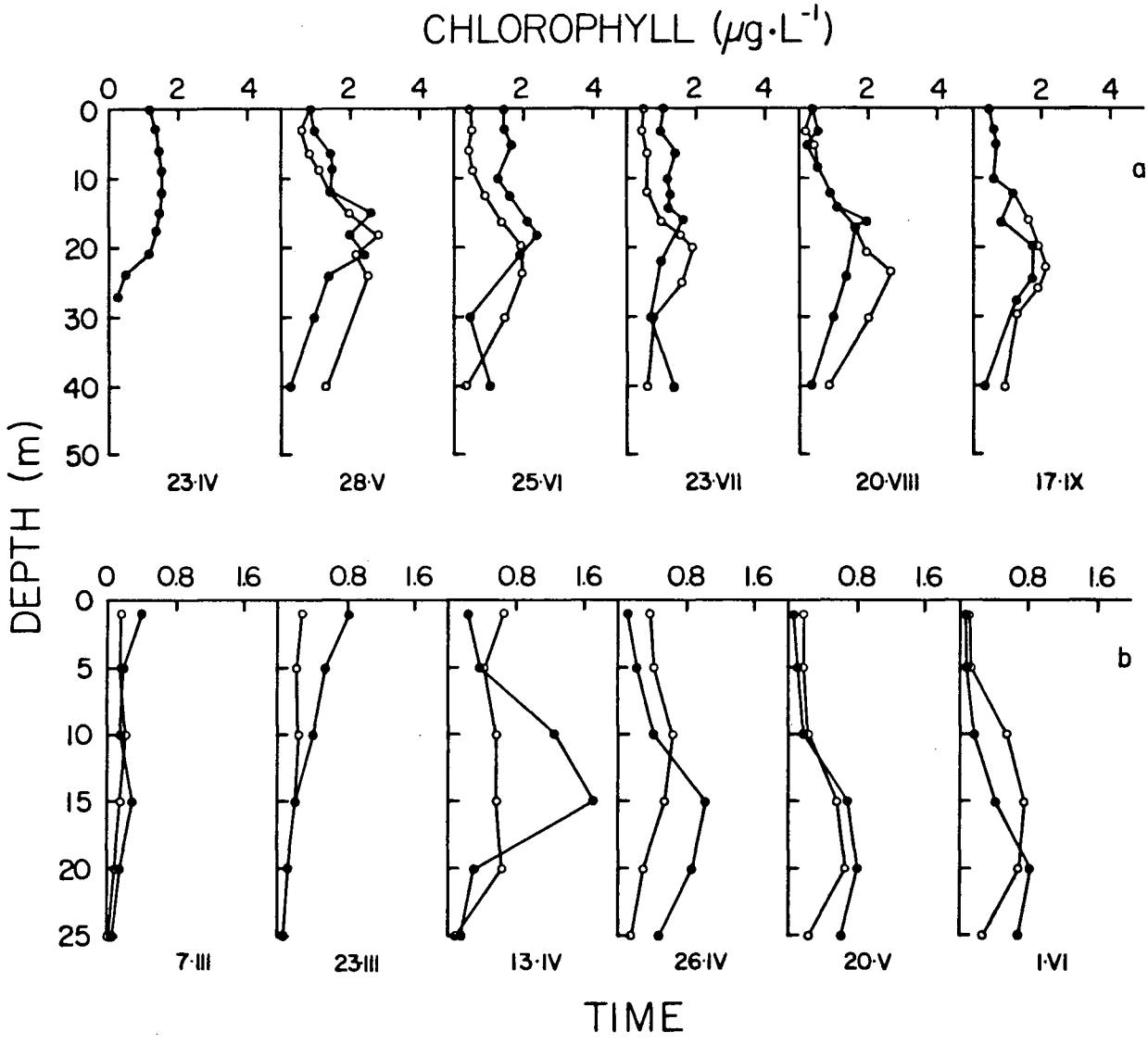

Figure 17. Chlorophyll a concentrations during 1986 (a) and 1987 (b) in Two Rivers (●) and Taylor (O) arms.

Epilimnetic chlorophyll was considerably less in Taylor arm than Two Rivers arm through 23 July. The maximum value of 0.63 ug Chl *a*·L^{-1} occurred on 28 May, approximately 6 weeks prior to the occurrence of the maximum in Two Rivers arm. Values were relatively constant throughout the seasonal sampling period, ranging from 0.44-0.63 ug Chl *a*·L^{-1}. Through July such values were much less than those of Two Rivers arm. Values in August and September were similar in both arms.

1987

The 7 March profile (Fig. 17), during conditions of isothermal mixing, showed nearly uniform concentrations of chlorophyll with depth. By 23 March there was an increase in surface chlorophyll in Two Rivers arm (1-10 m) but not in Taylor arm. The 13 April profile illustrates a maximum of ca. 1.70 ug Chl *a*·L^{-1} at 15 m. By 26 May the Two Rivers chlorophyll profile showed progressively more chlorophyll below the chlorophyll maximum as well as a deepening of the chlorophyll maximum to 20 m by 1 June.

In Taylor arm chlorophyll concentrations had not reached the same maximum concentrations that occurred in Two Rivers arm by 1 June. However, the *in vivo* fluorescence profiles illustrated a trend of an increasing maximum value through 1 June. The chlorophyll maximum was located at 20 m but there was also high chlorophyll at 10 m. Since my method was not directly compared to LEP's, possible different extraction efficiencies due to different extraction times can not be ascertained.

Phytoplankton

Many species and/or groups were enumerated during the two field seasons. These data are separated into two groups: i) data presented in the text of the thesis and ii) data contained in Appendix II. Therefore in the results section only data for R. eriensis, Cyclotella spp., small flagellates and Dinobryon sp. are presented.

1986

Rhizosolenia eriensis was present on 19 May sampling date in both Two Rivers and Taylor arms (Fig. 18 a). Through 9 June a large peak formed at 22.5 m with upper and lower limits of 10 and 27.5 m respectively. The peak was smaller in magnitude by 23 June and the upper limit was at 15 m. By 26 July R. eriensis was virtually absent from 0-30 m.

In Taylor arm R. eriensis cell density reached a maximum at 12.5 m on 19 May. The peak migrated to 10 m by 29 May, and the cell density at other depths decreased. There was an increase in cell density at 10 m on 9 June. Cell density increased at 15, 20 and 25 m and decreased at 5 m. The peak diminished and was absent by 26 July as was the case in Two Rivers arm.

Cyclotella spp.

Cyclotella spp. cell density formed a pattern opposite to R.eriensis (Fig. 18 b). On 19 May Cyclotella spp. was virtually absent and on 29 May cell densities were still extremely low. By

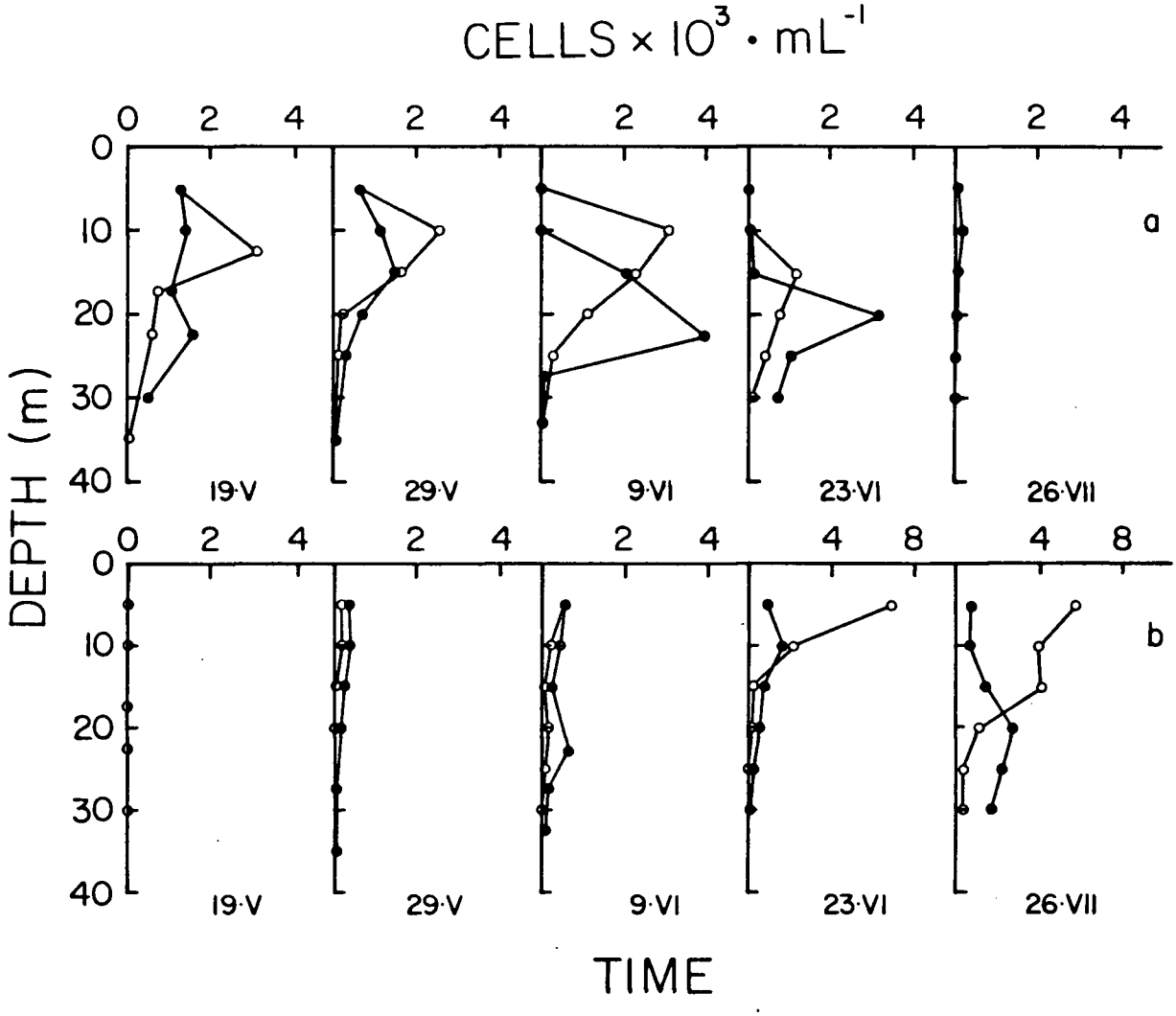

Figure 18. Depth profiles of Rhizosolenia eriensis (a) and Cyclotella spp. (b) in Two Rivers (●) and Taylor (○) arms, 1986.

9 June, Two Rivers arm had slightly higher cell densities than Taylor arm, and the maximum cell density of either arm was only ca. 0.7 x 10^3 cells·ml^{-1}. There was a slight peak in Cyclotella spp. at 10 m in Two Rivers arm but otherwise cell densities were low. In Taylor arm there was a large peak at 5 m on 23 June with cell density falling to near zero by 15 m. The peak in Taylor arm at 5 m had decreased but cell densities at 10, 15 and 20 m were all larger than on 23 June.

Flagellates (3-15 um)

In Two Rivers arm, flagellates were present at all the sampled depths (5-35 m) and cell densities were higher around 22.5-25 m (Fig. 19 a) than above and below. On 29 May cell density had increased from 5-15 m but remained similar at other depths. The 9 June profile shows that cell density at 5 m had declined dramatically but increased at 10, 15 and 20 m. This trend continued and by 23 June there was only a peak at 20 m. By 26 July the 20 m peak had disappeared but surface concentrations were again elevated.

The largest flagellate cell density measured in Taylor arm was at 12.5 m on 19 May (5.9 x 10^3 cells·ml^{-1}; Fig. 19 a). For other sampling dates, profiles were similar with the exception of the 20 m sample on 23 June; there was no peak in Taylor arm.

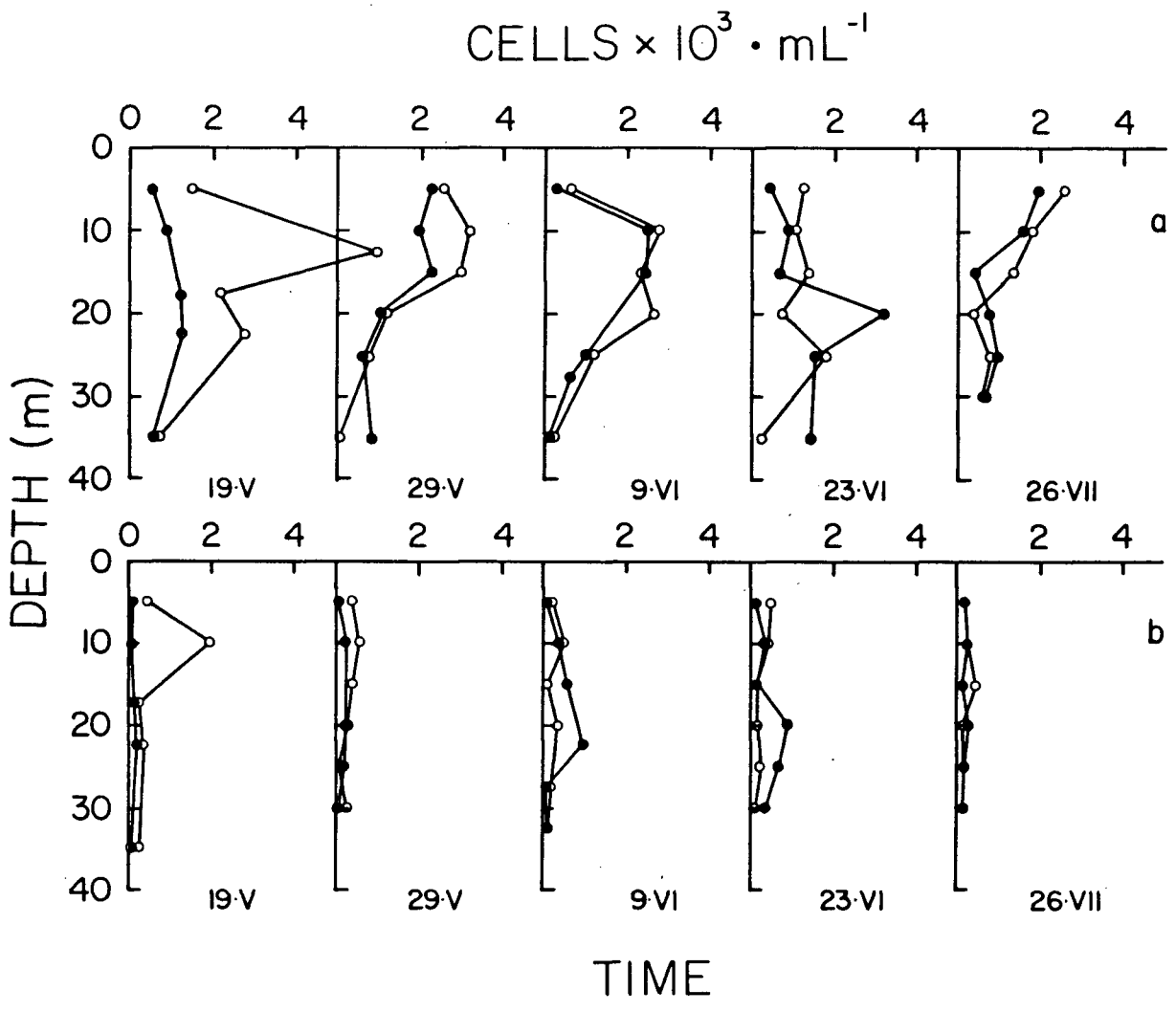

Figure 19. Depth profiles of small flagellates (a) and Dinobryon sp. (b) in Two Rivers (●) and Taylor (○) arms, 1986.

Dinobryon sp.

Dinobryon sp. was present at very low cell densities in Two Rivers arm at the beginning of the 1986 sampling period (Fig. 19 b; 19 May). Cell density increased at 10-25 m by 29 May and by 9 June a maximum had formed at 22.5 m. The cell density maximum was at 20 m on 23 June and while the cell density remained unchanged at 10 m, cell density at 15 m had decreased. By 26 July cell density was similar from 5-30 m.

On 19 May there was a maximum of Dinobryon sp. in Taylor arm at 10 m. Concentrations at other depths were low but still higher than those observed in Two Rivers arm. The maximum declined by 29 May, with concentrations at other depths remaining similar to 19 May. From 9 June through 26 July cell density was variable from 5-30 m, with no large increases.

1987

Rhizosolenia eriensis

On 15 March R. eriensis cell density was low (< 0.02×10^3 cells$\cdot$ml^{-1}) at all depths in Two Rivers arm (Fig. 20 a). On 13 April there was a pronounced peak in cell density at 10 m (0.26×10^3 cells$\cdot$ml^{-1}) and a small increase at 5 m but this peak was absent on 30 April. On 28 May a large peak was evident at 15 m (0.61×10^2 cells$\cdot$ml^{-1}) and cell densities had also increased at 10 and 20 m.

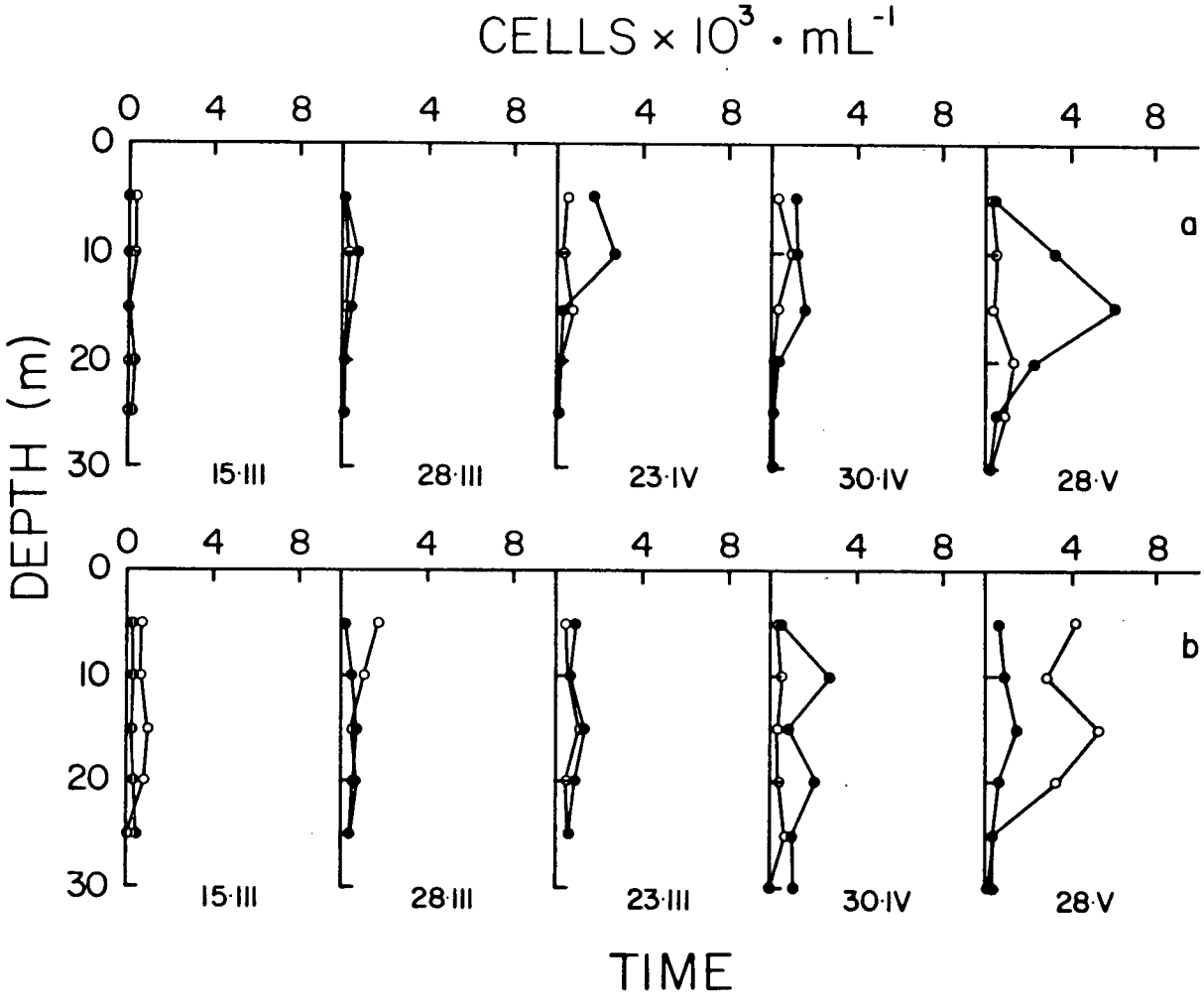

Figure 20. Depth profiles of Rhizosolenia eriensis (a) and Cyclotella spp. (b) in Two Rivers (●) and Taylor (○) arms, 1987.

In Taylor arm, R. eriensis cell density was low compared to that of Two Rivers arm throughout the sampling period. There was a small cell density maximum on 28 May at 20 m (0.12×10^3 cells$\cdot$ml^{-1}); otherwise cell density was usually below 0.05×10^3 cells$\cdot$ml^{-1}.

Cyclotella spp.

Cyclotella spp. in Two Rivers arm was found in low concentrations early in the sampling period similar to R. eriensis. Densities remained below 0.02×10^3 cells$\cdot$ml^{-1} until some time after 13 April (Fig. 20 b), where two small peaks were apparent on 30 April at 10 and 20 m; however, by 28 May these peaks had disappeared.

Taylor arm began the sampling period with low Cyclotella spp. cell density until 30 April. Between 30 April and 28 May there was a large increase in the surface layer and down to and including the 20 m depth. The maximum cell density was at 15 m while concentrations at 5, 10 and 20 m were lower.

Flagellates (3-15 um)

On 15 March in Two Rivers arm, flagellates were evenly distributed from 5-25 m (Fig. 21 a) at ca. 0.5×10^3 cells$\cdot$ml^{-1}. Through 30 April a broad peak developed at roughly 10-20 m with maximum cell density of 2.51×10^3 cells$\cdot$ml^{-1}. This broad peak decreased in size and intensity and by 28 May it was located at

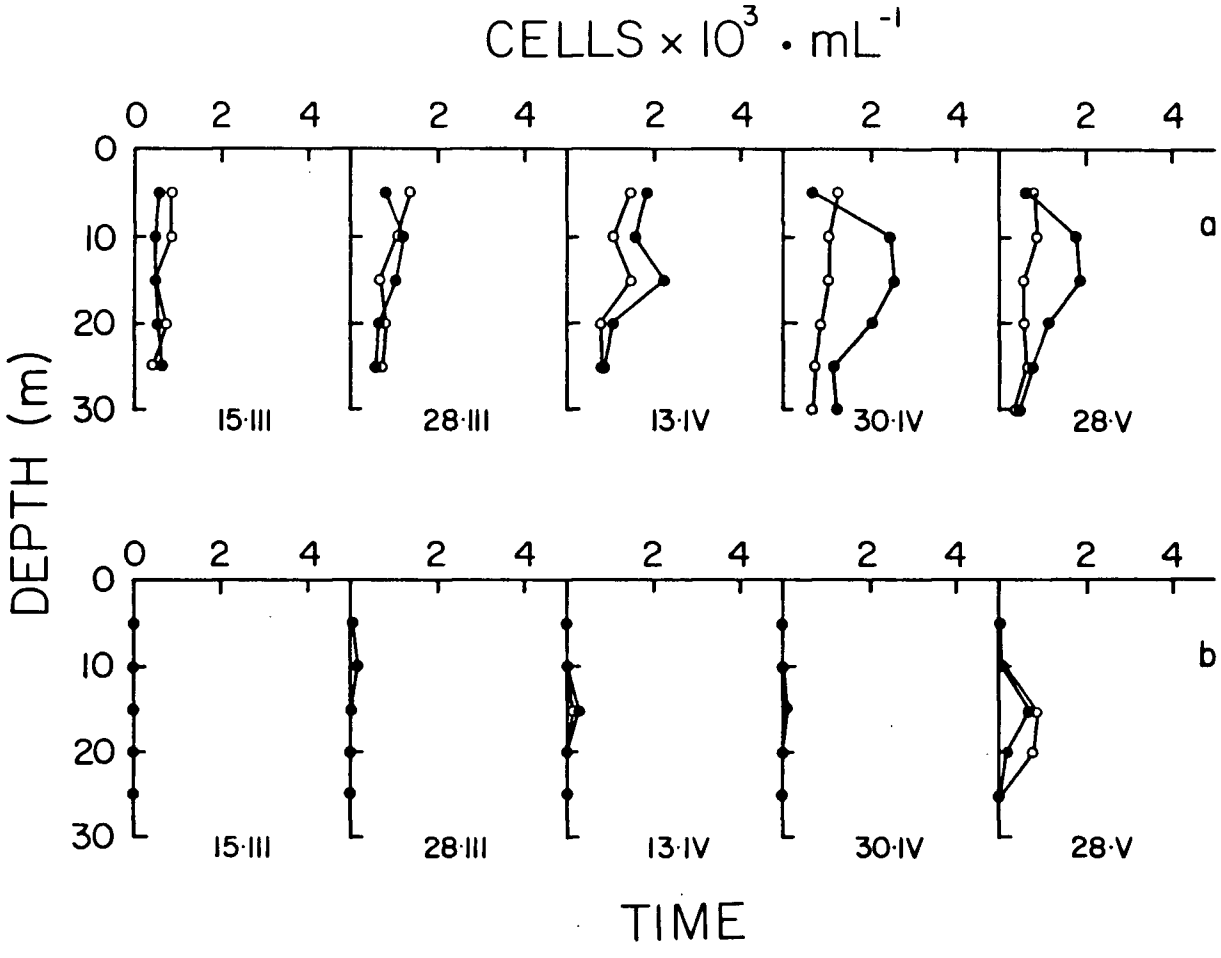

Figure 21. Depth profiles of small flagellates (a) and Dinobryon sp. (b) in Two Rivers (●) and Taylor (O) arms, 1987.

10-15 m. On 28 May the value at 5 m was similar to that of 30 April but values at 20, 25 and 30 m decreased.

In Taylor arm flagellates never reached the cell densities that occurred in Two Rivers arm (Fig. 21 a). Cell densities were similar to Two Rivers arm through 13 April. On 13 April there were small peaks at 5 and 15 m but by 30 April these had decreased (particularly at 15 m) so that from 5-30 m cell density ranged from 0.69-1.22 x 10^3 cells$\cdot ml^{-1}$. These cell densities had decreased even further by 28 May.

Dinobryon sp.

Dinobryon sp. was present in extremely low concentrations (Fig. 21 b) until 28 May (there were measurable concentrations of Dinobryon sp. between 30 April and 28 May but none exceeded the concentrations on 28 May). In Two Rivers arm there was a peak of cell density at 15 m and lower concentrations at other depths. Similar to Two Rivers arm, Taylor arm had a broader peak at 15 and 20 m but low concentrations at other depths.

Sinking rate determination

Sinking rate was determined by using a SETCOL apparatus twice (9 and 20 May) during 1987 representing two different stages of the spring bloom. Sinking rate was calculated for both R. eriensis and Cyclotella spp.. Results for these two groups were considered separately.

Rhizosolenia eriensis

Sinking rate of R. eriensis was similar for both sampling dates and both sites at 5 and 10 m and ranged from 1.8-2.2 $m \cdot d^{-1}$ (Fig. 22). One exception was the 10 m sample from Taylor arm on 20 May which had a value of 1.06 +/- 0.08 $m \cdot d^{-1}$. The lowest sinking rates occurred at 22.5 m during both 9 and 20 May. On 9 May, R. eriensis sank significantly faster ($p < 0.10$) at 17.5 m than at the same depth on 20 May at both sites.

Cyclotella spp.

On 9 May Cyclotella spp. had a faster sinking rate at 5 m than at 10 m in Two Rivers arm while on 20 May there was no significant difference between the two depths. The sinking rates at 5 and 10 m were ca. 0.8-1.0 $m \cdot d^{-1}$, approximately half the sinking rate of R. eriensis. There were no differences in the sinking rate of Cyclotella spp. between the 17.5 m samples on either date in either arm. The lowest sinking rates occurred at 22.5 m, similar to R. eriensis.

Sedimentation

1986

Cell flux data result from sediment trap measurements at 7 and 15 m. The highest cell flux of Rhizosolenia eriensis occurred in Two Rivers arm on 26 May at 7 m (Fig. 23 a). Generally, cell flux decreased through to 30 June. A similar trend occurred for R. eriensis at 15 m in Two Rivers arm (Fig. 23 b). However, following 9 June there was a sharp decrease in cell flux by 450%.

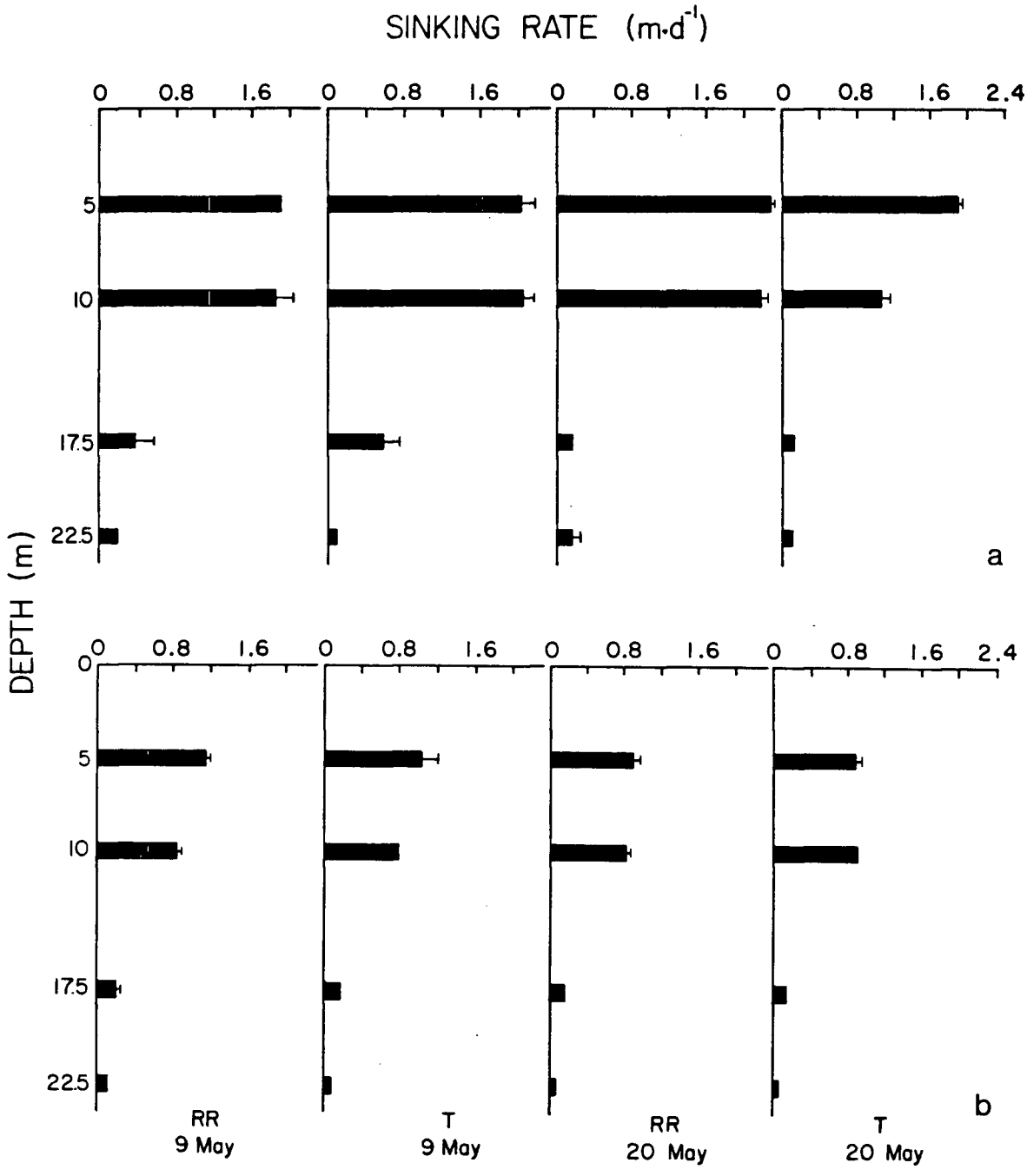

Figure 22. Sinking rates of Rhizosolenia eriensis (a) and Cyclotella spp. (b) on 9 and 20 May 1987 in Two Rivers (RR) and Taylor (T) arms, Error bars represent +/- 2 SD; n = 2.

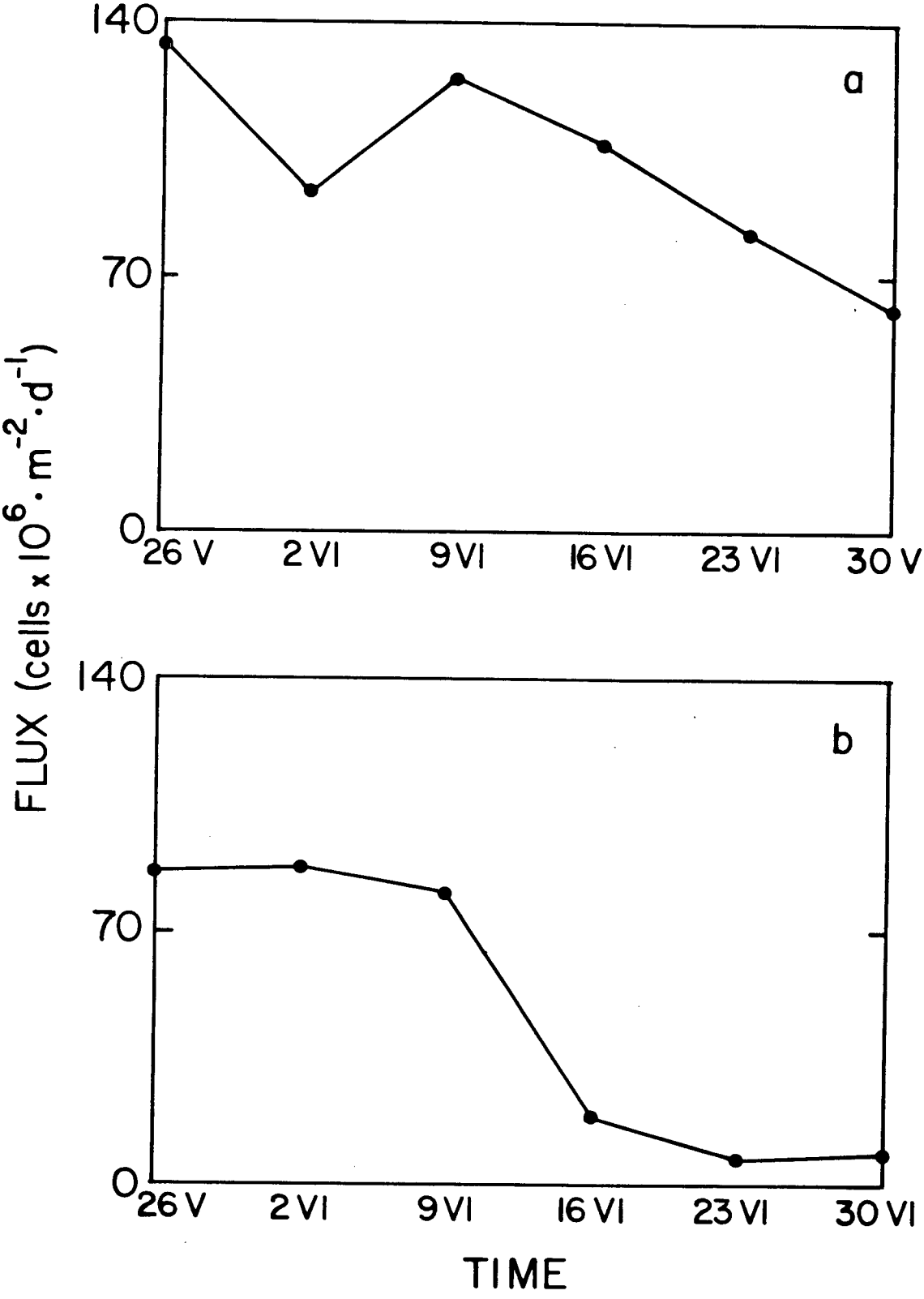

Figure 23. Sedimentation of Rhizosolenia eriensis at 7 m (a) and 15 m (b) in Two Rivers arm, 1986.

R. eriensis cell flux was always greater at 7 m than at 15 m in Two Rivers arm during the sampling period of 1986.

The general pattern of cell flux for Cyclotella spp. was quite different than that of R. eriensis. R. eriensis cell flux generally decreased through the sampling period while Cyclotella spp. generally increased (Figs. 23 to 26). Additionally, Cyclotella spp. cell flux at 15 m always exceeded that at 7 m in both arms.

At 7 m in Two Rivers arm (Fig. 25 a) cell flux of Cyclotella spp. increased gradually from 26 May to 30 June. At 15 m there was a similar pattern of increasing cell flux over time but it differed because the rate of increase was slightly greater at 15 m. The initial cell flux was lower at 15 m than 7 m on 26 May (by 25%) and by 23 June cell flux at 15 m was ca. 300% that at 7 m.

Cell flux for Cyclotella spp. followed a similar pattern in Taylor arm when compared to Two Rivers arm (Fig. 26). At 7 m the initial cell flux in Taylor arm was 40% that of Two Rivers arm. At 15 m, Cyclotella spp. flux was again lower initially in Taylor arm but exceeded cell flux in Two Rivers arm by 30 June.

1987

There was a lower flux of R. eriensis during the sampled portion of 1987 than during 1986 (Figs. 23 and 27). There was no overlap

of sampling time but the end of the 1987 field season approached the beginning of the 1986 season (24 and 26 May respectively).

R. eriensis cell flux doubled at 7 m in Two Rivers arm from 26 April to 4 May 1987. At 15 m the pattern remained similar to that at 7 m but with a larger increase in cell flux on 4 May. In Taylor arm R. eriensis cell flux again showed similar trends to that of Two Rivers arm (Fig. 28).

In Two Rivers arm at 15 m Cyclotella spp. cell flux decreased initially but increased near the end of the sampling period (Fig. 29 b). There was a sharp increase on 24 May at both 7 and 15 m (Fig. 29). At both 7 and 15 m the pattern of Cyclotella spp. cell flux in Taylor arm followed no overall trend and it fluctuated through the sampling period (Fig. 30).

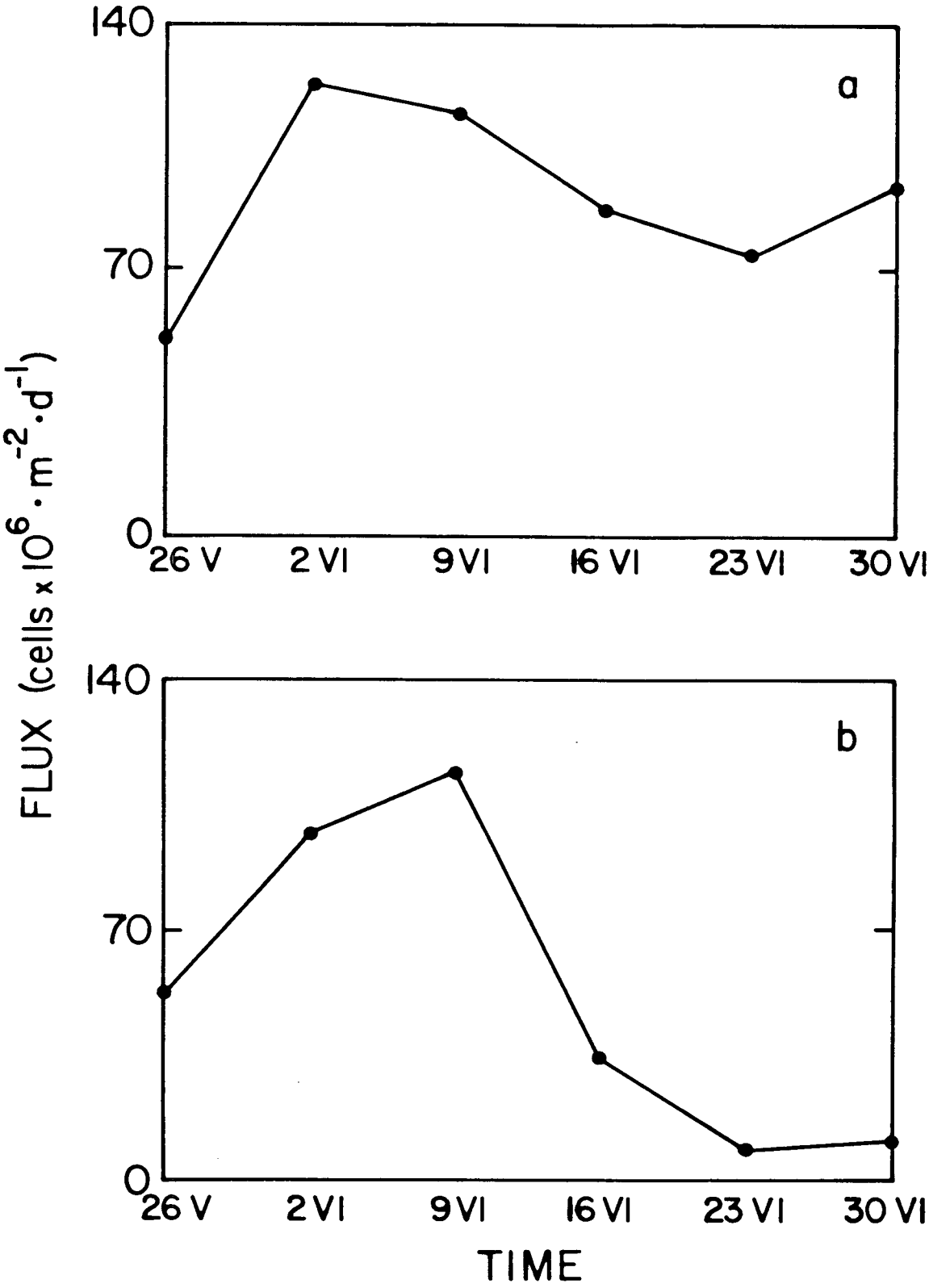

Figure 24. Sedimentation of Rhizosolenia eriensis at 7 m (a) and 15 m (b) in Taylor arm, 1986.

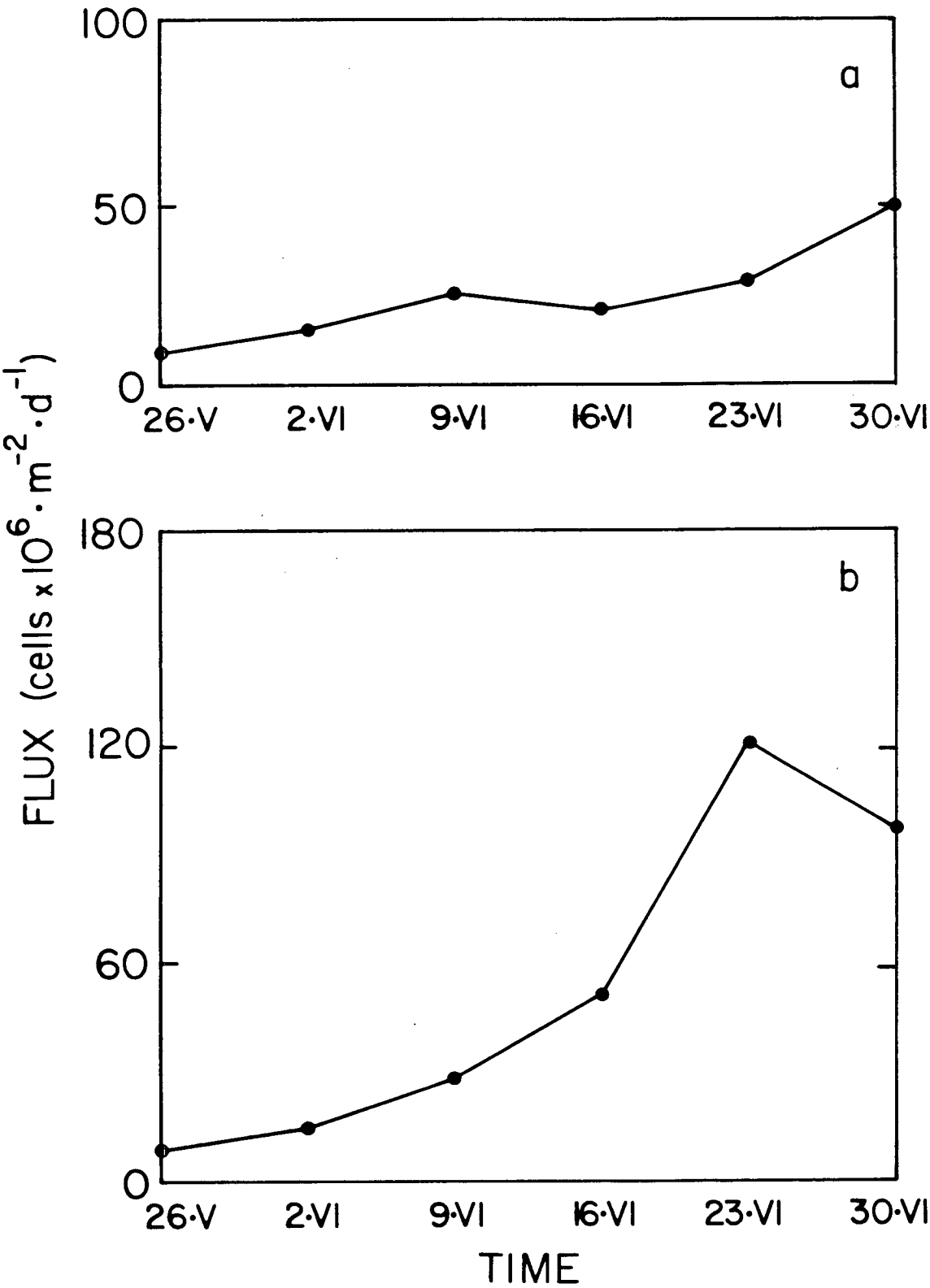

Figure 25. Sedimentation of Cyclotella spp. at 7 m (a) and 15 m (b) in Two Rivers arm, 1986.

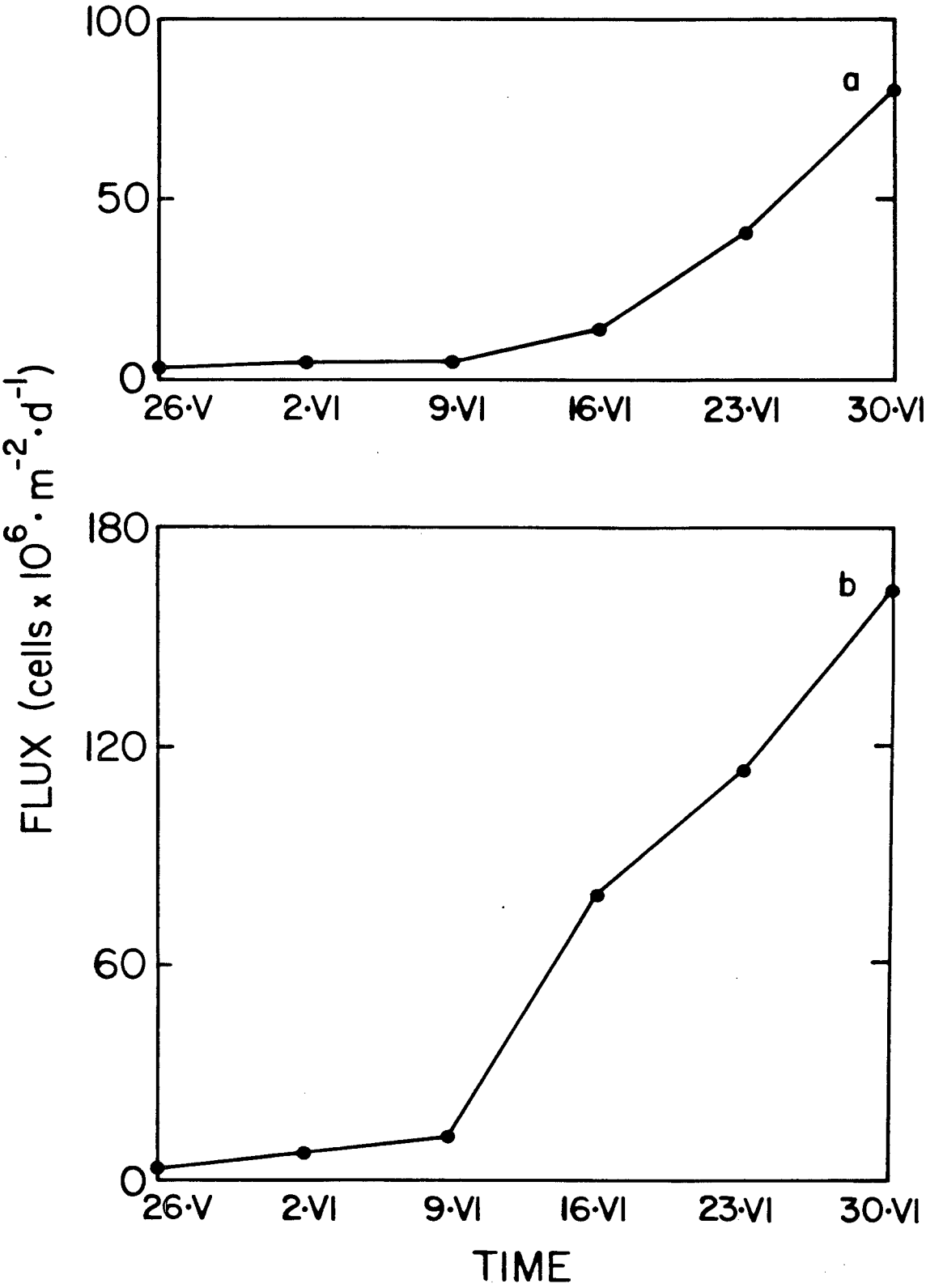

Figure 26. Sedimentation of Cyclotella spp. at 7 m (a) and 15 m (b) in Taylor arm, 1986.

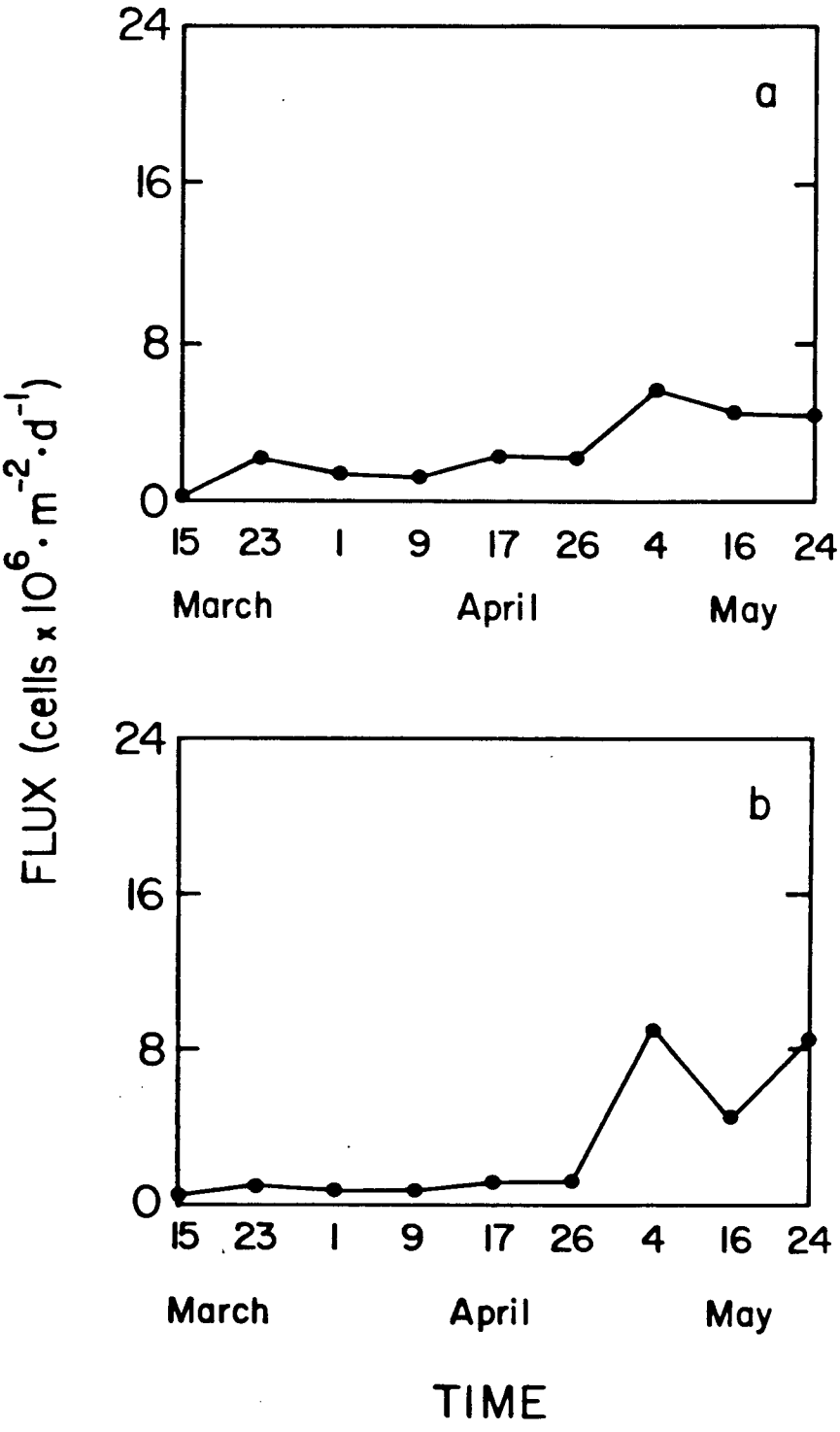

Figure 27. Sedimentation of Rhizosolenia eriensis at 7 m (a) and 15 m (b) in Two Rivers arm, 1987.

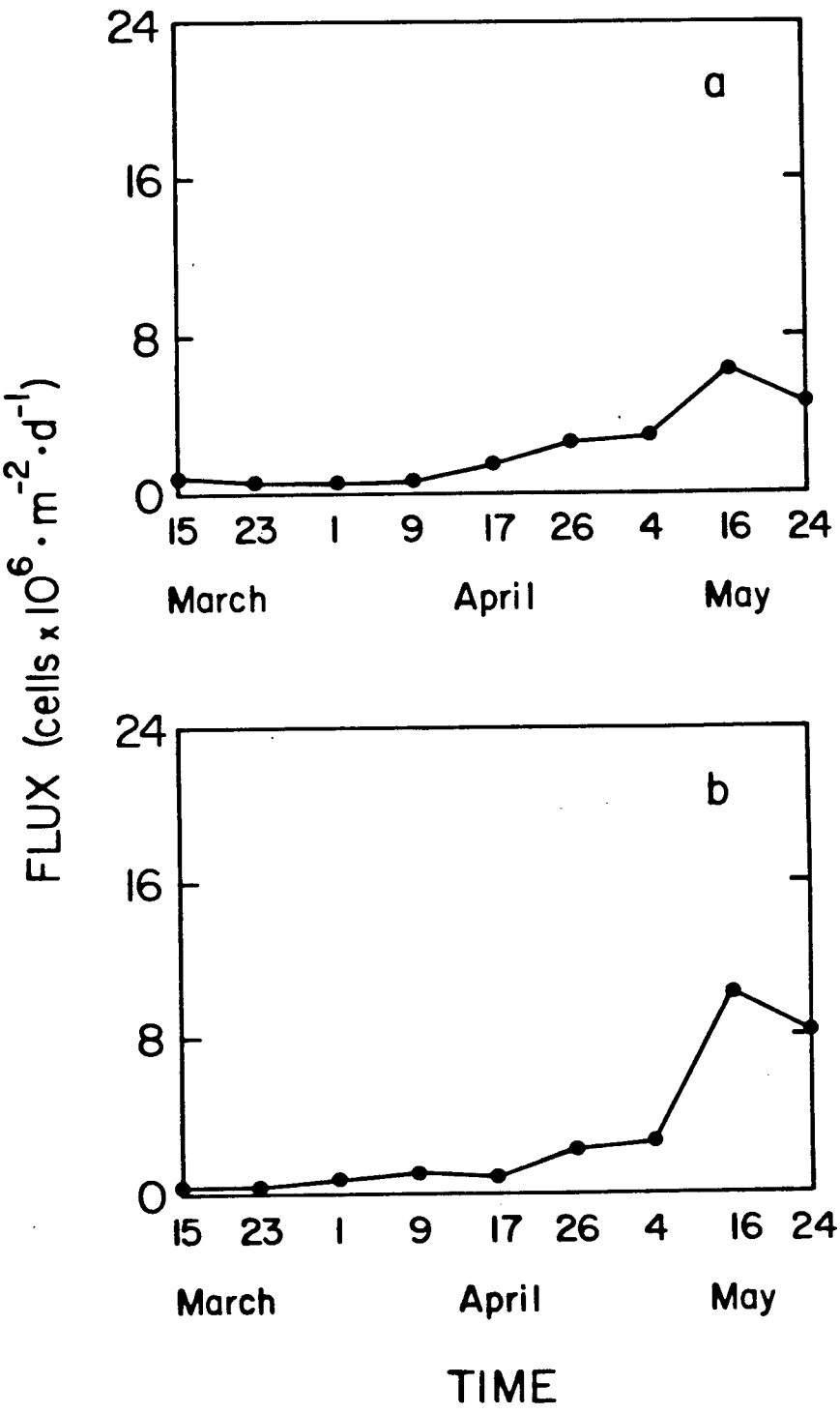

Figure 28. Sedimentation of Rhizosolenia eriensis at 7 m (a) and 15 m (b) in Taylor arm, 1987.

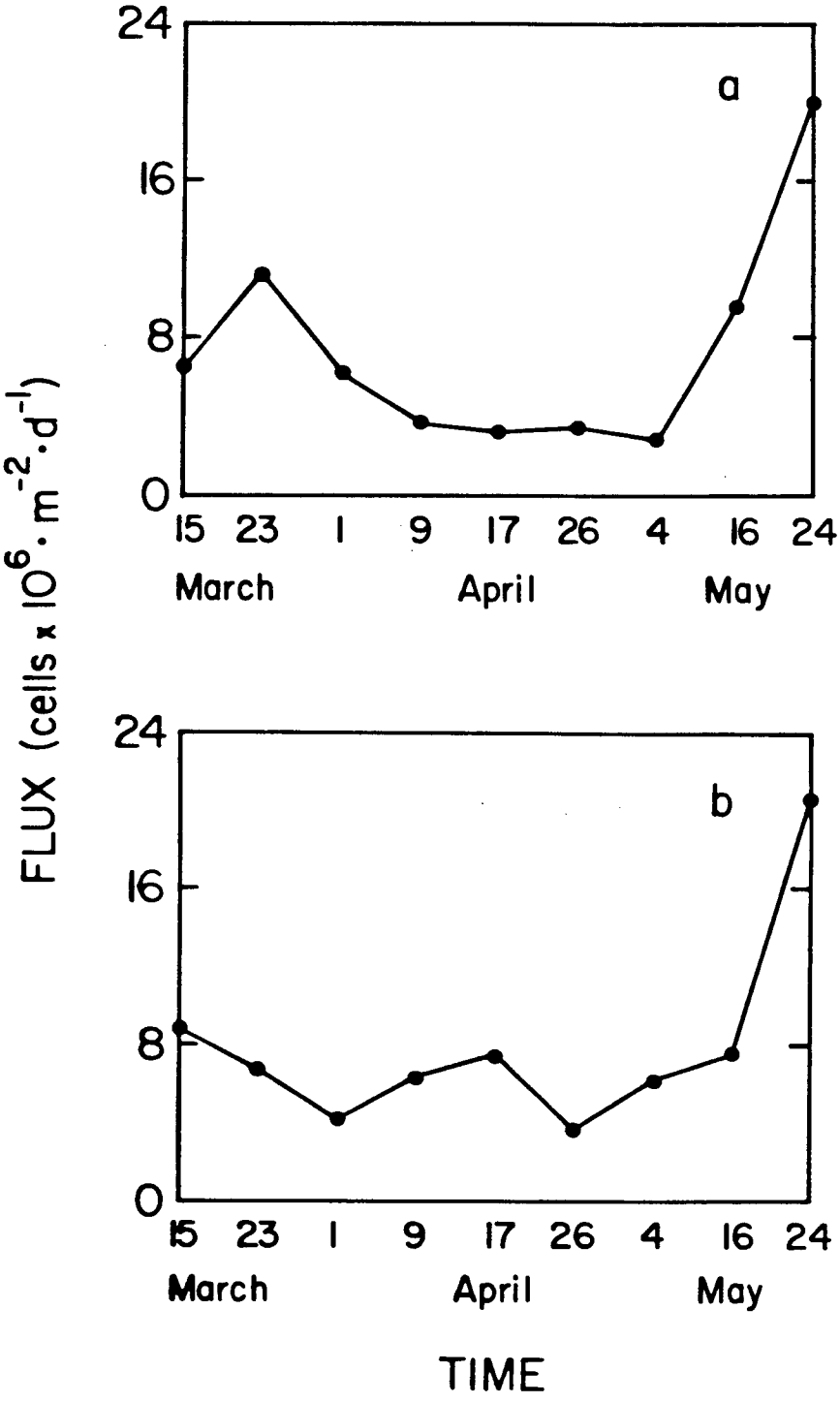

Figure 29. Sedimentation of Cyclotella spp. at 7 m (a) and 15 m (b) in Two Rivers arm, 1987.

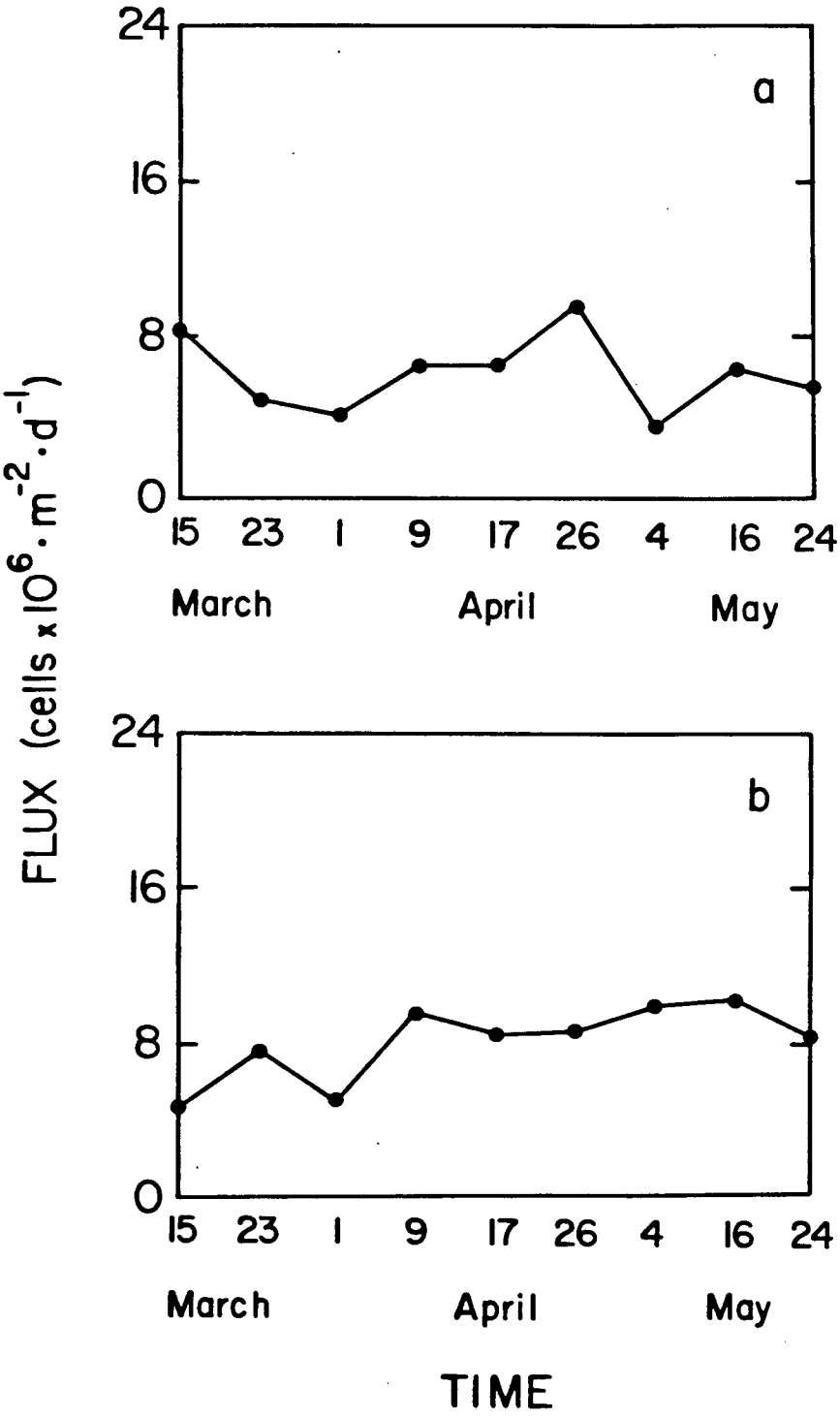

Figure 30. Sedimentation of Cyclotella spp. at 7 m (a) and 15 m (b) in Taylor arm, 1987.

Discussion

The definitions of spring and summer are operational at best. Variability of physical, chemical and biological processes between years prevents a rigid time-dependent definition. In this thesis and refering to water column temperature structure, spring is defined as the period of time from isothermal temperature conditions to development of seasonal stratification. Summer is the period of time following the establishment of seasonal stratification to fall overturn.

It is useful to discuss the data set in a context of seasonality in order to pool both year's data together. Since the original questions focused on gaining an understanding of the role of R. eriensis to the Sproat Lake phytoplankton community, this species will be discussed in more detail than other species. Throughout the discussion an emphasis will be placed on Taylor arm since it was the experimental site. Reference is made to Two Rivers arm where appropriate and comments regarding the usefulness of Two Rivers arm as a control site are also included.

Spring

The in vivo fluorescence profiles were closely spaced vertical profiles taken more frequently than either chlorophyll or phytoplankton cell counts and therefore illustrate the spring bloom in more detail. Appendix III contains a comparison of phytoplankton cell counts and in vivo fluorescence profiles.

This comparison demonstrates that the in vivo fluorescence measurements were consistent with phytoplankton bottle counts in indicating major profile features. On 11 March 1987 in vivo fluorescence was nearly uniform from 0-50 m (Fig. 16) as was chlorophyll and temperature on 7 March and phytoplankton profiles of 15 March. It is clear that the beginning of March 1987 was prior to the spring bloom in Sproat Lake.

Phytoplankton growth was slow until 23 March when there were increases in in vivo fluorescence and chlorophyll in the surface water to a depth of 10-12 m. At this time statification had begun to occur and the 1 % light depth was increasing. This was the initiation of the spring bloom. A subsurface fluorescence maximum formed quickly, as illustrated by the 28 March in vivo fluorescence profile (Fig. 16). This maximum may have resulted from increases in chlorophyll and/or changes in fluorescence per unit chlorophyll. On 13 April a well defined subsurface chlorophyll maximum formed at 15 m. This early peak may have been the result of growth of R. eriensis and small flagellates at 15 m or growth and subsequent sinking to 15 m. Nutrients were also present in the epilimnion during this period, but they were low.

In Sproat Lake, the in vivo fluorescence maximum formed around 10-12 m, and the 1 % light depth was deeper than the depth of the fluorescence maximum. Presumably, positive net rates of photosynthsis, and growth, were maintained in the chlorophyll

maximum throughout the spring. Light has been demonstrated to be important in determining the vertical position of the chlorophyll maximum (Moll et al., 1985). Cells were capable of growing in the subsurface chlorophyll maximum at low light levels. Moll et al., 1985 determined that cells within the chlorophyll maximum of Lake Michigan contributed ca. 60 % of areal (m^2) primary production.

Throughout the 1987 sampling season, nitrate was measurable throughout the water column; however, the trend of decreasing nitrate would probably have led to nitrate depletion in the epilimnion by the early summer.

Previous studies measuring soluble reactive silicon (SRS) values from Sproat Lake (Nidle et al., 1974; Nidle et al., in press) reported mean annual epilimnetic SRS concentrations of ca. 1050 ug $Si \cdot L^{-1}$. Considering the low concentrations of both phosphate and nitrate, Sproat Lake phytoplankton growth is rarely, if ever, silicate-limited.

During May nutrient concentrations and 1 % light depth were decreasing and in vivo fluorescence, R. eriensis cell density and stratification were increasing. R. eriensis sank significantly faster ($p < 0.05$) under conditions of high light and low nutrients than it did under conditions of low light and high nutrients (Fig. 20). The same was true for Cyclotella spp.. R. eriensis and Cyclotella spp. should have decreased their sinking

rates if a major factor leading to chlorophyll maximum formation was a decrease of sinking rate at depth. In fact, this was observed. On 9 May, when Cyclotella spp. was still increasing there were higher sinking rates in surface waters than at depth. Clearly, sinking rate is not always controlled by nutrient limitation.

Two major components of the spring and summer phytoplankton community were R. eriensis and Cyclotella spp.. Cell flux at 7 and 15 m was low for both of these groups early in 1987 before the spring bloom. Cells sedimenting out of the top 15 m early in the 1987 season were from the winter population while following the spring bloom, sedimenting cells were from the spring bloom.

Since sinking was a major mechanism of chlorophyll maximum formation and the chlorophyll maximum formed at 10-12 m, there was a higher cell flux at 7 m than at 15 m during chlorophyll maximum formation. This was particularly evident for R. eriensis, which bloomed earlier than Cyclotella spp.. Later in May, when R. eriensis growth rate slowed down, cell flux at 15 m approached that of 7 m (Fig. 23). Cyclotella spp. bloomed later in April and May, when the chlorophyll maximum was below 15 m and therefore more cell flux occurred at 15 m than at 7 m. This assumes that cells sank until they reached the depth of the chlorophyll maximum and then became neutrally buoyant. Cells caught in the 7 m traps represent cell flux out of the top 7 m while at 15 m, cell flux represents the whole epilimnion.

Summer

The 1986 summer began with stratification already developed and nutrient concentrations low in the epilimnion. During June and the remainder of the summer stratification intensified. By the end of June the nitracline began at
15 m. The *in vivo* fluorescence maximum was well developed at 22.5 m. Chlorophyll, *R. eriensis* and small flagellates were maximal at 20 m. A large proportion of phytoplankton biomass was therefore located in the chlorophyll maximum, an area of high nutriens and low light.

In late June and July *Cyclotella* spp. displaced *R. eriensis* in the epilimnion as the dominant diatom species. *Cyclotella* spp. probably benefited more from the nutrient enrichment than other species given the considerably higher increase in cell density during late June and July. Following the cessation of fertilization on 7 July 1986, nutrient levels would have remained low until fall overturn.

When comparing the profiles of *in vivo* fluorescence, chlorophyll and phytoplankton it is clear that events measured by these parameters did not occur at the same time each year. A possible reason is that the lake was at a different point of its seasonal cycle each year. It is probable that both these factors were important. The 1986 *in vivo* fluorescence and chlorophyll

profiles had deeper maxima than the 1987 profiles on the same date. Since these maxima formed at 10-12 m and then sank with time, it is suggested that the seasonal cycle had progressed further by 1 June in 1986 than 1987.

The phytoplankton in the chlorophyll maximum, located at 20-22.5 m, probably consumed nitrate as it was advecting through the hypolimnion toward the epilimnion assuming growth was not limited by phosphate. Measurements of orthophosphate in Sproat Lake are typically below the limits of detection (K. Shortreed, pers. comm.) and it is difficult therefore to determine the amount of inorganic phosphorus available for phytoplankton growth. Suttle (1987) suggested that in Sproat Lake different size fractions of phytoplankton may be growth limited by different nutrients. It is therefore possible that co-limitation by nitrogen and phosphorus may occur. Suttle (1987) demonstrated that a variety of factors were important to phytoplankton community composition in Sproat Lake, including N:P supply ratio, temporal patchiness of nutrient supply and size fraction of phytoplankton considered (Suttle, 1987).

Following the establishment of the chlorophyll maximum during April and May, it descended to 20-25 m for the duration of the summer. In the absense of measurable phosphate and nitrate, phytoplankton growth may have occurred at low rates in the epilimnion possibly utilizing remineralized phosphate, ammonium and urea.

At the chlorophyll maximum there was measurable nitrate; therefore, nitrate probably did not limit phytoplankton growth. Phytoplankton above the 1 % light depth (ca. 15 m) would have been capable of net photosynthesis. Cells between ca. 15 m and the 1 % light depth were probably phosphate-limited. Below the 1 % light depth growth was light-limited. Most of the chlorophyll maximum (not just the depth at which the chlorophyll maximum occurs) existed above the 1 % light depth and within the nitracline. At such depths, phosphate may have been supplied by zooplankton excretion and sloppy feeding (Williams, 1981).

In late June 1986 the abrupt loss of the chlorophyll maximum may have resulted from the picoplankton bloom, which caused a subsequent decrease in light at depth. This bloom occurred throughout Sproat Lake and its occurrence was not the result of lake fertilization but, it is likely that the fertilization increased the magnitude of the bloom in Taylor arm. (The picoplankton bloom consisted of more than one species but two large components were Synechococcus sp. and a "Synechococcus-like" gelatinous species; K. Shortreed, pers. comm.). The 3 July in vivo fluorescence profile had, in addition to the fluorescence maximum at 22.5 m, a smaller maximum at 10 m in Taylor arm. This may have been the beginning of the picoplankton bloom. Cyclotella spp. increased their cell density in the epilimnion at this time; likely benefiting from the fertilization, because a concurrent increase in cell density in Two Rivers arm did not

occur. A decrease in the 10 m maximum by 26 July was not accompanied by an increase in the maximum at 22.5 m as cells sank to depth. Cells must either have sank out of the region of the 22.5 m maximum or have been grazed. Without a sediment trap moored below the chlorophyll maximum it was not possible to ascertain the flux of cells out of the chlorophyll maximum. After the disappearance of the 10 m maximum and concurrent decrease in k_e, light penetrated deeper and a fluorescence maximum began to re-establish itself at 25 m (Fig. 13) by the end of August.

During July and August, nutrients remained similar at depths of the chlorophyll maximum; therefore, it appears that the position and maintenance of the chlorophyll maximum was affected more by the light environment than the nutrient environment.

Rhizosolenia eriensis autecology

During early lake fertilization projects in Great Central Lake, R. eriensis was shown to benefit greatly from nutrient enrichment (Parsons et al., 1972). It was important to know: 1) if R. eriensis was similarly enhanced in Sproat Lake, and 2) if R. eriensis was a nutrient sink. A consideration of the seasonal cycle of R. eriensis is important to understanding its importance to the Sproat Lake phytoplankton community and therefore indirectly to lake fertilization.

In the winter, during conditions of isothermal mixing, growth rates of R. eriensis were probably low. Nutrients were available for growth but the temperature was low (ca. 5°C) and light was limiting. R. eriensis existed at this time as an overwintering population. This population, or specifically what remained of it through the winter, formed the seed population for the following year's spring bloom. In Taylor arm, where the maximum depth is 270 m, cells which sank to the bottom would probably not have been resuspended. In the littoral zone, cells may be resuspended and form part of the seed for the spring bloom.

During the spring bloom R. eriensis reached its maximum cell density. The success of R. eriensis during the early spring and in the region of the chlorophyll maximum through the summer also indicated that it is well adapted to lower temperatures, i.e., 5-15°C. Since R. eriensis was one of the first species to bloom in the spring it may have a lower light requirement than other species at low temperatures.

Following the spring period, R. eriensis declined in the epilimnion and its importance centred around its contribution to the chlorophyll maximum. If storm events occurred during the summer it is unlikely that
R. eriensis would have been resuspended into the epilimnion because stratification was strong and the chlorophyll maximum was located in the hypolimnion. As previously mentioned, growth of R. eriensis was not nitrate-limited in the chlorophyll maximum

and growth was probably regulated by the supply rate of phosphorus and light intensity.

In 1986, the epilimnetic algal picoplankton bloom in the upper part of the water column caused a breakdown in the chlorophyll maximum, including losses of R. eriensis. The resulting decrease in the light reaching R. eriensis in the chlorophyll maximum, due to the bloom above it, argues for the importance of enough light reaching the chlorophyll maximum to allow R. eriensis to grow slowly and maintain itself at 20-22 m.

The time period including fall overturn was not monitored during 1986. However, it is clear that R. eriensis was present in sufficient numbers through the October 1986 - February 1987 period to form a seed population for the 1987 spring bloom.

Ecologically, R. eriensis is a species which is well adapted to conditions of low temperature and light, characteristic of the early spring. In late spring it sank out of the epilimnion, probably achieved neutral buoyancy, and became a major constituent of the hypolimnetic chlorophyll maximum. It is therefore unlikely that R. eriensis is a large nutrient sink for nutrients added as part of the lake fertilization programme because R. eriensis is present in substantial numbers in the epilimnion only during the early portion (March-May) of the spring bloom, prior to fertilization (at the end of May). R. eriensis may have been a small nutrient sink if, through the

summer, small numbers of cells sank out of the epilimnion to the chlorophyll maximum and were not grazed.

Rhizosolenia eriensis contains a large vacuole (ca. 90 % of the cell volume) and therefore has a low C:cell volume^{-1}. The large size of R. eriensis probably makes this cell difficult to graze by filter-feeding zooplankton. Rhizosolenia eriensis therefore probably does not represent a good food item for zooplankton.

Two Rivers arm as a control site

In using a control site it is desirable that one can compare differences between these observations and observations of the experimental site and attribute the differences to the experimental protocol. In fact, Two Rivers arm is not a good control site.

A shallower 1 % light depth in Taylor arm in the spring and higher extinction coefficients suggest Taylor arm had more non-biological suspended material than Two Rivers arm. If phytoplankton growth was the only factor affecting light penetration, both arms should have had similar properties early in the spring, before the spring bloom occurred. Logging occurs within the catchment basin of Taylor arm. Recently logged areas during one year may produce high levels of suspended material in the snow melt of the following spring, which in turn decrease light penetration.

Taylor arm is less sheltered than Two Rivers arm and was therefore more susceptible to breakdown of thermal stratification early in the spring. In 1986, both arms were beyond the onset of thermal stratification by the first sampling date however, in 1987, development of seasonal stratification was observed. Taylor arm stratified later than Two Rivers arm and until strong stratification occurred had a shallower epilimnion.

The initiation of the 1987 spring bloom was not as well defined in Taylor arm as it was in Two Rivers arm. Events occurred in Two Rivers arm ca. 2-4 weeks prior to their occurrence in Taylor arm. More mixing in Taylor arm early in the spring caused a delay in the onset of seasonal stratification. Comparing physiological processes must be done with caution if Taylor and Two Rivers arms are compared.

On a seasonal basis Two Rivers arm may be an adequate control site but on shorter time scales, ie., less than a few months, the validity of Two Rivers arm as a control site must be questioned. A better control site might be outside the fertilized portion of Taylor arm and towards the west end of the arm.

Lake Fertilization

In addition to affecting the physical environment, thermal stratification indirectly controls the temperature to which

phytoplankton cells are exposed. Fertilization of Sproat Lake typically commences around mid/late-May (e.g., 20 May in 1986). Takahashi and Nash (1973) demonstrated temperature inhibition of photosynthesis in nearby Great Central Lake between ca. mid-October and late May, while through the summer nutrients limited photosynthesis. The exact time of switch-over between temperature and nutrient-limitation on photosynthesis will vary. Fertilization prior to this point in time may result in some fertilizer loss because phytoplankton demand for nutrients (specifically nitrogen and phosphorus) may not be sufficient to use the additions.

One of the premises behind lake fertilization is that the fertilizer is added when the spring bloom is declining due to nutrient limitation so that the effect of the nutrient addition is to maintain bloom levels of phytoplankton growth through the summer but not to alter the trophic status of the lake. Stratification should be necessary for nutrient-limitation to occur because stratification creates a barrier to nutrient flux into the surface layers from depth. The N and P-load was doubled in 1986 and the resulting increase in primary production was obvious by the occurrence of the algal picoplankton bloom in July. During 8 weeks in 1986 almost the same amount of phosphorus was added as during 18 weeks in 1985. While the 1986 loading levels resulted in an algal picoplankton bloom, which may be undesirable, Cyclotella spp., a very grazable species, was also enhanced.

Fertilization was effective in increasing phytoplankton standing stock in 1985 but did not cause unwanted increases in standing stock (Nidle and Shortreed, in press). A shallower 1 % light depth, higher extinction coefficient and greater maximum fluorescence values illustrated that more plant material was present in Taylor arm throughout the summer of 1985 and can be directly attributed to lake fertilization. It is therefore suggested that lake fertilization can be an effective method of increasing phytoplankton standing stock, consistent with earlier reports (Parsons et al., 1972; Schindler and Fee, 1974; Stockner and Hyatt, 1984; Stockner and Shortreed, 1985).

Grazing

The observed standing stock of phytoplankton is a static measure of dynamic processes including growth, water transport, sinking and grazing. With respect to food chains grazing is particularly important because it represents a link between phytoplankton and higher trophic levels.

Growth of phytoplankton, with the exception of the picoplankton bloom in 1986, was low throughout the summer. Net growth of phytoplankton would primarily be the difference between growth and sinking plus grazing. In an ideal system all phytoplankton growth would be consumed by zooplankton grazing. Since grazing was not assessed in this study its importance as a phytoplankton

loss term cannot be determined although grazing was undoubtably occurring.

The chlorophyll maximum may represent a large food source for zooplankton. Changes in phytoplankton species composition with time and the shape and position of the chlorophyll maximum would be influenced by both grazing and sinking. The importance of the chlorophyll maximum as a food source cannot be determined without direct measurements of grazing.

Future work

The importance of picoplankton to marine and limnetic systems has become apparent (Stockner and Antia, 1987) but was not addressed in the present study. The relative importance of picoplankton to ecosystem and chlorophyll maximum dynamics should be considered in future studies.

Physiological rate processes of cells within the chlorophyll maximum have rarely been measured. To fully understand the contribution of the chlorophyll maximum requires quantification of such rates, which can then be used in dynamic models and energy budgets.

It is probable that zooplankton grazing plays a role, in various degrees, in controlling formation and influencing species composition with time by selectively grazing some species. What

is grazed and the rates of grazing in both the epilimnion and chlorophyll maximum need to be determined.

CONCLUDING REMARKS

Field measurements made during this study enabled observation of the spring and summer phytoplankton community in an oligotrophic coastal British Columbia lake. Over two seasonal periods it was clear that some events repeated themselves although the exact nature and timing of such events varied.

Sproat Lake phytoplankton form a seasonal hypolimnetic chlorophyll maximum following the onset of seasonal thermal stratification in late April and early May. Growth of phytoplankton within the chlorophyll maximum is probably phosphate-limited. Formation of the chlorophyll maximum began at 10-12 m and in late-May or early-June it descended to ca. 22.5 m for the duration of the summer. Some sinking phytoplankton (mainly R. eriensis) become neutrally buoyant at depth and play a major role in chlorophyll maximum formation. The position and maintenance of the chlorophyll maximum is possibly mediated by the light regime. Nitrate was present throughout the water column during mixing but became depleted during the spring bloom. A nitracline was present throughout the summer, beginning at 15 m. Phosphorus was always present in very low or undetectable concentrations. The sinking rate of two diatoms was measured and found to be highest in the epilimnion and lowest at the depth of the chlorophyll maximum.

A seasonal cycle of phytoplankton species succession and community structure was observed. R. eriensis and Cyclotella spp. were the two major diatom constituents during 1985 and 1986. R. eriensis bloomed prior to Cyclotella spp. in the spring. Throughout the spring and summer, medium-sized flagellates (3-15 um) were important numerically as was, on occasion, Dinobryon sp.. Later in the summer other diatoms, including Asterionella formosa, Synedra sp. and Fragilaria sp. became relatively more important numerically, but were still not as important as R. eriensis and Cyclotella spp.

Fertilization of the lake for enhancement of sockeye salmon can alter phytoplankton standing stock. If changes to the phytoplankton community are large, indirect changes, e.g., to the light regime, may occur. R. eriensis was not considered to be a large nutrient link or sink in Sproat Lake due to temporal and spatial separation from the portion of the lake directly affected by fertilization. It had already sunk out of the epilimnion and become a major component of the chlorophyll maximum (well below the depth of influence of fertilization; Fig. 18) by the time areal fertilization started in late May.

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APPENDICES

Appendix I. Sampling dates for various parameters during 1986 and 1987.

Table 1. Sampling dates for *in vivo* fluorescence and phytoplankton, 1986.

May	8	12	15	19	22	26	29
June	2	5	9	12	19	23	30
July	3	17	21	26	29		
August	6						

Table 2. Sampling dates for *in vivo* fluorescence and phytoplankton, 1987.

March	11	15	19	23	28		
April	1	5	9	13			
	18	22	26	30			
May	4	8	12	16	20	24	28
June	1						

Table 3. Sampling dates for light and temperature, 1987.

March	7	15	23
April	1	18	26
May	6	12	20
June	1		

Table 4. Sampling dates for total filtered phosphate, nitrate and chlorophyll, 1987.

March	7	23
April	13	26
May	12	
June	1	

Appendix II. Cell density (cells x $10^2 \cdot mL^{-1}$) for groups enumerated and discussed in the thesis text (lg = large, sm = small, and depths in metres).

Table 1. Cell densities for Two Rivers arm, 1986.

19 May	5	10	17.5	22.5
Other diatoms	11	18	13	13
lg flagellates	17	5	12	17
ciliates	4	5	3	3

26 May	5	10	17.5	20	25
Other diatoms	38	2	40	19	21
lg flagellates	21	43	64	24	11
ciliates	2	2	5	4	2

30 May	5	10	15	20	25	35
Other diatoms	15	14	15	15	12	22
lg flagellates	6	26	24	28	9	20
ciliates	4	1	2	1	3	1

2 June	5	10	15	20	25	30
Other diatoms	8	17	22	21	26	24
lg flagellates	12	56	60	48	6	5
ciliates	1	0	6	4	4	2

5 June	10	15	20	25
Other diatoms	9	20	31	18
lg flagellates	36	48	50	17
ciliates	5	1	4	2

9 June	5	10	15	22.5	27.5	32.5
Other diatoms	5	10	15	11	14	9
lg flagellates	8	35	56	92	4	8
ciliates	2	3	2	17	1	1

16 June	5	10	13	16	19
Other diatoms	13	18	12	23	36
lg flagellates	5	10	76	57	32
ciliates	0	1	5	8	4

19 June	5	10	15	20	25	30
Other diatoms	23	16	7	18	13	15
lg flagellates	13	29	16	53	32	28
ciliates	0	1	1	6	2	2

23 June	5	10	15	20	25	30
Other diatoms	13	19	15	17	29	19
lg flagellates	10	36	19	89	64	34
ciliates	0	3	2	5	4	1

30 June	5	10	15	20	25	30
Other diatoms	43	46	24	37	45	60
lg flagellates	11	30	17	29	29	16
ciliates	1	2	1	4	3	2

17 July	5	10	15	20	25	30
Other diatoms	18	20	24	31	24	23
lg flagellates	13	18	34	38	22	10
ciliates	1	2	4	2	1	2

26 July	5	10	15	20	25	30
Other diatoms	51	57	50	51	43	33
lg flagellates	17	24	12	27	11	11
ciliates	1	4	4	1	3	2

Table 2. Cell densities for Taylor arm, 1986.

23 April	5	10	17.5	22.5	35
Other diatoms	17	18	21	3	3
lg flagellates	23	36	24	12	1
ciliates	9	2	4	3	3

19 May	5	12.5	17.5	22.5	35
Other diatoms	0	63	8	19	5
lg flagellates	44	196	19	32	21
ciliates	1	6	1	3	3

26 May	5	10	17.5	22.5	27.5
Other diatoms	19	21	18	14	11
lg flagellates	20	33	12	15	16
ciliates	4	9	5	1	2

30 May	5	10	15	20	25	30
Other diatoms	28	13	21	6	7	27
lg flagellates	38	54	40	26	11	26
ciliates	7	13	4	1	1	2

2 June	5	10	15	20	25	35
Other diatoms	31	19	26	3	7	13
lg flagellates	7	84	91	15	12	16
ciliates	0	6	6	3	1	1

5 June	5	10	15	20	25	30
Other diatoms	169	32	18	37	34	32
lg flagellates	97	69	38	35	17	23
ciliates	0	10	6	7	0	3

9 June	5	10	15	20	25	30
Other diatoms	20	43	11	31	25	6
lg flagellates	6	53	27	20	13	5
ciliates	4	4	14	10	2	1

16 June	5	8	11	14	17	20
Other diatoms	29	21	27	49	38	14
lg flagellates	30	19	56	57	26	19
ciliates	3	1	5	7	7	6

19 June	1	5	10	15	20
Other diatoms	50	18	41	10	44
lg flagellates	21	11	50	37	67
ciliates	0	2	3	3	10

23 June	5	10	15	20	25
Other diatoms	51	16	21	31	35
lg flagellates	47	40	21	15	20
ciliates	1	1	3	3	1

1 July	5	10	15	20	25
Other diatoms	37	114	13	11	5
lg flagellates	11	47	9	5	1
ciliates	2	11	1	1	1

17 July	7.5	15	20	25	30	35
Other diatoms	77	51	21	30	22	25
lg flagellates	9	19	11	7	7	15
ciliates	6	0	1	1	2	1

26 July	5	10	15	20	25	30
Other diatoms	155	105	77	39	25	22]
lg flagellates	18	24	42	13	9	11
ciliates	0	4	6	4	1	2

6 August	5	10	15	20	25	30
Other diatoms	33	36	49	41	26	13
lg flagellates	18	16	25	28	7	3
ciliates	1	1	0	4	0	1

Table 3. Cell densities for Two Rivers arm, 1987.

11 March	5	10	15	20	25
Other diatoms	64	80	86	126	120
lg flagellates	65	98	54	37	54
dinoflagellates	0	4	0	0	4
ciliates	0.8	0	0	4	4

15 March	5	10	15	20	25
Other diatoms	87	25	70	53	35
lg flagellates	91	51	24	47	16
dinoflagellates	8	7	3	3	4
ciliates	12	7	10	8	5

19 March	5	10	15	20	25
Other diatoms	40	64	76	49	51
lg flagellates	166	126	54	43	45
dinoflagellates	8	0	3	6	0
ciliates	8	19	10	12	6

23 March	5	10	15	20	25
Other diatoms	22	98	90	45	97
lg flagellates	192	107	126	163	119
dinoflagellates	13	0	0	5	0
ciliates	22	13	0	10	13

28 March	5	10	15	20	25
Other diatoms	21	101	89	66	44
lg flagellates	98	218	124	73	62
dinoflagellates	4	23	29	4	3
ciliates	9	0	10	0	0

1 April	5	10	15	20	25
Other diatoms	71	127	65	71	118
lg flagellates	226	142	94	72	111
dinoflagellates	18	8	8	0	7
ciliates	6	0	0	13	11

5 April	5	10	15	20	25
Other diatoms	47	280	120	60	40
lg flagellates	226	433	113	46	43
dinoflagellates	6	0	0	4	0
ciliates	18	38	12	6	12

9 April	0.5	3	6	9	12	15
Other diatoms	244	83	67	110	268	198
lg flagellates	202	235	279	316	224	595
dinoflagellates	0	0	0	7	30	0
ciliates	8	12	0	13	0	0

9 April con't	18	21	24	27	30
Other diatoms	69	112	41	49	66
lg flagellates	157	96	89	95	110
dinoflagellates	5	0	4	0	0
ciliates	21	38	0	4	0

13 April	5	10	15	20	25
Other diatoms	205	108	158	526	321
lg flagellates	312	562	318	95	68
dinoflagellates	0	14	0	11	7
ciliates	18	28	0	0	4

18 April	5	10	15	20	25
Other diatoms	95	130	112	130	45
lg flagellates	220	142	257	119	134
dinoflagellates	6	0	0	12	4
ciliates	0	0	12	12	18

22 April	5	10	15	20	25	30
Other diatoms	37	180	152	89	67	39
lg flagellates	96	304	728	162	82	96
dinoflagellates	0	0	0	0	4	4
ciliates	0	9	14	16	0	4

26 April	5	10	15	20	25	30
Other diatoms	107	34	123	123	63	75
lg flagellates	128	23	234	275	115	82
dinoflagellates	12	0	0	7	21	4
ciliates	12	0	23	34	0	12

30 April	5	10	15	20	25	30
Other diatoms	74	59	155	45	73	71
lg flagellates	147	428	273	144	195	78
dinoflagellates	0	36	0	0	0	0
ciliates	5	6	24	5	12	6

4 May	5	10	15	20	25	30
Other diatoms	48	125	123	70	69	53
lg flagellates	226	257	187	155	131	147
dinoflagellates	0	0	0	0	5	0
ciliates	0	5	0	4	0	0

8 May	5	10	15	20	25	30
Other diatoms	85	64	115	105	100	89
lg flagellates	127	236	146	105	82	121
dinoflagellates	0	0	0	0	4	0
ciliates	0	0	0	5	0	11

12 May	5	10	15	20	25	30
Other diatoms	12	154	200	127	95	195
lg flagellates	127	321	278	225	145	315
dinoflagellates	0	0	0	0	0	16
ciliates	0	0	30	0	0	5

16 May	5	10	20	25	30
Other diatoms	84	62	55	79	55
lg flagellates	145	318	184	84	123
dinoflagellates	0	0	5	0	0
ciliates	0	0	5	0	4

20 May	0.5	3	6	9	12	15
Other diatoms	48	39	43	54	32	157
lg flagellates	35	56	63	120	125	228
dinoflagellates	4	5	6	0	0	8
ciliates	2	5	2	8	8	14

20 May con't	18	21	24	27	30
Other diatoms	147	89	63	93	37
lg flagellates	103	150	62	95	70
dinoflagellates	0	8	3	0	2
ciliates	27	21	0	10	7

24 May	5	10	15	20	25
Other diatoms	65	127	416	157	108
lg flagellates	149	200	394	206	64
dinoflagellates	0	22	64	34	9
ciliates	0	21	25	17	3

28 May	5	10	15	20	25	30
Other diatoms	32	54	145	112	141	21
lg flagellates	43	134	212	72	89	51
dinoflagellates	0	0	0	0	4	0
ciliates	0	0	9	17	0	0

Table 4. Cell densities for Taylor arm, 1987.

11 March	5	10	15	20
Other diatoms	32	36	82	102
lg flagellates	73	78	43	61
dinoflagellates	5	0	0	0
ciliates	5	0	4	4

15 March	5	10	15	20	25
Other diatoms	136	122	38	12	15
lg flagellates	93	82	61	53	21
dinoflagellates	7	12	0	0	0
ciliates	5	0	7	3	0

19 March	5	10	15	20	25
Other diatoms	52	70	94	52	24
lg flagellates	30	94	61	29	7
dinoflagellates	3	0	4	4	0
ciliates	3	12	12	0	4

23 March	5	10	15	20	25
Other diatoms	143	62	63	49	6
lg flagellates	172	101	100	77	50
dinoflagellates	0	0	0	0	0
ciliates	12	5	5	8	4

28 March	5	10	15	20	25
Other diatoms	44	121	79	175	48
lg flagellates	357	111	33	75	45
dinoflagellates	0	0	0	3	0
ciliates	6	0	6	4	4

1 April	5	10	15	20	25
Other diatoms	129	31	101	90	86
lg flagellates	192	34	71	58	56
dinoflagellates	22	9	4	4	9
ciliates	4	4	7	0	6

5 April	5	10	15	20	25
Other diatoms	78	154	71	78	78
lg flagellates	162	389	138	54	7
dinoflagellates	16	32	0	4	7
ciliates	5	24	9	0	4

9 April	0.5	3	6	9	12	15
Other diatoms	145	46	49	85	35	59
lg flagellates	173	128	104	178	112	188
dinoflagellates	5	0	0	0	0	5
ciliates	5	0	5	4	0	5

9 April con't	18	21	24	27	30
Other diatoms	48	38	79	93	64
lg flagellates	89	58	61	164	75
dinoflagellates	0	4	4	4	7
ciliates	4	0	4	0	0

13 April	5	10	15	20	25
Other diatoms	131	54	104	43	50
lg flagellates	165	99	208	50	70
dinoflagellates	0	0	0	0	4
ciliates	21	10	15	4	0

18 April	5	10	15	20	25
Other diatoms	46	49	123	38	71
lg flagellates	43	80	134	105	56
dinoflagellates	4	4	5	0	4
ciliates	4	4	0	11	0

22 April	5	10	15	20	25	30
Other diatoms	145	589	111	70	89	43
lg flagellates	288	95	154	73	48	116
dinoflagellates	28	8	0	4	4	0
ciliates	13	37	18	4	15	4

26 April	5	10	15	20	25	30
Other diatoms	23	129	85	127	47	36
lg flagellates	81	257	139	108	72	39
dinoflagellates	12	0	0	0	4	0
ciliates	4	0	0	4	4	0

30 April	5	10	15	20	25	30
Other diatoms	163	104	63	56	62	54
lg flagellates	71	243	120	128	93	120
dinoflagellates	0	0	9	0	4	4
ciliates	6	15	0	4	4	11

4 May	5	10	15	20	30
Other diatoms	78	56	77	75	54
lg flagellates	220	150	178	75	75
dinoflagellates	0	0	0	0	0
ciliates	0	4	26	9	14

8 May	5	10	15	20	25	30
Other diatoms	85	106	78	134	67	59
lg flagellates	38	190	74	168	108	113
dinoflagellates	0	0	0	0	0	0
ciliates	0	5	12	0	12	4

12 May	5	10	15	20	25	30
Other diatoms	89	83	48	54	123	52
lg flagellates	143	172	148	128	157	48
dinoflagellates	0	0	0	0	0	0
ciliates	6	6	0	7	4	4

16 May	5	10	15	20	25	30
Other diatoms	23	59	80	65	51	74
lg flagellates	178	345	248	113	78	55
dinoflagellates	4	0	0	6	0	0
ciliates	4	12	0	0	0	0

20 May	0.5	3	6	9	12	15
Other diatoms	38	55	66	116	86	71
lg flagellates	35	37	66	75	143	232
dinoflagellates	3	3	3	0	0	10
ciliates	3	5	5	6	8	9

20 May con't	18	21	24	27	30
Other diatoms	57	43	71	97	22
lg flagellates	75	64	74	121	64
dinoflagellates	0	0	0	0	0
ciliates	14	4	3	5	4

24 May	5	10	15	20	25	30
Other diatoms	10	59	178	112	95	48
lg flagellates	92	132	278	89	89	78
dinoflagellates	0	10	0	0	11	9
ciliates	7	10	24	9	7	6

28 May	5	10	15	20	25	30
Other diatoms	34	63	88	146	115	83
lg flagellates	34	43	147	139	86	36
dinoflagellates	0	18	20	4	4	0
ciliates	4	0	15	22	17	3

Appendix III. Comparison of *in vivo* fluorescence (○) to cell density of *Rhizosolenia eriensis* (■), *Cyclotella* spp. (●) and small flagellates (▲).