THE GROWTH OF PHYTOPLANKTON POPULATIONS IN NATURE AND IN CULTURE

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ABSTRACT

An investigation over a period of more than two years of phytoplankton, and physical and chemical conditions of the River Thames and the Wraysbury Reservoir in Southern England has indicated seasonal occurrence of phytoplankton populations with diatoms (chiefly Stephanodiscus ref. hantzschii Grun.) forming a large percentage of the populations. During 1984, 1985 and 1986; phytoplankton populations occurred most abundantly during the spring (mainly diatom populations) and during the summer (diatoms and green algae in the River Thames, and blue-green algae in the Wraysbury Reservoir).

Selected algal taxa were isolated and grown in culture in the laboratory and experiments carried out in which culture conditions have been manipulated in various ways. Such experiments included those involving suspected nutrient limiting factors (e.g. phosphate) as well as physical factors especially those of temperature and light.

Ecological records and experimental cultures indicate that the occurrence and growth of diatoms is encouraged by the increasing water temperatures and light intensity during the spring, and by higher levels of nutrient concentrations (i.e. nitrate-nitrogen, phosphate-phosphorus and silica) at all times. On the other hand, the growth of green algae (Chlorophyceae) and blue-green algae (Cyanophyceae) was

influenced by the maximum water temperatures and light intensity of the summer period and despite lower nutrient concentrations.

Thus,differences in physical and nutrient requirements by phytoplankton populations help to explain the presence of diatoms during the spring and green algae (in the River Thames) and blue-green algae (in the Wraysbury Reservoir) during the summer.

Simple investigation of the growth responses of the River Thames and Wraysbury Reservoir phytoplankton populations to River Thames and Wraysbury Reservoir water as natural culture media were performed.The results indicated that the River Thames and Wraysbury Reservoir are potentially able to support considerable crops of phytoplankton populations,and that the potential is present throughout the year.

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CHAPTER ONE

INTRODUCTION

The earth scientist views a river as a link in the hydrologic cycle;as a locus of erosion,transportation and deposition of dissolved,suspended and tractively carried geologic materials,and as a complete open physical system hydrodynamically balancing and distributing energy and work over the earth's land areas (Curry,1972).

Since prehistoric times the convenient water supply and means of communication afforded by a navigable river have lead to the habitation of river valleys.Man at any stage in culture and at any density is closely associated with and modifies rivers and streams.Naturally,sewage pollution occurred whenever man settled.The pollution of the River Thames became severe during the 1800s.The year 1851 was the "Year of the Great Stink" when the House of Parliament were forced to hang disinfectant-soaked sheets over the windows to dispel the appalling stench of hydrogen sulphide rising from the anoxic waters of the river (Whitton,1979).Victorian London expanding population was overloading the River Thames with raw sewage and turning it into little more than a sewer. It was not even an efficient outlet to the sea since the River Thames is tidal through London.It had become clear that legislation was needed to enforce a cleaning programme and to

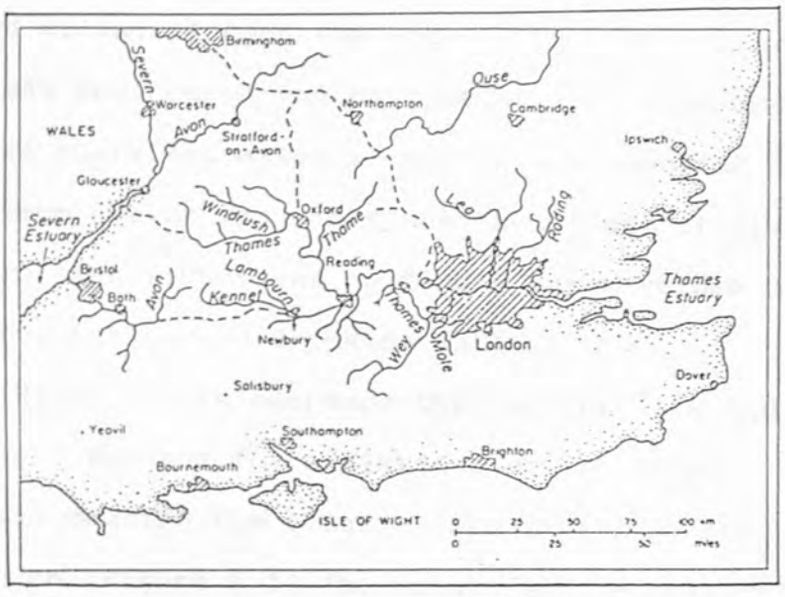


Figure 1.1 Map of southeast England showing the River Thames, its tributaries, and the major canals (broken lines) connecting with other watersheds.
(From: Mann, 1972)

encourage the revitalization.By 1839 they had power to control pollution in the whole watershed and within forty years some form of sewage treatment was provided for almost every town and village.Around the end of the 18th.century the River Thames was engineered for navigation,i.e.,provided with weirs and locks every few miles to maintain a constant depth of water (minimum 6ft.or 2m.).This has the effect of slowing the flow,controlling floods,and holding a large volume of water as reserve for London drinking water.

The River Thames meanders through the farmland and towns of Southern England for a distance of 147 miles (237 km.) before meeting the tidal waters of the Thames estuary at London (Figure 1.1).The total fall is only 370ft. (113m),so that average slope is 2.5ft.per mile or 0.47 per thousand.The rainfall in the catchment area averages 29 inches(74cm.),and the flow at Teddington Weir,the limit of tidal influence,averages about 800 MGD (million gallons per day,or 42 $m^3 s^{-1}$).The catchment area is 3845 sq.miles (9951 km^2),of which almost half is chalk and limestone.Thus, the water is hard,with a calcium content of the order of 100 mg l^{-1}.

For more than a century the River Thames has been of interest to waterworks undertakings,providing a large proportion of the raw water in South Eastern England.Since the 1920's routine records of the biological characteristics of the River Thames at Walton and Laleham have been kept by

the Metropolitan Water Board and general accounts have been published in the reports of the Director of Water Examination.

The phytoplankton of the River Thames was first studied by Fritsch (1902,1903),followed by Rice (1938).These studies were purely descriptive.Mc Gill (1969) initiated quantitative studies of the River Thames.Since then there have been several further studies of the River Thames.Lack (1971) investigated the River Thames and River Kennet at Reading as well as primary production and respiration of the phytoplankton in both rivers.Haffner (1974),Hardy (1977), Bowles (1978) and Yallop (1980) investigated seston distribution,phytoplankton production and environmental and physiological factors influencing phytoplankton productivity in the River Thames and Thames Valley Reservoirs.Speller (1984) carried out taxonomic and ecological investigations of centric diatoms in the River Thames.From previous studies it was found that regular cyclical fluctuations in abundance and species composition constitute one of the most striking characteristics of the phytoplankton populations in the River Thames and reservoirs.The factors that regulate the periodicity of specific populations are many and complex and they are incompletely understood (Reynolds,1982).Various factors have been taken into account to explain the periodicity and distribution of phytoplankton.These include light,temperature,hydrogen ion concentration,osmotic effects, mechanical factors and nutrient concentration.However,the

interactions between natural populations of organisms and their environment is not easy to understand.For example,it depends on drawing together many different scientific disciplines and methods of achieving such a blend of scientific expertise are not obvious nor simple and the solution to many of the problems in ecological research depends on techniques which may be lacking or in their infancy (Morris,1980).Therefore,it is understandable that the relationship between populations of organisms and those environmental factors controlling their survival,growth and distribution continues to be expressed in superficial descriptive terms.

The aim of this study was to investigate the growth of phytoplankton populations in nature and in culture selecting mainly populations from the River Thames and the Wraysbury Reservoir.In the natural systems,the aim was to describe the system as it exists in its natural state.This approach should provide a description of both standing state and dynamic features of the system with a minimum disturbance to its natural state.This approach should provide a description of both standing state and dynamic features of the system with a minimum disturbances to its natural status. At the organisms level,the factors controlling the success of the phytoplankton in question were determined through correlations between standing state and rate functions of the phytoplankton and various prevailing environmental

parameters,including the possible influence of other organisms.

In the study of the growth of phytoplankton species in culture,the system is manipulated in some way and the effects of manipulation are observed.The experimental manipulation should involve suspected limiting factors, including biotic components such as the number of algal cell, or the abundance of zooplankton grazers,as well as physical and other environmental parameters such as temperature,light intensity and nutrient concentrations.The experimental approach may provide more direct evidence for the various physical,chemical and biological factors which are responsible for the success of the phytoplankton populations in nature.

During the study selected species were isolated and grown in culture and subjected to laboratory growth experiments.As well as varying physical conditions such as temperature and radiation,nutrients which may influence the growth of phytoplankton populations were also investigated.

By a comparison of culture data with the growth of phytoplankton populations in nature the growth potential of some commonly occurring species might be more clearly understood.An additional approach was a simple investigation of the growth responses of the River Thames and Wraysbury Reservoir phytoplankton populations to the River Thames water as a natural culture medium.

1.1 PHYTOPLANKTON

1.1.1 TERMINOLOGY

The first use of the term 'plankton' is widely attributed to the German biologist,Hensen (Ruttner,1953; Hutchinson,1967),who,in the latter half of nineteenth century,began a series of expeditions to gauge the distribution,abundance and composition of microscopic organisms in the open ocean.The word 'plankton' which means 'wandering' was used to describe the suspended microscopic material at the mercy of winds,currents and tide.The dependence of plankton upon water movements for maintenance and transport is accurately implied in this definition but it immediately excluded other larger inhabitants (e.g.fish, animal of open water having the ability to substantially regulate their own position in space).The pelagic environment always contains particulate matter kept in suspension by water movement,known collectively as seston and divisible into living (bioseston) and non-living (abioseston or tripton).The components of the bioseston are the plankton and nekton and prefixes denote algal (phyto-) or animal (zoo-) types.Nekton encompasses the larger organisms such as fish, which move independently of turbulent water movement (Round, 1981).

Hensen's 'plankton' did not specifically exclude

non-living particles,and it is synonymous with 'seston' in Kolkwitz's (1912) later terminology,that continues to command common acceptance.There are criticisms of Hensen's definition of 'plankton' and it has taken nearly a century of subsequent investigations to resolve these.First,in general,plankton does not float:there are few planktonic organisms which are consistently buoyant;on the contrary,most are often or always more dense than the water they inhabit.The specific adaptations of planktonic organisms for pelagic life seem largely directed towards prolonged maintenance in suspension (Reynolds,1984).Moreover,there are occasions when it is beneficial for planktonic organisms to be able to avoid the immediate sub-surface water layers and when a positive sinking rate is actually advantageous.The second point is; many planktonic organisms are not exclusively confined to the pelagic zone but may spend part,or even most,of their life cycle on the sediments or in other littoral habitats,or in another way.Many organisms present in open waters are only facultatively planktonic (or meroplanktonic).

For these reasons,it is perhaps more useful to regard plankton as "the community of plants and animals adapted to suspension in the sea or in the fresh waters and which is liable to passive movement by wind and current" (Reynolds,1984).This definition does not exclude temporary inhabitants of the plankton or chance introductions to the pelagic (which is conceptually important in the context of

the evolution of the planktonic habit) but it nevertheless lays stress upon morphological and behavioural adaptations to survive there.

Many types of plankton have been distinguished according to the taxonomic range, individual sizes and places. The prefixes limno-, heleo- and potamo- are used to refer to the plankton of lakes, ponds and rivers respectively and marine plankton is often subdivided into neritic which occurs in coastal waters and oceanic in the open ocean. These sub-groups are characterized by certain species assemblages. The term euplankton (holoplankton) is used to refer to the permanent planktonic assemblage of organisms which complete its life cycle suspended in the water and may include, for example, Asterionella formosa. Species which spend part of each season resting on the sediments comprise the meroplankton (e.g. Melosira and Gleotrichia). Species which undergo sexual reproduction, e.g. desmids and many Chrysophyceae, are presumably meroplanktonic since the resulting zygospores are usually too heavy to be maintained for long in the water column. The statospores of Dinobryon have been shown to be capable of germinating immediately after they have been formed though those which reach the sediments do not germinate until after the ice melt of the next spring (Sheath, Hellebust and Takasi, 1975). From a dispersal-geographical aspect, lakes are comparable to islands, that is they are islands of water. Hutchinson (1967) points out that

the number of planktonic species does not increase as lake area increases, indeed a decrease may occur, which is the reverse of the situation for small islands where the diversity of bird, mammal and faunas usually increases with increasing area. This may be an indication that more freshwater species are meroplanktonic than generally recognized since increase in size presumably is of no consequence to euplanktonic but a disadvantage to meroplanktonic species which have a more intimate association with the sediments. Conversely large shallow lakes ought to have larger numbers of species unless shallowness imposes a constraint on the euplanktonic organisms. Casual species in any water mass which might be derived from the flora attached to detritus or transported by the nekton are referred to as pseudoplankton (tychoplankton). Pseudoplankton is quite common in lakes, especially after storms, and very common in rivers owing to inwash from ponds etc. and to suspension of scoured benthic species. Inclusion of such species produces impressive lists but is totally misleading, unless qualified, and such data should never be used for characterizing water types or for diversity studies. In rivers and coastal regions, such pseudoplankton may undergo some cell divisions whilst suspended and may have a temporary effect on the habitat (e.g. decreasing light penetration, removing nutrients, etc.).

Various authors have introduced prefixes to categorize the phytoplankton according to the individual

Table 1.1 THE SIZE RANGES OF PHYTOPLANKTON CATEGORIZED BY VARIOUS AUTHORS

AUTHORS	TERMINOLOGY	SIZE RANGE (μm)
Strickland, 1960	Macroplankton	>500
	Microplankton (netplankton)	ca. 50-500
	Nannoplankton	10-ca. 50
	Ultraplankton	0.5-10
Hutchinson, 1967	Macroplankton	>500
	Microplankton (Netplankton)	60-500
	Nannoplankton	5-60
	Ultraplankton (μ-plankton, μ-algae, μ-flagellates)	0.5-5
Drebes, 1974	Microplankton	>10
	Nannoplankton	5-20
	Ultraplankton	up to 5
Munawar and Munawar, 1985	Netplankton	> 64
	Microplankton	20-64
	Nannoplankton	< 64
	Ultraplankton	5-20
	Micro-algae	< 5

sizes of the organisms: the terms "nannoplankton" (Rodhe et al.,1958;Yentsch and Ryther,1959),"ultraplankton" (Wetzel, 1964) and "micro-algae" (Fogg and Belcher,1961) have been used to separate the lower size ranges of individuals from the larger (netplanktons) forms.

The range of cell size of phytoplankton populations indicated by other authors presented in Table 1.1.

Table 1.2 A SYSTEMATIC LIST OF REPRESENTATIVE SPECIES OF PHYTOPLANKTON POPULATIONS IN THE RIVER THAMES AND THE WRAYSBURY RESERVOIR DURING 1984 TO 1986

KINGDOM: PROKARYOTA

CLASS: Photobacteria

CYANOBACTERIA. (blue-green bacteria/algae)
(synonyms: CYANOPHYTA, MYXOPHYTA, SCHIZOPHYTA)
Prokaryotic algae lacking typical membrane-bound nuclei and plastids.

Order: Chroococcales; Solitary or colonial blue-greens.
Microcystis aeruginosa Kütz.

Order: Nostocales (Hormogonales, Oscillatoriales): Filamentous blue-greens, mostly capable of heterocyst and akinete formation.
Anabaena circinalis Rabenh.
Anabaena flos-aquae Breb.
Aphanizomenon flos-aquae Ralfs.
Oscillatoria spp.

KINGDOM: EUKARYOTA

Eukaryotic algae with typical nucleus and pigments localized within plastids (or chromatophores). Eight phyla (according to this treatment): two (RHODOPHYTA and PHAEOPHYTA) are without representatives in the freshwater phytoplankton.

CRYPTOPHYTA

Naked, biflagellate algae, with one or two large plastids; division longitudinal; sexual reproduction unknown; assimilatory product of photosynthesis, starch. One class and one order.

Order: Cryptomonadales
Cryptomonas erosa Ehrenb.
Cryptomonas ovata Ehrenb.
Rhodomonas minuta Skuja.

PYRRHOPHYTA (Dinoflagellates)

Unicellular flagellates, rarely colonial; two flagella of different length and orientation; naked, or with cellulose cell wall, sometimes sculptured into plates. Numerous discoid plastids or colourless; assimilation products, starch or oil. Mostly marine.

CLASS: Dinophyceae

Biflagellate cells, flagella located in transverse and longitudinal furrows. Planktonic representatives included within one order.

Order: Peridiniales
Ceratium hirundinella O.F.Müll.

CHRYSOPHYTA

Unicellular, colonial, filamentous or siphonaceous algae, with a preponderance of carotenoid pigments; cell walls pectinaceous, often in two pieces, sometimes impregnated with silica (especially in the Bacillariophyceae); assimilatory products, chrysose, chrysolaminarin, leucosin, lipids but never starch. Five classes, all with planktonic representatives.

CLASS: Chrysophyceae

Mainly unicellular or colonial; plastids brown, usually two; cell wall sometimes silicified or calcified; isogamous sexual reproduction; mainly freshwater. Three (out of eleven) orders represented in freshwater phytoplankton.

Order: Ochromonadales (=Chrysomonadales); Unicellular and colonial Chrysophyceae, without a rigid cell wall, but often bearing siliceous scales.
Dinobryon spp.
Synura spp.
Uroglena spp.
Mallomonas spp.

Table 1.2. (Continued)

CLASS: Bacillariophyceae (diatoms)
Unicellular and colonial algae usually with numerous discoid plastids; pectinaceous cell wall, impregnated with silica, in two distinct halves (valves); assimilatory products, chrysose, oils. Never flagellate. Two large orders, both with planktonic representatives.

Order: Centrales; Centric diatoms, sometimes forming filaments by adhesion of valve surfaces.
Aulacoseira granulata Ehrenb. Simonsen.
Aulacoseira granulata var. angustissima (O.Müll.) Simonsen.
Cyclotella spp.
Stephanodiscus rotula (Kütz.) Hendey
Stephanodiscus rotula var. minutula (Kütz.) R.Ross et Sims
Stephanodiscus hantzschii Grun.
Melosira varians Ag.

Order: Pennales; Pennate diatoms, sometimes forming filaments or coenobia.
Asterionella formosa Hass.
Diatoma vulgare Bory
Fragilaria crotonensis Kitt.
Meridion circulare (Grev.) Ag.
Synedra acus Kütz.
Synedra ulna (Nitzsch.) Ehrenb.
Tabellaria fenestrata (Lyngb.) Kütz.
Tabellaria floccusa (Roth.) Kütz.
Navicula viridula (Kütz.) Ehrenb.
Navicula spp.
Nitzschia acicularis (Kütz.) W.Sm.
Surirella ovata Kütz.
Pleurosigma elongatum W.Sm.
Gomphonema parvulum (Kütz.) Kütz.

CLASS: Xanthophyceae (yellow-green algae).
Unicellular, colonial, filamentous or siphonaceous algae. Motile cells usually unequally biflagellate; cell wall in two species but not obviously so; disc-like plastids; assimilation product, lipids (oil). Five (or six) orders mainly freshwater of which two have planktonic representatives. Only one order found in the River Thames and the Wraysbury Reservoir during the periods of study.

Order: Tribonematales (=Heterotrichales); Filamentous Xanthophytes.
Tribonema vulgare Pascher

EUGLENOPHYTA
Unicellular flagellates with one long and one very short flagellum; plastids numerous and irregular; reproduction by longitudinal fission; assimilatory products, paramylum, oil. One class (Euglenophyceae) and one order (a second order, Peranemales, are now regarded as protozoa).

Order: Euglenales
Euglena gracilis Klebs.
Phacus spp.
Trachelomonas volvocina Ehrenb.

CHLOROPHYTA (green algae)
Green pigmented unicellular, colonial, filamentous, siphonaceous and thalloid algae. One or more plastids with pyrenoids; assimilation product, starch. Authorities differ on number and extent of classes; these different classifications are avoided here by proceeding to the levels of orders (although various ascriptions to classes are noted). Only orders which were found in the River Thames and the Wraysbury Reservoir are listed.

Order: Volvocales; Unicellular or colonial biflagellates. Their inclusion within the class Chlorophyceae (Euchlorophyceae of Bourrelly, 1966) is undisputed.

Table 1.2. (Continued)

	Chlamydomonas spp.
	Eudorina elegans Ehrenb.
	Pandorina morum Bory
	Volvox aureus Ehrenb.
Order:	Chlorococcales;Non-flagellate,free-living or colonial (sometimes mucilagenous) Chlorophyceae.
	Ankistrodesmus falcatus (Corda)Ralfs
	Ankyra judayi (G.M.Sm.)Fott.
	Botryococcus braunii Kütz.
	Chlorella spp.
	Coelastrum spp.
	Pediastrum boryanum (Turp.)Meneghin.
	Pediastrum duplex Meyen
	Pediastrum tetras (Ehrenb.)Ralfs
	Scenedesmus acuminatus (Lagerh.)Chod.
	Scenedesmus obliquus (Turp.)Kütz.
	Scenedesmus quadricauda (Turp.)Breb.
Order:	Zygnematales;Unicellular or filamentous green algae, reproducing isogamously by conjugation.Christensen retains these in the Chlorophyceae,but separate class status has been proposed called Zygophyceae (by Bourrelly,1966) or Conjugatophyceae (by Fott, 1959).Planktonic genera are all members of the family Desmidaceae,mostly unicellular or (rarely) filamentous algae in which the cells are constricted into two semi-cells separated by an interconnecting isthmus.
	Closterium aciculare T.West
	Cosmarium spp.
	Staurastrum spp.

Authorities are not repeated in the text when stating the species.

1.1.2 BASIC BIOLOGICAL FEATURES OF PHYTOPLANKTON CELLS

Phytoplankton consists, for the most part, of single-celled organisms, physiologically similar to land plants, but far smaller, suspended in the liquid medium that nourishes them. They are drawn from a diverse range of, at best, distantly related phylogenetic groups (Table 1.2). From an evolutionary standpoint, it may be postulated that the planktonic habit has arisen on several occasions, suggesting that adaptive radiation into pelagic environments has been backed by powerful selective pressures. That the algae should have been relatively successful in exploiting the potential advantages offered by pelagic life has presumably depended upon a certain degree of pre-adaptation to a dispersed existence (Reynolds, 1984).

From the evolutionary point of view, plankton are the descendants of the ancestors which gave rise to both animals and plants more than 500 million years ago, the Cyanophytes (blue-green algae, Cyanobacteria) having a fossil record 1900 million years old. It is sometimes difficult (and probably pointless) to call them plants or animals except in a physiological sense because of this antiquity (Taylor, 1980).

Ecologically, the phytoplankton and the attached aquatic plants together contribute their productivity to the ecosystem in a way similar to that of land plants.

In terms of basic cell organization, organisms can

Table 1.3. Some basic differences between properties of prokaryotic and eukaryotic phytoplankton cells

CYANOPHYTES (Prokayotic)	Eukaryotic phytoplankters
Diameter: 1-55 μm, commonly 4 μm, rarely 15 μm	Diameter: 2 μm-2 mm, commonly 10-50 μm
1 DNA-containing compartments, (DNA lacking histones)	At least 3 DNA-containing compartments, (histones usually present in the nucleus)
Respiration and photosynthesis on general membranes	Respiratory and photosynthetic membrane specialization
'70S' ribosomes: streptomycin sensitive chloramphenicol sensitive cycloheximide insensitive	'80S' ribosomes ('70s' is mitochondrion and chloroplast): streptomycin insensitive chloramphenicol insensitive cycloheximide sensitive
Wall obligate, peptidoglycan, penicillin sensitive	Wall only in some groups various materials, Penicillin insensitive
No cytosis; membranes with only trace sterols	Cytosis common; membranes sterol-rich
No endosymbionts	Endosymbionts occasional
Surface gliding in some (other bacteria with 'flagella')	Locomotion common, varied mechanisms including flagellar propulsion and surface gliding.
Gas vacuoles in some	Only fluid vacuoles.
Nitrogen fixation in some	Nitrogen fixation absent
Tolerate low O_2 in dark	Obligate aerobes
High temperature tolerance (*Synechococcus lividus* can reach 73°C; other bacteria to 100°C)	Most cannot tolerate 40°C (*Cyanidium caldarum* tolerates 56°C at pH 5)

(From: Taylor, 1980)

be subdivided into two basic types: prokaryotic and eukaryotic.This distinction is thought to be so fundamental that some biologists recognize two kingdoms or 'superkingdoms' Prokaryota (= Monera) and Eukaryota,which transcend the traditional plant or animal kingdoms in importance.Both types occur within the phytoplankton groups.

Although the distinction was first proposed on the basis of the absence or presence of a clearly defined (i.e. membrane-limited) nucleus respectively (Chatton,1938),it is now known that the two types differ in many fundamental ways. Some of the most significant in the present context being summarized in Table 1.3.

The generally low level of structural organization and morphological plasticity of algal cells,the concomitant intracellular 'division of labour',which makes for considerable physiological and biochemical independence of individual cells,and the fact that the potential step into open water from adjacent aquatic habitats have existed for a long time.

The earliest attempts to distinguish separate groups of algae relied upon pigmentation and we still recognize this when we refer to groups such as the green or brown algae.Today we also consider the following characteristics important in defining major algal groups: presence or absence of flagella,flagellar characteristics (number,length,point of insertion,presence or absence of

hairs or scales);cell wall composition,and type of stored photosynthetic product.As more and more algae are examined with the electron microscope,it is becoming increasingly evident that ultrastructural features,especially details of chloroplast structure,are proving to be very useful taxonomic characters.It is possible to make rather clear distinctions among groups of algae at what many authors consider the class level by using this information.Darley (1982) suggested that the Chlorophyceae and Charophyceae are obviously closely related and the Xanthophyceae,Chrysophyceae,Bacillariophyceae and Phaeophyceae appear to be more closely related to each other than they are to other classes.Most algal classes show no obvious evolutionary relationships to one another.

One interesting bit of speculation on the origins of such a polyphyletic group of organisms relates to the theory that the chloroplasts and mitochondria in modern eukaryotic cells have evolved from endosymbiotic prokaryotic organisms.This theory is an old one which has gained support recently from biochemical data showing the similarity of the protein synthesizing system of these eukaryotic organelles with that of free-living prokaryotic cells.The eukaryotic, nuclear-cytoplasmic system is different in several respects. According to one suggestion (Raven,1970) at least three different oxygen-evolving,prokaryotic photoautotrophs existed at some time in the past:one containing phycobilins and containing chlorophyll _a_ as the only chlorophyll (similar to

extant blue-green algae);a second form lacking phycobilins and containing chlorophylls a and b (possibly related to a similar prokaryote reported by Lewin (1976) to be living symbiotically on tropical tunicates);and a third form lacking phycobilins and containing chlorophylls a and c (no similar extant forms are known).The many different groups of algae could have originated from several very different heterotrophic eukaryotes which acquired one of the three different photoautotrophs as an endosymbiont (the endosymbiont subsequently evolving into the chloroplast).This theory explains the presence of chlorophylls a and b in both the green algae and euglenoids,which differ in virtually every other character considered to be significant in algal systematics.The Xanthophyceae and the three (possibly) related algal classes mentioned by Darley (1982) could be derived from a common ancestoral heterotrophic eukaryote which acquired the hypothetical chlorophylls a and c - containing prokaryote.These four groups do not appear to be related to the Prymnesiophyceae even though all five contain similar pigments.Gibbs (1978) suggested that heterotrophic euglenoids and dinoflagellates acquired already evolved chloroplasts from other eukaryotic algae.The suggestion is supported by ultrastructural evidence in some dinoflagellates. This sort of thinking is speculative but at least it helps to rationalize the existence of so many different 'classes' of algae.

In contrast to the questionable evolutionary relationships among algal classes,evolutionary trends within algal classes are more obvious.In each of the various algal classes,evolution is assumed to have originated with a unicellular ancestor and proceeded,to various degrees,to multicellular forms along parallel pathways.Thus,most algal classes have extant representatives which are motile unicells and many classes include species which are uniseriate filaments.The green algae exhibit a spectacular diversity of body form while in other classes (e.g.the euglenoids) evolution in body form has scarcely advanced beyond the unicellular stage.

1.2 PHYSICAL AND CHEMICAL FACTORS AFFECTING THE GROWTH OF PHYTOPLANKTON POPULATIONS

1.2.1 LIGHT AND TEMPERATURE

The ecological effects of light and temperature on the photosynthesis and growth of algae are inseparable because of the interrelationships in metabolism and light saturation. Growth of algae and photosynthetic rates are directly related to quantitative light intensity. However, response to light intensity is variable among species and in many a considerable degree of adaptation to changing light intensities occurs. Two types of adaptive reaction can be distinguished (Steeman Nielsen and Jorgensen, 1968; Beale and Appleman, 1971). The most usual is the '*Chlorella* type' which is characterized by an inverse relationship between the light intensity to which the algae are exposed and their chlorophyll *a* content. That is, the light adaptation to this type is mainly accomplished by changes in pigment concentration. On the other hand, algae belonging to the '*Cyclotella* type' show an inverse correlation between the activities and/or concentrations of photosynthesis enzymes and light intensity.

It is equally clear that the specific responses of growth rate to temperature and light fluctuations will

interact with each other.For instance as metabolic activity increases with temperature,so the irradiance levels required to saturate growth rates might be expected to increase.The data of Foy et al.,(1976) show that growth rate of all four species of Cyanobacteria they investigated was saturated at a light intensity equivalent to 17.5 $\mu E\ m^{-2}s^{-1}$ at 10°C when grown in continuous light.Both Aphanizomenon flos-aquae and Anabaena flos-aquae showed higher light-saturation requirements at 20°C (~28 $\mu E\ m^{-2}s^{-1}$, ~40 $\mu E\ m^{-2}s^{-1}$ respectively) but no such increase was observed in Oscillatoria agardhii or Oscillatoria redekei cultures.

The growth rate of phytoplankton increases with increasing temperature up to some optimum temperature after which growth rate declines,often abruptly,to zero.The temperature optima for growth of many marine and freshwater phytoplankton lie in the range 18 to 25°C.Cold water forms generally have lower optima.

More information about the influence of light and temperature on the growth of phytoplankton populations will be discussed in Chapter Four and Five.

1.2.2 NUTRIENTS

The importance of inorganic nutrients,particularly the three major elements of phosphorus,nitrogen and silicon has been emphasized by many researchers (e.g.Tilman and

Kilham,1976;Goldman and Horne,1983 and Taylor,1985).

1.2.2.1 NITROGEN

Nitrogen appears to be the primary major nutrient limiting primary production in the world oceans (Smayda,1974) as well as in certain freshwater systems (Edmonson,1970; Likens,1972).

Under optimal conditions,there is a prescribed amount of nitrogen required for cell growth and division, depending on species.When nitrate is present in larger amounts,"luxury consumption" or uptake in excess of the requirements for growth (i.e.,uptake rates more than assimilation rates) can occur,resulting in internal pool of unreduced nitrate (Eppley et al.,1968).

1.2.2.2 PHOSPHORUS

Orthophosphate (PO_4^{-3}),is the only important inorganic phosphorus source for algae although most can obtain the element from various organic phosphates.Phosphorus plays major roles in nearly all phases of metabolism, particularly in energy transformation associated with phosphorylation reactions in photosynthesis.Phosphorus is required in the synthesis of nucleotides,phosphatides,sugar phosphates,and other phosphorylated intermediate compounds.

1.2.2.3 SILICON

Among the phytoplankton algae, the diatoms are by far the most important group which requires silicon. In addition to the silicon requirement for cell wall formation, diatoms require small amounts of silicon for net DNA synthesis, an unusual requirement which resides in the translation step in the synthesis of DNA polymerase.

Further discussions of the influence of nutrients on the growth of phytoplankton populations are presented in Chapter Three.

1.3 PHYTOPLANKTON SPECIES SUCCESSION

The taxonomic composition of phytoplankton communities,and the abundance and relative dominance of the different species and algal groups present undergo continuous change.This process of continuous community reorganization is termed succession (Smayda,1980)."These range between frequent reorganizations of existing community structures,in response to advective mixing processes,through annually recurrent cycle of compositional change that accompany underlying cyclical fluctuations in insolation,temperature and vertical differentiation (stratification) of the environment,to longer-term floristic changes,where one recognizably recurrent cycle is supplanted by another,in response to sustained limnological shifts in morphometry,hydraulic throughput and nutrient loading.The responses are observed relatively easily,either directly or,as in the case of long term floristic changes, in the retrospective synopses that can be gained from systematic analyses of the fossilized remains of species representative of past assemblages,recovered from intact cores of lacustrine sediments"(Round,1971).

The phenomenon of succession of phytoplankton has been viewed traditionally as a floristic phenomenon of limited significance to overall community dynamics,or to the food web. Although the phenomenon of succession of phytoplankton has

fascinated phytoplankton ecologists for over half a century, yet the factors that regulate the periodic wax and wane of specific populations are many and complex and they are incompletely understood.Kalff and Knoechel (1978) expressed their view that "although this (research) activity has resulted in an enormous and growing literature,progress in understanding and prediction has been very slow".There are still no widely accepted explanations either of the mechanisms that drive the seasonal waxing and waning of phytoplankton,or of the factors that condition long-term floristic changes (Reynolds,1984).

Succession traditionally has been viewed as a floristic phenomenon of limited significance to overall community dynamics,or to the food web.

A distinct periodicity in the biomass of phytoplankton is observed in polar and temperate fresh waters. Growth is greatly reduced or negligible during the winter period or low light and temperatures.Phytoplankton numbers and biomass normally increase greatly in the spring under improved light conditions,building up to a spring maximum.The spring maximum can begin under the ice in late winter,and often consists predominantly of diatoms adapted to low temperatures. In many dimictic lakes,the spring maximum does not develop fully until after the spring circulation and the period of summer stratification have begun.

The spring maximum of phytoplanktonic biomass

generally is short-lived,usually less than 3 months in duration.This maximum is followed by a period of low numbers and biomass that may extend throughout the summer.The summer minimum is often brief among more eutrophic lakes of the temperate region and phases into a late summer profusion of blue-green algae that persists into the autumn until the disruption of thermal stratification begins.The summer populations of phytoplankton are often low throughout the summer in temperate oligotrophic lakes and a second maximum develops in the autumn generally, but is not as strongly developed as that of the spring period.Decline of the populations into the winter minimum frequently also is more rapid and irregular in the autumn.

Generalizations are easy to make but difficult to justify because of the great variability observed among phytoplanktonic numbers and biomass from lake to lake.However, several points are reasonably consistent (Wetzel,1975):

(a) The successional seasonal periodicity of phytoplanktonic biomass is approximately constant from year to to year.If the freshwater system is not perturbed by outside influences,such as the activities of man in modifications of the watershed,nutrient loading,etc.,the characteristic seasonal changes in the phytoplanktonic populations are very repetitious from year to year on a short-term basis.

(b) The seasonal amplitude of changes in phytoplanktonic numbers and biomass is usually very great,of

the order of a thousandfold in temperate and polar fresh waters. In keeping with the relatively constant environmental conditions, the seasonal variation in tropical waters is much lower, often as little as fivefold (Fogg, 1965).

(c) The maxima and minima observed in numbers and biomass of phytoplankton often are quite out of phase with measured periodicity of rates of primary production. The spring maximum, if conspicuously developed, often is composed of larger algae such as diatoms with slower turn over rates than summer algae which occur in warmer and more favourable light conditions.

The interpretation of seasonal periodicity has been done from the study of interactions between environmental variables and the organisms (Lund, 1965; Hutchinson, 1967; Round, 1971; Talling, 1971; Vidal, 1973; Fogg, 1975; Reynolds, 1976, 1982, 1984) and also according to ecological theory (Margalef, 1964, 1968, 1974; Odum, 1969).

Flowing waters like rivers develop phytoplankton crops only in the slower moving parts. For example in the River Thames; since it is modified from its original state to produce a series of relatively slow-flowing basins, phytoplankton is the major source of primary production. In the River Nile the quantity was shown to be inversely proportional to the current speed (Brook and Rzoska, 1954). Brook (1954) listed over 160 species of plankton algae from the Blue and White Niles, several species being new records for Africa. However,

ecological studies by Rzoska,Brook and Prowse (1955);Brook and Rzoska (1954);Prowse and Talling (1958) and Talling and Rzoska (1967) have shown that very few of these are important in the plankton.The dominant species in the Blue Nile and White Nile are Aulacoseira granulata and its variety angustissima, Anabaena flos-aquae,Lyngbya limnetica,Microcystis flos-aquae and Phormidium mucicola.Diatoms and coccoid Chlorophyta tend to be the common phytoplankton in the rivers.Szemes (1967) reported that diatoms were the dominant forms in the River Danube throughout its length,both in number of species and of cells.The small centric species of the genera Stephanodiscus and Cyclotella are the most common diatoms found in the rivers (e.g.in the River Thames (Mc Gill,1969;Evans,1971;Lack,1971; Haffner,1974;Hardy,1977;Bowles,1978;Yallop,1980;Speller,1984), in the River Lee,Stour and Severn (Swale,1964,1969) and in the River Avon (Aykulu,1978)).Other group of algae regularly recorded in any quantity in river plankton are the flagellate Volvocales and coccoid Chlorococcales of the Chlorophyta (e.g. Chlamydomonas,Gonium,Pandorina,Pediastrum,Scenedesmus, Ankistrodesmus,Crucigenia,Lagerheimia,Golenkinia,Micractinium, Actinastrum,Dictyosphaerium).Species of Cyanophyta (Microcystis,Anabaena),Euglenophyta (Euglena,Trachelomonas, Phacus),Dinophyta,Cryptophyta and Chrysophyta are relatively rare and only very occasionally form large populations in rivers (Round,1981).

The River Rhine has for the public two faces.One

face is the romantic river between mountains with wineyards and old castles.The other face can be described as "Cloaca of Europe",because the river has to take the sewage from cities and industries of an important part of several European states,however,at the same time it must supply good drinking water for about 20 million people (Friedrich and Viehweg,1984). Centric diatoms dominate the plankton in the Rhine,especially Stephanodiscus hantzschii and Stephanodiscus tenuis.Besides diatoms,only Chlorococcalian green algae are common in this river.In a comparison of three river systems in Hungary, Uherkovich (1969) found Cyclotella-Nitzschia acicularis-Synedra acus-Actinastrum hantzschii-dominant in the River Danube,Cyclotella-Nitzschia acicularis-Synedra ulna and Scenedesmus spp. in the River Theiss and Ceratoneis acus-Cyclotella-Diatoma vulgare-Synedra ulna in the River Drau.

The seasonal cycle of river plankton is not so well pronounced as in lakes or the oceans but there are clear winter lows and spring blooms and autumn blooms.Early workers (e.g.Krieger,1927;Butcher,1932,1940) believed that the river phytoplankton originated from headwaters,lakes and pools along the river or was recruited from the sediments.There seems to be little doubt that in fact all these and others (e.g. epiphytic populations) contribute cells to the (pseudo) plankton and that in certain rivers,or sections of rivers, plankton is mainly a miscellaneous collection from such sites (Swanson and Bachmann,1976;Roeder,1977),carried along in the

stream and perhaps dividing to some extent in the open water. Bowles (1978) considered the phytoplankton in the River Thames as true phytoplankton populations.This suggestion was made by investigating the effects of flow on algal populations in relation to volume changes (dilution),velocity changes and the relationships between velocity,length of river,turbidity, buoyancy of algae and algal growth.Comparisons between algal populations in the River Thames and River Murray in Australia indicated that despite differences in climatic conditions and nutrient concentrations,the floras of the two rivers had marked similarities.This was considered to be further evidence of the presence of true phytoplankton populations in large rivers (Bowles,1978).

From this study,it was found that phytoplankton populations especially Stephanodiscus ref.hantzschii, Stephanodiscus rotula var.minutula,Stephanodiscus rotula, Chlamydomonas spp.,Scenedesmus spp.,Rhodomonas minuta, Cryptomonas spp. etc.,remain in the river for considerable lengths of time and divide many times,often to form rich blooms (especially Stephanodiscus ref.hantzschii) and must be regarded as euplanktonic.These phytoplankton populations are also trapped amongst debris and epiphytes in the river and doubtless these masses form an inoculum which is maintained in benthic habitats (Aykulu,1978).In fact,on theoretical grounds it is difficult to see how in a flowing system any species can remain in the water unless a few cells are trapped in backwaters or between vegetations (Round,1981).

1.4 PROBLEMS IN THE METHODOLOGY OF STUDYING PHYTOPLANKTON

1.4.1 INTRODUCTION

The problems involved in field studies of phytoplankton are formidable and arise mainly from two features (Sakshaug,1980):

(i) phytoplankton communities are highly dynamic, with cells which,under the appropriate conditions, have the ability to divide rapidly;

(ii)pelagic communities constitute numerous groups of organisms:bacteria,phytoplankton,zooplankton, etc.with a wide range of sizes within each group.

The first feature mentioned implies large short-term fluctuations in phytoplankton biomass as well as the transport of matter and energy through the community.This has consequences for the choice of a sampling programme.

The other feature raises persistent problems with regard to the determination of chemical properties for the various groups of organisms.The problem of separation between groups of organisms and detritus is far from adequately solved.

To follow patterns of growth and succession the habitat must be sampled thoroughly and at frequent intervals.

Phytoplankton may move vertically in the water column during the period of observation.Heaney (1976) found that the distribution of Ceratium was found to be non-uniform in both vertical and horizontal planes even in a small lake and frequently vertically stratified so that a sample from the surface may contain a different association of species from one at one metre depth and this may differ from one at 5 metre and so on.An attempt to overcome this situation during this study was made by sampling from the Wraysbury Reservoir at various depths ranging from 1 to 21 metres every week. Traditionally,discussions of phytoplankton patchiness have been restricted to heterogeneities in the horizontal.But aquatic systems are three-dimensional,and it will not be possible for us to ignore the vertical structure,particularly since recent work shows that vertical and horizontal fluctuations are closely related (Evans et al.,1976;Herman and Derman,1977).

In phytoplankton ecology,in particular when dealing with chemical methods,it is crucial to separate groups of organisms from each other and from detritus (dead organic matter) so that chemical data can be assigned correctly to the various groups of organisms and a correction made for detritus.This is one of difficult methodology problems in phytoplankton ecology because:

(i) it is necessary to separate phytoplankton from bacteria and zooplankton,

(ii) it may even be necessary to separate groups of

phytoplankton, for instance diatoms from dinoflagellates, because of their different biological and chemical properties.

There are no direct treatment of a water sample., so far, which meets these requirements adequately under all circumstances, and the existing indirect methods for estimations of biomass can be burdened with rather large errors. These problems increase with the maturity of a community.

The classical approach for concentrating and separating groups of organisms involves the use of nets. Nylon nets are today obtainable in size ranges down to 1 µm. Collection by towing is not a quantitative method and is used mainly for taxonomic purposes and for chemical analyses when large amounts of matter are necessary. However, it should be used with caution in chemical analysis. According to Hegseth (1977), there are indications, at least for the commonly used nets of 25-35 µm mesh size, that nauplii are collected more efficiently than phytoplankton.

To collect the phytoplankton quantitatively, membrane, glass-fibre, polycarbonate or metal filters are employed, with a stated pore size of 0.5-0.8 µm. These filters will always retain some of bacteria. Sheldon (1972) has discussed the merits of various filters. He found that none of the filters acted as true screens in that they did not separate two size fractions quantitatively. Typically, a filter

with a stated pore size of 0.5 µm might let through particles up to 0.7-1.0 µm.A better description of filter characteristics was therefore their median retention size. This size was close to the stated pore size for metal (Selas Flotronics) and polycarbonate (G.E.Nucleopore) filters,and in the 0.45-0.8 µm range for membrane filters (Millipore).For the very much used glass-fibre filters Whatman GF/C and GF/A the median retention size was 0.7 and 0.9 µm ,respectively and,for Whatman GF/F 0.5 µm.Thus the characteristics of the filters in common use are not much different.

Fractionated filtration of plankton has become popular in later years (Durbin et al.,1975).The method is very laborious since the work performed on one sample has to multiplied by the number of fractions collected.However,a true screen effect will not be achieved unless there is an oligospecific community with species or colonies of considerable size differences.Data from Durbin et al.,(1975) indicate that biomass calculated per cell in mixed diatom populations may be as high for the 'smaller' size fractions as for the 'larger' ones.

Bayne and Lawrence (1972) described a new principle for separation of freshwater species from each other and from detritus.The method employs continuous particle electrophoresis and is based on the fact that living phytoplankton cells are negatively charged.This method is probably unusable for marine phytoplankton since the algae

have to be transferred to freshwater buffer.The seawater has a conductivity far higher than the instrumentation can bear.

There is no method available which can yield a quantitative separation between algal species or between groups of species and detritus.Neither can bacteria and zooplankton be separated quantitatively from phytoplankton. What then remains is the long standing tradition of using coarse nets to remove macrozooplankton,and filters in the 0.5-0.8 μm range of medium retention size to separate the algae from the water and partly from the bacteria.Further distinction between group of organisms and detritus has to be derived from an adequately chosen set of parameters to be measured.

1.4.2 MEASUREMENTS OF ALGAL BIOMASS

The determination of algal biomass is central to most studies of phytoplankton.Numerous quantitative methods have been adopted including cell counts,optical methods using using live cells or extracted pigments,and chemical determinations (e.g.Strickland and Parson,1972;Stein,1973; Hallaegraeff,1977;Sournia,1978).

(a) COUNTING OF CELLS

The oldest method of determining biomass,direct

cell counting,is still in extensive use and should remain so in the future.This method was employed during this study as no other method yields as much information on one samples as do the enumeration and identification of phytoplankton. Butterwick et al.,(1982) studied and made a comparison of eight methods for estimating the biomass and growth of planktonic algae.The methods were based on cell counts by visual microscopy and electronic means,optical properties and chemical estimations.They found that visual cell counts, although relatively slow and fatiguing,were unsurpassed for low limit of detection,economy of sample,and assessment of cell condition.

There is a wide range of methods and devices available for the identification and enumeration of phytoplankton.Most preferred is the inverted microscope technique of Utermöhl (1931),employing sedimentation of preserved samples in 2-100 ml.chambers.Counting and identification is made through the bottom of the chamber, which consists of glass of cover-slip thickness.This method is adequate for concentrations in the $10\text{-}10^{6}$ cells l^{-1} range.

A main problem in all methods using preserved samples is that a number of organisms,in particular naked flagellates,disintegrate or become misshapen so that identification becomes impossible.In the inverted microscope technique,sedimentation may be incomplete due to attachment of cells to the side walls of the chambers,or simply because

the cells do not gain enough weight by preservation. In that particular context Lugol's solution is superior to neutralized formaldehyde as fixing agent, but the former will destroy coccolithoporids. Hasle (1978) found that some species e.g., Chaetoceros sp., are not distributed randomly on the bottom of the chamber, but tend to accumulate along the periphery, causing erroneous results when inspecting only a part of the bottom area.

The reliability of phytoplankton counts has been studied by a number of researchers and is reviewed by Venrick (1978). Statistics of subsamples from one given sample indicate that for most solitary species a log normal or Poisson distribution can be assumed (excluding patchiness on a scale greater than the size of the sample). At least 20-50 cells should be counted for solitary species. For species forming multicellular colonies, contagion or 'clumping' must be taken into account when using cell number as a base for calculation. These procedures, all of which involve use of the microscope, allow estimation of cell volume and cell surface area. By measuring the volume of vacuoles as well, plasma volume can also be determined. The necessary calculations usually involve application of formulae for stereometric figures of shapes related to the organisms in conjunction with measurement of cell dimensions.

Hastings et al., (1962) and Maloney et al., (1962) introduced electronic particle counting as a means of

enumerating phytoplankton.The method has been applied to natural waters rather extensively (Cushing et al.,1968;Evans and Mc Gill,1970;Haffner,1974 and Yallop,1980).This method was also employed during the presently described investigations of phytoplankton populations in the River Thames and the Wraysbury Reservoir.Modern particle counters yield a size distribution spectrum of particles as well as total particulate numbers and volumes.The principle involved is a measurement of the electrical resistance of a particle to an electric current flowing across an aperture through which the particle passes.Because of this,neither enumeration nor size measurement in a mixed community is equivalent to measurenments carried out with the microscope,a point which must be emphasized.Dead and living matter will be counted indiscriminately,and the shape of particles will affect the size estimate,colony-forming phytoplankton being a particularly serious problem.However,a notable advantage of this method is that measurements can be carried out very precisely and rapidly for the total seston.

(b) CHLOROPLAST PIGMENTS

Among the numerous chloroplast pigments in algae, chlorophyll a has an outstanding position since it is common to all photosynthetic organisms and is the receptor of radiant energy,directly or via the accessory pigments.In

other words,all energy available for the total ecosystem is fixed by chlorophyll a.Therefore,considerable efforts have been put into the development of methods for analysis of chlorophyll a,and chlorophyll a data have been extensively used for estimating phytoplankton biomass as well as (in combination with data for irradiance) primary production.

Simple,colorimetric methods for the measurement of chlorophyll a were presented as early as the thirties (Kreps and Verjbinskaya,1930;Harvey,1934).Routine measurements today are usually carried out according to the handbook of Strickland and Parsons (1972) for the spectrophotometric method,and of Holm-Hansen et al.,(1965) for the fluorometric methods.Both methods involve the extraction of pigments from particulate material by the use of organic solvents,usually acetone or (preferably) methanol.A crucial problem in the analyses is that chlorophyll a has to be measured in a mixture of pigments,of which some interfere with the chlorophyll a analysis,chlorophylls b and c and some derivatives of chlorophyll in particular.

Further discussions of the methods used for this present study are presented in Chapter Two.

1.5 EUTROPHICATION

1.5.1 INTRODUCTION

There has been international attention directed toward the problem of eutrophication in recent years. The process of eutrophication is one of the problems of impairment of standing and flowing surface waters, which represent an important part of the environment, and is conditioned by civilization. Eutrophication is defined as an increase in the rate of income of nutrients (Edmonson, 1974). The income of nutrients may be considered as artificial or cultural eutrophication if the increase is due to human human activities, or natural eutrophication if the rate of increase is caused by non-human process, such as forest fire. Eutrophication includes the enrichment of water by plant nutrients. It is a natural process in the ageing of lakes and impounded waters. If we sum up all the data available and if we bear in mind the wider meaning of this conception, then the term eutrophication embraces everything that contributes to the occurrence of nutrients outside and inside the water body, and which manifests itself directly in an increase of its productivity. This supplementary criterion is important, for the mere increase of the level of nutrients in water remains non-significant unless biocenosis is included in the process of eutrophication and unless this produces undesired

effects on water metabolism (Stepanek,1979).The consequences of the increased nutrient supply depend on a whole complex of factors determining the manner of organic production in a given ecosystem: the morphometrical features of the water body,mixing of water masses,temperature,light,the species composition of the plankton and benthic producers, participation of primary and secondary consumers and,perhaps not least,the factor of time.

The term oligotrophic and eutrophic were originally introduced by Weber in 1907 to describe nutrient conditions in the development of peat bogs.Naumann (1919) introduced the terms to the limnological world,classifying lakes as having oligotrophic water if they were clear in summer and eutrophic water if they were turbid due to the presence of algae.As other definitions have arisen considerable confusion over these terms has developed.Oligotrophic lakes have been defined as having a low productivity and eutrophic lakes as having a high productivity.Whilst in general terms high nutrient levels and high productivity go together this may not always the case.For instance,marl lakes have highly calcareously,nutrient rich water ("eutrophic"),with a heavy precipitation of carbonates.Under these conditions phosphates and many micro-nutrients form very insoluble compounds which precipitate to the bottom of the lake.Thus algal productivity is low and it has described as oligotrophic by Wetzel (1968).

Planktonic algae occupy a central position in the

eutrophication problems,especially for waterworks authorities. Such algae are the primary producers of organic matter,and so of troubles arising from biological factors.

It has been suggested that eutrophication is not yet a major economic problem in the British water industry (Lund,1970).However,it could became one and therefore further ecological investigations on the growth of phytoplankton populations is needed.

1.5.2 CAUSES AND CONSEQUENCES OF EUTROPHICATION

The problems of water and man (which is closely associated with eutrophication) can be in principle divided into two basic functions:

(i) The importance of water for man,and

(ii) the effect of human activities on water resources.

The advance of civilization which involves a continuous rise in the demand and use of water by the population,industry and agriculture,leads simultaneously to a growing water pollution not only by quantity but by a variety of different compounds,an increasing portion of which are toxic (Allen and Kramer,1972).

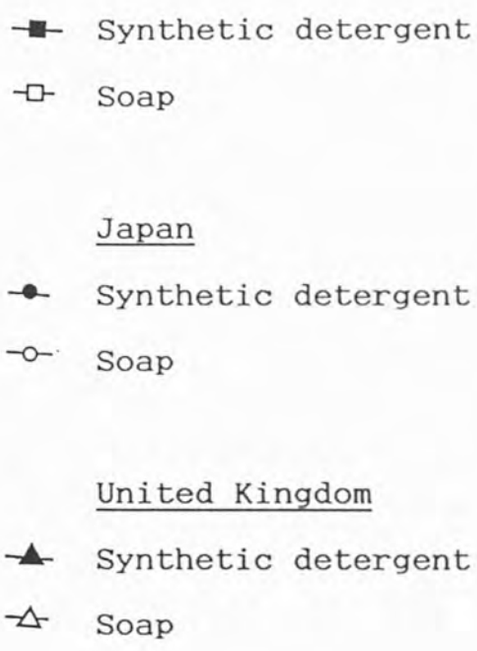
The majority of polluting nutrients enter watercourses and lakes in effluents from sewage treatment works,in untreated sewage or from farming activities.It has

been proved that the washings of nutrients from the soil and surface runoffs are one of the primary sources of contamination and eutrophication of surface waters (Jones et al.,1971).

Nutrients from urban sources may be derived from domestic sewage,industrial wastes and storm drainage.The contribution of nitrogen and phosphorus per person averages 10.8 g N/capita/day and 2.18 g P/capita/day,though there is a considerable range (Vollenweider,1968).Detergents have become a very important source of phosphorus in domestic sewage since it was first developed in the 1940's.Figure 1.2 shows the increase in usage of detergents in the United States, Japan and Britain.Phosphorus from detergents made up 47-65% of the total phosphorus in sewage from six English sewage works in 1971,compared with 10-20% in 1957 (Devey and Harkness,1973).Industrial sources of nutrients may be locally important,depending on the type of industry,the volume of effluent and the amount of treatment it receives.For instance,the brewing industry which released some 10,680 m^3 effluent each day into rivers in England and Wales in 1975 (Department of the Environment,1978),produces an effluent containing some 156 mg l^{-1} N and 20 mg l^{-1} P (Vollenweider, 1968).

Rural sources of nutrients include those from agriculture,forest management and rural dwellings.Rural dwellings tend to dispose of their sewage into septic tanks

Figure 1.2. Trends in the consumption of synthetic detergents and soap (metric tons X 10^3) for:



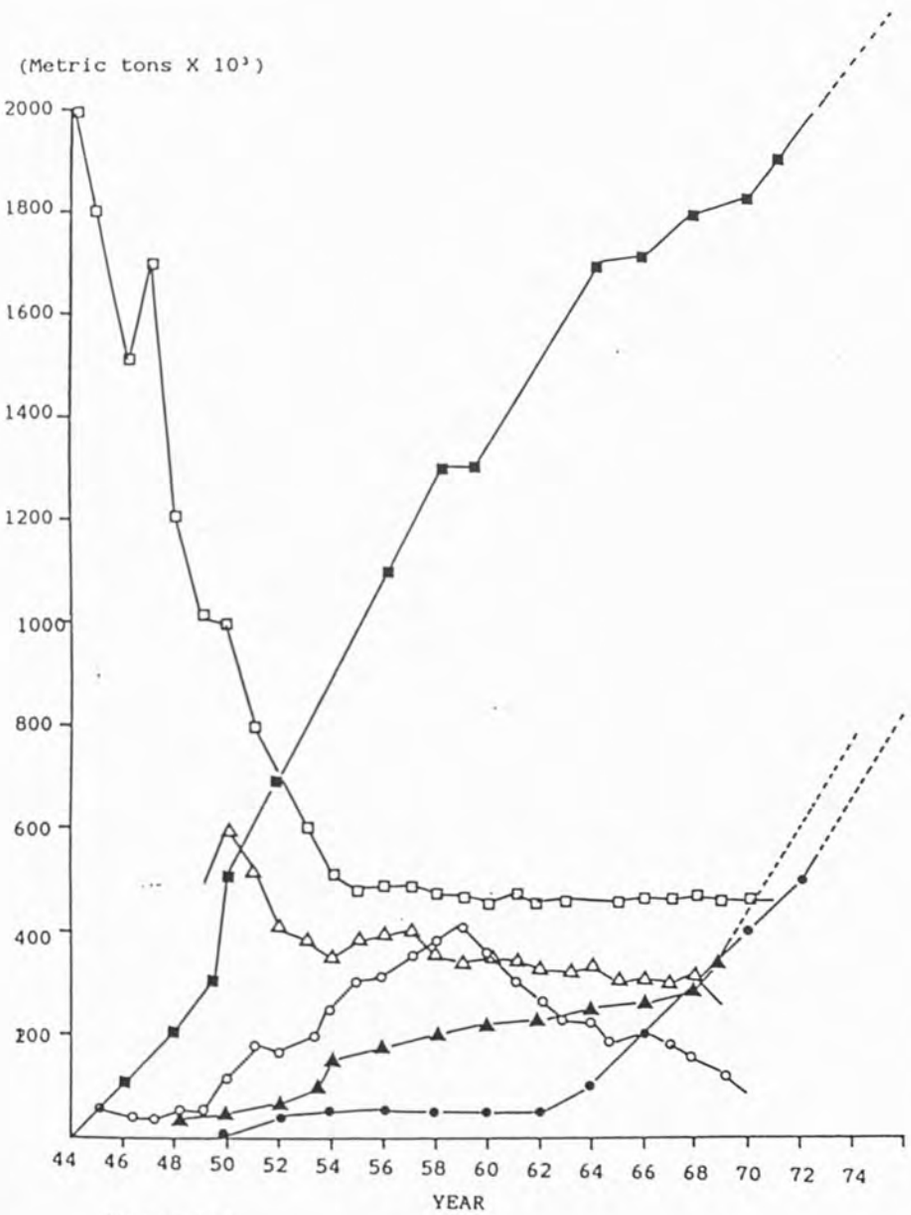


Figure 1.3

(Reconstruct after Devey and Harkness, 1973)

which might cause local pollution, though Lee et al., (1978) consider them generally unimportant.

Nutrients are lost from farmland in three ways Tomlinson (1971):

(i) by drainage water percolating through the soil leaching soluble plant nutrients;

(ii) by inefficient return to the land of the excreta of stock;

(iii) by the erosion of surface soils or by the movement of fine soil particles into subsoil drainage systems.

CHAPTER TWO

METHODS

SAMPLING, ANALYTICAL AND CULTURE TECHNIQUES

2.1 SAMPLING PROGRAMME

During 1984, from mid-March, samples were collected regularly once a fortnight from the River Thames and Wraysbury Reservoir. For more reliable data, samples were collected weekly from February 1985 until September 1986. Routine collection of water samples from Wraysbury Reservoir were made by the staff of the Thames Water Authority during their own regular sampling programme from several different depths that is: 1, 3, 5, 7, 9, 11, 13, 15, 17, 19 and 21 metres. On most occasions samples were provided from the Limnology Tower Two. Limnology Tower Two is the most centrally situated station in the reservoir and nearly opposite the main jet stream of the river input (Figure 2.1).

River samples were collected from the south side of the River Thames near Egham at the Bells of Ouzely (992735); as shown in Figure 2.2.

Volumes samples were collected in size polythene bottles of 1000 ml. and net samples were obtained by using a

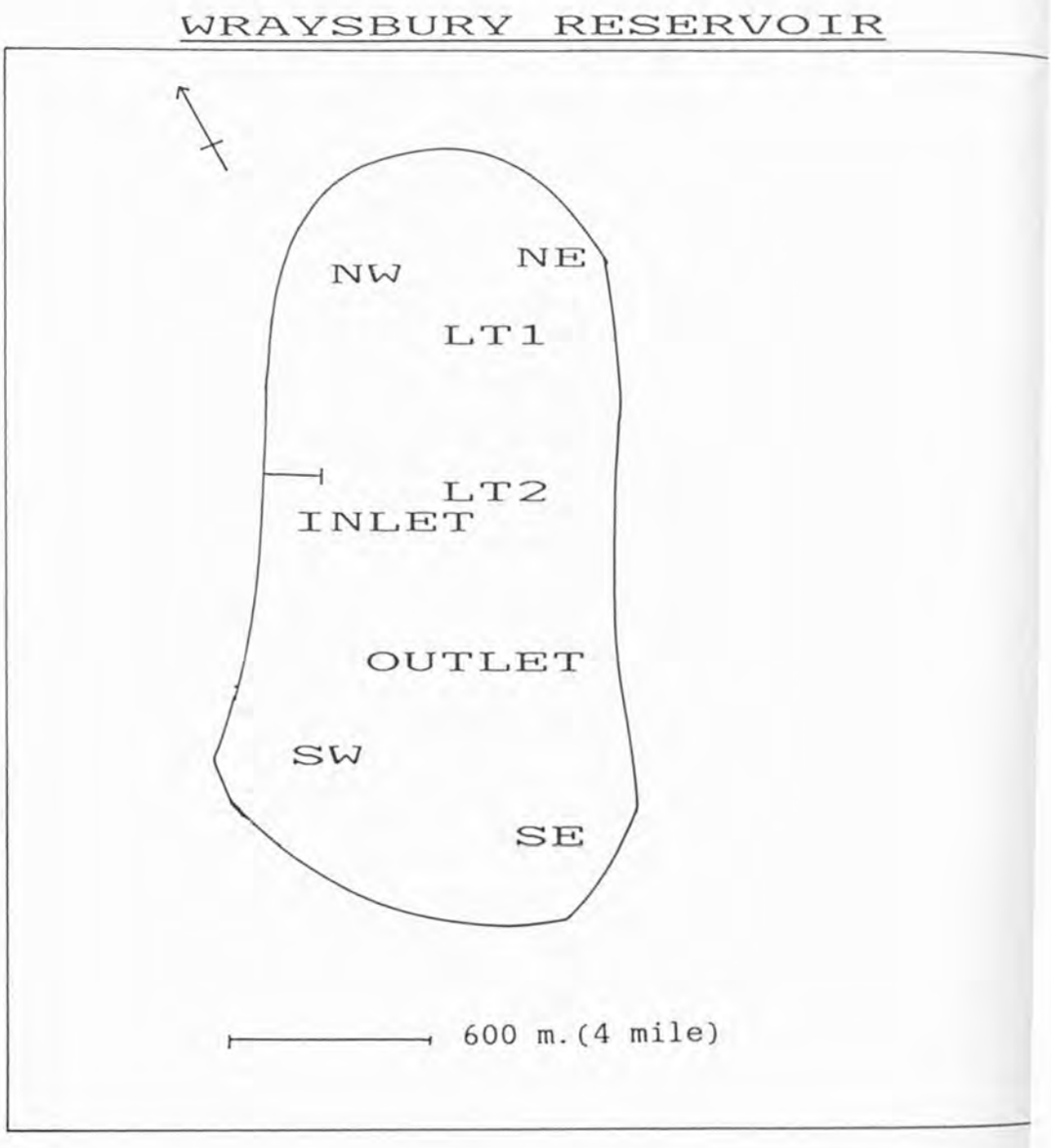


Figure 2.1 Plan of the Wraysbury Reservoir showing sampling stations.

LT1 = Limnology Tower One

LT2 = Limnology Tower Two

(From: Hardy,1977)

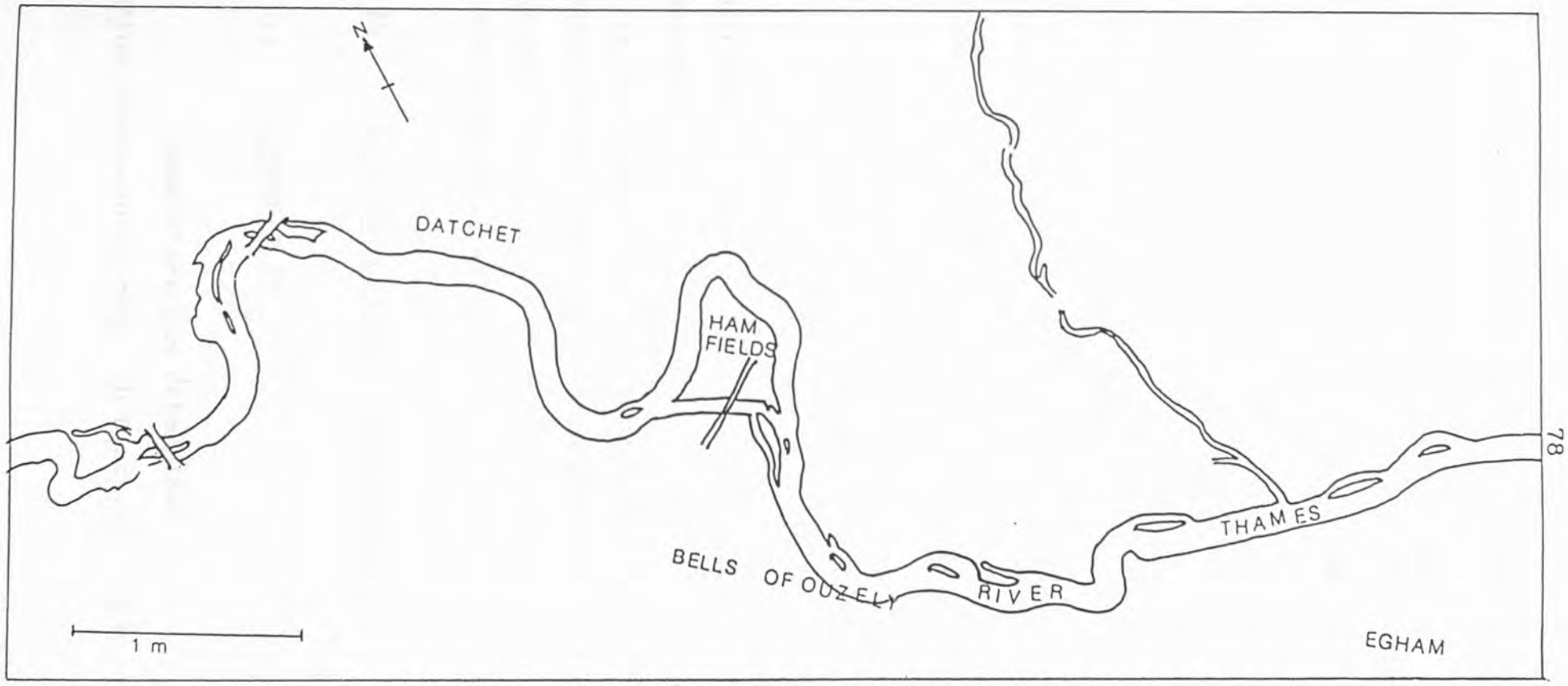


Figure 2.2. Sketch map of the section of the River Thames, showing sampling stations.

'Hydrobios' plankton net with mesh size about 30 microns. Plankton nets are not to be recommended for either extensive qualitative or quantitative sampling of phytoplankton as the cells of large percentage of important algal species are much smaller than the mesh opening dimension of nets,even of the finest mesh size.Furthermore,the volume of water passing through most nets is very difficult to measure.Samples collected by plankton net were examined to aid in the identification of live phytoplankton populations.

The depth of water at the end of the landing stage from which River Thames samples were collected was measured using a 1.5 metre stick,graduated in cm.

Weekly field trips were made to investigate the following: temperature,dissolved oxygen concentration, conductivity,pH,light attenuation,chlorophyll a,alkalinity, nitrate-nitrogen,phosphate-phosphorus and silica concentrations,carbon concentrations and phytoplankton population numbers and Calculated Algal Volume determined with the inverted microscope and Coulter Counter.

2.2 PHYSICAL FACTORS

2.2.1 TEMPERATURE

Temperature was determined using the YSI (Yellow Spring Instruments) Model 58 Dissolved Oxygen Meter with

reading taken to $\pm$0.1°C.

2.2.2 CONDUCTIVITY, ALKALINITY, pH AND DISSOLVED GASES

The electrolytic conductivity of a solution of electrolytes refers to the ability of the solution to carry an electric current. Since electricity is carried in the solution by migration of ions, the conductivity under standard conditions (of electrode geometry and temperature) may be expected to bear some relationship to the total ion concentration. The relationship is to some extent dependent on the nature of the major ions in solution, so that waters of different ionic composition will display a different relationship between ionic concentration and conductivity.

The specific conductance or conductivity was measured using a temperature-compensating conductivity meter (manufactured by Evershed and Vignoles Limited); with the reading given at 20°C and expressed in μmhos cm^{-1}. The conductivity data have not been corrected to the more usual standard (at 25°C) because it was found reliable for broad comparisons of the data and the temperature chosen is more or less similar to the laboratory where the measurement was taking place.

Alkalinity is a useful single measure, as it may be correlated with important general characteristics such as

total ion content (and hence conductivity),calcium concentrations (excepting in high alkalinity water,more than 5 meq l^{-1}) and pH.

In most natural waters bicarbonates,and sometimes carbonates,are present.These salts are hydrolyzed in solution because of the weakness of carbonic acid (H_2CO_3),with the production of hydroxyl ions and consequent rise in pH:

$$M^+ + HCO_3^- + H_2O \rightleftharpoons M^+ + H_2CO_3 + OH^-$$

The concentration of bicarbonate in solution can be determined by titrating the samples with standard acid which will remove OH^- until the above equilibrium has moved completely to the right.Since this occurs when pH is 4.5,an indicator is chosen to give a colour change at this pH.The amount of acid consumed will often approximate the equivalent of bicarbonate in samples near neutrality (pH 6-8.5),but generally reflects the sum of alkalinity components,as equivalents:

$$[HCO_3^-] + 2[CO_3^{2-}] + [A^-] + [OH^-] - [H^+]$$

where A^- represents anions of weak acids other than H_2CO_3 (e.g.$H_3SiO_4^-$).In very alkaline waters $[OH^-]$ and $[CO_3^{2-}]$ can be considerable.In very acid waters the sum of alkalinity components will be negative (Stumm and Morgan,1970) and constitute a positive acidity.

The calcium carbonate alkalinity was determined by titration (Mackereth et al.,1978).Results were expressed in mg l^{-1}.

Free carbon dioxide concentration was determined approximately by the use of Moore's nomogram.Results have been expressed in mg l^{-1}.This method although simple was found reliable and has been used by the American Water Works Associations (A.P.H.A.,1976).

Dissolved oxygen provides valuable information about the biological and biochemical reactions going on in waters;it is a measure of one of the important environmental factors affecting aquatic life,and of the capacity of water to receive organic matter without causing nuisance.Oxygen gas dissolves freely in fresh waters.Oxygen may be added to the water from the atmosphere or as a by product of photosynthesis from aquatic plants,and is utilized by many respiratory biochemical,as well as by inorganic chemical reactions.The concentration in water depends also upon temperature,pressure and concentrations of various ions (Wetzel,1975).

To be successful,a method for measuring dissolved oxygen needs two requirements.First,owing to the small amount of substance to be determined (a few mg l^{-1});it must be exact and second;it must be carried out with apparatus suited for field operation.The determination of dissolved oxygen in natural waters is most conveniently carried out by means of an oxygen-temperature probe.

Dissolved oxygen was measured as % air saturation

($\pm$0.3) with the YSI Model 58 Dissolved Oxygen Meter.The % air saturation feature allows quick determination of the degree of air saturation occurring in water.The % air saturation is the saturation which would occur if the samples were saturated with air under a normal barometric pressure of 1013 millibars (760 mm Hg.or 29.92 inches Hg.).

pH: Besides its use in the direct estimation of CO_2, pH is widely used as a general characteristic of a water and its value in this respect is greatly enhanced if the titration alkalinity is also known as the air-equilibrium pH of a water will rise with increasing alkalinity (an increase by approximately 1 pH unit for each tenfold increase in alkalinity).Natural variability of the free CO_2 content will,however,produce considerable deviations from this idealized relationship.Since the pH of a water sample is liable to be modified by biological activity or by CO_2-exchange with the air,long intervals (a few hours) between collection and measurement should be avoided.Given constancy of alkalinity during CO_2 exchanges,the elevation of pH (a widely measured factor) is an indication of CO_2 depletion, especially if it can be compared with the pH at air-equilibrium (Talling,1985).Therefore effects of biologically-generated depletion or accumulation of CO_2 can be judged relative to the pH/alkalinity relationship for air-equilibrium.According to Talling (1985),CO_2 depletion is

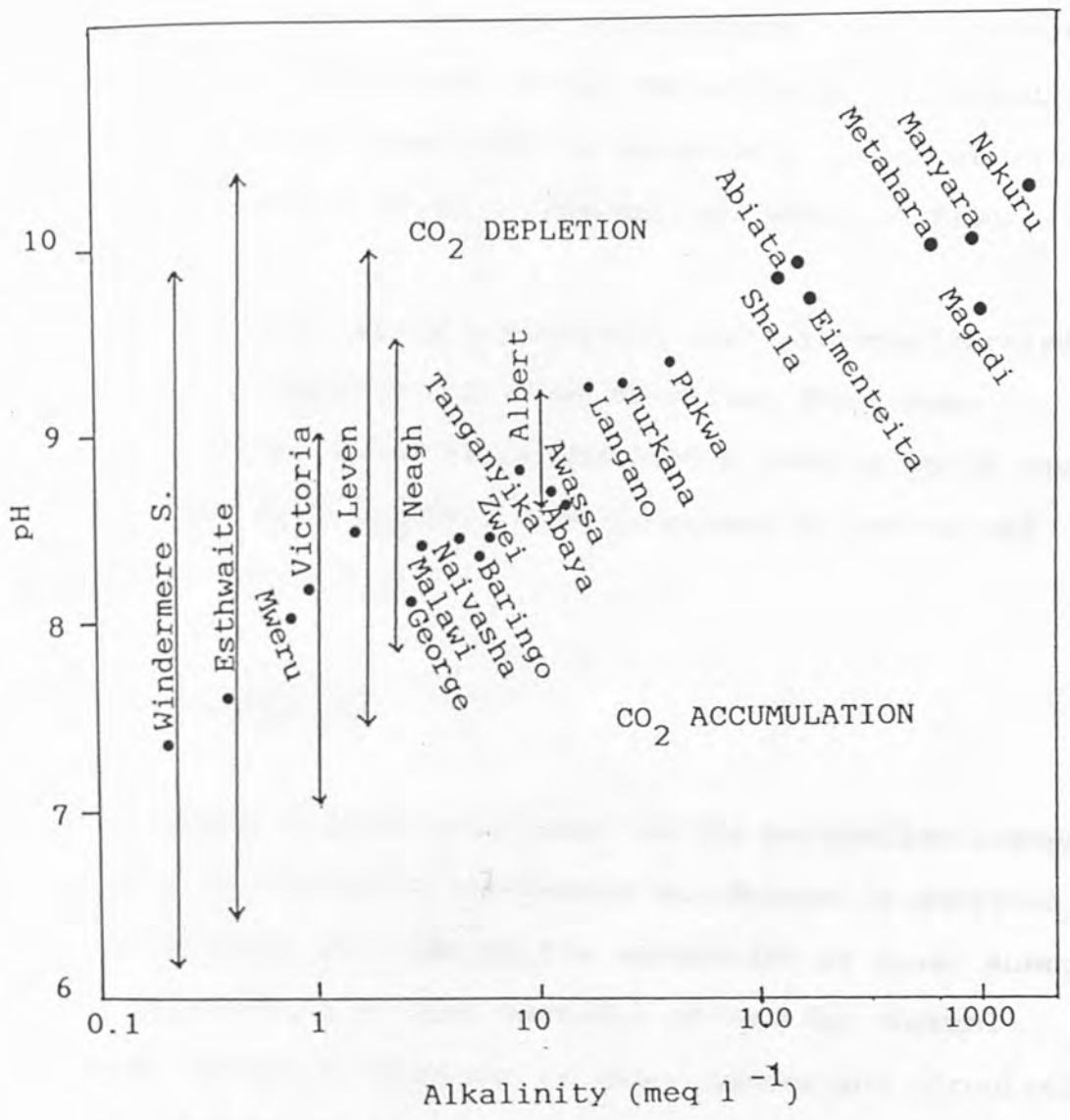


Figure 2.3. The variation of pH at air-equilibrium (15 to 20°C) measured for lake waters of varying alkalinity and range (arrows) due to CO_2 depletion or accumulation recorded in nature. The sources are African lakes, Talling and Talling (1965); L. Leven, Scotland, Bindloss (1974); L. Neagh, N. Ireland, Gibson et al., (1971); Winderemere and Esthwaite Water, England (Talling, unpublished).
(From: Talling, 1985)

approximately tenfold per unit pH rise over most of the pH range involved. Indications of the depletion of CO_2 based on pH shifts at known alkalinity (a relatively conservative quantity unaffected by CO_2 exchange) are shown in Figure 2.3 (Talling, 1985).

Although it is appreciated that air-equilibrated samples would indicate different pH values from those determined in the field, it is the latter results which have been recorded here as indicating responses to biological influences.

2.2.3 LIGHT

Solar radiation is vital to the metabolism, indeed, to the very existence of freshwater ecosystems. In addition to direct biological utilization, the absorption of solar energy and its dissipation as heat markedly affects the thermal structures and stratification of water masses, and circulation pattern of lakes, reservoirs and streams. Solar radiant energy that reaches the surface of the earth has a spectral range from about 300 nm (ultraviolet) to about 3000 nm (infrared) and about half of the total radiant energy that can be detected by the human eye (380 to 780 nm). Photosynthetically active radiation (PAR) occurs between 46 to 48% of the total energy impinging in the earth's surface (Strickland, 1958; Talling, 1957; Westlake, 1965). The irradiance (=intensity) is

To convert Into	Wm^{-2}	Wm^{-2} PAR	Cal cm^{-2} min^{-1}	Cal cm^{-2} min^{-1} PAR	$\mu E\ m^{-2}s^{-1}$	Photons (quanta $m^{-2}s^{-1}$)	MJ $m^{-2}d^{-1}$	Lux
Watt per square metre	1	2.17; 0	6.98; +2	1.51; +3	4.65; -1	7.72;-19	2.31; +1	8.70; -3
Watt per square metre (PAR)	4.60; -1	1	3.21; +2	6.98; +2	2.14; -1	3.55;-19	1.06; +1	4.00; -3
Calorie per square centimetre min.	1.47; -3	3.11; -3	1	2.17; 0	6.85; -4	1.14;-21	3.40; -2	1.25; -5
Cal.per square centimetre min (PAR)	6.58; -4	1.47; -3	4.60; -1	1	3.15; -4	5.23;-22	1.52; -2	5.75; -6
Micro-Einsteins per square metre sec.	2.15; 0	4.67; 0	1.46; +3	3.17; +3	1	1.66;-18	4.97; +1	1.75; -2
Photons (Quanta per square metre sec.	1.30;+18	2.82;+18	9.07;+20	1.96;+21	6.02;+17	1	3.00;+19	1.13; -4
Mega Joule per square metre day (12 hour)	4.33; -2	9.43; -2	2.94; +1	6.58; +1	2.01; -2	3.33;-20	1	3.55; -4
Lux (Lumen per square metre)	1.15; +2	2.66; +2	8.00; +4	1.80; +5	5.71; +1	8.85;-17	2.82; +3	1

Table 2.1. UNITS AND CONVERSION FACTORS FOR SOLAR RADIATION DATA

Definitions and expressions

Watt = Joules s^{-1}; Joule = 1 Nm(Newton-metre); 1 Newton = 1 Kg m s^{-2}; Wm^{-2} = K erg $cm^{-2}s^{-1}$; Langley = cal cm^{-2}; 1 mg carbon fixation = 39 Joules as energy storage.

Notes

Use of Table: E.g. (1) To convert Wm^{-2} into cal $cm^{-2}min^{-1}$ multiply by 1.47×10^{-3}; (2) To convert Wm^{-2} into Photons multiply by 1.30×10^{18}

N.B. All conversions are approximate and all but one of these units represent irradiance or energy flux (photon flux density) or PFD integrated over time. Lux (Lumens m^{-2}) are units of illuminance and not strictly comparable, but are included for convenience.

$\mu E\ m^{-2}s^{-1}$ = $\mu mol\ m^{-2}\ s^{-1}$

(From: Evans, 1985)

the quantity of energy is expressed in a number of ways:

(a) in the meter-kilogram-second system as Joules per area-time, J m^2 sec^{-1}.

(b) Watts per area-time, Wm^{-2} (time is implied, e.g. Watt = Joules s^{-1}), or as gram-calories per area-time, g cal cm^2 min^{-1}.

The relationships among these values are summarized in Table 2.1 (Evans, 1985).

2.2.3.1 MEASUREMENT OF SURFACE IRRADIANCE

A pre-calibrated Kipp and Zonen solarimeter connected to a sensitive DC microvoltmeter (Comark Type 1221) has been used to indicate surface radiation. The amount and spectral composition of solar radiation impinging on the surface of a lake or stream are influenced by an array of dynamic environmental factors. Direct solar radiation reaching the water surface varies with the angular height of the source of the radiation and, therefore, with time of day, season and latitude (Wetzel, 1975).

2.2.3.2 MEASUREMENT OF UNDERWATER IRRADIANCE

As solar radiation penetrates water, portions are absorbed both by water itself and by dissolved and suspended materials contained in it.

The attenuation of total irradiance from direct and indirect insolation within a river can be measured with a variety of instruments. Ideally the total underwater irradiance would be measured with a receptor system at a specific depth. It is this amount of energy, whether from direct incident light or from scattered light sources, that is collectively important to phytoplankton for photosynthesis or as behavioural stimuli. This amount of irradiance is the photon scalar irradiance, defined as the total number of photons, from all directions about the point of measurement when all directions are weighted uniformly (Smith and Wilson, 1972). Techniques for measuring photon irradiance are available but as yet are complex and in only limited use.

Approximations of underwater irradiance may be made with less sophisticated but very reliable instruments. In this investigation a Macam SD 101 Q Sensor wired to a Levell Type TM 9 BDC multimeter was used and read out in μA transferred to Wm^{-2} PAR via a calibration constant supplied with each sensor.

The design, construction, testing and use of an underwater relative radiation multifilter sensor are described by Evans (1985).

2.3 ADDITIONAL METEOROLOGICAL DATA

Reports from the Meteorological Offices were used to obtain data on temperature,rainfall and hours of sunshine over the study period.

2.4 NUTRIENT ANALYSIS

Compounds of nitrogen,silicon and especially phosphorus,are major cellular components of phytoplankton. Since the availability of these elements may be less than biological demand,environmental sources can be regulate or limit of the production of the phytoplankton populations in the river or reservoir.Other elements such as iron and sulphur are essential constituents but are required in relatively low concentrations in relation to availability in most freshwaters.The major cations;calcium,magnesium,sodium and potassium,are usually required in very low quantities,but their concentrations in freshwaters can influence the osmoregulation of phytoplankton.Certain nutrients,such as magnesium and sodium,are conservative in concentration in that their solubility is high,they are usually abundant in relation to metabolic demands,and their concentrations are relatively unaffected by metabolically altered reduction-oxidation conditions of the water.On the other hand,

concentrations of nitrogen and phosphorus compounds are highly dynamic because they may be utilized,stored, transformed and excreted rapidly and repeatedly by various aquatic organisms.

Great care in collection and analysis of water samples for determining the concentrations of nutrients (i.e. nitrate-nitrogen,phosphate-phosphorus and silica) is very important.To avoid contamination,all equipment and glassware were thoroughly cleaned by:

(a) Detergent (Teepol) washing in tap water,rinsed in tap water,three rinses in glass distilled water.

(b) Soaked in concentrated sulphuric acid (H_2SO_4) saturated with $NaNO_3$ followed by thorough rinsing with distilled water.

Only Pyrex glassware,distilled water and analytical grade reagents were used.Storage of water samples before analysis was generally avoided.

It is often meaningful to the biologist,from the standpoint of availability,to separate analysis of total nutrient concentrations into those fractions that occur in particulate form.This separation was done by filtration through Millipore membrane acetate filter paper size 0.45 μm.

2.4.1 NITRATE-NITROGEN (NO_3-N)

The total nitrogen content of a water sample is divisible into particulate (largely organic) nitrogen and total soluble nitrogen.The latter comprises inorganic forms at various levels of oxidation:ammonia-nitrogen,nitrite, nitrate-nitrogen and dissolved organic nitrogen.

The phenyldisulphonic acid method described by Mackereth (1963) was used to determine nitrate-nitrogen concentrations.One disadvantage of this method is the interference of chloride,as this will promote loss of nitrogen as nitrosyl chloride.Holden (1970) states that levels of up to 100 mg l^{-1} can be tolerated.As chloride levels in the River Thames and Wraysbury Reservoir were usually below 45 mg l^{-1} and fairly constant (Hardy,1977; Yallop,1980),this method could be used.This was confirmed by results for chloride provided by Thames Water Authority and the North Surrey Water Company.

2.4.2 PHOSPHATE-PHOSPHORUS (PO_4-P)

Intense ecological interest in phosphorus stems from its major role in metabolism in the biosphere.In comparison to the relatively rich supply of other major nutritional and structural components of the biota (C,N,O,S), phosphorus is least abundant and commonly limits biological

productivity.Phosphorus occurs in a number of inorganic and organic components in both particulate and dissolved forms (Strickland and Parsons,1968).Differentiation of forms is based on their reactivity with molybdate,ease of hydrolysis and particulate size.

Filterable orthophosphate was measured following the method described by Golterman (1969).In this procedure, the filtered water sample is allowed to react with a composite reagent of ammonium molybdate,sulphuric acid, antimony potassium tartrate and ascorbic acid.This method was selected as it involves the modification of Murphy and Riley (1962),who suggested the use of antimony potassium tartrate which promotes a faster colour development.Furthermore, ascorbic acid is used as the reductant,replacing stannous chloride.KH_2PO_4 was used as a standard for the calibration curve,results being expressed as mg l^{-1} PO_4-P.

2.4.3 SILICA (SiO_2)

Dissolved silica (SiO_2) usually occurs in moderate abundance in freshwaters.Although essentially non-ionized and relatively unreactive chemically,dissolved silica is assimilated in large quantities by diatoms in the synthesis of their cell walls or frustules.Since diatoms are major algal components in the River Thames and Wraysbury Reservoir, diatom utilization can modify greatly the concentrations and

flux rates of dissolved silica in the river and reservoir.

The standard picric acid method was used to determine silica in the water samples (Mackereth,1963). Results are expressed throughout as mg l^{-1} SiO_2.

2.5 PIGMENT ANALYSIS

Chlorophyll was determined by a very simplified method and calculation.

500 ml. of water samples was filtered through membrane filter paper,placed in 20 ml.100% methanol in a 100 ml.beaker and left overnight in the dark at 5°C.The extract was subsequently made up to 60 ml. and reading taken at 601 µm (value of phaeophytin) and 608 µm (value for chlorophyll a) in 10 cm.cells using a long-celled EEL absorptiometer.Values for chlorophyll a and phaeophytin concentrations were determined using the calculation:

$$\text{e.g. Chlorophyll } a = \frac{D \times 100}{V} \quad \text{where;}$$

D = optical density,

V = volume filtered in ml.

2.6 QUANTITATIVE EVALUATION OF NUMBERS AND BIOMASS OF SPECIES

2.6.1 TOTAL PARTICULATE VOLUME

Samples were routinely analysed with the Coulter Counter Model ZB with a 200 μm aperture tube to size and enumerate seston in water samples from selected depths in the reservoir and sample from the river.Results obtained represent the total seston present but during periods of dense phytoplankton populations,may accurately reflect the phytoplankton biomass (Evans and Mc Gill,1970;Haffner,1974).

The methodology involved has been described fully by Mc Gill (1969) and Haffner (1974).In brief,the Coulter Counter operates by electronic sensing and counting of the number of particles in a suspension in a dilute electrolyte as they pass through a standard aperture.The diameter of the aperture may be varied,by the use of different aperture tube, so that the overall size range of the particles being counted may be varied within wide limits.Control settings on the instrument allow the selection of wider or narrower size ranges within the overall range.Thus not only numbers,but size distributions of algal populations may be determined.

A 10% solution of NaCl (membrane filtered) was added to the sample to make a final concentration of a 0.5%

saline solution.This was found to be a suitable concentration for algal populations (Mulligan and Kingsbury,1968;Evans and Mc Gill,1970).Particles were counted in eighteen size classes from 4.6 μm diameter to 48.5 μm diameter and a corresponding volume range of 50 to 60,000 μm^3.Such a range included the majority of the unicellular algae present in the water samples but excludes very large colonies of Microcystis flos-aquae.Some phytoplankton algae in their naturally occurring form are clearly unsuitable for size analyses with the Coulter Counter.For example,long filaments of large cells may tangle together and block the aperture and it is necessary to reduce such algae (eg. Trichonema vulgare, Anabaena spp.) to a more manageable form and for this purpose a Maxomatic ultrasonic shaker was used.

Such treatment could distort numerical results but the Total Particulate Volume should not be greatly altered.

This method does not distinguish between algal and non-algal particles but comparison with other methods for biomass determination showed clear relationship.Previous researchers have shown relationship between Total Particulate Volume with Calculated Algal Volume obtained by visual measurements,providing the level of non-algal detritus was low (Evans and Mc Gill,1970).There is also clear relationship between Total Particulate Volume with inverted microscope counts of large centric diatom Stephanodiscus rotula (=S.astrea,(Hardy,1977)) and chlorophyll a determinations (Yallop,1980).

My results provide further evidence that the Coulter Counter is a very useful and reasonably accurate instrument for measuring phytoplankton biomass in combination with other biomass determinations such as Calculated Algal Volumes, enumeration of phytoplankton and chlorophyll a determinations. This method was also used to determine numbers of cells and Total Particulate Volumes of phytoplankton populations in unialgal culture and comparisons have been made with visual measurements. The results have revealed clear relationship between them, providing that the unialgal culture was not contaminated by particles other than algae (e.g. dust, cotton wool).

2.6.2 PHYTOPLANKTON IDENTIFICATION AND ENUMERATION

For identification purposes, live specimens as well as preserved ones were observed. The samples of river and reservoir were preserved in Lugol's iodine solution (about 1 ml. added to a 100 ml. sample) in bottles with tight fitting lids. A distinct yellowing of the sample is generally an indication that the correct amount of preservatives has been added. Excessive amount was avoided as it will discolour and deform the plankton algae to an extent that identification is impossible. The absorption of iodine from the Lugol's solution by the cells also promotes settling when the sedimentation-inverted microscope technique, is used. To determine

phytoplankton biomass by calculation of the total volume of the various species it is necessary for sedimentation in a counting chambers (Utermöhl,1925;1931;1958) of different sizes.The literature gives varying lenghts of time necessary for sedimentation in a counting chambers.Lund,Kipling and Le Cren (1958) recommend 18 hours for a 100 ml.chamber,3 hours for 10 ml.and 1 hour for 1 ml. chamber.Javornicky (1958) considers that 20 minutes to $1\frac{1}{2}$ hours sufficient for a 1 ml. chamber and that several hours,preferably overnight,are needed for counting chambers.

In the present study,an appropriate sub-sample, usually between 1 to 2 ml.,was placed in a split-tube sedimentation chamber (Evans,1972) and the contents allowed to sediment out for one hour.

Phytoplankton counts were made using an inverted microscope (Utermöhl,1931;Lund,Kipling and Le Cren,1958).The phytoplankton were counted in the microscope at different magnifications,dependent upon their size.Larger forms were counted under low magnification,while high magnification was used for small forms.

Detailed analyses of phytoplankton population requires determination of number and volume of each species. Phytoplankton consist of individual cells,filaments and colonies.Although phytoplankton analyses using the counting method are very time consuming,especially in the case of many multicellular colonies.It is however a reliable method.In

this study the number of cells of phytoplankton were counted. For colonial species,determination of the average number of cells per colony were made.The number of cells per colony can vary spatially within lakes and seasonally with changes in the population vigour of a species.

Cell numbers often do not represent true biomass because of considerable variation in sizes of cells among algal species.This disparity can be dealt with by multiplying the number of cells of a given species by its average cell volume and then summing these volumes over all species.Cell volume is estimated from knowledge of mean cell dimensions and correspondence of cellular shape to geometric solids or combinations of simple solids spheres,cones,truncated cones, cylinders,etc.(Sicko-Goad et al.,1977;Nauwerck,1963; Vollenweider,1969).

For taxonomic purposes and the identification of phytoplankton species,reference was made using various taxonomic works.A survey of the phytoplankton of the inland waters of the world has been undertaken by Huber-Pestalozzi (1938,1942,1950,1955 and 1968) but much of this is a collation of the work of other authors,reference have been obtained from these books.Useful illustrations and information concerning phytoplankton populations have been obtained from Hustedt (1927-1937;1967),Bellinger (1980) and the microfiche edition of the Fritsch Collection available in the Botany Department,Royal Holloway and Bedford New Colleges.

Among the earlier works the various volumes of the Süswasserflora Deutschlands,Hustedt's Kieselalgen,Geitler's Cyanophyceae etc.in the Rabenhorst series are useful.The second edition of Ward and Whipple's Freshwater Biology (Edmonson,1959) gives concise keys to the North American genera and species of phytoplankton populations.

Details concerning the phytoplankton can be found in various general texts including Morris (1967;1980),Round (1973;1981),Chapman and Chapman (1973),Wynne and Bold (1978). Ultrastructural features are reviewed by Dodge (1973).The classical work of Fritsch (1935) is still an essential guide to earlier knowledge for English readers.A thorough grounding in classical phytoplanktology is best obtained from Hutchinson's classic treatise (1967).The ecology of phytoplankton are reviewed by Reynolds (1984) and Harris (1986) recently.Hartley (1986) has published a check list of the freshwater,brackish and marine diatoms of the British Isles and adjoining coastal waters.

2.7 CULTURE TECHNIQUES

2.7.1 CHEMICALS

The media were prepared from 'Analar' chemicals containing known maximum amounts of impurities.Accurate analytical procedures were followed when weighing small quantities of reagents.

2.7.2 AGAR

Agar is a neutral polymer of galactose which has low viscosity in water solution,a sharp,stable gelling temperature and a strong gel structure.It has a melting point about 95°C and solidifies about 45°C.During this study agar (manufactured by DIFCO Laboratory) was routinely used to solidify growth media.As a general rule it is unsafe to autoclave agar in media with very acid pH (Stein,1973). Huttner et al.,(1966) suggested that a slight hydrolysis of the agar liberate acid which accelerates further hydrolysis and liberation of additional acid.Therefore agar and growth media were autoclaved separately and they were mixed aseptically while hot.Agar was generally used at concentrations of 2%.Petri dishes (sterile) were poured when the temperature of the medium was about 50°C (warm to the inside wrist) to avoid condensation.

2.7.3 GLASSWARE

Only Pyrex glassware was used.To prevent contamination of media during sterilization,glassware was washed or cleaned as follows: detergent (Teepol) washing in tap water,rinsed in tap water,three rinses in glass distilled water.Glassware which failed to respond to the detergent cleaning was soaked in concentrated sulphuric acid (H_2SO_4) saturated with $NaNO_3$ followed by thorough rinsing with distilled water.Then the glassware was autoclaved.

2.7.4 WATER

Glass-distilled water was used during this study.

2.7.5 SOIL

Garden soil was used to prepare soil extract media. Pringsheim (1946) suggested that soil should not have a high humus content and should not have had commercial fertilizers added recently.

2.7.6 MEDIA

Media were prepared from pre-mixed stock solutions. Aliquots from these stocks were measured and added to a given

volume of water. Improper procedure may result in precipitation of one or more of the components of the medium especially nitrates and phosphates (Stein, 1973) or a failure of some of the constituents to go into solution.

Chu 10 (Chu, 1942) medium was used during this study:

	($g\ l^{-1}$)
$Ca(NO_3)_2$	0.04
K_2HPO_4	0.01
$MgSO_4 \cdot 7H_2O$	0.025
Na_2CO_3	0.02
Na_2SiO_3	0.025
$FeCl_3$	0.008 mg l^{-1}

This medium was chosen because during preliminary investigations, the best growth was found in Chu 10 medium compared to other culture media which have been studied (e.g. Rodhe VIII).

2.7.7 ISOLATION

The isolation of a single algal unit (unicell, colony, filament) into medium suitable for growth is required to establish a unialgal culture.

2.7.7.1 STERILE PASTEUR-TYPE PIPETTE TECHNIQUE

Cultures were set up in sterile conditions by the

pipetting and washing method of Pringsheim (1946).A sterile Pasteur-type pipette with a rubber bulb on the wide end was held by a forcep at the narrow end so that part of the pipette is in a low or pilot flame of a burner.As the glass softens and reddens,gently and with a smooth lenghtwise pulling action,the pipette was removed from the flame.Sudden jerking and/or pulling while the pipette is in the flame does not result in a capillary pipette.The tip of the capillary pipette was broken off near point where the glass bends under its own weight.The bore of the pipette should be several times (ca.75-150 µm) the diameter of the algal units being isolated.

By means of a microscope,the alga selected from the mixture using the capillary pipette and placed in a drop of culture medium on a slide.The alga was transferred in this manner through a series of washes in the sterile culture medium to ensure removal of particles on the surface.Care had to be taken not to damage the cells.Finally,the alga was transferred to a culture flask,plugged with cotton wool and placed in a growth cabinet.

2.7.7.2 STREAK PLATING

When algal units are 10 µm or less in diameter they are isolated more easily by streak plating.Petri dishes containing growth medium solidified with 2% agar medium were

prepared.The agar should be $\frac{1}{2}$-$\frac{2}{3}$ the depth of the dish.Plastic sterile petri dishes were used.One to two drops of phytoplankton samples were placed near the periphery of the agar and parallel streak of the suspension were make on the agar using a sterilized wire loop.The petri dishes were covered,inverted and incubated for 4 to 8 days under suitable growth conditions in the incubator (relative light intensity about 26 Wm^{-2} total radiation;12hr.light:12hr.dark and temperature at 18 ± 1°C.The desire species that were free of other organisms were observed and selected under a microscope for further isolation.A sample was removed using a fine capillary pipette and placed in a drop of sterile culture medium on a cover glass.Using the high power objective ($\frac{1}{6}$th.inch.=4 mm.) of the microscope,the desired species that had been isolated was observed.The streaking procedure was repeated and this second streaking reduced the possibility of bacterial contamination and of colonies originating from more than one algal unit.Algal units from a desired colony were transferred to liquid or agar medium.

2.7.8 CULTURE METHODS

Media were dispensed in amounts of 10 ml.per test tubes or 50 ml.per 100 ml.,150 ml.per 300 ml.,and 2000 ml.per 5000 ml.flasks with cotton plugs,and sterilized by autoclaving (120°C) for 20 minutes.

Light was provided by cool-white fluorescent lamps which maintained a relative light intensity of about 26 Wm^{-2} total radiation at the surface of the culture vessels. The incubator was usually maintained at $18\pm1°C$. However, light intensity and temperature were changed according to the purpose of the experiment. In this investigation batch cultures were employed.

Phytoplankton for nutritional studies was first precultured until it reached the exponential growth phase. To minimize carry over from the old media, the algal were washed three times with glass-distilled water.

Growth was measured by Calculated Algal Volumes and cell numbers using an inverted microscope and Coulter Counter (Model ZB).

Growth rates were calculated from cell counts taken on days 0, 7, 14 and 21 from (Hoogenhout and Amesz, 1965):

$$k(day^{-1}) = \frac{\ln N_2 - \ln N_1}{t_2 - t_1}$$ where,

N_1 and N_2 = cell numbers of phytoplankton and

t_1 and t_2 are culture time in days.

All experimental results were the average of either two or four replicate culture flasks from at least two separate experiments.

Other experimental methods will be mentioned in detail in the material and methods of each chapter.

CHAPTER THREE

THE INFLUENCE OF NUTRIENTS ON THE GROWTH OF PHYTOPLANKTON POPULATIONS

3.1 INTRODUCTION

In addition to carbon, hydrogen and oxygen, algae require some 13-15 additional elements to grow and reproduce. About 20 elements may comprise the substance of algae (and all other plants), either as compounds of varying complexity or as ions maintained within the protoplast. Of the 20 elements, about 11 that is, C, O, H, N, P, S, K, Mg, Ca, Na and Cl which each typically constitute $\geq 0.1\%$ of the ash-free dry weight and referred to as macronutrients. The remainder (micronutrients), which include Fe, Mn, Zn, B, Si, Mo, V and Co, are required to be present in traces (often $\leq 0.1\%$ by weight) but are no less essential to the functioning of the healthy cell. For members of the Chrysophyta and of diatoms, in particular, Si(silicon) is a major components of the cell wall and hence, occupies the role of a micronutrient (Reynolds, 1984).

Most of these nutrients are usually present in sufficient amounts, relative to the requirements, so as not to be potential limiting factors for growth. However, the

concentrations of nitrogen and phosphorus are often low enough to limit phytoplankton growth in surface waters. Phosphorus limitation is more common in lakes whereas nitrogen limitation is more common in the sea.Silicon concentrations can be low enough to limit diatom growth in both freshwater and marine systems (Darley,1982).

Various nutrients must be obtained from the external medium (by a process termed 'uptake',and almost always in the chemical forms in which they naturally occur, before they can be assembled into the structures of the living cell.Many are assumed to be in solution as relatively simple inorganic compounds or ions.Uptake by autotrophic organisms is limited to sources which are both soluble and diffusible,so that they may pass through the semi-permeable membrane or plasmalemma;many soluble complexes and insoluble (particulate) polymers are unavailable.Heterotrophs are not restricted,although absorption and final assimilation into the cell still requires that such substances are first broken down by enzymatic digestion.

The variations in the chemical composition of natural waters are important in regulating the abundance, composition and the geographical and periodic distribution of phytoplankton and this was recognized by early investigators. Pearsall (1930,1932) carried out a series of field studies on the composition of the phytoplankton in relation to dissolved substances in lakes in North West England.He concluded that:

diatoms increased when the water was richest in dissolved silica;that development of Chrysophytes (especially Dinobryon) was favoured at low silica levels and high ratios of nitrogen to phosphorus;that desmids were associated with waters of low calcium content and a low nitrogen/phosphorus ratio and that the abundance of Cyanobacteria (Cyanophyceae) was correlated with the concentration of albuminoid nitrogen (organic nitrogen).Pearsall's work stimulated a great deal of research throughout the world on the link between phytoplankton and water chemistry or nutrients.

Culture studies are required to attempt to establish the absolute nutrient requirements for each phytoplankton species.Some particularly successful culture media resemble many natural waters in their major ionic composition (Chu,1942,1943,1949;Rodhe,1948;Provasoli and Pintner,1953).

Concentration requirements established in cultures for nutrients particularly nitrate and phosphate,are often much greater than those known to permit growth in nature.This feature has been related to the generally larger volumes of natural media (Gerloff and Skoog,1954;Provasoli,1958),but for many of the more evenly distributed populations of phytoplankton this seems implausible.The comparatively high cell densities and rapid growth rates usual in cultures may be partly responsible.Evidence of nutrient requirement in specific natural populations is provided by correlations

between algal growth and water chemistry, estimates of the quantities of nutrients removed by the crop (e.g. Gardiner, 1941; Lund, 1950; Hughes and Lund, 1962; Fay et al., 1968; Donaghay et al., 1978; Eppley, 1981; Dring et al., 1982; Ahlgren, 1985), comparisons of the chemical composition of naturally grown cells with that known to develop in cultures under limiting conditions (e.g. Mackereth, 1953; Gerloff and Skoog, 1954, 1957b; Healey, 1973; Tilman and Kilham, 1976; Kilham, 1978; Olsen and Paasche, 1986) and enrichment experiments (e.g. Strom, 1933; Potash, 1956; Fish, 1956; Gerloff and Skoog, 1957b; Goldman, 1977; Lynch and Shapiro, 1981; Goldman, 1983). In planktonic blue-green algae, gas vacuoles function in a buoyancy regulating mechanism. There are two leading hypotheses on buoyancy regulation in these algae; and they have different implications with respect to limiting nutrients. In one proposed mechanism, algal growth rate is the main determinant of relative gas vacuole volume, the two varying inversely (Reynolds, 1972); in the other (Walsby, 1971) relative gas vacuole volume is a function of cell turgor pressure in that weaker gas vacuole subunits collapse as cell turgor increases. Whereas the turgor-collapse hypothesis allows for positive effects on gas vacuolation in that higher levels of limiting nutrients (other than Carbon) may lower the concentration of osmotically active photosynthate molecules, such increases in limiting nutrients could have a negative effect on buoyancy according to the growth rate hypothesis.

3.2 CULTURE STUDIES OF SELECTED ALGAE

The distribution and variations in abundance of the phytoplankton are as yet difficult to account for except in vague and general terms.More extensive and detailed observations of phytoplankton populations and environmental factors in natural waters will contribute greatly to our understanding of what is taking place.However,studies in laboratory with cultures of phytoplankton algae under controlled conditions also have a very important role to play.The experimental use of algal cultures offers an excellent method for attempting to solve problems concerning algae as well as the interplay between biota and environmental factors in natural and disturbed waters (Rodhe, 1978).As in ecology generally,full understanding of the growth of organisms in their natural habitats will be achieved only by the synthesis of the results of physiological and biochemical investigations and the results of field studies (Fogg,1965).

There has been increasing international attention directed toward the problem of eutrophication in recent years. Eutrophication includes the enrichment of water by plant nutrients.It is a natural process in the ageing of lakes and impounded waters.The consequences of the increased nutrient supply depend on a whole complex of factors

determining the manner of organic production in a given ecosystem: the morphometrical features of the water body, mixing of water masses, temperature, light, the species composition of the plankton and benthic producers, participation of primary and secondary consumers, the time factors etc.

We should study and measure not only the actual manifestation of eutrophication, but also the potential basis for its materialization. The most natural way to this purpose is the testing of water by algal assays or bioassays.

Bioassay is a technique for determining the potential fertility of water without, in the first place, necessarily knowing or assuming what controls it (Schreiber, 1927; Ström, 1933; Lund, 1970). In its simplest form, algal bioassay consists of the addition of a given species, the so-called test alga, or of two or more test algae, to a series of waters which are then exposed to constant conditions of light and temperature for a given time. The growth of the test alga in the water samples is a measure of the relative potential fertilities of these waters. Alternatively, water samples can be compared without removing the algae in them. In this case, herbivorous animals or parasites of algae may also be present. Since waters may support the growth of one kind of alga but not of another, the use of different kinds of algae, such as a green alga, a blue-green alga and a diatom, can also give

information about the potential qualitative as well as quantitative fertilities of waters.Bioassay can also be used to determine the growth of algae in natural waters to which certain nutrients or conditioning factors are added or from which they have been removed.The tests can also be carried out under varied physical conditions.

The factors which determine the growth of phytoplankton populations in nature are so numerous and complex that they can only be elucidated by a combination of observations on natural populations and extensive experimentation.It is not suggested that bioassay alone can solve ecological problems.Nevertheless it is a valuable technique,the full potential of which has not yet been fully realized.

Algal culturing can principally be divided into three different types:

(i) Batch cultures,

(ii) Chemostat cultures and

(iii) Dialyse cultures.

The first one was used in these studies because it is more convenient and appropriate.

Batch cultivation is a cultivation of single-species or mixed algal populations suspended or dispersed in aqueous medium usually.It is an open system into which both energy and material enter and where they are transformed and accumulated according to their biological possibilities.

Simultaneously the unused part of the energy and material is released into the surroundings of the system.

Batch cultivation is the fundamental,simple and the oldest type of cultivation of algal populations.With the development of technical refinements and the appearance of new applications,this type of cultivation has undergone various useful modifications.

It was first used for long term maintenance of single species populations,for yields of greater amounts of material in examination of specific taxonomical, cytomorphological and generally biological problems,or for simple physiological experiments.Later on,it became part of the methodology of studying life cycles of algae,stability and variability of algal strains,interaction of physical and chemical factors related to population growth,uptake and accumulation of nutrition,trace and radioactive elements.Due to its relatively smaller technical requirements it became the basis of most mass cultivation of algae,or rather of the periods between the particular technological interferences with their development (separation of algal mass,supply of nutrients).It also can be used for simulating natural eco-systems in studies of phytoplankton dynamics in stagnant waters with a large retention time (in ponds,lakes,reservoirs or in running waters) when horizontal mixing is neglected.

Batch cultivation certainly represents one of the fundamental organization models of the algae-water system.For

assays of the trophic potential which set out to provide information on the reserves of biologically utilizable nutrients,batch cultivation is the only rational method to be used.

3.2.1 HISTORICAL DEVELOPMENT OF THE CULTURE MEDIA

The earliest attempts to culture algae started about a century ago with solutions of a few inorganic salts, actually devised for studies of vascular plants.The first culture solution specifically designed for algae was the medium of Beijerinck from 1898 and it has long been in use at various dilutions and often with addition of trace elements (Stein,1973).Beijerinck (1890) was also the first to achieve pure cultures of algae.E.G.Pringsheim,the famous pioneer in the art of culturing algae realized that many algae do not thrive on inorganic salts alone,but can be cultured if a small amount of soil extract is added to the medium. Pringsheim (1946,1950) introduced biphasic soil-water technique which was close to mother earth.This technique primarily intended to keep algae in a kind of quarantine while acceptable monophasic media are being prepared for them and it also can serve manifold purposes where an indefinable medium can be permitted.

The first investigator who purposely tried and succeeded to cultivate freshwater plankton algae in

Table 3.1 MAJOR COMPOSITION, IN mg l^{-1}, OF ALGAL CULTURE MEDIA AND STANDARD LAKE WATER*

	BEIJERINCK	CHU 10	RODHE VIII	PROVASOLI & PINTNER	LAKE WATER
CATIONS					
Ca	27.3	9.8	14.7	13.0	16.7
Mg	19.7	2.5	1.0	2.0	2.8
Na	-	18.1	7.5	14.8	4.7
K	89.8	4.5	2.2	9.2	1.8
NH_4	112.7	-	-	-	-
Others	-	0.3	0.2	19.7	-
ANIONS					
Cl	48.2	0.5	-	49.1	4.7
SO_4	77.9	9.7	4.0	7.8	10.1
CO_3 or HCO_3	-	11.3	-	-	59.2
NO_3	387.3	30.2	45.3	14.6	-
HPO_4 or H_2PO_4	110.2	5.5	2.8	10.0	-
SiO_3	-	15.6	12.5	-	-
Others	-	-	1.8	32.5	-
	873.1	108.0	92.0	172.7	100.0

* (From: RODHE, 1949)

completely synthetic and bacteria free solutions was Chu (1942,1943).His comprehensive paper on the influence of mineral composition on the growth of several planktonic algae in unialgal cultures opened the gate for experiments with clearly defined solutions adapted to the needs of the algae. He started with media that were similar to natural waters in their composition and concentration of dissolved chemicals and his final recipes were based on the nutritional demands on the algae concerned,as evidenced by numerous growth tests with gradually changed concentrations of the constituents in the solution.His highly successful medium No.10 which is comparable in composition and degree of dilution to the water of eutrophic lake was used during this studies (Table 3.1, Rodhe,1949).

A few years after Chu,Rodhe (1948) continued culture investigations of freshwater phytoplankton and his culture solution VIII is rather similar to Chu 10,although based on growth experiments with algae not used by Chu.

Since that time many investigators have been involved in creating new recipes for media and there are perhaps as many media and modifications as there are active phycologists today.Each investigator generally employs his or her own particular medium for successful cultivation of freshwater algae.The media that have been successful for growing of algae are Beijerinck (Stein,1966);Bold Basal (also known as Bristol solution;Nichols and Bold,1965);Bozniak

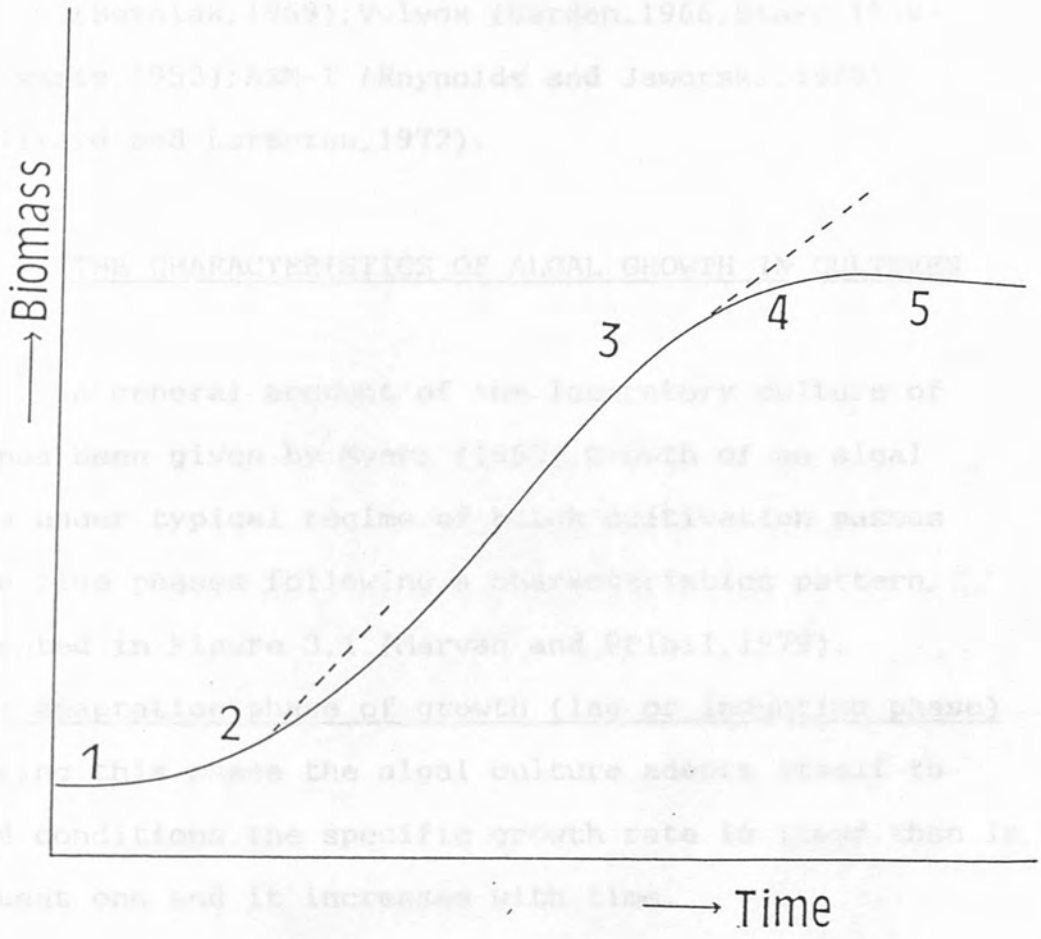


Figure 3.1 THE IDEAL PROGRESS OF THE ALGAL GROWTH IN A BATCH CULTURE

(FROM: MARVAN AND PŘIBIL, 1979)

Community (Bozniak,1969);Volvox (Darden,1966;Starr,1969), Waris (Waris,1953);ASM-1 (Reynolds and Jaworski,1978); WC (Guillard and Lorenzen,1972).

3.2.2 THE CHARACTERISTICS OF ALGAL GROWTH IN CULTURES

A general account of the laboratory culture of algae has been given by Myers (1962).Growth of an algal culture under typical regime of batch cultivation passes through five phases following a characteristics pattern, represented in Figure 3.1 (Marvan and Přibil,1979):

(1) The adaptation phase of growth (lag or induction phase)

During this phase the algal culture adapts itself to altered conditions,the specific growth rate is lower than in subsequent one and it increases with time.

(2) The exponential phase of growth

By now the algal culture has adapted itself to the given cultivation conditions.The light intensity is not limiting,mutual screening of cells (coenobia) is negligible. Changes in the concentration of the individual nutrients caused by the uptake by cells are so small (and,moreover,lie in the range of high concentrations) that their effect on culture growth is not significant.The specific growth rate (μ) of a culture during exponential phase of growth is constant.In cultures with a low nutrient content (e.g.when

testing the trophic potential of natural waters) the duration of the exponential phase may be greatly reduced (one day or less).The same holds for cultures with a higher initial concentration of algal biomass.

(3) The linear phase of growth

If the culture has enough nutrients,the algal cells may multiply after a certain time to such extent that they begin to screen one another and gradually an almost complete absorption of incident light may ensue.Hence the amount of light absorbed by a cell decreases and the specific growth rate reduced.This limitation becomes apparent in a linear rather than an exponential increase in biomass.

(4) The phase of decreasing growth rate

As the culture thickens the light supply per cell decreases and respiration plays an increasing role.Oxidative breakdown of the synthesized substance (respiration,etc.) begins to reduce the constant increment.The growth curve approaches asymptotically a certain limiting value which may be described as the maximum attainable concentration of algal biomass.

(5) The stationary phase

Maximum concentration of the algal biomass under given cultivation conditions represents attainment of equilibrium

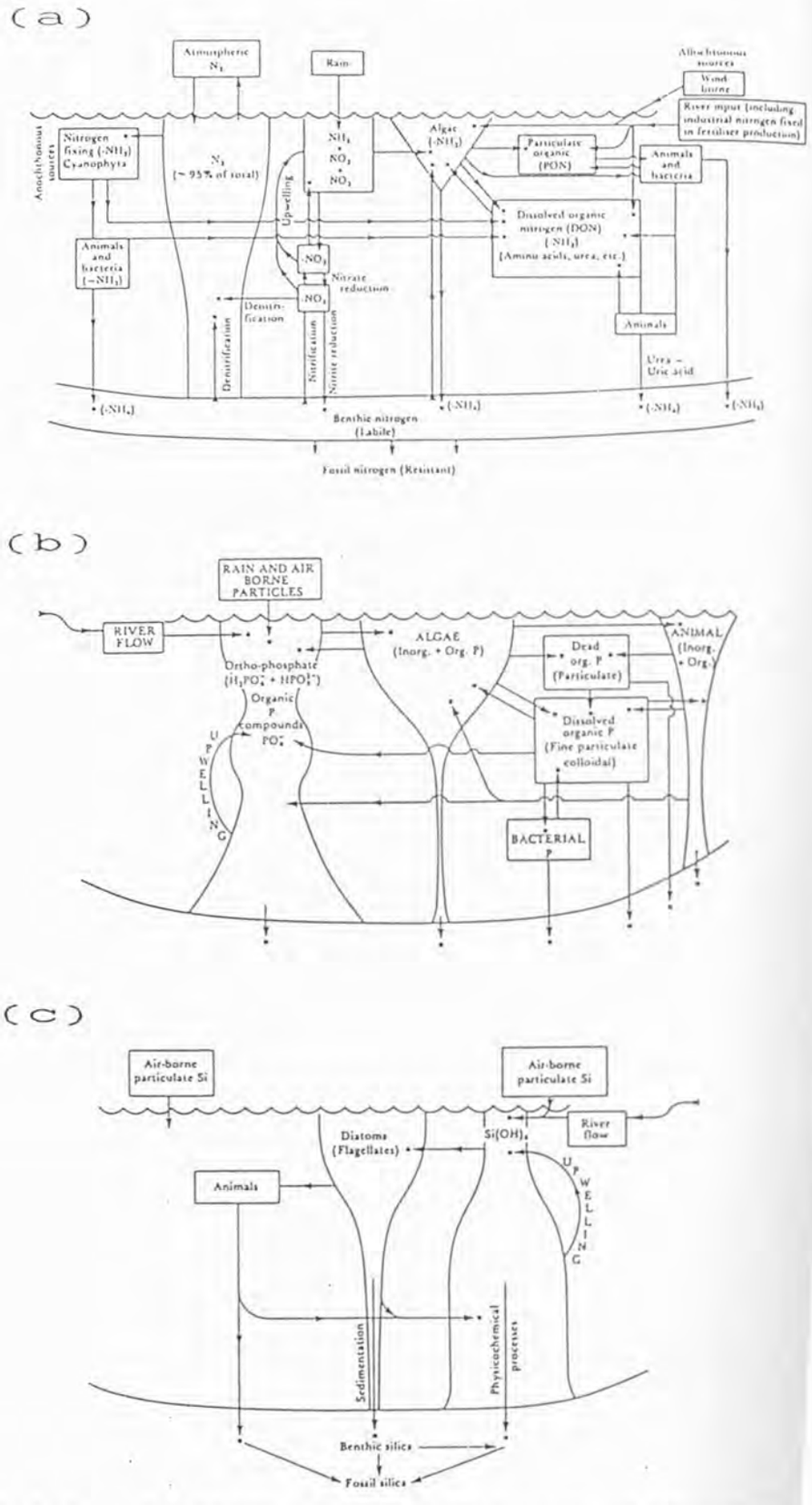


Figure 3.2. Diagrams of the (a)Nitrogen; (b)Phosphorus and (c)Silicon cycles.

(From: Round, 1981)

between photosynthesis and respiration, i.e. the onset of the stationary phase.

3.3 NITROGEN

Nitrogen in the aqueous environment has been the subject of many reviews and most often, however, the emphasis has been on either the distribution of nitrogenous nutrients in natural waters or the physiology of algae. The comprehensive nature of many such reviews (Vaccaro, 1965; Painter, 1970; Brezonik, 1972; Fogg, 1973; Morris, 1974) and others which have treated both nutrient cycles (Dugdale, 1976) and eutrophication (Goering, 1972; Hutchinson, 1973) simplifies the task of addressing the ecological dimension of phytoplankton nitrogenous nutrition.

A major source of nitrogen of the biosphere originates from fixation of atmospheric molecular nitrogen. The nitrogen cycle is a biochemical process in which concentration of molecular nitrogen occurs by nitrogen fixation, assimilation and denitrification in which nitrate is reduced to N_2.

Nitrogen is utilized by algae in the form of nitrogen, ammonium ions, nitrite ions, nitrate ions and various organic compounds. Figure 3.2a (Round, 1981) shows how nitrogen is cycled through algae and that in general nitrogen compounds only move through the biochemical cycle.

The principle requirement of algae for nitrogen is in the synthesis of amino acids and proteins,wherein it constitutes about one-eighth to one-sixth by weight;the minimum nitrogen content of cells is about three to four per cent of dry weight (Reynolds,1984).Certain Cyanophyceae are also able to fix atmospheric nitrogen dissolved in the water. For example,Aphanizomenon,Anabaena,Gleotrichia,Nodularia and Nostoc dominate nitrogen fixation in lakes and streams (Horne,1977).

3.4 PHOSPHORUS

Phosphorus plays a significant role in most cellular processes,especially those involved in generating and transforming metabolic energy.As a compound of nucleic acids and of adenosine triphosphate (the basis of enzyme synthesis and intracellular energy transfer systems), phosphorus is essential to the function and growth of all plants including phytoplankton.In water,phosphorus usually occurs in the oxidized state,either as inorganic ortho-phosphate ions (HPO_4^{2-} ,$H_2PO_4^-$) or in organic largely biogenic compounds.Dissolved phosphate are derived from weathering of phosphatic minerals (e.g.apatite) present in catchment soils and are generally present in aqueous concentrations within the range 0.1-1000 $\mu g\ P\ l^{-1}$.Real progress in the study of the phosphorus cycle of inland waters was not made until Atkins

(1923) introduced into oceanography and limnology the colorimetric method for the determination of phosphate elaborated by Deniges (1920).It soon became evident that more phosphorus was usually present in inland waters than could be determined as phosphate ions.

Dissolved orthophosphate is evidently the major source of phosphorus for phytoplankton and it is taken up rapidly by phosphorus deficient cells until very low concentrations (1 μg P l^{-1}) remain in the water (Rigler, 1966).

The phosphorus cycle is illustrated in Figure 3.2b; the element is present in algal cells in relatively small amounts but it is even less abundant in the primary drainage sources and therefore is the element most likely to limit freshwater algal production and it certainly does so in many lakes (Schindler,1977;Schindler et al.,1978),but not so often in the sea where the limiting value (often quoted as about 0.40-0.55 μg at.l^{-1}) is usually not reached before nitrate or silicate limitation occurs.

3.5 SILICON

All phytoplankton have a requirement for the small amounts of silicon involved in protein and carbohydrate synthesis.Among the Chrysophytes genera and among the diatoms in particular,the requirement becomes ecologically important.

The siliceous frustules constitute the basic structural unit of the wall in the diatoms. In Chrysomonads the silica is incorporated into the delicate scales that clothe the cell. In either case, the completed structure is unique to that species. In addition to the silicon requirement for cell-wall formation, diatoms require small amounts of silicon for net DNA synthesis, an unusual requirement which resides in the translation step in the synthesis of DNA polymerase. The adaptive significance of the latter silicon requirement is not clear (Darley, 1982).

Silicon is an essential element for diatom growth (Lewin, 1955) and its concentrations have frequently been described as playing an important role in limiting natural populations (Paasche, 1980). Although the mechanism by which diatoms take up silicate in culture has been extensively studied by various groups of workers (Swale, 1963; Darley, 1974; Werner, 1977; Paasche, 1980; Paasche and Olsen, 1986) relatively few species have been studied and there are still considerable gaps in our knowledge, especially with regard to the responses of different ecological groups, and the differences between freshwater and marine forms.

Growing diatoms obtain their silicon from dissolved $Si(OH)_4$ (orthosilicic acid). Silicon is present in solution in natural waters in the form of monomeric orthosilicic acid, $Si(OH)_4$, virtually all of it undissociated except in extremely alkaline waters (Stumm and Morgan, 1970).

The silica valve is the basic wall structure in all diatoms.Owing to the peculiar mode of cell division in these algae,the formation of new valves is restricted to the period just after nuclear division and cytoplasmic separation.This is also the stage in the cell cycle when most of the $Si(OH)_4$ uptake from the medium takes place.The time needed by the cell to complete the various parts of the silica wall can be stated quite accurately.The formation of the valve face and valve mantle may require 10 to 20 minutes,depending on the species (Reimann,1960).Spines and similar projections from the valve,which may contribute significantly to the total silica content in many planktonic diatoms,usually need 1 to 2 hours (von Stosch and Drebes,1964;Eppley et al.,1967; von Stosch et al.,1973).In diatoms with a long pervalvar axis,further deposition of silica may take place during the formation of girdle bands in connection with cell elongation (von Stosch,1975).This is usually a slow process compared with valve formation.Completion of the entire cell cycle in planktonic diatoms may require 10 to 20 hours under optimal conditions and the morphological observations indicate that the bulk of silica is deposited during one-tenth of the cycle.

The silica cycle illustrates the nearly one-way flow of this element from rocks in the watershed to the lake sediments (Figure 3.2c).The cycle is very different from the cycles of nitrogen,phosphorus,iron or other nutrients where plant and animal cells take up and excrete large amounts in

various forms.There are only two major sources of silica in lakes,from inflows and from below the photic zone.Generally animal recycling of silica is generally believed to be unimportant in lake waters,but some release of silica occurs from anoxic sediments.According to Nelson et al.,(1976) certain diatoms release up to 15% of the silica they take up.

3.6 MATERIALS AND METHODS

Investigations of seasonal occurrence of phytoplankton populations in relation to nutrient concentrations (i.e.nitrate-nitrogen,phosphate-phosphorus and silica) in natural waters (i.e.River Thames and Wraysbury Reservoir) were carried out during 1984 to 1986.The methods are described in Chapter Two.

All phytoplankton populations used in the studies on their growth in culture were derived from cultures,originally started from a single cell,colony or filament.The phytoplankton were isolated from fresh plankton samples collected from the River Thames and the Wraysbury Reservoir (refer Chapter Two).

Stock cultures were grown in Chu 10 medium,and 50 ml of this,contained in a 250 ml Pyrex conical flask were maintained in the growth phase at temperature of 18 ± 1°C using a light-dark regime of 12 hours of light and 12 hours of darkness.A light-dark cycle is recommended as being a more

natural condition than constant light.Many diatom species will not grow well under conditions of constant light, especially if they are nutrient limited.Stock cultures were subcultured monthly and used as an inoculum for the culture experiments.

Modified Chu 10 media with varying nutrients concentrations were inoculated with each of the test organisms.The nitrogen concentrations varying from 0 to 28 mg l^{-1} NO_3-N with $Ca(NO_3)_2$ as the source of nitrogen.The range of phosphate-phosphorus concentrations varied from 0 to 2 mg l^{-1} PO_4-P,with K_2HPO_4 as the source of phosphorus.The range of silica concentrations varied from 0 to 30 mg l^{-1} with Na_2SiO_3 as the source of silica in Chu 10 medium.The range of concentrations were selected as it is similar to or include to that found in the River Thames and the Wraysbury Reservoir.

All the flasks for each experiment were duplicated and kept in culture incubator under conditions as described for stock cultures (see Chapter Two).

Growth rates were derived from measurements to determine Calculated Algal Volumes and from cell numbers.An inverted microscope and a Coulter Counter (Model ZB) were used throughout.

All experimental results reported represent means of four replicate culture flasks from two separate experiments.

Table 3.2 CONCENTRATION OF INORGANIC NITROGEN ($\mu g\ l^{-1}$) IN THE SURFACE WATERS OF VARIOUS LAKES AND RIVERS

Note the very wide range of total inorganic nitrogen (NO_3+NH_4)available for plant growth. Values less than 100 $\mu g\ l^{-1}$ may limit growth, while levels above 400 would not. Both eutrophic and oligotrophic lakes may have very low or very high levels of total inorganic nitrogen.

Lake or river	Relative trophic state and mixing type	NO_3-N*		NH_4-N*		References!
		Summer	Winter	Summer	Winter	
Tahoe, Calif.	Oligotrophic monomictic	4	μ-25	<2		1
Castle, Calif.	Mesotrophic dimictic	<5	10-50	<5	10-50	2
Clear, Calif.	Eutrophic polymictic	μ-100	400-600	μ-300	μ-20	3
Superior	Oligotrophic monomictic	~230	~280	<10		4
Windermere	Mesotrophic monomictic	100-200	300-400	~10		5
Esthwaite Water	Eutrophic monomictic	μ-100	400-500	~30		6
George, Uganda	Eutrophic polymictic	μ		<10		7
Baikal, U.S.S.R.	Oligotrophic dimictic	0-20	45-80	μ		8
Titicaca, Andes	Mesotrophic monomictic	40-110	100-200	μ		9
Cayuga, N.Y.	Eutrophic monomictic	50-180	~800	100-300	~80	10
Uganda Rivers (annual mean)		530		24		11
Truckee River at km 3	...	20	...	<10		12
Hubbard Brook	...	440	2500	40		13

μ - undetectable, generally 10 $\mu g\ l^{-1}$.

! References: (1,2) Goldman, various sources; (3) Horne and Goldman, 1972; (4) Dobson et al., 1974; (5,6) Heron, 1961; Horne and Fogg, 1970; (7) Viner, 1969; (8) Kozhov, 1963; (9) Richerson et al., 1977; (10) Oglesby, 1978; (11) Viner and Smith, 1973; (12) Mc Laren, 1977; (13) Likens et al., 1977. (From: Goldman and Horne, 1983).

3.7 RESULTS AND DISCUSSIONS

3.7.1 THE INFLUENCE OF NITROGEN ON THE GROWTH OF PHYTOPLANKTON POPULATIONS

3.7.1.1 GROWTH IN NATURE

The concentration of most nitrogen compounds in lakes and streams tend to follow regular seasonal patterns. Biological uptake lowers concentrations in spring and summer in the photic zone.During the autumn and winter,releases from sediments,tributary inflows,precipitation and replenishment from the hypolimnion increase the nitrate and sometimes the ammonia concentrations (Goldman and Horne,1983).Nitrate is the most highly oxidized form of nitrogen and is usually the most abundant form of combined inorganic nitrogen in lakes and streams (Table 3.2;Goldman and Horne,1983).

The seasonal fluctuations of nitrate was observed in the River Thames and the Wraysbury Reservoir (Figures 3.3 a and b).Spring and summer minima have been observed which gradually increase in late autumn to maxima in winter.This study showed that high levels of nitrates are maintained in the River Thames and the Wraysbury Reservoir.The range of concentration of nitrate-nitrogen during 1984 to 1986 were 1.3 to 13.2 mg l^{-1} in the River Thames and 0.98 to 7.6 mg l^{-1} in the Wraysbury Reservoir.The seasonal distribution

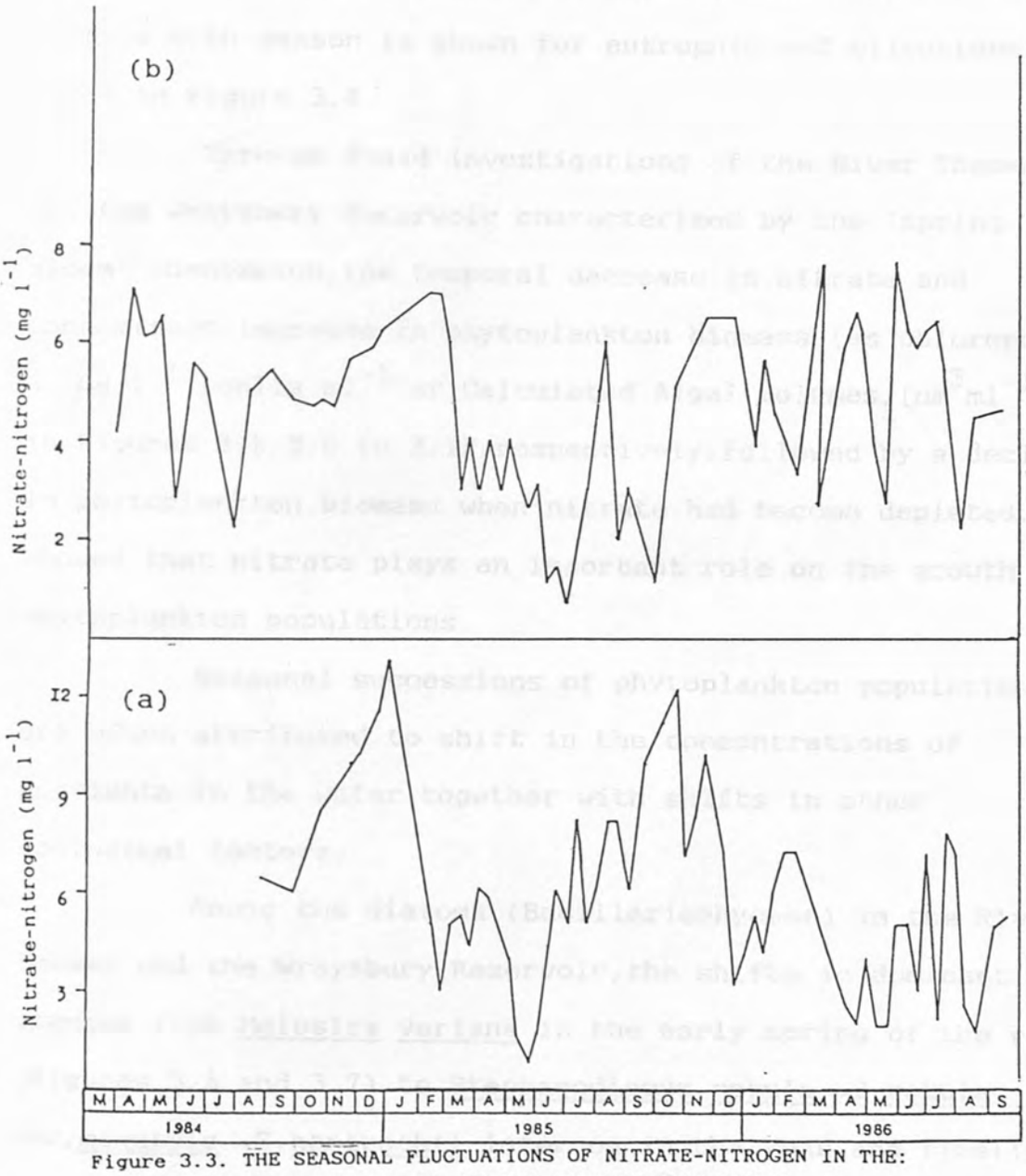


Figure 3.3. THE SEASONAL FLUCTUATIONS OF NITRATE-NITROGEN IN THE:
(a) RIVER THAMES, AND (b) WRAYSBURY RESERVOIR

of nitrogen in the River Thames and the Wraysbury Reservoir is similar to that commonly found in numerous lakes of temperate regions.The changes in overall concentrations of nitrate with season is shown for eutrophic and oligotrophic lakes in Figure 3.4.

Through field investigations of the River Thames and the Wraysbury Reservoir characterized by the 'spring bloom' phenomenon,the temporal decrease in nitrate and concomitant increase in phytoplankton biomass (as chlorophyll a ($\mu g\ l^{-1}$);cells ml^{-1} or Calculated Algal Volumes,($\mu m^3 ml^{-1}$)) in Figures 3.5,3.6 to 3.12,respectively;followed by a decline in phytoplankton biomass when nitrate had become depleted, showed that nitrate plays an important role on the growth of phytoplankton populations.

Seasonal successions of phytoplankton populations are often attributed to shift in the concentrations of nutrients in the water together with shifts in other ecological factors.

Among the diatoms (Bacillariophyceae) in the River Thames and the Wraysbury Reservoir,the shifts in dominant species from Melosira varians in the early spring of the year (Figures 3.6 and 3.7) to Stephanodiscus rotula→S.rotula var.minutula→S.hantzschii later on in the year and finally in late summer Aulacoseira granulata after blooms of other algae.This phenomenon is believed to be due to lower requirements of the successive species for nitrogen.From

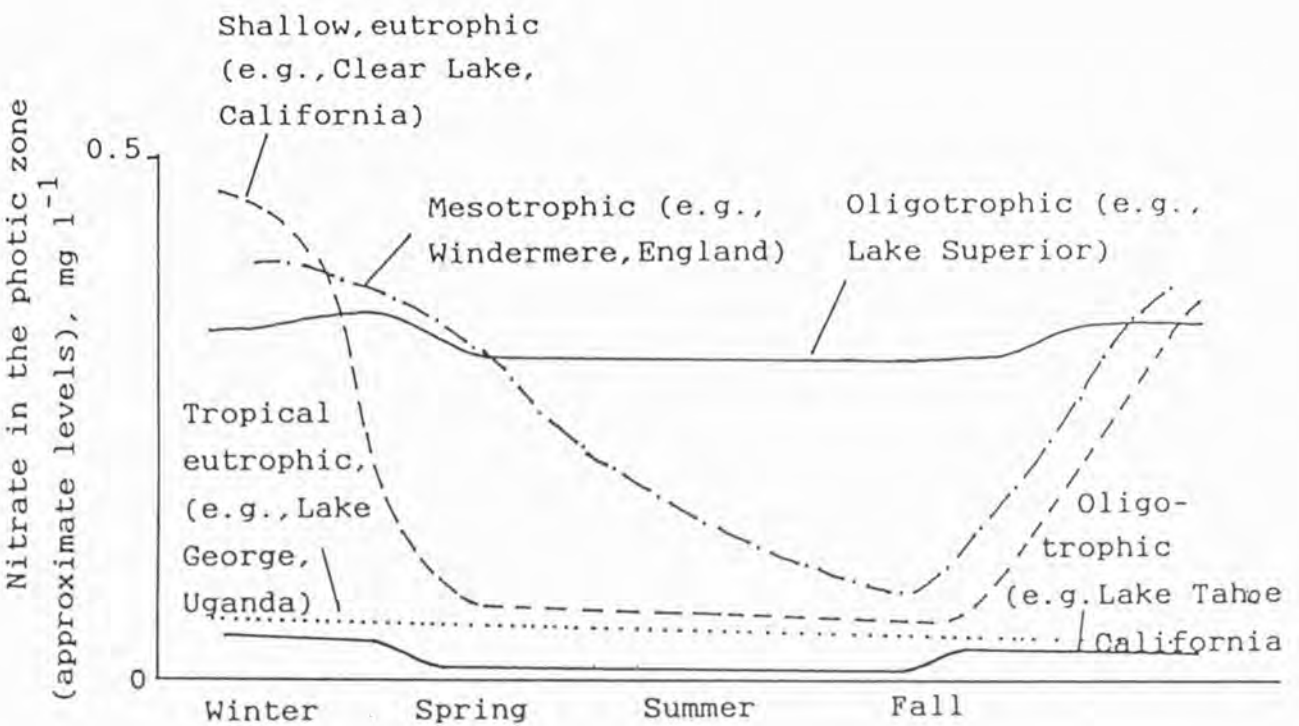


Figure 3.4. Idealized representation of seasonal changes in nitrate available for plant growth in temperate-zone eutrophic, mesotrophic and oligotrophic lakes and a tropical eutrophic lake.

(From: Horne and Goldman, 1972)

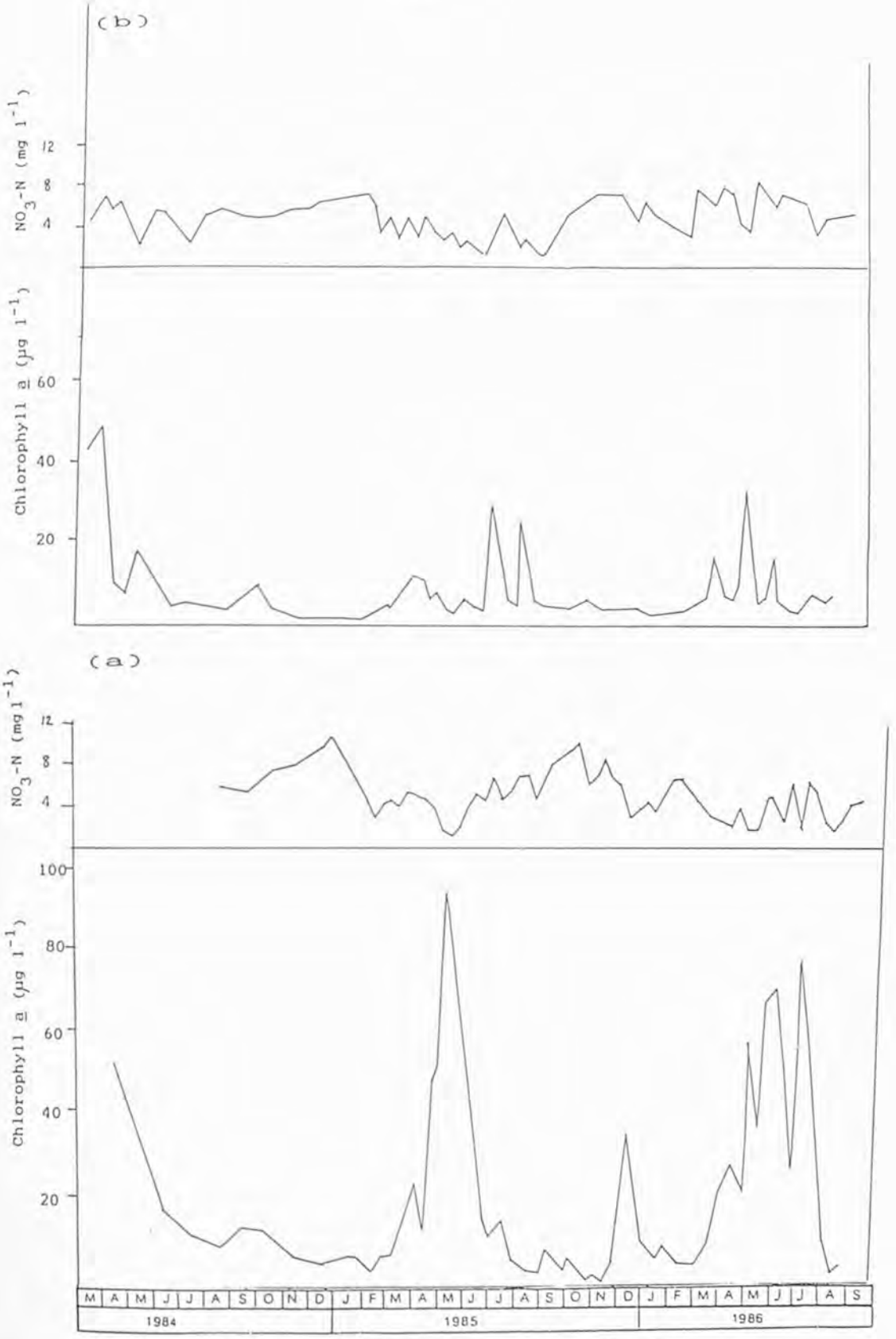


Figure 3.5 Relationships between nitrate-nitrogen concentrations and chlorophyll a concentrations in the (a) River Thames, and (b) Wraysbury Reservoir.

Figure 3.6. Relationships between *Melosira varians* and *Aulacoseira granulata* and nitrate-nitrogen concentrations in the River Thames.

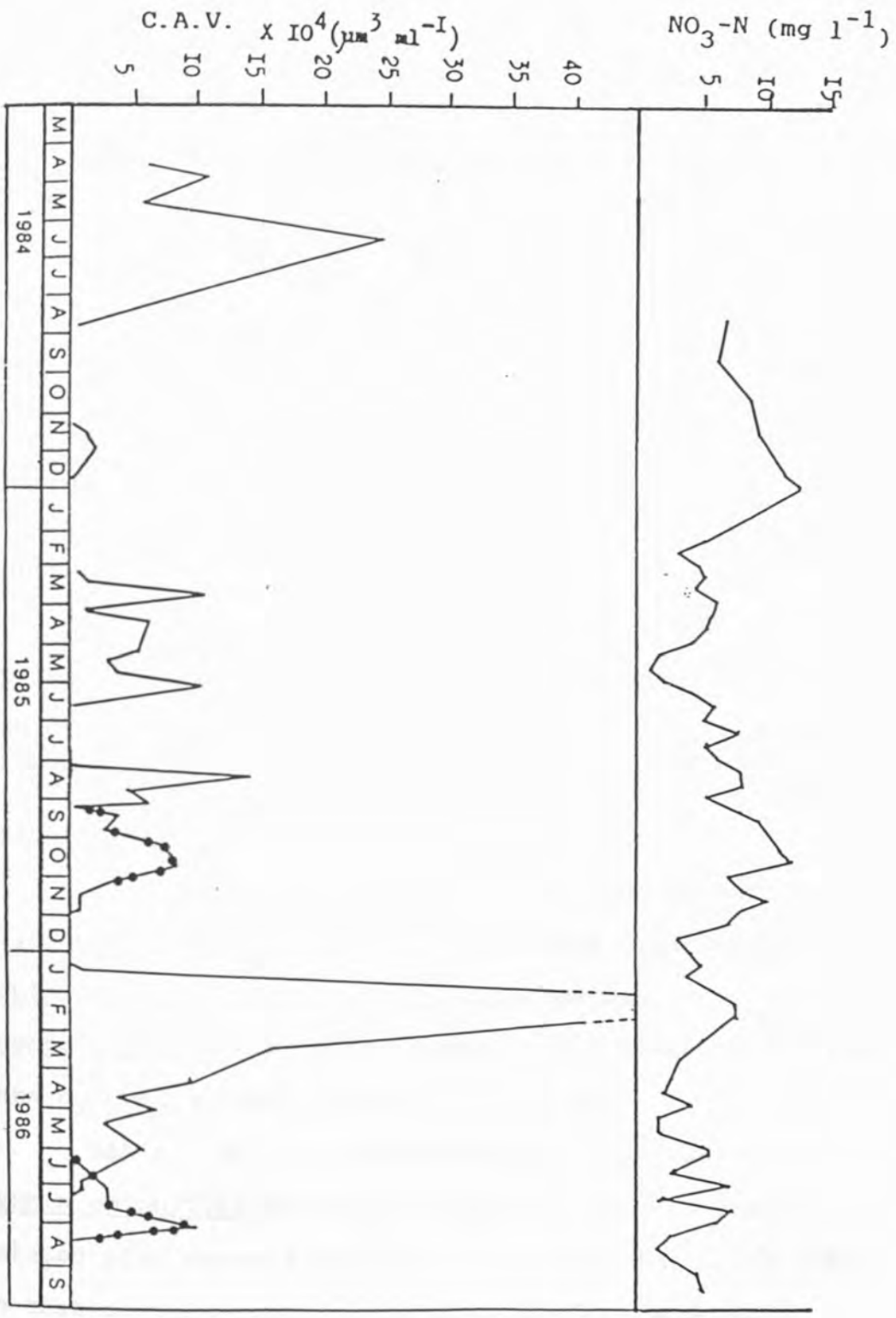

C.A.V. x 10^4 (μm^3 ml^{-1})
5
10
15
20
25
30
35
40
NO_3-N (mg l^{-1})
5
10
15
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.6

Figure 3.6, it was found that Melosira varians declines in June, 1985 when nitrate concentrations in the River Thames decreased to 5.2 mg l^{-1} and re-appears again when nitrate concentration increased to 7 mg l^{-1}. But when the concentration drops to 1.8 mg l^{-1}, Aulacoseira granulata was dominant. The same patterns tend to appear during 1984 to 1986 in the River Thames and the Wraysbury Reservoir (Figures 3.6 and 3.7).

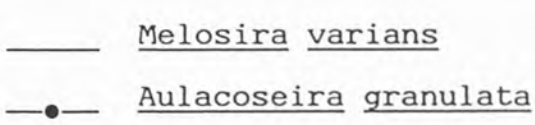
Stephanodiscus hantzschii became dominant in the spring (Figures 3.8 and 3.9) and the shifts to the dominance of Stephanodiscus rotula var. minutula took place when the concentrations drop to 1.8 mg l^{-1}.

Nitrate-nitrogen decreased in concentration in the River Thames and the Wraysbury Reservoir whenever a sustained growth of diatoms occurred. This agrees with the suggestion that low nitrate levels might be a contributory factor in restricting diatom growth.

In streams in eastern parts of the USA, Patrick (1977) found that Melosira varians, Synedra ulna, Navicula viridula, Navicula mutica, Cocconeis placentula and Cyclotella pseudostelligera, become very common in the presence of high nitrate concentrations in water (2 to 3 mg l^{-1}).

Bahls (1973) has found that the optimum growth of Nitzschia epiphytica and Navicula minima are positively correlated with ammonia concentrations. Schoeman (1973) has shown that certain species of diatom prefers organic

Figure 3.7. Relationships between Melosira varians and Aulacoseira granulata and nitrate-nitrogen concentrations in the Wraysbury Reservoir.



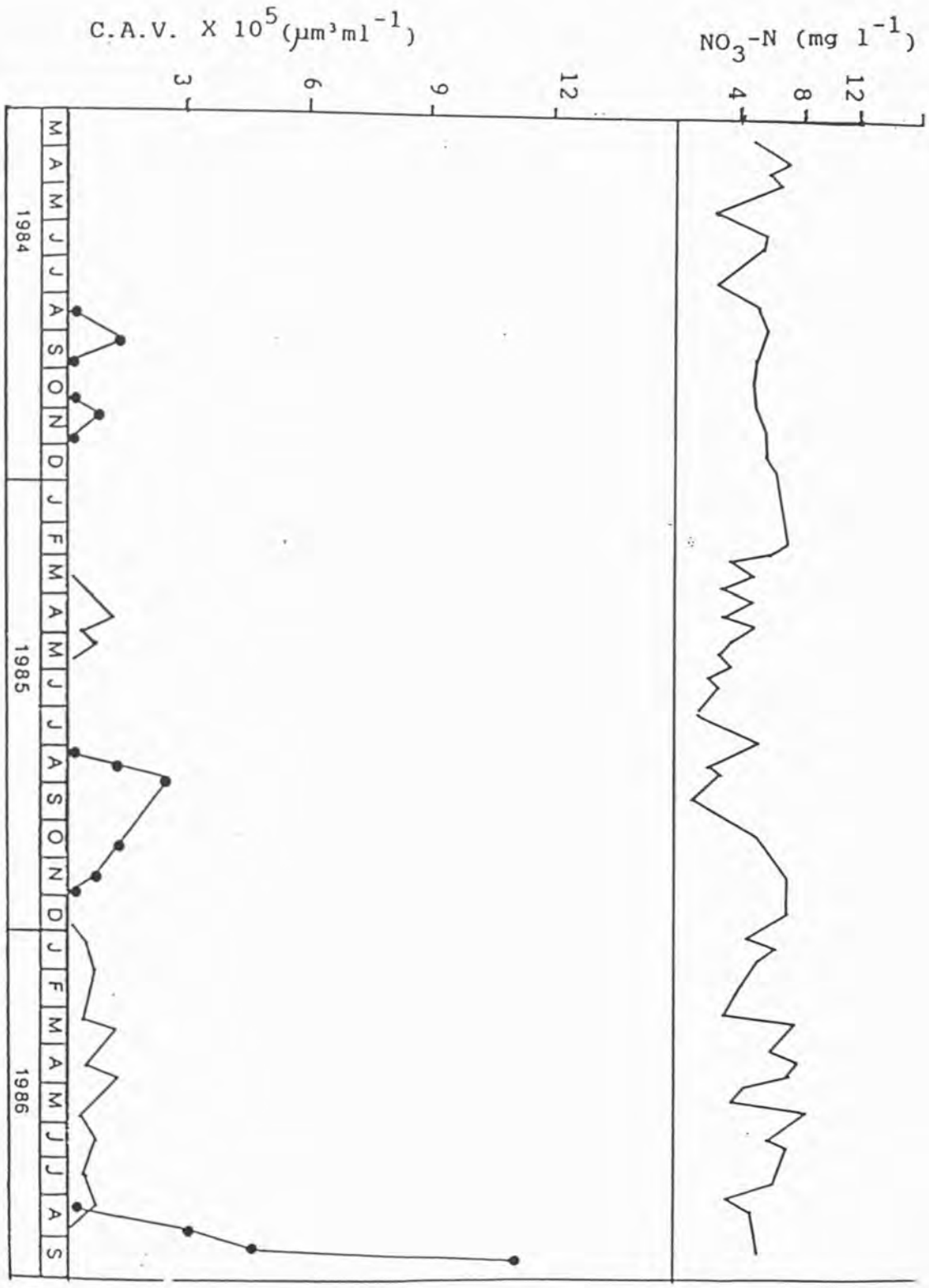

C.A.V. X 10^5 ($\mu m^3 ml^{-1}$)
3
6
9
12
NO_3-N (mg l^{-1})
4
8
12
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.7

Figure 3.8. Relationships between Stephanodiscus spp. and nitrate-nitrogen concentrations in the River Thames.

——— Stephanodiscus rotula

—•— Stephanodiscus rotula var.minutula

—o— Stephanodiscus ref.hantzschii

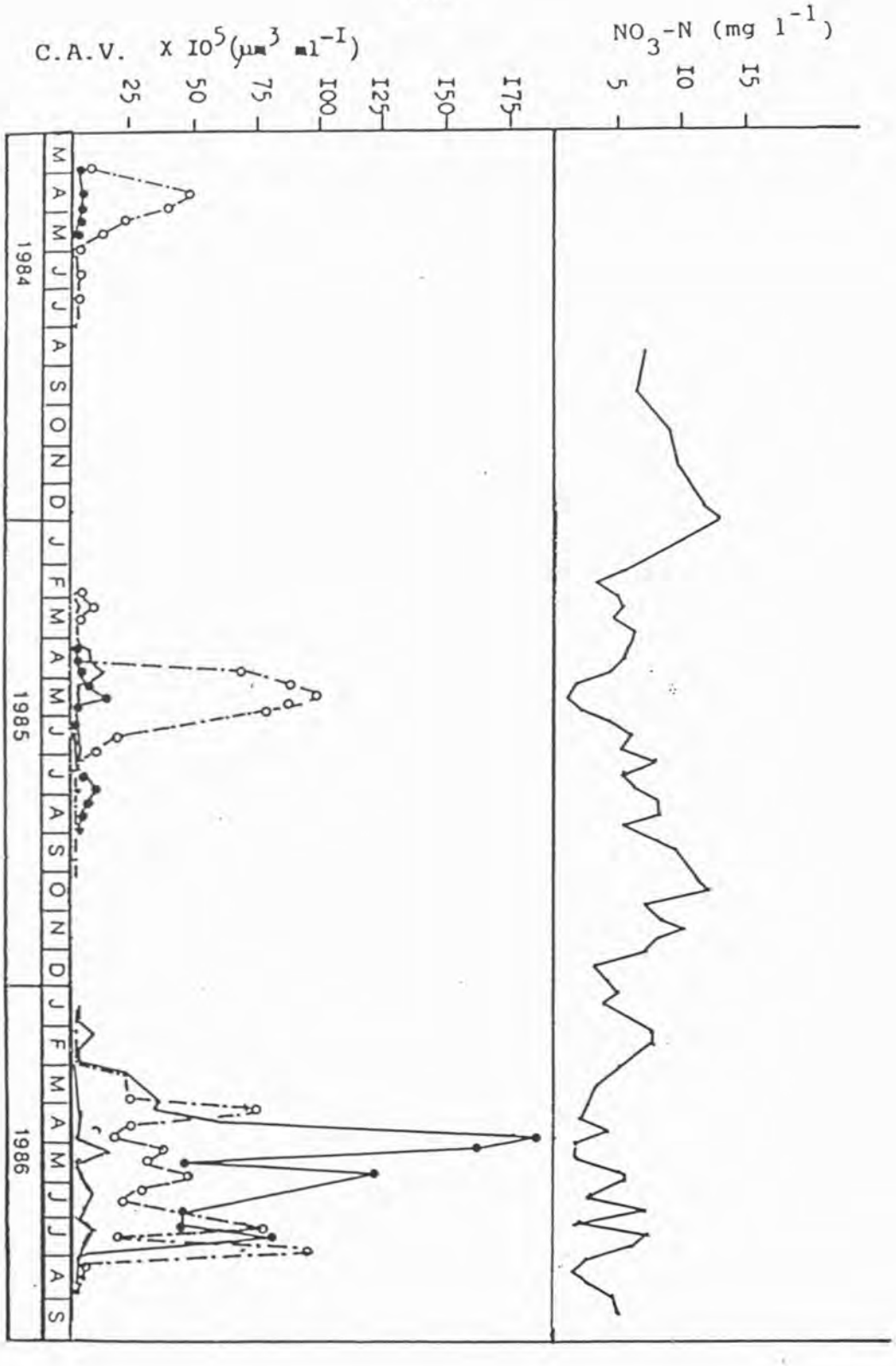

C.A.V. X 10^5(μm^3 ml^{-1})
25
50
75
100
125
150
175
NO_3-N (mg l^{-1})
5
10
15
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.8

Figure 3.9. Relationships between *Stephanodiscus spp.* and nitrate-nitrogen concentrations in the Wraysbury Reservoir.

———— *Stephanodiscus rotula*

—•— *Stephanodiscus rotula* var. *minutula*

—o— *Stephanodiscus* ref. *hantzschii*

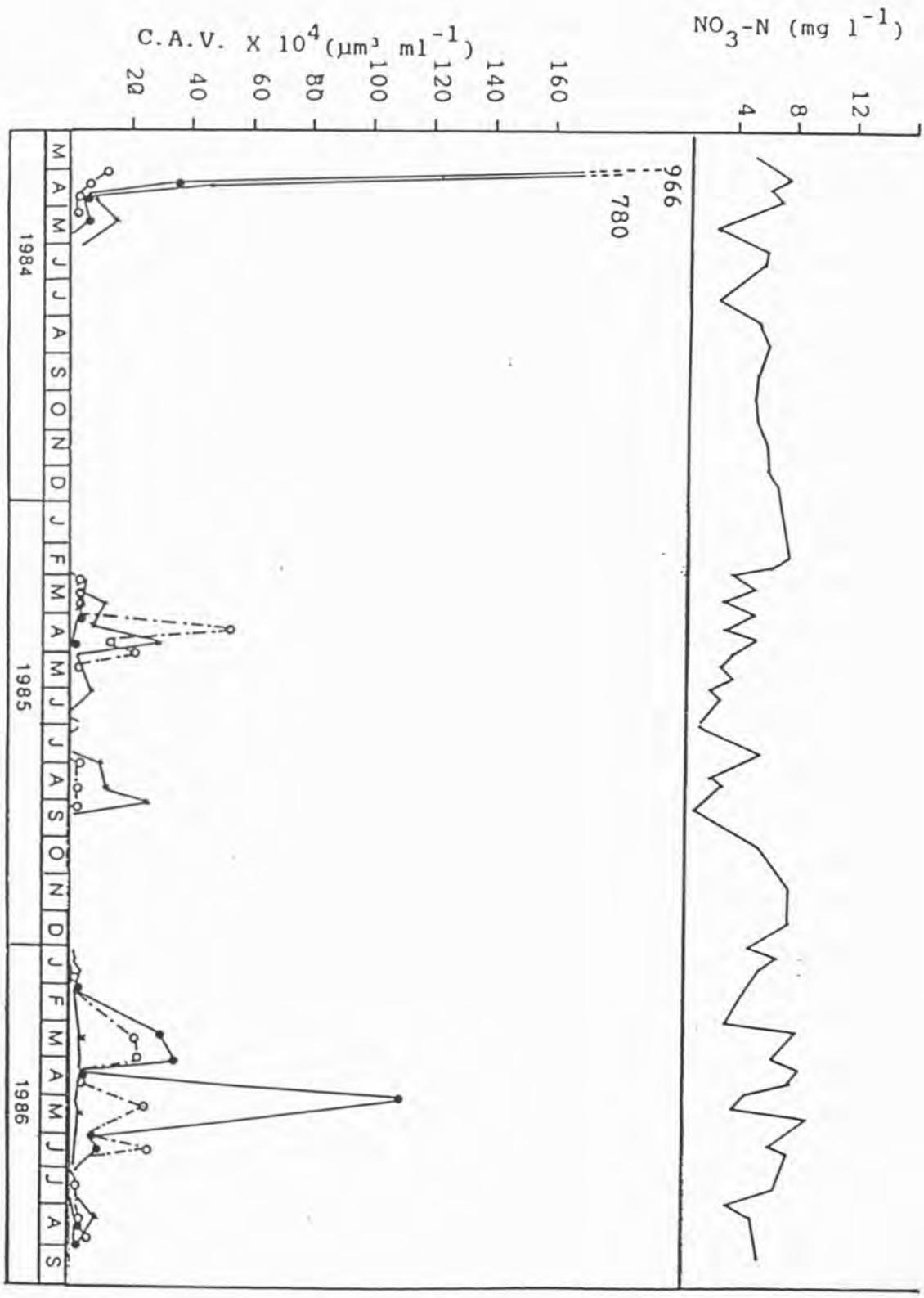

NO3-N (mg l-1)
4
8
12
C.A.V. X 10^4 (µm³ ml-1)
20
40
60
80
100
120
140
160
966
780
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.9

Figure 3.10. Relationships between Cryptophyceae and nitrate-nitrogen concentrations in the River Thames.

_____ Rhodomonas minuta

—•— Cryptomonas spp.

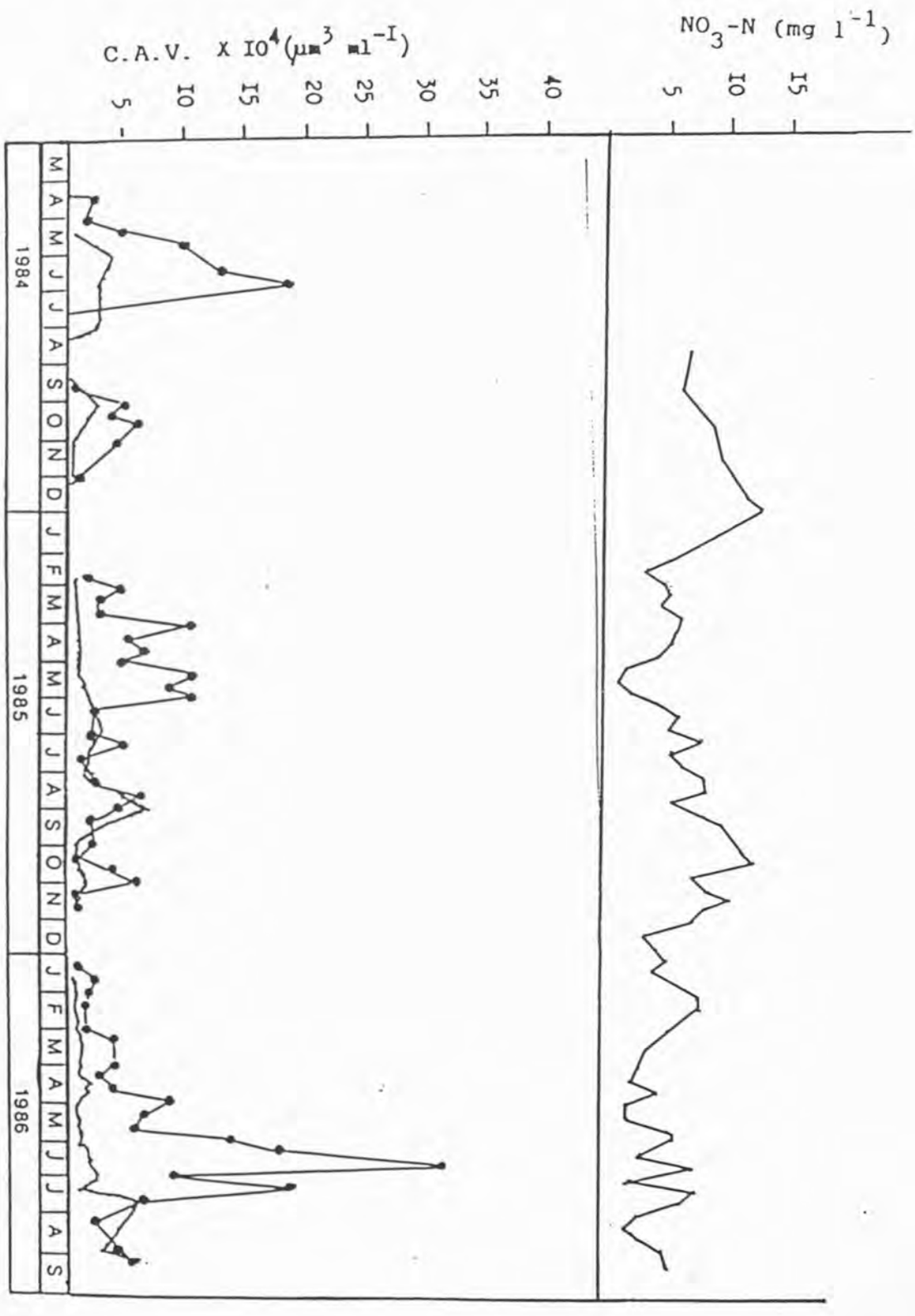

C.A.V. X IO⁴(μm³ ml⁻¹)
5
IO
I5
20
25
30
35
40
NO3-N (mg l⁻¹)
5
IO
I5
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.10

Figure 3.11. Relationships between Cryptophyceae and nitrate-nitrogen concentrations in the Wraysbury Reservoir.

_____ Rhodomonas minuta

—•— Cryptomonas spp.

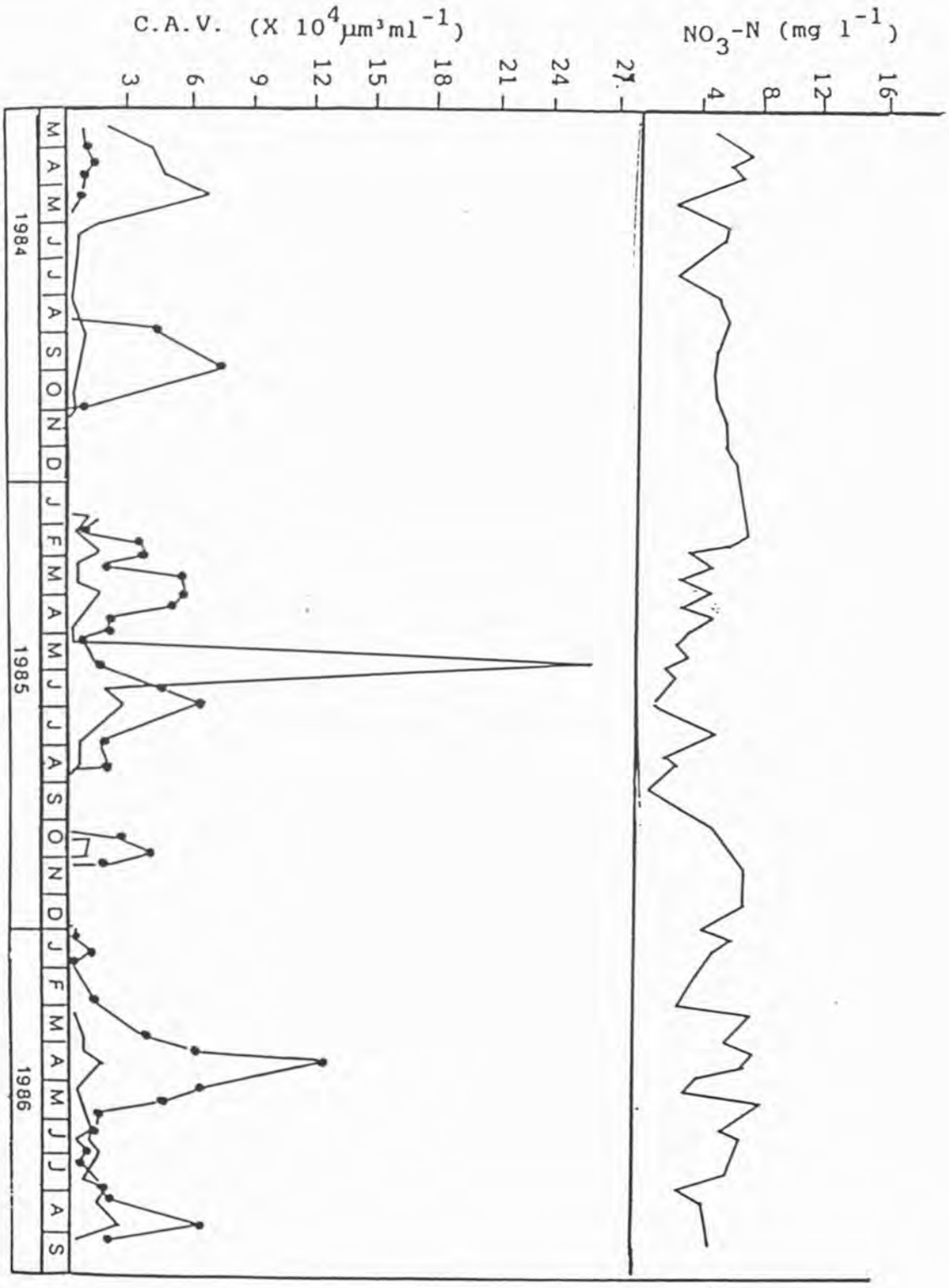
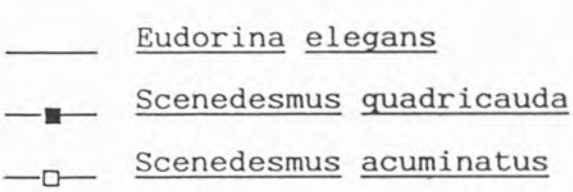

C.A.V. (X $10^4 \mu m^3 ml^{-1}$)
3
6
9
12
15
18
21
24
27
NO_3-N ($mg\ l^{-1}$)
4
8
12
16
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.11

Figure 3.12. Relationships between Chlorophyceae and nitrate-nitrogen concentrations in the River Thames.



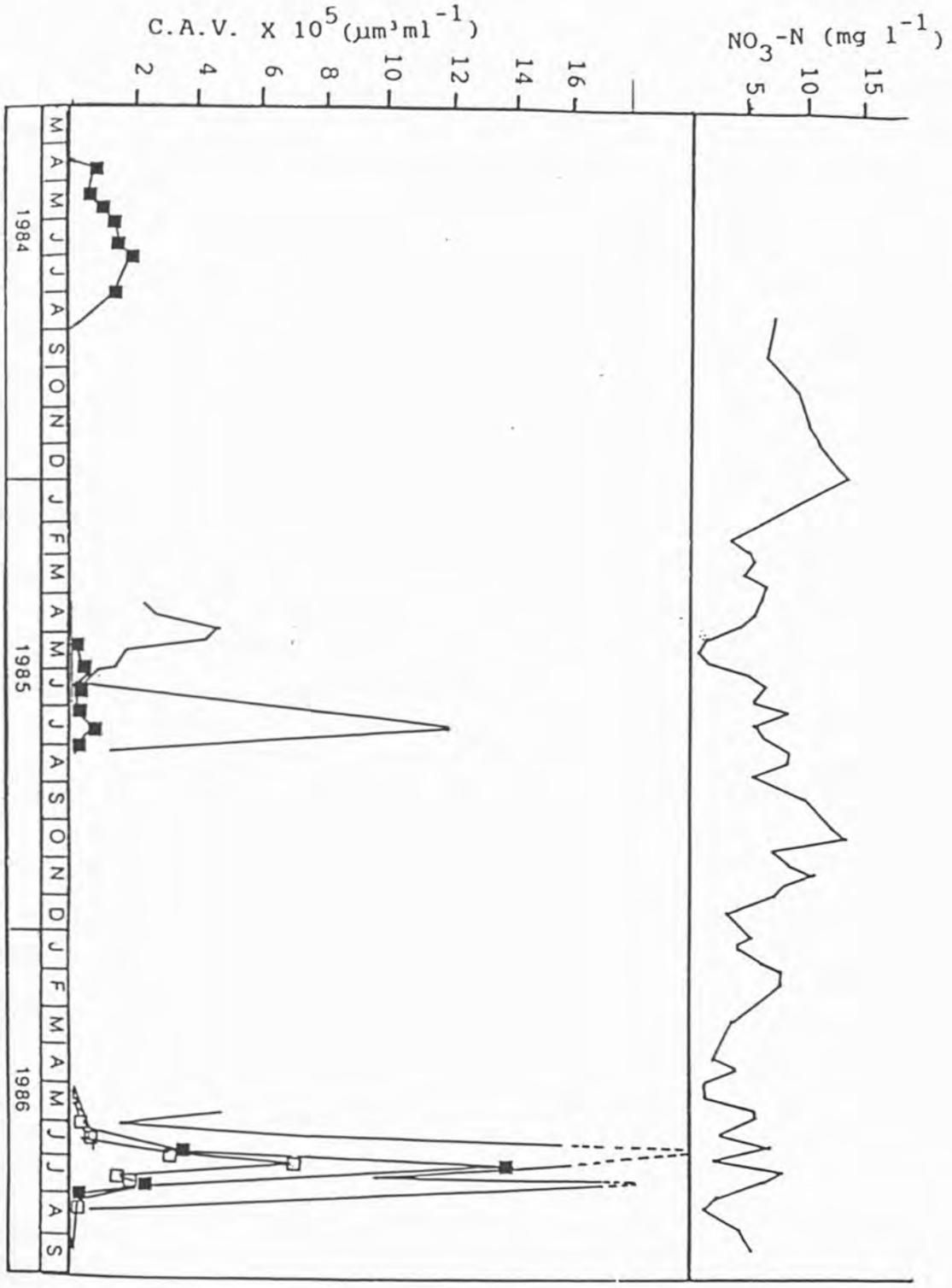
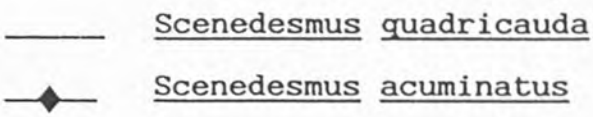

C.A.V. X 10^5 ($\mu m^3 ml^{-1}$)
2
4
6
8
10
12
14
16
NO_3-N (mg l^{-1})
5
10
15
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.12

Figure 3.13. Relationships between Scenedesmus spp. and nitrate-nitrogen concentrations in the Wraysbury Reservoir.



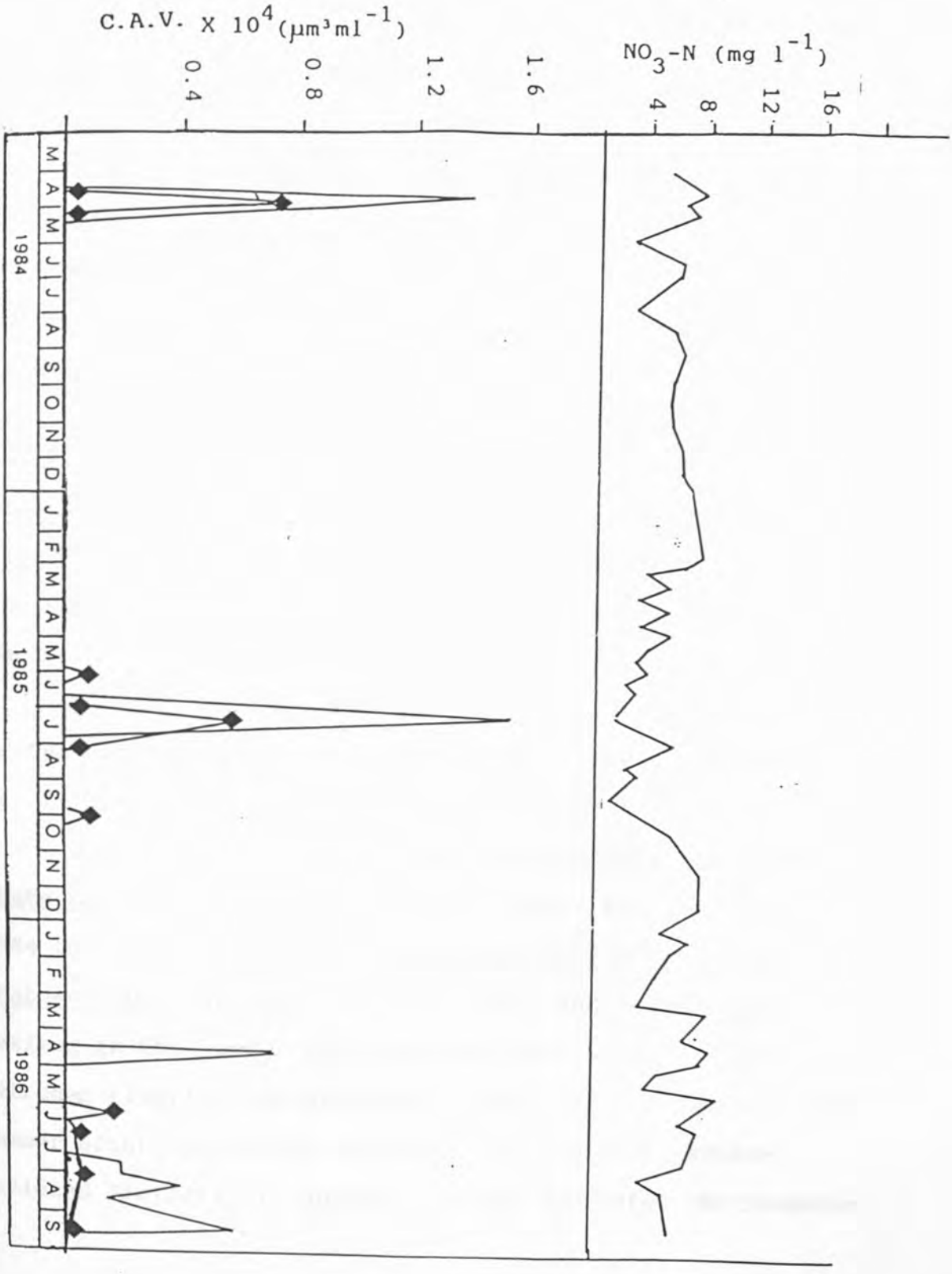

C.A.V. X 10^4 ($\mu m^3 ml^{-1}$)
0.4
0.8
1.2
1.6
NO_3-N (mg l^{-1})
4
8
12
16
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.13

compounds as a source of nitrogen.Some of these are facultative nitrogen heterotrophic species such as Nitzschia epiphytica,Navicula seminulum,Cyclotella meneghiniana, Nitzschia amphibia,Nitzschia formalis,Nitzschia frustulum, Nitzschia intermedia,Gomphonema parvulum and Navicula confervacea.Other species seems to be obligate nitrogen heterotrophic forms.These are Navicula muralis,Navicula perparva,Nitzschia fonticola,Nitzschia palea and Nitzschia formalis.

The evidence that certain Cyanophyceae were able to assimilate dissolved atmospheric nitrogen (N_2,chemically a relatively inert gas) was first confirmed by Dugdale et al., (1959) in a study of Anabaena in Sanctuary Lake,Pennsylvania. It is now clear that this property is exclusive to certain bacteria and Cyanobacteria (especially the order Nostocales).

The importance of nitrogen fixation in the ecology of Cyanobacteria has been stressed many times (e.g.Fogg et al.,1973;Stewart,1973;Magne,1977).

Oscillatoria spp.,Aphanizomenon flos-aquae and Anabaena spp. were found in the Wraysbury Reservoir during 1984 to 1986 (Figure 3.14).Aphanizomenon flos-aquae and Anabaena spp. appeared in early spring and reached their maximum in the summer and persisted until autumn.Without nitrogen fixation the bloom would possibly collapse in late summer after the winter accumulation of nitrate became depleted.Similarly,in autumn Anabaena dominated the plankton

Figure 3.14. Relationships between Cyanobacteria and nitrate-nitrogen concentrations in the Wraysbury Reservoir.

_____ Anabaena spp.

—•— Aphanizomenon flos-aquae

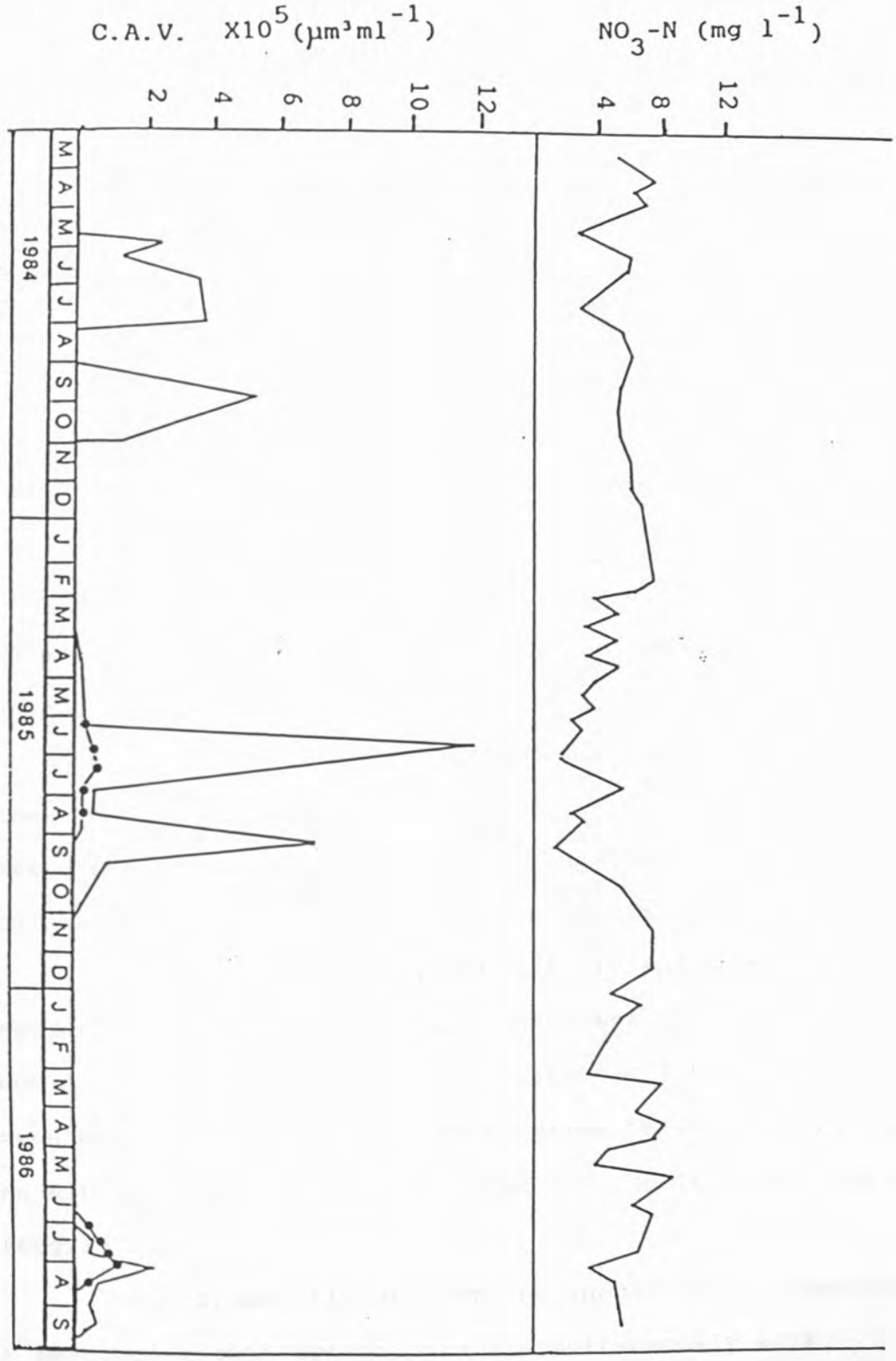

C.A.V. X10^5(µm^{3}ml^{-1})
NO_3-N (mg l^{-1})
2
4
6
8
10
12
4
8
12
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

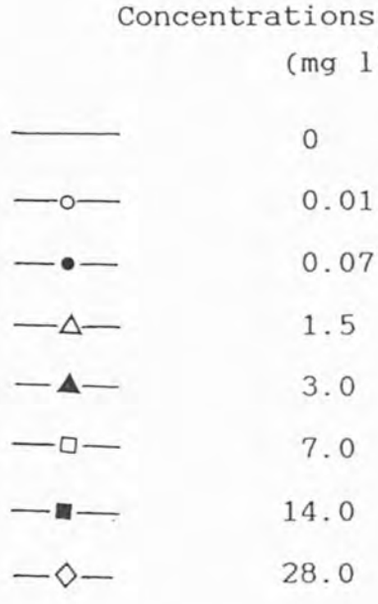
Figure 3.14

with its ability to grow in a nitrogen-depleted situation (Figure 3.14).This is supported by the evidence that the heterocyst:vegetative cell ratio increases in natural populations of Anabaena and Aphanizomenon as external sources of combined nitrogen fall,below about 300 $\mu g\ N\ l^{-1}$ (Reynolds, 1972;Horne and Goldman,1972) and,accordingly,the nitrogen-fixing capability is facultative.Many field measurements of limnetic nitrogen fixation per unit area per unit time have been made (e.g.Brezonik,1972;Vanderhoef et al.,1974),and show that,at times,it can represent the major contribution to the nitrogen requirements of the dominant plankton.In some cases, nitrogen fixation by Cyanobacteria contributes as much as 50% of the annual nitrogen input into the lake (Mc Carthy,1980). Furthermore,the ability to change from the use of NH_4 to NO_3 and then to N_2 as each nitrogen sources is depleted has been demonstrated in experiments on an Anabaena bloom in Smith Lake,Alaska,using ^{15}N labelling (Billaud,1968).

In mesotrophic Windermere,nitrate and ammonia become depleted in late summer when Anabaena reaches its maximum.Although amounting to only 1% of the lake's annual nitrogen budget,nitrogen fixation supplies between 10 and 70% of the nitrogen used by the alga,depending on the year (Horne and Fogg,1970).

The nitrogen-fixing forms (Cyanobacteria) commence their seasonal growth approximately simultaneously with Eudorina and Scenedesmus acuminatus,Scenedesmus quadricauda

Figure 3.15 The growth of Scenedesmus quadricauda in Chu's medium No.10 with different concentrations of nitrate-nitrogen.



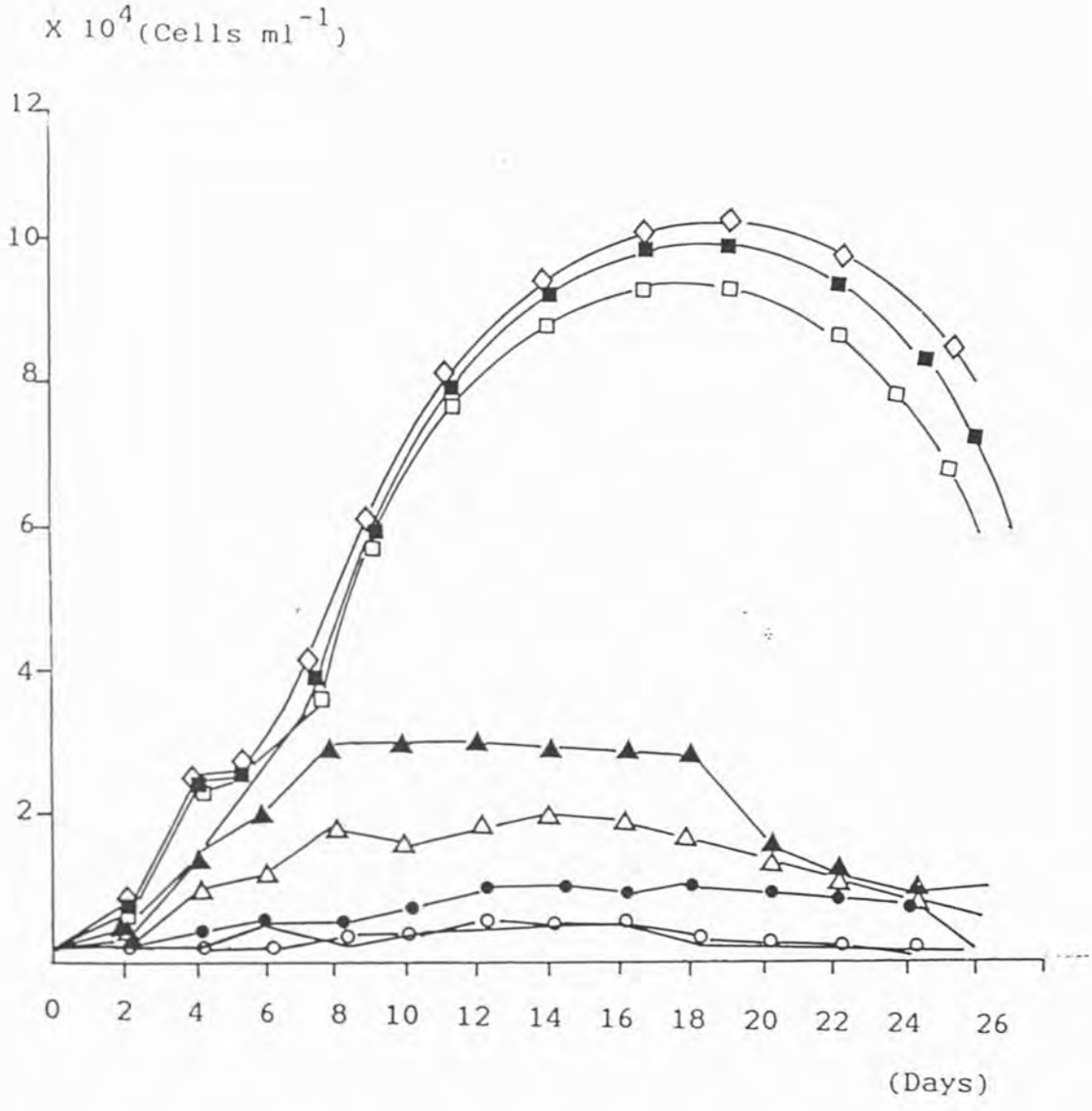


FIGURE 3.15

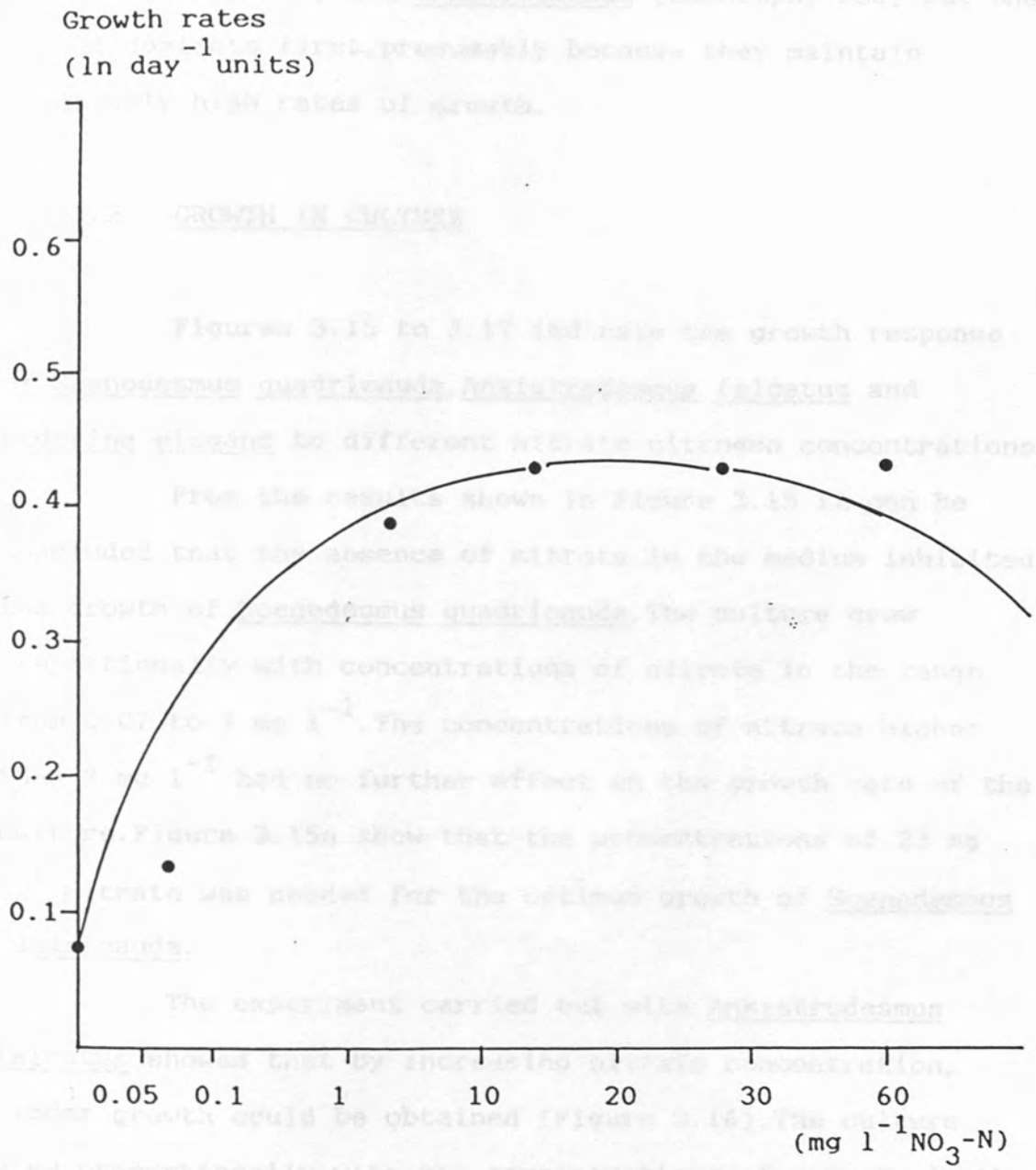


Figure 3.15a Effects of nitrate-nitrogen on the growth rates of Scenedesmus quadricauda.

(Figures 3.12,3.13) and Chlamydomonas (Chlorophyceae) but the latter dominate first,presumably because they maintain relatively high rates of growth.

3.7.1.2 GROWTH IN CULTURE

Figures 3.15 to 3.17 indicate the growth response of Scenedesmus quadricauda,Ankistrodesmus falcatus and Eudorina elegans to different nitrate-nitrogen concentrations.

From the results shown in Figure 3.15 it can be concluded that the absence of nitrate in the medium inhibited the growth of Scenedesmus quadricauda.The culture grew proportionally with concentrations of nitrate in the range from 0.07 to 7 mg l^{-1}.The concentrations of nitrate higher than 7 mg l^{-1} had no further effect on the growth rate of the culture.Figure 3.15a show that the concentrations of 23 mg l^{-1} nitrate was needed for the optimum growth of Scenedesmus quadricauda.

The experiment carried out with Ankistrodesmus falcatus showed that by increasing nitrate concentration, higher growth could be obtained (Figure 3.16).The culture grew proportionally with the concentrations of nitrate in the range from 0.5 to 20 mg l^{-1}.

In both algae which have been investigated it was found that culture with lower nitrogen concentrations (less than 0.1 mg l^{-1} nitrate for Ankistrodesmus falcatus and less

Figure 3.16 The growth of Ankistrodesmus falcatus in Chu's medium No.10 with different concentrations of nitrate-nitrogen.

	Concentrations of NO_3-N ($mg\ l^{-1}$)
———	0
—o—	0.01
—●—	0.07
—△—	1.5
—▲—	3.0
—□—	7.0
—■—	14.0

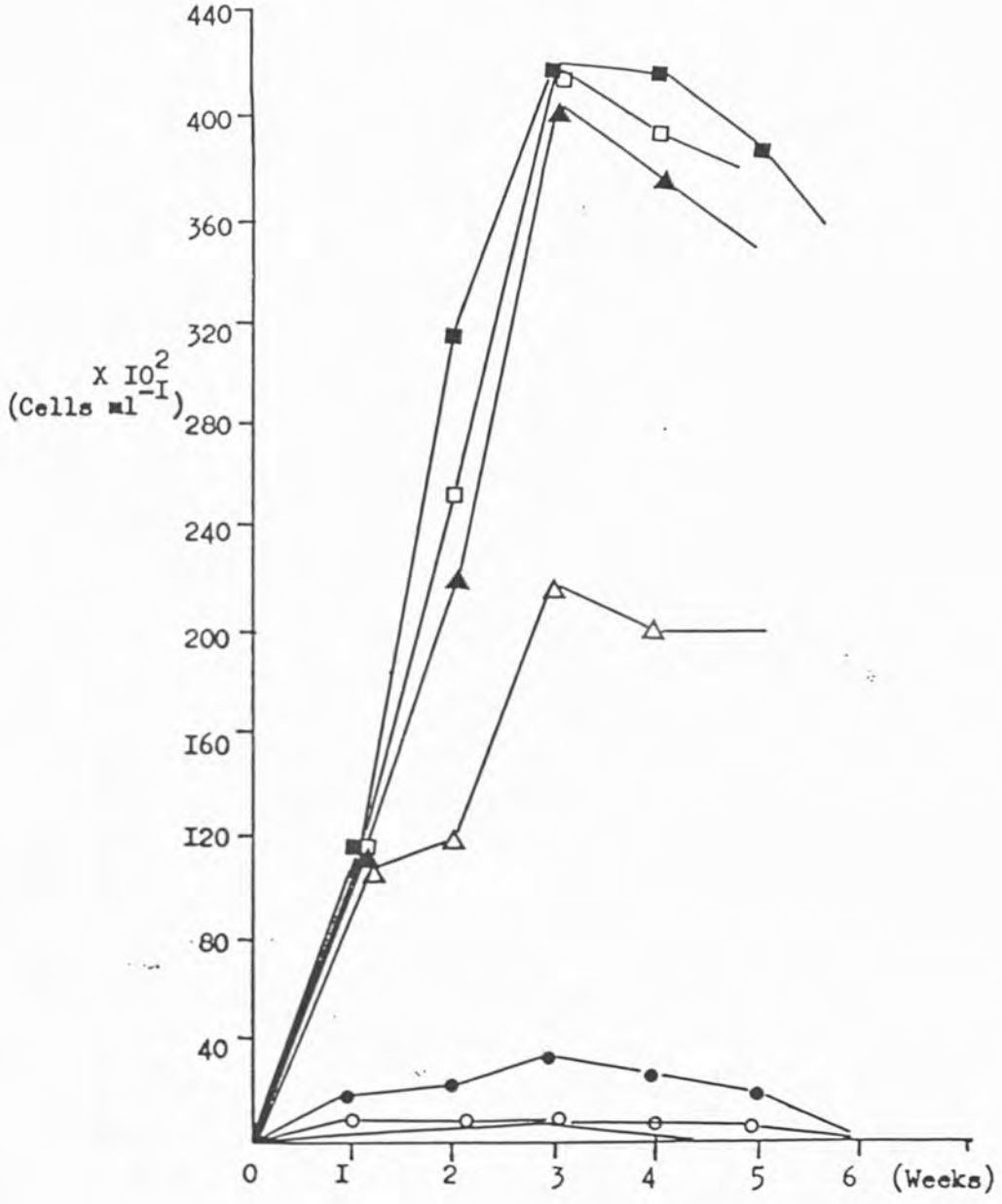

440
400
360
320
280
240
200
160
120
80
40
X 10^2
(Cells ml^{-1})
0
1
2
3
4
5
6
(Weeks)

Figure 3.16

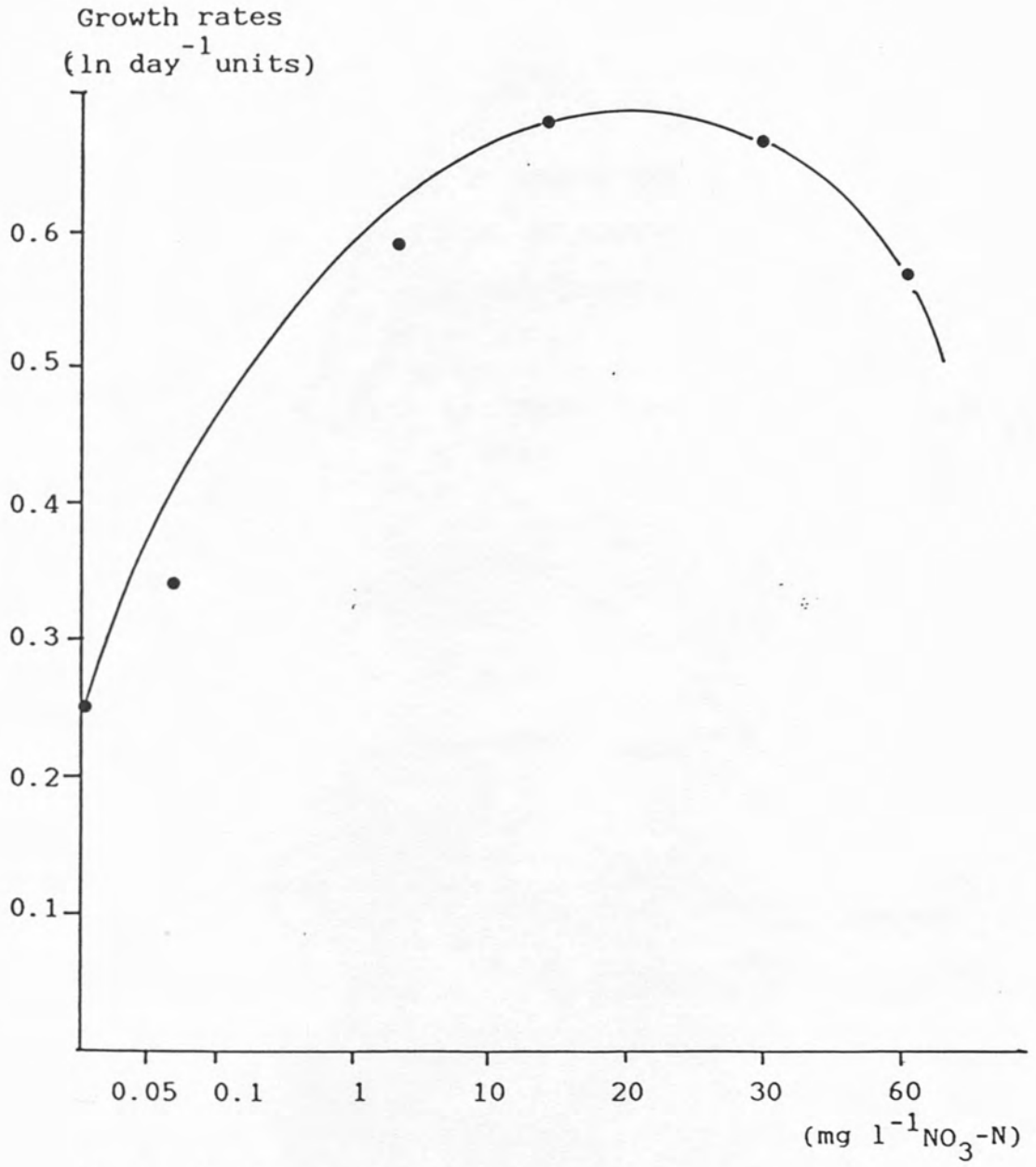


Figure 3.16a Effects of nitrate-nitrogen on the growth rates of Ankistrodesmus falcatus

Figure 3.17 The growth of Eudorina elegans in Chu's medium No.10 with different concentrations of nitrate-nitrogen.

	Concentrations of NO_3-N ($mg\ l^{-1}$)
———	0
—○—	0.01
—●—	0.07
—△—	1.5
—▲—	3.0
—□—	7.0
—■—	14.0
—◇—	28.0
—◆—	60.0

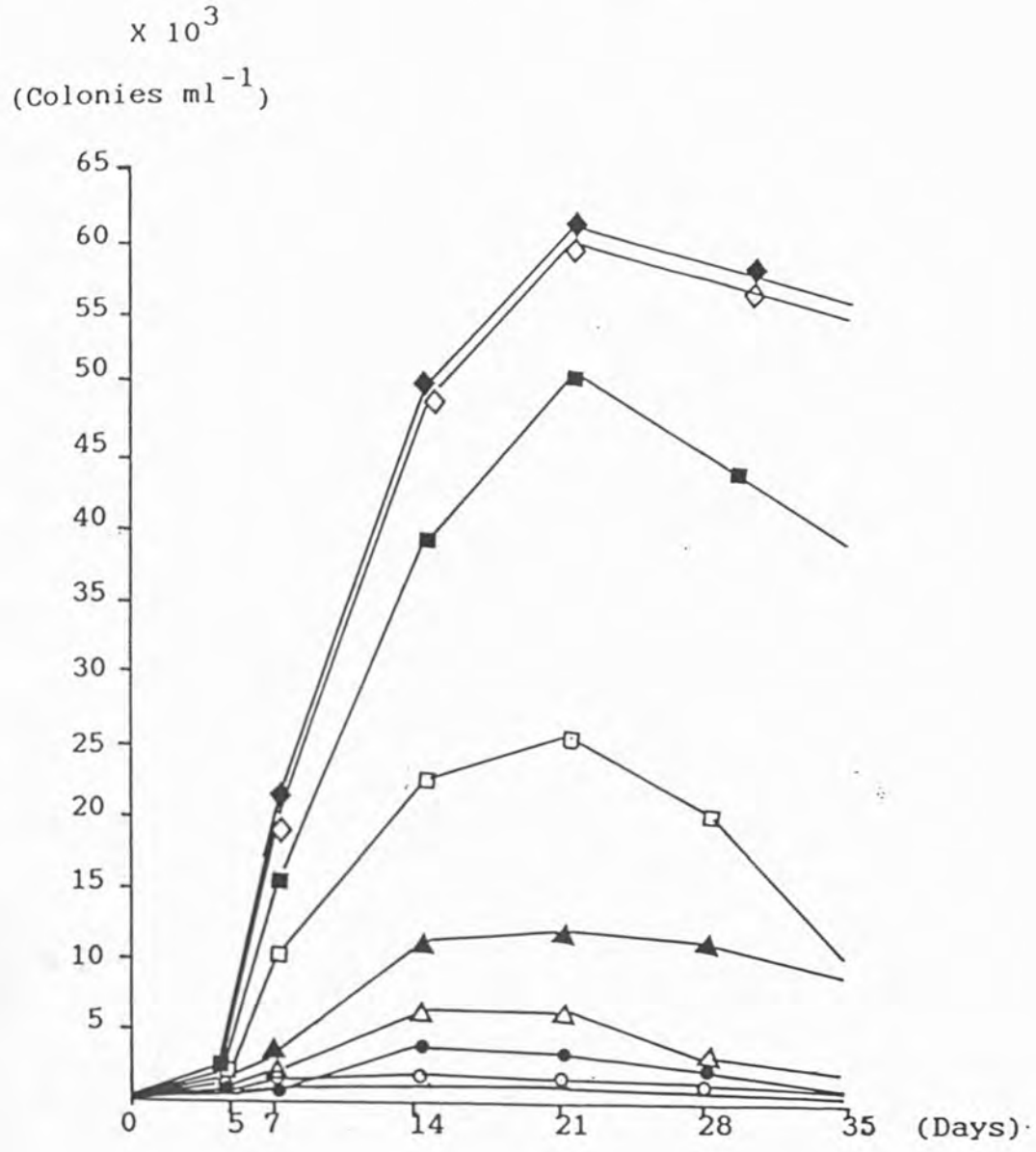

X 10^3
(Colonies ml^-1)
65
60
55
50
45
40
35
30
25
20
15
10
5
0
5
7
14
21
28
35
(Days)

Figure 3.17

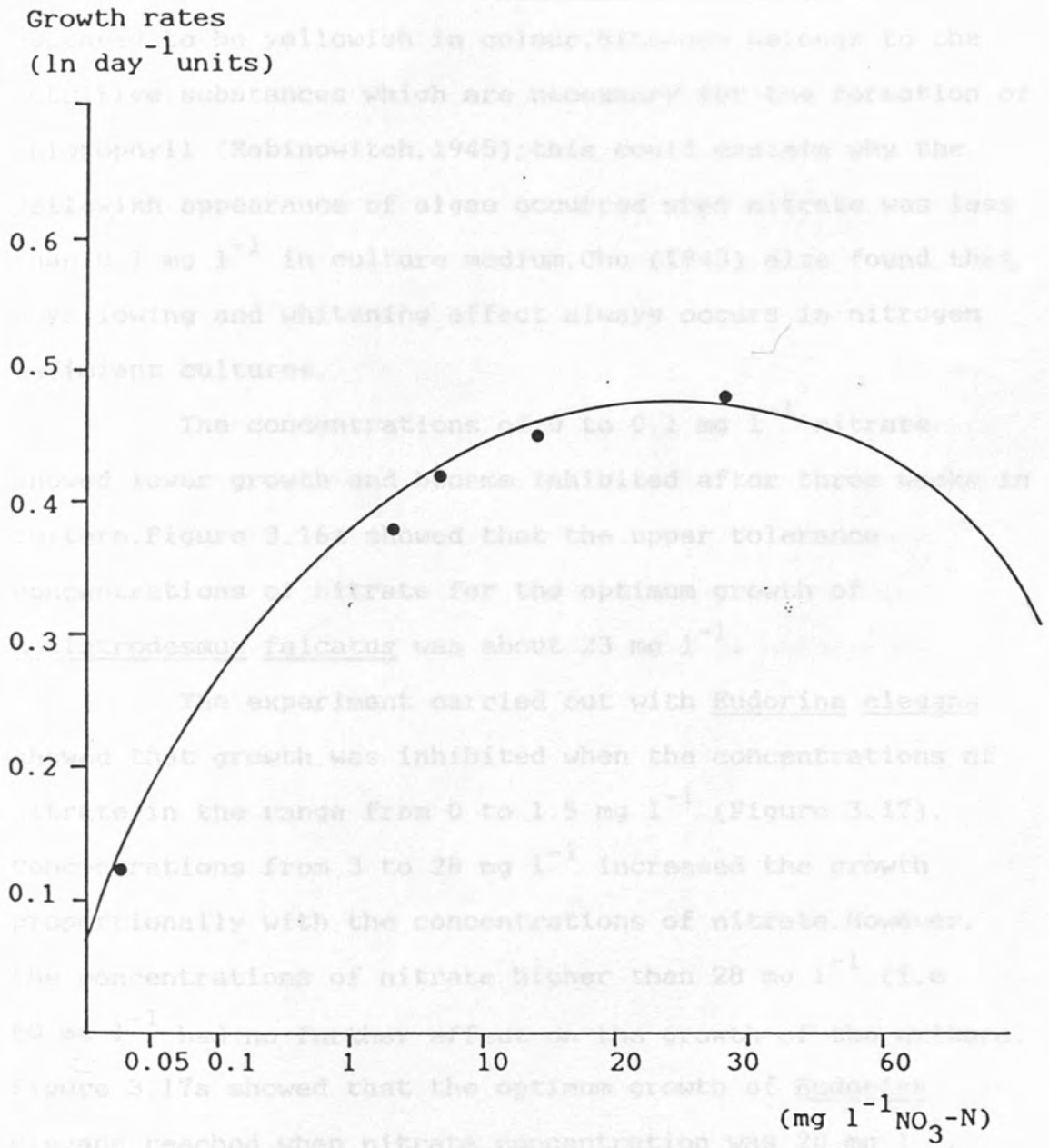


Figure 3.17a Effects of nitrate-nitrogen on the growth rates of Eudorina elegans.

than 0.01 mg l^{-1} nitrate for Scenedesmus quadricauda) appeared to be yellowish in colour.Nitrogen belongs to the nutritive substances which are necessary for the formation of chlorophyll (Rabinowitch,1945);this could explain why the yellowish appearance of algae occurred when nitrate was less than 0.1 mg l^{-1} in culture medium.Chu (1943) also found that a yellowing and whitening effect always occurs in nitrogen deficient cultures.

The concentrations of 0 to 0.1 mg l^{-1} nitrate showed lower growth and became inhibited after three weeks in culture.Figure 3.16a showed that the upper tolerance concentrations of nitrate for the optimum growth of Ankistrodesmus falcatus was about 23 mg l^{-1}.

The experiment carried out with Eudorina elegans showed that growth was inhibited when the concentrations of nitrate in the range from 0 to 1.5 mg l^{-1} (Figure 3.17). Concentrations from 3 to 28 mg l^{-1} increased the growth proportionally with the concentrations of nitrate.However, the concentrations of nitrate higher than 28 mg l^{-1} (i.e 60 mg l^{-1} had no further effect on the growth of the culture. Figure 3.17a showed that the optimum growth of Eudorina elegans reached when nitrate concentration was 28 mg l^{-1}.

Growth rate limitation of phytoplankton by nitrogen has been investigated by various researchers (Thomas and Dobson,1972;Caperon and Meyer,1972a,b;Eppley and Renger,1974; Conway et al.,1976;Harrison et al.,1976;Conway,1977;Goldman

and Mc Carthy,1978;Wyman and Fay,1986).

Most of the field studies addressing the dynamics of nitrogenous nutrient cycling in aquatic systems have been executed in marine or estuarine regions.The highly individual character of lakes and rivers makes it more difficult to generalize about freshwater plankton ecology.In the absence of good tracer data for the nitrogenous nutrition of phytoplankton in inland waters;short-term recycling has not been considered in the development of many ecosystem models and management strategies.Nevertheless,existing data support a generalization that the well-characterized importance of nitrogenous animal excretory products as plant nutrients in marine and estuarine waters is also a common occurrence in lakes (Mc Carthy,1980).

Figure 3.18 The seasonal fluctuations of phosphate-phosphorus in the:

(a) River Thames, and

(b) Wraysbury Reservoir.

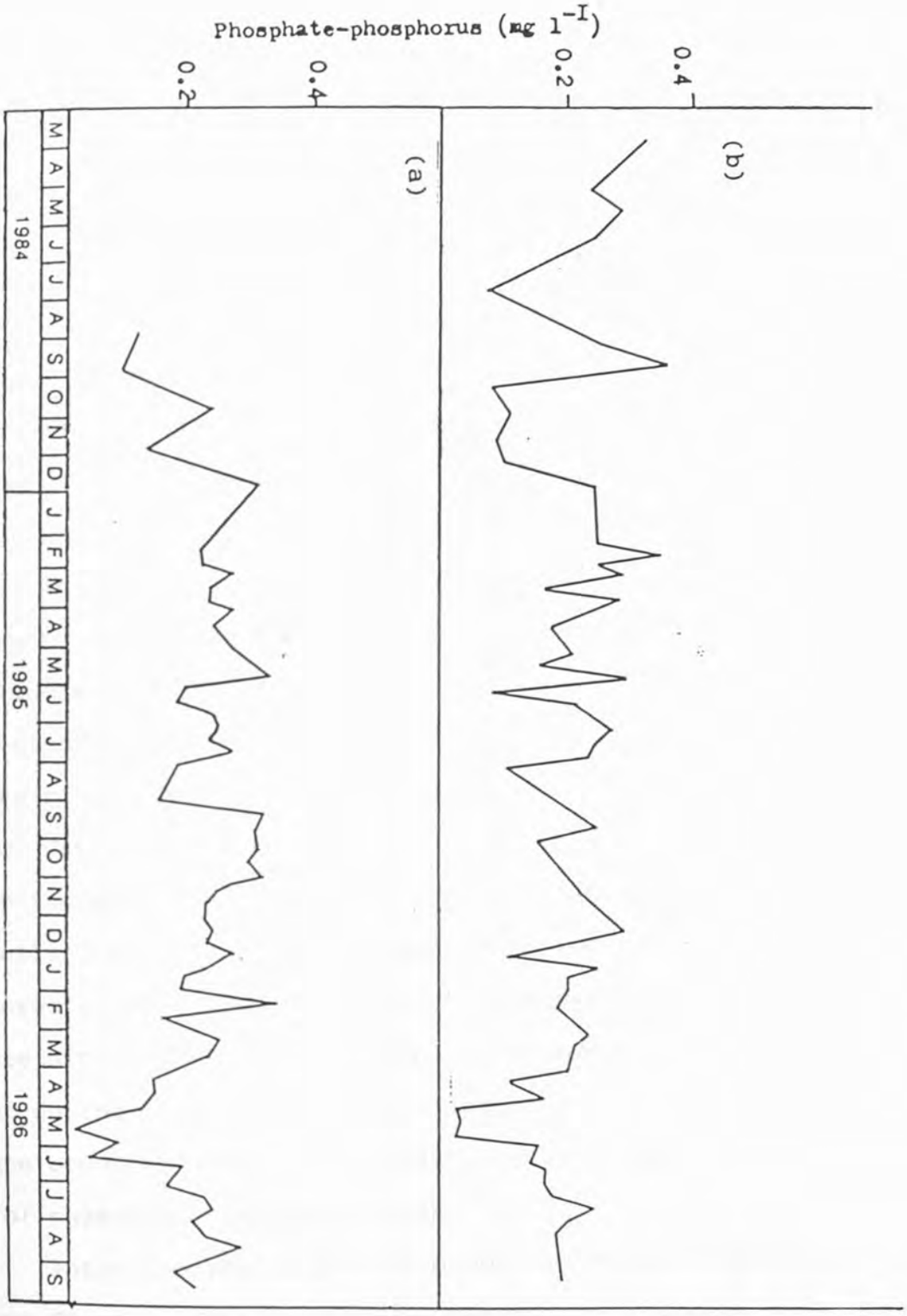

Phosphate-phosphorus (mg l^{-1})
0.2
0.4
0.2
0.4
(a)
(b)
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.18

3.7.2 THE INFLUENCE OF PHOSPHATE ON THE GROWTH OF PHYTOPLANKTON POPULATIONS

3.7.2.1 GROWTH IN NATURE

The range of concentration of phosphate-phosphorus in the River Thames was 0.15-0.33 mg l^{-1} and the Wraysbury Reservoir was 0.06-0.32 mg l^{-1} during 1984 to 1986.Phosphate-phosphorus drops to low levels in the spring during intensive growth of phytoplankton populations especially diatoms (Figure 3.18a,b).Phytoplankton population growth is limited in winter mainly by decreased light and,to a lesser extent by lower temperatures.Consequently the utilization of phosphate by phytoplankton is lessened and the concentration of phosphate rises.From about February,with the increasing length of day,the utilization of phosphate by phytoplankton commonly increases and the concentration of phosphate in the water falls.The decrease in the concentration of phosphate is often especially marked and noticeable before that in inorganic nitrogen (Heron,1962).This phenomenon was not apparent during this study.The decline of the nitrate and phosphate occurred almost simultaneously with the maximum growth of phytoplankton populations.

Intensive phytoplankton growth in spring depletes the River Thames and the Wraysbury Reservoir phosphate relatively to low levels (Figures 3.18a,b).In deep stratified

lakes there is limited replenishment,and the quantity of 'available' phosphorus in late winter may determine the maximum phytoplankton standing crop that can develop in summer.Growth during summer usually occurs using phosphate excreted by animals feeding on phytoplankton.In eutrophic lakes,animal recycling,especially that due to zooplankton,may supply all the daily phosphate needs for phytoplankton growth. Direct sediment resupply is important in summer in shallow areas.After migration through the thermocline to the epilimnion,zooplankton and fish return phosphorus to the euphotic zone.When surface phosphate levels are low, phytoplankton excrete extracellular enzymes called alkaline phosphatases.These enzymes have the ability to free phosphate bound to organic molecules.

Devices for overcoming phosphorus deficits have been evolved by algae.These are:

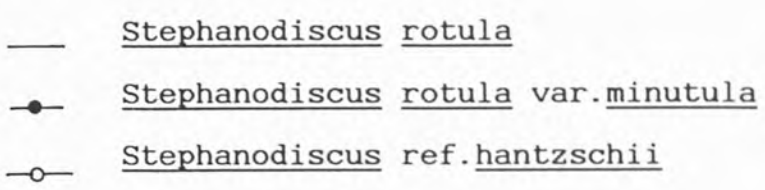
(1) luxury consumption,

(2) an ability to use phosphate at low levels,and

(3) alkaline phosphatase production.

Luxury consumption of phosphate is probably found in all phytoplankton.The process entails the uptake of more phosphate than is required for growth and it is storage within the cell (Goldman and Horne,1983).Luxury consumption of phosphate by Cyanobacteria results in the storage of polyphosphate granules in the cell.They tend to form very rapidly when phosphate is added to a phosphorus-deficient

Figure 3.19 Relationships between Stephanodiscus spp. and the phosphate-phosphorus concentrations in the River Thames.



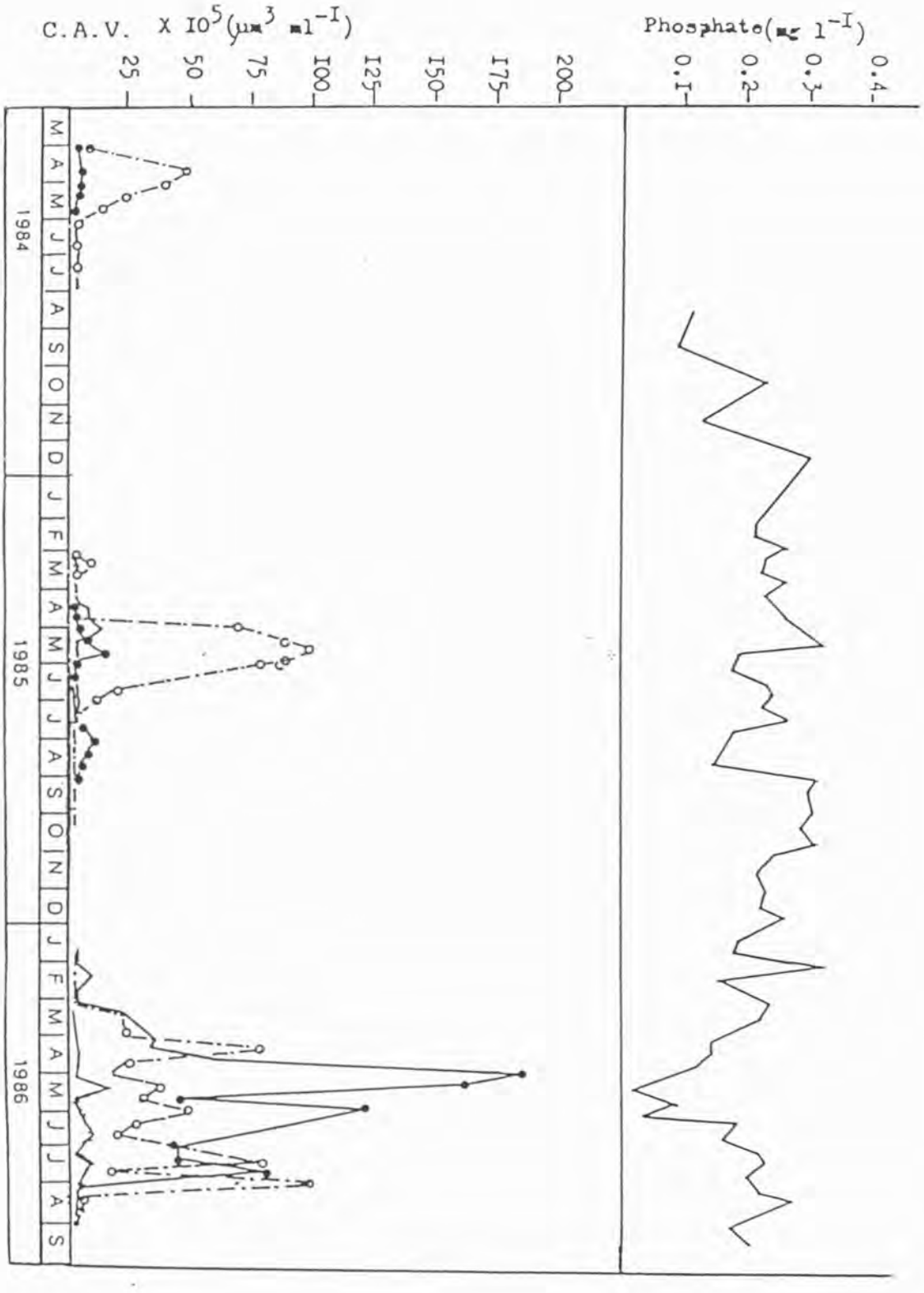

C.A.V. x 10^5 (μm^3 ml^{-1})
25
50
75
100
125
150
175
200
Phosphate(μg l^{-1})
0.1
0.2
0.3
0.4
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.19

Figure 3.20 Relationships between Stephanodiscus spp. and the phosphate-phosphorus concentrations in the Wraysbury Reservoir.

Stephanodiscus rotula

Stephanodiscus rotula var.minutula

Stephanodiscus ref.hantzschii

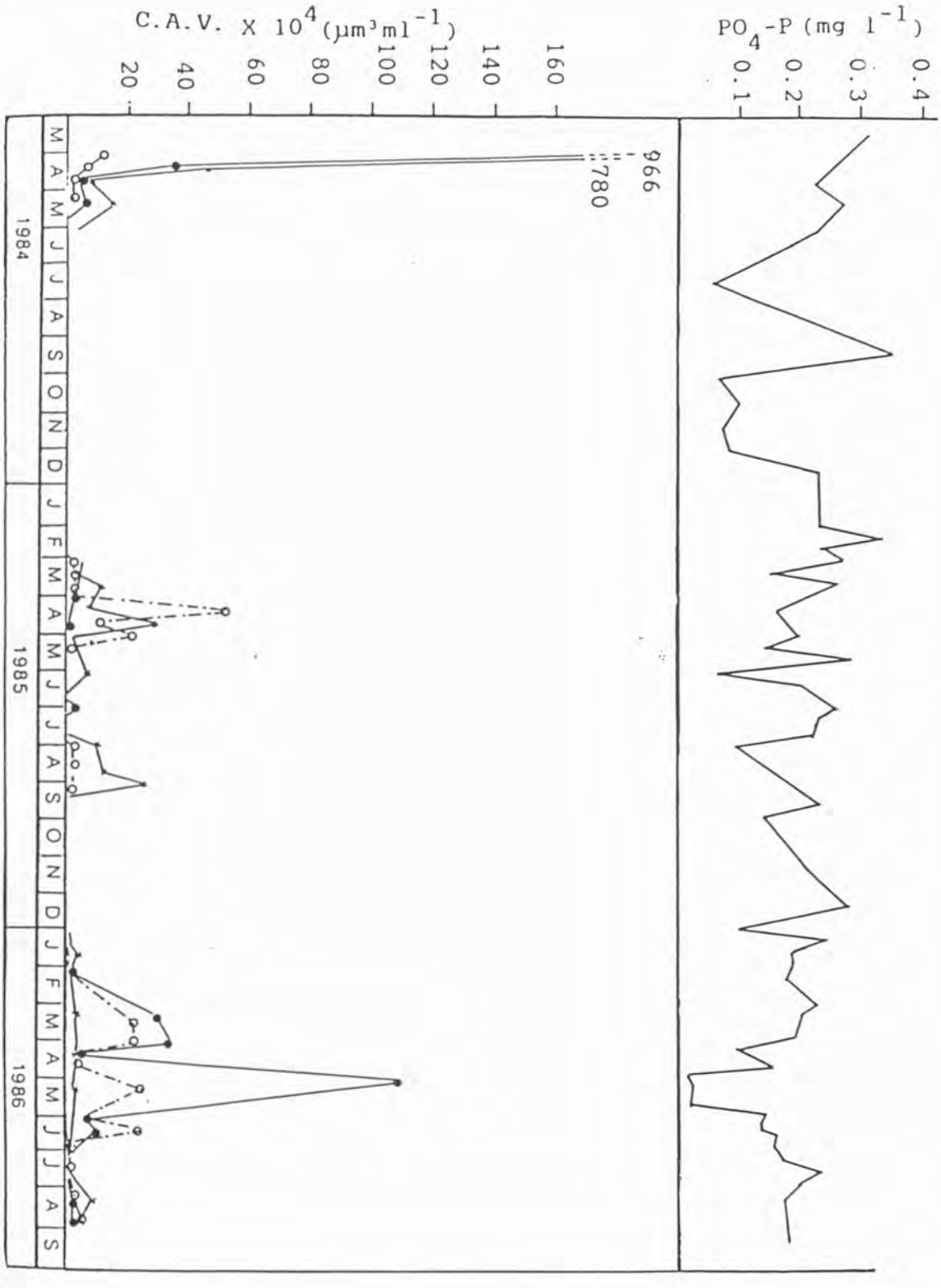

C.A.V. X 10^4 (µm³ml⁻¹)
20
40
60
80
100
120
140
160
966
780
PO4-P (mg l⁻¹)
0.1
0.2
0.3
0.4
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.20

Figure 3.21 Relationships between Bacillariophyceae and phosphate-phosphorus concentrations in the River Thames.

——— *Melosira varians*

—●— *Aulacoseira granulata*

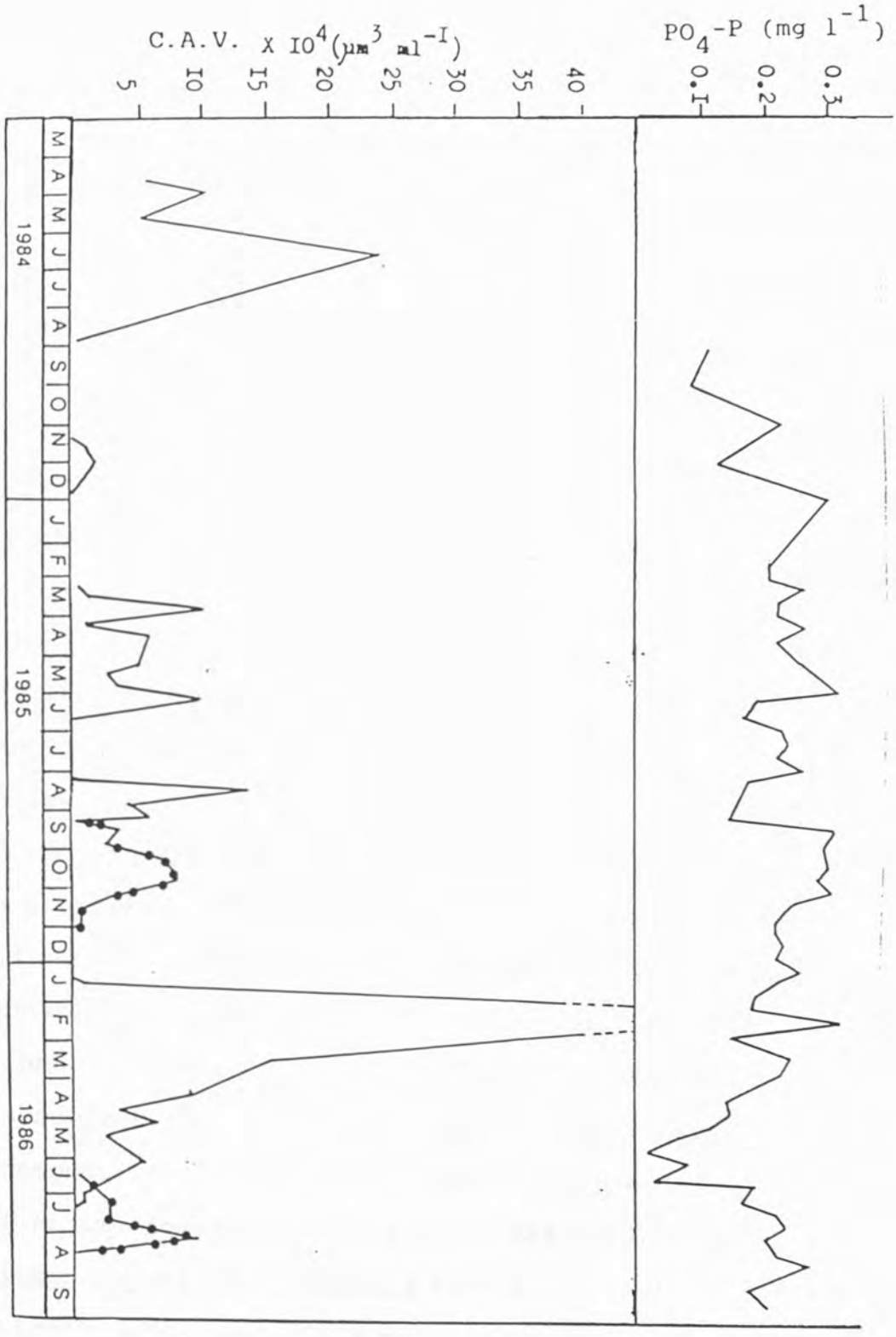

C.A.V. X IO^4(μm^3 ml^{-1})
5
IO
I5
20
25
30
35
40
PO$_4$-P (mg l^{-1})
0.I
0.2
0.3
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.21

culture (Stewart and Alexander,1971).These may contain sufficient phosphorus for many cell divisions and help to carry phytoplankton through short periods of phosphorus depletion.

The influence of phosphate-phosphorus concentrations in nature upon the growth of phytoplankton species was investigated.Figures 3.19-3.27 shows that there were inverse relationships between them.

Among Bacillariophyceae,there were shifts in dominant species from Stephanodiscus rotula in the early spring to Stephanodiscus hantzschii during the late spring, followed by Stephanodiscus rotula var.minutula during the summer and the reappearance of Stephanodiscus rotula during the autumn (Figures 3.19,3.20).This succession is believed to be due to lower requirements of successive species for phosphate-phosphorus.Stephanodiscus rotula dominated the diatom populations in the Wraysbury Reservoir during early spring and autumn when phosphate concentrations were higher. When phosphate concentration decreased gradually to about 0.18,0.09 and 0.08 mg l^{-1} in 1984,1985 and 1986,respectively, in the Wraysbury Reservoir and 0.16 and 0.02 mg l^{-1} in 1985 and 1986,respectively,in the River Thames,Stephanodiscus hantzschii became dominant.The shifts to the dominance of Stephanodiscus rotula var. minutula took place when the concentrations increased to 0.23 mg l^{-1}.

The shifts of Melosira varians in the early spring

Figure 3.22 Relationships between Bacillariophyceae and the phosphate-phosphorus concentrations in the Wraysbury Reservoir.

——— Melosira varians

—●— Aulacoseira granulata

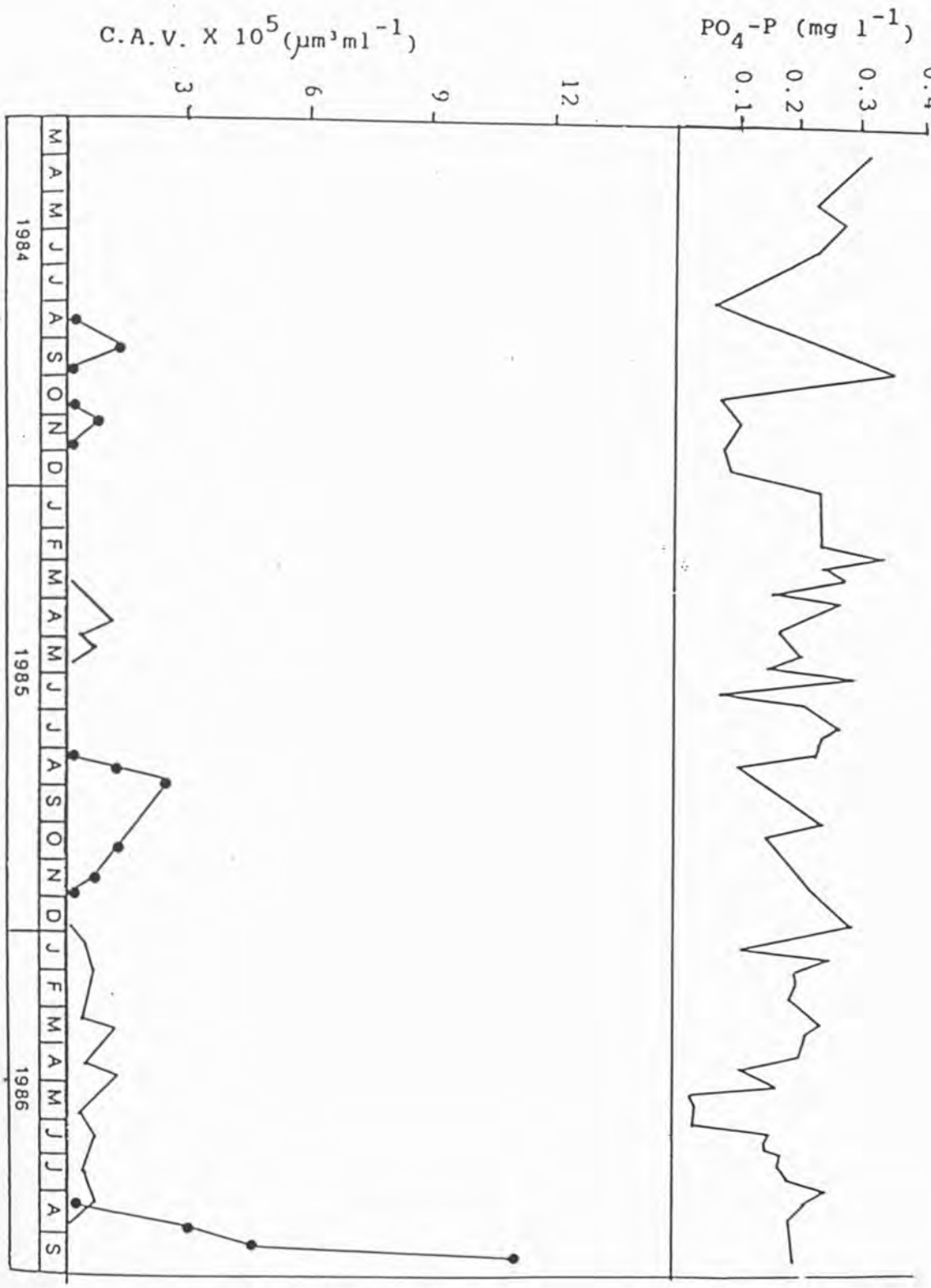

C.A.V. X 10^5 ($\mu m^3 ml^{-1}$)
3
6
9
12
PO_4-P (mg l^{-1})
0.1
0.2
0.3
0.4
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.22

Figure 3.23 Relationships between Chlorophyceae and the phosphate-phosphorus concentrations in the River Thames.

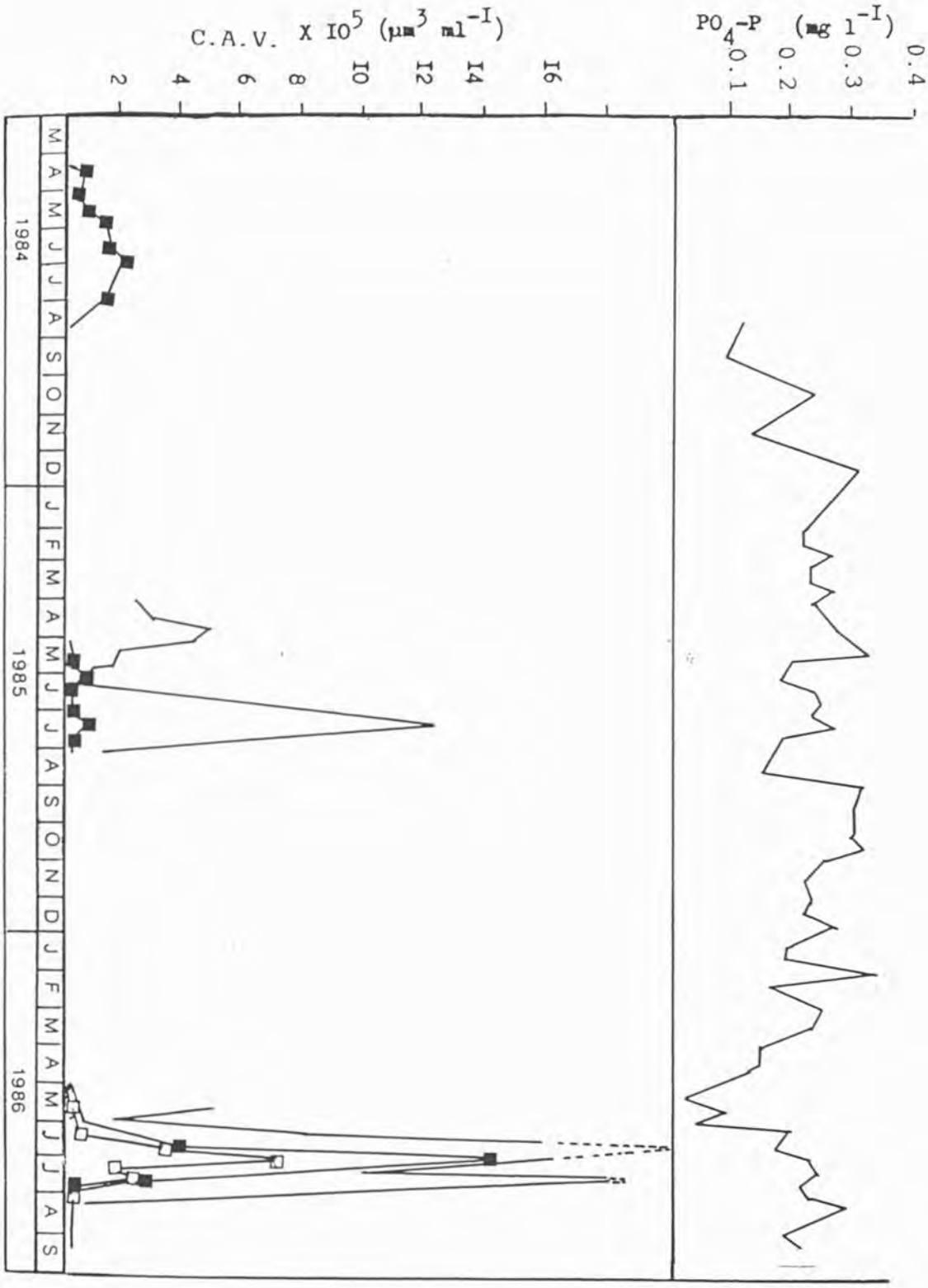

C.A.V. X IO^5 (μm^3 ml^{-1})
2
4
6
8
IO
I2
I4
I6
PO_4-P (mg l^{-1})
0.1
0.2
0.3
0.4
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.23

Figure 3.24 Relationships between Chlorophyceae and the phosphate-phosphorus concentrations in the Wraysbury Reservoir.

—◆— Scenedesmus quadricauda

—— Scenedesmus acuminatus

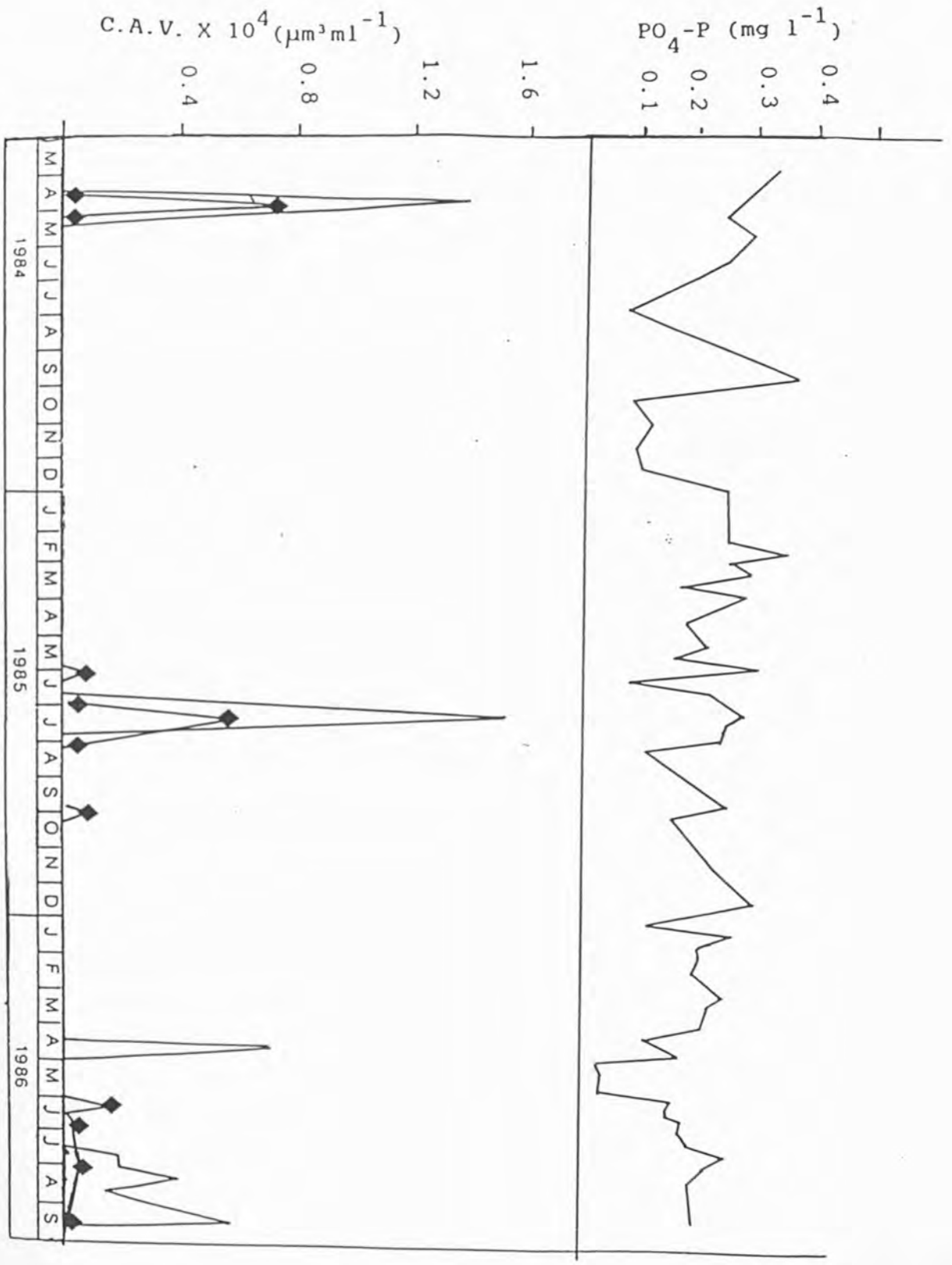

C.A.V. X 10^4 ($\mu m^3 ml^{-1}$)
0.4
0.8
1.2
1.6
PO_4-P (mg l^{-1})
0.1
0.2
0.3
0.4
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.24

Figure 3.25 Relationships between Cryptophyceae and the phosphate-phosphorus concentrations in the River Thames.

——— Rhodomonas minuta

—●— Cryptomonas spp.

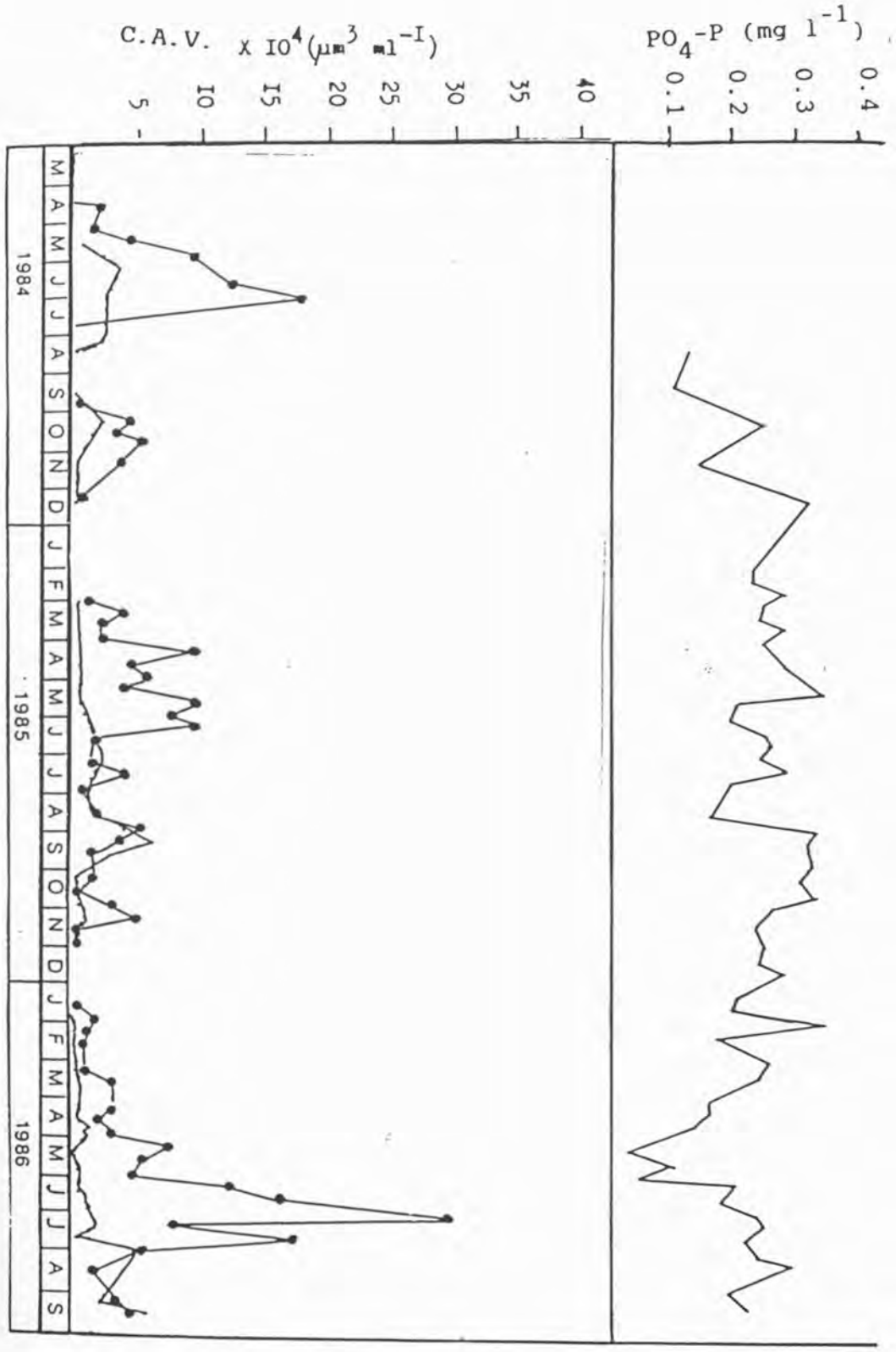

C.A.V. x 10^4 (μm^3 ml^{-1})
5
10
15
20
25
30
35
40
PO_4-P (mg l^{-1})
0.1
0.2
0.3
0.4
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.25

Figure 3.26 Relationships between Cryptophyceae and the phosphate-phosphorus concentrations in the Wraysbury Reservoir.

——— *Rhodomonas minuta*

—●— *Cryptomonas spp.*

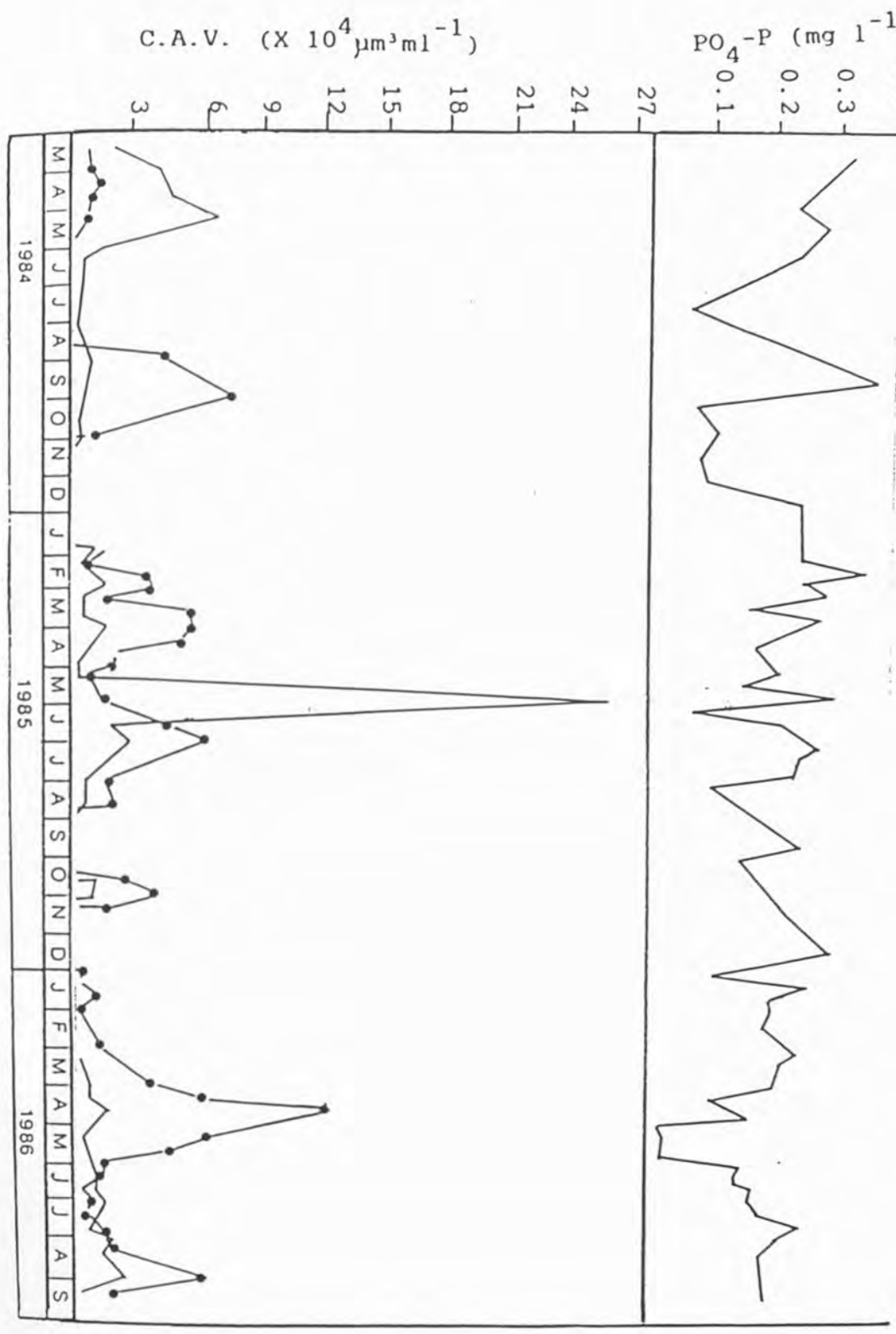

C.A.V. (X $10^4 \mu m^3 ml^{-1}$)
3
6
9
12
15
18
21
24
27
PO_4-P (mg l^{-1})
0.1
0.2
0.3
0.4
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.26

Figure 3.27 Relationships between Cyanobacteria and the phosphate-phosphorus concentrations in the Wraysbury Reservoir.

—— *Anabaena spp.*

—●— *Aphanizomenon flos-aquae*

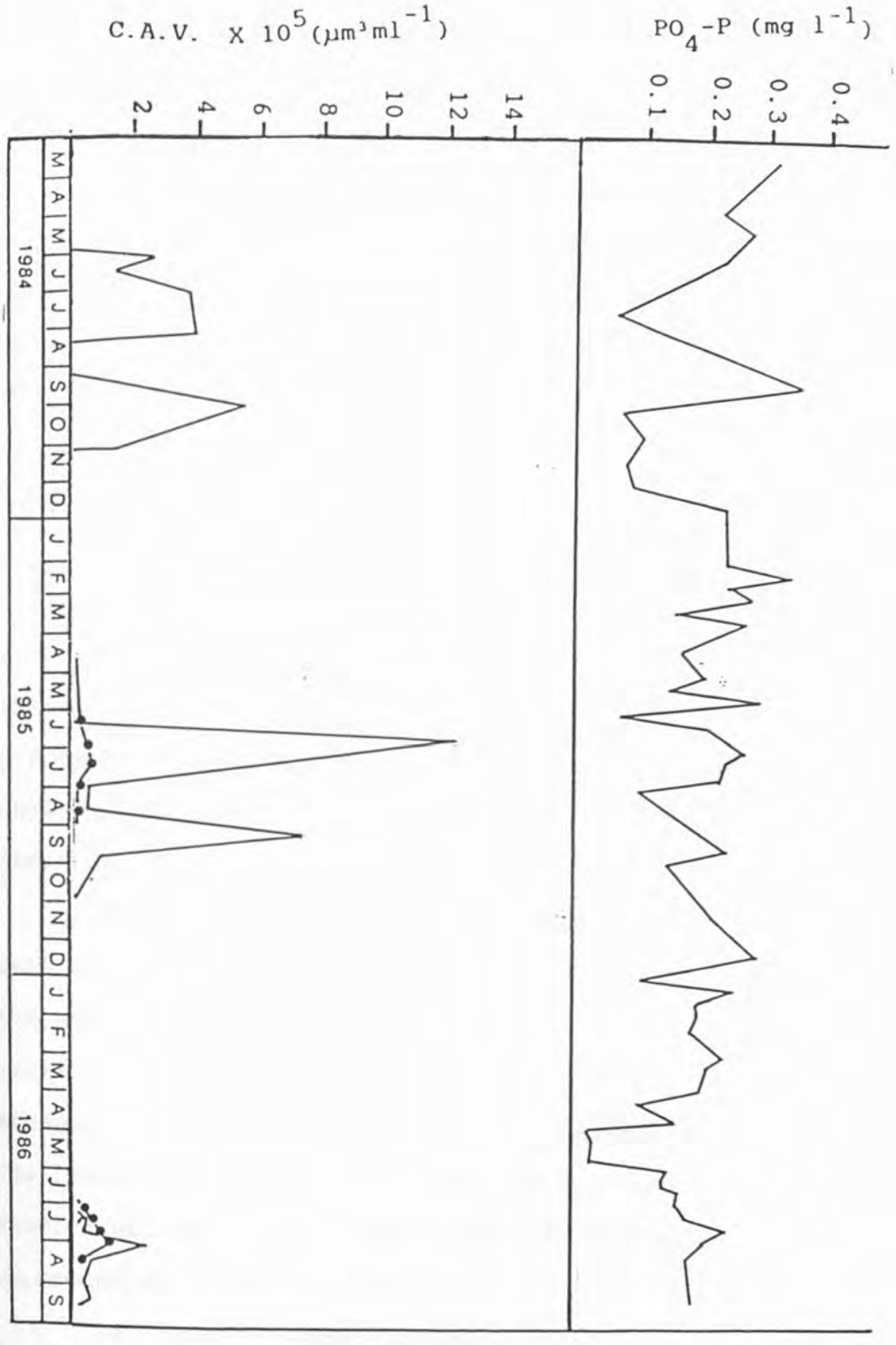

C.A.V. X 10^5 ($\mu m^3 ml^{-1}$)
PO_4-P (mg l^{-1})
0.1
0.2
0.3
0.4
2
4
6
8
10
12
14
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 3.27

(Figures 3.21,3.22) to Aulacoseira granulata in late summer occurred when phosphate-phosphorus concentration decreased to 0.1 mg l^{-1}.

Scenedesmus quadricauda and Scenedesmus acuminatus (Figures 3.23,3.24) appeared during the summer when high temperature and light occurred but nutrients concentrations were relatively low.

3.7.2.2 GROWTH IN CULTURE

The first important work specifically directed towards the solution of the limnological problems raised by nutritive requirements of planktonic algae appears to have been done by Frantzev (1932),whose contributions mainly established the possibility of such researches.His work was followed in the USSR by Guseva (1935).

From an ecological standpoint,the growth of algae in both natural and laboratory culture exhibits dependency on the amount of available phosphorus and the rate at which it cycled in the trophogenic zone.Extensive investigations of minimal and maximal phosphorus concentrations,especially by Chu (1943) and Rodhe (1949),grouped freshwater algae into categories according to whether their tolerance ranges fell below,around or above 20 µg PO_4-P l^{-1}:

(a) Species whose optimum growth and upper tolerance limit is below 20 µg PO_4-P l^{-1},e.g.

Dinobryon divergens, Uroglena americana and some species of Chara.

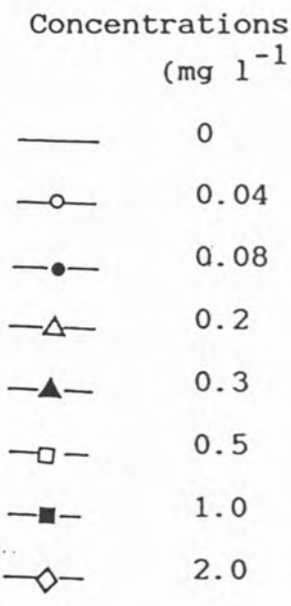
(b) Species whose optimum growth is below 20 µg PO_4-P l^{-1}, but whose tolerance limit is well above that level, e.g. Asterionella formosa and other diatoms.

(c) Species whose optimum growth and upper tolerance limit is above 20 µg PO_4-P l^{-1}, e.g. green algae such as Scenedesmus, Ankistrodesmus and many others.

Most planktonic algae fall into the groups with low or medium phosphorus tolerance. Vollenweider (1968) comments that exceptions to this grouping have been reported and that he and his co-worker have been unable to confirm the results with Dinobryon or Uroglena. On the basis of culture work, it is difficult to accept the idea of phosphate toxicity at µg l^{-1} levels (Nalewajko and Lean, 1980). Various media devised by Chu (1942) and found to be suitable for a great variety of planktonic algae, contain phosphate at the level of mg PO_4-P l^{-1}. His work on upper tolerance limits for phosphate in cultures showed values above 9-18 mg PO_4-P l^{-1}, far in excess of concentrations found in natural waters.

Figures 3.28, 3.29, 3.30, 3.31 and 3.32 showed the growth response of Scenedesmus quadricauda, Ankistrodesmus falcatus, Eudorina elegans, Tribonema vulgare and Stephanodiscus ref. hantzschii to different phosphate-

Figure 3.28 The growth of Scenedesmus quadricauda in Chu's medium No.10 with different concentrations of phosphate-phosphorus.



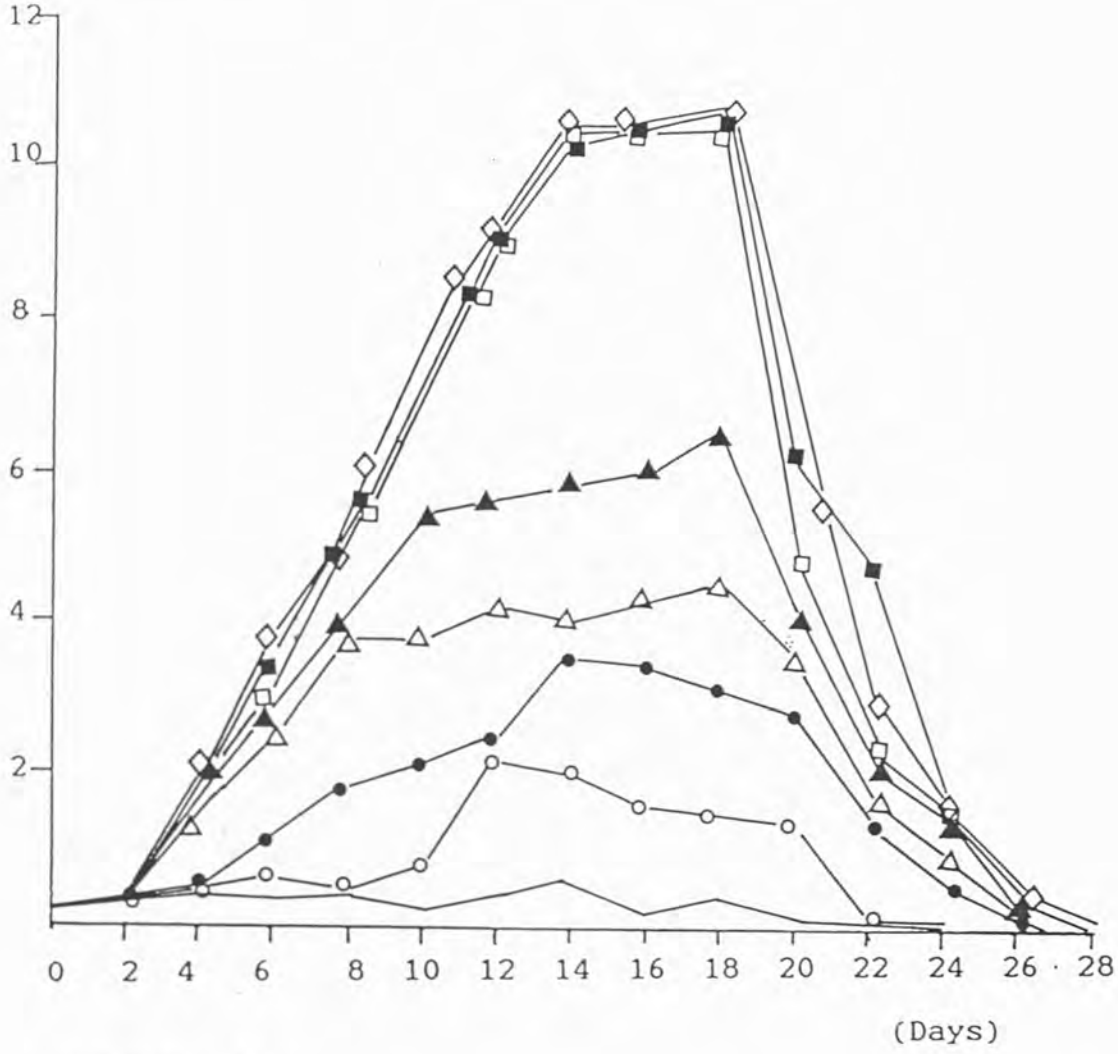


Figure 3.28

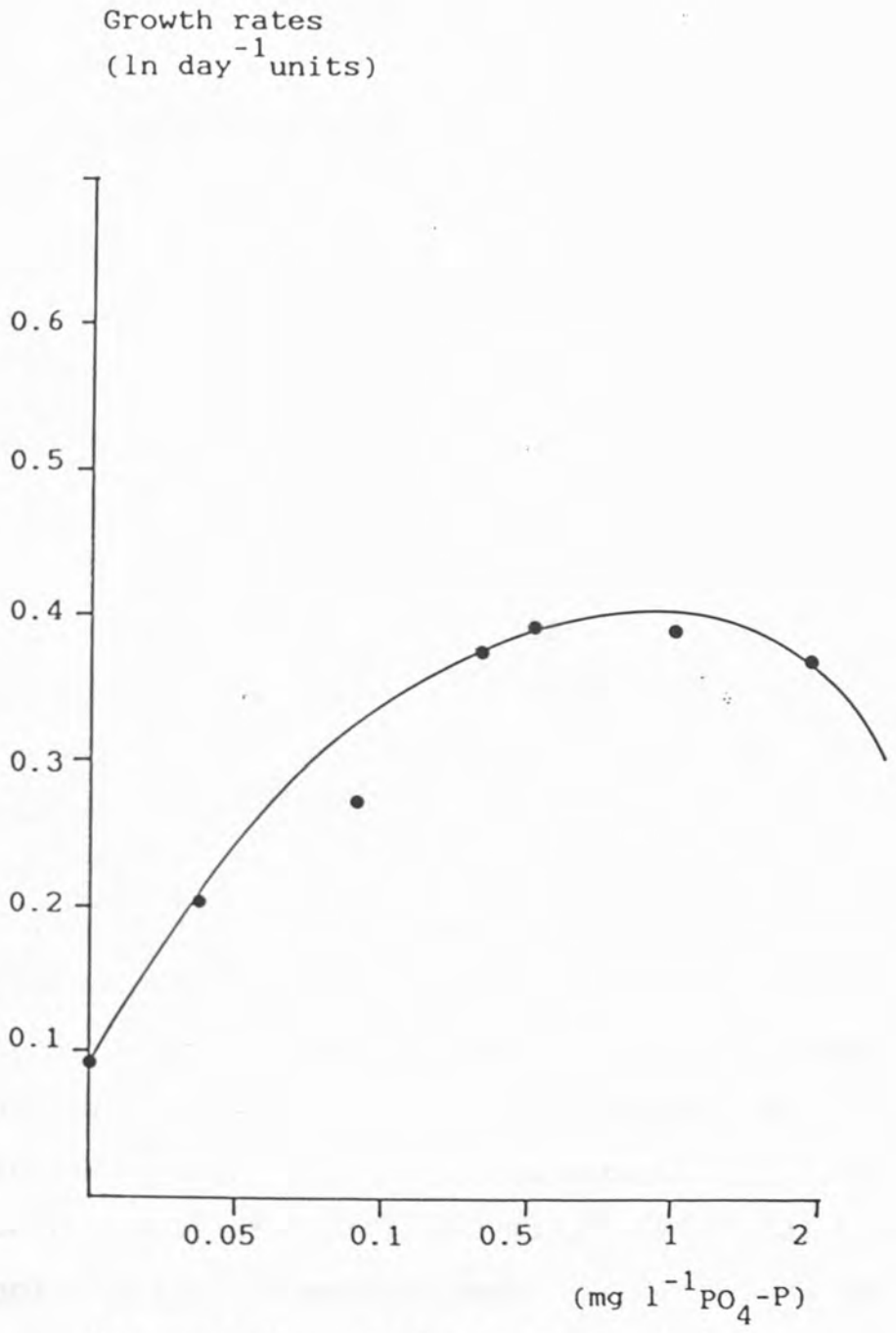


Figure 3.28a Effects of phosphate-phosphorus on the growth rates of Scenedesmus quadricauda.

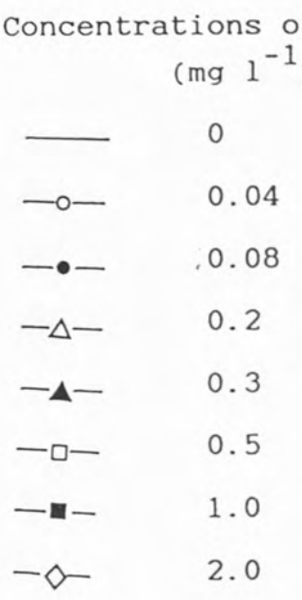
phosphorus concentrations.

From the results presented in Figure 3.28 it was found that the absence of phosphate in the medium inhibited the growth of Scenedesmus quadricauda. The culture grew proportionally with concentrations of phosphate in the range 0.04 to 0.5 mg l^{-1}. The slope of the growth curves was not affected by increasing concentrations of phosphate, but the maximum of growth was affected.

The Monod model was found to describe adequately the relationship between phosphate concentration and growth rate in chemostats in Monochrysis lutheri (Droop, 1974) and has been extended by Titman (1976) to studies of inter-specific competition for phosphate and silicate between Asterionella formosa and Cyclotella meneghiniana. This model was used during this study to find the level of nutrients concentration for the optimum growth rate. From Figure 3.28a it was found that a concentration of 0.5 mg l^{-1} phosphate was needed for the optimum growth of Scenedesmus quadricauda. Growth was inhibited when the concentrations were more than 1 mg l^{-1} phosphate. This agrees with the category of freshwater algae established by Chu (1943) and Rodhe (1948) indicating that Scenedesmus spp. are species whose optimal growth and tolerance limit is above 20 μg PO_4-P l^{-1} although the concentrations found in this study were high.

The experiment carried out with Ankistrodesmus falcatus showed that by increasing phosphate concentration,

Figure 3.29 The growth of Ankistrodesmus falcatus in Chu's medium No.10 with different concentrations of phosphate-phosphorus.



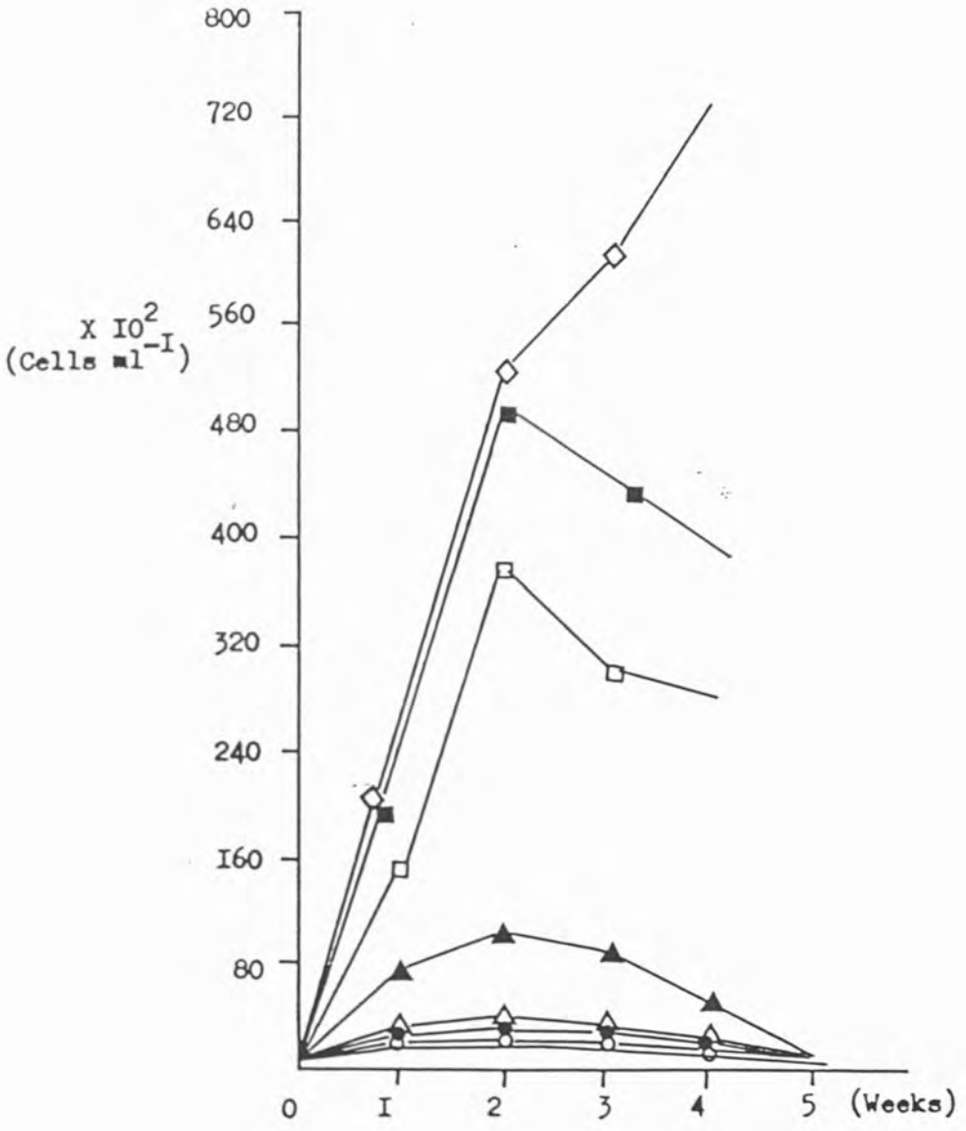

800
720
640
560
480
400
320
240
160
80
X 10^2
(Cells ml^{-1})
0
1
2
3
4
5
(Weeks)

Figure 3.29

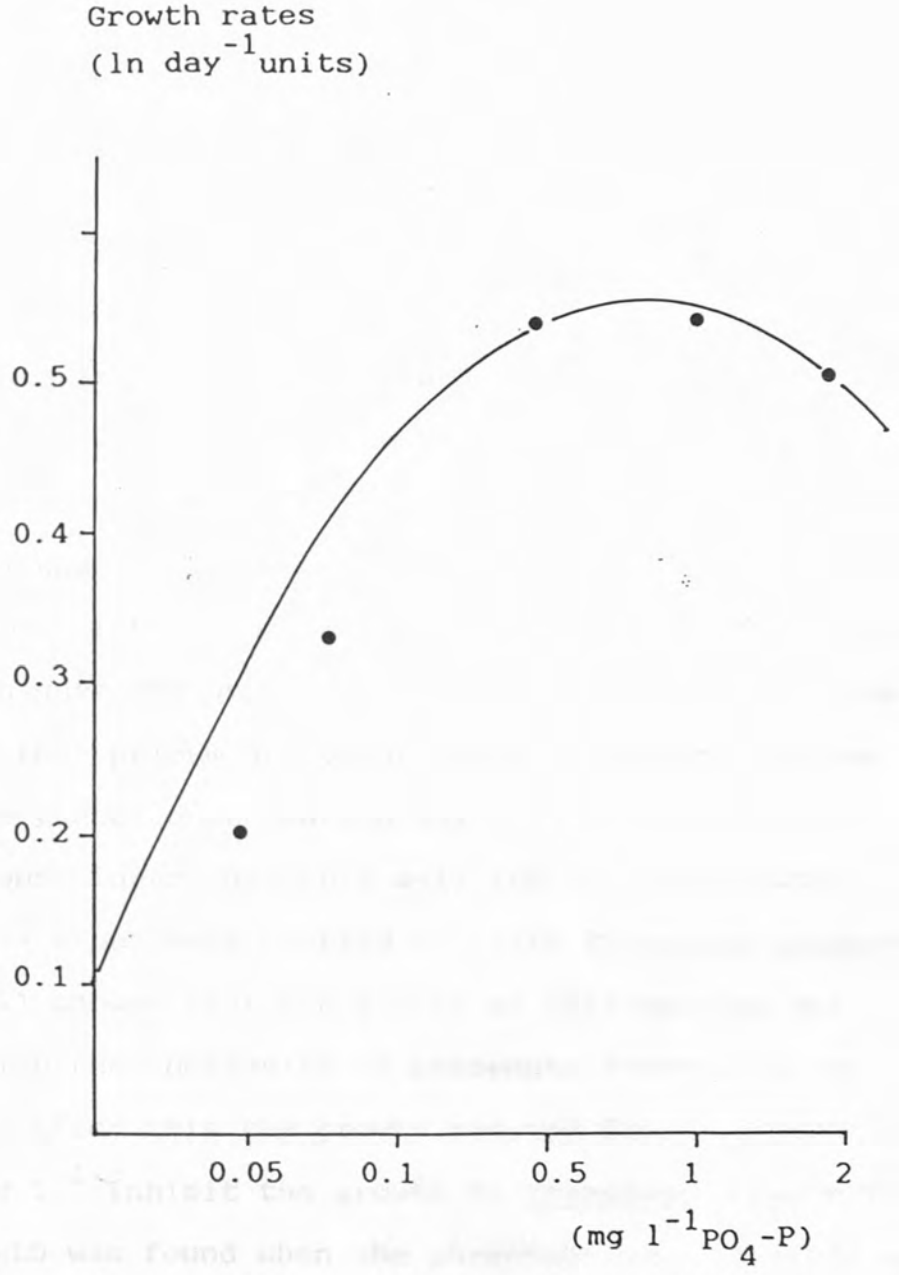


Figure 3.29a Effects of phosphate-phosphorus on the growth rates of Ankistrodesmus falcatus.

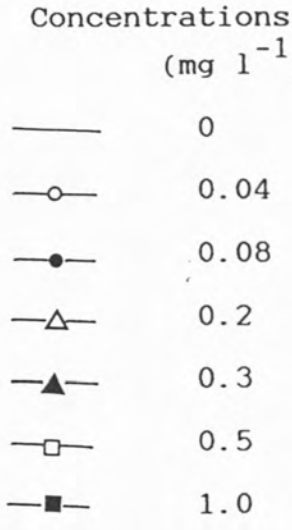
higher growth could be obtained (Figure 3.29).The culture grew proportionally with the concentrations of phosphate in the range 0.2 to 2 mg l^{-1}.The concentrations of 0 to 0.08 mg l^{-1} of phosphate inhibited the growth of Ankistrodesmus falcatus.Figure 3.29a showed that the upper tolerance concentrations of phosphate for the optimum growth of Ankistrodesmus falcatus was 0.2 mg l^{-1}.The result also agreed with those of Chu(1943) and Rodhe (1948).

Eudorina elegans (Figure 3.30) showed the inhibition of growth when the concentrations of phosphate in in the range 0 to 0.04 mg l^{-1}.Concentrations from 0.08 to 0.3 mg l^{-1} increased the growth proportionally with the concentrations of phosphate.However the growth of Eudorina elegans in higher concentrations was inhibited.Figure 3.30a showed that the optimum growth of Eudorina elegans reached when the phosphate concentration was 0.35 mg l^{-1}. Concentrations higher than this will inhibit the growth.

The experiment carried out with Tribonema vulgare (Figure 3.31) showed that the growth of this species was increased with the increasing of phosphate concentrations until day 21.After this the growth reduced.Concentrations 0 to 0.08 mg l^{-1} inhibit the growth of Tribonema vulgare.The optimum growth was found when the phosphate concentration was 0.1 mg l^{-1} (Figure 3.31a).

From the culture experiments (Figure 3.32) with Stephanodiscus ref.hantzschii it was found that the growth of

Figure 3.30 The growth of Eudorina elegans in Chu's medium No.10 with different concentrations of phosphate-phosphorus.



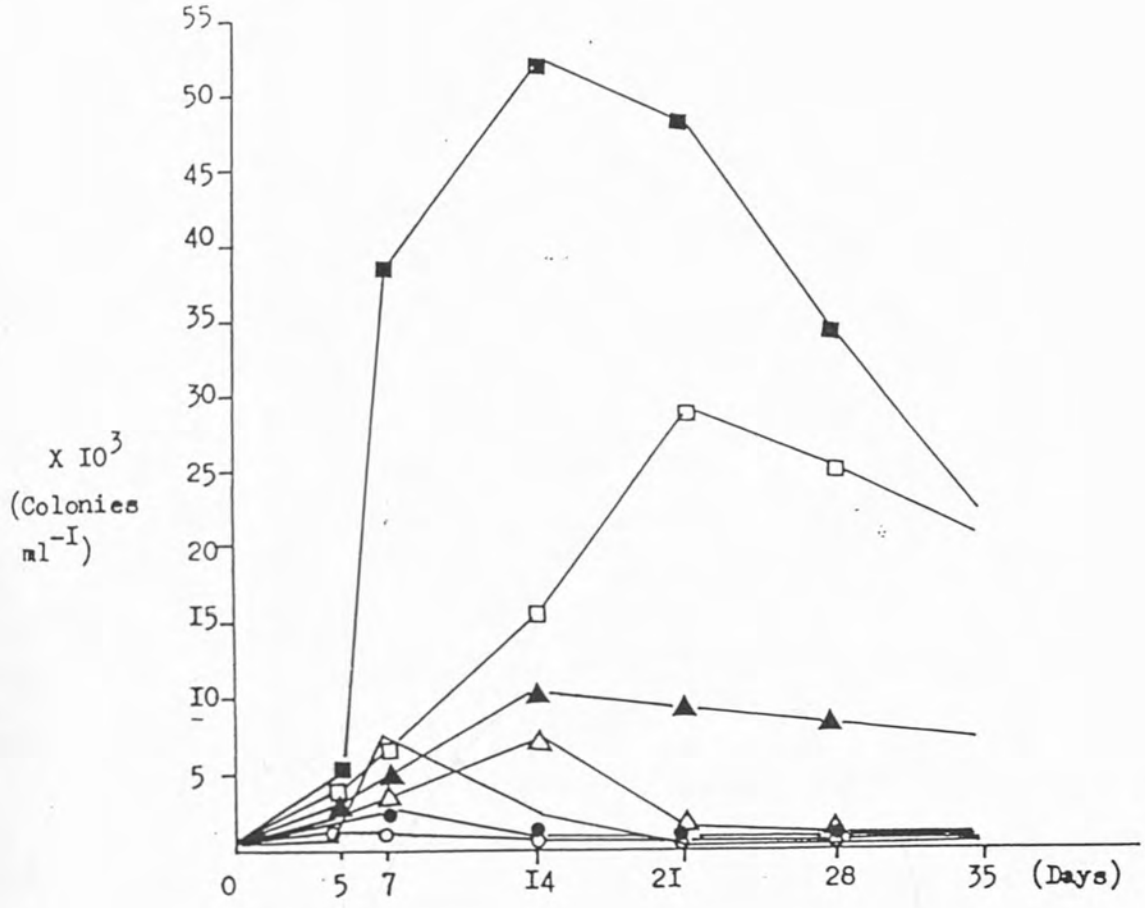

55
50
45
40
35
30
25
20
I5
I0
5
X I0^3
(Colonies
ml^{-I})
0
5
7
I4
2I
28
35
(Days)

Figure 3.30

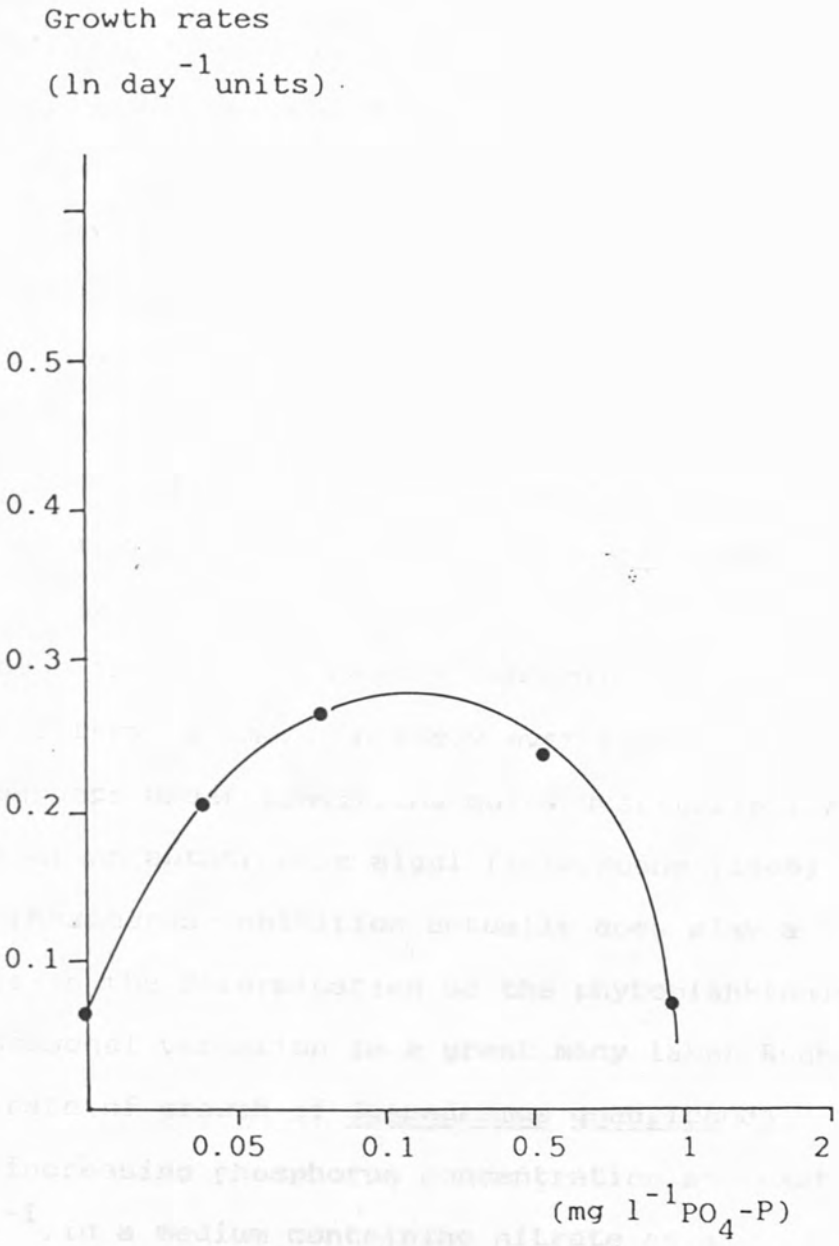


Figure 3.30a Effects of phosphate-phosphorus on the growth rates of Eudorina elegans.

this species yielded proportionally with the concentrations of phosphate in the range from 0.02 to 3 mg l^{-1}. The lower concentrations of phosphate that is 0 and 0.01 mg l^{-1} inhibited the growth of Stephanodiscus ref. hantzschii. The optimum growth of Stephanodiscus ref. hantzschii reached when the phosphate concentration was 0.8 mg l^{-1} (Figure 3.32a).

There appeared to be a rather wide range of concentrations at which further increase of the phosphorus had no effect in increasing the growth of Scenedesmus quadricauda, Ankistrodesmus falcatus and Stephanodiscus ref. hantzschii but inhibition occurred when sufficiently large amounts of phosphorus were added to the medium with Tribonema vulgare and Eudorina elegans.

Although the high phosphorus concentrations found to be inhibitory are most unlikely ever to occur in nature, except perhaps under conditions quite unsuitable for the development of an autotrophic algal flora, Rodhe (1948) indicates that phosphorus inhibition actually does play a significant role in the determination of the phytoplanktonic flora and its seasonal variation in a great many lakes. Rodhe found that the rate of growth of Scenedesmus quadricauda increased with increasing phosphorus concentration, at least up to 1000 mg l^{-1}, in a medium containing nitrate as a nitrogen source. Up to about 500 mg l^{-1} the growth rate was proportional to the phosphorus concentration, and very slight growth was detected in a medium containing 10 mg l^{-1}. The

Figure 3.31 The growth of Tribonema vulgare in Chu's medium No.10 with different concentrations of phosphate-phosphorus.

	Concentrations of PO_4-P ($mg\ l^{-1}$)
———	0
—○—	0.04
—●—	0.08
—△—	0.2
—▲—	0.3
—□—	0.5
—■—	1.0

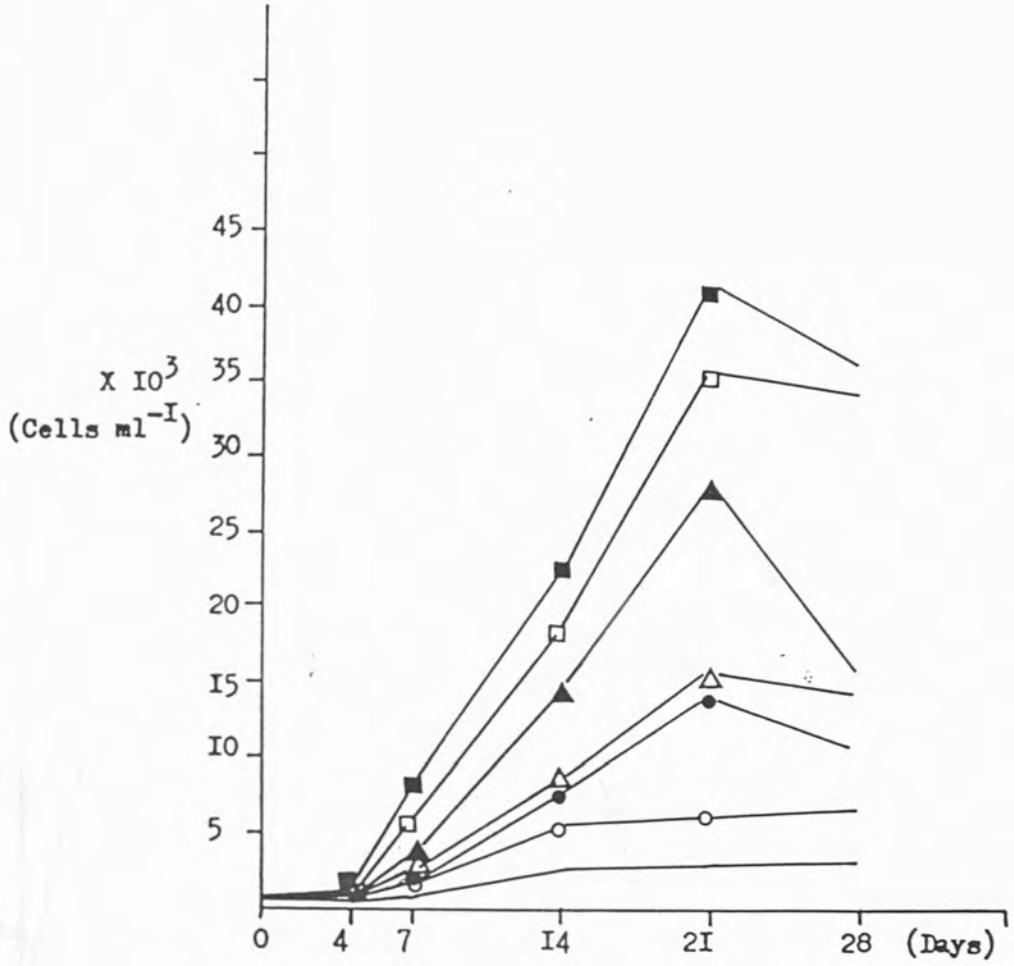


Figure 3.31

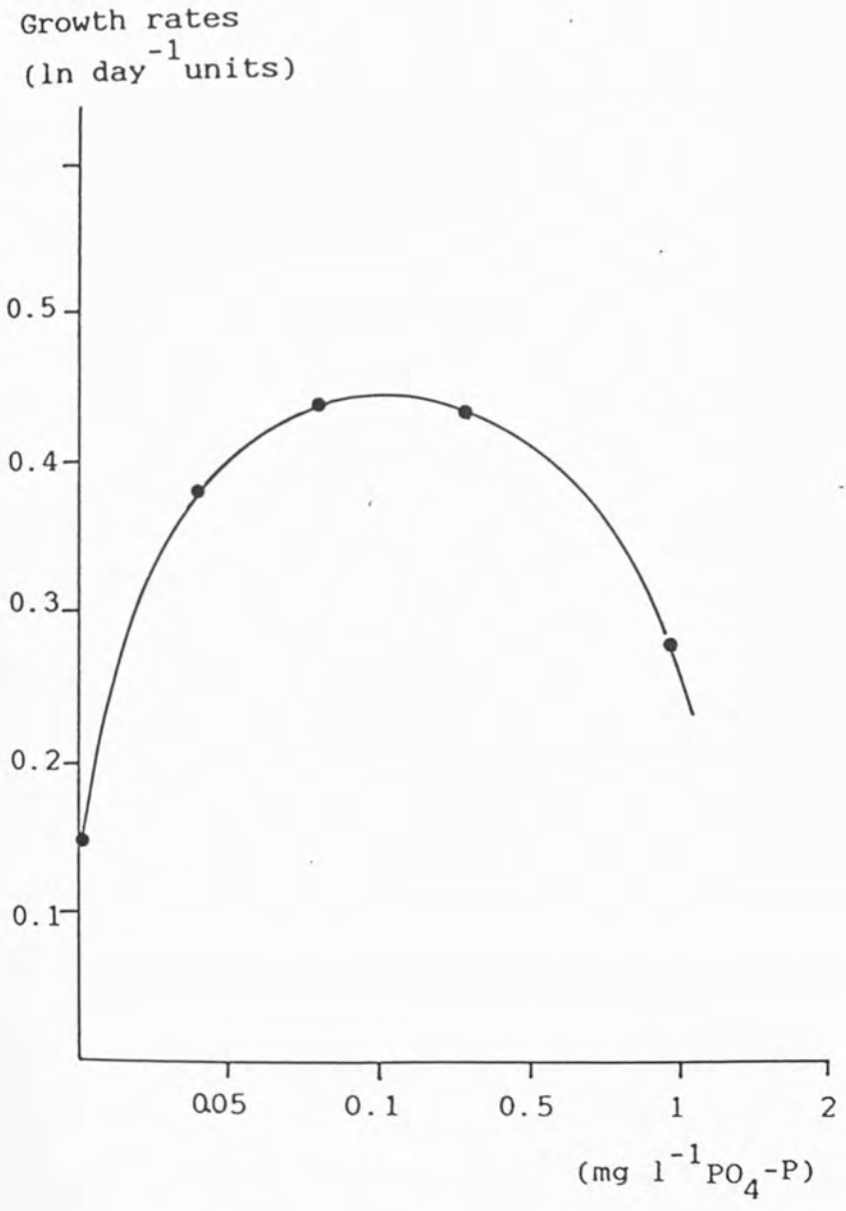
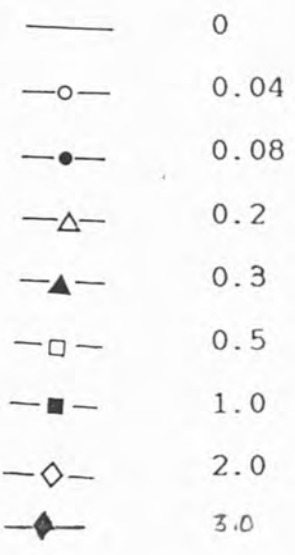


Figure 3.31a Effects of phosphate-phosphorus on the growth of Tribonema vulgare.

Figure 3.32 The growth of Stephanodiscus ref.hantzschii in Chu's medium No.10 with different concentrations of phosphate-phosphorus.



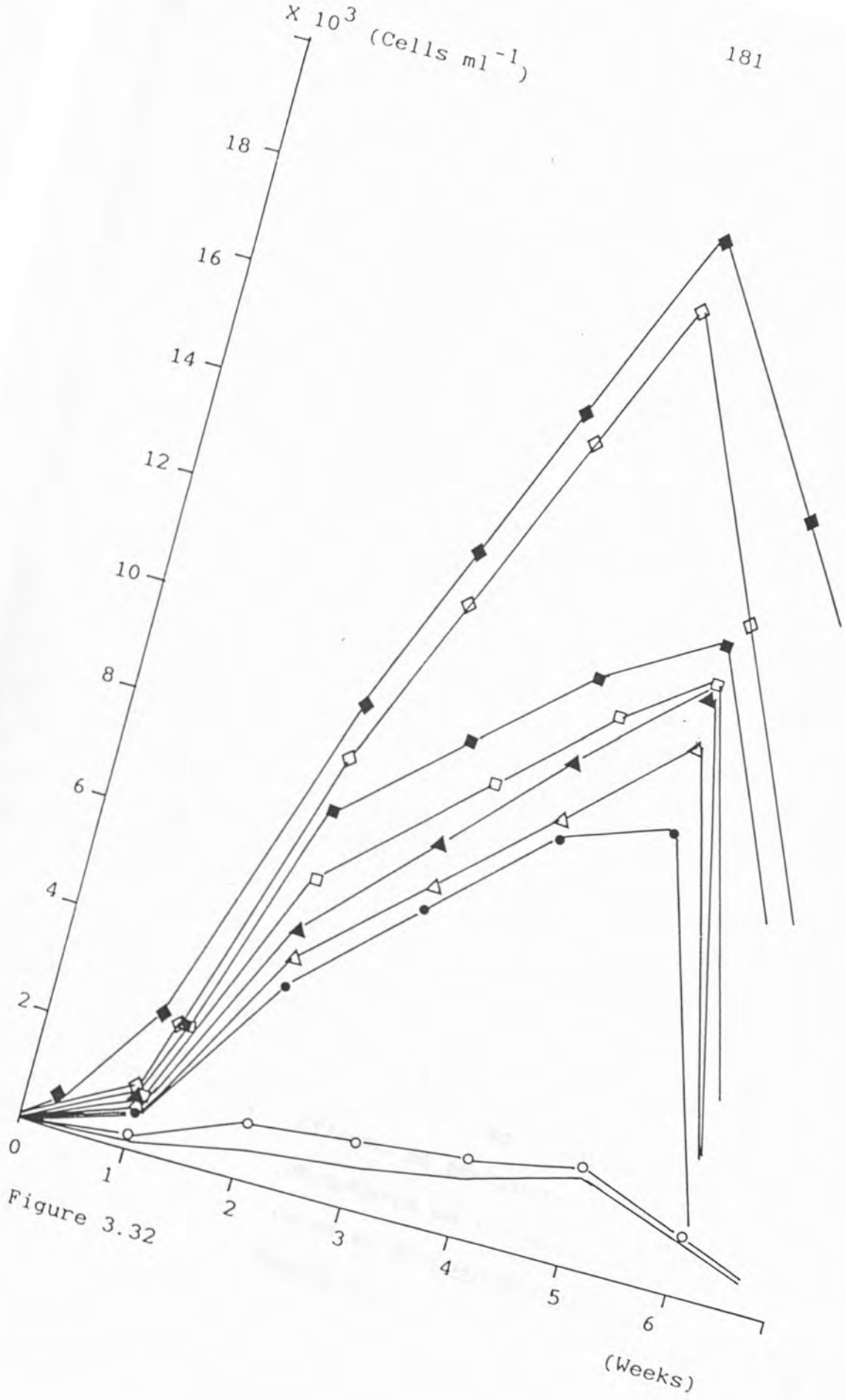


Figure 3.32

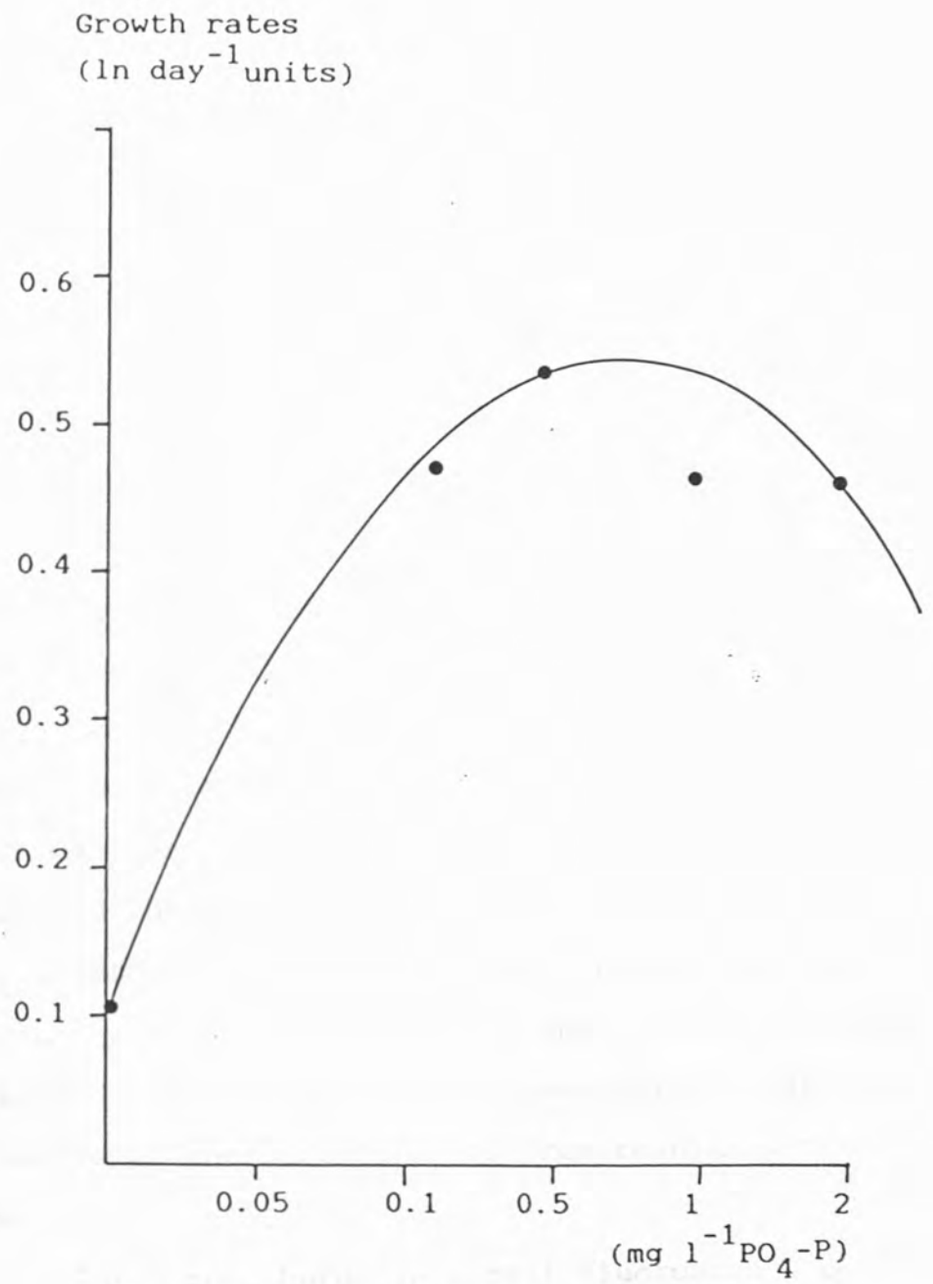


Figure 3.32a Effects of phosphate-phosphorus on the growth rates of Stephanodiscus ref. hantzschii.

concentrations investigated by Rodhe were much higher than those considered in the present work.

The occurrence and periodicity of a species is seldom, if ever, determined by one factor, let alone by one nutrient; and Pearsall (1930, 1932), in addition to attaching importance to concentrations of a certain nutrient, also regarded ratios, of nitrate to phosphate for example, as as important factors in species succession. For example, with regard to the autecology of Dinobryon divergens, he noted that it appears when this ratio rises, although concentrations of calcium and silica were also thought to be important. Since changes in nitrate concentrations at the time of the Dinobryon appearance were small, a decrease in phosphate concentration emerged as the controlling factor (Lund, 1965) and this was confirmed by Rodhe's (1948) culture experiments which showed the growth of the species was inhibited by 5 $\mu g\ l^{-1}$ PO_4-P. Yet the occurrence of other Dinobryon species at much higher phosphate levels (Hutchinson, 1967; Lund, 1965) must be a warning to ecologists not to generalize about nutrient requirements at the generic level from results with a single species.

Total phosphorus in a cell fluctuates with changes in the phosphorus supply. The C:N:P atomic ratio also changes. Fuhs et al., (1972) cited ratios for growing algae are 106:16:1 or 100:15:1. Over large areas of the ocean C:N:P ratios in phytoplankton approximate to 108:15.5:1 (Redfield

et al.,1963).In culture,the 100:15:1 ratio was reached when the phosphorus supply permitted growth to occur at 50-75% of the maximum rate.Severe phosphorus limitation resulted in N:P ratio rising to 35:1.Under phosphorus starvation cells reach a minimum cell phosphorus content below which no further growth occurs (Droop,1973).

The interest in storage or 'luxury consumption' of phosphorus by algae was initiated by Mackereth (1953),who showed that Asterionella formosa stored 25 times the minimum cell content of phosphorus before the spring outburst of growth and then continued dividing,with a concomitant decline in the cell phosphorus level.This phenomenon could explain the reason for the increase of the growth of phytoplankton in culture with the increase of phosphate concentration higher than phosphate concentration in the nature.

From culture experiments it was found that Stephanodiscus ref.hantzschii have the highest maximum growth rate (û) (0.55 cell divisions per day) of all the species which have been experimentally investigated (Scenedesmus quadricauda,Ankistrodesmus falcatus,Eudorina elegans and Tribonema vulgare).It also has the highest half saturation constant,that is,the substrate concentration at which half the maximum growth rate occurs (Ks),relative to other species except Scenedesmus quadricauda in which Ks (0.035 mg l^{-1} PO_4-P) is equal.This showed that Stephanodiscus ref. hantzschii requires high concentrations of nutrients for

Figure 3.3 3 Seasonal variations of silica concentrations in the River Thames.


Silica (mg l⁻¹)
3
6
9
12
15
18
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.33

Figure 3.34 Seasonal variations of silica concentrations in the Wraysbury Reservoir.

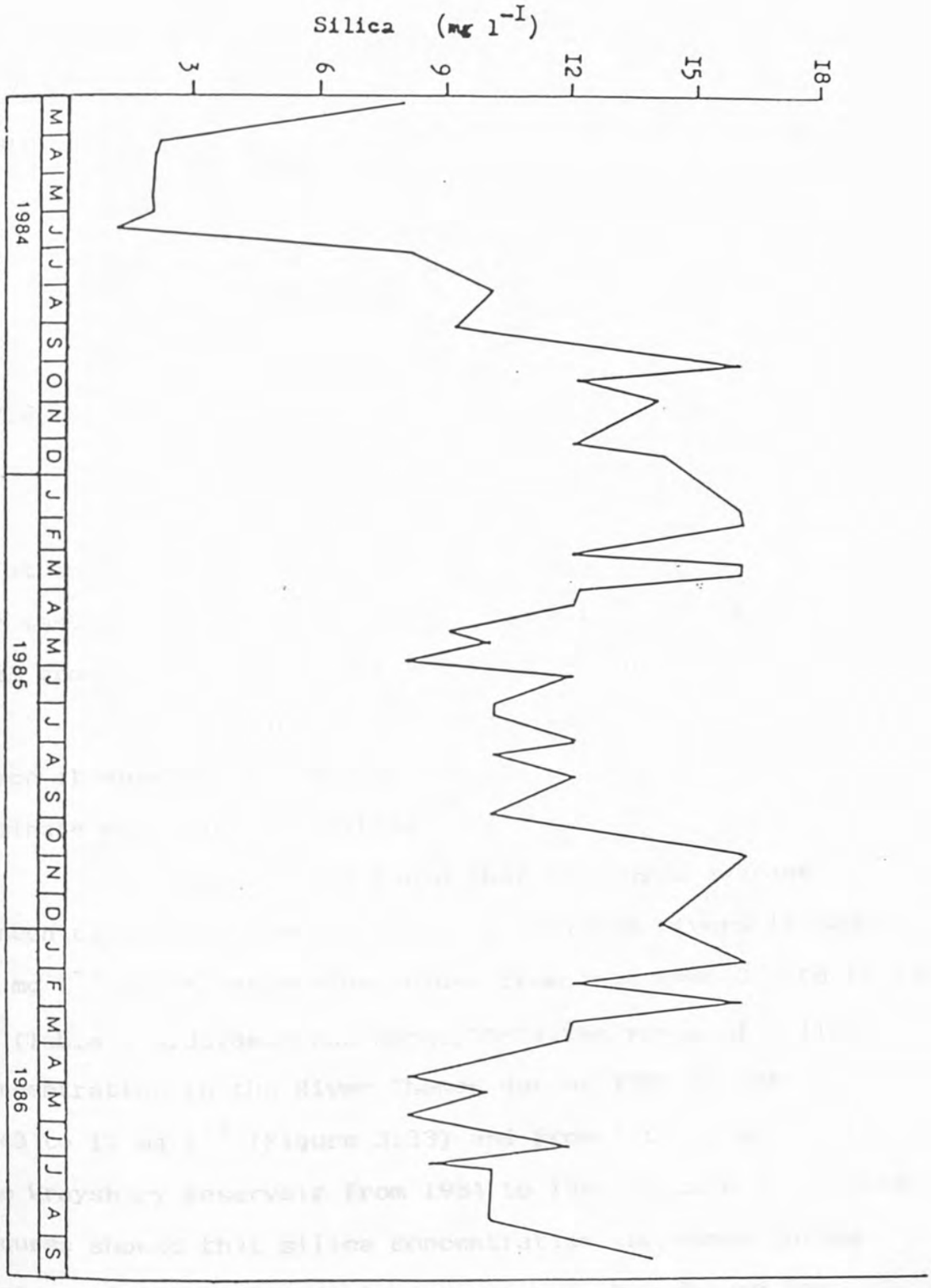

Silica (mg l⁻¹)
3
6
9
12
15
18
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 3.34

growth. Therefore, from studies on the growth of phytoplankton populations in nature it was found that diatoms, particularly, Stephanodiscus ref. hantzschii dominates phytoplankton populations in spring when high nutrient concentrations occur.

3.7.3 THE INFLUENCE OF SILICA ON THE GROWTH OF PHYTOPLANKTON POPULATIONS

3.7.3.1 GROWTH IN NATURE

Silica may be said to be a limiting nutrient either if it is depleted to the point where no further diatom growth can take place, or if it occurs in such low concentrations that growth rates are significantly reduced.

In lakes and seas silica plays an intriguing role since it apparently accounts for the success of diatoms which dominate most aquatic systems.

Various workers found that the world average concentration for dissolved silica in large rivers is about 13 mg l^{-1} while lakes show values from less than 0.5 to 60 mg l^{-1} (Table 3.3, Goldman and Horne, 1983). The range of silica concentration in the River Thames during 1985 to 1986 was 1.43 to 17 mg l^{-1} (Figure 3.33) and from 1 to 16 mg l^{-1} in the Wraysbury Reservoir from 1984 to 1986 (Figure 3.34). Both figures showed that silica concentration increased during winter and decreasing during summer and when diatom was

Table 3.3. CONCENTRATIONS (mg l^{-1}) OF SOLUBLE SILICA IN THE SURFACE WATERS OF VARIOUS LAKES AND RIVERS.

Lake or River	SiO_2	References
Castle, Calif.	1.3	Goldman, various sources
Titicaca, Andes	0.07-1.1	Richerson et al.; 1977
Baikal, Siberia	~3	Kozhov, 1963
World average lakes and rivers	12	Livingstone, 1963
North American rivers, average	9	Livingstone, 1963
European rivers average	7.5	Livingstone, 1963
Nile, Khartoum	26	Livingstone, 1963
Rhine, Netherlands	5.7	Livingstone, 1963
Amazon (Narrow Santarem)	11.1	Livingstone, 1963
Truckee at km 15	16	Livingstone, 1963,

(Modified from Goldman and Horne, 1983)

Figure 3.35 Relationships between Bacillariophyceae and silica concentrations in the River Thames.

—— *Melosira varians*

—●— *Aulacoseira granulata*

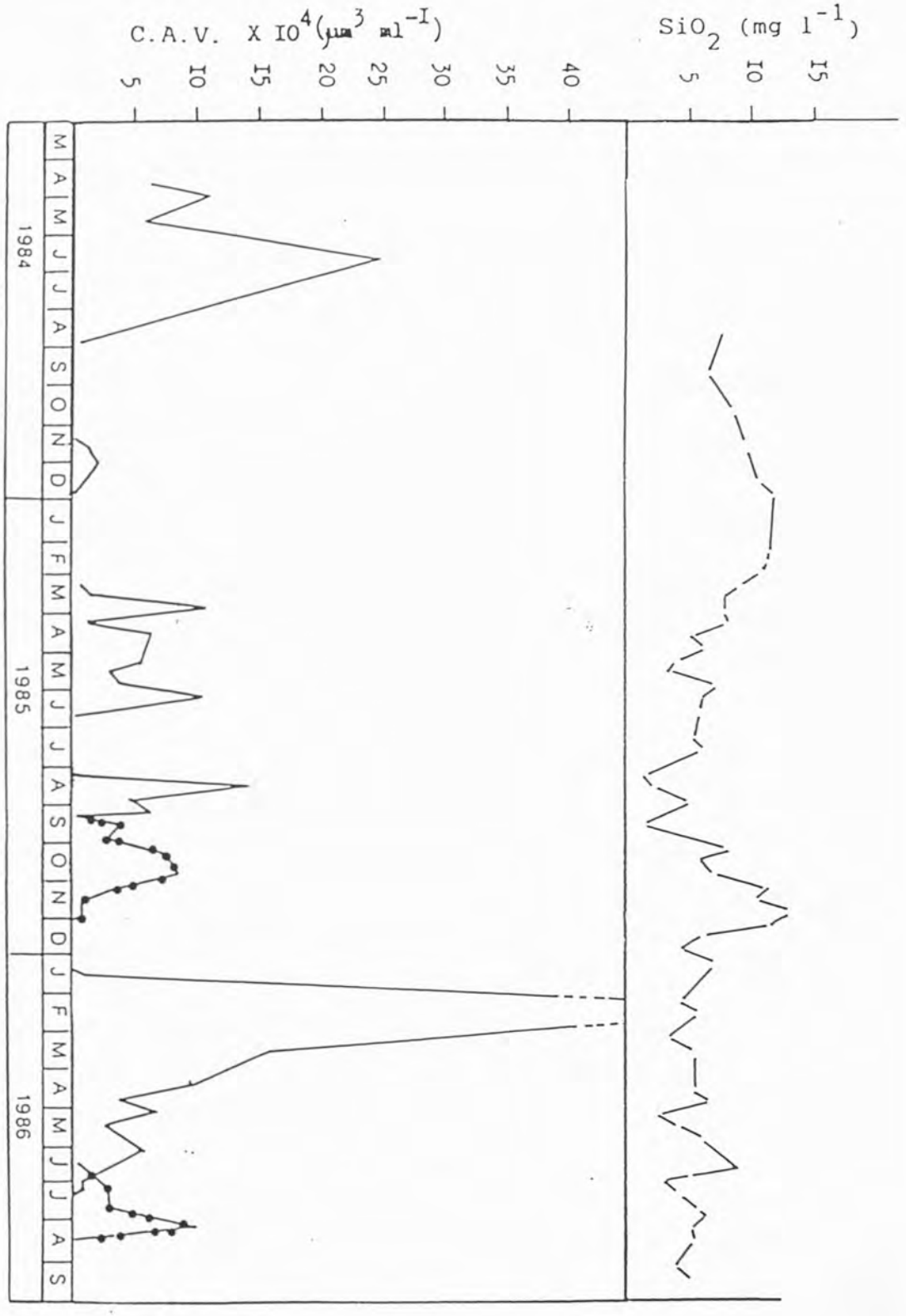

C.A.V. X IO^4(µm^3 ml^{-1})
5
IO
I5
20
25
30
35
40
SiO_2 (mg l^{-1})
5
IO
I5
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.35

Figure 3.36 Relationships between Bacillariophyceae and silica concentrations in the Wraysbury Reservoir.

—— Melosira varians

—●— Aulacoseira granulata

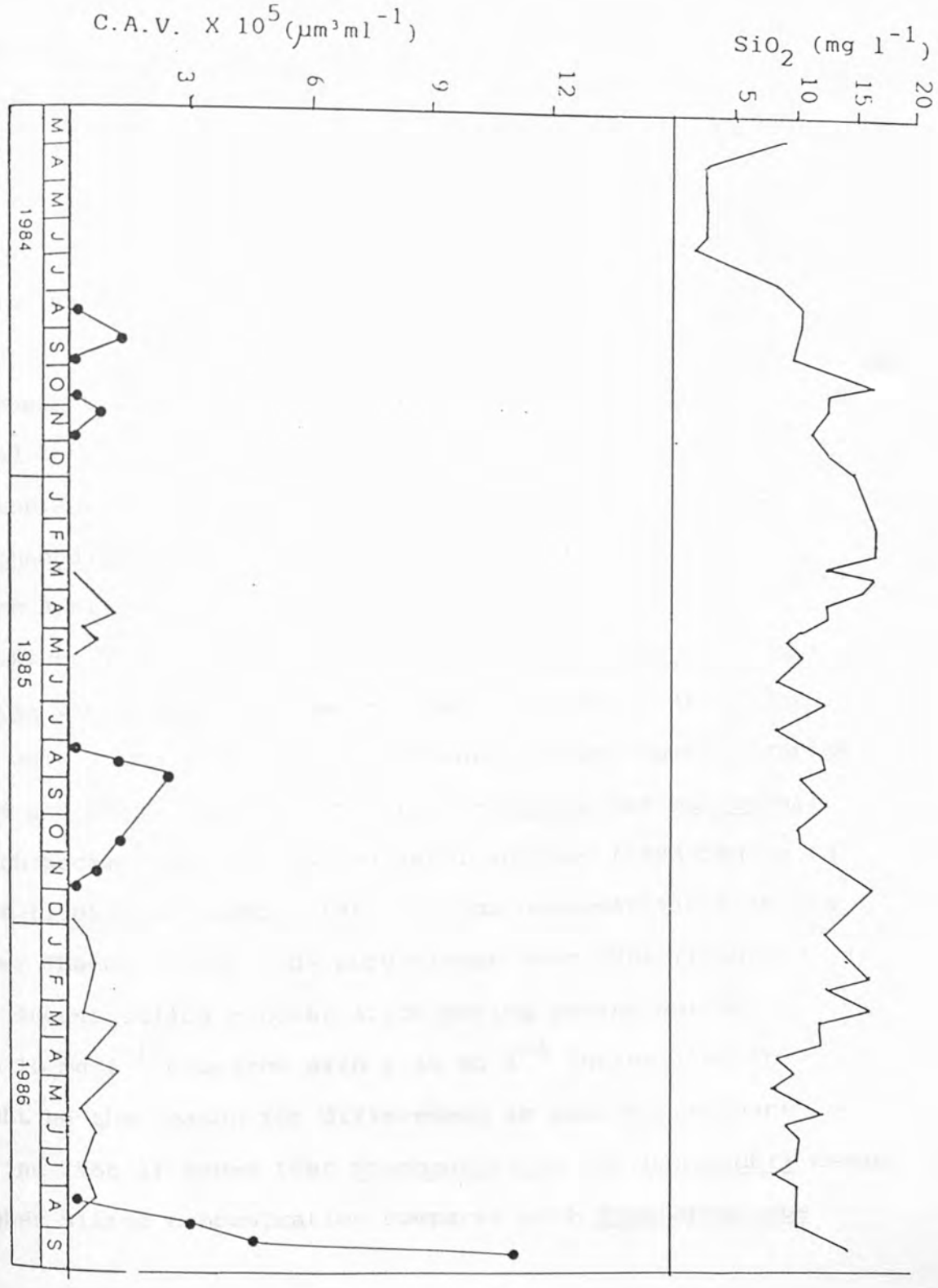

C.A.V. X 10^5 ($\mu m^3 ml^{-1}$)
3
6
9
12
SiO_2 (mg l^{-1})
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.36

dominated.

Of all the aspects of chemical determination of succession and productivity,the relation between diatoms and silica concentrations is among the most apparent.The development of phytoplankton algae in the River Thames and the Wraysbury Reservoir may begin as soon as light conditions improve during the winter,but is most conspicuous during and following spring circulation when the water is relatively rich in nutrients as the winter accumulations are mixed throughout the water column.During the present study it was found that diatoms formed a large percentage of the phytoplankton populations during the spring maximum growth. Stephanodiscus ref.hantzschii became dominant throughout March,April and May (1984 and 1985) and in August (1986) in the River Thames (Figure 3.37).During 1986 Stephanodiscus rotula var.minutula became dominant from March,April,May,June and July although they were present in lower numbers during 1984 and 1985 compared with Stephanodiscus ref.hantzschii which became dominant during April and May (1984);March to June (1985) and August (1986).Silica concentrations in the River Thames during 1985 were higher than 1986 (Figure 3.33). The lowest silica concentration during spring maximum in 1985 was 10 mg l^{-1} compared with 1.43 mg l^{-1} during 1986.This might be the reason for differences in species dominant during 1986.It seems that Stephanodiscus ref.hantzschii needs higher silica concentration compared with Stephanodiscus

rotula and Stephanodiscus rotula var.minutula.

In the Wraysbury Reservoir during 1984 to 1986 silica concentrations range from 1 to 16 mg l^{-1}(Figure 3.34). Concentrations were higher than in the River Thames.During 1984;silica concentrations decreased to 1 mg l^{-1} when Stephanodiscus rotula became dominant.However,the phenomenon did not occur during 1985 and 1986.Stephanodiscus ref. hantzschii and Stephanodiscus rotula var.minutula became dominant during 1985 and 1986 respectively.The lowest silica concentrations during these years were 8 mg l^{-1}.Silica concentration was higher in the Wraysbury Reservoir compared with the River Thames related with the higher concentration of diatoms in the River Thames.As diatoms used up silica in the River Thames;the silica concentration decreased.In his studies of Lake Windermere (Lund,1950;Lund et al.,1963);Lund found that the populations of Asterionella formosa produced during the spring ceased to grow before the silicate was completely exhausted from the water.At concentrations of less than 0.5 mg l^{-1},the loss of cells by sinking and death tended to exceed the production of new cells,suggesting that growth was impeded by lack of silicon.More than 15 years of detailed observations,summarized by Lund (1964),testify to the amazing regularity with which the Asterionella maximum in Lake Windermere coincides with a concentration in the epilimnion of about 8 μ mol $Si(OH)$ l^{-1}.The nature of this growth limitation could be seen in the Wraysbury Reservoir and the

Figure 3.37 Relationships between Stephanodiscus spp. and silica concentrations in the River Thames.

—— Stephanodiscus rotula

—●— Stephanodiscus rotula var.minutula

—○— Stephanodiscus ref.hantzschii

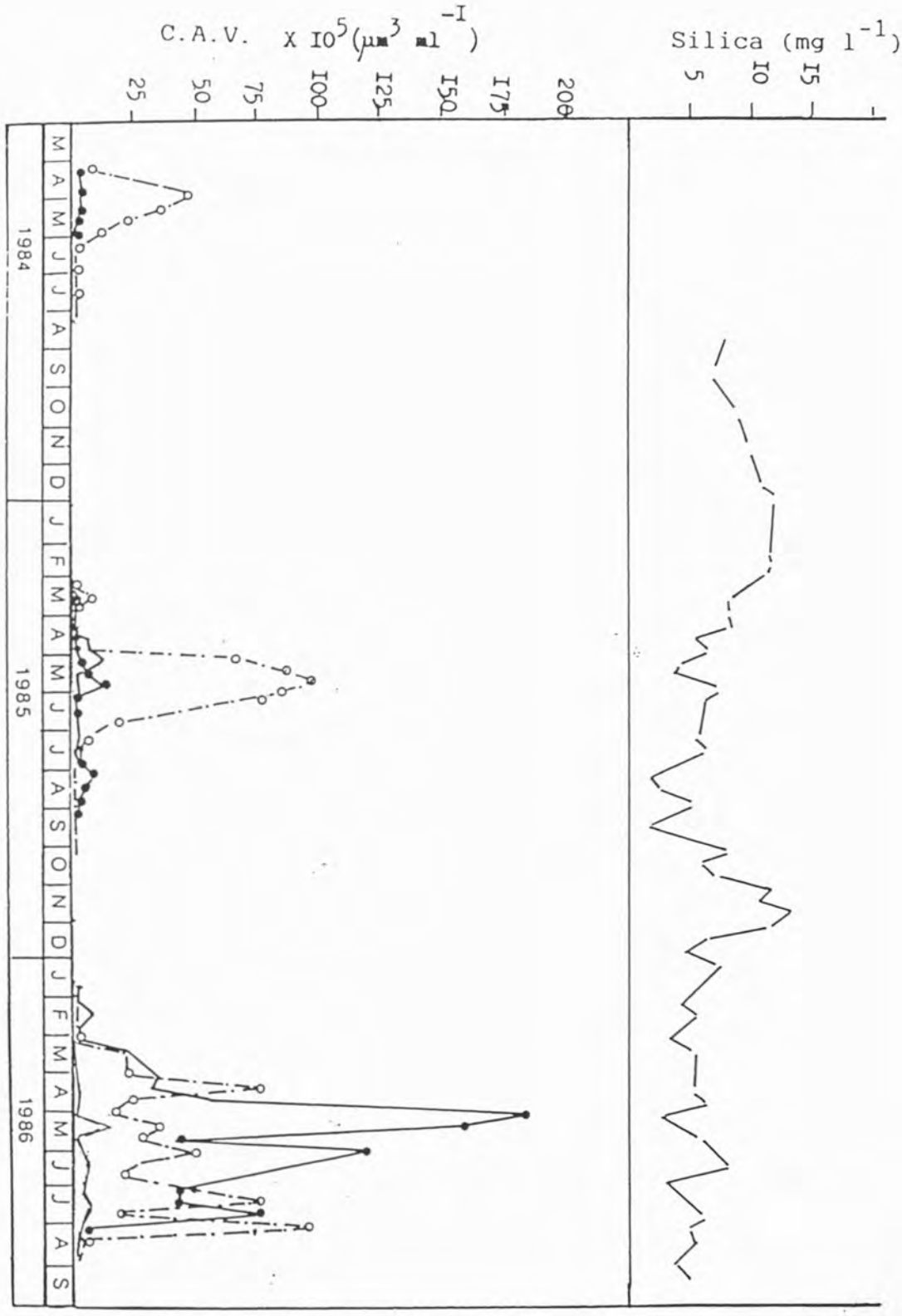

C.A.V. X 10^5 (μm^3 ml^{-1})
25
50
75
100
125
150
175
200
Silica (mg l^{-1})
5
10
15
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.37

Figure 3.38 Relationships between *Stephanodiscus* spp. and silica concentrations in the Wraysbury Reservoir.

——— *Stephanodiscus rotula*

—●— *Stephanodiscus rotula* var. *minutula*

—○— *Stephanodiscus* ref. *hantzschii*

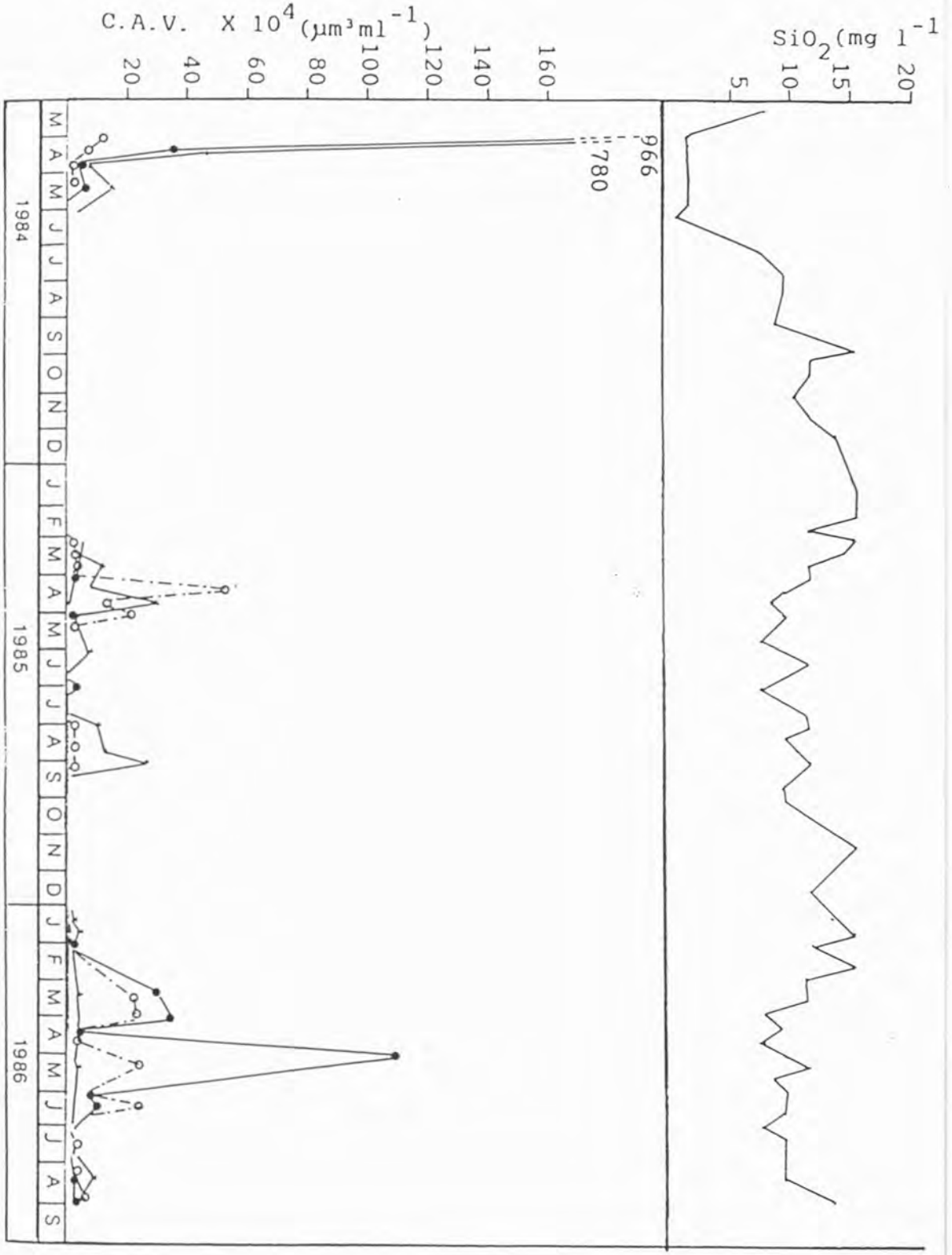

C.A.V. X 10^4 ($\mu m^3 ml^{-1}$)
20
40
60
80
100
120
140
160
966
780
SiO_2 (mg l^{-1})
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.38

Figure 3.39 Relationships between Chlorophyceae and silica concentrations in the River Thames.

Eudorina elegans

Scenedesmus quadricauda

Scenedesmus acuminatus

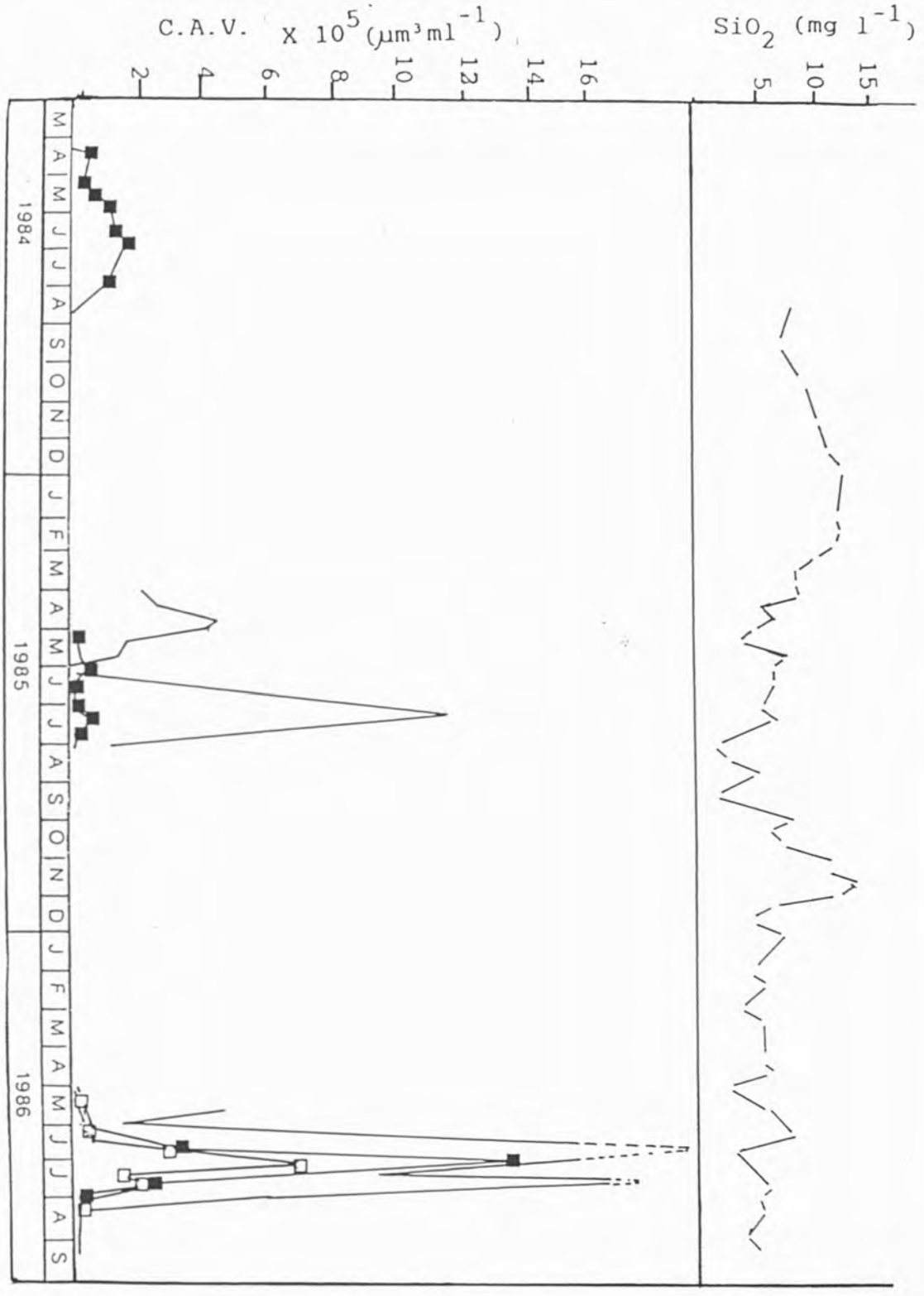

C.A.V. X 10^5 ($\mu m^3 ml^{-1}$)
2
4
6
8
10
12
14
16
SiO_2 (mg l^{-1})
5
10
15
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.39

Figure 3.40 Relationships between Chlorophyceae and silica concentrations in the Wraysbury Reservoir.

Scenedesmus quadricauda

Scenedesmus acuminatus

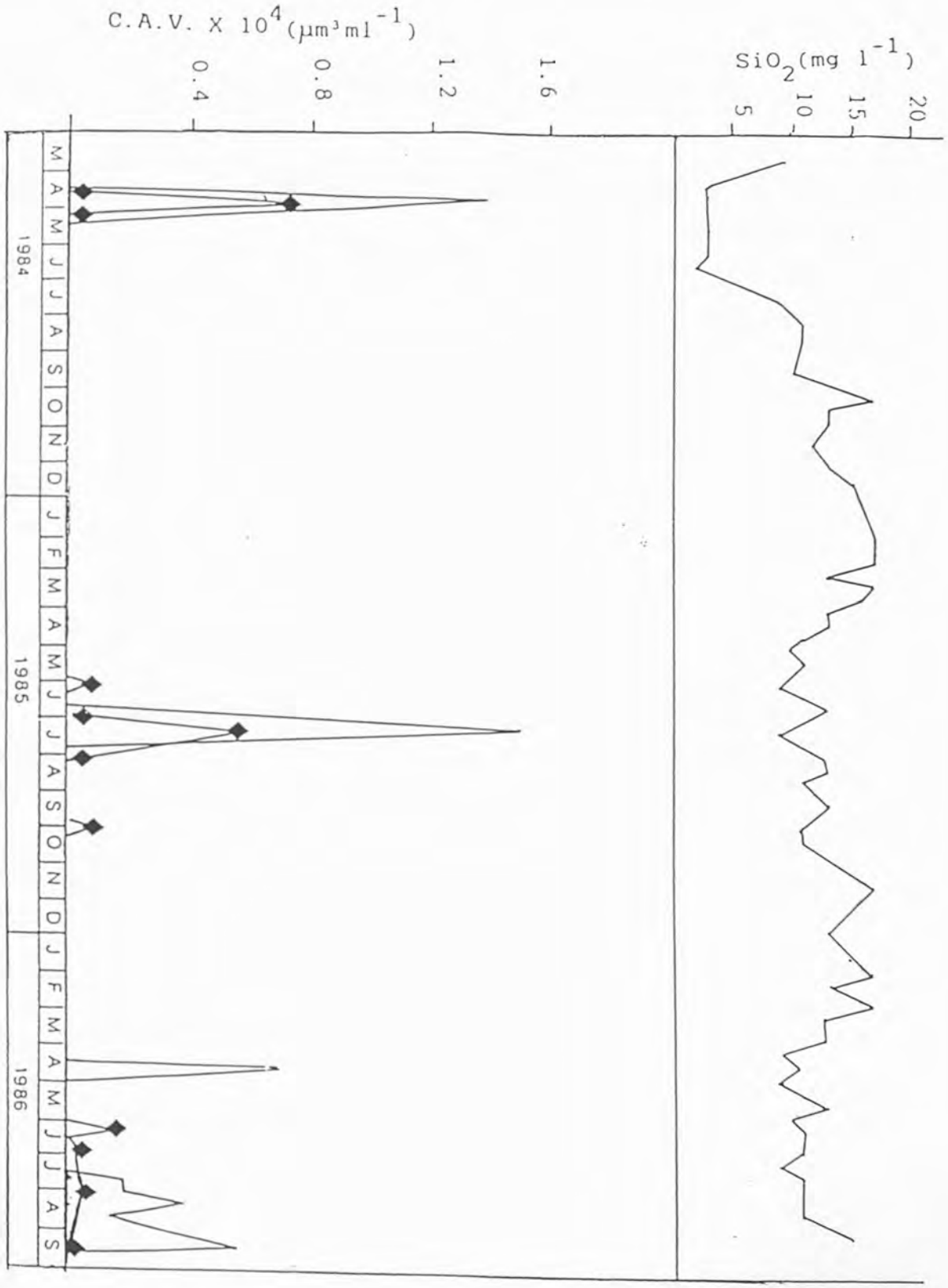

C.A.V. X 10^4 ($\mu m^3 ml^{-1}$)
0.4
0.8
1.2
1.6
SiO_2 ($mg\ l^{-1}$)
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.40

Figure 3.41 Relationships between Cryptophyceae and silica concentrations in the River Thames.

——— *Rhodomonas minuta*

—●— *Cryptomonas spp.*

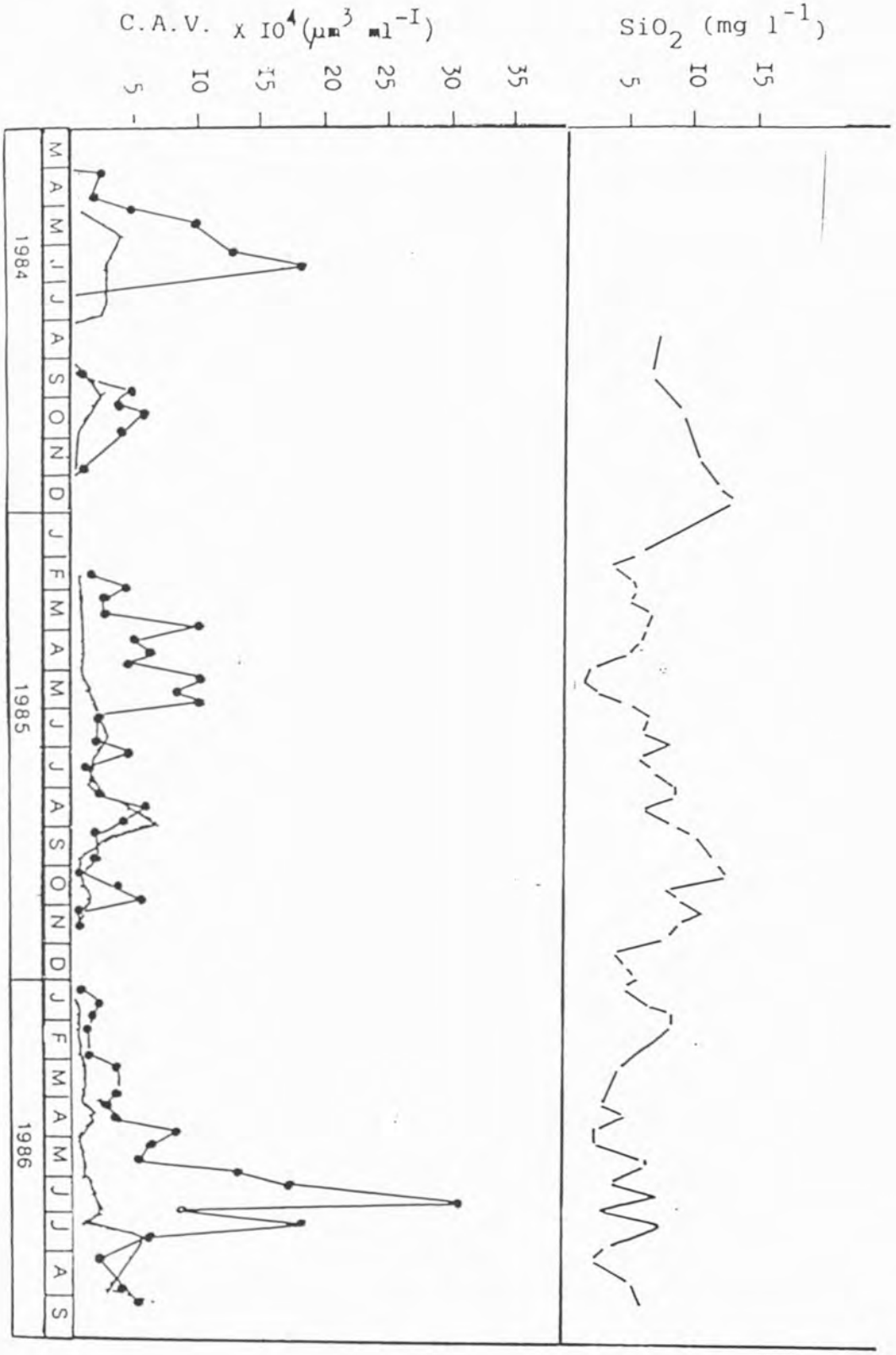

C.A.V. x 10^4 (μm^3 ml^{-1})
5
10
15
20
25
30
35
SiO_2 (mg l^{-1})
5
10
15
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.41

Figure 3.42 Relationships between Cryptophyceae and silica concentrations in the Wraysbury Reservoir.

—— *Rhodomonas minuta*

—●— *Cryptomonas spp.*

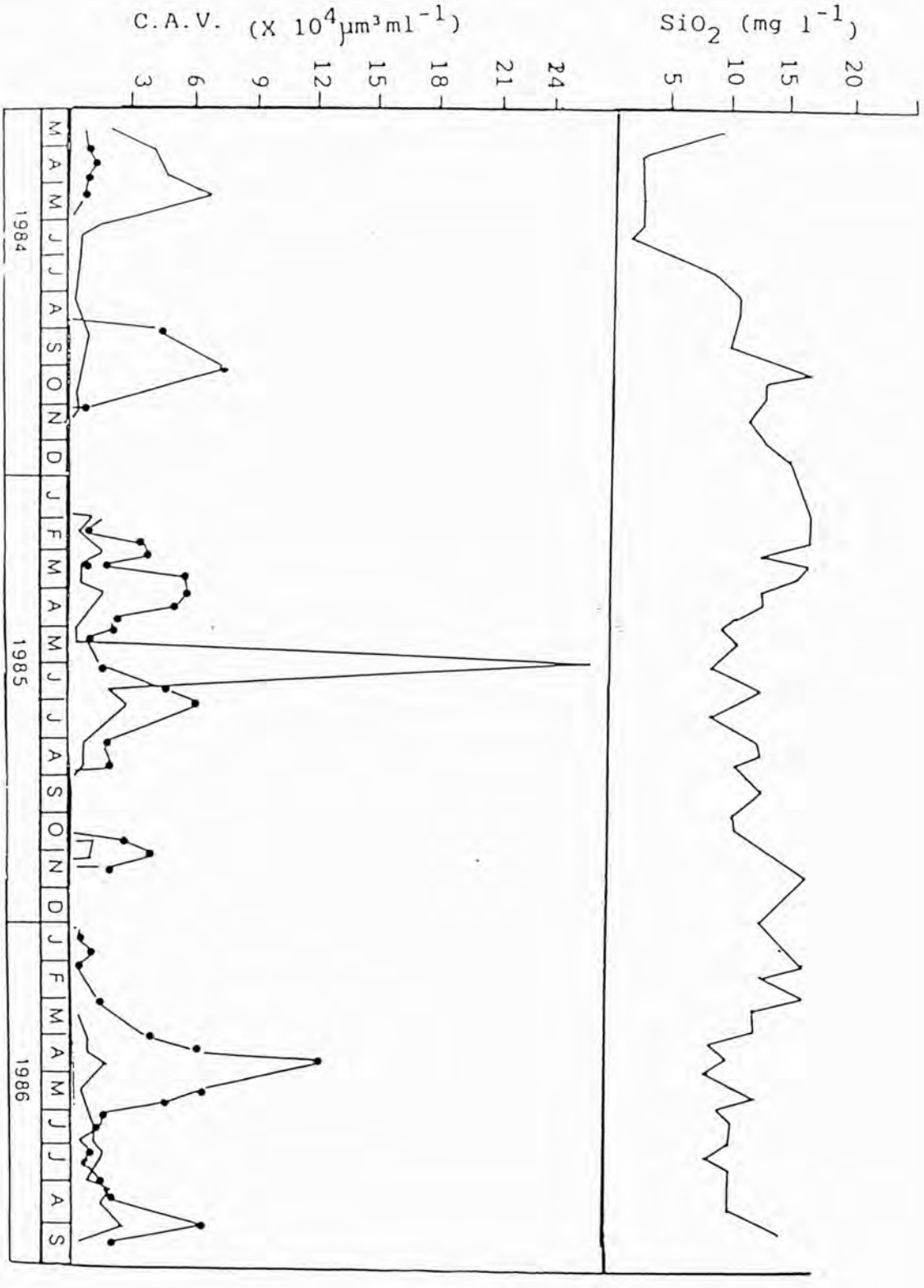

C.A.V. (X 10^4 µm³ml^{-1})
3
6
9
12
15
18
21
24
SiO_2 (mg l^{-1})
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.42

Figure 3.43 Relationships between Cyanobacteria and silica concentrations in the Wraysbury Reservoir.

—— Anabaena spp.

—●— Aphanizomenon flos-aquae

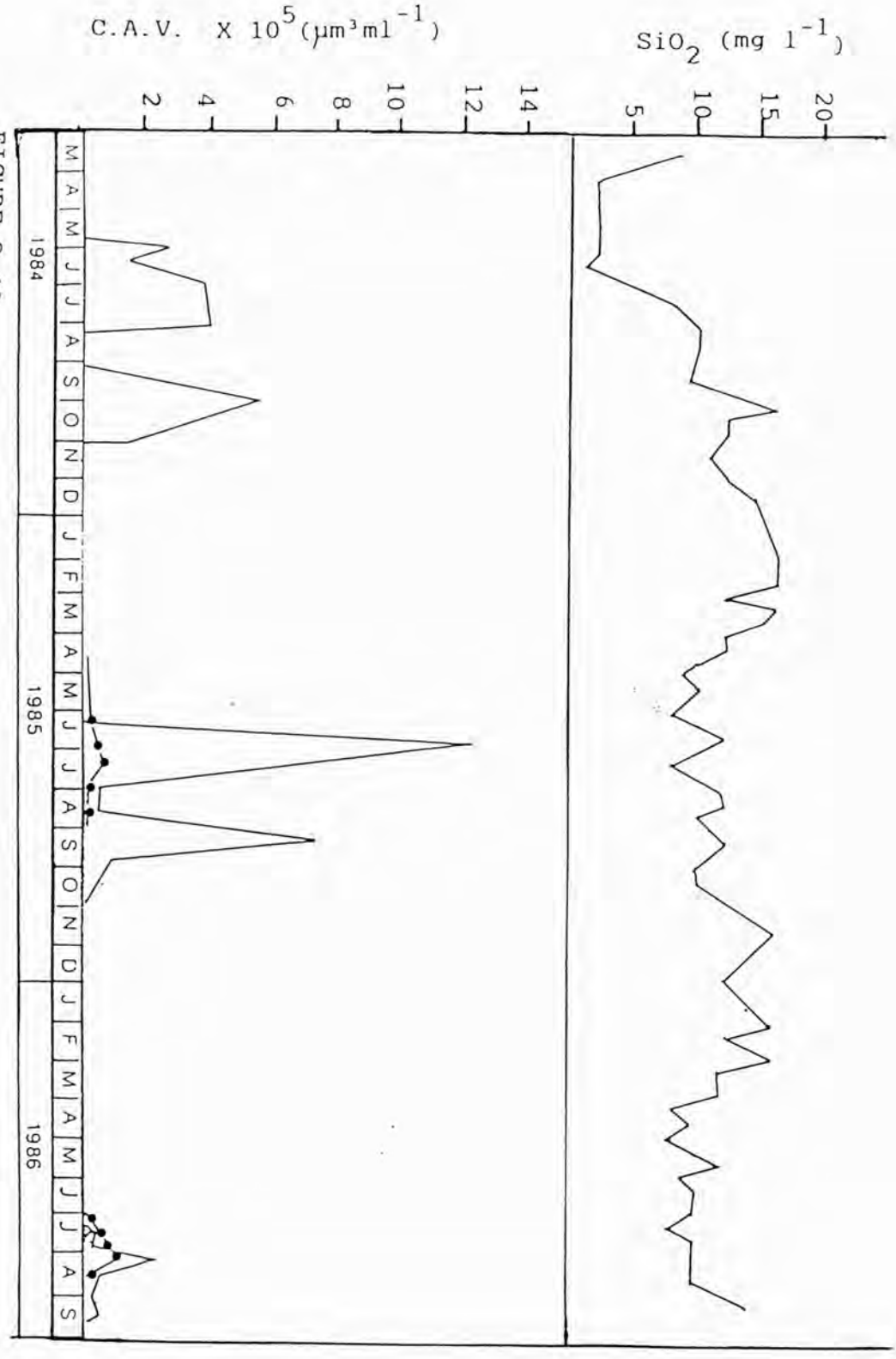

C.A.V. X 10^5 ($\mu m^3 ml^{-1}$)
SiO_2 (mg l^{-1})
2
4
6
8
10
12
14
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.43

River Thames.From Figures (3.35 to 3.38) suggested that low silica levels were a contributory factor in restricting diatom growth.Exponential growth of phytoplankton populations especially diatoms,in the River Thames and the Wraysbury Reservoir had reduced the silica level (Figures 3.39 to 3.43).

It has been pointed out by several workers that the relationships between the state of the diatom plankton and the ambient dissolved silicon concentration is complicated by the fact that the latter is merely the net balance of two mutually opposed processes,the rate of supply and the rate of utilization.The growth of mixed populations or of selected species may continue for extended periods at low silicate concentrations,a continuous supply being maintained by river inflow (Lund et al.,1963),by admixture from the hypolimnion (Tessenow,1966),or by contact between water and sediments (Bailey-Watts,1976a).

The growth of diatoms in the Wraysbury Reservoir was reduced during 1985 and 1986 although silica concentrations were higher than those of 1984.This showed that growth may depend upon other environmental variables than dissolved silica such as temperature and light.In addition grazing may influence population density.Tom (1986, personal communication) stated that fish populations have changed in the Wraysbury Reservoir during the last 15 years or so and as a result there has been marked increase in the zooplankton,notably of Daphnia Magna.Heavy grazing has reduced the phytoplankton including diatoms and improved the

water quality for supply. However, it is desirable to retain some phytoplankton algae as they help to maintain high oxygen levels when growing healthily.

The question to what concentrations of silicate can be expected to limit phytoplankton growth in nature deserves closer attention. Kilham (1975) thought that the $Si(OH)_4$ concentration giving 90% of the maximum growth rate might provide an estimate of incipient limitation, and in a Windermere clone of Asterionella formosa, a concentration of 6.5 μ mol l^{-1} was found to be limiting by this definition. This values compares favourably with the 8 μ mol l^{-1} (0.5 mg $l^{-1} SiO_2$) which Lund (1950) considered limiting to Asterionella in Lake Windermere. Parker et al., (1977b) accepted Kilham's value as the concentration likely to limit diatom growth rates in general in Lake Michigan, although it is evident from their data that much growth took place at considerably lower concentrations. The very low post-bloom $Si(OH)_4$ which is characteristic of the euphotic zone in Lake Michigan as well as in many other lakes may indicate one of the following possibilities:

(1) diatom populations are able to grow for extended periods at a rate which is severely limited by low ambient silicon concentrations;

(2) low $Si(OH)_4$ concentrations may have comparatively less severe effect on growth in nature than in laboratory, since growth in the

euphotic zone is normally light-limited (Davis, 1976);

(3) the kinetics of silicon-limited growth of diatoms tend to be distorted in culture experiments, for some reason that is not understood at present; or

(4) the exhaustion of $Si(OH)_4$ from lake water is normally caused by diatom species that are better than Asterionella formosa to grow rapidly at low silicon concentrations.

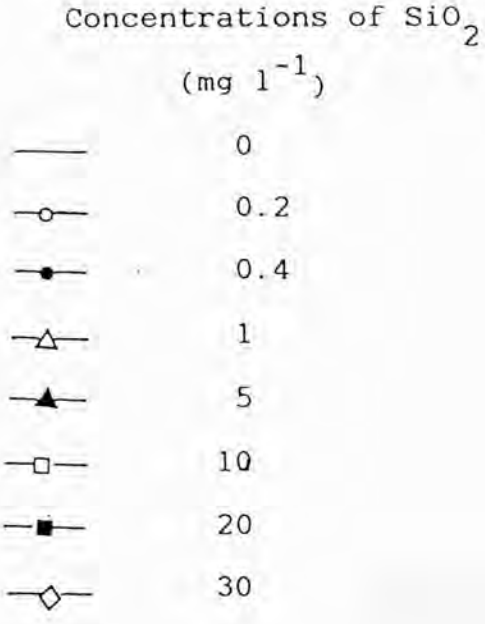
Although there is some evidence for this last possibility (Schelske and Stoermer, 1972; Moed et al., 1976; Tilman et al., 1976), the whole questions need much more study.

3.7.3.2 GROWTH IN CULTURE

Figures 3.44 to 3.47 show the growth response of Stephanodiscus ref. hantzschii, Scenedesmus quadricauda, Ankistrodesmus falcatus and Eudorina elegans to different silica concentrations.

It was found that lower concentrations (0-0.4 mg l^{-1}) of silica in the medium inhibited the growth of Stephanodiscus ref. hantzschii (Figure 3.44). The culture grew proportionally with concentrations of silica in the range from 1 to 40 mg l^{-1}. From microscopical investigation of morphology of Stephanodiscus ref. hantzschii it was found that

Figure 3.44 The growth of Stephanodiscus ref.hantzschii in Chu's medium No.10 with different concentrations of silica.



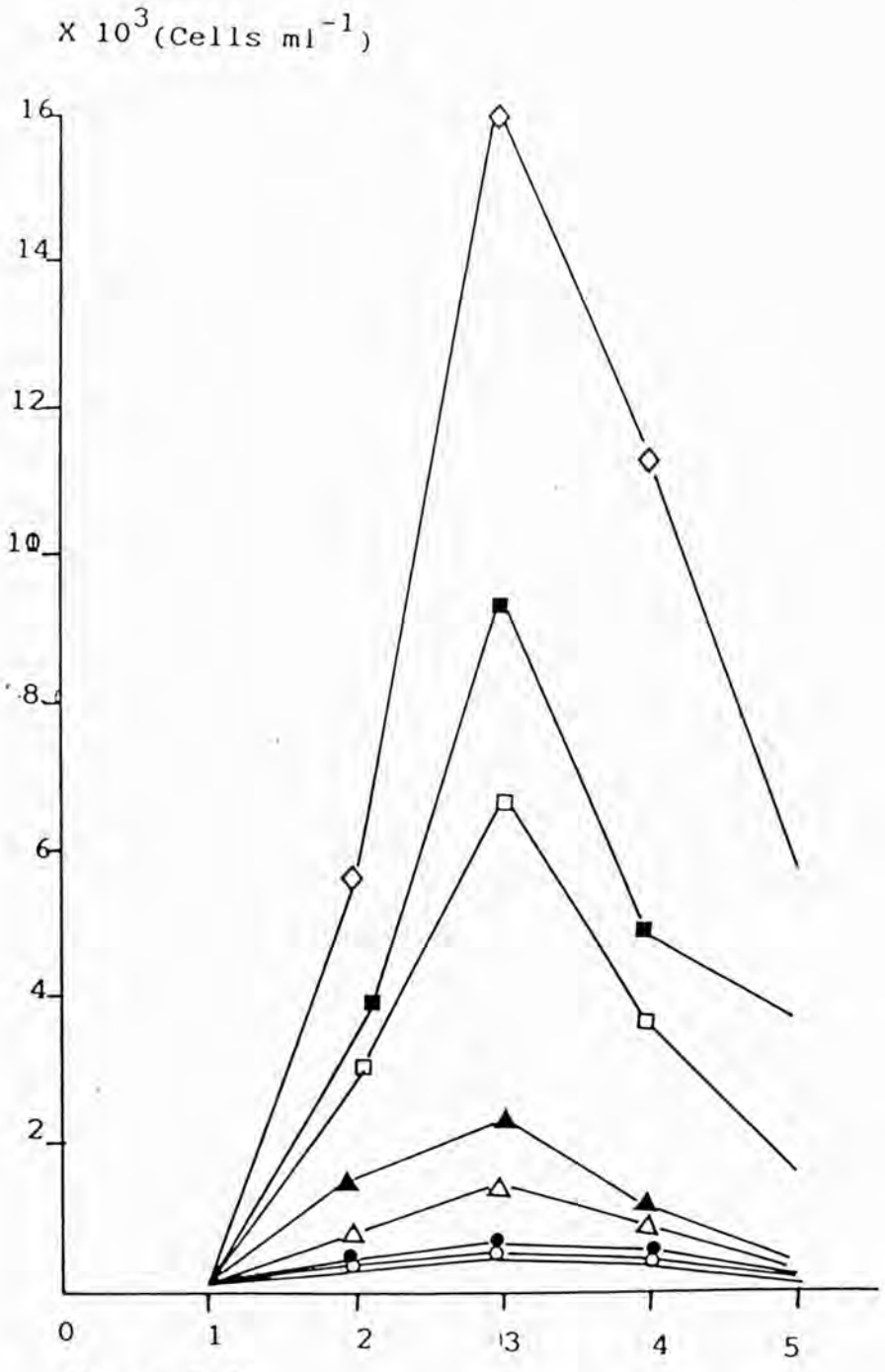


Figure 3.44.

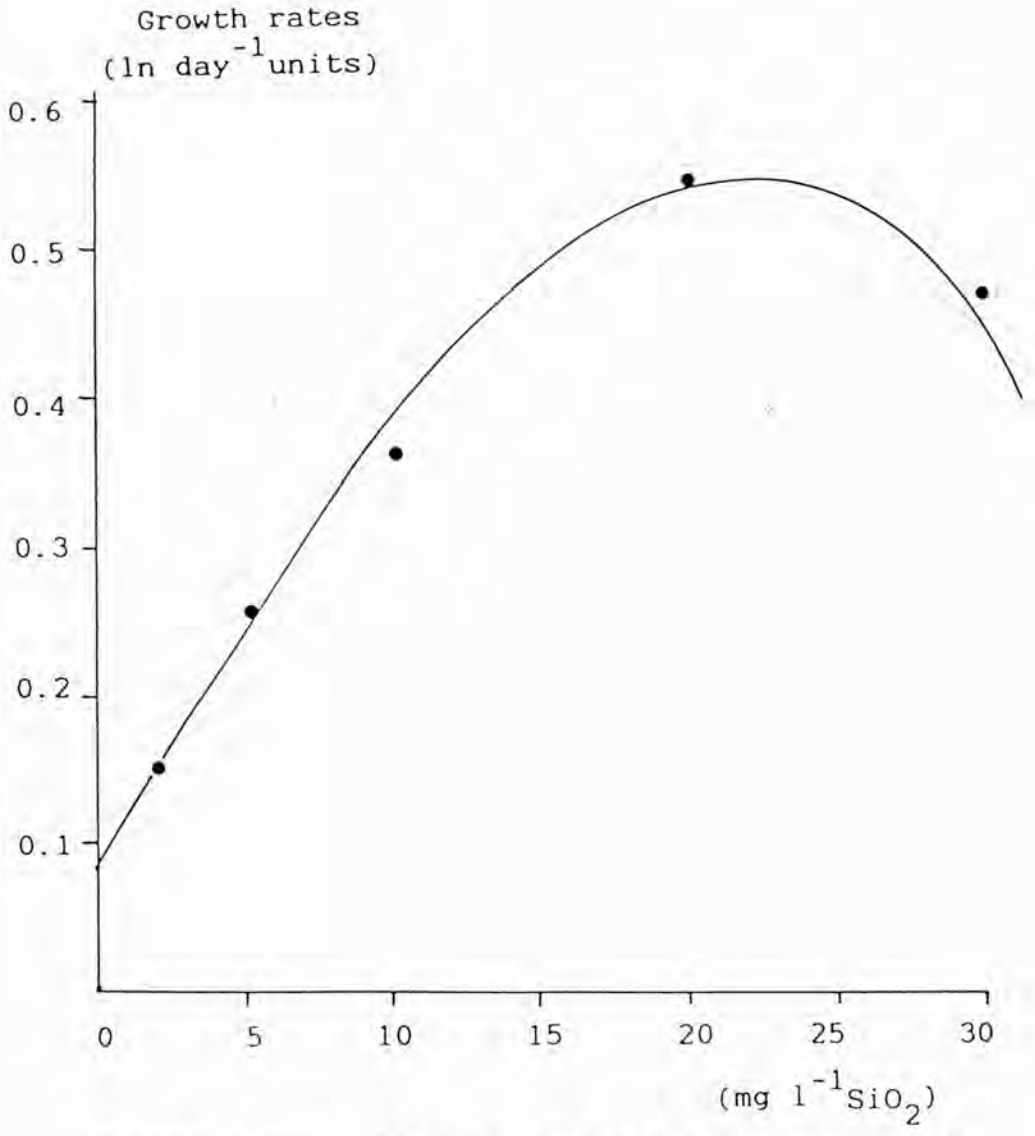
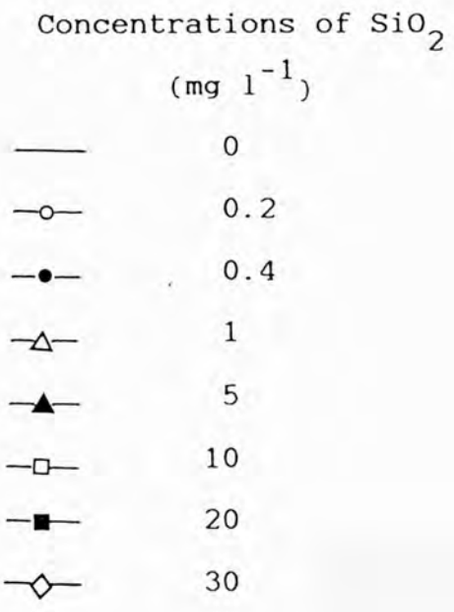


Figure 3.44a Effects of silica on the growth rates of *Stephanodiscus* ref. *hantzschii*.

elongation of cells in culture medium with concentrations (10 to 40 mg l^{-1}) of silica after three weeks.Valves that were formed before growth stopped tend to be thinner and poorly silicified.This may be due to limitation of silica.The same conditions were found by several researchers where silicon deficiency is accompanied by morphological changes in the cell wall.Braaud,1948;Paasche,1973a;Harrisons et al.,1977 found that silicon deficiency made the valves thinner than normal,also,specialized silica structures such as the connecting rods in the Skeletonema,the areolar cross-walls in Thallasiosira,or the spines in Chaetoceros,fail to develop properly.In Cyclotella pseudostelligera grown to the point of silicon depletion,the valvar fine structure may be affected to such an extent that the cells take on the morphological aspect of a different species.

Elongation of the cells of Stephanodiscus ref. hantzschii after 3 weeks may be due to limitation of silica. Diatom cell division stops with the depletion of silicic acid from the culture medium (Lewin,1955;Werner,1966;Lewin and and Chen,1968).Detailed studies have shown that silicon metabolism is closely involved in cell division processes (Darley,1974).In cultures grown to the point where silicic acid [$Si(OH)_4$] is exhausted from the medium,prolonged silicon starvation may lead to the accumulation of cells that have gone through nuclear and cytoplasmic division but remained united in pairs as long as no walls can be formed (Coombs et

Figure 3.45 The growth of Scenedesmus quadricauda in Chu's medium No.10 with different concentrations of silica.



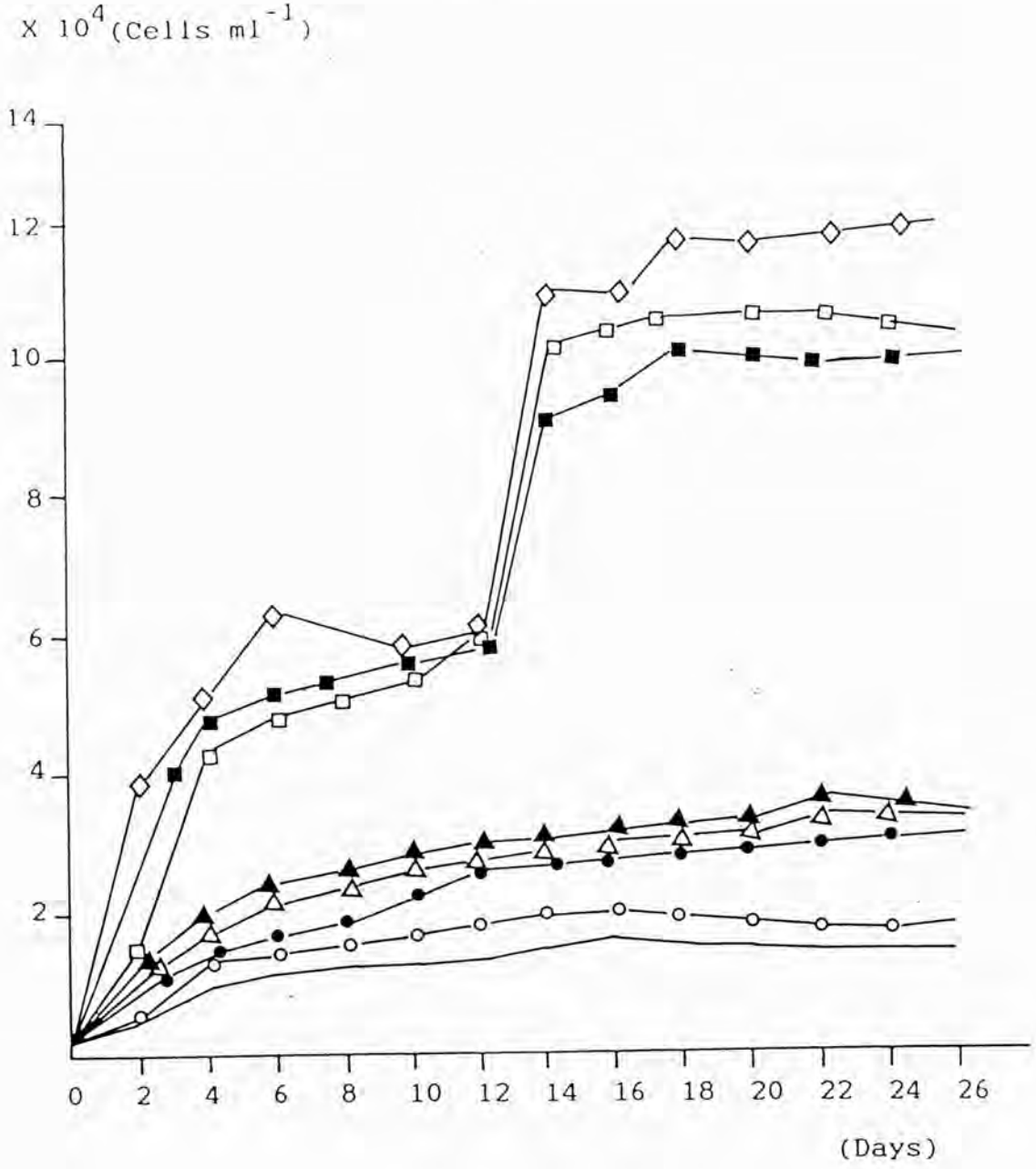


Figure 3.45.

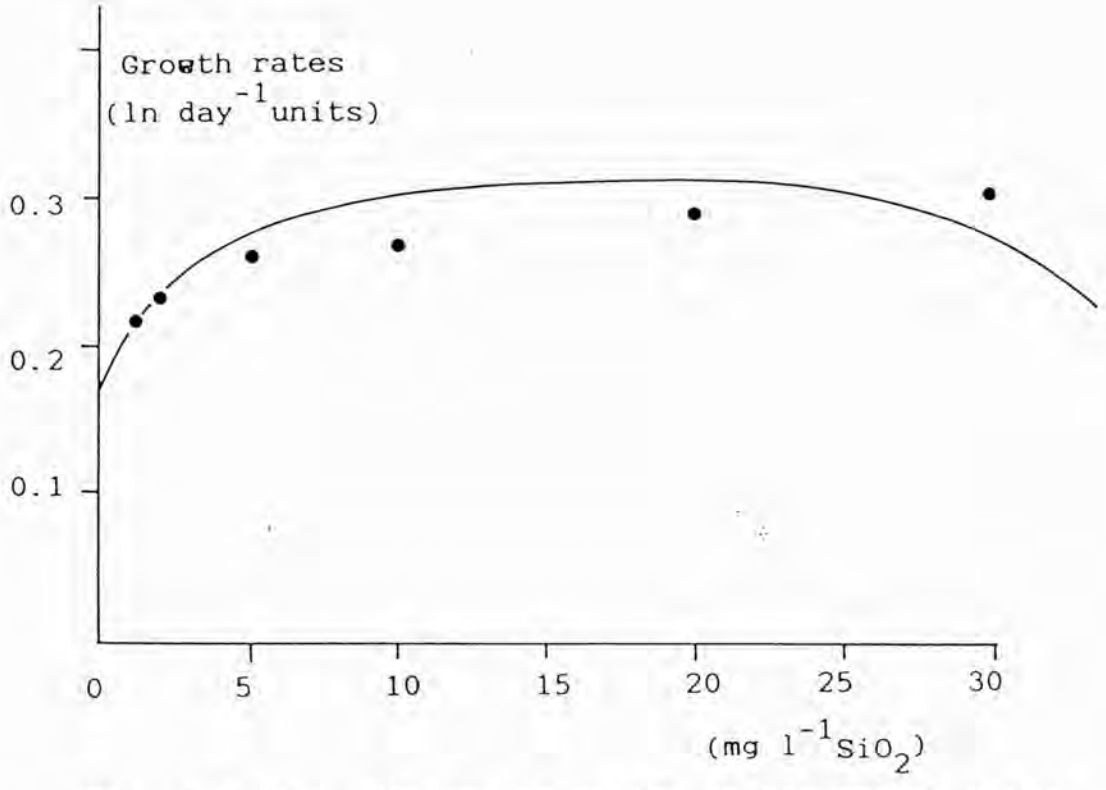


Figure 3.45a Effects of silica on the growth rates of Scenedesmus quadricauda.

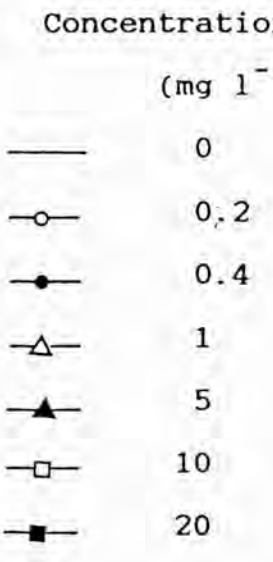
al.,1967).

The data in Figure 3.44 also indicate that the absence of silica in the medium inhibited the growth of Stephanodiscus ref.hantzschii.The upper tolerance concentrations of silica for the optimum growth of Stephanodiscus ref. hantzschii was 20 mg $l^{-1}SiO_2$.

The experiments carried out with Scenedesmus quadricauda (Figure 3.45) showed that the growth was proportional to the concentrations of silica from 10 to 30 mg $l^{-1}SiO_2$.However,the growth between 0 to 5 mg $l^{-1}SiO_2$ showed lower increases in numbers of cells compared with higher concentrations.As shown in Figure 3.45a it was found that the growth rates of Scenedesmus quadricauda was almost constant during exponential growth.Even a small concentrations of silica can support the growth of Scenedesmus quadricauda.From Figure 3.45,the growth decreased during days 8 to 12 in the concentrations between 10 to 30 mg $l^{-1}SiO_2$. However,growth was increased from about days 12 to 14.This might have been due to technical faults in the growth incubator.The upper tolerance concentrations of silica for the optimum growth of Scenedesmus quadricauda was 13 mg l^{-1}.

The growth of Ankistrodesmus falcatus and Eudorina elegans as influenced by silica concentrations was also investigated.Ankistrodesmus falcatus (Figure 3.46) showed lower growth in the concentrations from 0 to 1 mg $l^{-1}SiO_2$ compared with higher concentrations (5 to 20 mg $l^{-1}SiO_2$).

Figure 3.46 The growth of Ankistrodesmus falcatus in Chu's medium No.10 with different concentrations of silica.



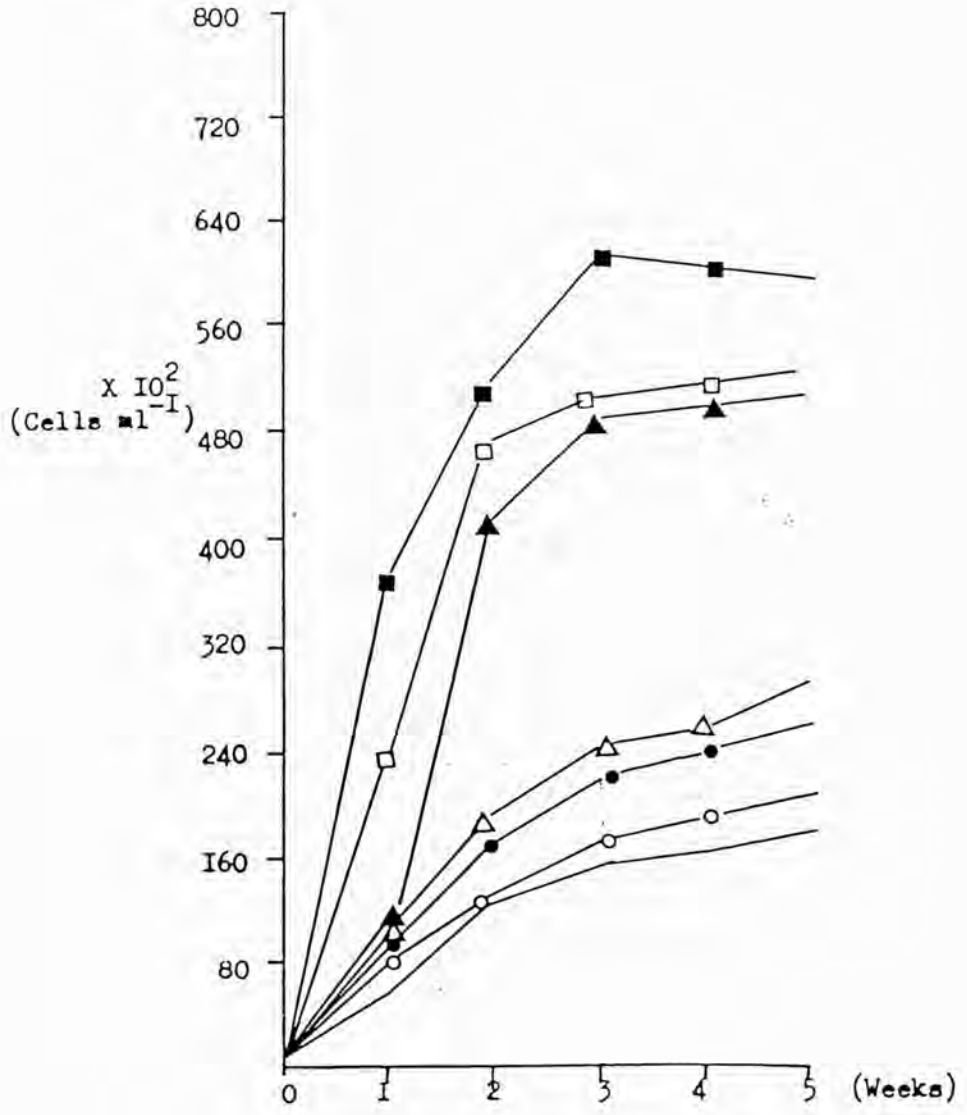

800
720
640
560
480
400
320
240
160
80
X 10^2
(Cells ml^{-1})
0
1
2
3
4
5
(Weeks)

Figure 3.46.

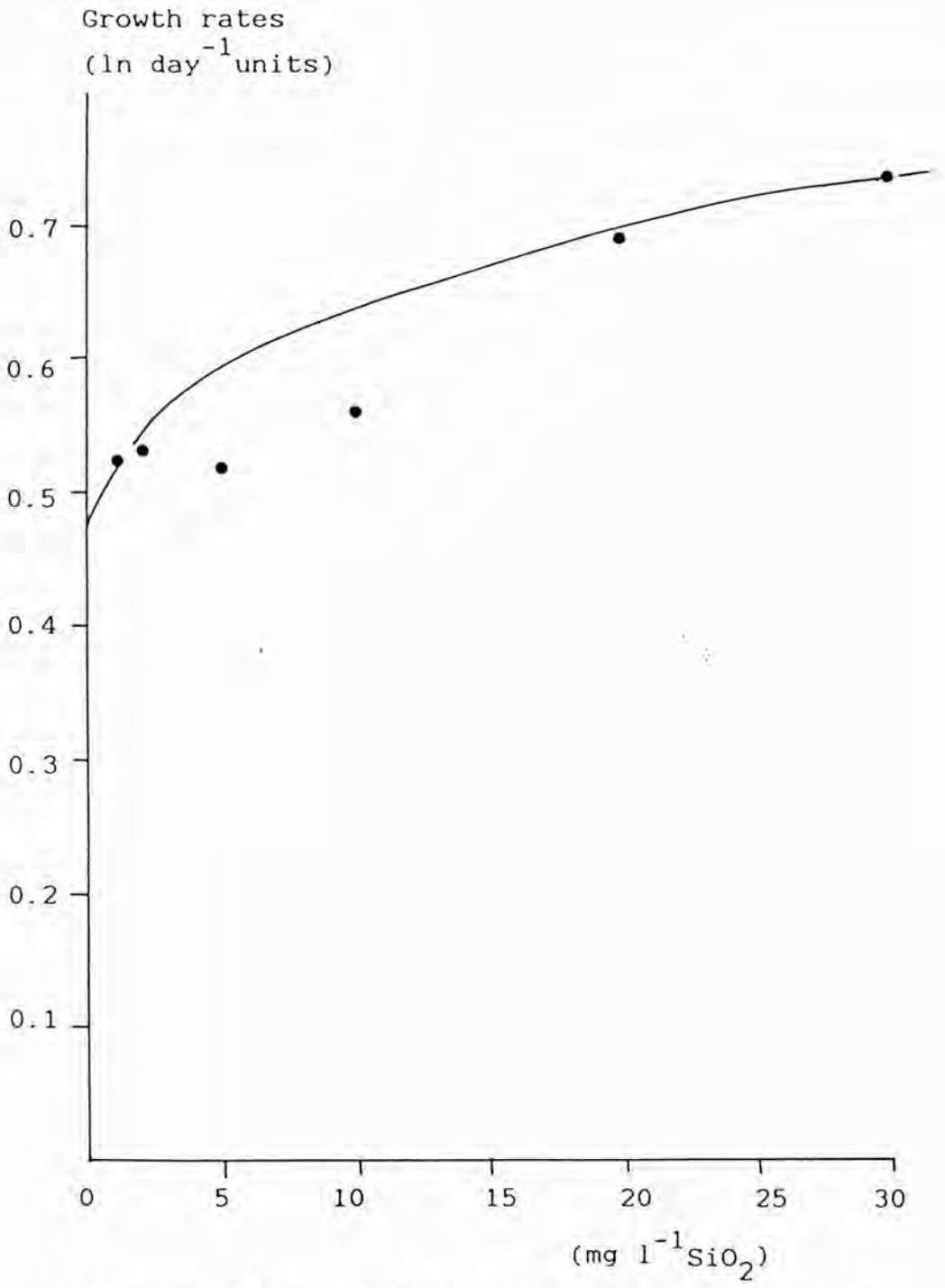
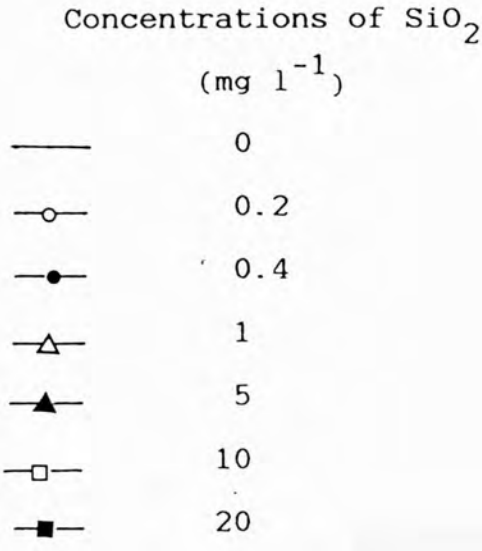


Figure 3.46a Effects of silica on the growth rates of Ankistrodesmus falcatus.

Figure 3.47 The growth of Eudorina elegans in Chu's medium No.10 with different concentrations of silica.



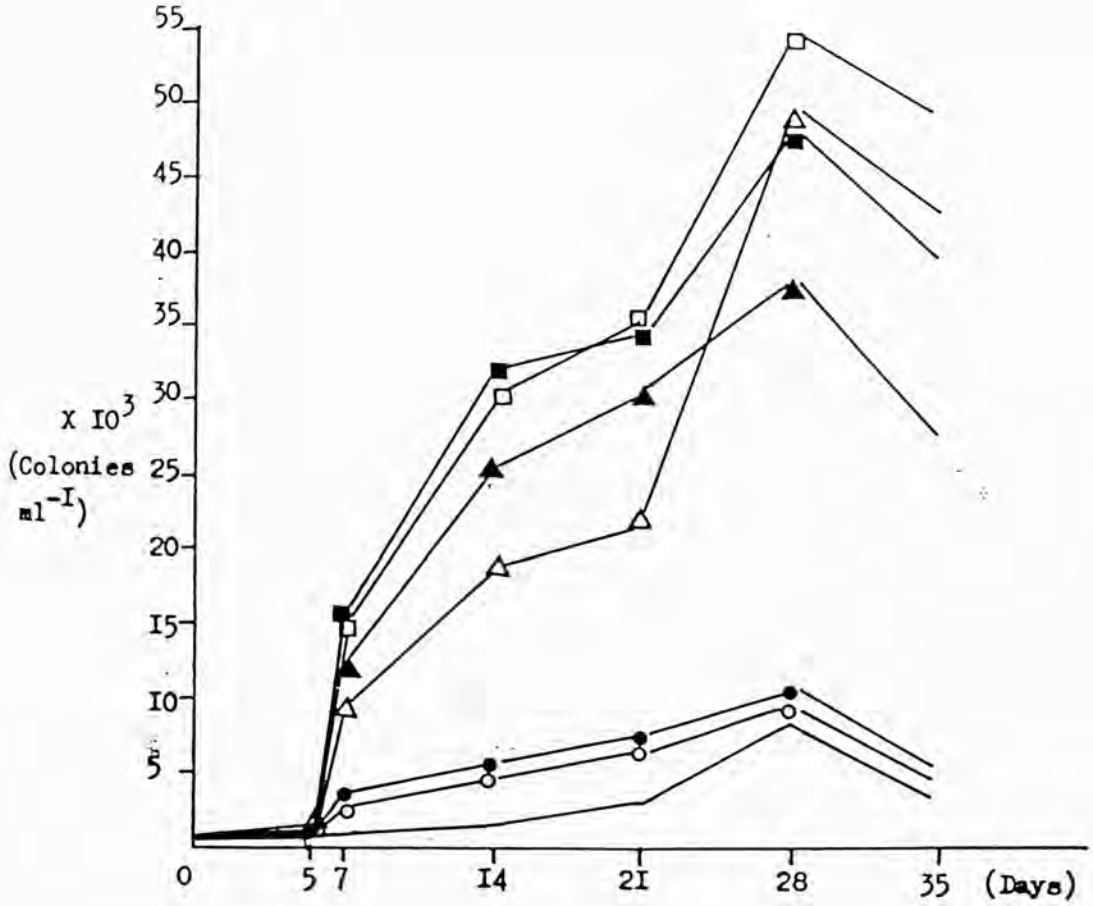

55
50
45
40
35
30
25
20
I5
I0
5
X I0^3
(Colonies
ml^-I)
0
5 7
I4
2I
28
35
(Days)

Figure 3.47.

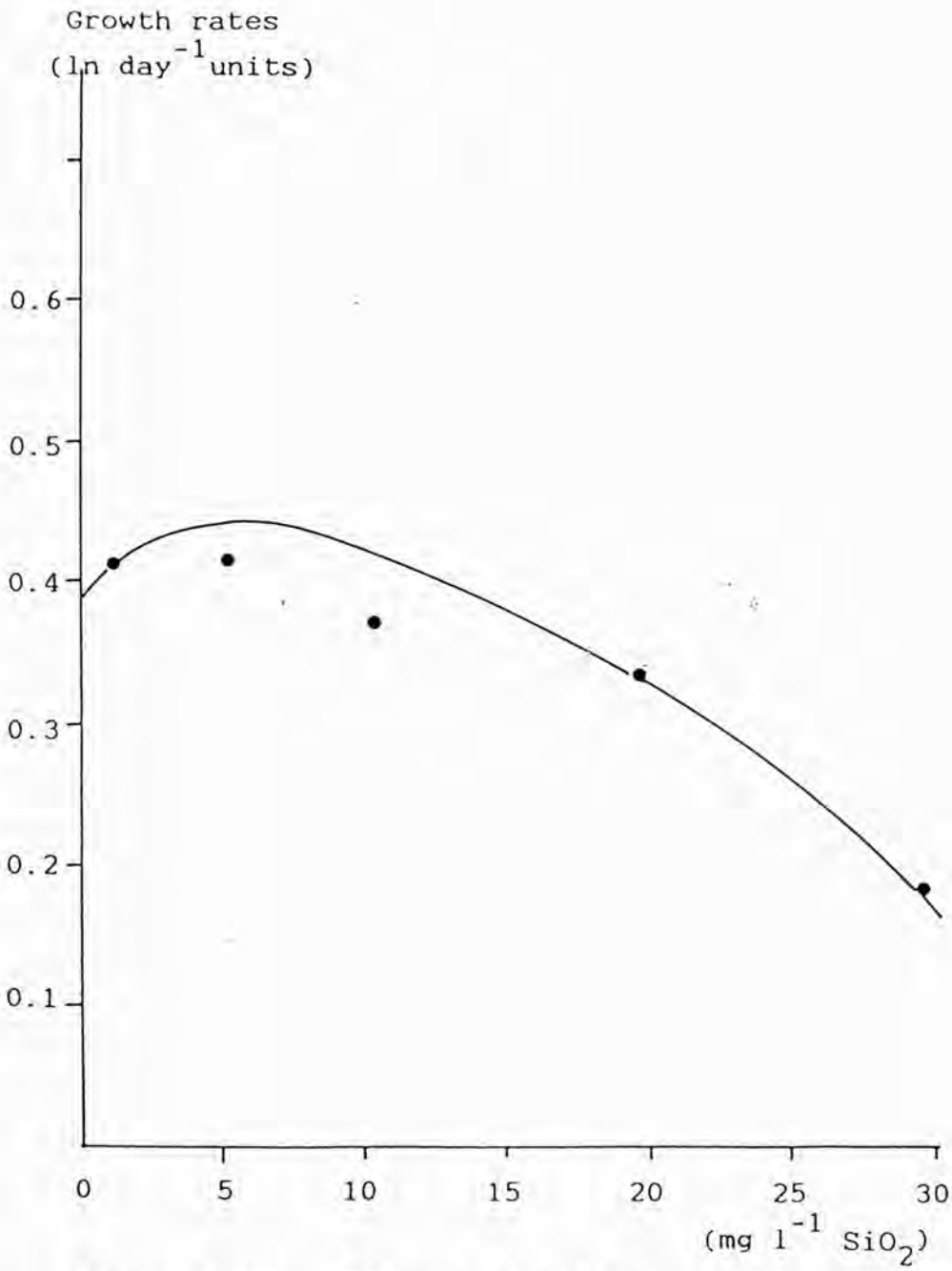


Figure 3.47a Effects of silica on the growth rates of Eudorina elegans.

Figure 3.46a showed that the growth of Ankistrodesmus falcatus increased with the increasing concentrations of silica.The highest concentrations (30 mg l^{-1})of silica showed the maximum growth.The differences of the growth rates between the highest and lowest concentrations of silica were not larger.This showed that even lower concentrations of silica could support the growth of Ankistrodesmus falcatus.

However,different results was found with experiments carried out with Eudorina elegans (Figure 3.47). Results indicated that the growth of Eudorina elegans increased with the increasing concentrations of silica from days 5 to 14.However,after 3 weeks in culture medium,the growth in highest concentrations (30 mg l^{-1}) decreased compared with 20 mg l^{-1} silica (Figure 3.47).As shown in Figure 3.47a,it was found that the growth rates of Eudorina elegans was higher when concentrations of silica lower than 10 mg l^{-1}during exponential growth.On the contrary, concentrations higher than about 10 mg l^{-1} inhibited the growth of Eudorina elegans.The results are consistent with the field observations.Eudorina elegans occurred during the summer when silica concentrations were low.

3.8 A COMPARISON BETWEEN PHYTOPLANKTON POPULATIONS AT TWO SITES ON THE RIVER THAMES

3.8.1 INTRODUCTION

During the period October,1985 to June,1986;with co-operation from Professor Li (a visiting Professor from Peoples Republic of China);samples were taken from the River Thames at Datchet (refer Figure 2.2,Chapter Two) as well as those from the regular sampling station.Comparison between physical and chemical environmental factors (i.e.light,pH, temperature,conductivity,alkalinity,dissolved oxygen and carbon dioxide concentrations,nitrate-nitrogen,phosphate-phosphorus and silica concentrations)as well as phytoplankton fluctuations in both places were made.Similar methods were used throughout.

3.8.2 RESULTS AND DISCUSSIONS

From the investigations during the period of observations from October,1985 to June,1986;it was found that generally temperature,pH,alkalinity,conductivity,dissolved oxygen,carbon dioxide and light were more or less similar at the two sites (River Thames at the Bells of Ouzely and Datchet)(Table 3.4;Figures 3.48-3.50).However,there were certain periods when there were variations between the two in

Table 3.4 PHYSICAL AND CHEMICAL FACTORS AT TWO SITES ON THE RIVER THAMES

	RIVER THAMES AT THE BELLS OF OUZELY	RIVER THAMES AT DATCHET
PHYSICAL FACTORS		
(1) Temperature (°C)	2.5-19.8	2.4-19.7
(2) pH	6.7-8.3	6.4-8.3
(3) Alkalinity (mg l^{-1} $CaCO_3$)	135-358	128-300
(4) Conductivity (μ mhos cm^{-1})	550-680	520-630
(5) Dissolved Oxygen (% saturation)	82-128.8	95-129.8
(6) Free Carbon dioxide (mg l^{-1})	4-144	4- 100
(7) Surface radiation (Wm^{-2} PAR)	10-350	3-250
(8) Light Attenuation (ln $unit^{-1}$)	6.8-5.7	0.1-3.8
CHEMICAL FACTORS		
(1) Nitrate-nitrogen (mg l^{-1})	2.6-13.2	1.2-10
(2) Phosphate-phosphorus (mg l^{-1})	0.01-0.33	0.005-0.31
(3) Silica (mg l^{-1})	1.27-12	2.2-6.7

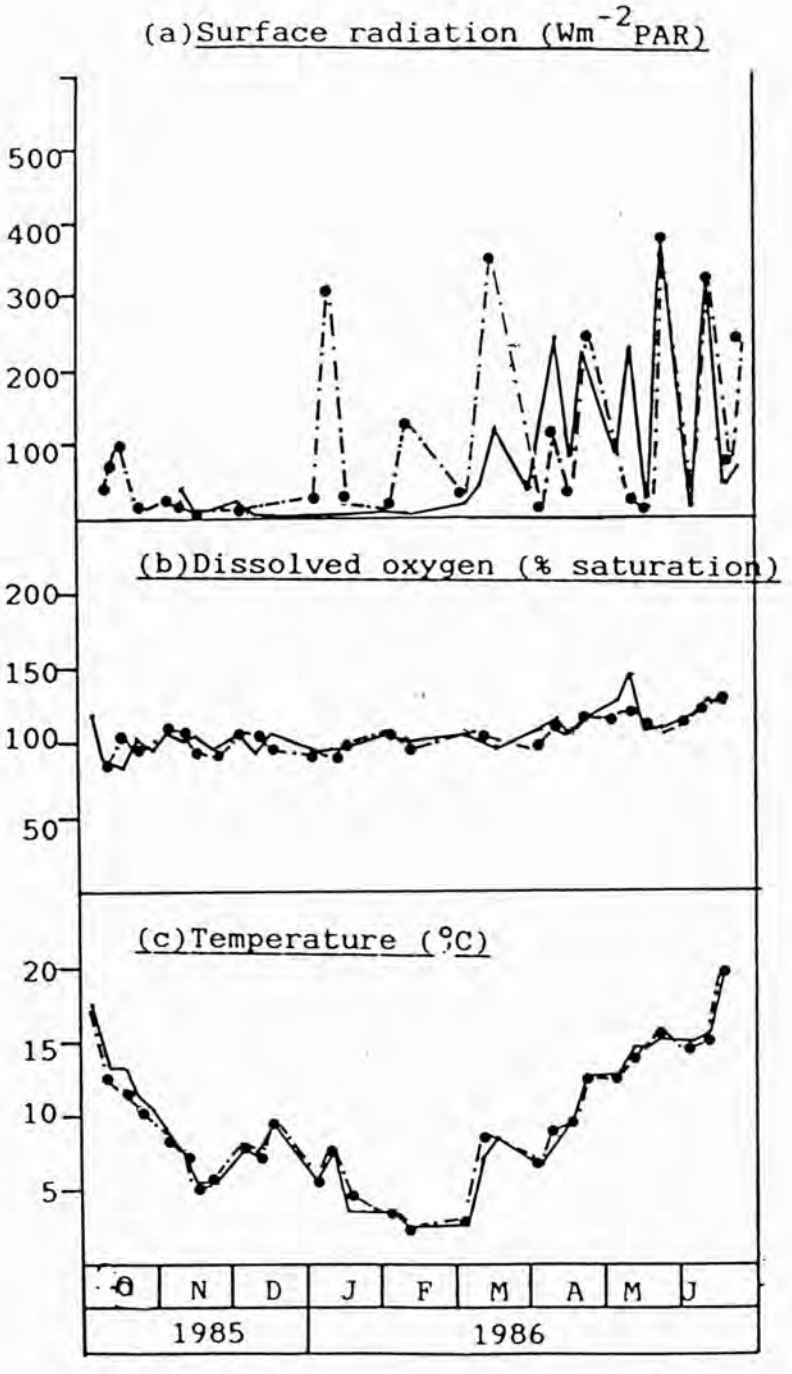


Figure 3.48

—•— Bells of Ouzely

——— Datchet

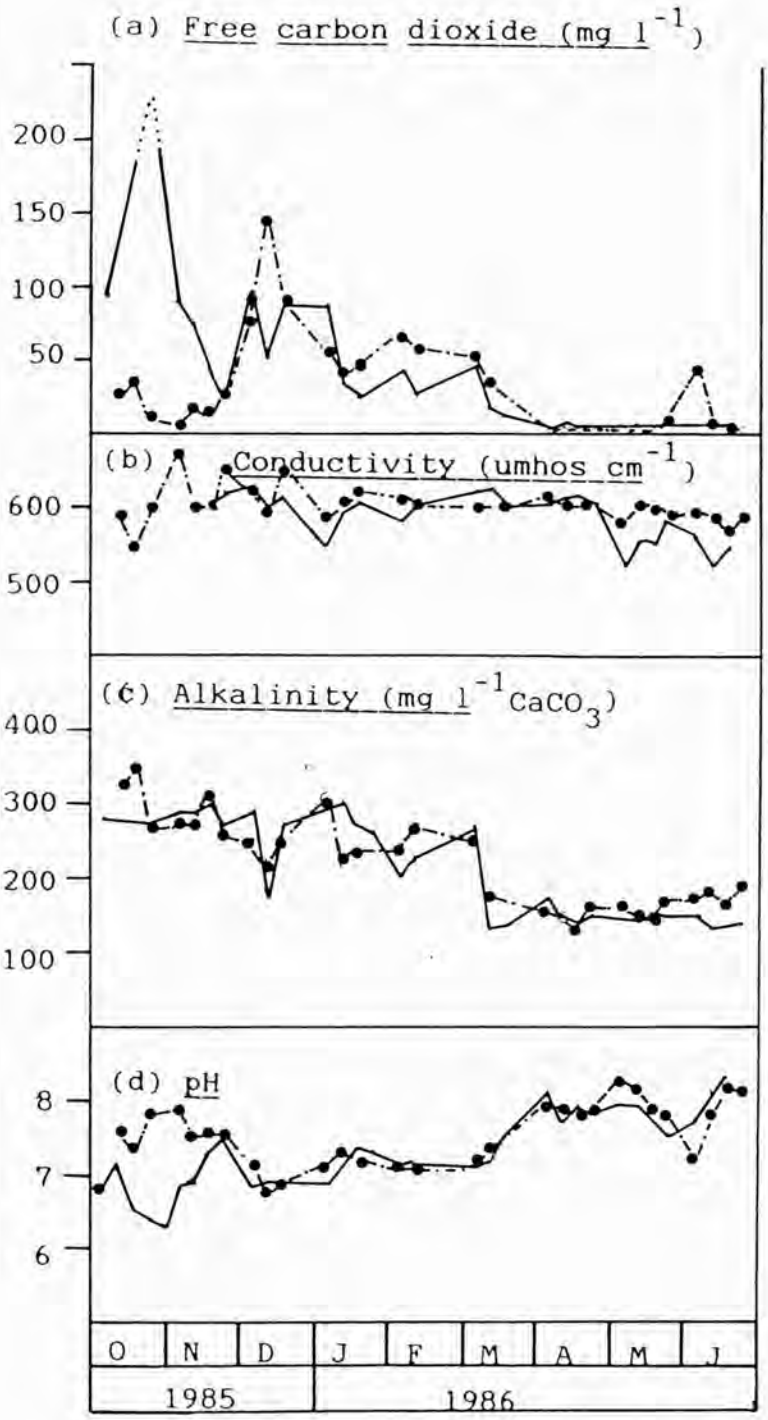


Figure 3.49

—●— Bells of Ouzely

—— Datchet

Light attenuation

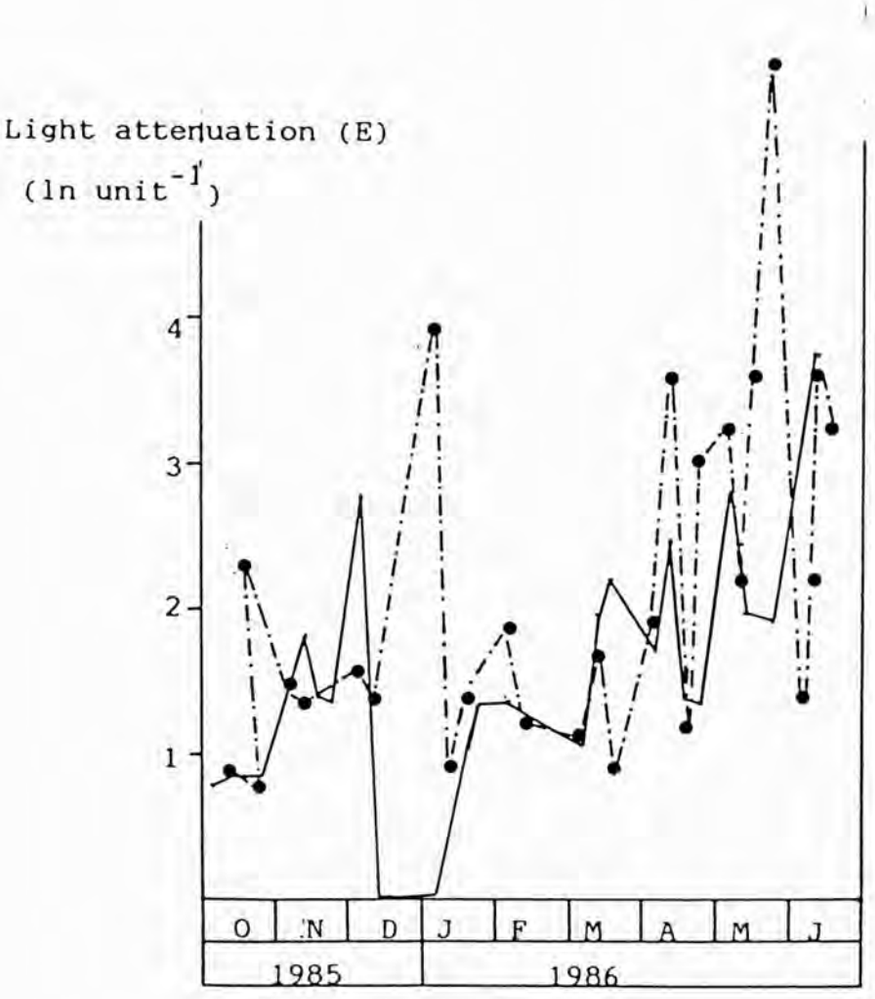


Figure 3.50

Bells of Ouzely

Datchet

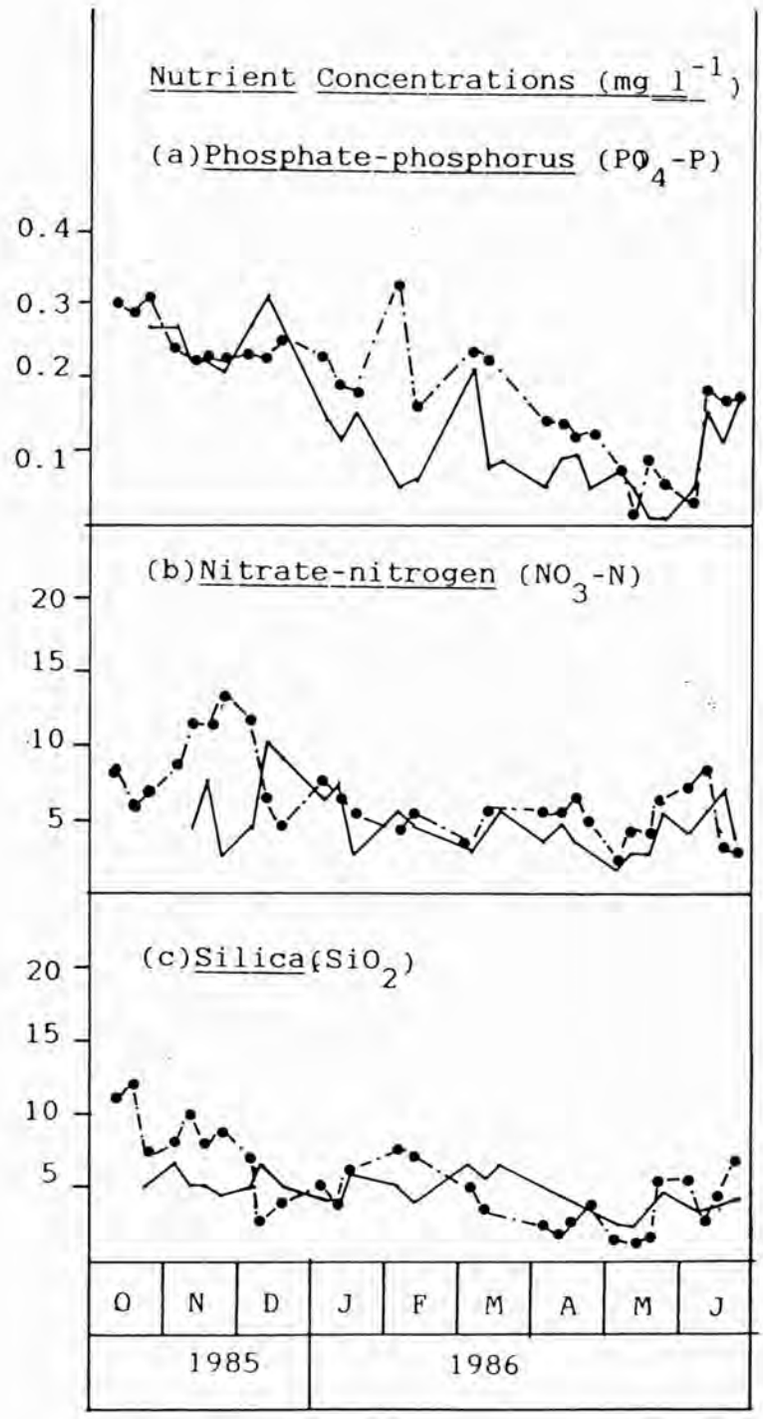


Figure 3.51

—●— Bells of Ouzely

—— Datchet

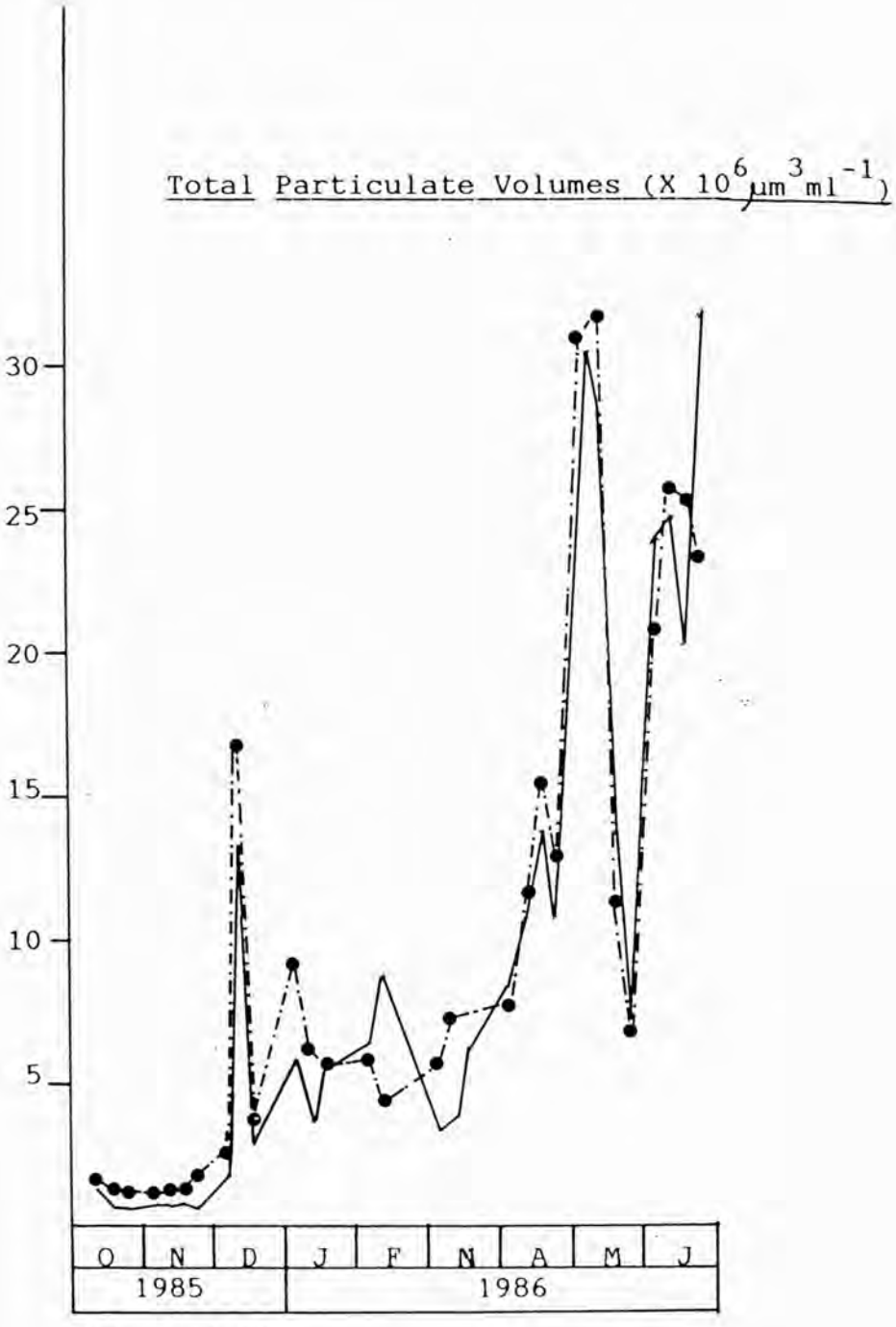


Figure 3.52

—●— Bells of Ouzely

—— Datchet

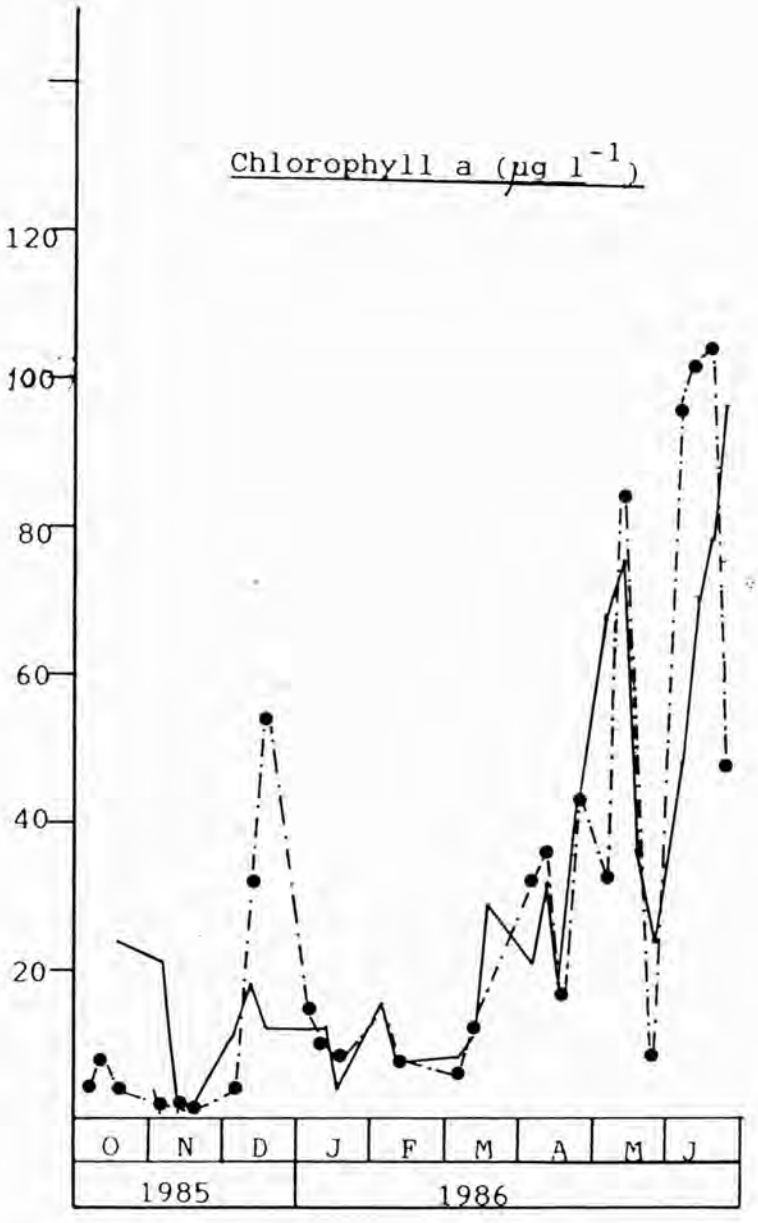


Figure 3.53

—●— Bells of Ouzely

—— Datchet

physical and chemical environmental factors.Light attenuation were higher in the River Thames at the Bells of Ouzely during December(1985) to January(1986) and during May(1986) (Figure 3.50).This condition was coincided with the higher concentrations of chlorophyll a (Figure 3.53),in the River Thames at the Bells of Ouzely.It can be concluded,therefore, that there is a correlation between chlorophyll a and attenuation in the PAR region of the light spectrum.This correlation was also shown in Figure 4.11 (see Chapter Four).

Surface radiation (Figure 3.48a) was also higher in the River Thames at the Bells of Ouzely during January to March.The differences was due to cloudy sky at Datchet when the measurements was performed.

From Figures 3.51a,b,c it could be concluded that nutrients concentrations (nitrate-nitrogen,phosphate-phosphorus and silica) in the River Thames at the Bells of Ouzely were higher than at Datchet.This might probably due to the effluents from sewage treatment works from Ham Fields (refer to Figure 2.2,Chapter Two).

Phytoplankton populations in the River Thames at both places showed no clear differences either in species or cells number (Figures 3.54 to 3.61).This might be due to river water flowings within one day from Datchet to the Bells of Ouzely.There were also relatively steady relationship between Total Particulate Volumes in both places (Figure 3.52).

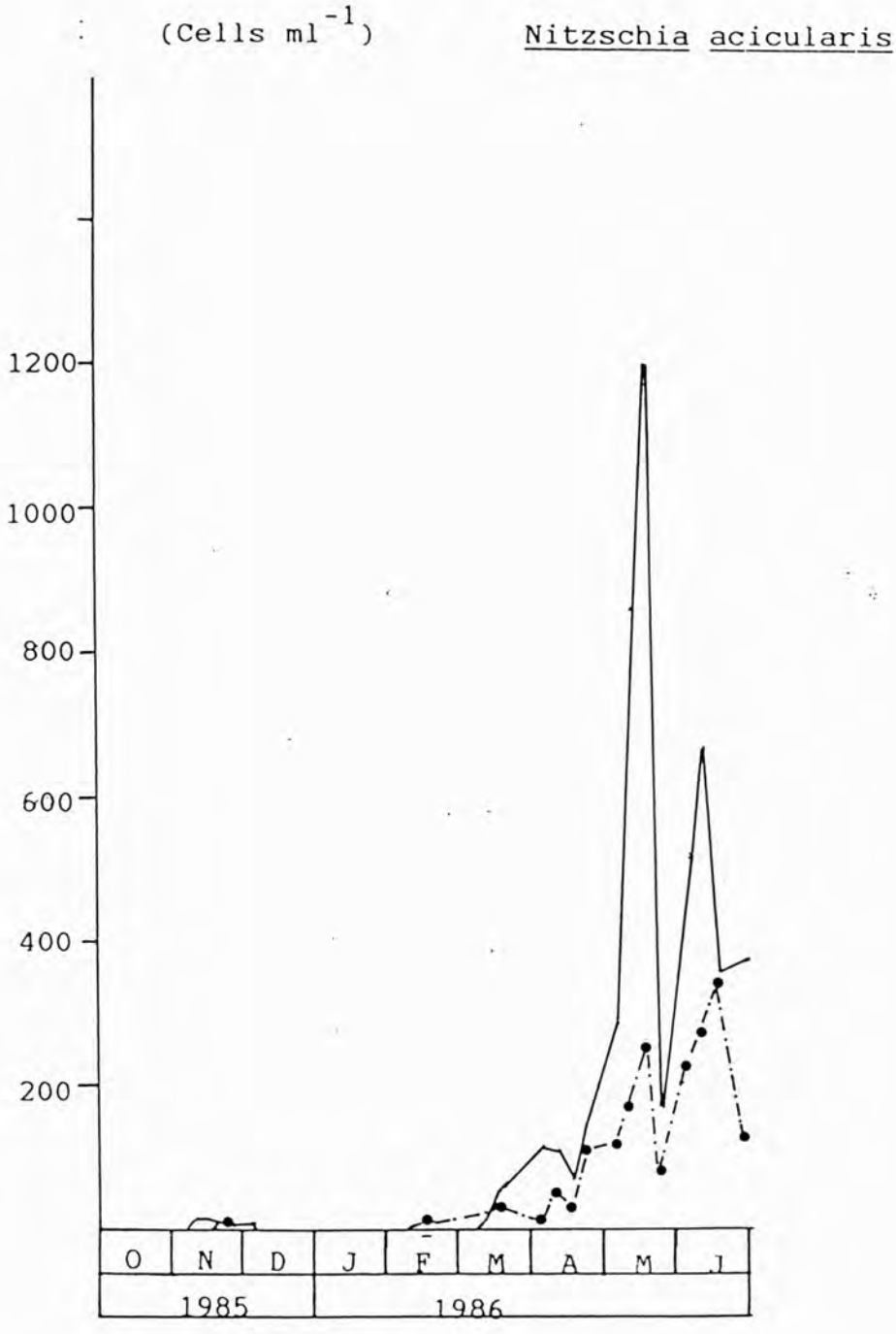


Figure 3.54

—·●·— Bells of Ouzely

——— Datchet

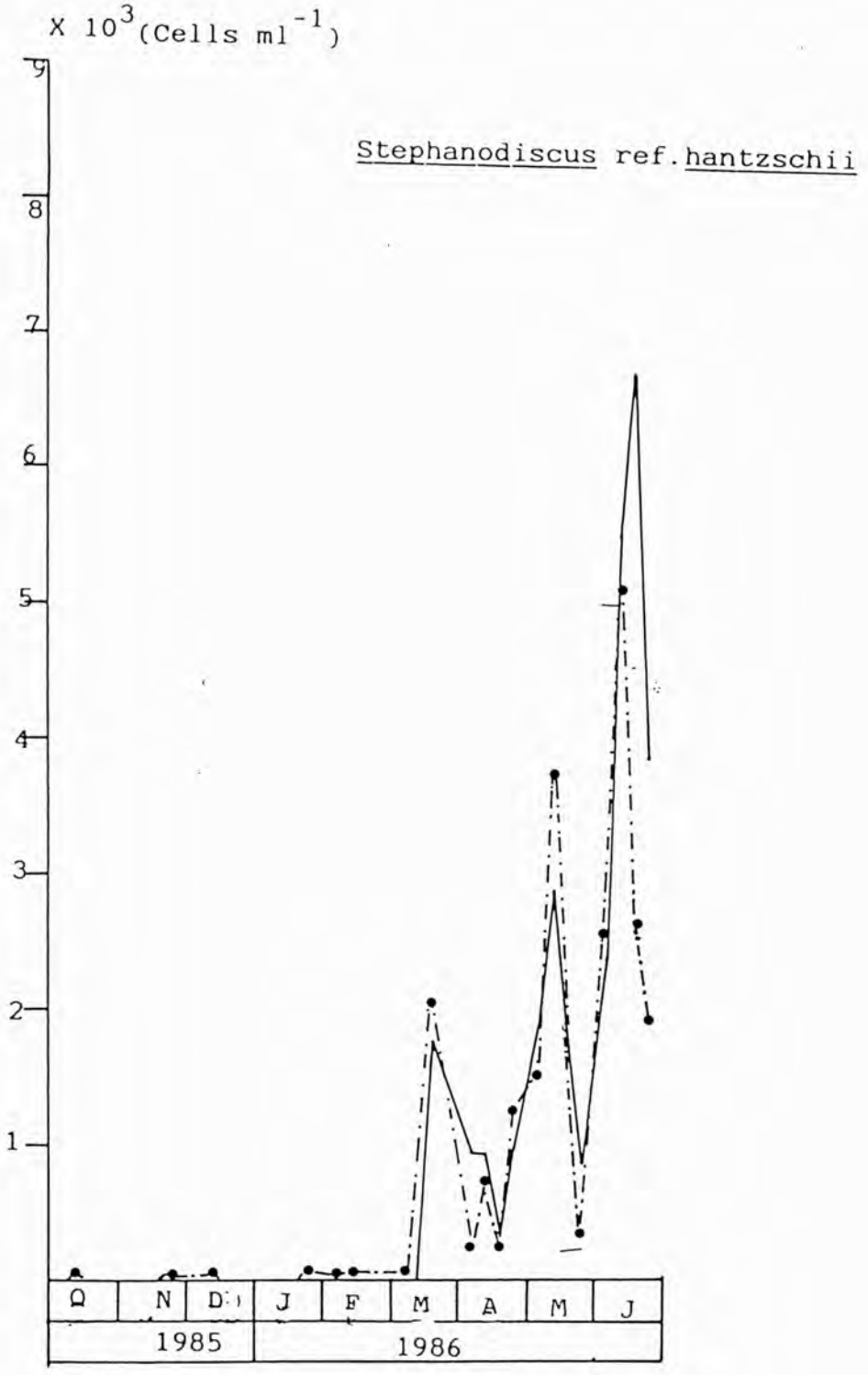


Figure 3.55

—·●·— Bells of Ouzely

——— Datchet

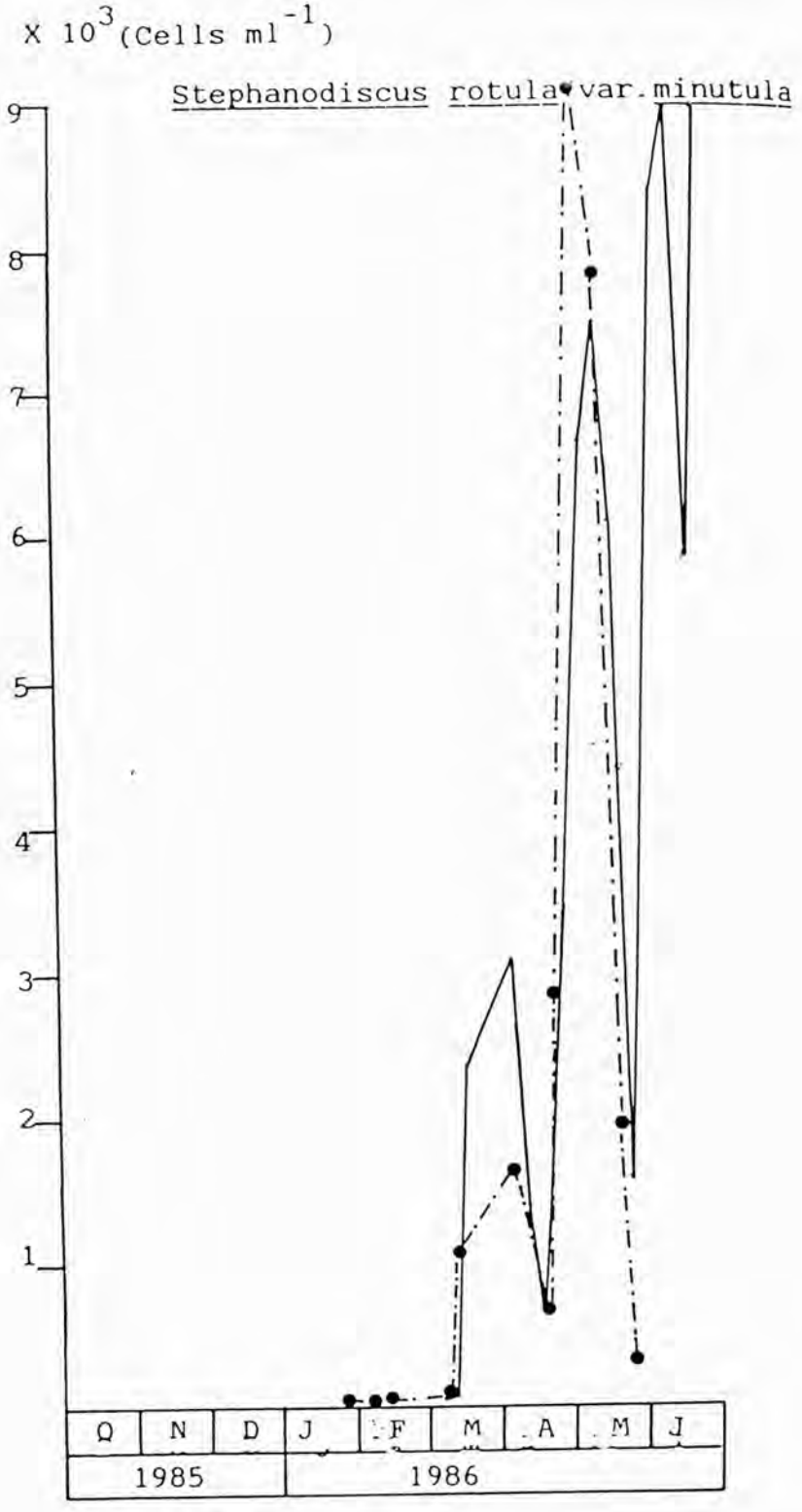


Figure 3.56

—·●·— Bells of Ouzely

—— Datchet

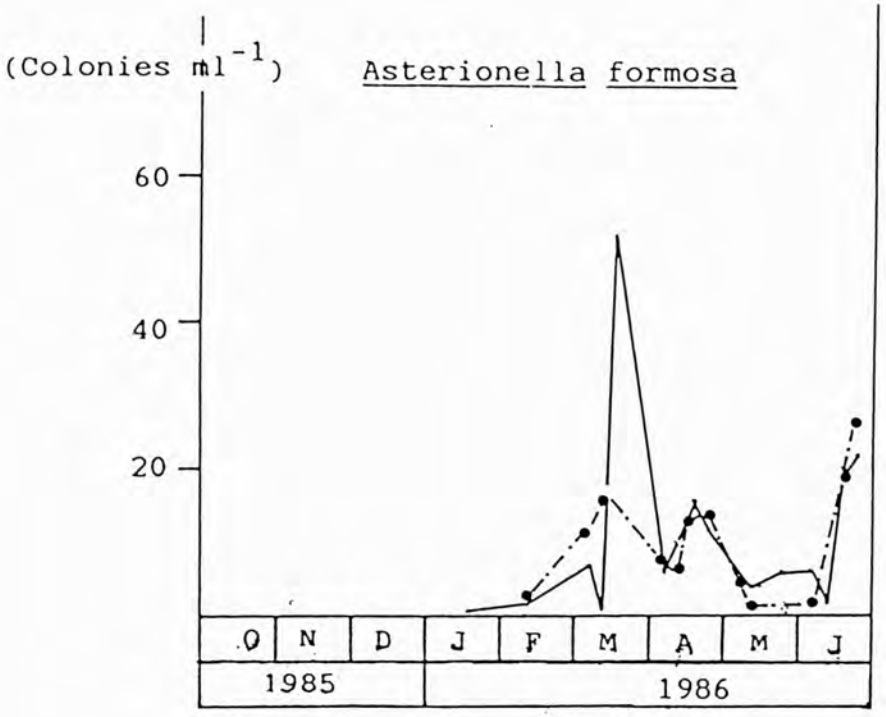


Figure 3.57

—·●·— Bells of Ouzely

——— Datchet

Figure 3.58 Scenedesmus spp

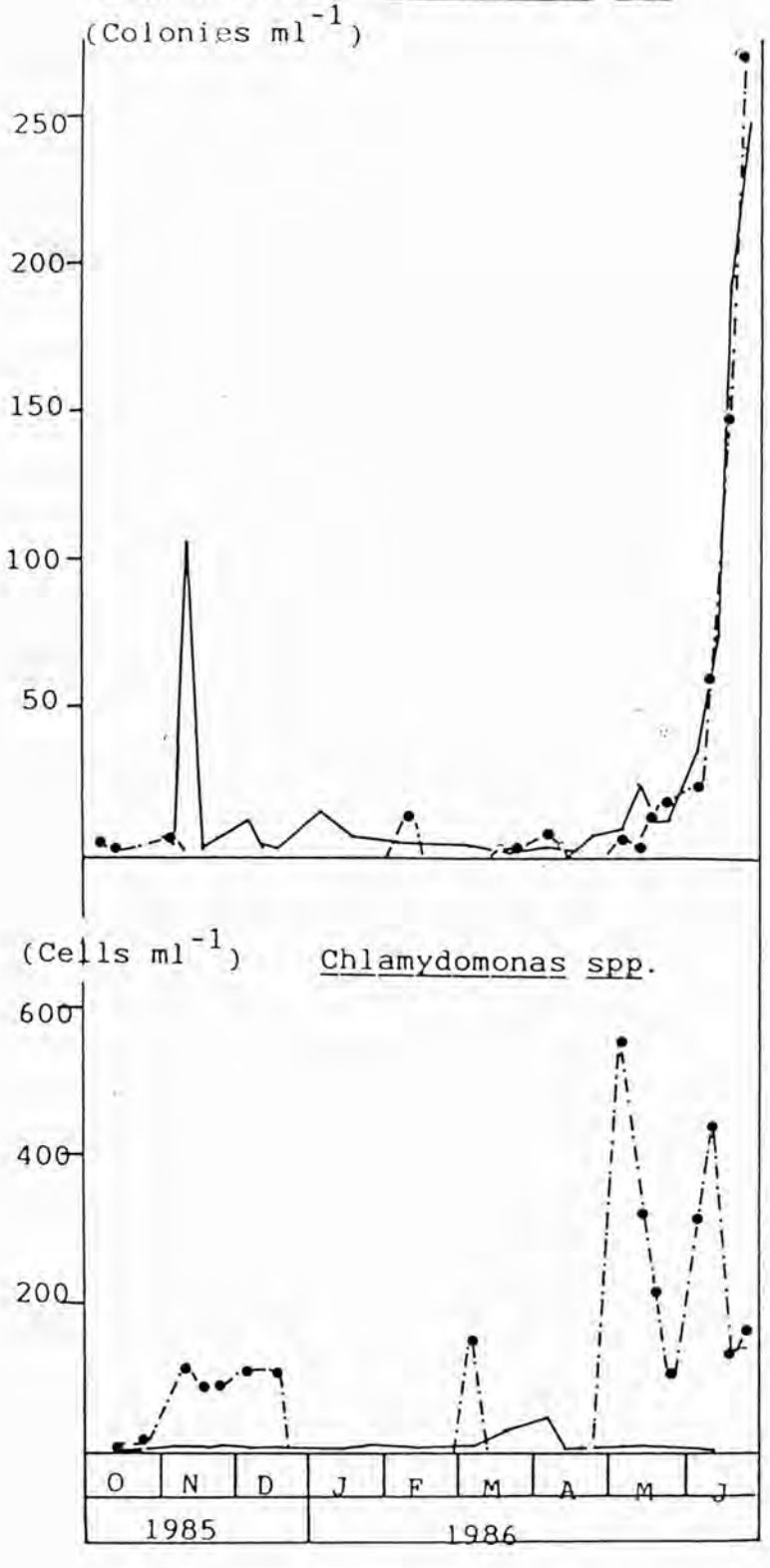


Figure 3.59

—·—·— Bells of Ouzely

——— Datchet

Figure 3.60 Cryptomonas spp.

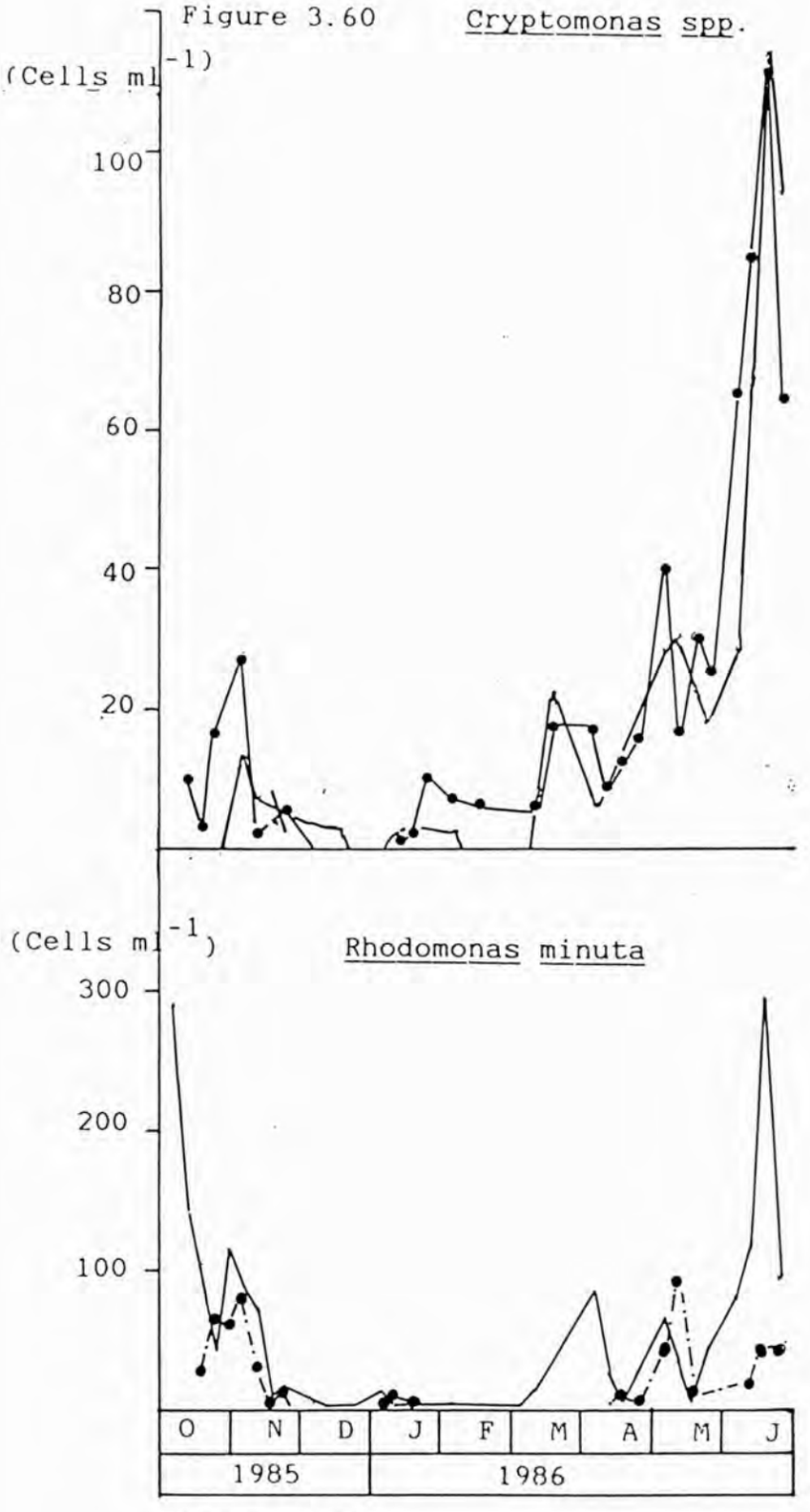


Figure 3.61

—●— Bells of Ouzely

—— Datchet

3.9 GROWTH RESPONSES OF THE RIVER THAMES AND THE WRAYSBURY PHYTOPLANKTON POPULATIONS IN THE RIVER THAMES WATER

3.9.1 INTRODUCTION

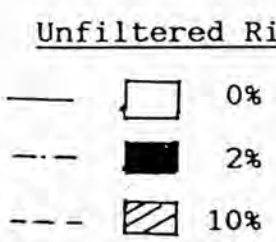
Growth responses of the River Thames and the Wraysbury Reservoir phytoplankton populations in the River Thames water were investigated.The aim of this study was to investigate the effects of nutrient inputs on phytoplankton in the river and reservoir and the fate of the phytoplankton being transported by the river to the reservoir.

3.9.2 MATERIALS AND METHODS

Water samples (collected from the River Thames) were collected in polythene containers.The sample was filtered to remove the algae and herbivorous organisms which could be present and might subsequently graze the inoculated test alga. Filtration was carried out using vacuum.Millipore filters (0.45 μm) were used to obtain filtered river waters.Treatments were unfiltered river water (URW),filtered river water (FRW), and phosphorus additions.In this experiment filtered and unfiltered river water and phosphorus were added to samples of the Wraysbury Reservoir water taken at the depth of sub-

Figure 3.62a Growth responses of the River Thames and the Wraysbury Reservoir phytoplankton populations in the River Thames water.

y axes: Growth rates (ln day^{-1} units) and concentrations (X 10 cells ml^{-1}) of phytoplankton populations.



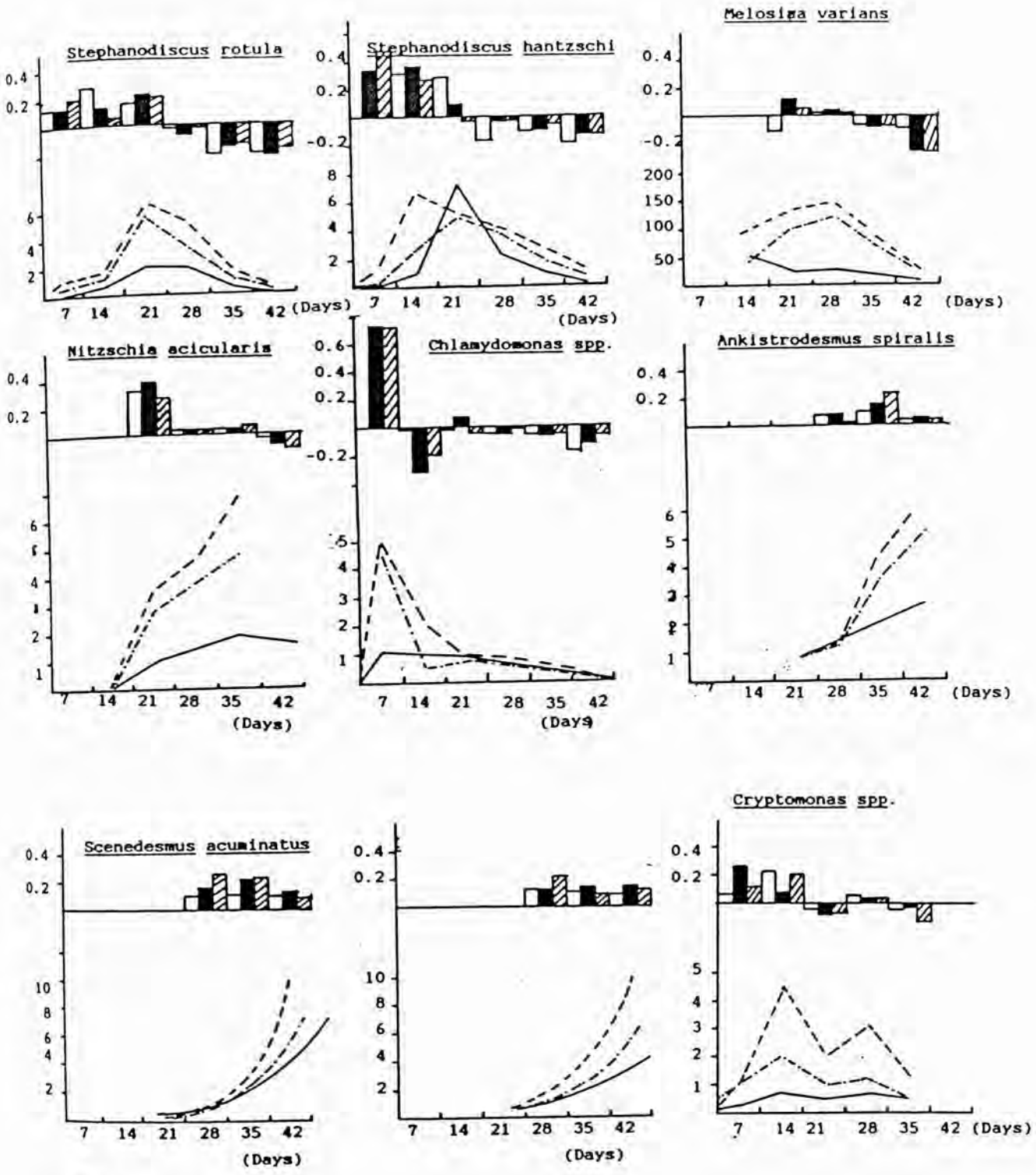

Stephanodiscus rotula
Stephanodiscus hantzschi
Melosira varians
Nitzschia acicularis
Chlamydomonas spp.
Ankistrodesmus spiralis
Scenedesmus acuminatus
Cryptomonas spp.
(Days)

Figure 3.62a

phytoplankton cells acted as inoculum for the experiments.

Greatest community responses, as measured by increases in cell numbers per ml were obtained in the unfiltered river water treatments with doublings in concentrations for 2 and 10% treatments (Figures 3.62, 3.63). Phytoplankton crops increased with the treatment because of the phytoplankton added with unfiltered river water. Phytoplankton populations growth decreased after day 21 presumably because nutrient supplies were depleted.

Greater increases in phytoplankton cells were obtained with phosphate-phosphorus treatments for unfiltered than filtered river water treatments. The concentration tripled in the 0.2 mg l^{-1} PO_4-P treatment but only doubled in the 10% filtered water treatment between days 7 to 14 (Figures 3.62, 3.63). This result showed that addition of phosphate-phosphorus alone stimulated the growth of phytoplankton in the River Thames and the Wraysbury Reservoir. It is presumed that phosphate-phosphorus added with river water also was responsible for increasing phytoplankton growth. In the unfiltered river water treatments, phosphorus was added with phytoplankton as internally stored phosphorus (Stoermer et al., 1980), and in other particulate forms. This phosphorus was responsible for doubling the phytoplankton growth on day 14 in 10% unfiltered river water.

River and reservoir populations that responded in the treatments followed two patterns of growth:

Figure 3.62b Growth responses of the River Thames and the Wraysbury Reservoir phytoplankton populations in the River Thames water.

y axes: Growth rates (ln day^{-1} units) and concentrations (X 10^2 cells ml^{-1}) of phytoplankton populations.

Filtered River Water

— □ 0%

—·— ■ 2%

--- ▨ 10%

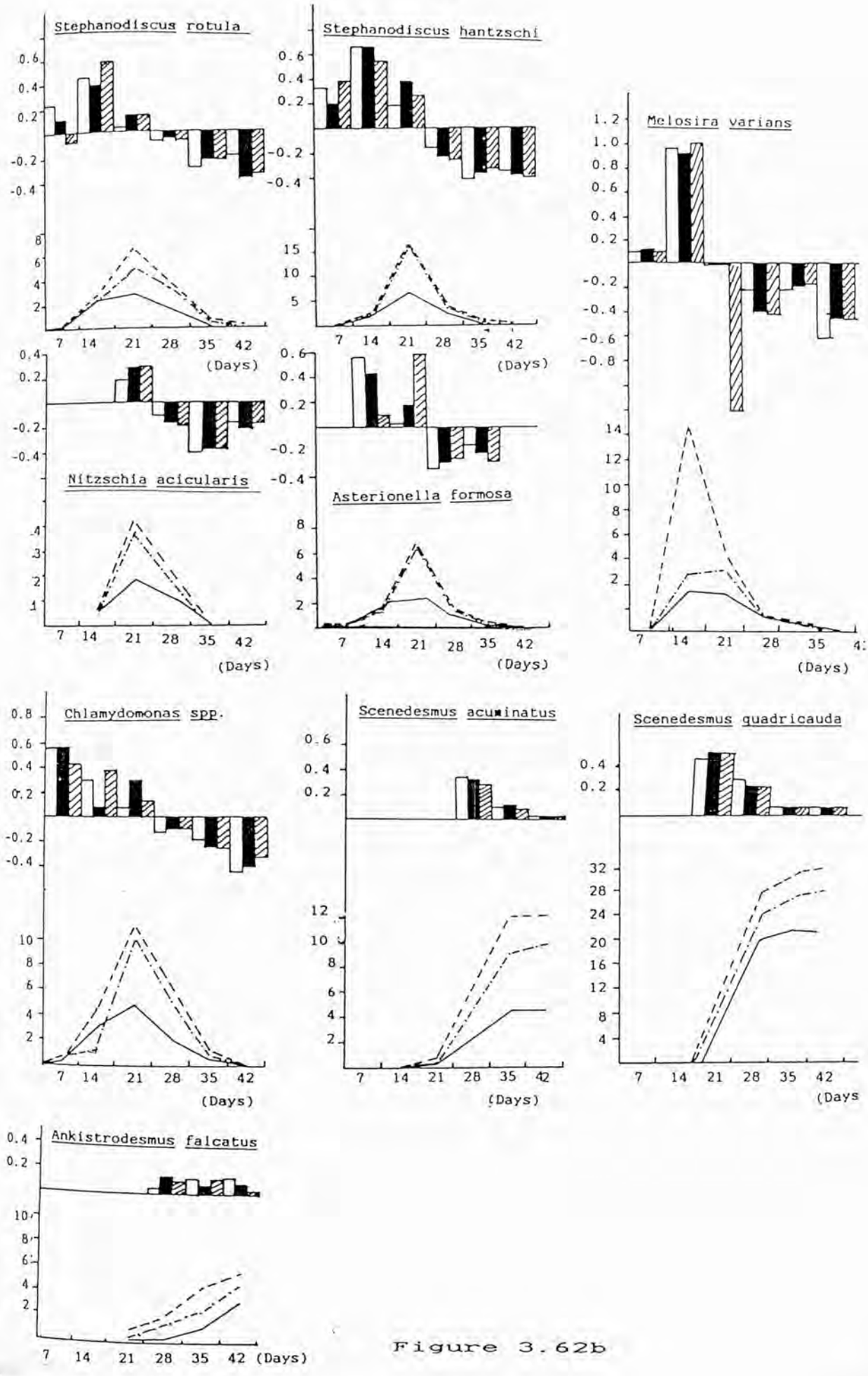
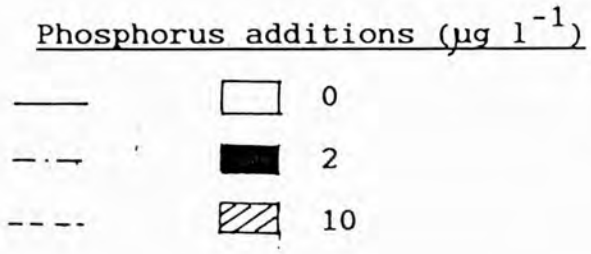

Stephanodiscus rotula
Stephanodiscus hantzschi
Melosira varians
Nitzschia acicularis
Asterionella formosa
Chlamydomonas spp.
Scenedesmus acuminatus
Scenedesmus quadricauda
Ankistrodesmus falcatus
(Days)

Figure 3.62b

Figure 3.63 Growth responses of the River Thames and the Wraysbury Reservoir phytoplankton populations in the River Thames water.

y axes: Growth rates (ln day^{-1} units) and concentrations (X 10^2 cells ml^{-1}) of phytoplankton populations.



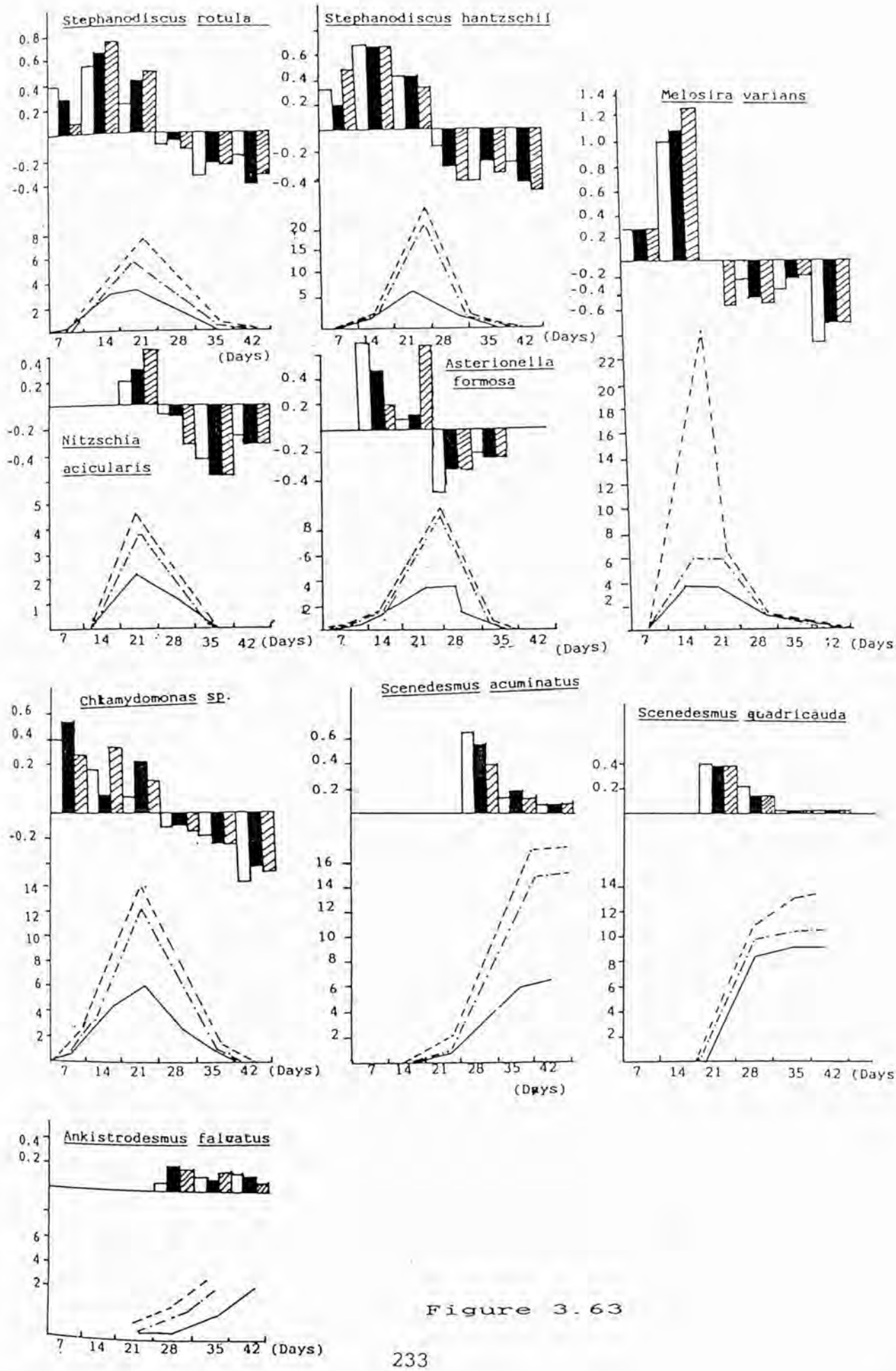

Stephanodiscus rotula
Stephanodiscus hantzschii
Melosira varians
Nitzschia acicularis
Asterionella formosa
Chlamydomonas sp.
Scenedesmus acuminatus
Scenedesmus quadricauda
Ankistrodesmus falcatus
(Days)

Figure 3.63

surface chlorophyll maximum (1 metre).For the experiments, 200 ml of water were added to 500 ml conical flasks.All flasks were duplicated.Additions of river water were 0,1,2,5 and 10% and of phosphorus 0,1,2,5 and 10 µg l^{-1} PO_4-P.Flasks were maintained at a constant temperature ($18\pm1°C$) and were manually shaken daily.Light was programmed with a 12 hours light and 12 hours dark.Each flask was sampled on days 0,3,7 and 13 and analysed for phytoplankton species composition and abundance.Growth rates were calculated from cell counts taken on days 0,3,7 and 13.Counts were also made for each replicate on day 0 to ensure that growth rates were independent of variation in initial cell densities.Growth rates were calculated from Hoogenhout and Amesz (1965);(see Chapter Two).

3.9.3 RESULTS AND DISCUSSIONS

Chemical conditions and phytoplankton in the River Thames and the Wraysbury Reservoir during the periods of this study (14th.January,1986) were as shown in Tables 3.5 and 3.6. In the River Thames and the Wraysbury Reservoir;Stephanodiscus rotula,Stephanodiscus rotula var.minutula,Stephanodiscus ref. hantzschii,Melosira varians and Rhodomonas minuta were present in very low numbers.Samples such as these provided an opportunity to observe the growth of phytoplankton when transferred from winter conditions (cold,lower temperature) to higher temperature in the laboratory.Lower numbers of

Table 3.5 PHYSICAL AND CHEMICAL CONDITIONS IN THE RIVER THAMES AND WRAYSBURY RESERVOIR ON 14th.JANUARY,1986

	RIVER THAMES	WRAYSBURY RESERVOIR
(1)Temperature(°C)	5.9	6.7
(2)Dissolved Oxygen(%)	99	79
(3)Chlorophyll *a* ($\mu g\ l^{-1}$)	14	1.9
(4)NO_3-N ($mg\ l^{-1}$)	7.6	4
(5)PO_4-P ($mg\ l^{-1}$)	0.21	0.10
(6)SiO_2 ($mg\ l^{-1}$)	6	12

Table 3.6 COMPARISON OF PHYTOPLANKTON SPECIES COMPOSITION AND ABUNDANCE IN THE RIVER THAMES AND WRAYSBURY RESERVOIR ON 14th.JANUARY,1986

	RIVER THAMES (Cells ml^{-1})	WRAYSBURY RESERVOIR (Cells ml^{-1})
Stephanodiscus rotula	+	+
Stephanodiscus rotula var.*minutula*	+	+
Stephanodiscus ref. *hantzschii*	+	+
Melosira varians	+	+
Nitzschia acicularis	+	+

(1) Some populations decreased between day 7 and 14 (negative growth rates), whereas;

(2) some populations exhibited positive growth rates from day 7 and 42 (when experiments were terminated).

The populations that responded to pattern (1) were Stephanodiscus rotula, Stephanodiscus ref. hantzschii, Asterionella formosa, Nitzschia acicularis and Melosira varians. Growth rates for Chlamydomonas spp., Scenedesmus acuminatus, Scenedesmus quadricauda and Ankistrodesmus spiralis were as pattern (2).

Reservoir and river populations (Table 3.6) with cell densities < 12 cells ml^{-1} at the beginning of the experiment bloomed in all treatments. This may have been due to light and temperature conditions during the experiments. Phytoplankton in both treatments showed dominant growth of diatoms from day 7 to 14 and then replacement by green algae from day 14 to 42. This simulated succession in the nature. It is well known that diatoms dominate when more nutrients are available and decrease when there is nutrient limitation, especially silica (see page 187).

The results obtained show that river populations can grow in the Wraysbury Reservoir. The decrease in growth after day 21 of most of the phytoplankton populations suggests that nutrient supplies may have become limiting. The growth of phytoplankton populations in the Wraysbury Reservoir was lower

than in the River Thames.

The results obtained also showed that addition of phosphate-phosphorus stimulated the growth of river phytoplankton.This was consistent with the results obtained from the experiments of the influence of phosphate-phosphorus on the growth of phytoplankton populations (see page 168).

3.10 THE PREDICTION OF PHYTOPLANKTON GROWTH BY BIOASSAY

3.10.1 INTRODUCTION

Many of man's agricultural, industrial and domestic activities enrich water bodies with nutrients and some support crops of microscopic algae which interfere with water treatment. Algal blooms, undesired types and the excessive development of phytoplankton represent a serious hygienic as well as water management problem in reservoirs and in all surface waters, regardless the purpose they serve, including fishing and recreation. Management of such waters requires a knowledge of algal populations, and biologists are frequently asked to predict algal growth in existing and proposed reservoirs. It was found by several researchers that the most natural way that offers itself to this purpose is algal assays or bioassays (Forsberg, 1972; Marvan, 1979).

3.10.2 MATERIALS AND METHODS

Four 500 ml aliquots were prepared from each test water sample (River Thames and Wraysbury Reservoir). The samples were filtered as described in Section 3.9.2. The test algae inocula were then prepared and the aliquots inoculated

with Stephanodiscus ref.hantzschii and Scenedesmus quadricauda. The flasks were swirled to ensure thorough mixing of the test algae into the test waters.Each test alga was duplicated.Then each 500 ml aliquot was distributed into four 250 ml conical flasks.Each flask was filled with 125 ml of aliquots.The flasks were incubated for a week under conditions as decribed in section 3.9.2.

An aliquot of unfiltered,uninoculated test water was also distributed between test flasks and the naturally present algae were allowed to grow in them for a period of one week.

Control aliquots were also prepared.This consisted of 500 ml of unmodified Chu No.10 medium which was inoculated with Stephanodiscus ref.hantzschii and Scenedesmus quadricauda distributed and incubated as describe above.

3.10.3 RESULTS AND DISCUSSIONS

RIVER THAMES

The results (Figure 3.64 ,refer to appendix Table 3) show that River Thames water is potentially able to support considerable crops of Stephanodiscus ref.hantzschii and Scenedesmus quadricauda,and that the potential is present throughout the year.The tests showed that the River Thames water supported higher growth of Scenedesmus quadricauda than Stephanodiscus ref.hantzschii.This was found

Figure 3.64 River Thames:

(a) The growth of Stephanodiscus ref. hantzschii in the:

—□— Control

—■— River Thames water

(b) The growth of Scenedesmus quadricauda in the:

—△— Control

—▲— River Thames water

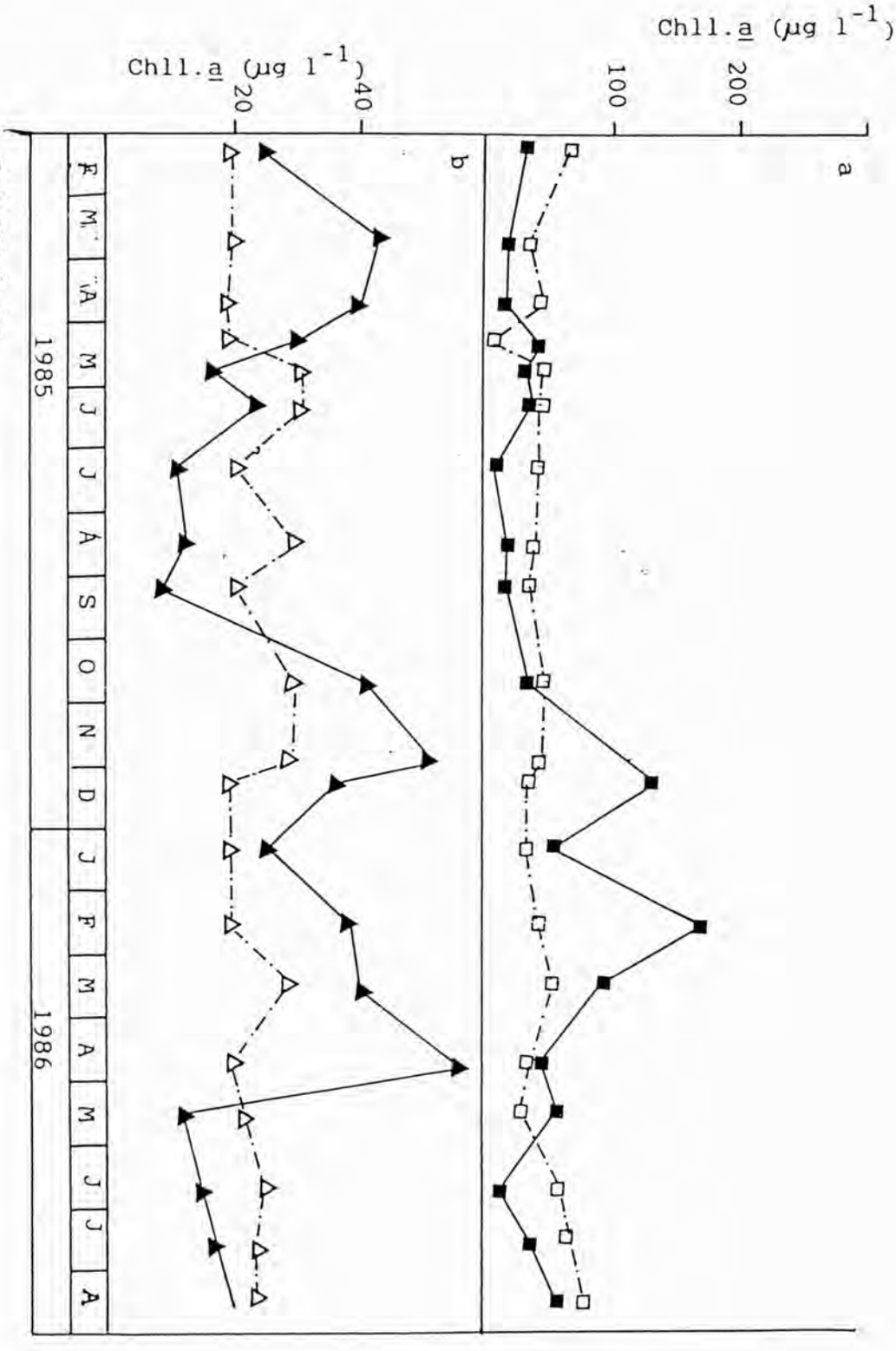

Chll.a (µg l-1)
100
200
a
Chll.a (µg l-1)
20
40
b
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
1985
1986

FIGURE 3.6.4

to be the reverse of what occurred in nature where Stephanodiscus ref.hantzschii was the dominant alga.However, the observations on untreated River Thames samples (Figure 3.6 5 and refer to appendix Table ^{7}) showed that Stephanodiscus ref.hantzschii was the most frequently observed species.The observations on untreated River Thames samples also suggested that the River Thames is potentially able to support high population growths of phytoplankton.

Observations of the River Thames during these studies (1984 to 1986) and by previous researchers (Haffner, 1974;Hardy,1977;Yallop,1980) have shown that the growth of phytoplankton populations occurs mainly in the period of March to September with diatoms (mainly Stephanodiscus ref. hantzschii) forming a large percentage of the population.Green algae including Scenedesmus quadricauda,Ankistrodesmus spp., Actinastrum hantzschii,Eudorina elegans and Pediastrum boryanum also occur but they were of secondary importance to the Stephanodiscus spp.During the rest of the year (October to February) only relatively low concentrations of phytoplankton populations were recorded.The factors which may influence the growth of phytoplankton have been discussed in Chapter Three, Four and Five.Tables(3,7.5) may give some indication of how large is the potential for algal growth in the River Thames.

Figure 3.65 Variations in the chlorophyll a concentrations of untreated River Thames and Wraysbury Reservoir samples.

—■— River Thames samples.

—□— Wraysbury Reservoir samples.

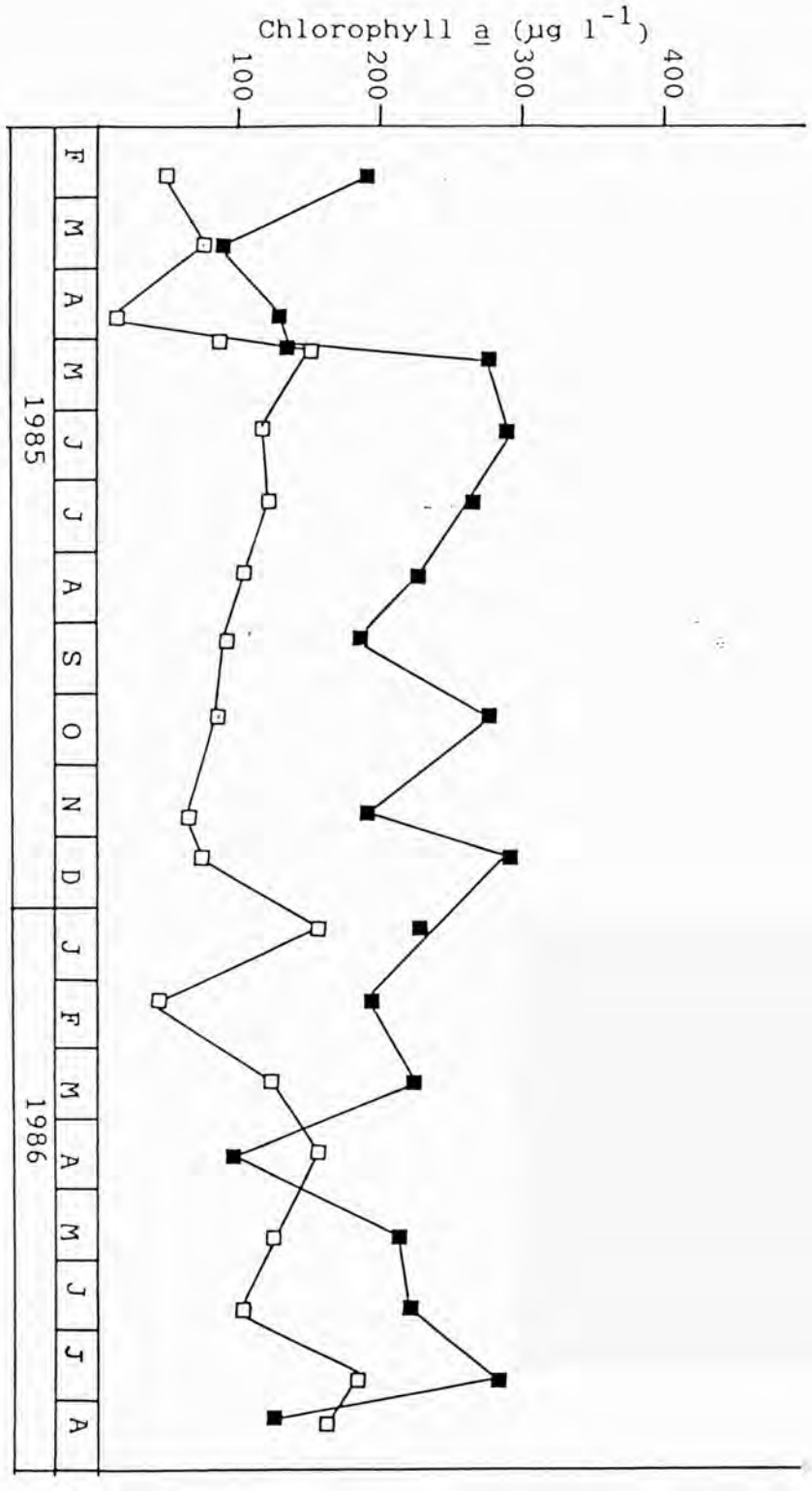

Chlorophyll a (µg l-1)
100
200
300
400
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
1985
1986

FIGURE 3.65

Figure 3.66 Wraysbury Reservoir:

(a) The growth of Stephanodiscus ref.hantzschii in the:

—□— Control

—■— Wraysbury Reservoir water

(b) The growth of Scenedesmus quadricauda in the:

—△— Control

—▲— Wraysbury Reservoir water

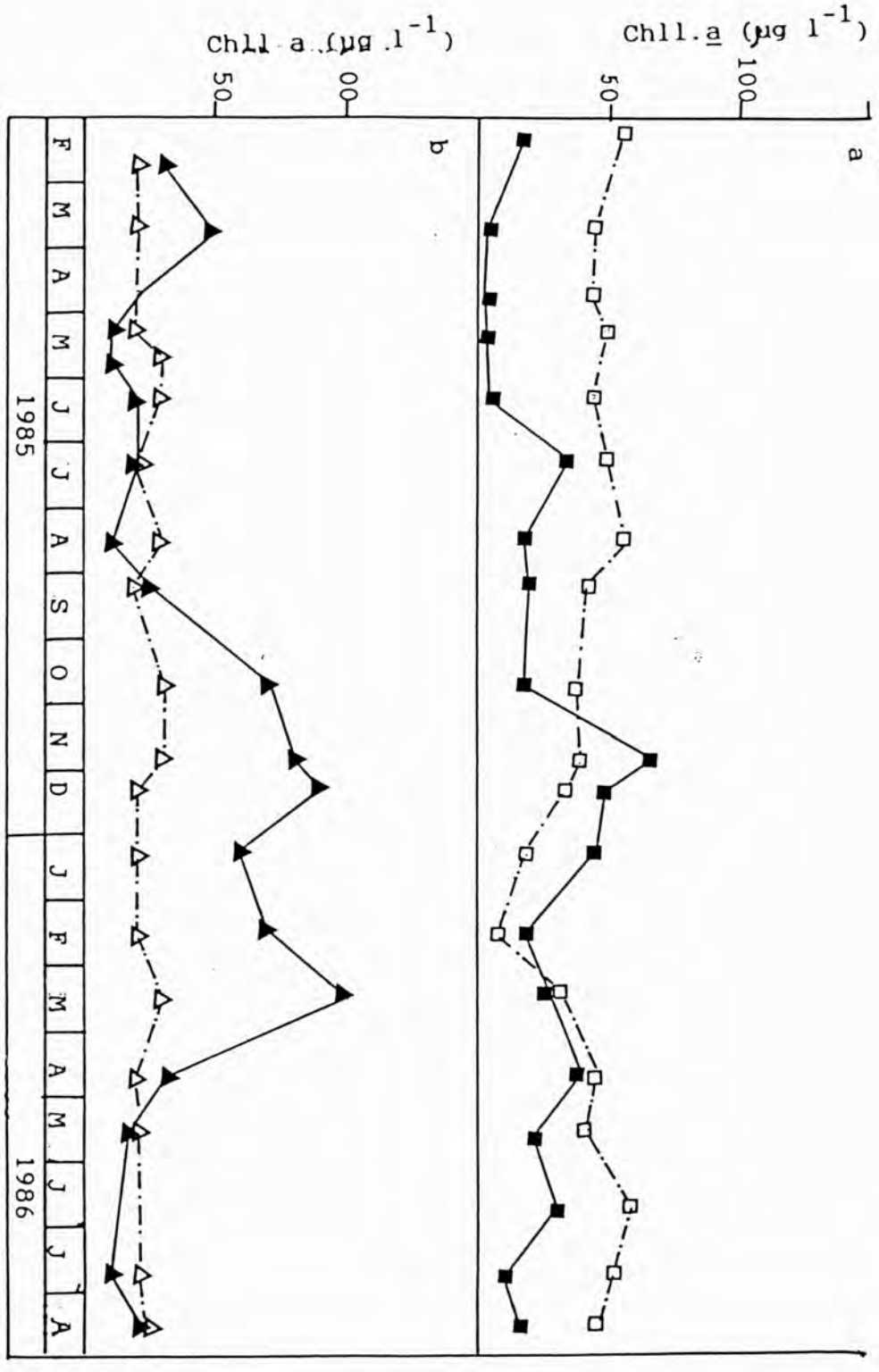

Chll.a (µg l-1)
100
50
a
Chll.a (µg l-1)
50
00
b
F M A M J J A S O N D J F M A M J J A
1985
1986

FIGURE 3.66

WRAYSBURY RESERVOIR

The results (Figure 3.66,and refer to appendix Tables 4,6) showed that the reservoir is potentially able to support considerable growth of Stephanodiscus ref.hantzschii and Scenedesmus quadricauda at any time of the year.As in the River Thames,observation on untreated samples (Figure 3.65 and refer to appendix Table 8) suggest that potentially high populations of algae may be supported.However,the tests showed that Scenedesmus quadricauda did not appear to grow quite as well as in the River Thames samples.

During the period that the bioassay tests were being carried out,the Wraysbury Reservoir supported a succession of phytoplankton populations of many different species (refer to Chapter Six).The observed chlorophyll a maxima were,however,nothing like as large as indicated by the chlorophyll a potential (Figures 3.65,3.66,and refer to appendix Tables 4,6,8).The growth which is observed in the reservoir results from a complex interaction of factors that is temperature,depth,light regime,nutrient status (refer to Chapter Three,Four and Five),retention time, competition with other phytoplankton,grazing by zooplankton and the activities of algal parasites.

3.10.4 CONCLUSIONS

Comparisons of the results for two different waters (that is,River Thames and Wraysbury Reservoir) can indicate that growth of the test organisms is likely to be less in one water than in another.

The bioassay test results appear to give a broad indication of the level of phytoplankton growth which may be observed.However,bioassay tests do not allow one to make precise predictions of how much of what will grow where and when,but they appear to provide a tool for producing a general statement on potential algal quantity and quality for any water body.

CHAPTER FOUR

THE INFLUENCE OF LIGHT AND PHOTOPERIOD ON THE GROWTH OF PHYTOPLANKTON POPULATIONS

4.1 INTRODUCTION

Light, which must be considered in terms of photoperiod and quality (wavelength) as well as intensity, is very important to phytoplankton. In addition to its obvious significance as an energy source for photosynthesis, the fact that light fluctuates widely in both space (depth and latitude) and time (daily and seasonally) suggests that light will often be limiting for phytoplankton growth.

In their natural habitats, phytoplankton experience light conditions that vary continuously. These variations are due to rapid changes in incident irradiance, vertical mixing and the more gradual changes in daylength (Marra, 1980). Daylength is known to invoke diurnal patterns in photosynthesis and cell division of natural phytoplankton populations consisting of diatoms and green algae (e.g. Sournia, 1974; Harris, 1978). Synchronous division and growth of chlorococcal green algae like Chlorella, Ankistrodesmus and Scenedesmus is a well studied phenomenon (Pirson and Lorenzen, 1966; Lorenzen and Hesse, 1974; Post et al., 1985; Osborne and Raven, 1986).

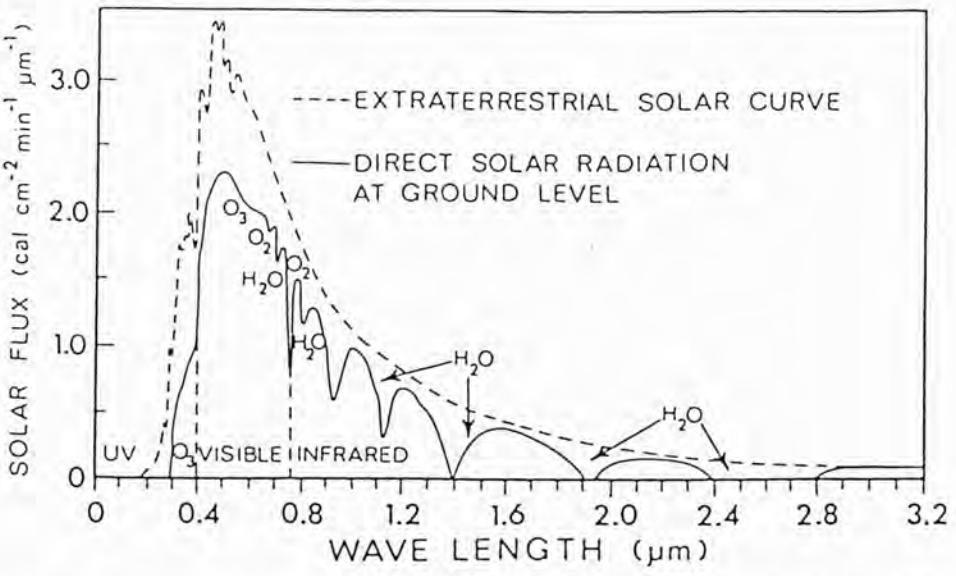


Figure 4.1 Extraterrestrial solar flux and that at the surface of the earth with major absorption bands from atmospheric O_2, O_3, and water vapour. (Modified from Gates, 1962) (From: Wetzel, 1975).

4.2 LIGHT IN THE ATMOSPHERE

Light leaving the sun has a wide and uneven spectral distribution ranging from very short ultraviolet to very long infrared wavelengths.The penetration of light through the earth's atmosphere and through water results in the selective absorption and scattering of light,especially at the ends of the spectrum.The spectral composition and percentage of light at various wavelengths arriving at the lake surface is crucial since the physical properties of photons (scattering,absorption,reflection) and their suitability for photosynthesis depend on the wavelengths actually reaching the plant pigments (Goldman and Horne,1983). Figure 4.1 illustrates the spectral distribution of light outside the atmosphere,after it passes through the earth's atmosphere,and the portion of the spectrum visible to the human eye.About half the total energy occurs in the visible part of the spectrum,and the peak energy input lies near 380 nm.The visible portion of the spectrum,with maximum energy in the green (480 nm) portion of the visible range,is only a small part of the total energy radiated by the sun. Ultraviolet energy is strongly absorbed by ozone and oxygen and infrared by water vapour,ozone and carbon dioxide (Wetzel,1975).

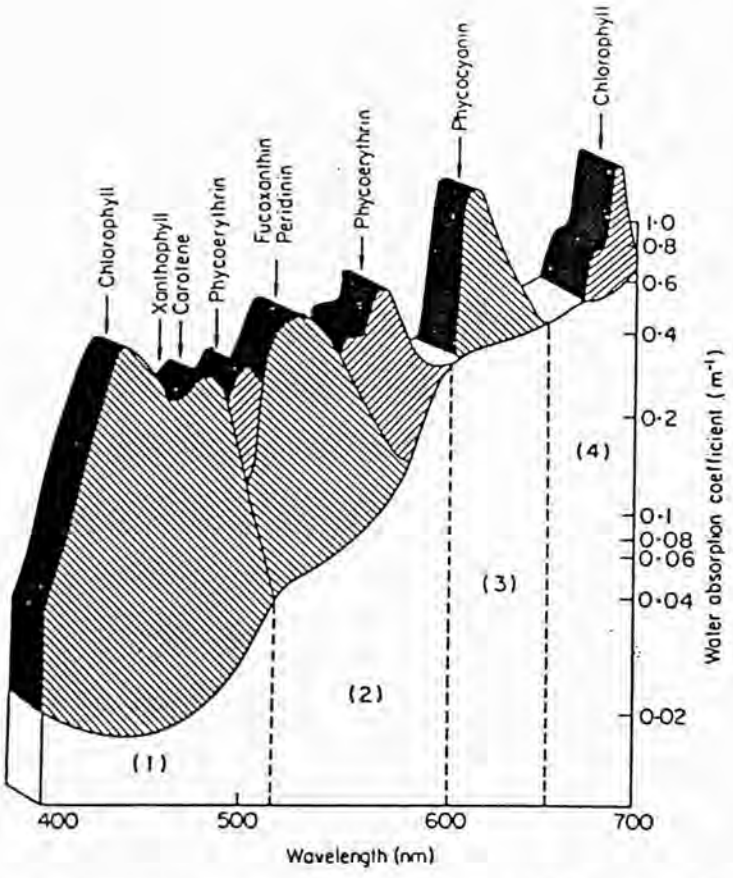


Figure 4.2 The absorption of light by different algal pigments and the 'windows of clarity' in water absorption. The spectra for the pigments approximate to those measured in vivo. For the sake of this illustration, fucoxanthin and peridinin absorption are considered identical. (From: Yentsch, 1980).

4.3 LIGHT UNDER WATER

The factors that attenuate light in water can be divided into four main groups: water itself, dissolved or colloidal (or both) organic coloured substances (also known as dissolved yellow substances, yellow ultraviolet absorbing material or Gelbstoff (Yentsch, 1980)), inorganic turbidity and phytoplankton (Robarts and Zohary, 1984). The influence of these factors on PAR (Photosynthetically Available Radiation; ca. 400-700 nm) is of interest here. Jewson (1977) noted that the water itself absorbs mainly outside the PAR region. Gelbstoff has its major effects also outside this region and mainly absorbs in the ultraviolet region.

Measurement of the amount of light absorbed by pure water has been hampered because of the difficulties of removing impurities and the precision required for making the measurement (Smith and Tyler, 1977). In Figure 4.2, the curve for the highly purified water is shown where the attenuating components, scattering and absorption, have been resolved (Morel, 1974). A case can be made for an apparent relationship between the absorption by major algal pigments and the major windows of clarity in the water spectrum. The major 'clear window' for water lies between 425-450 nm, is filled with the absorption bands of chlorophyll *a*, *b*, *c* and carotenoid bands from all groups of algae found in the marine environment. The windows of clarity between 525-575 nm are filled with

absorption by carotenoids (fucoxanthin and peridinin) of diatoms and dinoflagellates and the phycoerythrins of red and blue-green algae (Cyanobacteria).The third conspicuous window between 525-650 nm is filled by another blue-green algae chromoprotein,phycocyanin.The fourth window between 665-680 nm,positioned next to a strong water absorption band,is filled with the long wavelength absorption bands of chlorophyll a.

In many areas of the open ocean,euphotic zones exceed 100 metres in depth.If the water is not mixed, organisms residing at these depths must rely on short wavelength pigment absorption to gather their light energy needs.Whether algae growing under these conditions function in a metabolic fashion similar to algae exposed to a more equal mixture of red and blue light characteristic of the upper regions of the euphotic is an interesting topic yet to be investigated (Yentsch,1974).In particular,there is interest in the possibility that some aspects of algal kinetics are accelerated by blue light.Some research has included attempts to simulate blue light conditions of the lower reaches of the euphotic zone by adding blue filters to light incubators.Lorenzen (1979) suggested that photosynthesis fixation of carbon-14 by phytoplankton is slightly inhibited by ultraviolet wavelengths passed by quartz bottles.Smith et al.,(1980) have demonstrated that photosynthetic inhibition at high light is due to short wavelengths.

4.4 MATERIALS AND METHODS

Seasonal occurrence of phytoplankton populations in relation to light radiation were investigated in the River Thames during 1984 to 1986.The methods employed are described in Chapter Two.

All phytoplankton species used in the culture experiments were prepared as described in Chapter Two and were grown in unmodified Chu 10 medium.All the flasks for each experiment were duplicated and subjected to the relative total light radiation of 20,40,60 and 80 Wm^{-2} and photoperiods of 24 hours light;12 hours light:12 hours dark and 16 hours light:8 hours dark.

Scenedesmus quadricauda,Stephanodiscus ref. hantzschii and Eudorina elegans were subjected to a study of the effects of light radiation on their growth.Growth rates and numbers of cells per ml were employed during this study to measure the growth of phytoplankton populations (refer to Chapter Two).

4.5 THE INFLUENCE OF LIGHT ON THE GROWTH OF PHYTOPLANKTON POPULATIONS

4.5.1 GROWTH IN NATURE

Smayda (1980) suggested that the extent to which light influences species succession cannot be assessed adequately,partly because sufficient relevant data are lacking.Even if adequate data were available extrapolation to in-situ conditions would have to take into account numerous complicating factors.Furthermore,their location within the euphotic zone and the degree of turbulence influence the amount of photosynthetically available light that will be absorbed.

It is well known that light intensity and photo-period influence phytoplankton growth,including the timing of cell division (Paasche,1968;Smayda,1975).It is also difficult to separate the effects of light and temperature because of the interrelations of these factors in photosynthesis.

Over the period of study,the trends in light intensity in the River Thames were paralleled by corresponding changes in water temperature (Figures 4.3 and 4.4).The results also consistent with hours of bright sunshine (Figure 4.5) data obtained from the Meteorological Offices Reports.In winter the light was of low intensity and

Figure 4.3 Surface Radiation at the River Thames.

Figure 4.4 Seasonal variation of water temperatures in the River Thames.

_____ 0 metre

-·-·-· 1 metre

Figure 4.5 Meteorological Data

Hours of bright sunshine (Monthly means).

Figure 4.5

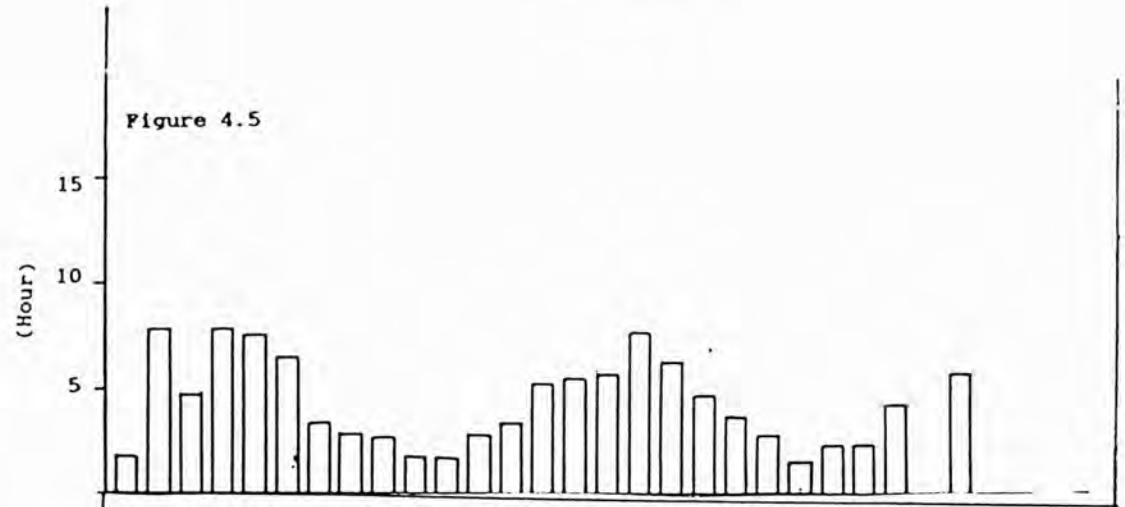


Figure 4.4

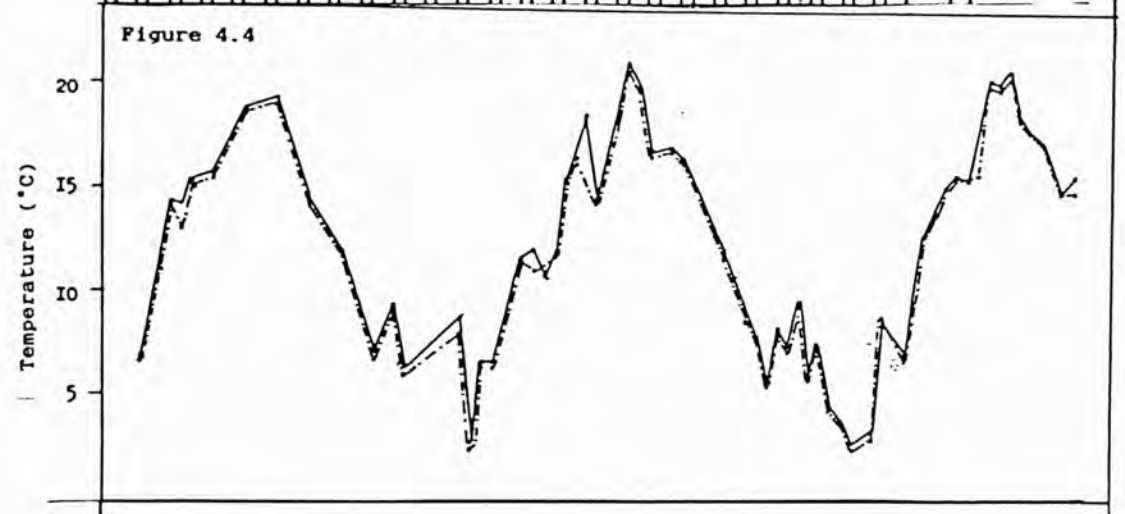
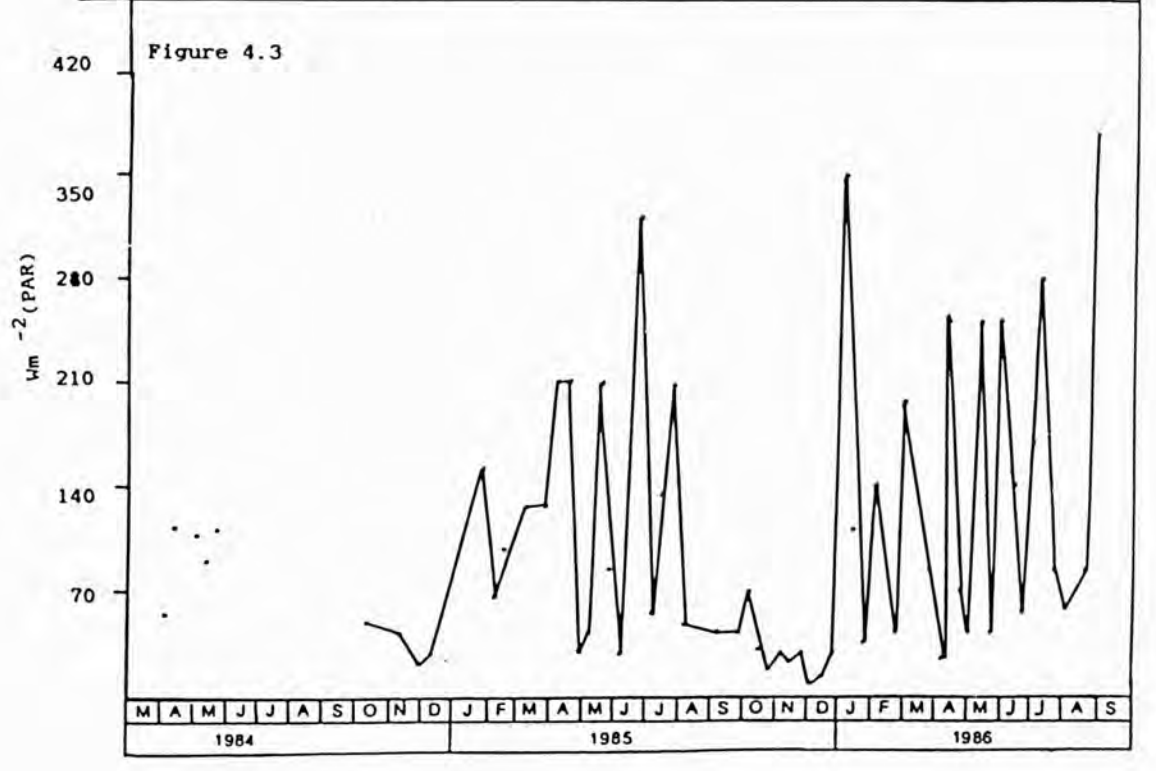


Figure 4.3



short duration.This coincided with the lowest temperature giving a situation which is unsuitable for the growth of nearly all phytoplankton.Increasing light (higher intensities and longer days) in the early spring is thought to be the principle factor which stimulates the spring outburst of phytoplankton growth since temperature remained low during this period.

Melosira varians started the spring growth where it became dominant during early January 1986 (Figure 4.6).The light was 20 Wm^{-2} PAR during Melosira varians blooms. Stephanodiscus rotula,Stephanodiscus rotula var.minutula and Stephanodiscus ref.hantzschii grew during this period but in lower numbers.Stephanodiscus ref.hantzschii became dominant when light intensity increased to about 50 Wm^{-2} PAR and about 60 Wm^{-2} PAR for Stephanodiscus rotula var.minutula. Asterionella formosa did not became dominant in the River Thames but it appeared in quite high numbers on 24th.June, 1986 and 22nd.May,1985 when the light intensity was 70 Wm^{-2} PAR and temperature was about 17°C.The amount of light and duration of light necessary for optimum growth vary greatly depending on the species under consideration.Just as in higher plants,there are some species which prefer abundant light while others live in regions of low light intensity.Diatoms that prefer abundant light are usually found in the plankton or in shallow littoral zones (Schroeder,1939).From Figures 4.6 and 4.7 it was found that Melosira varians grew at low

Figure 4.6 Relationships between Bacillariophyceae and the light intensity at the River Thames.

—— Melosira varians

—●— Aulacoseira granulata

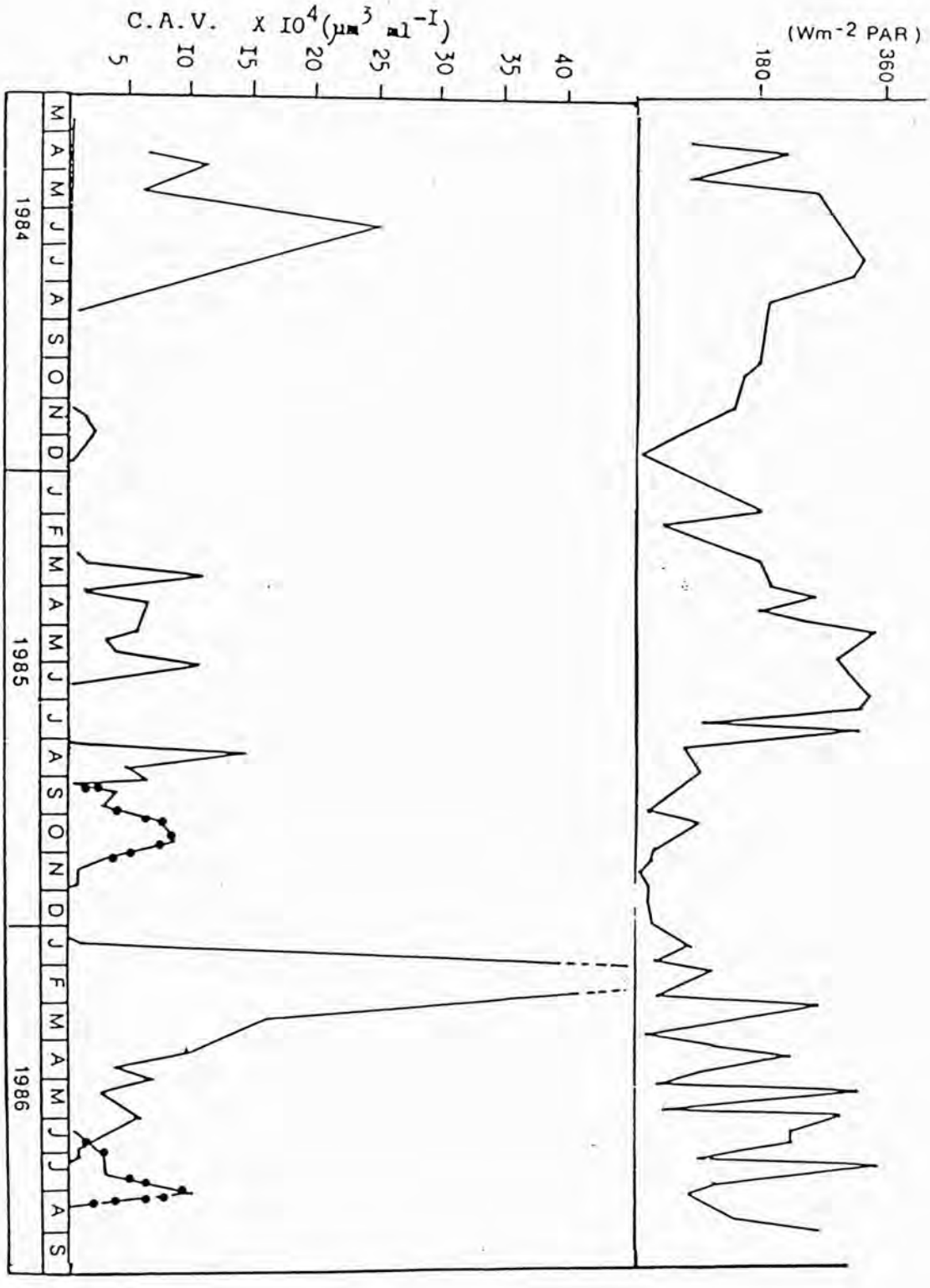

C.A.V. x 10^4(μm^3 ml^{-1})
5
10
15
20
25
30
35
40
(Wm^{-2} PAR)
180
360
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 4.6

Figure 4.7 Relationships between Asterionella formosa and the light intensity at the River Thames.

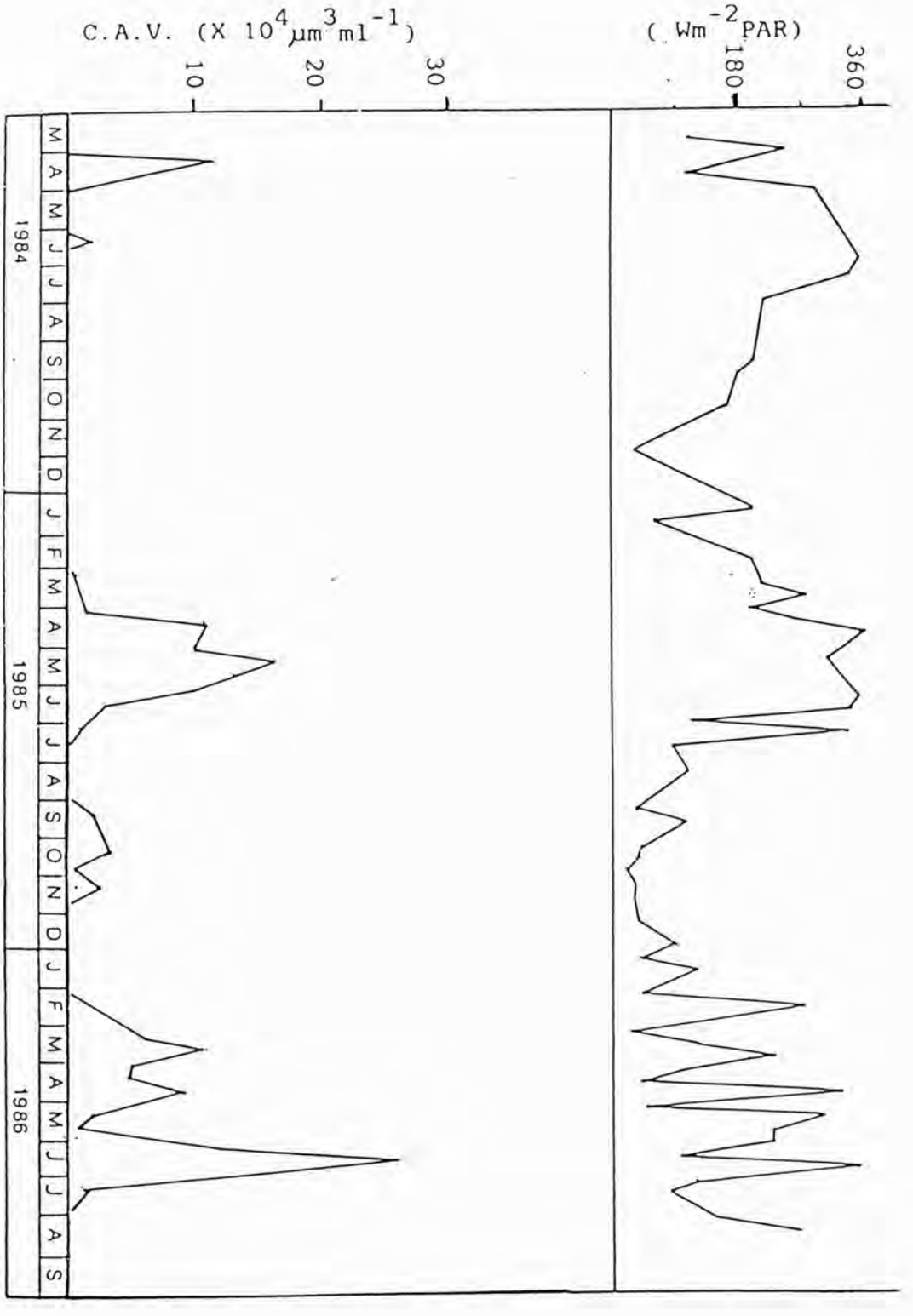

C.A.V. (X $10^4 \mu m^3 ml^{-1}$)
10
20
30
(Wm^{-2} PAR)
180
360
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 4.7

Figure 4.8 Relationships between Stephanodiscus spp. and the light intensity at the River Thames.

——— Stephanodiscus rotula

—●— Stephanodiscus rotula var.minutula

–·o·– Stephanodiscus ref.hantzschii

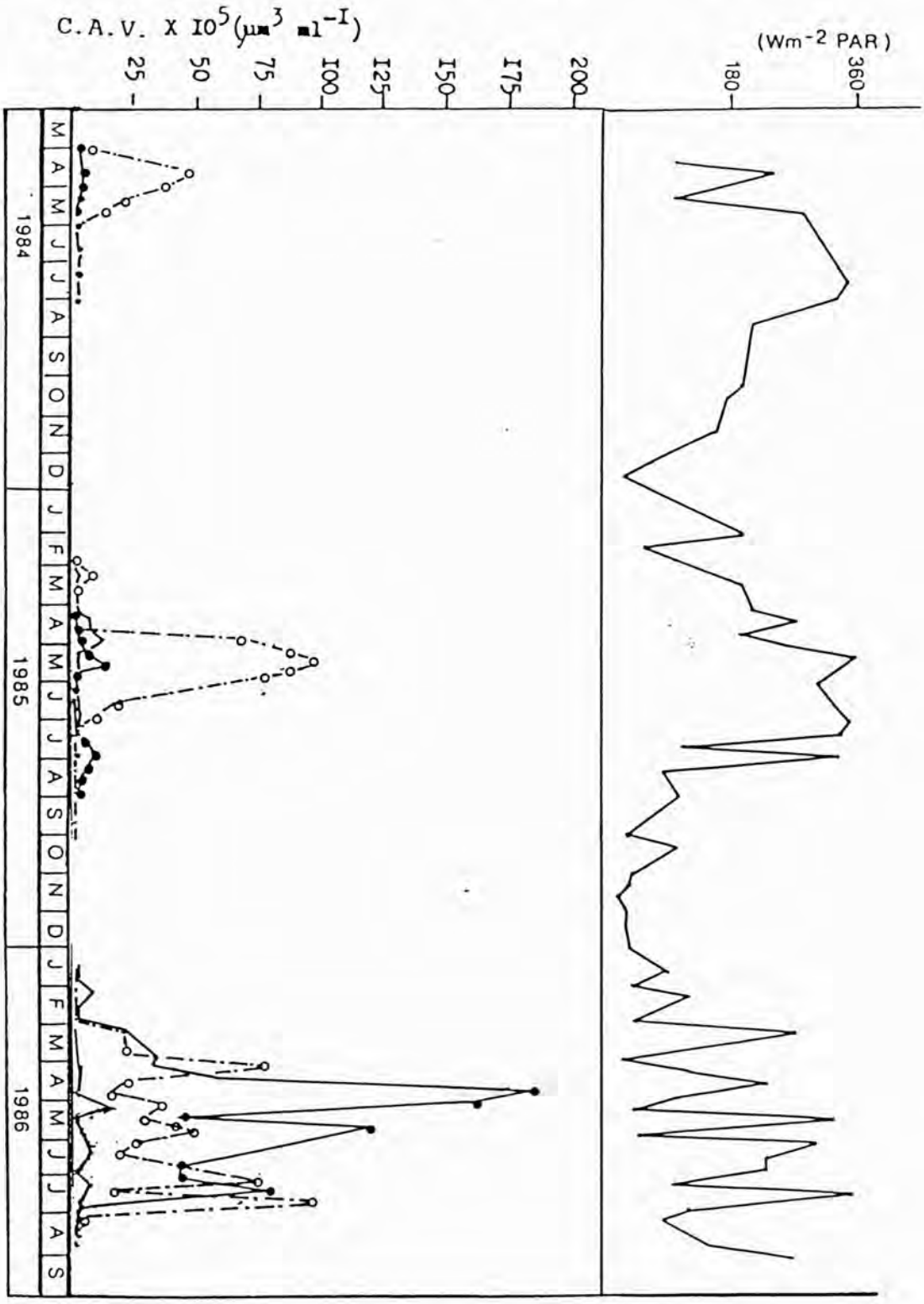

C.A.V. X 10^5 (μm^3 ml^{-1})
25
50
75
100
125
150
175
200
(Wm^{-2} PAR)
180
360
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 4.8

Figure 4.9 Relationships between Cryptophyceae and the light intensity at the River Thames.

——— Rhodomonas minuta

—●— Cryptomonas spp.

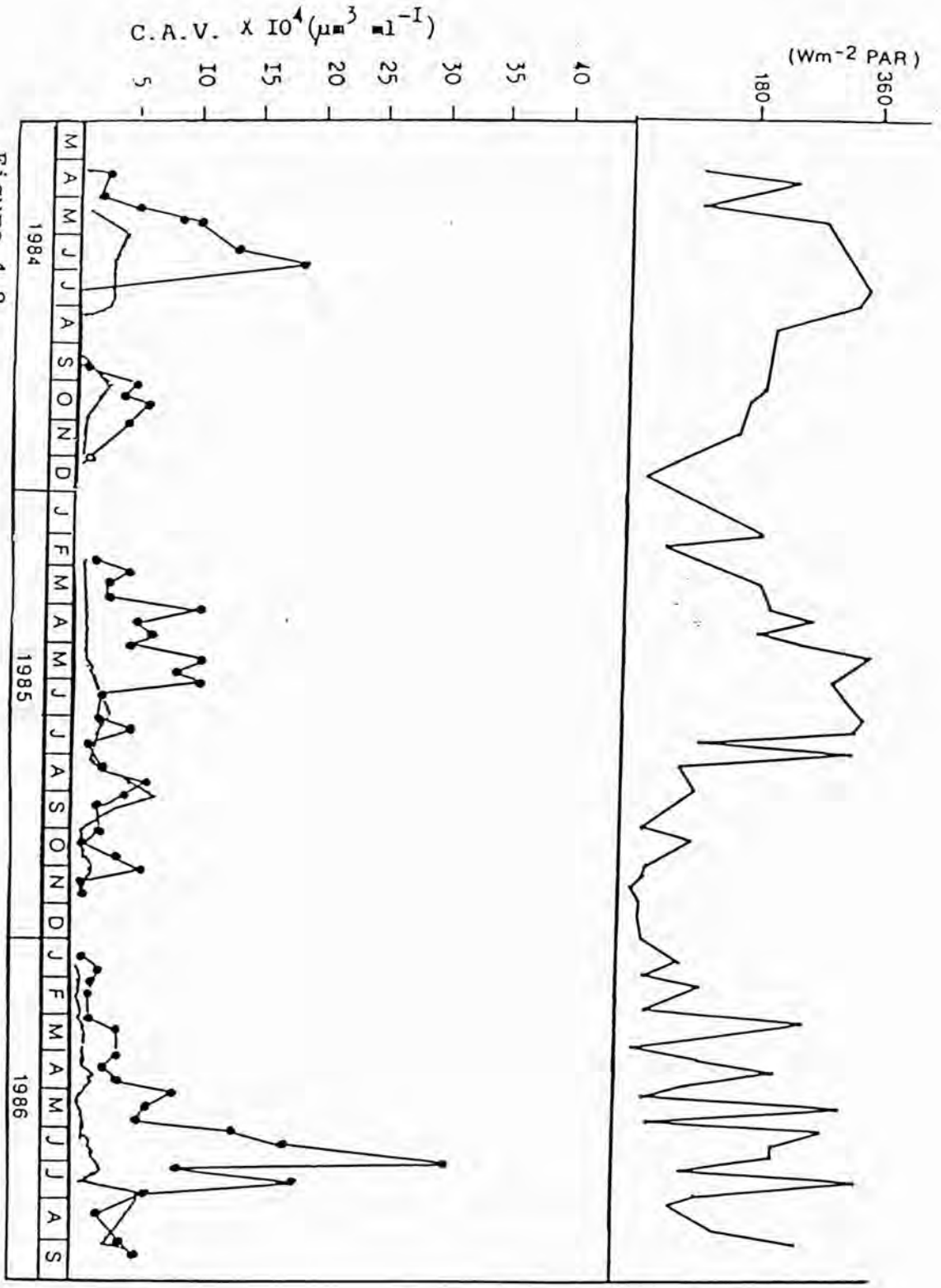

C.A.V. x 10^4 (μm^3 ml^{-1})
5
10
15
20
25
30
35
40
(Wm^{-2} PAR)
180
360
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 4.9

Figure 4.10 Relationships between Chlorophyceae and the light intensity at the River Thames.

Eudorina elegans

Scenedesmus quadricauda

Scenedesmus acuminatus

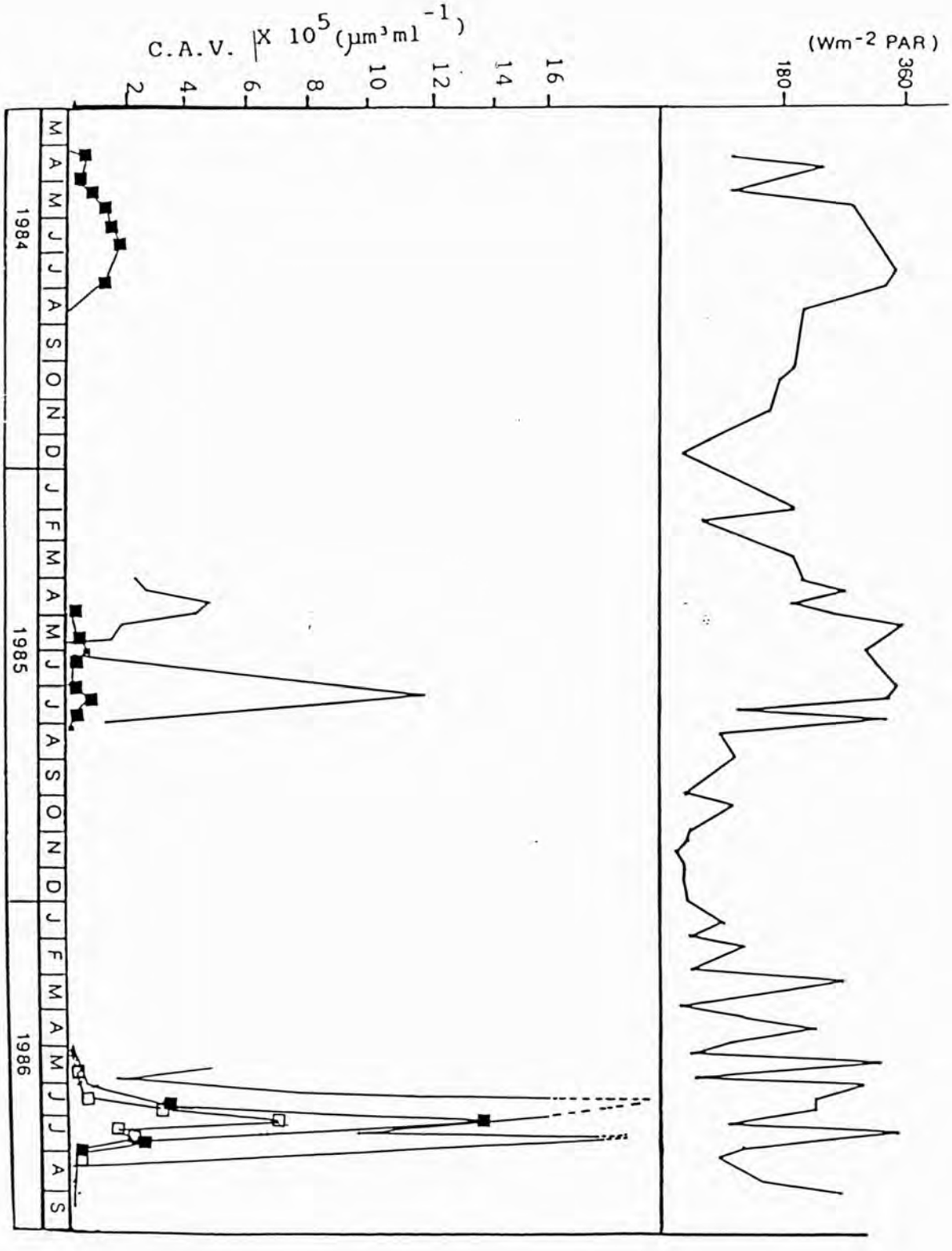

C.A.V. X 10^5 (µm³ml^-1)
2
4
6
8
10
12
14
16
(Wm^-2 PAR)
180
360
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 4.10

light intensity and low temperature whereas Asterionella formosa grew at high light and low temperature.However,on 17th.and 24th.June,1986;Asterionella formosa appeared in relatively high numbers (77 and 172 cells ml^{-1},respectively) in the River Thames although temperatures were high (i.e. 19.8 and 20°C).The growth of Asterionella formosa coincided with the growth of other phytoplankton species which appeared in quite large numbers (Figure 4.8,4.9 and 4.10).Lund (1954) noted that Aulacoseira italica var.subarctica grew at low light intensities and low temperatures.On the other hand, Asterionella formosa was a high-light and low-temperature species.Swale (1964) and Lund (1965) both stated that the increase in daylength was the most likely factor initiating the onset of spring diatom growth.From experiments on cultures of Stephanodiscus hantzschii Swale (1963) showed that the natural daylight of early spring was of more than sufficient intensity to permit the active increase in population even though the water may be at a low temperature. Rice (1938),Lack (1971),Hardy (1977) and Yallop (1980) also believed that increased duration of light encouraged certain diatoms to bloom in the River Thames.

The spring maximum in both River Thames and Wraysbury Reservoir was dominated by Stephanodiscus ref. hantzschii.

Aulacoseira granulata grew during summer and early autumn in the River Thames and Wraysbury Reservoir.They

appeared when the light and temperature were high.

Green algae such as Scenedesmus quadricauda, Scenedesmus acuminatus, Eudorina elegans, Chlamydomonas spp. and Actinastrum hantzschii grew during the summer when both light and temperature were high.

4.5.1.1 UNDERWATER LIGHT ATTENUATION

There is no straightforward evaluation of the vertical attenuation coefficient (E) of light. This is owing to the non-linear (hyperbolic) attenuation of light and its spectral composition with depth (Reynolds, 1984). Perhaps the most direct way is to look first at the percentage of transmission or absorption of monochromatic light through given depth of water. This percentile absorption, or Birgean percentile absorption (after E.A. Birge who used the relationship extensively), is based on the expression (Wetzel, 1975):

$\frac{100(Io-Iz)}{Io}$ where,

Io = irradiance at the lake surface,

Iz = irradiance at depth z.

The vertical attenuation coefficient (E) can be calculated from:

$Iz = Io.10^{-Ez}$ or $E = \frac{1}{z}(\log Io - \log Iz)$

or $Iz = Ioe^{-Ez}$ or $E = \frac{1}{z}(\ln Io - \ln Iz)$ which is used in this study.

Figure 4.11 shows the relationship between chlorophyll a and underwater light attenuation in the River Thames during the periods of study. It can be concluded, therefore, that there is a relationship between chlorophyll a and attenuation in the PAR region of the light spectrum. The presence of even a relatively small concentration (2 $\mu g\ l^{-1}$) of chlorophyll a significantly increases the absorption of light.

The seasonal variation of the attenuation coefficient during 1985 to 1986 is shown in Figure 4.12. There was a relatively steady relationship between the values of attenuation coefficient throughout the year under a wide range of phytoplankton populations canopies. The seasonal variation suggested that the underwater light in the River Thames was related to changes in chlorophyll a concentrations.

4.5.2 GROWTH IN CULTURE

The exponential decrease in light level with depth in marine environments can result in about 10-50% of the incident photons (=350-700 nm) being absorbed at a depth of 10 metres (Jerlov, 1976). In freshwaters, light is attenuated more rapidly due to the presence of higher concentrations of dissolved pigments and particulate matter (Kirk, 1983). The large reduction in the photon fluence rate (PFR, =400-700 nm) with depths suggests that algae can survive at light levels considerably lower than full sunlight (i.e. 1200 $\mu mol\ m^{-2}s^{-1}$),

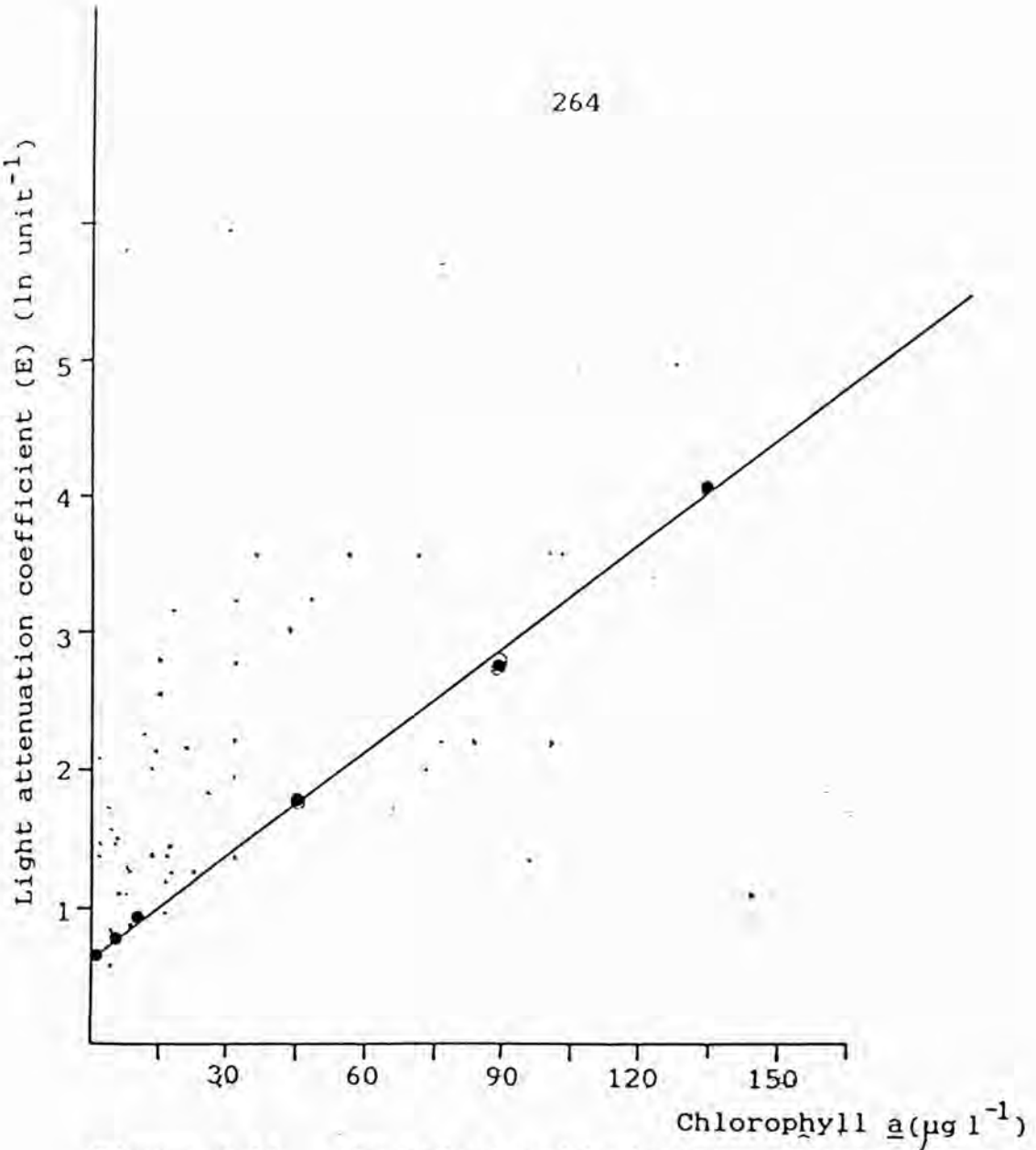


Figure 4.11 The Relationship between chlorophyll a and underwater light attenuation in the River Thames.

$y = 0.024x + 0.64$

$r = 0.71$

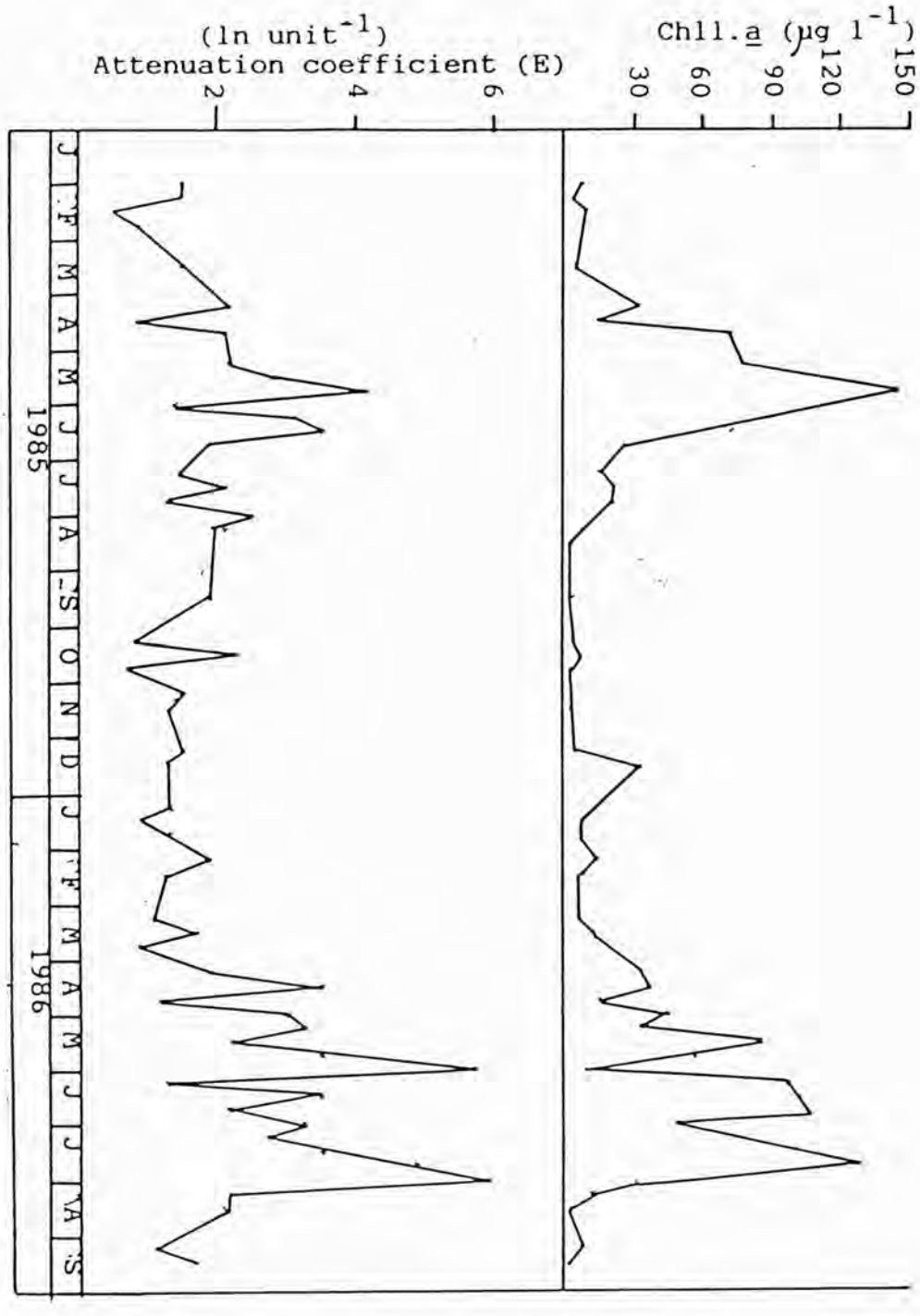


Figure 4.12 The seasonal variation of the attenuation coefficient and chlorophyll a during 1985 to 1986 in the River Thames.

Many algae, for instance, exhibit low light saturated rates of photosynthesis (100 to 200 μmol $m^{-2}s^{-1}$) and lower light compensation points in comparison with terrestrial vascular plants (Beardall and Morris, 1976; Harris, 1978; Bjorkman, 1981; Richardson et al., 1983). Fallowfield and Osborne (1985) studied the growth and light absorption of Anabaena variabilis Kütz. and Scenedesmus obliquus Pringsheim by measuring changes in the photon absorption of algae. There are number of reports directly relating cell synthesis and growth to the amount of light available (Tamiya et al., 1953; Gons and Mur, 1975; Van Liere and Mur, 1978; Droop et al., 1982; Foy and Gibson, 1982; Gibson and Foy, 1983).

Growth under light limited conditions may depend primarily on the efficient capture and utilization of the available photons (Fallowfield and Osborne, 1985).

Stephanodiscus ref. hantzschii, Scenedesmus quadricauda and Eudorina elegans were used in these experiments in adaptation to different light conditions as they occur commonly in the River Thames and Wraysbury Reservoir and became dominant at different time of the year.

Figures 4.13, 4.14 and 4.15 shows the growth rates and density (cells ml^{-1}) of phytoplankton at 20, 40, 60 and 80 Wm^{-2} total radiation (12 hour light:12 hour dark) relative light intensities, at which the phytoplankton have been cultured. The highest rate for the growth of Stephanodiscus ref. hantzschii was found at 40 Wm^{-2} relative light intensity.

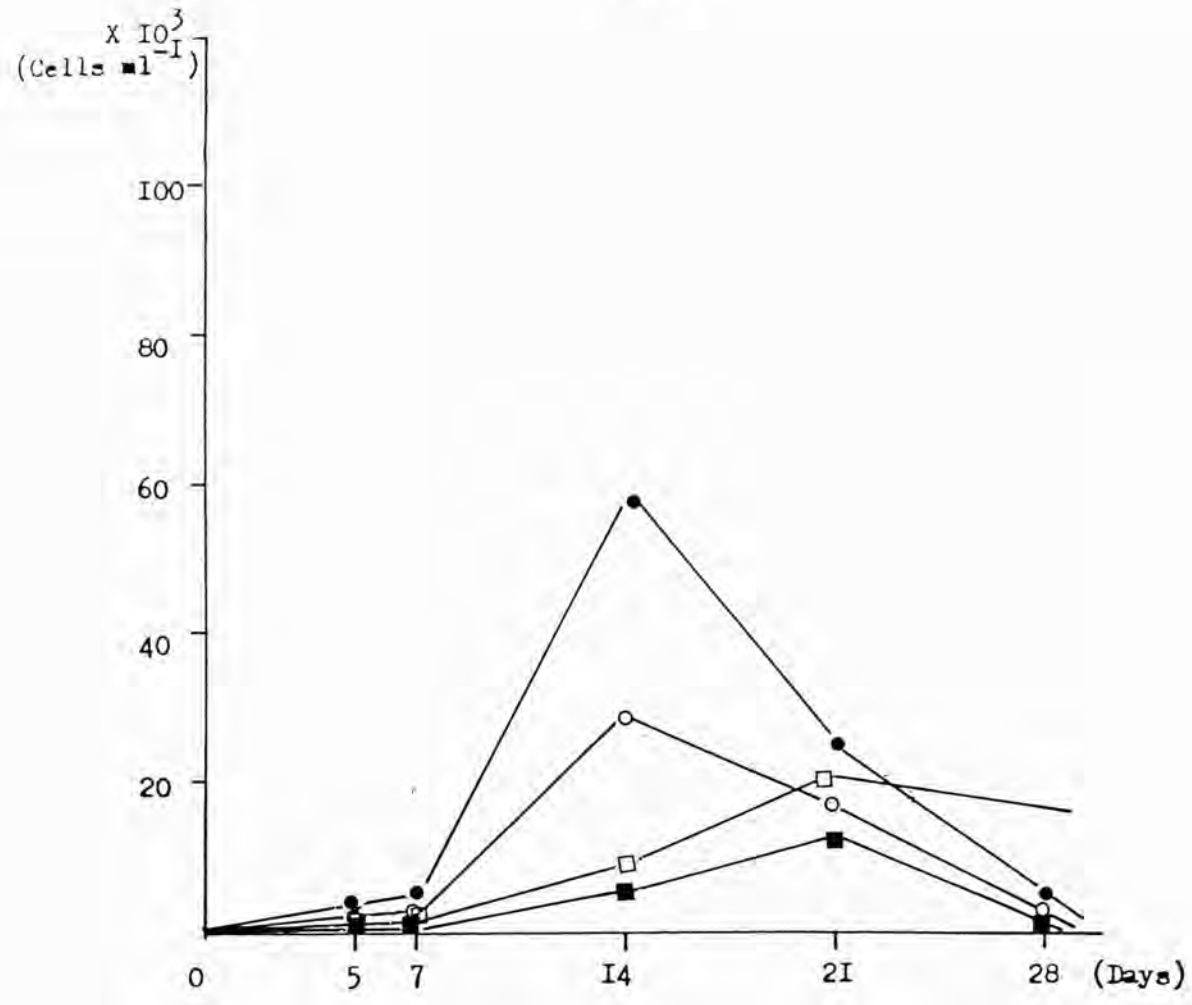


Figure 4.13 The growth of Stephanodiscus ref. hantzschii under different relative light intensities.

LEGEND: Relative radiation (Wm^{-2})

—○— 20

—●— 40

—□— 60

—■— 80

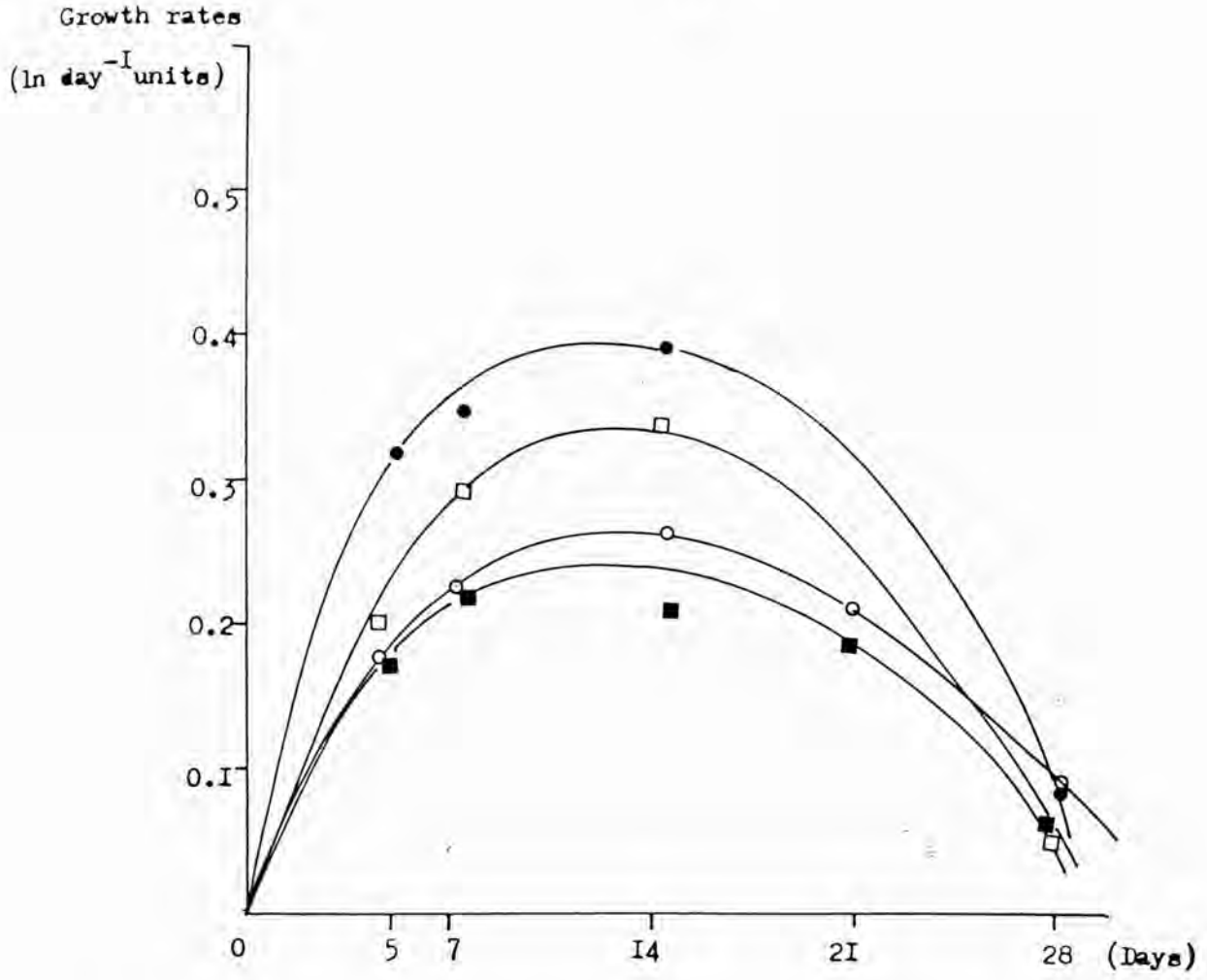


Figure 4.13a Growth rates of Stephanodiscus ref.hantzschii under different relative light intensities.

LEGEND:

Relative radiation (Wm^{-2})

—○— 20

—●— 40

—□— 60

—■— 80

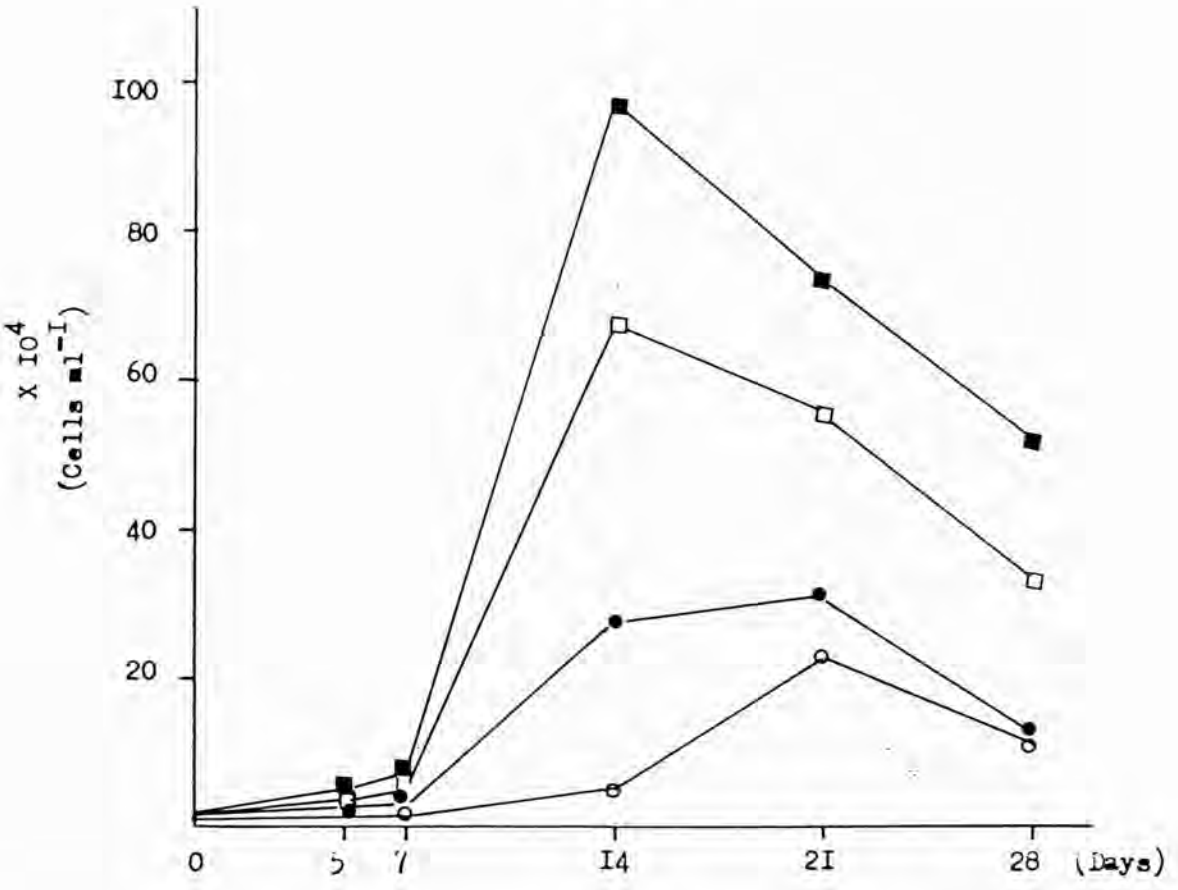


Figure 4.14 The growth of Scenedesmus quadricauda under different relative light intensities.

LEGEND:

Relative radiation (Wm^{-2})

—○— 20

—●— 40

—□— 60

—■— 80

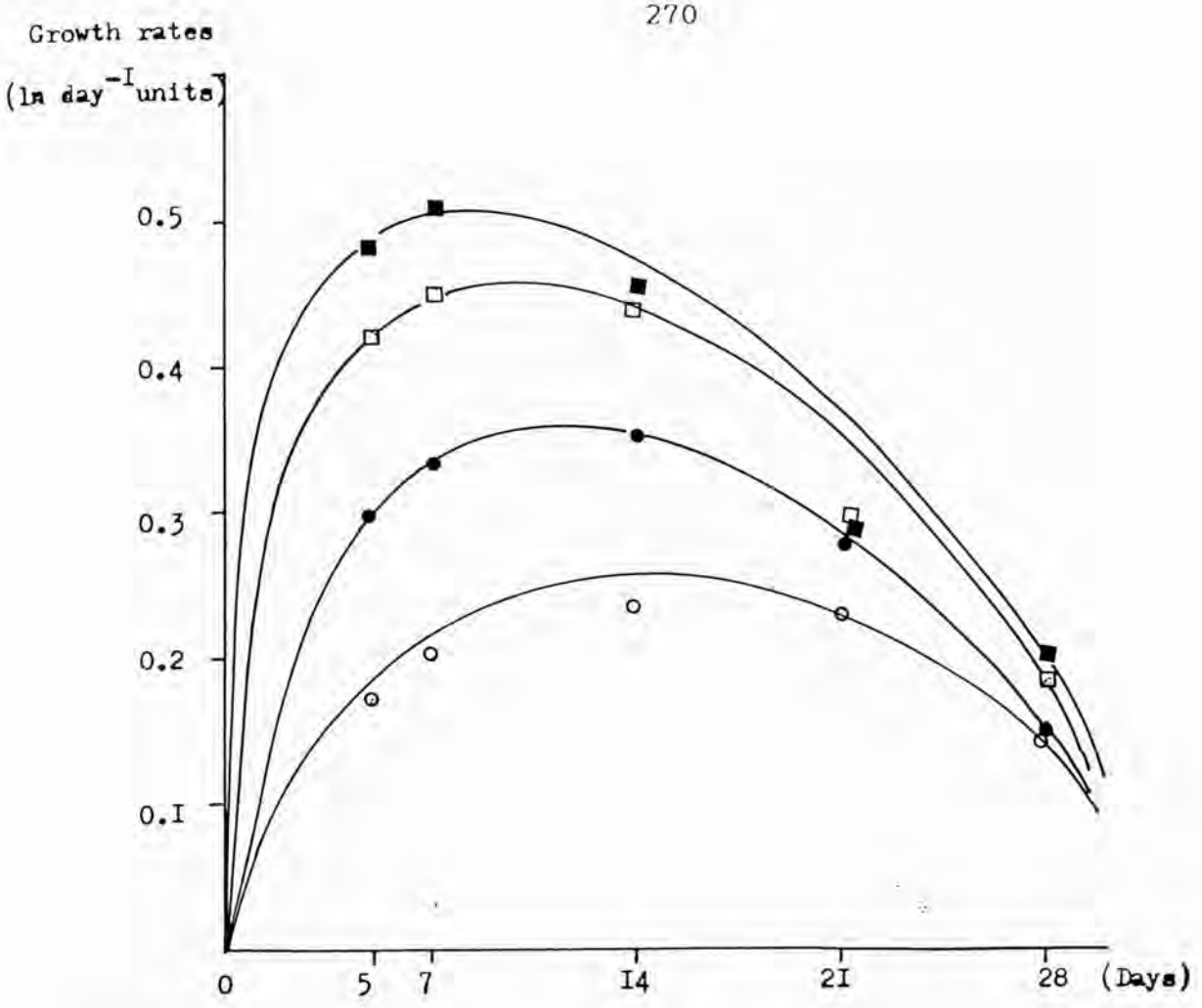


Figure 4.14a Growth rates of Scenedesmus quadricauda under different relative light intensities.

LEGEND:

Relative radiation (Wm^{-2})

—○— 20

—●— 40

—□— 60

—■— 80

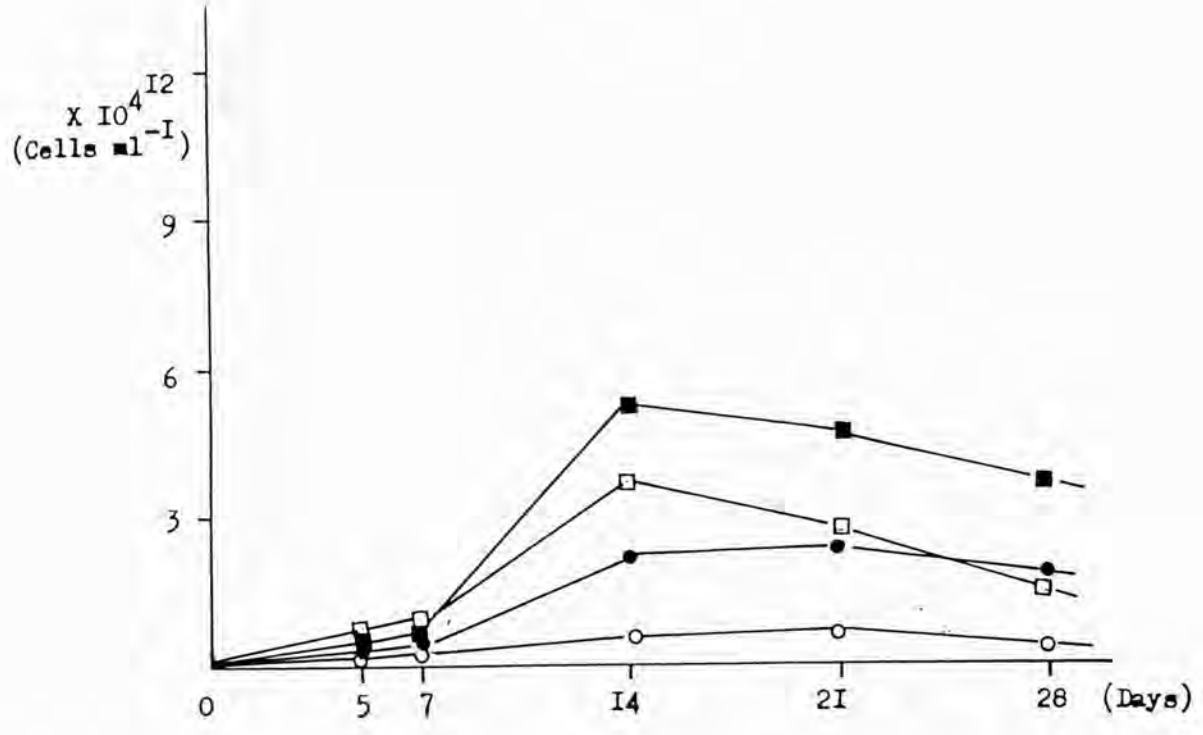


Figure 4.15 The growth of Eudorina elegans under different relative light intensities.

LEGEND:

Relative radiation (Wm^{-2})

—○— 20

—●— 40

—□— 60

—■— 80

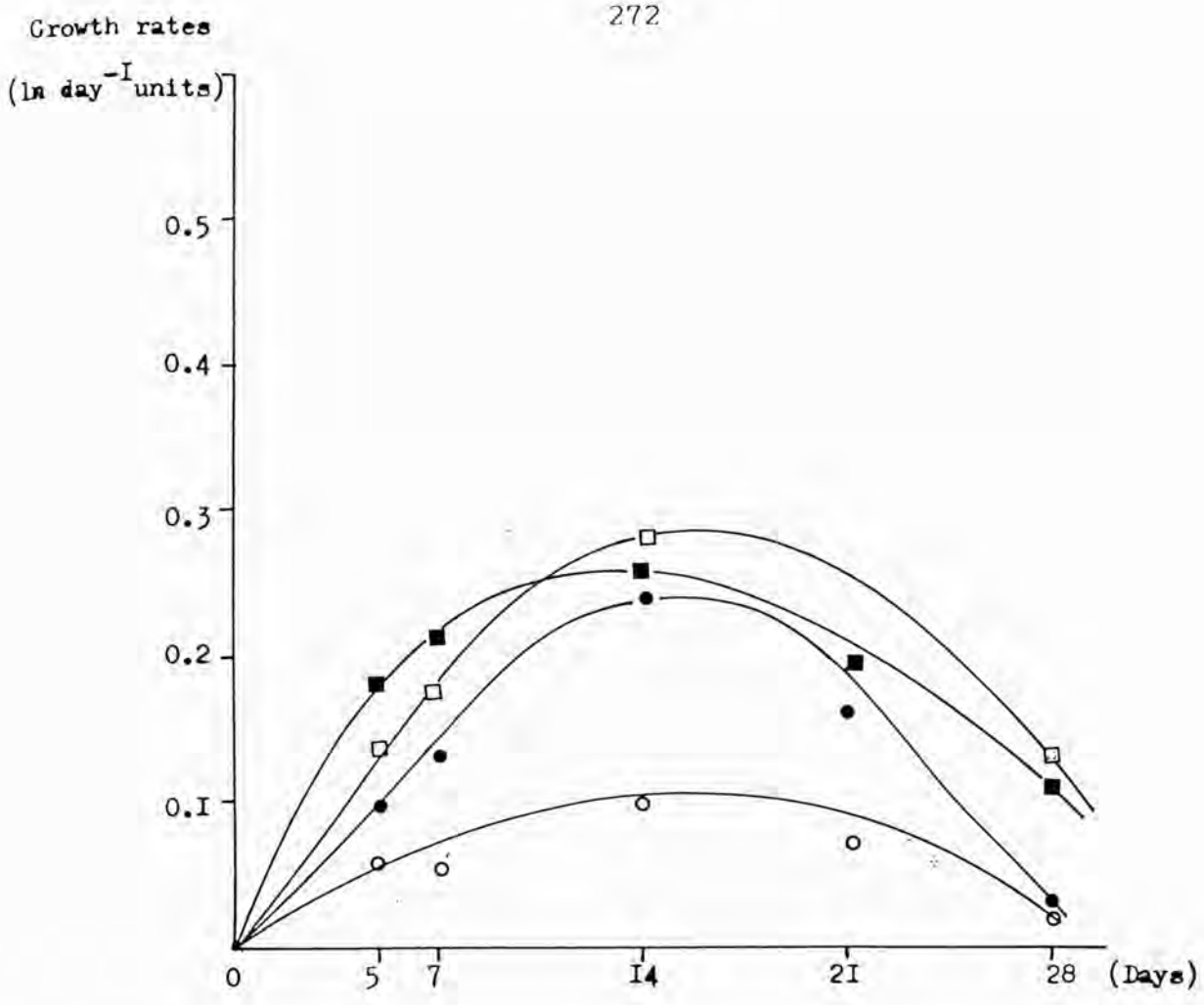


Figure 4.15a Growth rates of Eudorina elegans under different relative light intensities.

LEGEND:

Relative radiation (Wm^{-2})

—○— 20

—●— 40

—□— 60

—■— 80

Light intensities of 60 and 80 Wm^{-2} total radiation were found for the highest growth rates of Eudorina elegans and Scenedesmus quadricauda (Figures 4.15a and 4.14a).

The light intensity at which the phytoplankton have been cultured affects both the morphology and the physiology of the cells.The effect on the morphology has not been investigated to any great extent during this study.However,it has been studied by many researchers.For example;Brown and Richardson (1968) showed that the cell volumes of Nitzschia closterium depends on the light intensity,the cell volume being greatest at light intensities below 2 klux.The size of the chloroplasts of the same species also found to decrease with increasing light intensities.The effect of light intensity on the ultrastructure of chloroplasts in diatom species has been studied in Detonula by Jupin (1973c).Studies by Myers and Graham (1971) and Sheridan (1972) in Chlorella species show further that light intensity in this alga affects the size of photosynthetic unit with the highest number of chlorophyll molecules per unit at low light intensity and the number of chlorophyll molecules per unit decreasing with increasing light intensity.

The changes in their physiology which takes place when the cells of phytoplankton adapt from one light intensity to another is best illustrated by the changes in the light-photosynthesis curves.Jorgensen (1964,1969) studied the adaptation of several algal species to different light

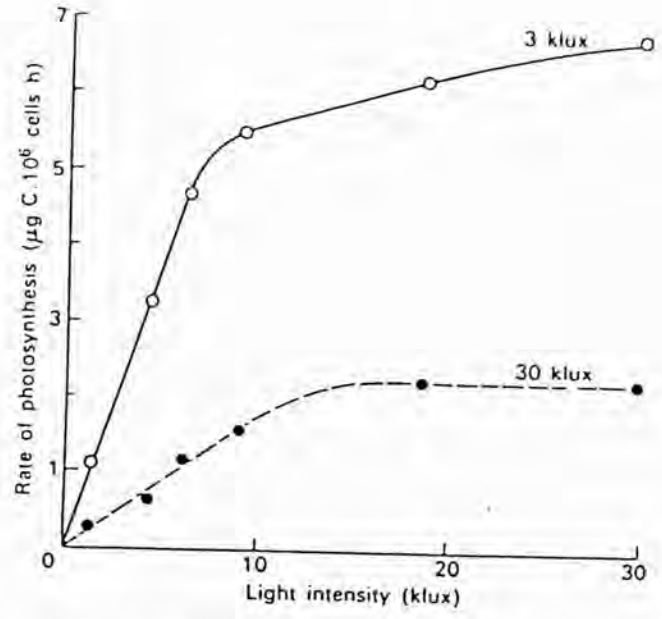


Figure 4.16 The '<u>Chlorella-type</u>' of adaptation. Light intensity-photosynthesis curves for <u>Chlamydomonas moevusii</u> grown at 3 klux and 30 klux, respectively. After Jorgensen, 1969

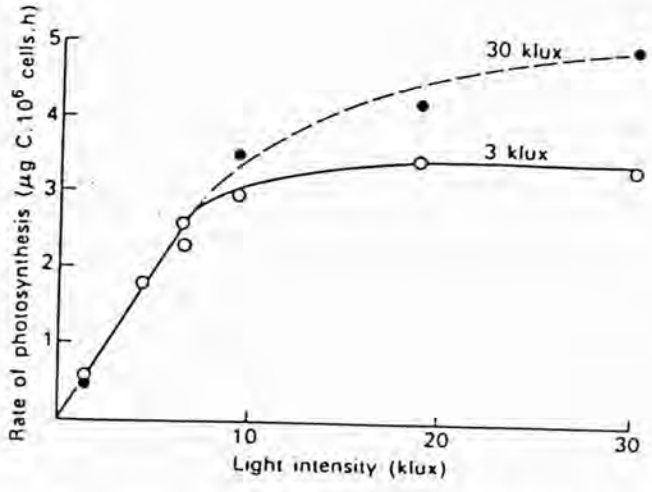


Figure 4.17 The '<u>Cyclotella-type</u>' of adaptation. Light intensity-photosynthesis curves for <u>Cyclotella meneghiniana</u> grown at 3 and 30 klux, respectively. After Jorgensen, 1964.

intensities.He distinguishes between two main types of adaptation: the Chlorella-type and the Cyclotella-type.The Chlorella-type is characterized by changes in chlorophyll content per cell with changes in light intensity.More chlorophyll per cell is formed at low light levels than at high (Figure 4.16).In the Cyclotella-type the chlorophyll content is about the same in cells grown at high and low levels of light,while the actual photosynthetic rate is considerably higher in cells developed at high intensities.It is assumed that in the latter case increased contents of photosynthetically active enzymes in the dark reaction steps of photosynthesis has caused the rise in the rate of photosynthesis (Figure 4.17).

4.6 THE INFLUENCE OF PHOTOPERIOD ON THE GROWTH OF PHYTOPLANKTON POPULATIONS

In natural environments phytoplankton populations will experience 'an apparent daylength',that is,the result of total daylength and the time that phytoplankton are in the euphotic zone (Post et al.,1985).This allows for an extended range of daylengths occurring under natural conditions,that may exert its influence on photosynthesis and timing of cell division for phytoplankton populations.

It has been shown by Gibson and Foy (1983) that

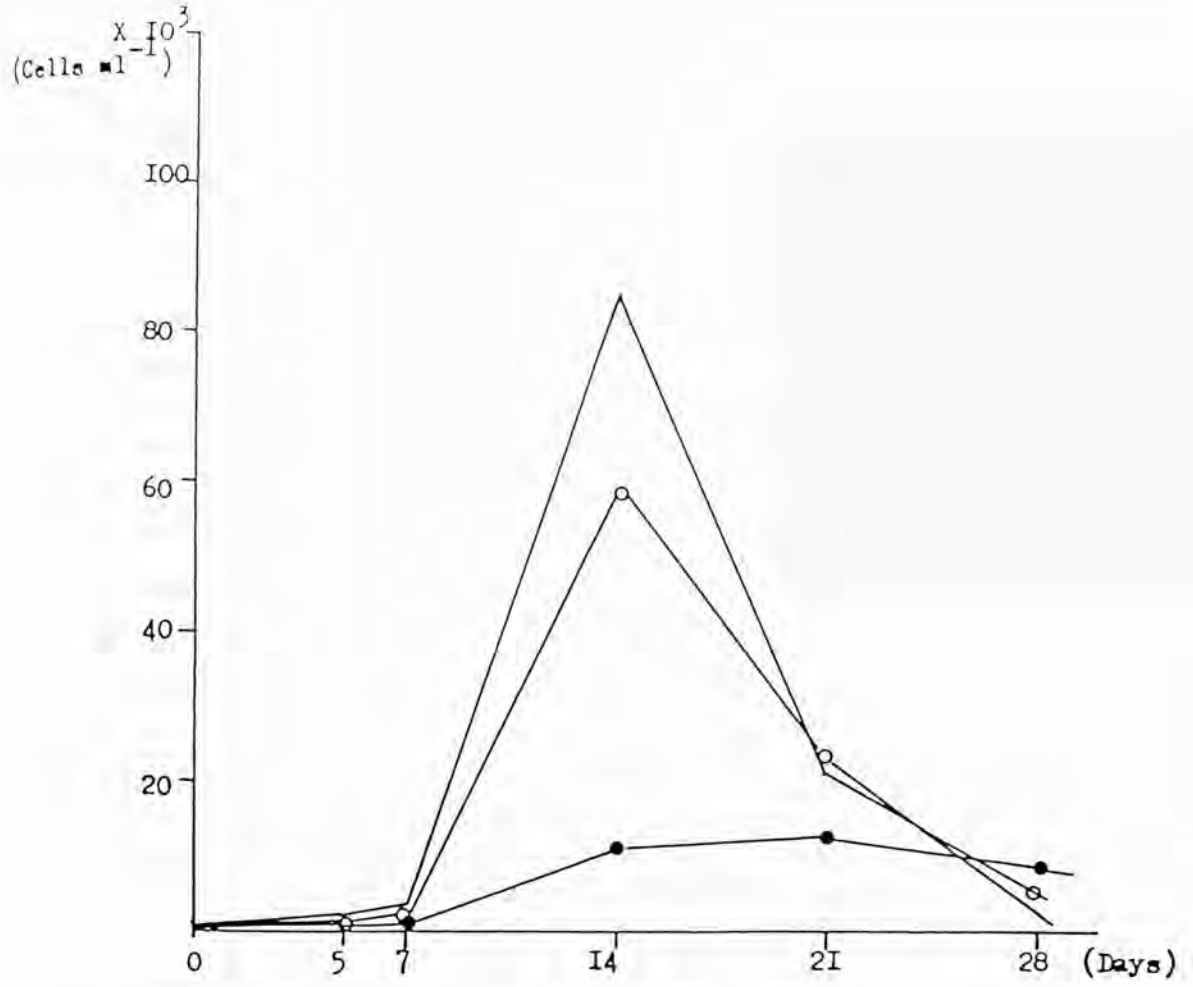


Figure 4.18 The growth of Stephanodiscus ref.hantzschii under various photoperiods.

LEGEND:

Photoperiods

——— 24 hr.light.

—o— 12 hr.light:12 hr.dark

—●— 16 hr.light:8 hr.dark

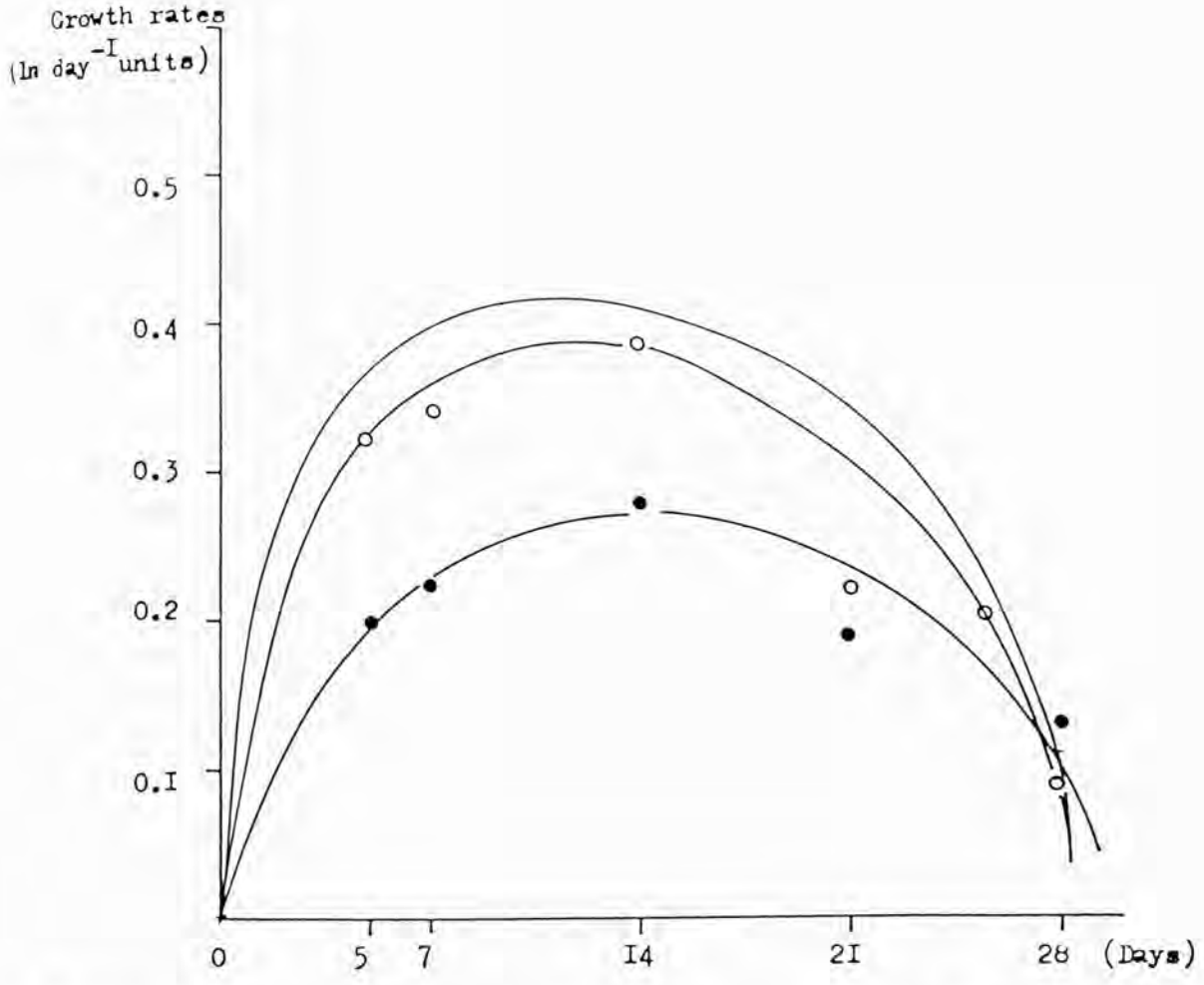


Figure 4.18a Growth rates of Stephanodiscus ref.hantzschii under different photoperiods.

LEGEND:

Photoperiods

——— 24 hr.light

—○— 12 hr.light:12 hr.dark

—●— 16 hr.light:8 hr.dark

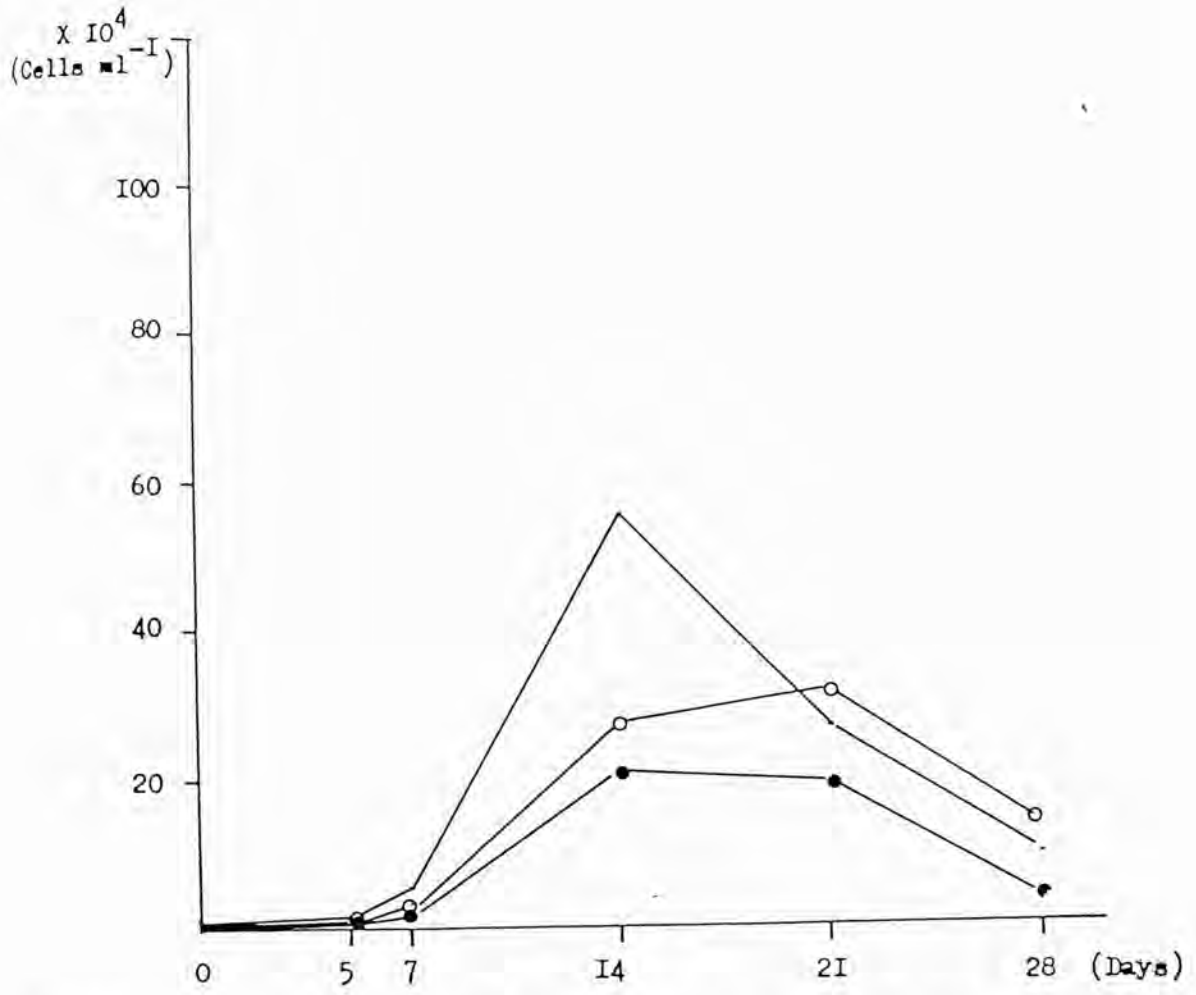


Figure 4.19 The growth of Scenedesmus quadricauda under different photoperiods.

LEGEND:

Photoperiods

——— 24 hr.light

—o— 12 hr.light:12 hr.dark

—●— 16 hr.light:8 hr.dark

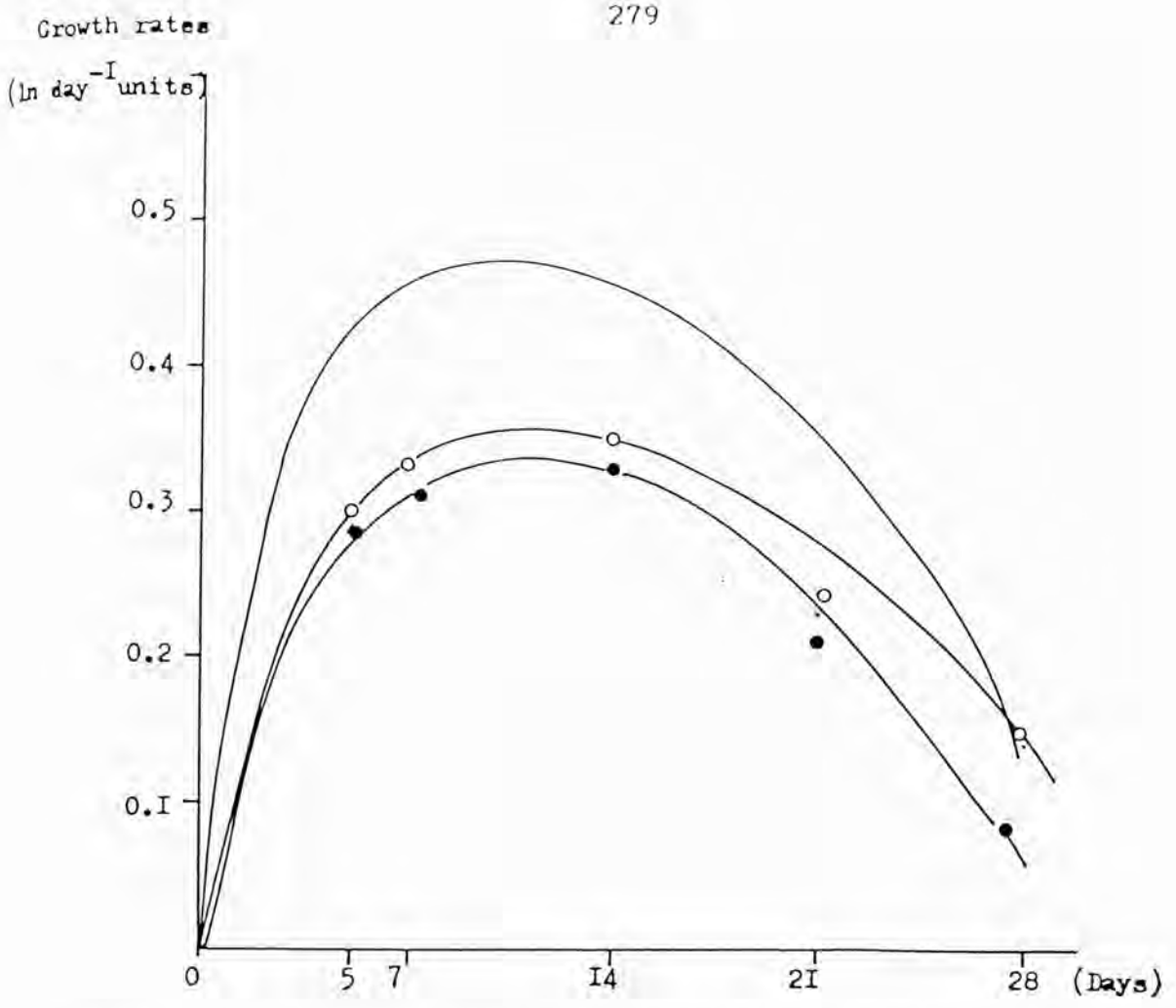


Figure 4.19a Growth rates of Scenedesmus quadricauda under different photoperiods.

LEGEND:

Photoperiods

——— 24 hr.light

—○— 12 hr.light:12 hr.dark

—●— 16 hr.light:8 hr.dark

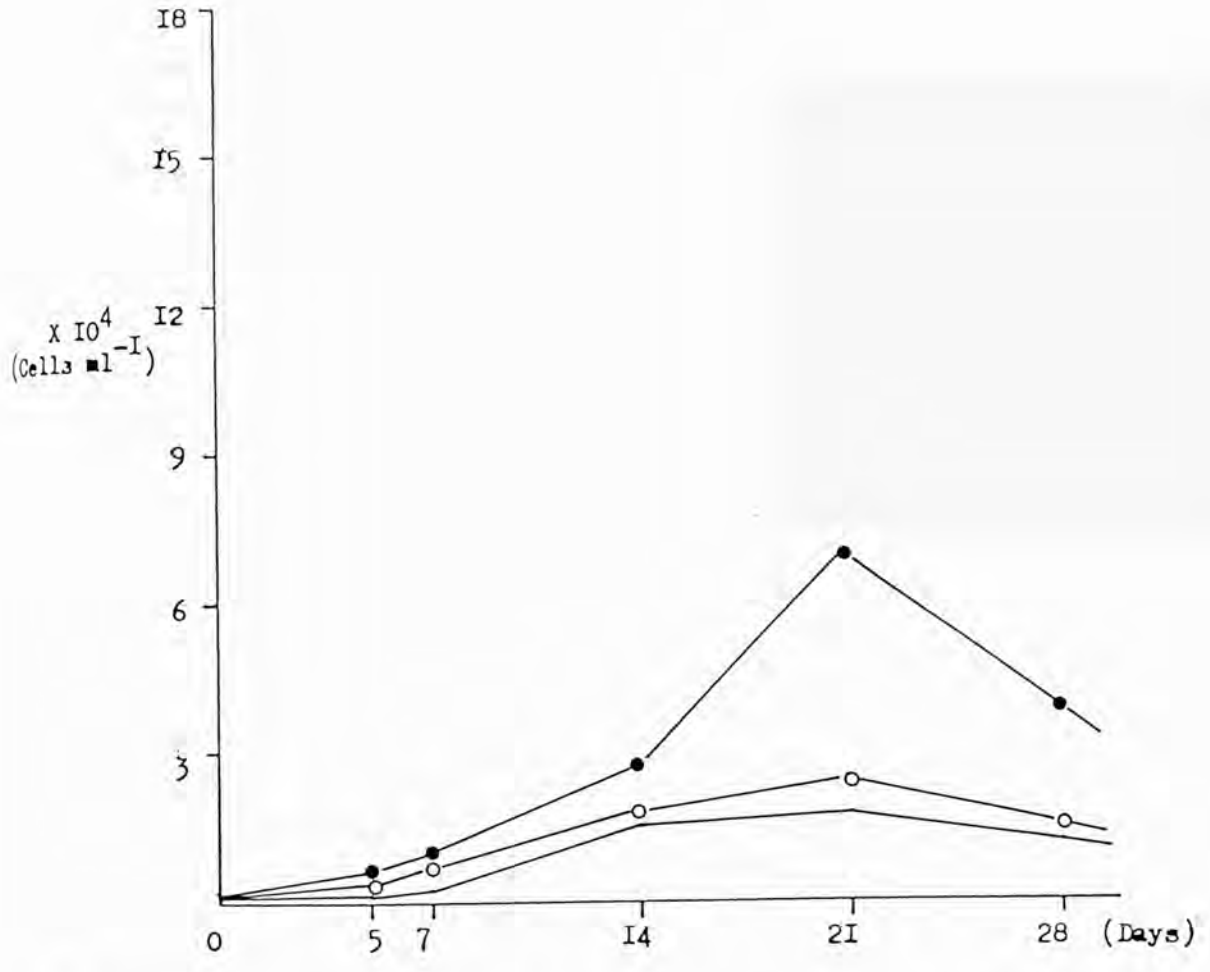


Figure 4.20 The growth of Eudorina elegans under different photoperiods.

LEGEND:

Photoperiods

——— 24 hr.light

—○— 12 hr.light:12 hr.dark

—●— 16 hr.light:8 hr.dark

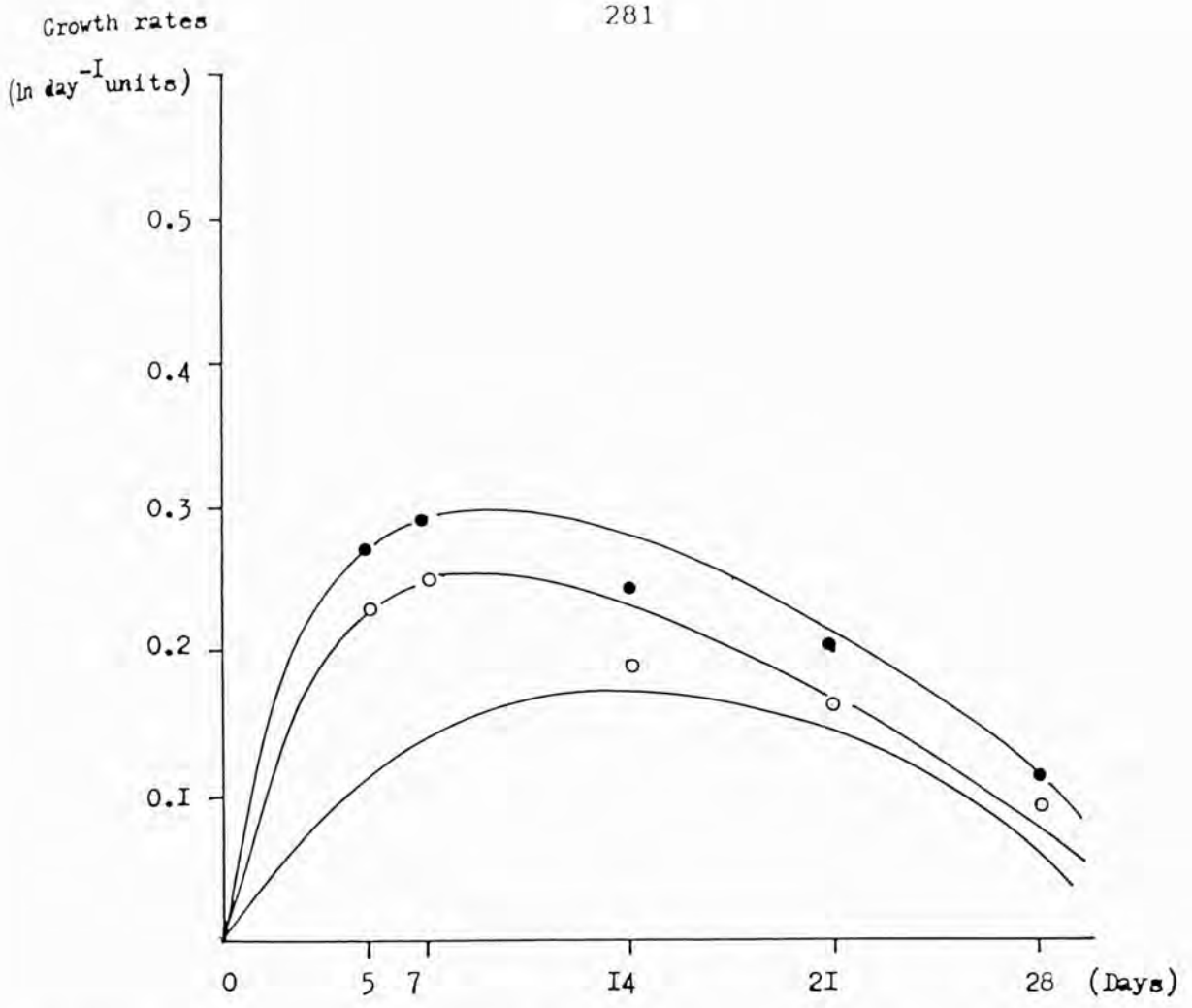


Figure 4.20a Growth rates of Eudorina elegans under different photoperiods.

LEGEND:

Photoperiods

——— 24 hr.light

—○— 12 hr.light:12 hr.dark

—●— 16 hr.light:8 hr.dark

light saturation of the growth rate of Oscillatoria redekei Van Goor occurs at lower photon fluence rates on a light:dark cycle than on a light:light treatment.

Three photoperiods which have been chosen during the experiments were 24 hours light;12 hours light:12 hours dark and 16 hours light:8 hours dark cycles.

Experiments carried out with Stephanodiscus ref. hantzschii showed that the growth of this species was higher when subjected to 24 hours light than to 12 hours light:12 hours dark and 16 hours light:8 hours dark cycles (Figures 4.18 and 4.18a).

The same results were found in the experiments carried out with Scenedesmus quadricauda (Figures 4.19 and 4.19a).

However, Eudorina elegans showed higher growth and growth rates when the experiments were carried out under 16 hours light:8 hours dark (Figures 4.20 and 4.20a).

4.7 CONCLUSIONS

From the field and culture investigations it was found that light intensity and photoperiod influence phytoplankton growth. However, numerous complicating factors would have to be taken into account for the interpretation of such data. Algal cells are exposed to a continuously changing intensity over a daily cycle. Furthermore, their location

within the euphotic zone and the degree of turbulence influences the amount of photosynthetically available light that will be absorbed.

It is well known that light intensity and photoperiod influence phytoplankton growth, including the timing of cell division (Paasche, 1968; Smayda, 1975; Fallowfield and Osborne, 1985). Over an annual cycle, the trends in light intensity in the River Thames are paralleled by corresponding changes in water temperature. It was found experimentally (see page 267) that Scenedesmus quadricauda had the highest growth rates at a higher light intensity than Stephanodiscus ref. hantzschii (Figure 4.13). This was consistent with the conditions of light in nature where Scenedesmus quadricauda was found abundant during periods of high light intensity. The same conditions occurred for Eudorina elegans although the growth rate of this species was lower than that of Scenedesmus quadricauda. Stephanodiscus ref. hantzschii showed the highest growth rate at 40 Wm^{-2} total radiation relative light intensity. This was lower than those of Scenedesmus quadricauda and Eudorina elegans.

CHAPTER FIVE

THE INFLUENCE OF TEMPERATURE ON THE GROWTH OF PHYTOPLANKTON POPULATIONS

5.1 INTRODUCTION

Temperature is one of the major environmental factors that may influence the growth of phytoplankton populations. Since the temperature of large bodies of water is relatively constant on a diel basis and is usually below 30°C, phytoplankton ecologists are more concerned with the seasonal and latitudinal impact of temperature and with long-term adaptation to temperature rather than with the impact of daily temperature fluctuations. Phytoplankton organisms exhibit the usual relationship between temperature and biological activity by increasing growth rate with increasing temperature up to some optimum temperature after which growth rate declines, often abruptly, to zero (Figure 5.1).

Rodhe (1948) has stressed the concept that an optimum temperature or optimum illumination is not necessary absolute, since a considerable increase in growth may be produced momentarily by an increase in temperature or illumination to levels that also produce a slow irreversible injury to the living system under investigation. Therefore we

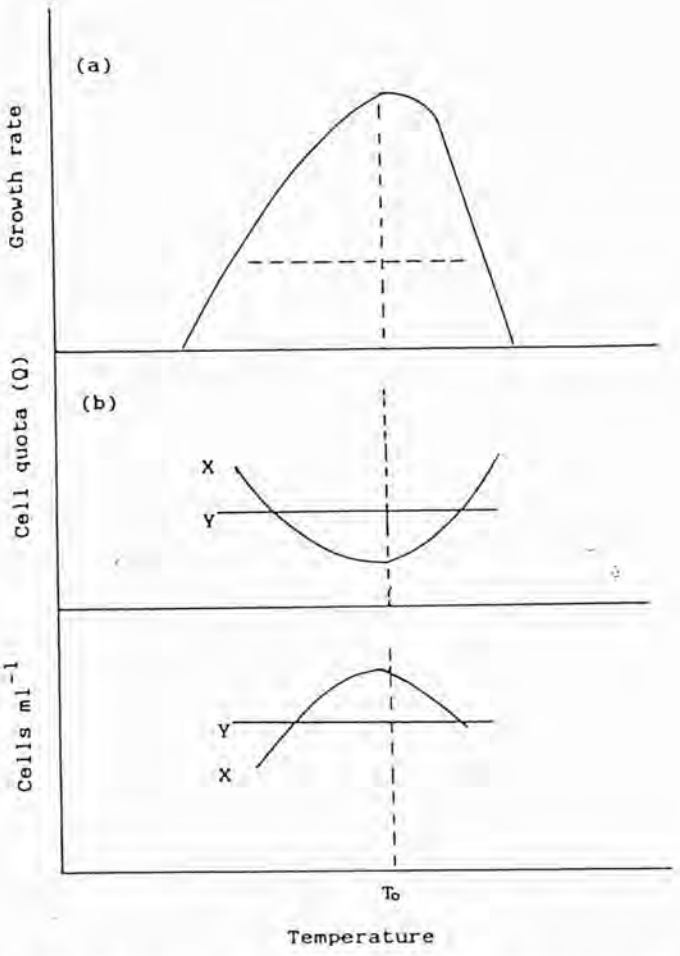


Figure 5.1 Interactions between temperature and nutrient limitation. (a) The solid line represents the typical temperature-dependent growth rate in nutrient- and light-saturated cells, obtained in batch-culture experiments; T_o is the temperature optimum for growth. The horizontal dashed line represents the constant, nutrient-limited growth rate at different temperatures obtained in chemostat culture. (b) The cell quota of the nutrient-limited cells in the chemostat culture in (a). (c) The equilibrium cell density of the nutrient-limited cells in the chemostat culture in (a). X and Y represent the responses of two different species. (After Goldman and Mann, 1980).

can distinguish between momentary optima under any given set of conditions and the lower limit at which irreversible inhibition by light or temperature sets in.Whatever may happen at higher temperatures or higher illumination over short periods of time,the lower limit of irreversible inhibition will always appear to be optimal if all environmental factors are held constant and the time of observation is sufficiently long.

Different species of phytoplankton undoubtedly have different temperature requirements,and it could be that a particular species predominates at a particular season because the prevailing temperature favours it.Numerous investigators have pointed out that changes in species predominance accompany changes in temperature.Gran (1929) reported that in Northern European waters,the annual diatom maxima and temperature minima tend to coincide. Coccolithoporids predominate in Norwegian fjords primarily during late summer when the temperature is at its annual maximum (Schei,1974).

Temperature is also an important factor determining the general geographical distribution of certain algae.For example the relationship in benthic algae between heat hardiness and geographical latitude (Biebl,1970).Algal life at extreme temperatures has been reviewed by Brock (1969) with special reference to the heat tolerance of thermophilic forms,the upper limit of which seems to be 74°C.The monograph

by Kol (1968) deals with algae inhabiting the surfaces of snow and ice and the physiological characteristics of cryophilic algae are dealt with by Fogg and Horne (1968).The vertical zonation of benthic marine algae in the littoral zone,once thought to be due solely to heat hardiness on the basis of cytological examination of the tissue after temperature shock does not in fact appear to be the whole answer as studies on the restoration kinetics of photosynthesis by the algae show clearly (Ried,1969b).

Temperature is an extremely important variable in the mixing process because of its well-known effect on the density of water and therefore on the stability of the water column (Figure 5.2).In temperate lakes and oceans during the winter,temperature (and therefore density) differences between surface and deeper waters usually are not sufficient to prevent complete mixing by the wind.As surface waters are warmed during the spring and early summer,they become less dense and less likely to be mixed with deeper,colder and denser water.Eventually,density differences are great enough to prevent mixing and the water column becomes stratified into an upper mixed layer (called the epilimnion) which is separated from the bottom water (hypolimnion) by a zone in which temperature (and density) of the water changes abruptly (Figure 5.3).The significance of this zone,called the thermocline,is that it severely restricts the mixing of the deeper,nutrient rich water with the surface,mixed layer where

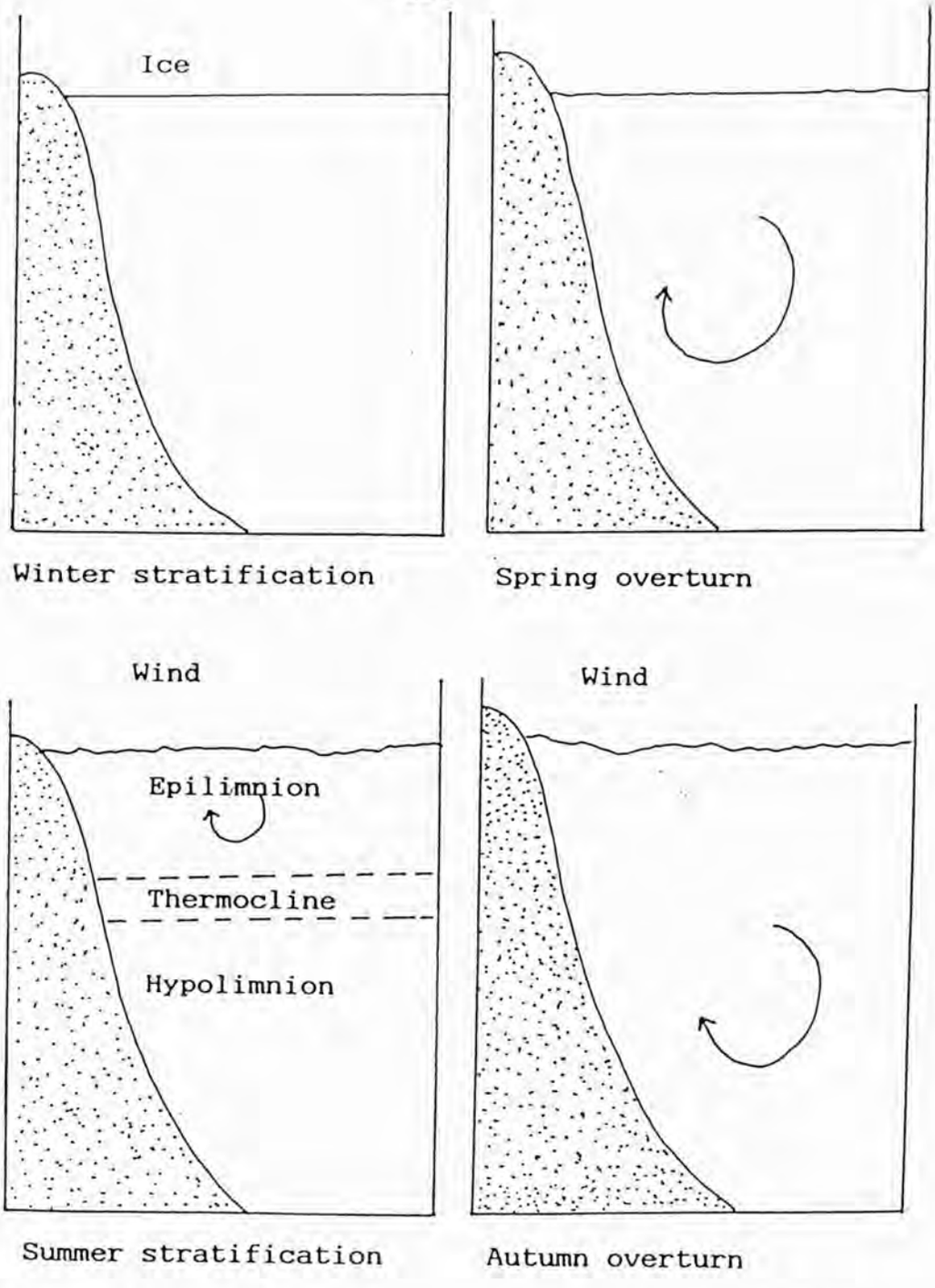


Figure 5.2 Effect of seasonal temperature changes on vertical mixing in a temperate lake. (From: Darley, 1982).

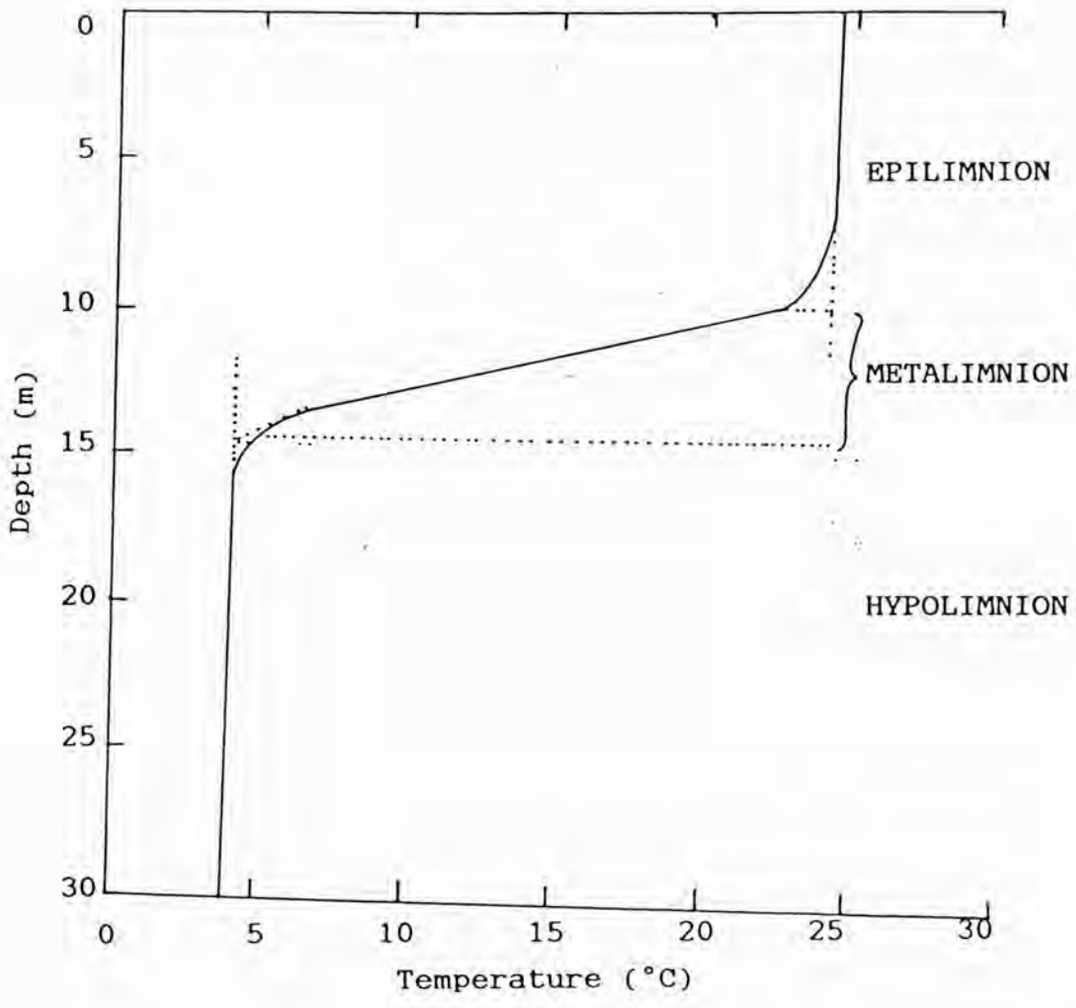


Figure 5.3 Typical thermal stratification of a lake into the epilimnetic, metalimnetic, and hypolimnetic water strata. Dashed lines indicate planes for determining the approximate boundaries of the metalimnion.
(From: Wetzel, 1975)

phytoplankton growth has stripped the water of nutrients. Thus, two important requirements of algal growth, light and nutrients, are most abundant in separate water masses (Darley, 1980).

The term thermocline refers to the plane or surface of maximum rate of decrease of temperature with respect to depth (Wetzel, 1975). An extensive discussion of these terms and their conceptual basis is given by Hutchinson (1957). Terms in wide use that are functionally synonymous with the term metalimnion include the German 'Sprungschicht', and discontinuity layer as used in the United Kingdom.

Stratification breaks down in the autumn when surface waters cool and wind-induced circulation results in the autumn overturn. Winter stratification may also occur in lakes, particularly if there is a cover of ice.

Some attempts have been made to upset the thermal stratification of lakes in the USA (Ford, 1963; Grim, 1952; Hooper et al., 1953; Irwin et al., 1966; Stroud, 1959, 1965). This has been established in the Wraysbury Reservoir where thermal stratification was upset by inducing water circulation using jet inputs. Two pairs of high energy jets, angled at $22\frac{1}{2}°$ and 45° from the reservoir floor are capable of injecting 200 M.G.D. (10.52 $m^3 s^{-1}$) of river water into the reservoir under high pressure; less energy is transferred with the use of the two horizontal (low velocity) jets. Internal circulation of the reservoir water is provided by three recirculation pumps

which are operated when river abstraction restrictions prevent the normal intake from the River Thames (Hardy,1977). The design of the Wraysbury Reservoir has turned out to be quite accidentally close to ideal from the point of view of efficient mixing and the maintenance of good supply water (Tom,personal communication).

Besides jet inputs there are other ways to upset thermal stratification.For example,180 hours of pumping of warm surface water into the bottom of a small German lake increased the temperature of the bottom water by 5°C (Grim, 1952).

In an experiment in a 3.6 acre Michigan Lake,water was pumped from near the bottom (hypolimnion) to the surface. This caused a progressive increase in the depth of the upper warm layer of the uniform temperature,a sinking of the thermocline (transition zone) at a nearly constant rate,and a decrease in the thickness of hypolimnion as the bottom water was displaced.The upper limit of the thermocline was lowered from 13 to 25 ft.,and the volume of the epilimnion was increased by 50%.An attempt was made to follow the movement of cold bottom water after its release at the surface. Apparently the cool water became mixed rather thoroughly with surface water within the upper 4 to 5 ft.

Compressed air,released from perforated tubes on the lake bottom,has been used widely in winter to carry water currents from deep water to the surface and melt thick or snow-covered ice for the prevention of winterkill.This

technique has been applied with some success in breaking up thermal stratification in summer.The thin streams of air bubbles escaping from holes in the plastic tubes create upward movement of water,some of which eventually reaches the surface (Ford,1963;Irwin et al.,1966).This method is more efficient than the pumping of water either from the top to the bottom of the lake or from the bottom to the top.

Probably the most efficient method yet devised for carrying large amounts of water from the depths to the surface is through the use of invention called a hydraulic air gun consisting of a tube 12 in.in diameter and 12 ft.long supported vertically above the lake bottom.At the bottom of the tube is a chamber arrangement into which compressed air collects until the chamber is full,then a 'bubble' of air large enough to fill the diameter of the 12 in.tube is suddenly released to pass up the 12 ft.tube pushing water ahead of it and drawing water in behind it through holes near the bottom of the 'gun'.These 'bubbles' are released intermittently,providing a good continuous flow of water through the gun.The water leaving the upper end of the 12 ft. tube acts as a free turbulent jet which carries additional water along in its upward movement.Air comes in contact with water throughout the tube and after escape from the upper end of the tube.Compressed air is supplied to the guns through tubes leading from a compressor on the lake bank.

Using a compressor that delivered 72 $ft.^3$ of air per

minute,Wirth and Dunst (1967) supplied six guns with air and estimated that they moved a total of 16.8 ft.of water per second through the tubes.This water escaping from the ends of of the tubes activated other water to increase the total upward movement to an estimated 84 $ft.^2$ per second or 166 acre-ft.per day.Tests run with the six air guns in Cox Hollow Lake (36 acres,maximum depth 29 ft.),demonstrated that temperature stratification could be completely broken up in less than five weeks beginning with surface temperatures of 29°C and bottom temperatures of about 10°C.This stratification process may have significance in increasing fish production and controlling algal blooms.

5.2 MATERIAL AND METHODS

Seasonal occurrence of phytoplankton populations in relation to temperature were investigated in the River Thames and the Wraysbury Reservoir during 1984 to 1986.The methods employed are described in Chapter Two.

All phytoplankton species used in the culture experiments were prepared as described in Chapter Two and were grown in unmodified Chu 10 medium.All the flasks for each experiment were duplicated and kept in culture incubators with temperatures 10,20 and 25°C.

Scenedesmus quadricauda,Stephanodiscus ref. hantzschii and Eudorina elegans were subjected to a study of the effects of temperature on their growth.Growth rates and numbers of cells ml^{-1} were employed during this study to measure the growth of phytoplankton populations.Each growth rate and numbers of cells ml^{-1} was calculated with the average of four or more flasks from at least three separate experiments for each test organism.

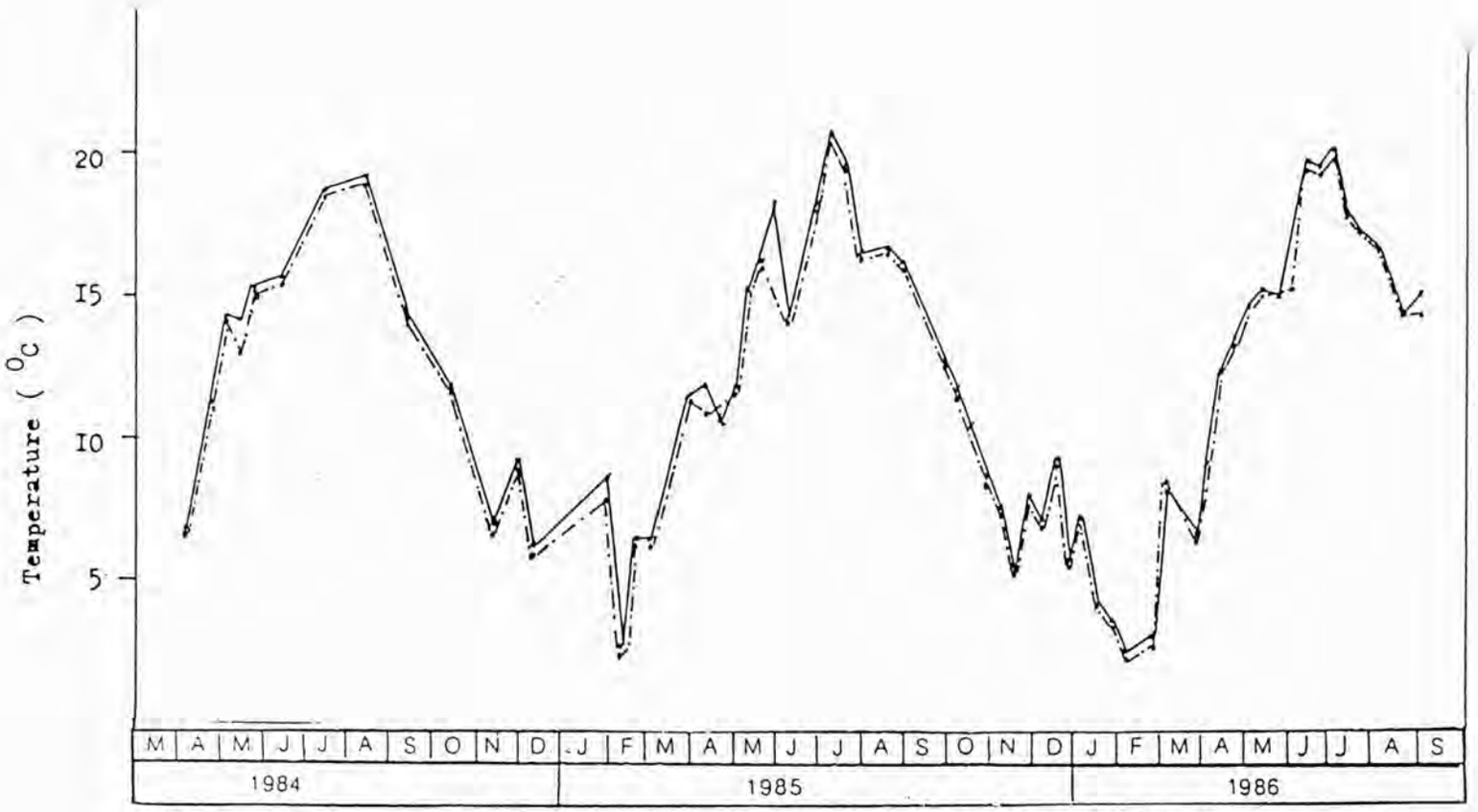


Figure 5.4 Seasonal variations of temperature in the River Thames.

LEGEND: _____ 0 metre

_.-.-._ 0.5-1 metre (Bottom of the river).

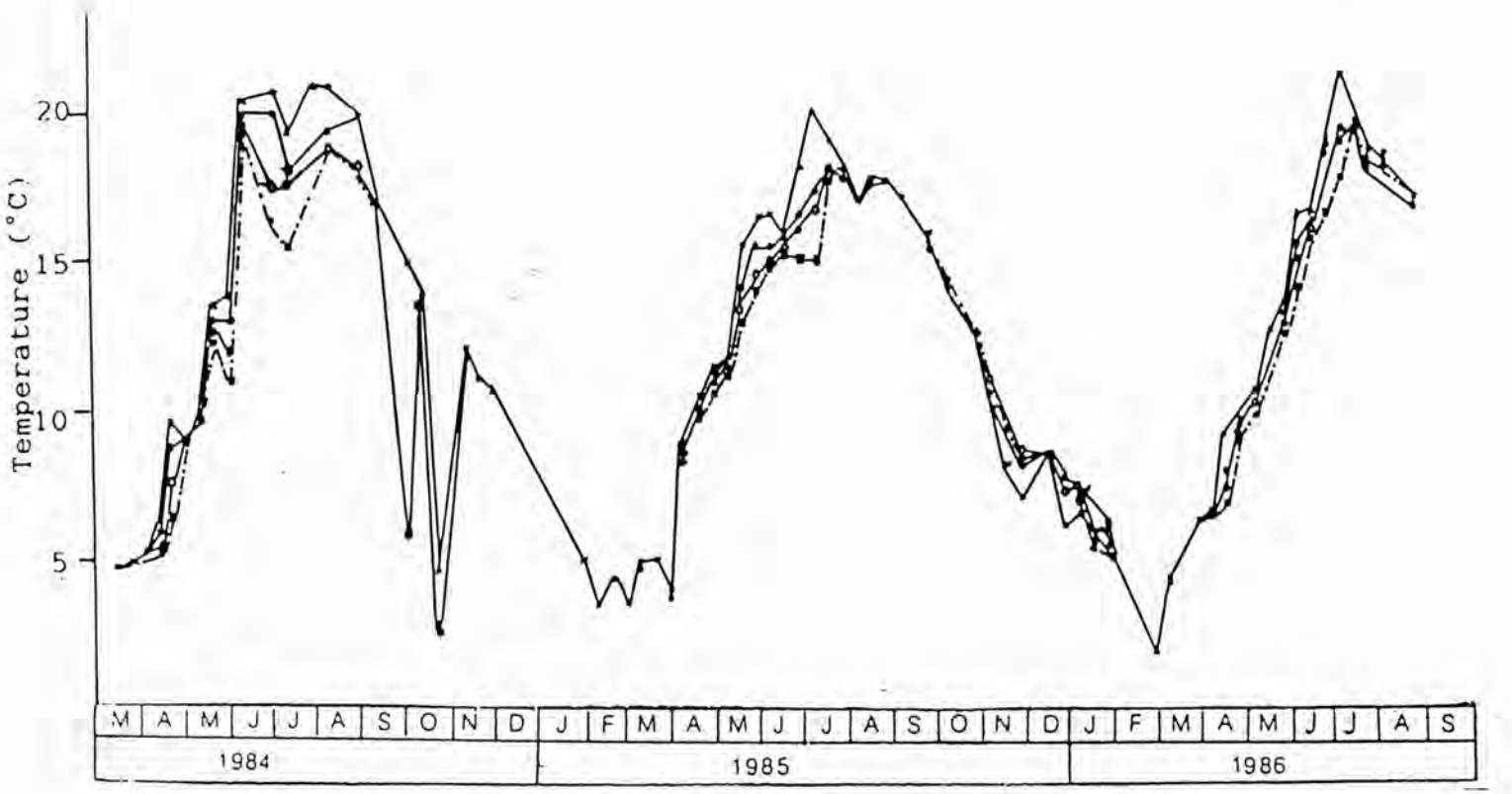


Figure 5.5 Seasonal variations of temperatures in the Wraysbury Reservoir.

LEGEND:

	Metre
———	1
—●—	7
—o—	15
—·—·—	21

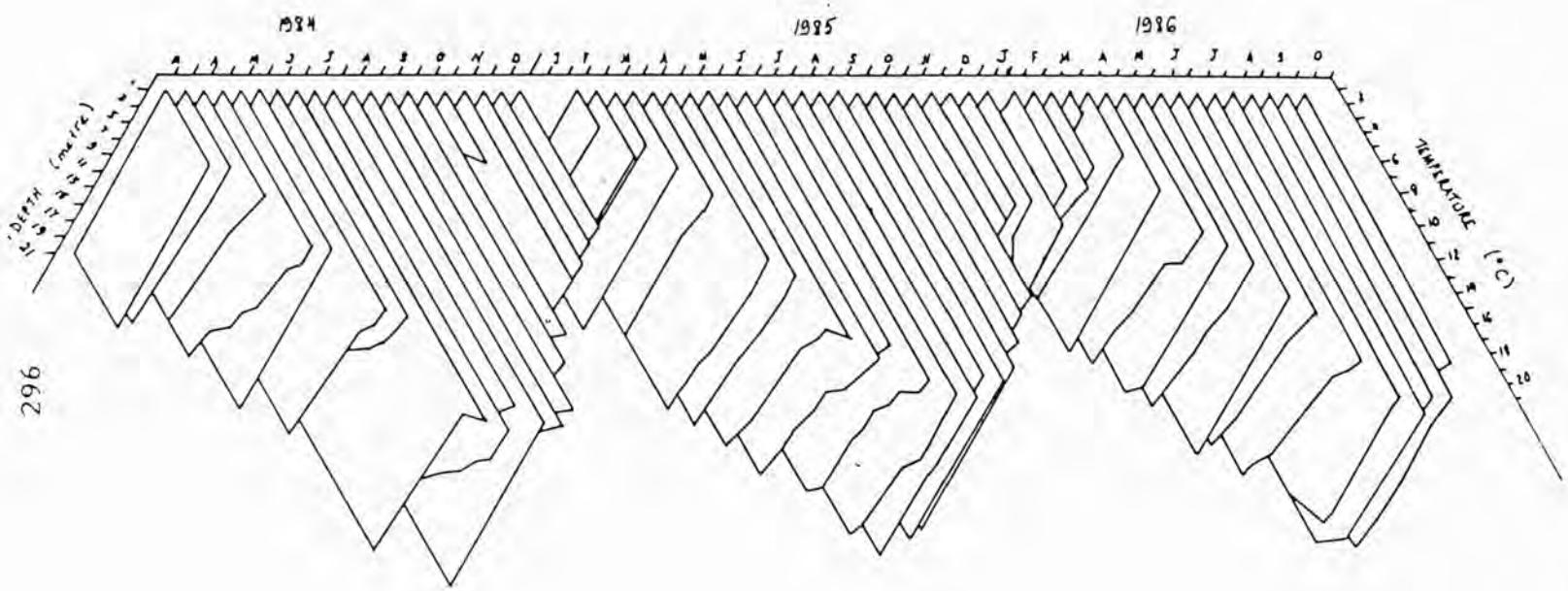


Figure 5.5a Vertical distributions of water temperatures in the Wraysbury Reservoir.

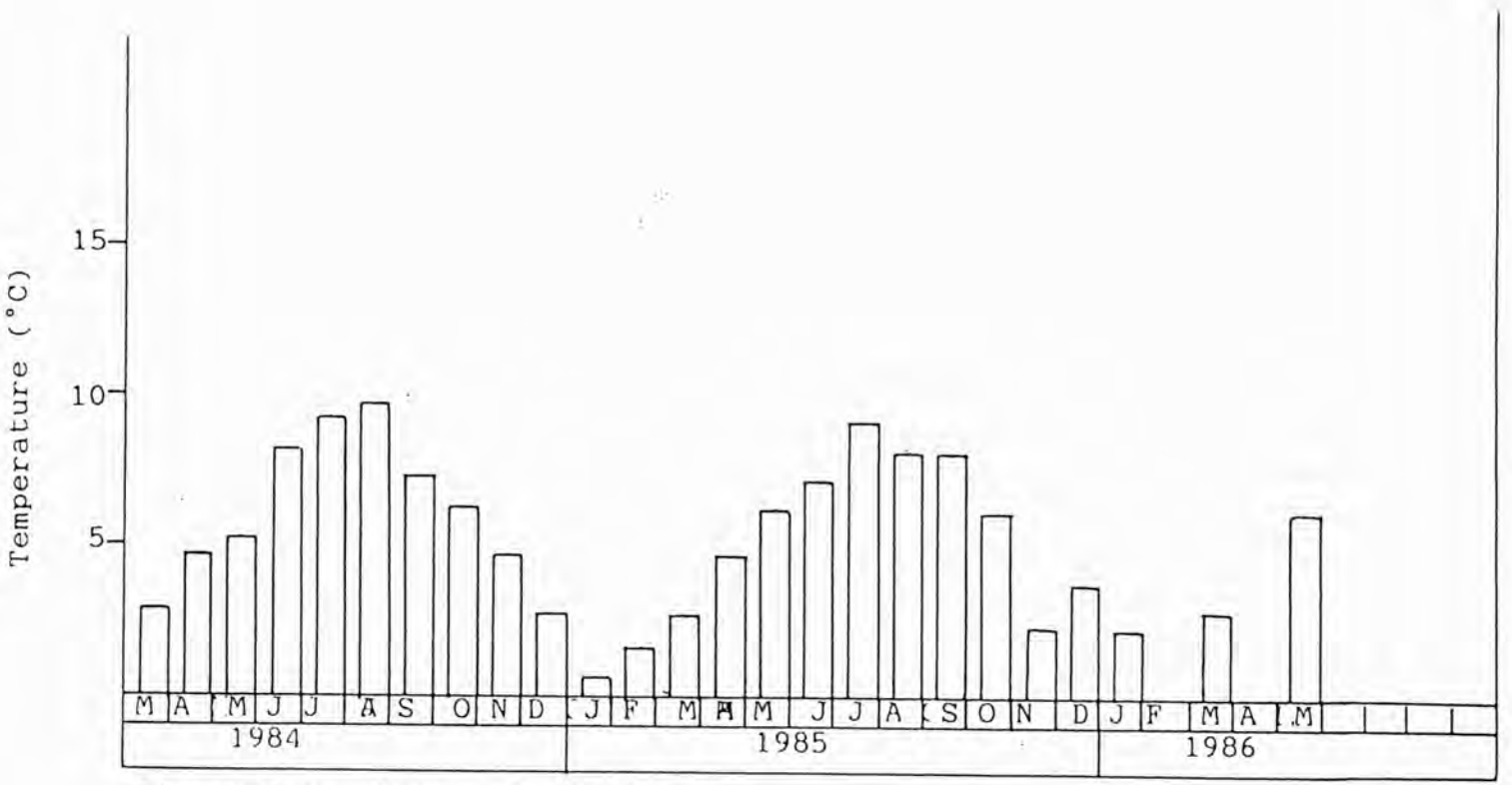


Figure 5.6 Meteorological Data:

Monthly mean temperature.

March, 1984 to May, 1986.

5.3 RESULTS AND DISCUSSIONS

5.3.1 GROWTH OF PHYTOPLANKTON POPULATIONS IN NATURE

The greatest source of heat to lakes and rivers is solar radiation and most is absorbed directly by the water. Some transfer of heat from the air and sediments does occur, but in lakes of moderate depth this input is small in comparison to direct absorption.In shallow waters,either for the entire lake or in its littoral regions,sediments can absorb significant quantities of solar radiation and this heat is transferred in part to the water.However,such terrestrial heat is generally very small in comparison to direct absorption of solar radiation by the water.

Temperatures in the River Thames and the Wraysbury Reservoir tends to follow regular seasonal patterns that is low during the winter and increased gradually during the spring until summer and decreased again during the autumn (Figures 5.4,5.5 and 5.5a).The results were consistent with the monthly mean temperature provided by the Meteorological Offices (Figure 5.6).The highest temperatures during the period of sampling were 21°C (on 15th.July,1986) in the River Thames and 19.2°C (29th.July,1986) in the Wraysbury Reservoir. Whereas the lowest temperatures during the period of sampling were 2.5°C (18th.February,1986) in the River Thames and 1.5°C (4th.May,1986) in the Wraysbury Reservoir.

Figures 5.7 to 5.15 showed the relationship between temperatures and species occurrence in the river and reservoir. Generally, diatoms became dominants in the spring when the temperature was low and blue-green and green algae became dominants in the summer when the temperatures were high.

Temperature effects on phytoplankton growth may be both direct and indirect. The reduction in temperature seems to be the most profound density-independent environmental effect in the production of biomass to many temperate zone species. It is well known that certain species have a narrow temperature range and others are able to withstand rather large temperature ranges. During this investigation it was evident that most of the species had wide ranges of tolerance and that species composition in the winter and summer as well as in the autumn and spring were quite similar. However, the dominance or the development of large populations of given species seemed to be quite clearly correlated with temperature. Some species growing best under cool water conditions and others under warm. Stephanodiscus rotula, Stephanodiscus rotula var. minutula and Stephanodiscus ref. hantzschii were found during the spring where the temperatures ranged between 6.5 and 18.4°C in the River Thames. However, they only became dominant when the temperatures were between 12.5 and 13.5°C. Mean temperature of maximum growth of Stephanodiscus rotula was 12.8°C. For

Figure 5.7 Relationships between Stephanodiscus spp. and the water temperatures in the River Thames.

Stephanodiscus rotula

Stephanodiscus rotula var.minutula

Stephanodiscus ref.hantzschii

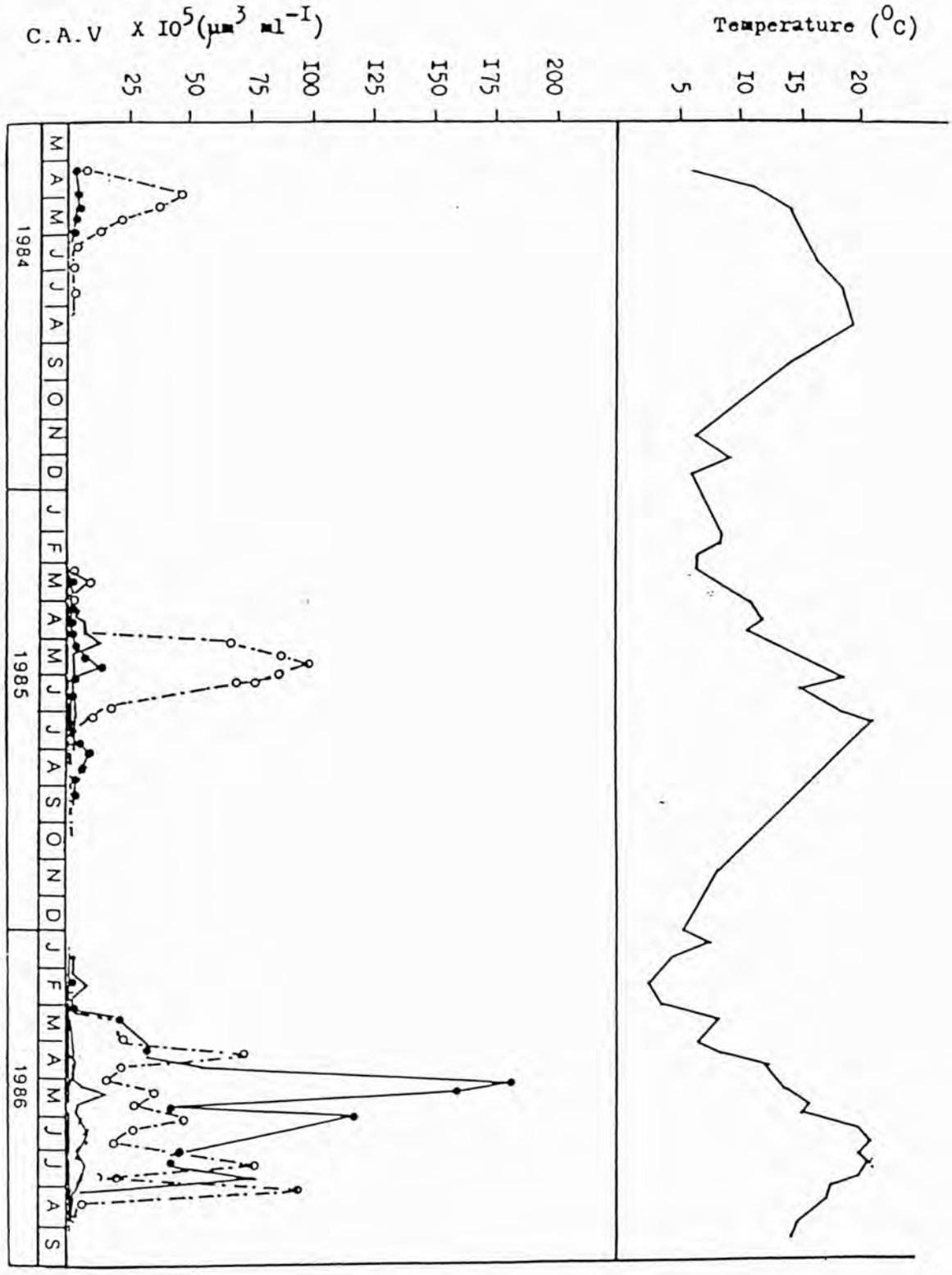

C.A.V X 10^5 (μm^3 ml^{-1})
25
50
75
100
125
150
175
200
Temperature (^{0}C)
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 5.7

Figure 5.8 Relationships between Stephanodiscus spp. and the water temperatures in the Wraysbury Reservoir.

———— Stephanodiscus rotula

—●— Stephanodiscus rotula var.minutula

—○— Stephanodiscus ref.hantzschii

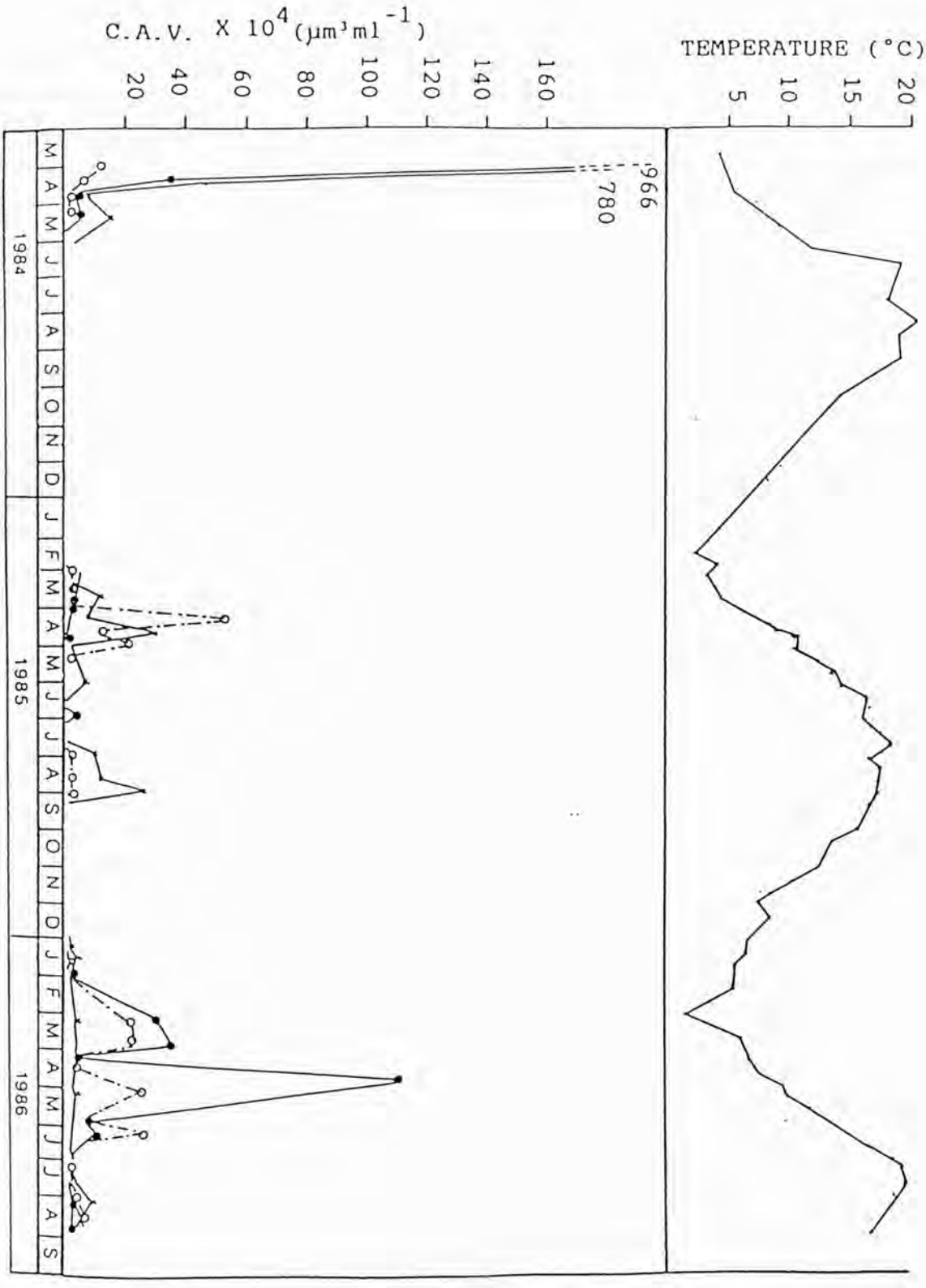

C.A.V. X 10^4 ($\mu m^3 ml^{-1}$)
20
40
60
80
100
120
140
160
966
780
TEMPERATURE (°C)
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 5.8

Figure 5.9 Relationships between Bacillariophyceae and the water temperatures in the River Thames.

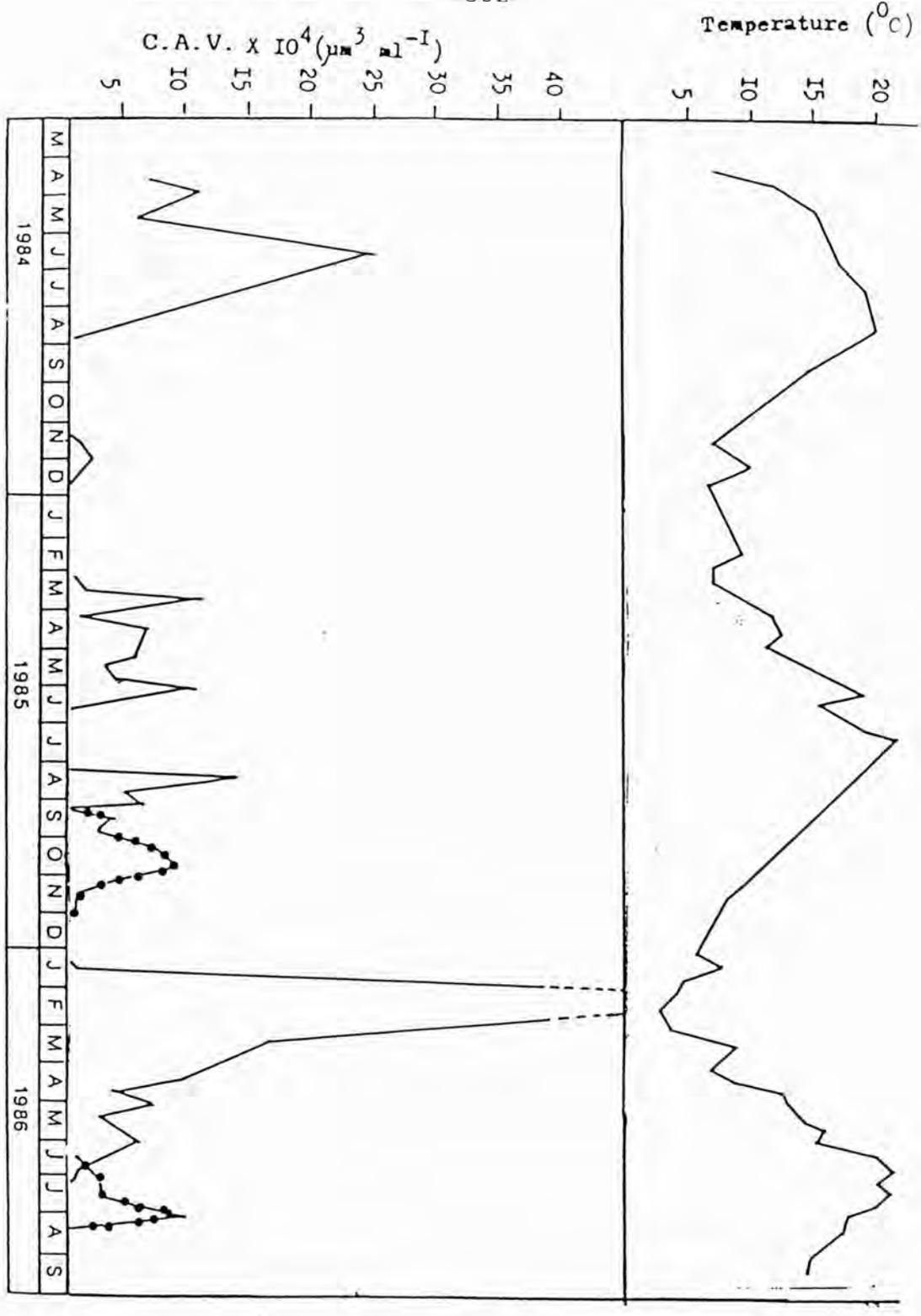

Temperature (°C)
5
10
15
20
C.A.V. x 10⁴(µm³ ml⁻¹)
5
10
15
20
25
30
35
40
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 5.9

Figure 5.10 Relationships between Bacillariophyceae and the water temperatures in the Wraysbury Reservoir.

Melosira varians

Aulacoseira granulata

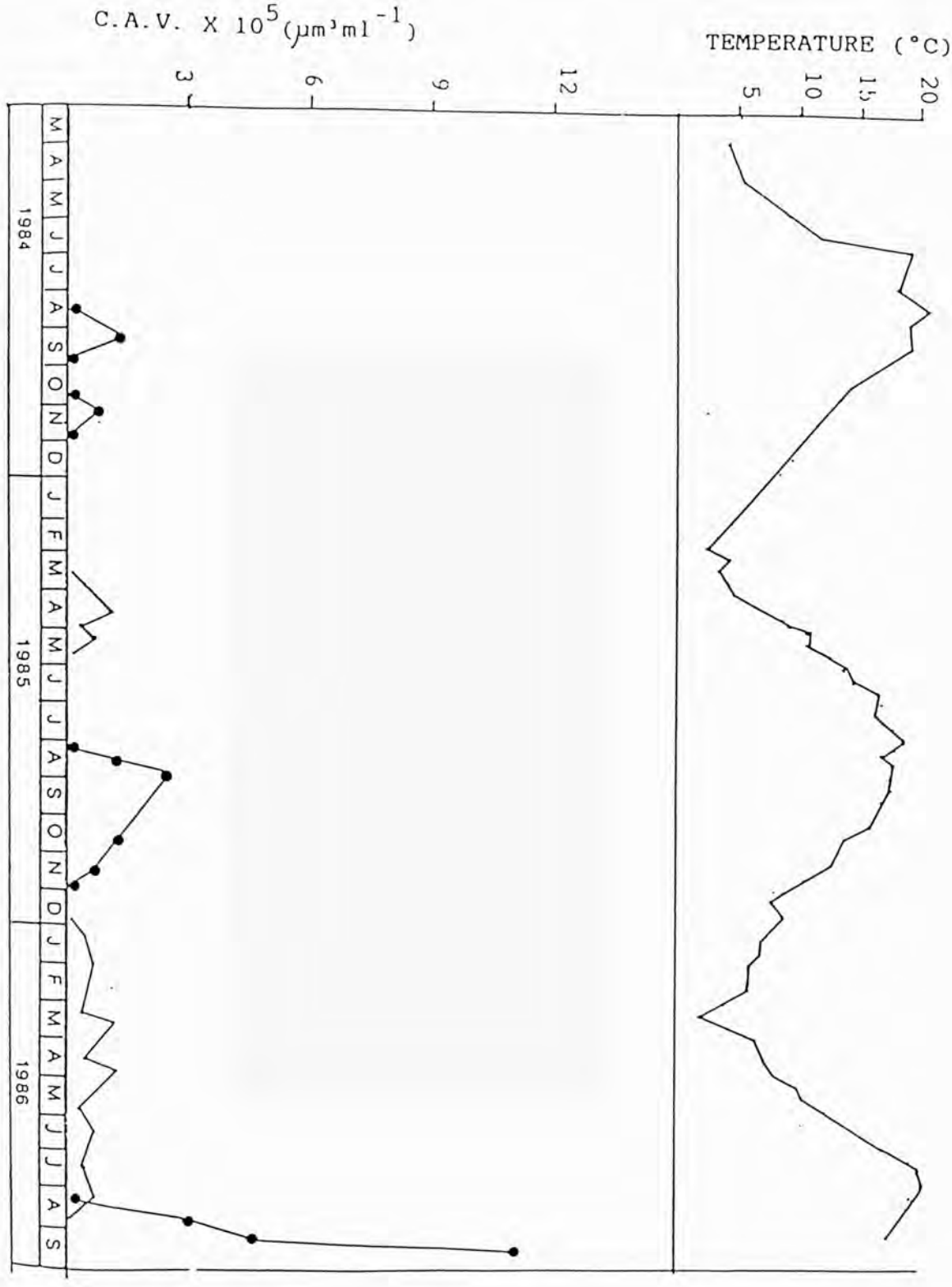
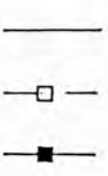

C.A.V. X 10^5 ($\mu m^3 ml^{-1}$)
3
6
9
12
TEMPERATURE (°C)
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 5.10

Figure 5.11 Relationships between Chlorophyceae and the water temperatures in the River Thames.



Eudorina elegans

Scenedesmus quadricauda

Scenedesmus acuminatus

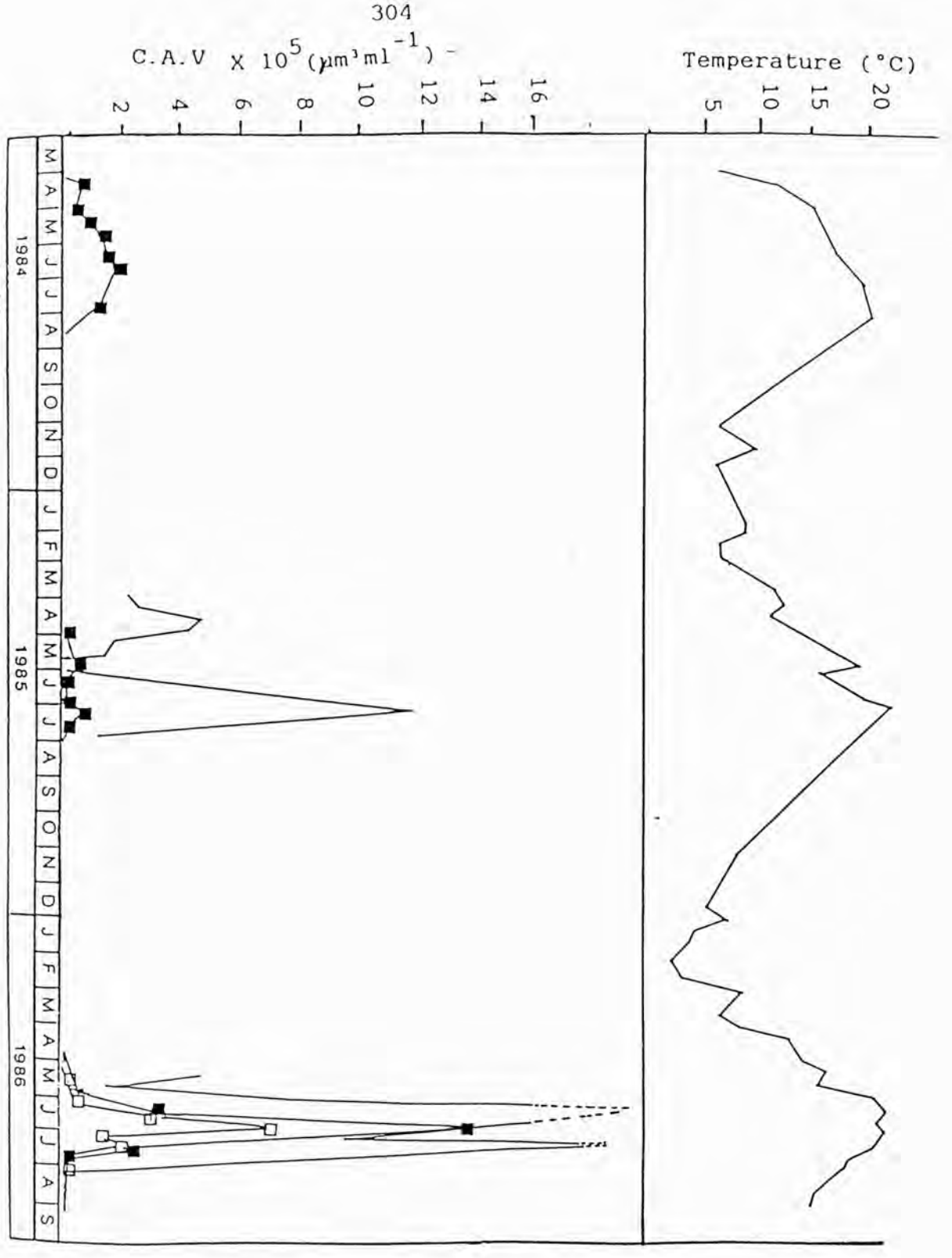

C.A.V X 10^5 ($\mu m^3 ml^{-1}$)
2
4
6
8
10
12
14
16
Temperature (°C)
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 5.11

Figure 5.12 Relationships between Chlorophyceae and the water temperatures in the Wraysbury Reservoir.

Scenedesmus quadricauda

Scenedesmus acuminatus

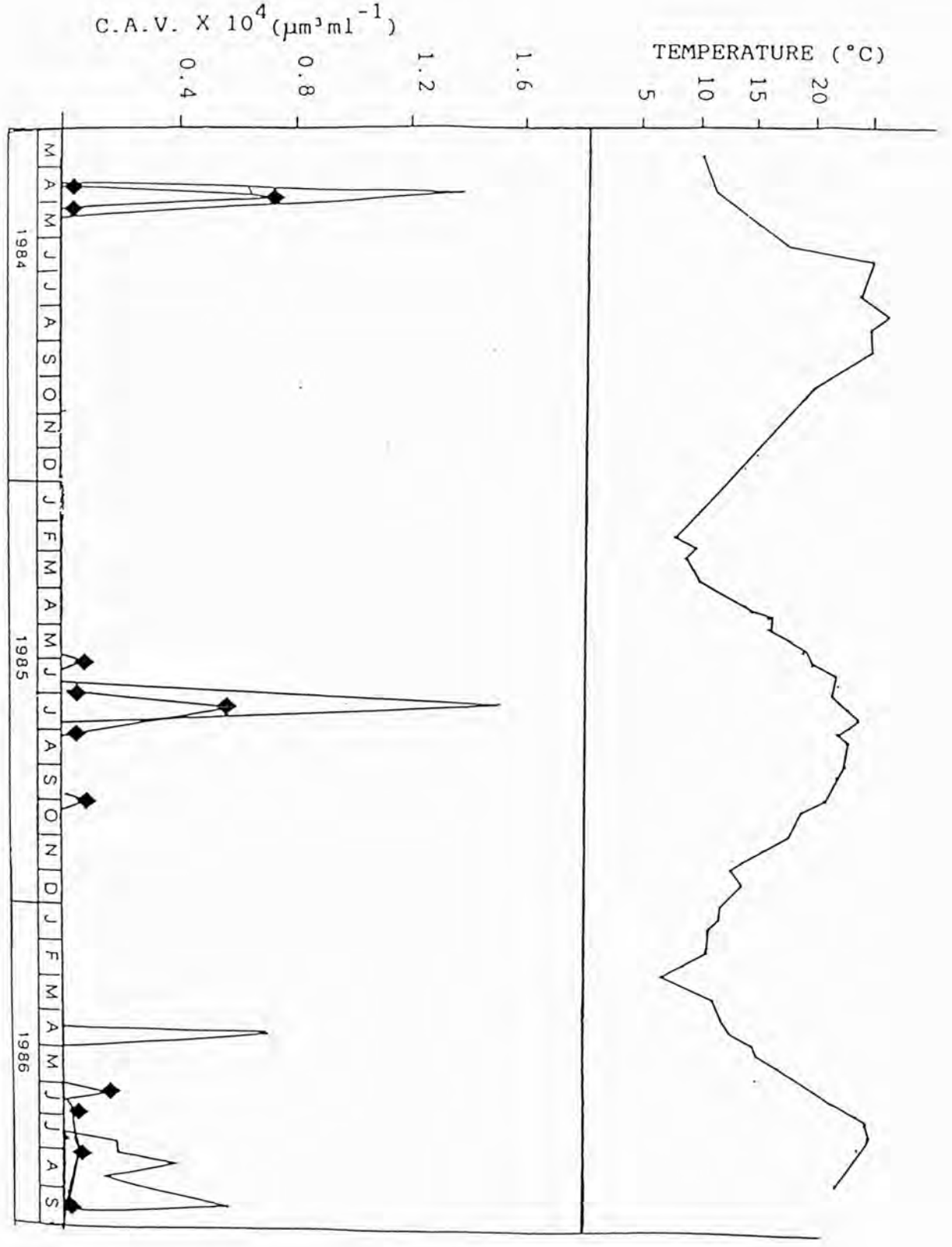

C.A.V. X 10^4 ($\mu m^3 ml^{-1}$)
0.4
0.8
1.2
1.6
TEMPERATURE (°C)
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 5.12

Figure 5.13 Relationships between Cryptophyceae and the water temperatures in the River Thames.

——— *Rhodomonas minuta*

—●— *Cryptomonas spp.*

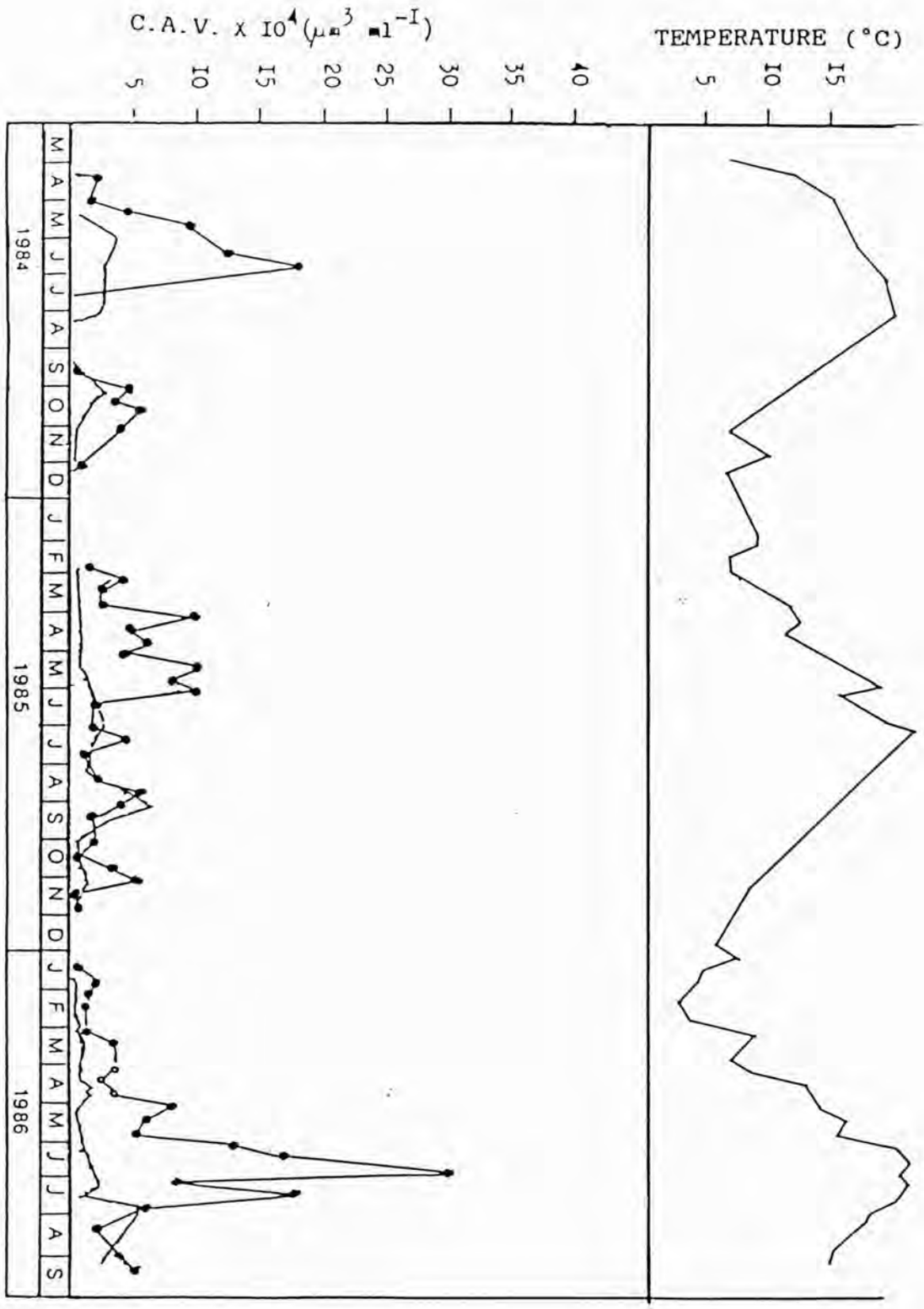

C.A.V. x 10^4 (μm^3 ml^{-1})
5
10
15
20
25
30
35
40
TEMPERATURE (°C)
5
10
15
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 5.13

Figure 5.14 Relationships between Cryptophyceae and the water temperatures in the Wraysbury Reservoir.

——— Rhodomonas minuta

—●— Cryptomonas spp.

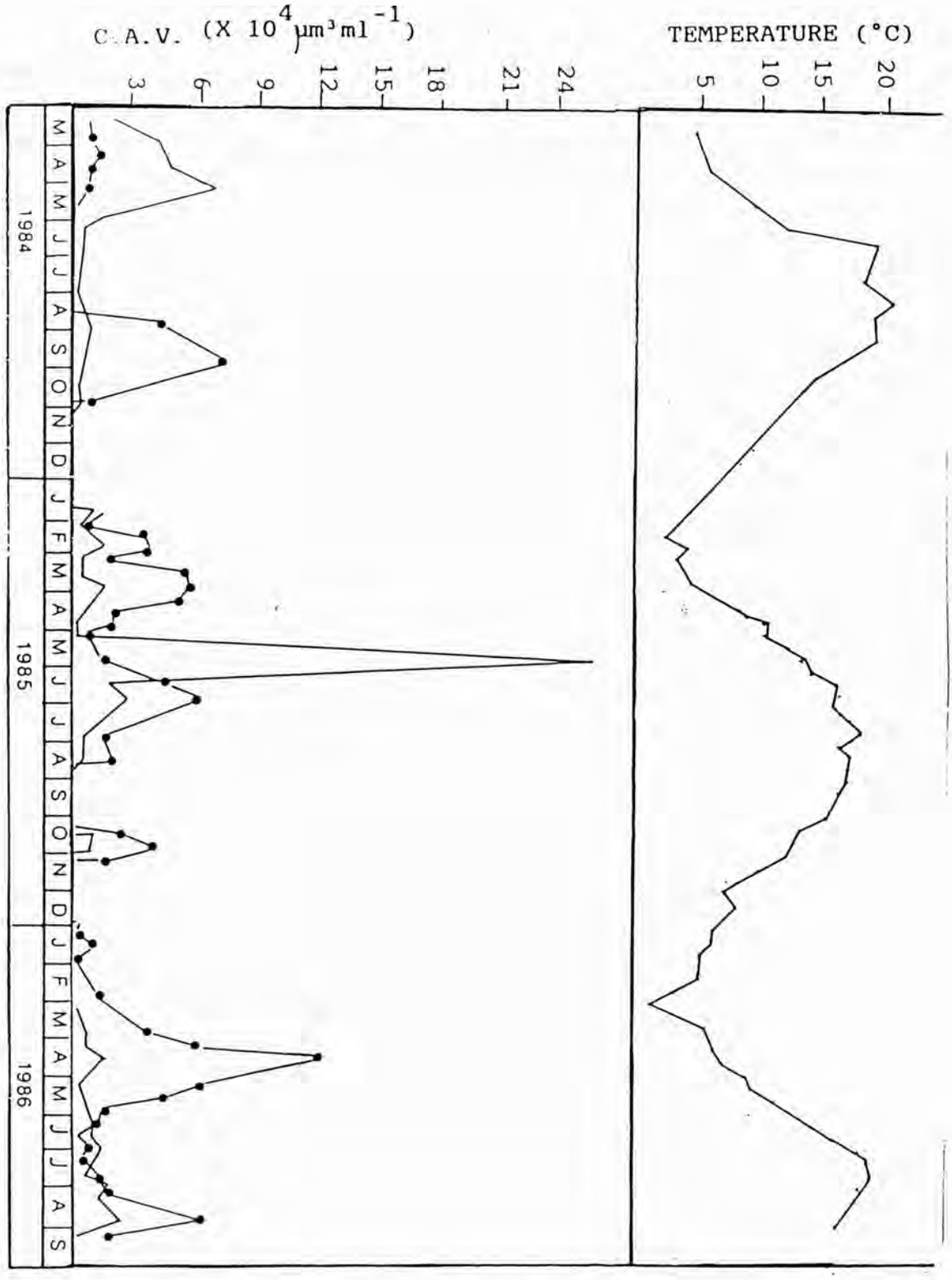

C.A.V. (X 10⁴ µm³ml⁻¹)
3
6
9
12
15
18
21
24
TEMPERATURE (°C)
5
10
15
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 5.14

Figure 5.15 Relationships between Cyanobacteria and the water temperatures in the Wraysbury Reservoir.

——— Anabaena spp.

—•— Aphanizomenon flos-aquae

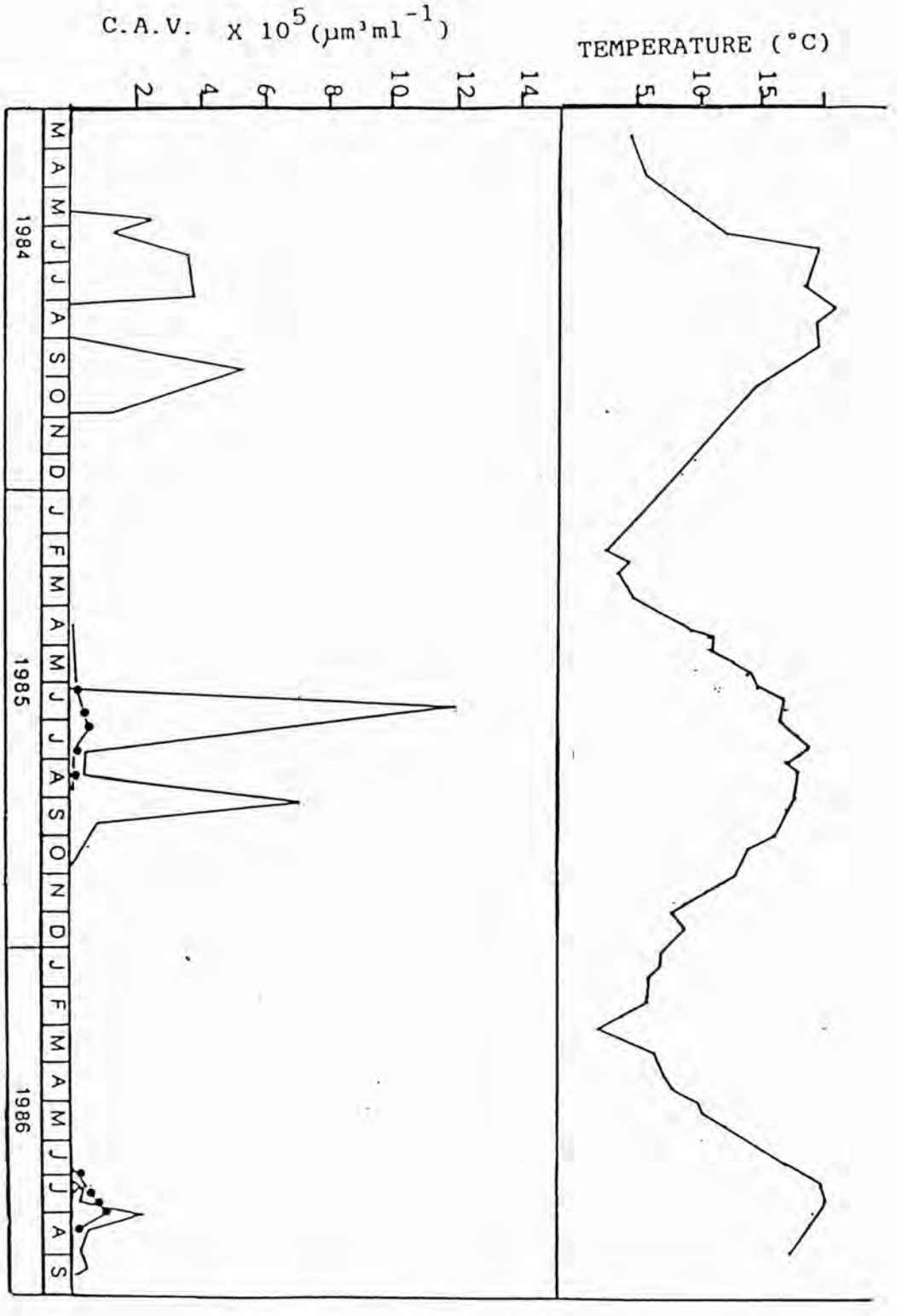

C.A.V. X 10^5 ($\mu m^3 ml^{-1}$)
2
4
6
8
10
12
14
TEMPERATURE (°C)
5
10
15
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 5.15

Stephanodiscus rotula var.minutula it was 12.4°C and for Stephanodiscus ref.hantzschii it was 13.5°C.Diatoms were all replaced by green and blue-green algae in summer when the temperature ranged between 19°C and 21°C.Scenedesmus quadriacauda occurred in higher numbers when the temperature reached about 20°C.

General diatom diversity seemed to increase as one approached the optimum range of temperature within the range of tolerance for most of the species of a community.When the temperature regime moved away from the optimum either by becoming colder or hotter the diversity was decreased and the biomass was also affected (Patrick,1977).This phenomenon was apparent during this study.The optimum temperature for Stephanodiscus ref.hantzschii,Nitzschia acicularis,Melosira varians and Aulacoseira granulata were in the range from 8.2°C to 15.1°C.When the temperature regime moved away from the optimum either by becoming colder (less than 2°C) or hotter (more than 20°C) diatom growth and diversity were decreased.

Some diatoms seemed able to stand fairly wide temperature ranges and maintain fairly good growth rates (e.g.Stephanodiscus ref.hantzschii,Stephanodiscus rotula var. minutula),whereas other diatoms seemed to have small ranges of temperature tolerance (e.g.Nitzschia acicularis,Melosira varians,Aulacoseira granulata).

Hustedt (1956) has classified diatoms as in Table

Table 5.1 THERMAL TOLERANCE CLASSIFICATION OF DIATOMS*

Stenotherms	
Cold-water stenotherms	15°C
Temperate stenotherms	15°-25°C
Warm-water stenotherms	above 25°C
Meso-stenotherms: those forms that can withstand 10°C variation in temperature.	
Tropical cold-water forms	10°-20°C
Temperate forms	15°-25°C and 20°-30°C
Warm-water forms	25°-35°C and 30°-40°C
Meso-eurytherms: those forms that can withstand 15°C variation in temperature.	
Cold-water to temperate forms	10°-25°C
Temperate forms	15°-30°C
Temperate to warm-water forms	30°-45°C
Eu-eurytherms: those forms that can live in 20°C or more variation in temperature.	

* From Hustedt (1956)

Table 5.2 Temperature ranges of common species of phytoplanktonic algae.

	Findenegg	Ruttner	Stanković	Wesenberg-Lund
Oscillatoria nubescens	5-8°C	5.8-10.4°C	-	4-10°C
Stephanodiscus astrea(=S.rotula)	6-12	-	6.5	4-6 (rarely to 15
Synedra acus delicatissima	5-10	4.8-7.6	-	1-10
Asterionella formosa var. hypolimnetica	-	5.1-8	8.0	-
Dinobryon divergens	5-8	8.5-13.2	10.5	-
Fragilaria crotonensis	8-14	7.1-14.1	-	13-16
Rhodomonas lacustris	8-12	5.1-13.2	-	-
Cyclotella bodanica	10-15	6.3-12.3	-	-
Cyclotella comensis	12-15	6.4-12.8	-	-
Cyclotella comta	8-15	(4.6)-14.7	-	-
Ceratium hirundinella	12-19	8.9-13.7	16.5-23.0	Warmest period of year
Anabaena flos-aquae	16-21	11.6-14.5	-	16-18

Modified from (Hutchinson, 1967).

5.1. For example, Stockner (1967) has found that some diatoms can live in very high temperatures. However, most diatoms living in the temperate zone seem to prefer temperatures lower than 30°C. There are, however, exceptions to this. Barker (1935) found that Nitzschia palea reached its maximum rate of photosynthesis at 33°C and at 40°C the rate of photosynthesis was irreversibly lowered. Wallace (1955) found that the growth of Nitzschia linearis was greatly reduced or inhibited at 30°C and Nitzschia filiformis at 34°C. In contrast, Gomphonema parvulum could grow fairly well at 34°C, although the rate of cell division was not as great as at 20°C.

Ruttner (1937b) and Findenegg (1943b) also have published lists of extreme temperature ranges of occurrence, temperature ranges of marked development, and mean temperatures for the maxima of a number of species found in the lakes of Austria. Findenegg investigated a group of Carinthian lakes and Ruttner investigated principally the lakes of the Salzkammergut. Ruttner's temperature data are largely based on vertical series, and his range of temperatures for well-marked development on any occasion is the range within which the population density is at least 10% of the maximum density. Stankovič (1960) has published comparable data for Lake Ohrid. The mean temperature of maxima and the ranges for well-marked development for species common to the list of at least two of these authors are given in Table 5.2 with data of Wesenberg-Lund (1904) as comparison.

Among green algae or Chlorophyceae; Scenedesmus quadricauda reached a maximum number of 2804 cells per ml. in the River Thames during 1986 but only 128 cells per ml. during 1985. However, the maximum number of Scenedesmus quadricauda cells coincided with the highest temperature during the years (i.e. 20.7°C and 20°C in 1985 and 1986, respectively). Scenedesmus quadricauda was less than 100 cells per ml. in the Wraysbury Reservoir during the investigation and appeared when the temperature was high (i.e. 15°C to 19°C).

Rhodomonas minuta reached a maximum of 515 cells per ml. in the River Thames on 29th. July, 1986 when water temperature was 18.5°C. During 1985, Rhodomonas minuta reached a maximum number of 463 cells per ml. when the water temperature was 16.3°C. In the Wraysbury Reservoir; Rhodomonas minuta reached a maximum number of 1669 cells per ml. on 4th. June, 1985 when the water temperature was 16°C. During 1986 only 160 cells per ml. of Rhodomonas minuta occurred as a maximum number when the water temperature was 16.8°C. These observations showed that Rhodomonas minuta occurred in the River Thames and the Wraysbury Reservoir when water temperatures were between 16°C to 18.5°C.

Trachelomonas volvocina was recorded in the River Thames during March, April, May, June and July with maximum number of 308 cells per ml. (during 1985) and 211 cells per ml. when water temperature was about 20°C.

Cyanobacteria, Oscillatoria ref. limosa, Oscillatoria

ref.agardhii and Anabaena spp. were found occasionally in the River Thames during the summer but in low numbers.Hardy (1977) also found that Anabaena flos-aquae and Aphanizomenon flos-aquae appeared only sporadically in the Thames and the counts did not indicate that rapid growth took place.However, Cyanobacteria including Anabaena flos-aquae,Anabena circinalis (counted together and classified as Anabaena spp.),Aphanizomenon flos-aquae and Microcystis aeruginosa were found in quite high numbers in the Wraysbury Reservoir when the water temperature were high (between 15°C and 20°C).

5.3.2 GROWTH OF PHYTOPLANKTON POPULATIONS IN CULTURE

Batch cultures have been used for many years to study autecological relationships between specific growth rate and temperature in diatoms (Braarud,1937;1945).

The effects of temperature on the physiology of phytoplankton are as complex as the effects of nutrients and light.The time scale of variation in temperature are less rapid than either of the parameter as,while variance in light and nutrients are influenced by temperature (and hence density) differences,the mean temperature of surface water changes rather slowly in a seasonal pattern or not at all.The temperature 'signal' is one of slow seasonal change in temperate waters but,even so,there are discernible effects of both the mean and the variance components (Harris,1986).

Eppley (1972), Goldman and Carpenter (1974) have shown a clear overall temperature effect on the growth rate of phytoplankton, and the maximum rate of growth doubles, roughly, every 10°C increase in temperature (a Q_{10} of approximately 2.0). Temperature, therefore sets an upper limit to the rate of growth.

Controlled laboratory conditions of continuous saturating illumination, near constant temperature and a plentiful availability of nutrients supplied in artificial media presumably afford the best opportunity for most 'algal' species to realize their highest potential growth rates (Reynolds, 1984). However, during this study the optimum temperature and the maximum growth rate of the phytoplankton species studied were obtained using light-dark cycle. A light-dark cycle is a more natural condition than constant light. Phytoplankton are not active during the daytime only; during the night various biochemical processes take place, and also the biomass increases somewhat during the start of the dark period (Nyholm, 1978).

Figures (5.16, 5.16a; 5.17, 5.17a; 5.18, 5.18a) show the relationships between phytoplankton concentrations (cells per ml. or colonies per ml.) and the growth rate (in ln unit day^{-1}) with temperatures.

From this investigation it was shown that Stephanodiscus ref. hantzschii (Figures 5.16, 5.16a) grew well in three conditions where temperatures were 10°C, 20°C and

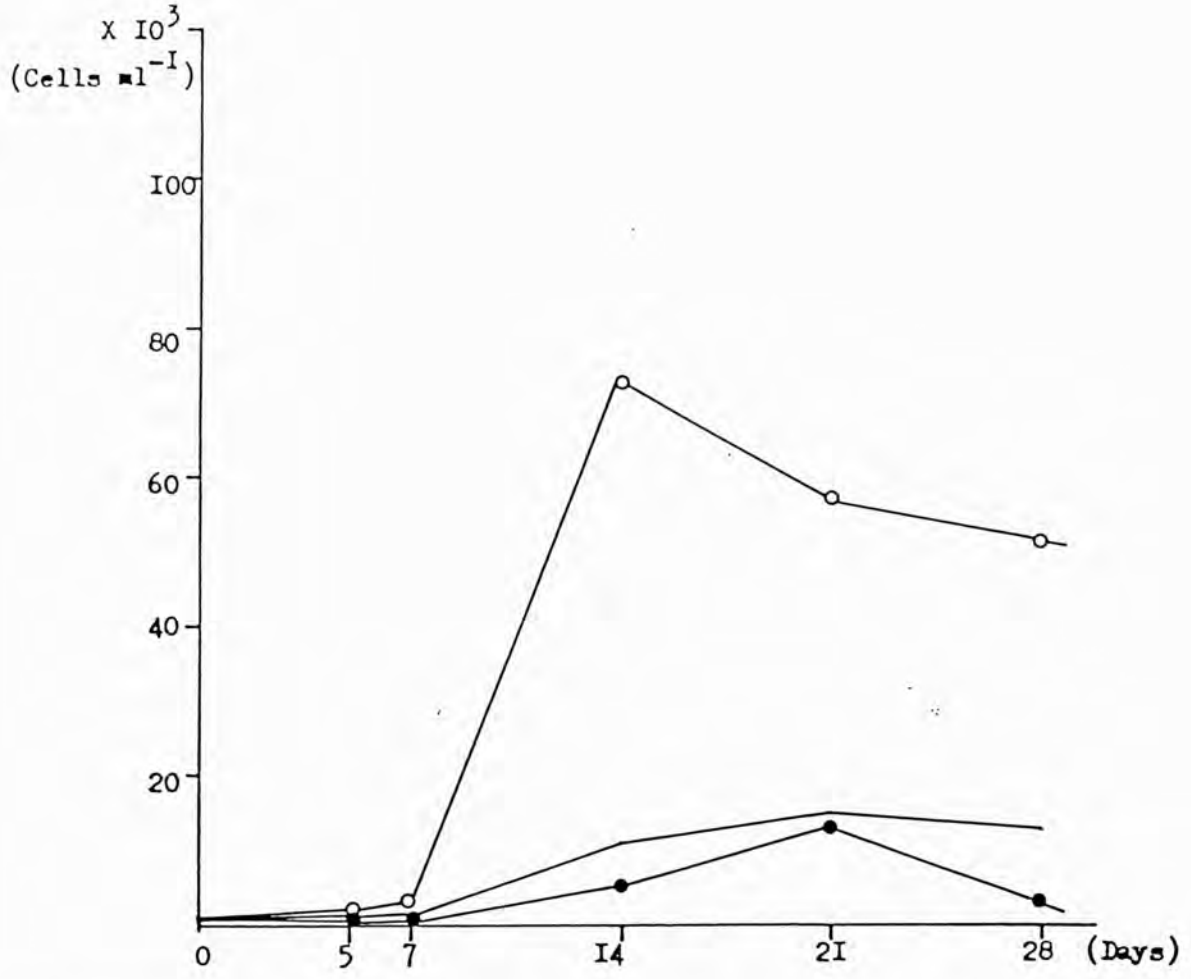


Figure 5.16 The growth of Stephanodiscus ref.hantzschii at different temperatures.

LEGEND: Temperature (°C)

—— 10

—○— 20

—●— 25

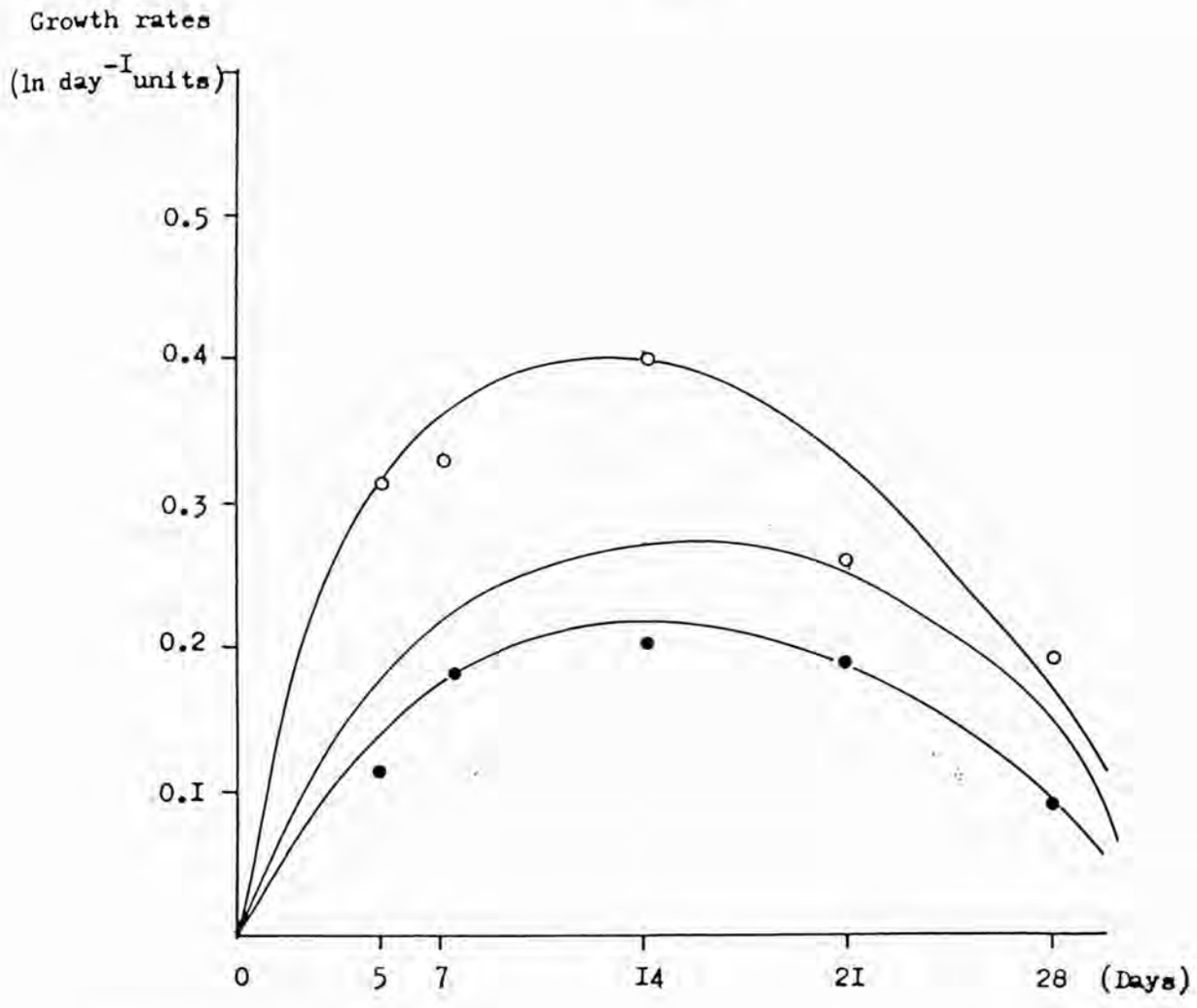


Figure 5.16a Growth rates of Stephanodiscus ref.hantzschii at different temperatures.

LEGEND: Temperature (°C)

—— 10

—o— 20

—•— 25

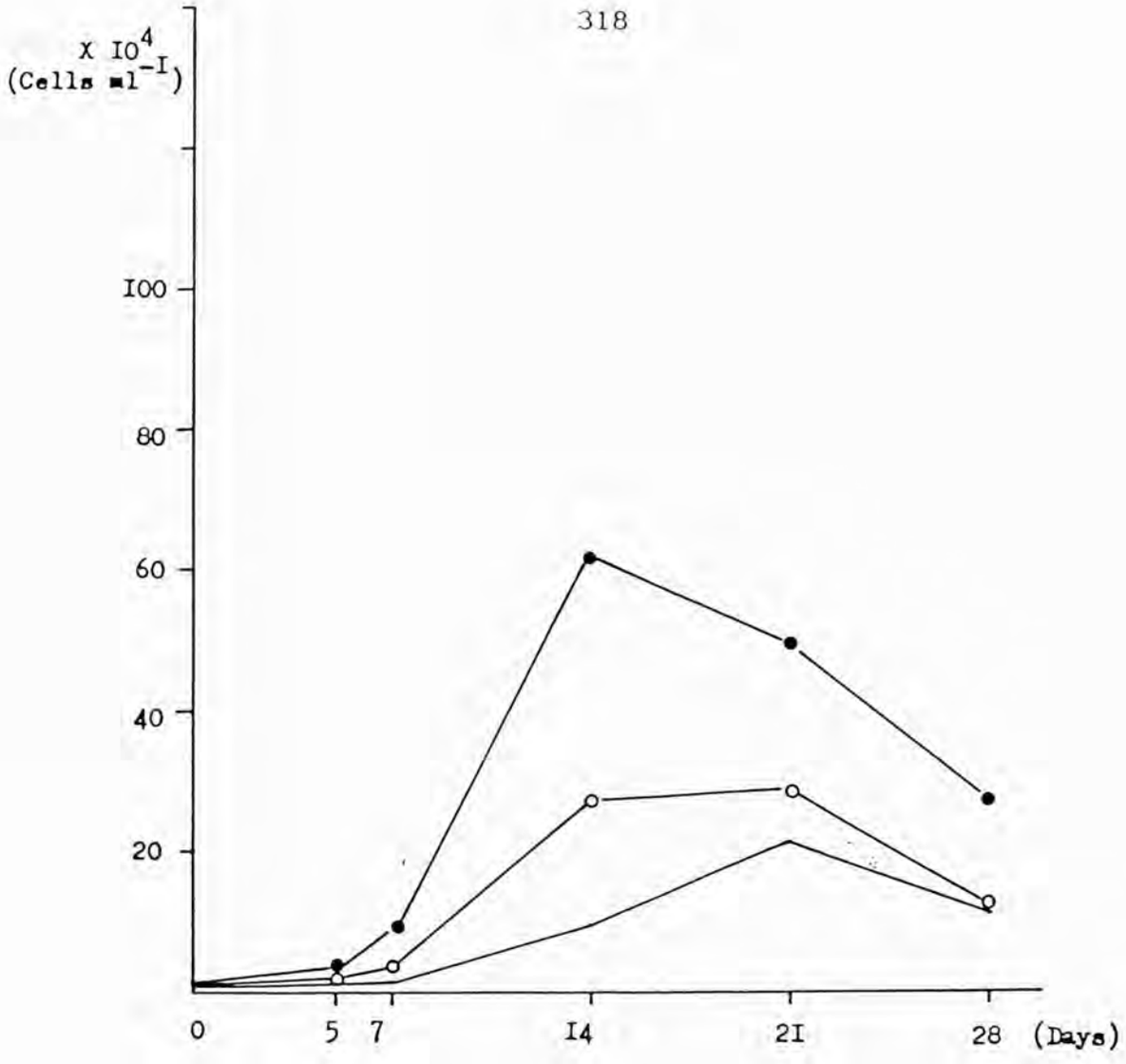


Figure 5.17 The growth of Scenedesmus quadricauda at different temperatures.

LEGEND: Temperature (°C)

—— 10

—o— 20

—●— 25

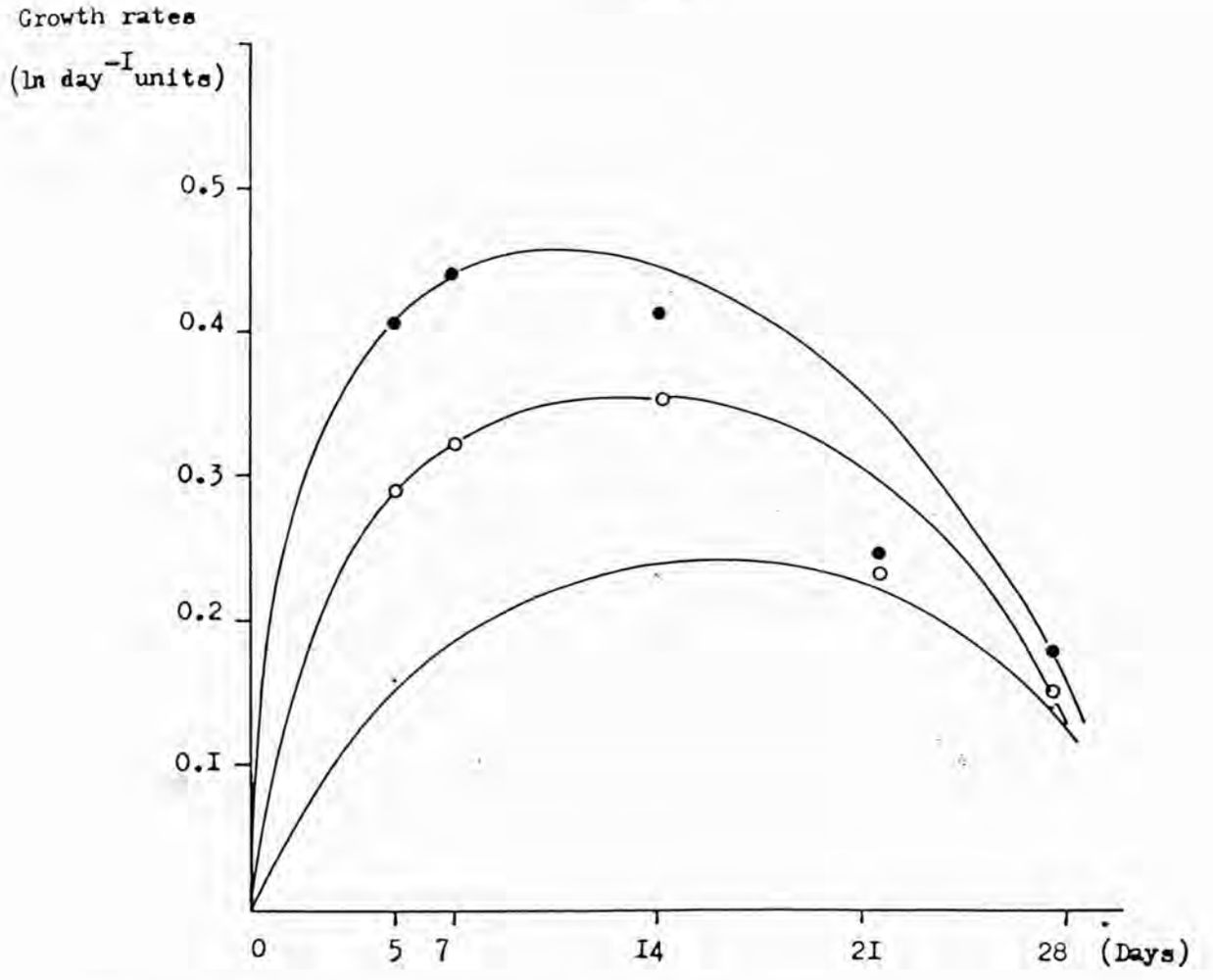


Figure 5.17a Growth rates of Scenedesmus quadricauda at different temperatures.

LEGEND: Temperature (°C)

—— 10

—o— 20

—•— 25

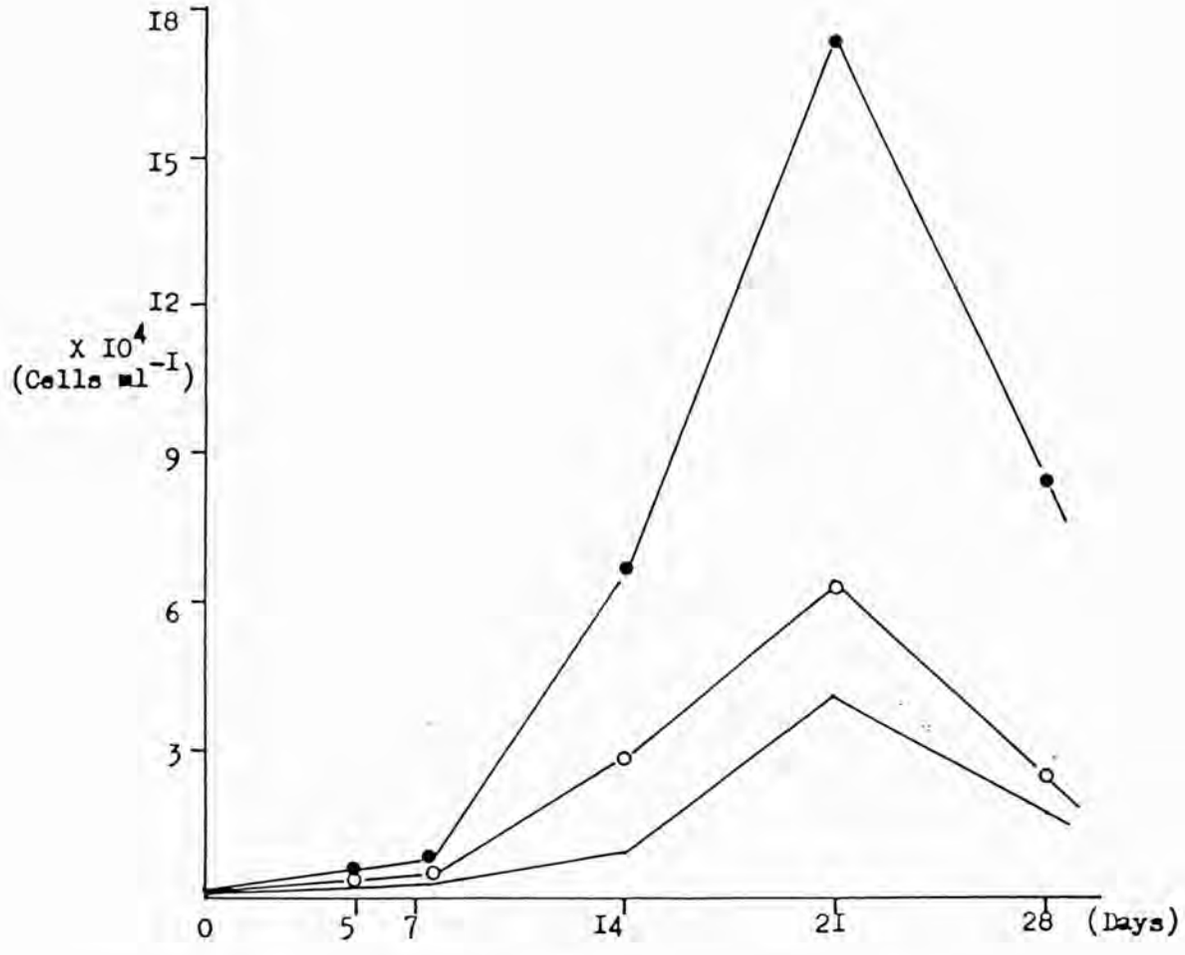


Figure 5.18 The growth of Eudorina elegans at different temperatures.

LEGEND: Temperature (°C)

—— 10

—o— 20

—●— 25

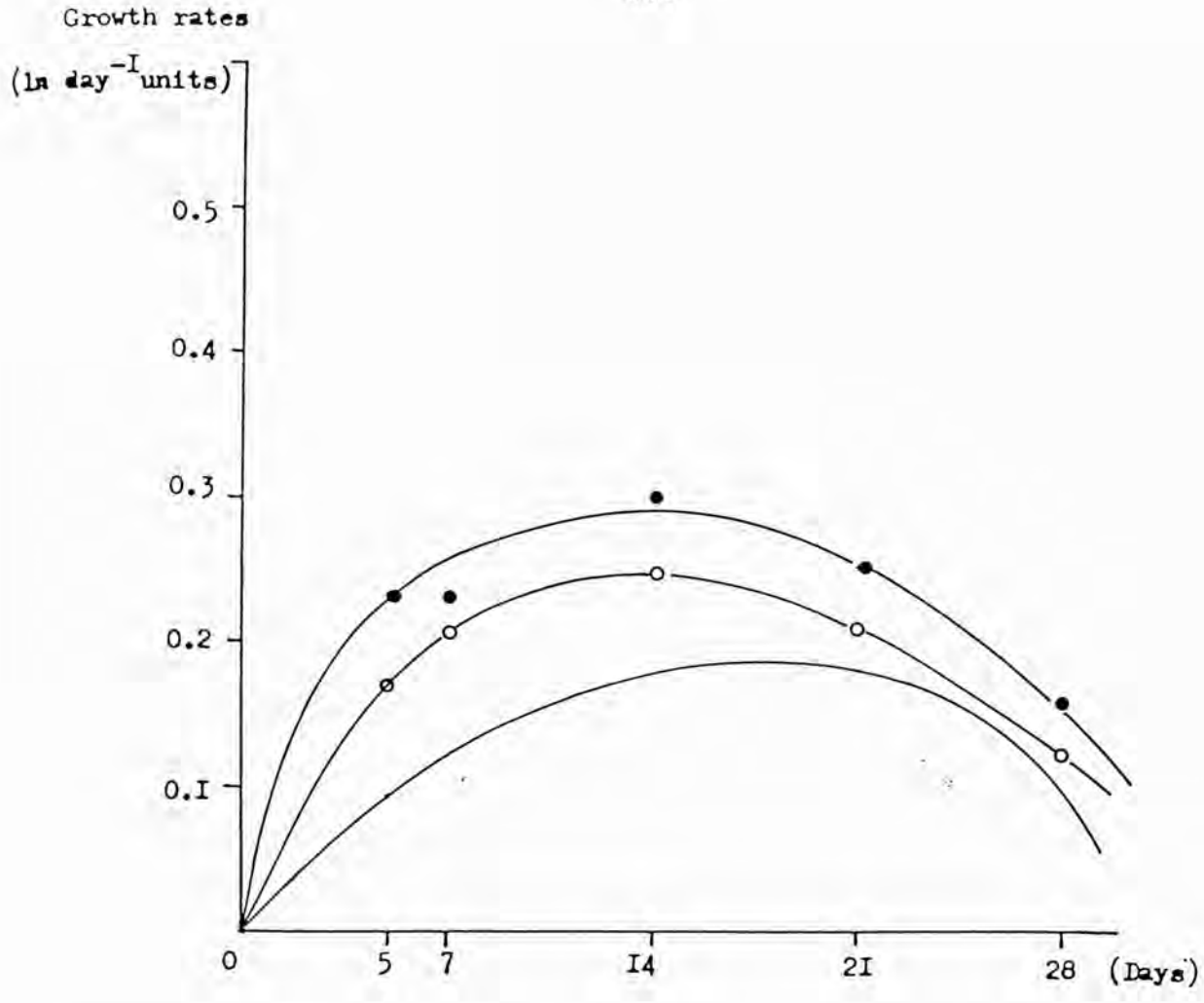


Figure 5.18a Growth rates of Eudorina elegans at different temperatures.

LEGEND: Temperature (°C)

—— 10

—○— 20

—●— 25

25°C.However,the maximum growth rate occurred when temperature was 20°C.The optimum temperature found in the culture experiments was higher than the water temperature when Stephanodiscus ref.hantzschii reached maximum growth in nature (i.e.about 14°C).One of the puzzling results of μ vs.T measurements with cultures is that T_{opt} (optimum temperature) exceeds by several degrees the natural water temperatures where the species are found to be most abundant (Braarud, 1961;Smayda,1969).

Figures (5.17,5.17a) show that Scenedesmus quadricauda did not grow very well when the temperature was low (10°C).It reached its maximum growth rate when the temperature was 25°C.Similar results were obtained with the Eudorina elegans.

Scenedesmus quadricauda and Eudorina elegans are green algae which occurred during the summer.Therefore they need a higher temperature than Stephanodiscus ref.hantzschii. However,the maximum temperature in the River Thames and the Wraysbury Reservoir did not exceed 23°C during the period of study.

There have been few systematic attempts to compare individual performances of a range of species or even to collect published values together in a single review (Reynolds,1984).Exceptions to both statements are presented by the work of Hoogenhout and Amesz (1965) and to the latter in Fogg (1975).

The highest specific growth rate yet recorded for any 'alga' is ranging between less than 1 division day^{-1} and the 11.5 divisions day^{-1} recorded for Anacystis nidulans (=Synechococcus) at 41°C by Kratz and Myers (1955).This species is evidently thermophilic.However,many phytoplankton fail to grow much faster,if at all,at temperatures exceeding 30°C-35°C than they do at 20°C-25°C (Hoogenhout and Amesz, 1965).Even so,the optimum rates of growth of Synechococcus and of other several other small,unicellular (e.g. Chlamydomonas,Chlorella spp.) or simple coenobial (e.g. Scenedesmus quadricauda) algae exceed 2.7 divisions day^{-1} at 20°C-25°C (Reynolds,1984).Maximum growth rate (ln units day^{-1}) for Scenedesmus quadricauda was 2.84 at 25°C (recorded by Hoogenhout and Amesz,1965).This value was higher than the maximum growth rate for Scenedesmus quadricauda found in culture experiments during this study (1.8 divisions day^{-1}). This differences might possibly have been due to differences in light regimes obtaining during the experiments.Hoogenhout and Amesz (1965) used a continuous illumination whereas a light and dark cycle (12 hr.light:12hr.dark) was set up during my investigation.The effect of photoperiod on the growth rate of Scenedesmus quadricauda (see Chapter Four) seemed to agree with this result.

In contrast,many larger,filamentous and colonial phytoplankton grow relatively more slowly.The maximum growth rate of Tribonema vulgare was 0.33 divisions day^{-1} whereas

the maximum growth rate of Eudorina elegans was 0.42 divisions day^{-1} during this study. Indeed, although growth rates are undoubtedly influenced by a variety of physiological and metabolic factors, they are widely recognized to be generally coupled to size and structural organization (e.g. Belcher and Miller, 1960; Findenegg, 1966a; Fenchel, 1974; Fogg, 1975; Laws, 1975; Banse, 1976). The implication that habit influences growth rate is strengthened by the available data for the growth of Microcystis aeruginosa. In most cultures, this species loses the colonial organization that characterizes natural populations (Reynolds et al., 1981).

According to data in Lund (1949) and Foy et al., (1976) growth rates of Asterionella, Anabaena, Aphanizomenon and Oscillatoria increase between 1.8 and 2.9 fold over the range 10°C-20°C, while the average Q_{10} for Kratz and Myers (1955) Synechococcus between 25°C and 41°C is ~2.4. Cloern's (1977) data from Cryptomonas ovata, however, indicated that its growth rate increased about nine-fold between 8°C and 20°C (Q_{10}~6.1). The growth rate increased more slowly above 20°C to an optimum at about 23.5°C, above which it decreased significantly. The maximum growth of Cryptomonas spp. (Cryptomonas ovata and Cryptomonas erosa) occurred between 7.5°C to 19.1°C of water temperatures in the River Thames and Wraysbury Reservoir.

Laboratory studies have demonstrated certain features that were consistent with the field observations for

Scenedesmus quadricauda, Eudorina elegans and Stephanodiscus ref. hantzschii although the optimum temperature found in the studies were higher than field observations.

Stephanodiscus ref. hantzschii occurred in the River Thames and Wraysbury Reservoir during periods when water temperatures were between 6.5°C-18.4°C but they were abundant and became maximum when water temperature was around 14°C.

Scenedesmus quadricauda and Eudorina elegans occurred and became maximum in the River Thames and Wraysbury Reservoir during periods when water temperatures were 20°C or higher.

5.4 OTHER ENVIRONMENTAL FACTORS WHICH INFLUENCE THE GROWTH OF PHYTOPLANKTON POPULATIONS

5.4.1 OXYGEN

Oxygen is the most fundamental parameter of the water bodies, aside from water itself. Dissolved oxygen is essential to the metabolism of all aquatic organisms. Therefore, the properties of solubility, and especially the dynamics of oxygen distributions in aquatic environment, are basic to the understanding of the distributions, behaviour and physiological growth of aquatic organisms. Oxygen participates in many important chemical and biological reactions and has become the most widely studied chemical in the aquatic environment.

Figure 5.19 showed the concentrations of oxygen (in percentage saturation) in the River Thames and Wraysbury Reservoir. The oxygen concentration were at or near 100 percent saturation. However, deviations were found, frequently in the form of slight supersaturation resulting from intense photosynthetic activity by dense algal crops. Alternately, saturation to the value below 60% of oxygen in the Wraysbury Reservoir means that it is easily depleted by respiration and decomposition. Organic matter from natural sources or domestic and industrial sewage may result in serious depletion of dissolved oxygen. When this occurs for a long enough time, most aquatic organisms perish or

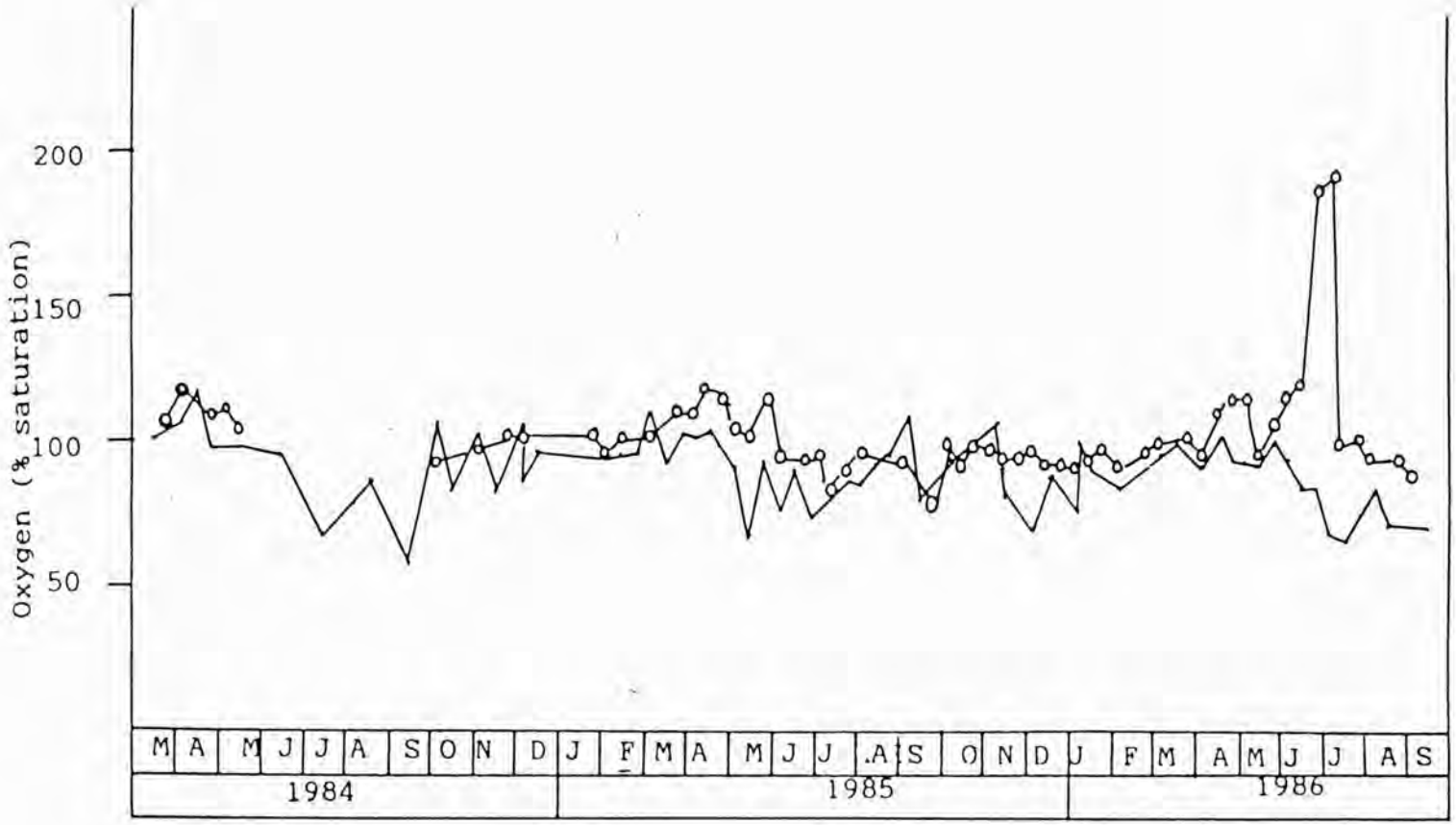


Figure 5.19 Oxygen concentrations in the River Thames (—o—) and the Wraysbury Reservoir (——).

are replaced by a few specialized organisms tolerant of low oxygen.This saturation occurred downriver (at Chelsea) in the River Thames during 5th. and 6th.July,1986.During the weekend of 5th. and 6th.July,water from storms washed sewage into the river.Concentrations of dissolved oxygen in parts of the River Thames fell to nil and because of this,thousands of fish died in the tidal reaches of the River Thames in Central London (New Scientist,1986).However,River Thames near Egham is not affected, judging from the results of dissolved oxygen concentrations during that time.

5.4.2 CARBON DIOXIDE

Carbon dioxide is a product of respiration by both plants and animals,provides the major carbon source for photosynthesis,and generally shows an inverse relationship to oxygen in water.Although only a minor component of air,carbon dioxide is quite abundant in water because its solubility is about 200 times that of oxygen.Carbon dioxide dissolves in water to produce carbonic acid (H_2CO_3),which dissociates into various fractions (HCO_3^-,CO_3^{2-}) depending upon the hydrogen-ion concentration (pH).Figure 5.20 shows concentrations of free carbon dioxide in the River Thames and Wraysbury Reservoir. Vertical distributions of carbon dioxide in the Wraysbury Reservoir shows in Figure 5.21.The carbon dioxide concentrations were usually higher in the River Thames than the Wraysbury

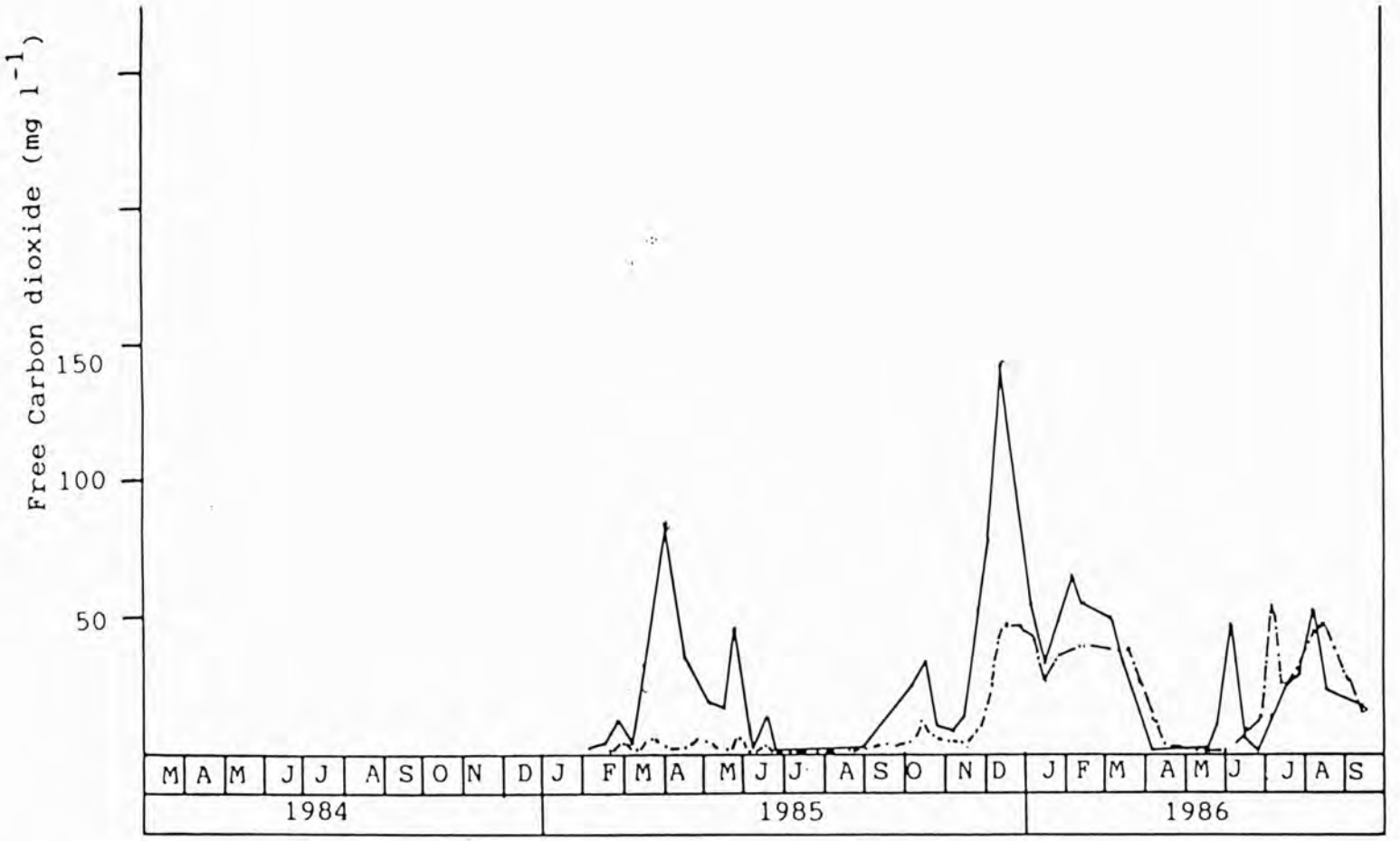


Figure 5.20 Free carbon dioxide concentrations in the River Thames (——) and the Wraysbury Reservoir (–.–.–).

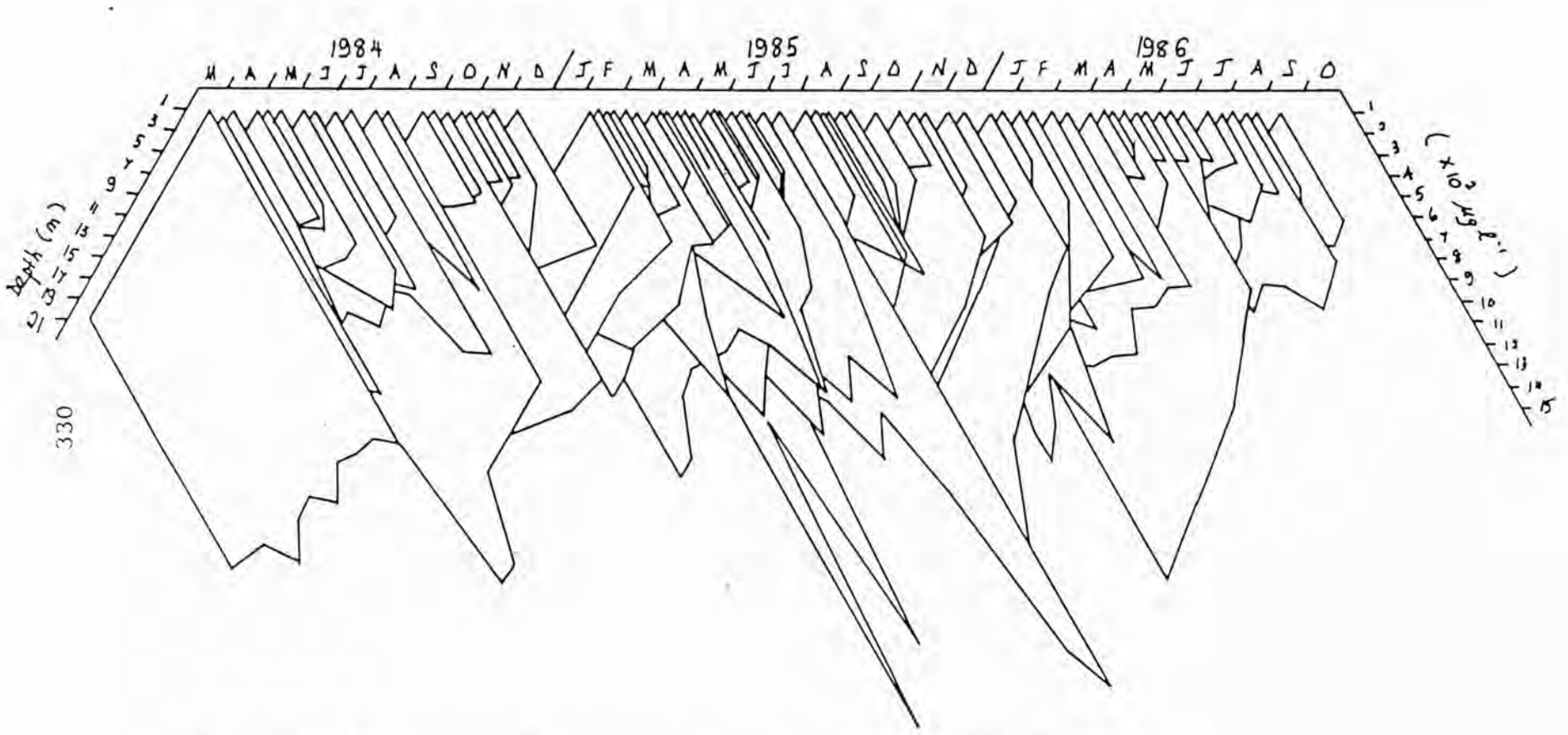


Figure 5.21 Vertical distributions of carbon dioxide concentrations in the Wraysbury Reservoir.

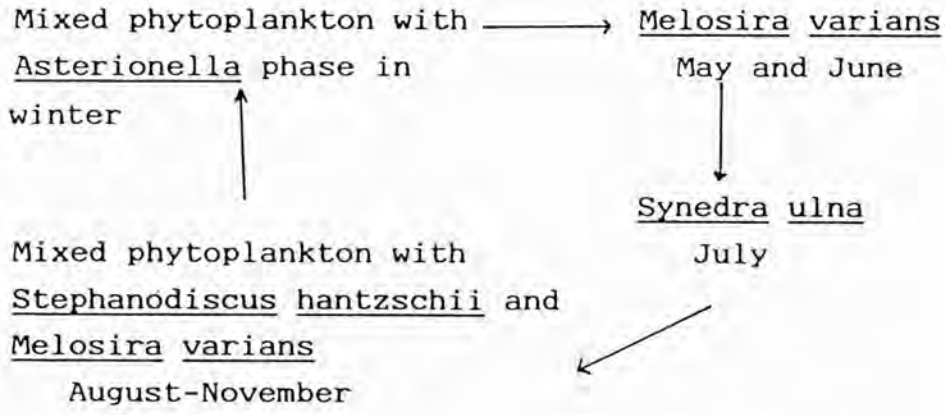
Reservoir.However,the pattern of distribution is more or less similar,with the highest concentrations from March to June and September to December in 1985 and from January to March and June to August in 1986.

CHAPTER SIX

DISCUSSIONS

6.1 PHYTOPLANKTON PERIODICITY

Fritsch (1902,1903) carried out the earliest study of the phytoplankton of the River Thames.He sampled near Teddington Lock and found that algae were present throughout the year with diatoms forming a large percentage of the populations.Phytoplankton populations that he studied followed the cycle as follows:



During 1928-32,Rice (1938) found several members of phytoplankton which successively became dominant in the River Thames.The cycle was shown as:

January: Asterionella gracillima (Hantz.) (which would now be referred to Asterionella formosa Hass.).

February : Synura uvella Ehr.

March : Nitzschia linearis W.Sm.,Surirella ovata Kütz., Synedra ulna (Nitzsch.)Ehr.,Navicula viridula Kütz.

April : Diatoma vulgare Bory

May : Melosira varians Agardh.and green algae.

June and July : Stephanodiscus hantzschii Grun.

August-November : Melosira varians Agardh.

Mc Gill (1969) reported over 150 genera and species of algae in the River Thames.Of these twenty types were found frequently or in abundance,and could cause concern to water undertakings.She found that Cyclotella spp.and Stephanodiscus hantzschii were the dominant species in the River Thames.

Lack (1971) in his study of the River Thames in the Reading area found that centric or discoid forms were by far the most abundant diatoms found in the phytoplankton with Stephanodiscus hantzschii as the dominant species.Other centric diatoms such as S.tenuis Hust.,Melosira spp.and Cyclotella comta (Ehr.)Kütz.were recorded but never became dominant.

Since then several researchers have investigated phytoplankton populations in the River Thames and almost all of them found that algae were present throughout the year with diatoms forming a large percentage of the population (Haffner,1974;Hardy,1977;Bowles,1978;Yallop,1980).Speller

(1984) carried out taxonomic and ecological investigations of centric diatoms in the River Thames.The findings obtained in the taxonomic part of the investigation have shown that the separation of small centric diatoms into 'types' visibly different by light microscopy forms a valid basis for the study of the ecology of these diatoms.Some of the 'types' described can be referred to species of Cyclotella (e.g. C.compta (Ehrenb.)Kütz. and C.meneghiniana Kütz.).

During the present study seasonal succession or periodicity of phytoplankton populations was found although they were present in lower numbers compared with previous years.

The biomass of phytoplankton populations in terms of chlorophyll a,cell numbers and calculated algal volumes,and total particulate volumes (Figures 6.1,6.2,6.3,6.4) of the winter season was low in the River Thames and Wraysbury Reservoir.As nutrient concentrations were high during the winter,growth is limited to species that are adapted to low temperatures and low light irradiance.Only few cells (less than 10 cells per ml) of Rhodomonas minuta,Cryptomonas spp.and Stephanodiscus spp.(i.e.Stephanodiscus rotula,S.rotula var. minutula and S.hantzschii) occurred during this period.Wright (1964),Rodhe (1955),Verduin (1959),Tilzer (1972) and Maeda and Ichimura (1973);found the population of winter algae beneath ice usually is dominated by small and often motile algae such as Rhodomonas,Cryptomonas,Chlamydomonas,Dinobryon,Synura,Synedra,

Figure 6.1a Seasonal variations of chlorophyll a in the River Thames.

Dominance species are represented by the abbreviations:

S.r	Stephanodiscus rotula
S.r var.m	Stephanodiscus rotula var.minutula
S.h	Stephanodiscus ref.hantzschii
A.f	Asterionella formosa
A.g	Aulacoseira granulata
M.v	Melosira varians
N.a	Nitzschia acicularis
S.a	Scenedesmus acuminatus
S.q	Scenedesmus quadricauda
E.e	Eudorina elegans
Cry.	Cryptomonas spp.
R.m	Rhodomonas minuta
Trach.	Trachelomonas spp.

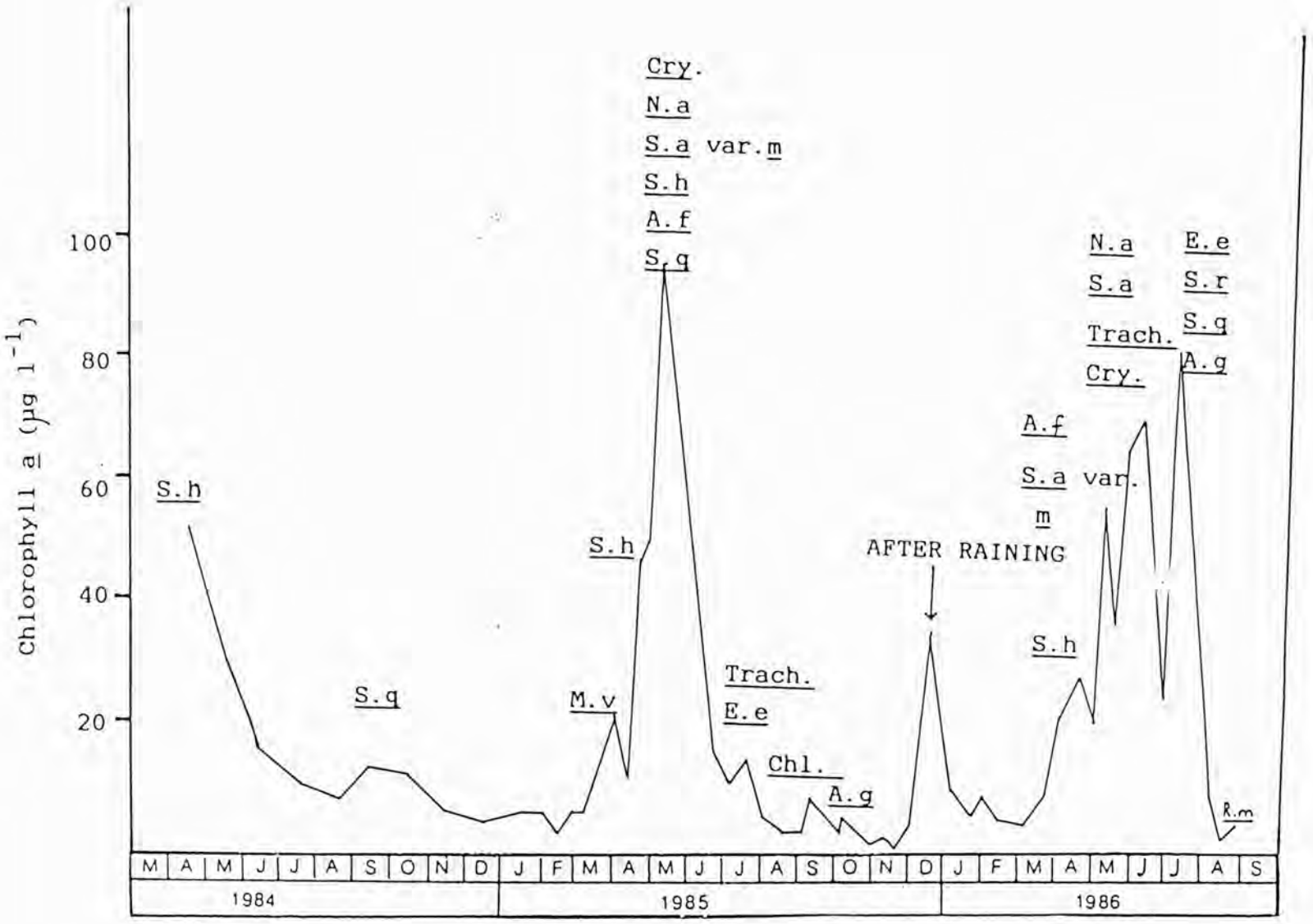

Chlorophyll a (µg l⁻¹)
100
80
60
40
20
S.h
S.q
M.v
S.h
Cry.
N.a
S.a var.m
S.h
A.f
S.q
Trach.
E.e
Chl.
A.g
AFTER RAINING
A.f
S.a var.
m
S.h
N.a
S.a
Trach.
Cry.
E.e
S.r
S.q
A.g
R.m
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 6.1a

Figure 6.1b Seasonal variations of chlorophyll *a* in the Wraysbury Reservoir.

Dominance species are represented by the abbreviations:

S.r	*Stephanodiscus rotula*
S.r var. *m*	*Stephanodiscus rotula* var. *minutula*
S.h	*Stephanodiscus* ref. *hantzschii*
A.f	*Asterionella formosa*
A.g	*Aulacoseira granulata*
M.v	*Melosira varians*
N.a	*Nitzschia acicularis*
S.a	*Scenedesmus acuminatus*
S.q	*Scenedesmus quadricauda*
E.e	*Eudorina elegans*
Cry	*Cryptomonas spp.*
R.m	*Rhodomonas minuta*
Trach.	*Trachelomonas spp.*

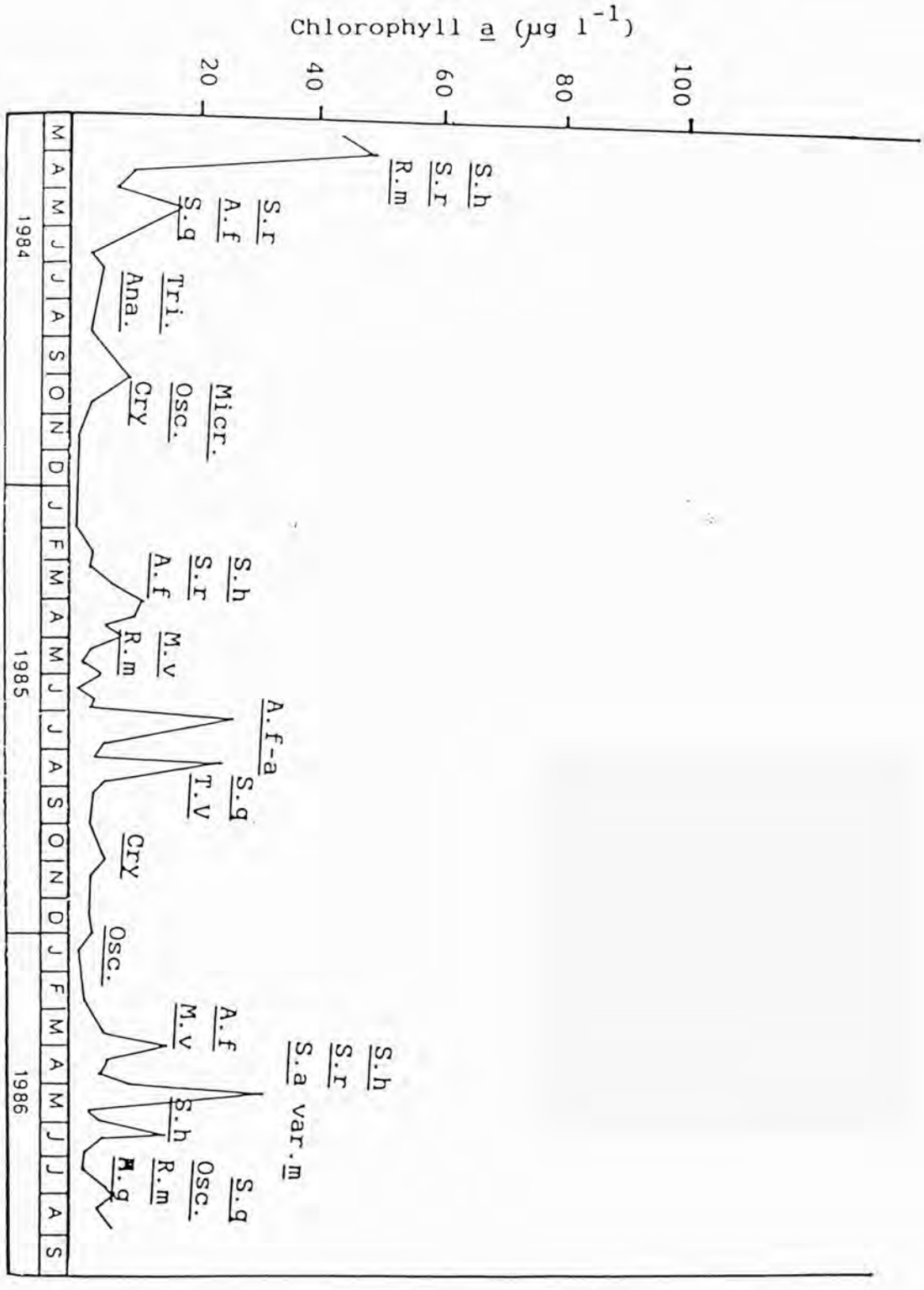

Chlorophyll a (µg l-1)
20
40
60
80
100
S.h
S.r
R.m
S.r
A.f
S.g
Tri.
Ana.
Micr.
Osc.
Cry
S.h
S.r
A.f
M.v
R.m
A.f-a
S.g
T.V
Cry
Osc.
A.f
M.v
S.h
R.m
S.g
Osc.
S.h
S.r
S.a var.m
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

Figure 6.1b

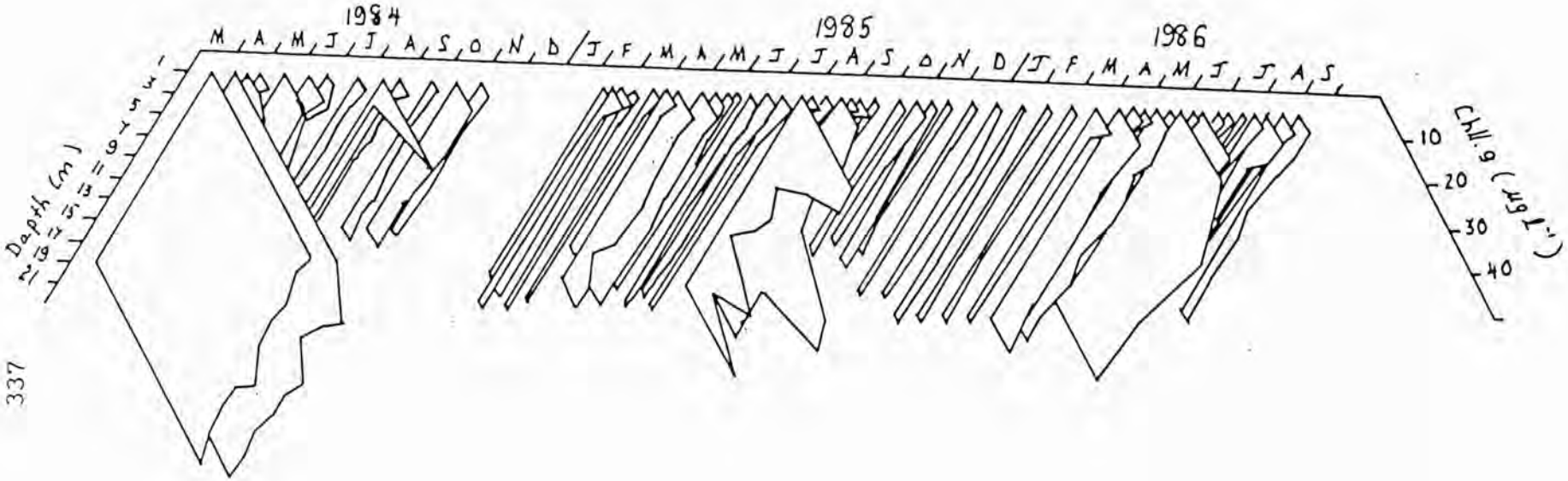


Figure 6.1c Vertical distributions of chlorophyll a in the Wraysbury Reservoir during 1984-1986.

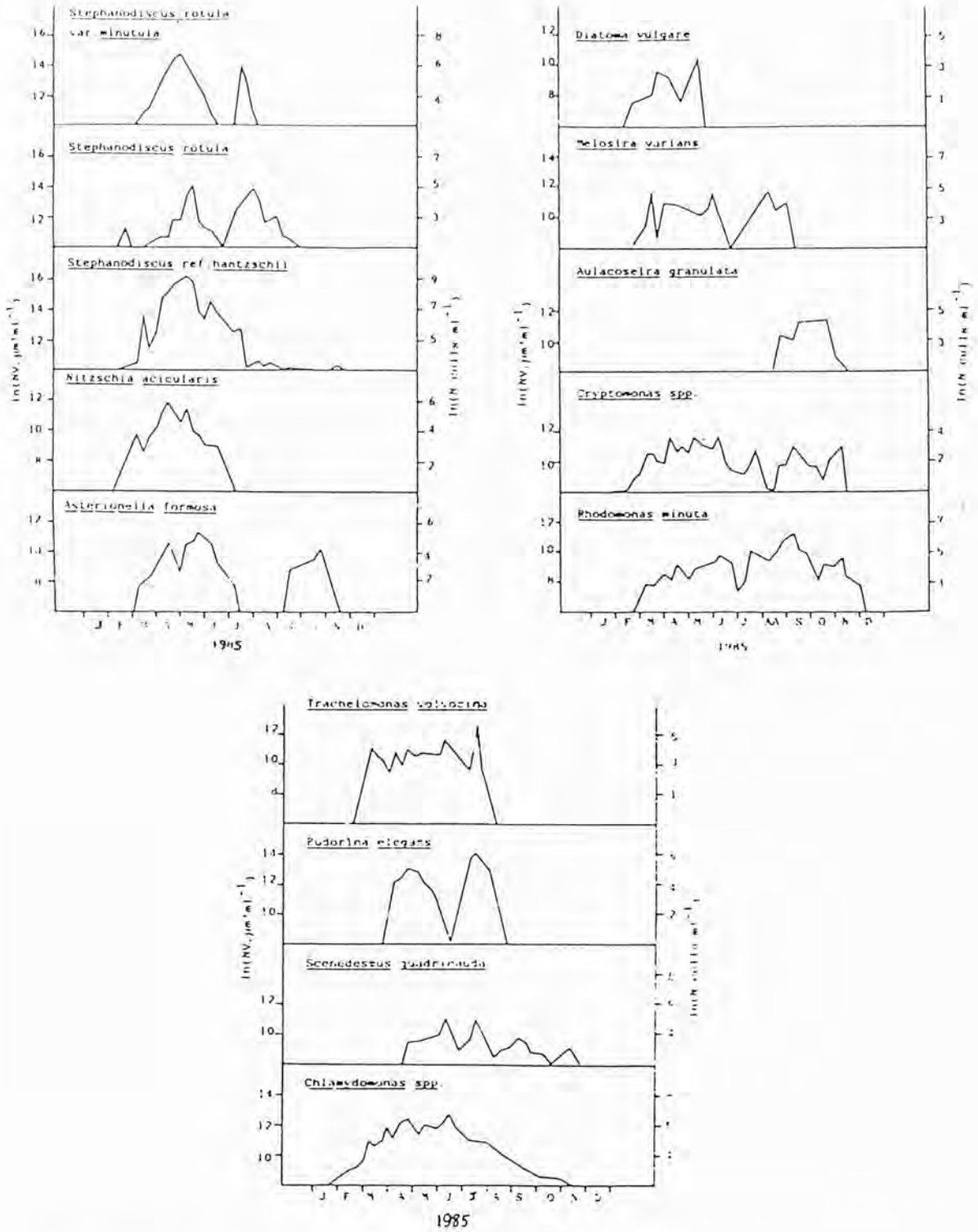
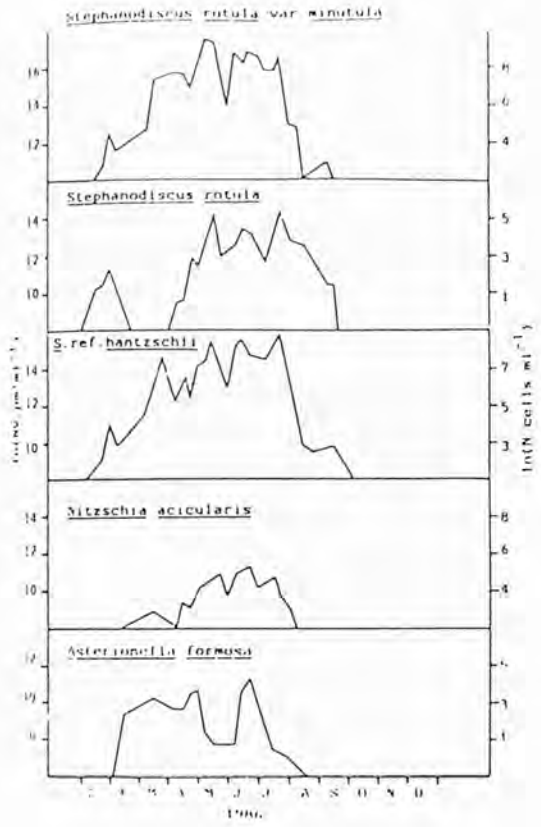
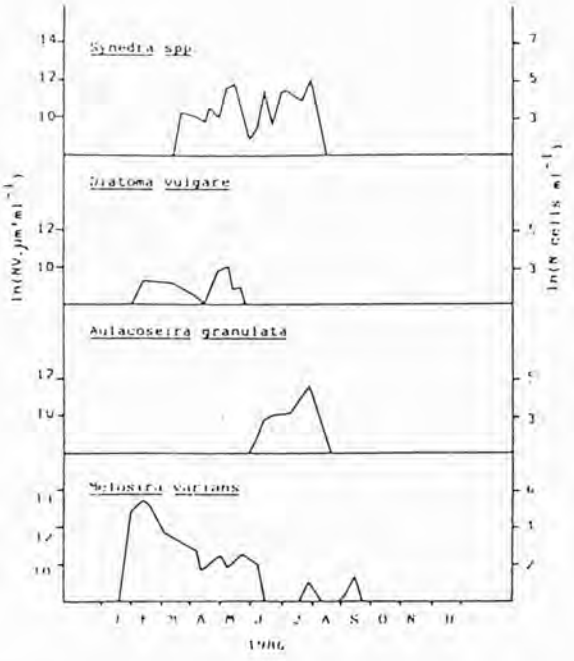
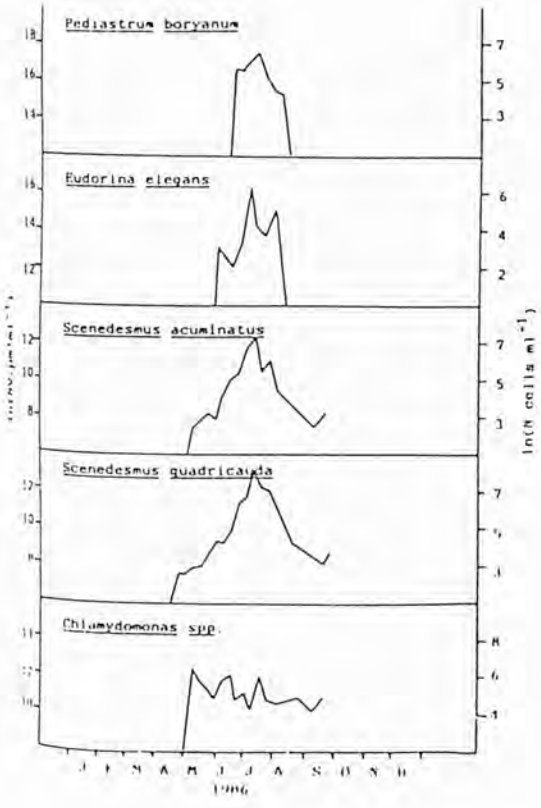


Figure 6.2a Phytoplankton populations concentrations (C.A.V. and cell number) in the River Thames during 1985.







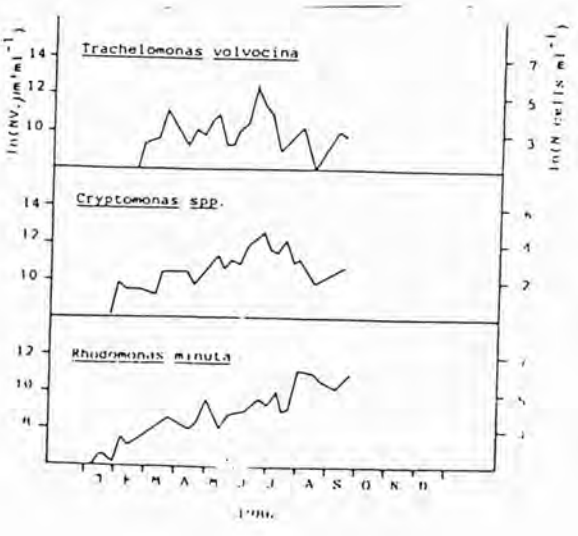


Figure 6.2b Phytoplankton populations concentrations (C.A.V and cell number) in the River Thames during 1986.

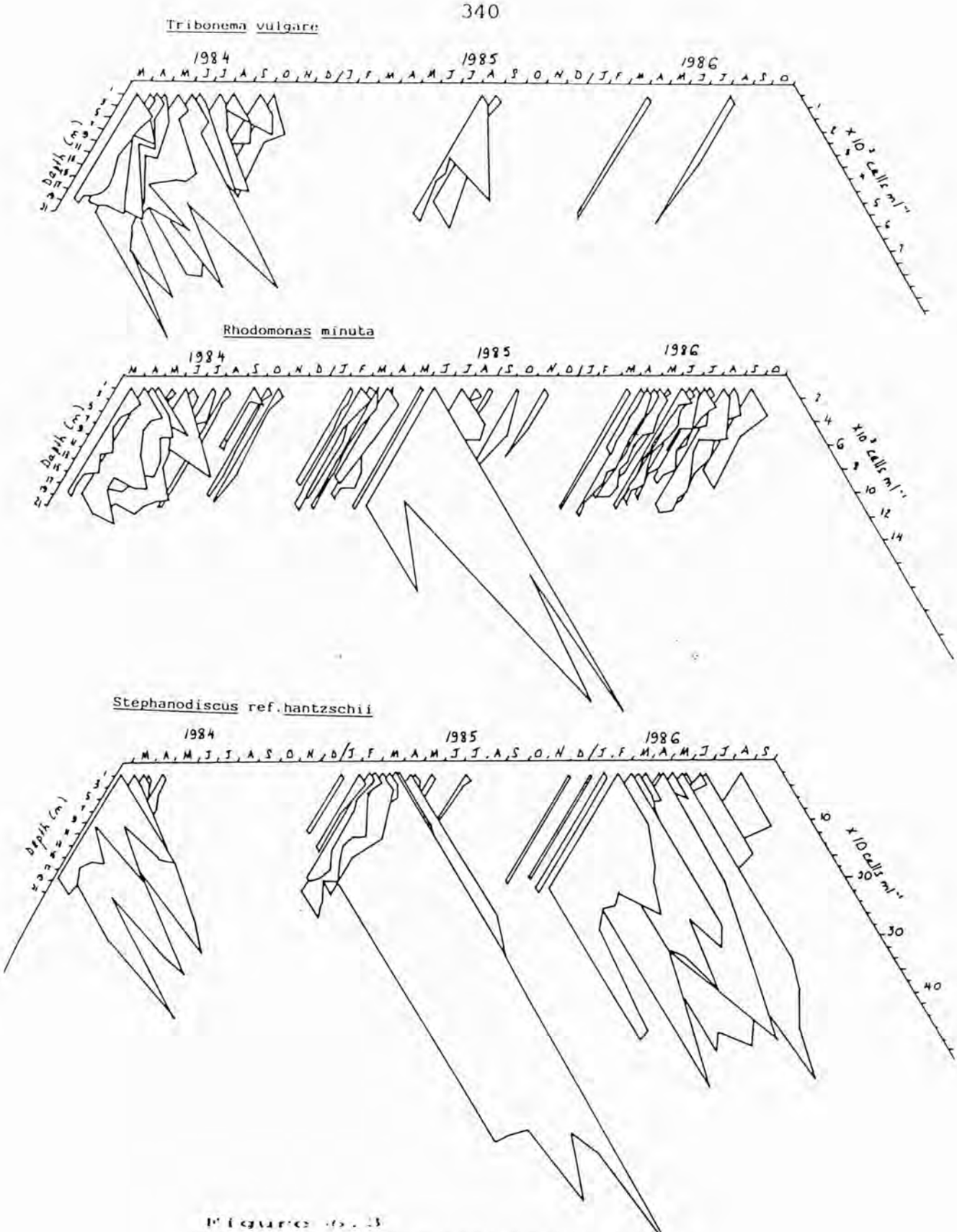


Figure 6.3
Vertical distributions of phytoplankton populations in the Wraysbury Reservoir during 1984-1986.

Tabellaria, Fragilaria and Trachelomonas.

From the study it was found that Stephanodiscus spp. (chiefly S. hantzschii) predominates spring growth in the River Thames and Wraysbury Reservoir and the same observations was found by previous workers (e.g. Hardy, 1977; Yallop, 1980).

From the culture experiments (see Chapter Three, Four and Five) it was found that Stephanodiscus ref. hantzschii has higher growth rates than other phytoplankton species which have been tested. Therefore, once light begins to increase, after mid-winter, Stephanodiscus ref. hantzschii was the phytoplankton which became dominant until nutrient limitation arises. There is little question that increasing light in the spring is the dominant factor contributing to the development of the spring "outburst", even though water temperature are still low. The relative rates (e.g. growth rates) of the dominant algae of the spring maximum during exponential growth are usually much less than those observed under "optimal" conditions of light and temperatures of cultures (Fogg, 1965). The growth rates of Stephanodiscus ref. hantzschii calculated from culture experiments (see Chapter Three, Four and Five) was about 0.40 ln day^{-1} units compared to only 0.14 ln day^{-1} units calculated from the field observations. This difference is variously attributable to restrictions of light, temperature, nutrients and losses of cells by sedimentation and other causes (Wetzel, 1975). Other diatom species that can increase their numbers during winter or early spring in the River Thames and

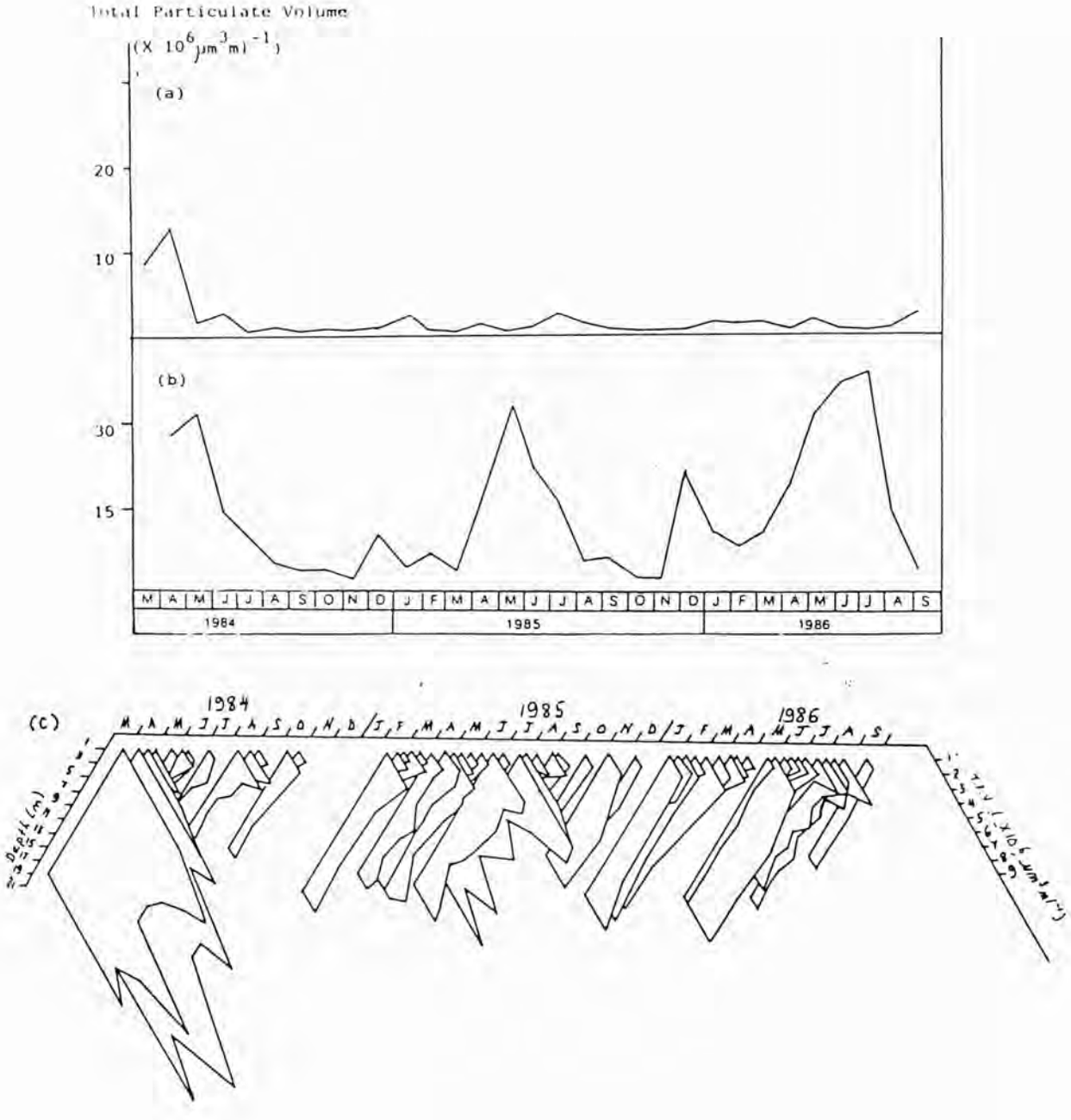
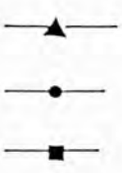


Figure 6.4 Seasonal variations of Total Particulate Volume in the (a)Wraysbury Reservoir, (b)River Thames, and (c)Vertical distributions of Total Particulate Volume in the Wraysbury Reservoir.

Figure 6.5 Effects of nitrate-nitrogen concentrations on the growth rates of phytoplankton populations.



Scenedesmus quadricauda

Ankistrodesmus falcatus

Eudorina elegans

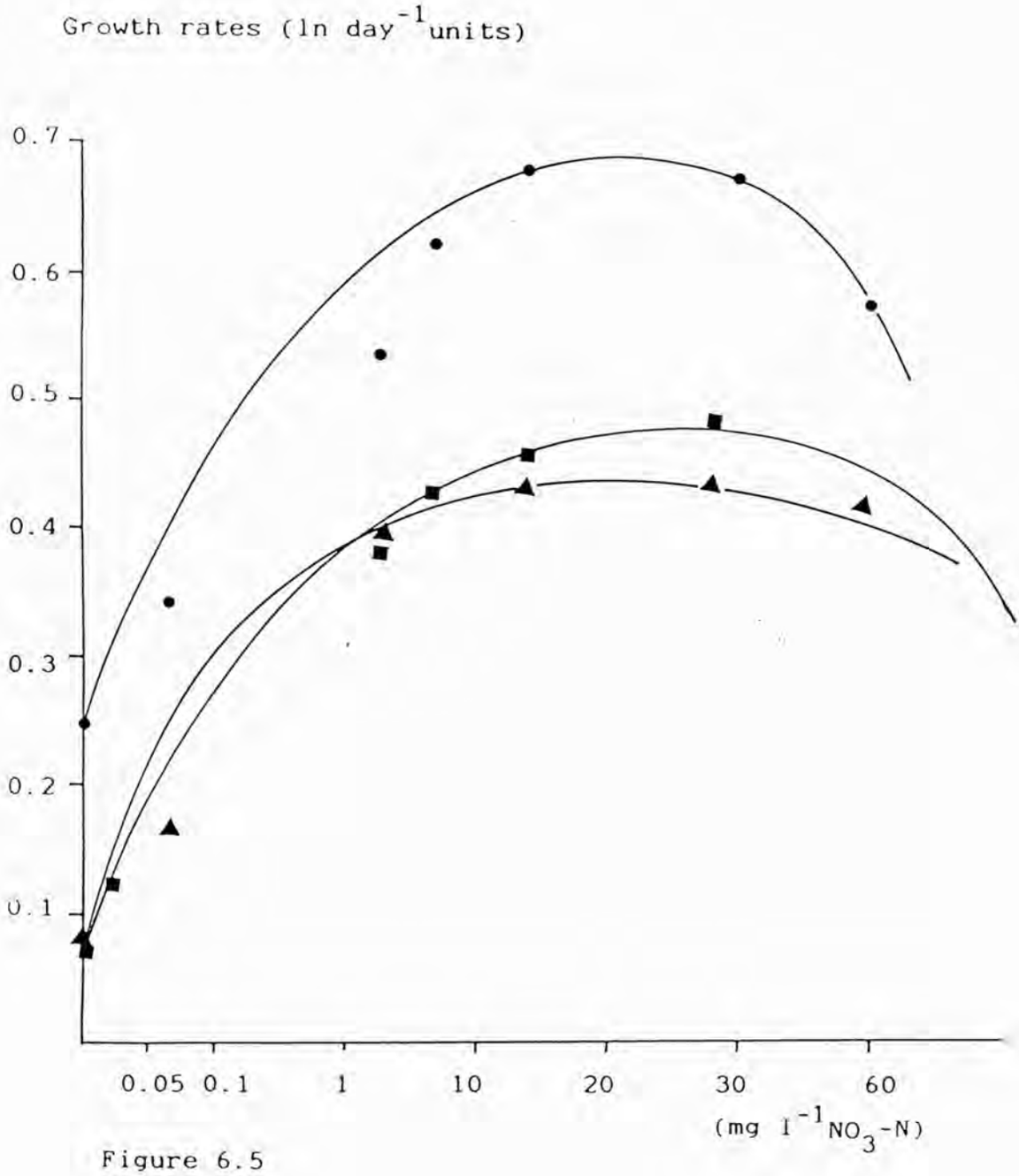

Growth rates (ln day^{-1} units)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.05 0.1 1 10 20 30 60
(mg l^{-1} NO_3-N)

Figure 6.5

Figure 6.6 Effects of phosphate-phosphorus concentrations on the growth rates of phytoplankton populations.

Stephanodiscus ref.hantzschii

Scenedesmus quadricauda

Ankistrodesmus falcatus

Eudorina elegans

Tribonema vulgare

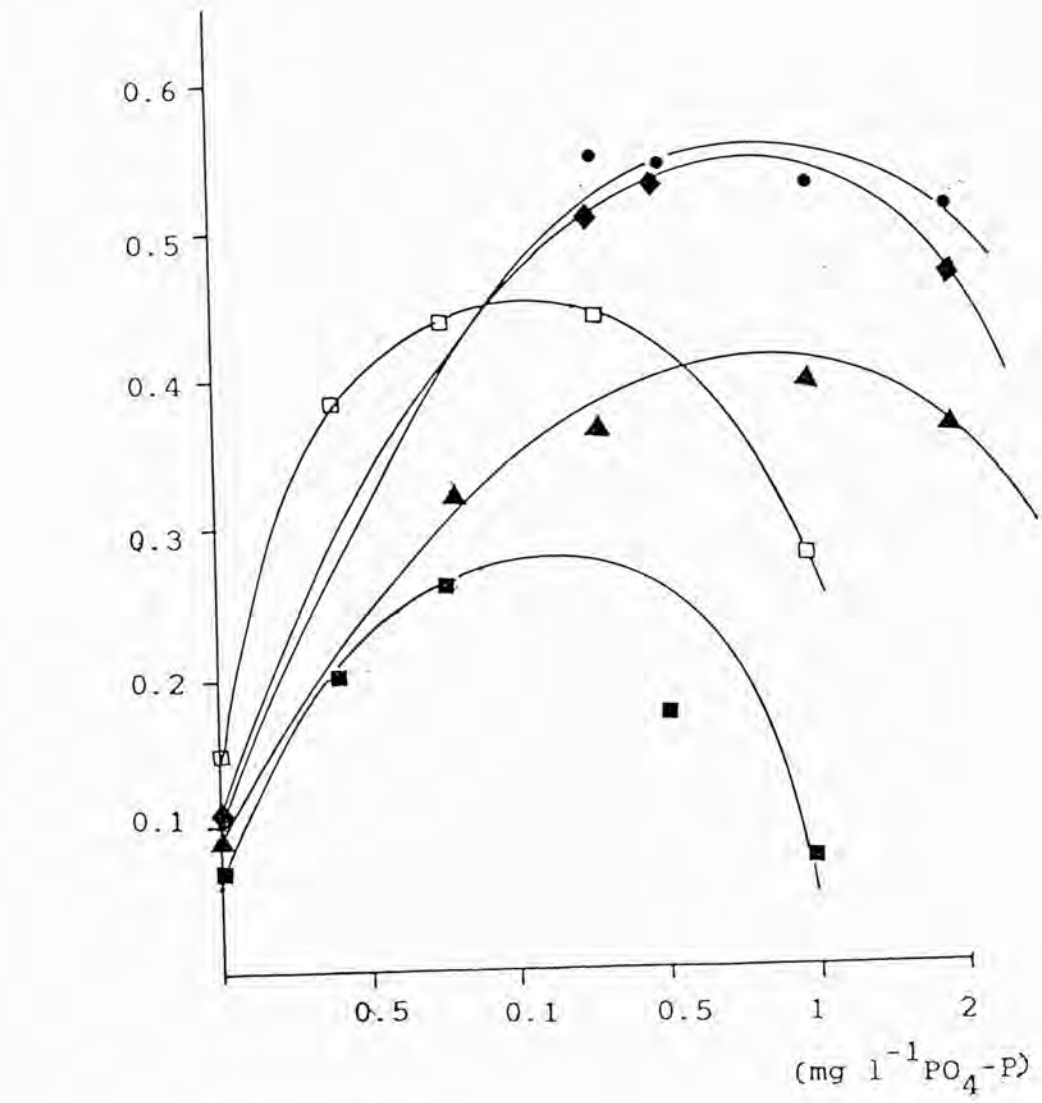

Growth rates (ln day^{-1} units)
0.6
0.5
0.4
0.3
0.2
0.1
0.5
0.1
0.5
1
2
(mg l^{-1} PO_4-P)

Figure 6.6

Figure 6.7 Effects of silica concentrations on the growth rates of phytoplankton populations.

Stephanodiscus ref. hantzschii

Scenedesmus quadricauda

Ankistrodesmus falcatus

Eudorina elegans

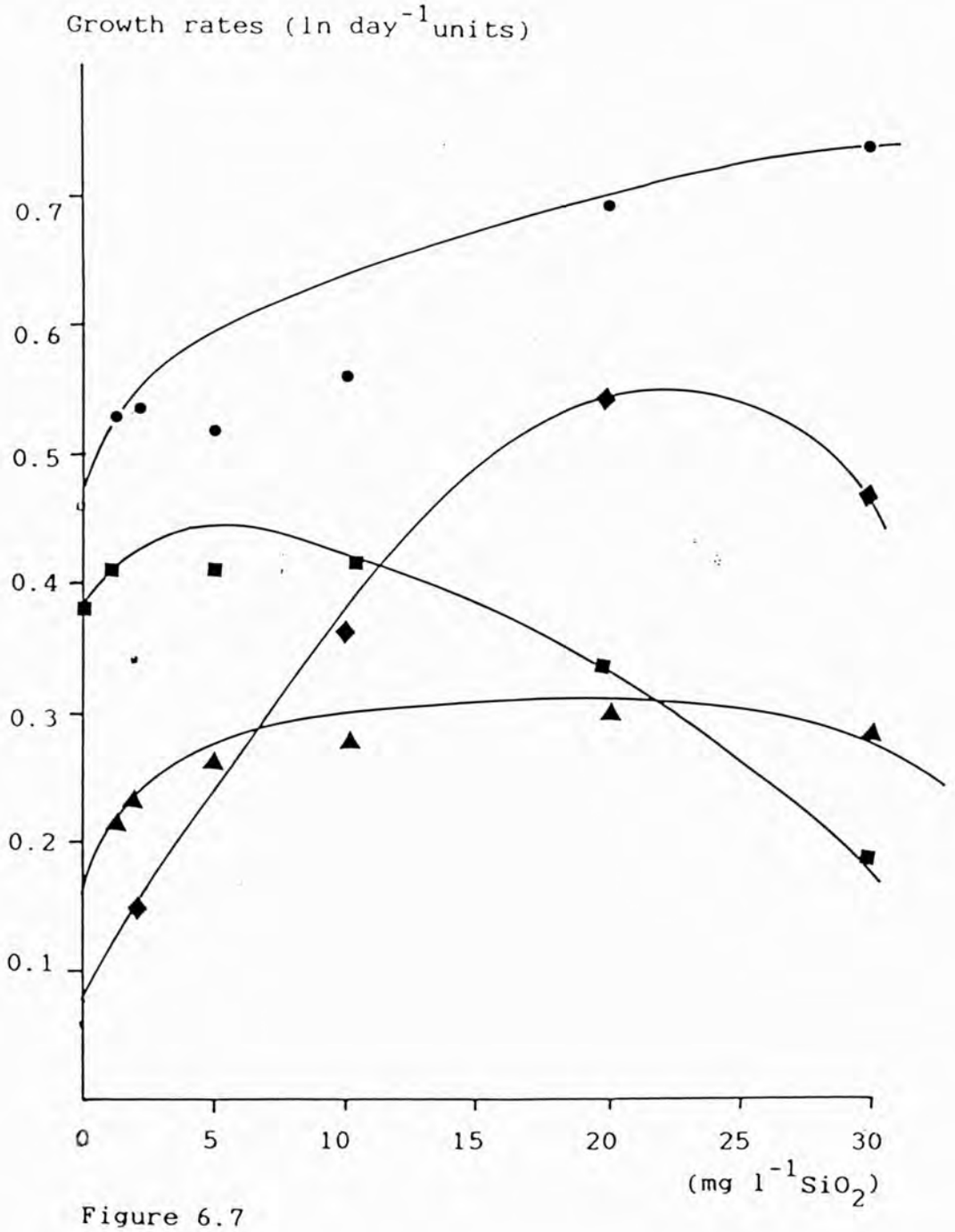

Growth rates (ln day^{-1} units)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
5
10
15
20
25
30
(mg l^{-1} SiO_2)

Figure 6.7

Wraysbury Reservoir were Nitzschia acicularis,Nitzschia sigmoidea,Asterionella formosa,Melosira varians (they occurred at fewer than 10 cells per ml as did Stephanodiscus ref. hantzschii at that time).Stephanodiscus ref.hantzschii, however,then grew most rapidly and became the dominant diatom in the river.Present knowledge of their precise specific environmental requirements,adaptabilities and dynamic is still poorly developed and does not permit a predictive appraisal of likely interactions.However,the literature does provided some pointers to the critical mechanisms.Since Pearsall's (1932) important observations on the phytoplankton periodicity of the English Lakes were published,many subsequent workers have tried to explain periodic change primarily in terms of specific nutrient requirements and changes in time of nutrient availability.The reason for the predominance of Stephanodiscus ref.hantzschii would seem to be it ability to utilize nutrients more efficiently at low concentrations.From culture experiments (Figures 6.5,6.6 and 6.7) by comparing the growth rates of Stephanodiscus ref.hantzschii and other phytoplankton species (Scenedesmus quadricauda,Eudorina elegans and Tribonema vulgare) it was shown that Stephanodiscus ref. hantzschii has higher growth rates at low concentrations of silica and phosphate.Application of Tilman (1977) resource-based competition theory to limiting resource-ratios provides a strong basis for selection between potential alternative dominants.The results of interalgal competition can only be

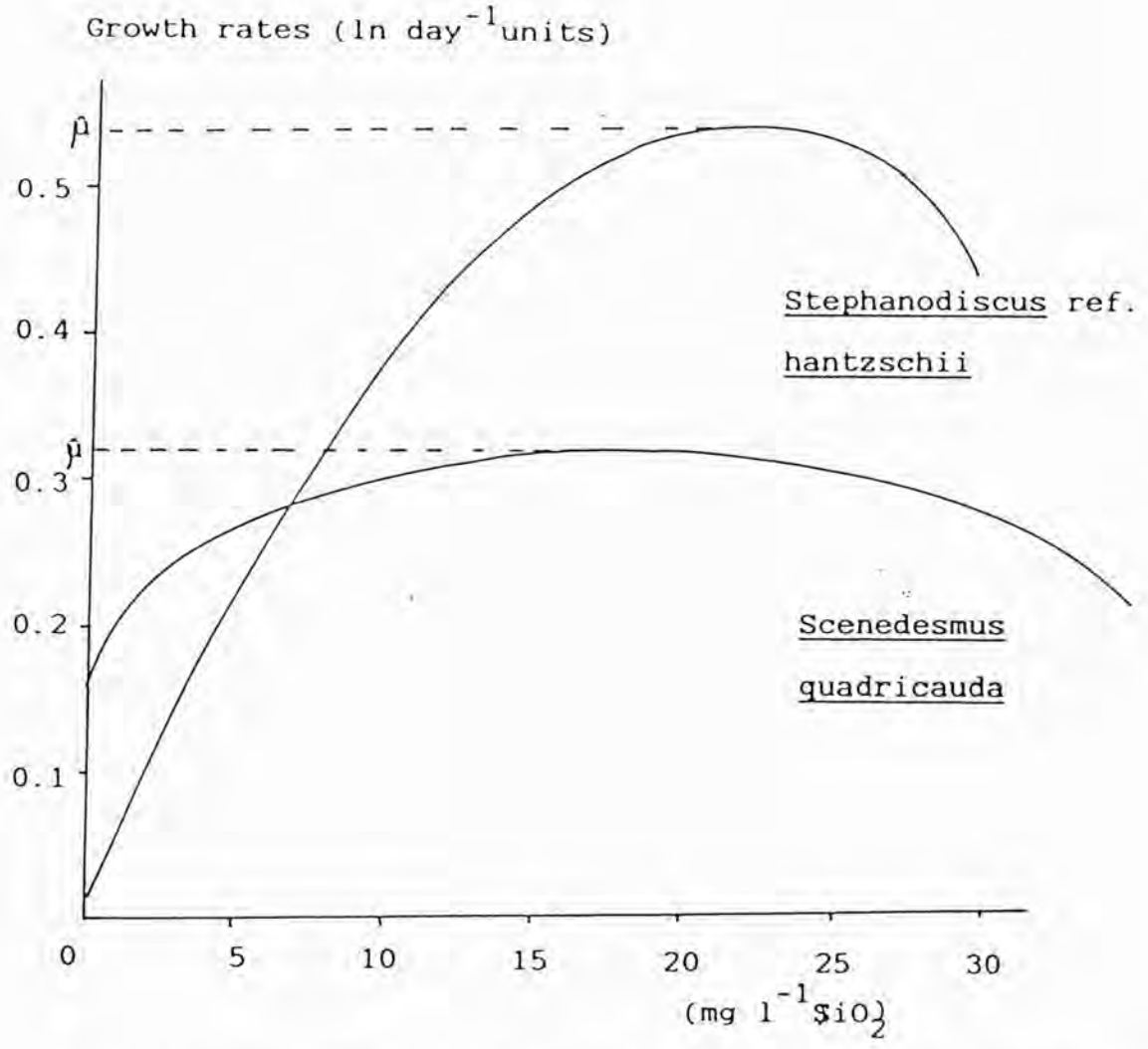


Figure 6.8 Effects of silica concentrations on the growth rates of Stephanodiscus ref.hantzschii and Scenedesmus quadricauda.

predicted if the differences in the maximum growth rate ($\hat{\mu}$) or Ks(half saturation constant,i.e.,the substrate concentration at which half the maximum growth rate occurs) are large and constant and the same factor remains limiting.From Figure 6.8; by comparing the maximum growth rate ($\hat{\mu}$) and half saturation constant (Ks) between Scenedesmus quadricauda ($\hat{\mu}$=0.32 ln day^{-1}units,Ks=0.4 mg $l^{-1}SiO_2$) and Stephanodiscus ref. hantzschii ($\hat{\mu}$=0.54 ln day^{-1}units,Ks=6.9 mg $l^{-1}SiO_2$);it was found that Scenedesmus quadricauda become dominant when low concentrations of silica.However,when silica concentrations increased about 7 mg l^{-1},Stephanodiscus ref.hantzschii starts to be dominant.

Ankistrodesmus falcatus showed higher growth rates at higher concentrations of nitrate-nitrogen,phosphate-phosphorus and silica (Figures 6.5,6.6,6.7).This showed that Ankistrodesmus falcatus requires high concentrations of nutrients for growth.This may explain the reason why Ankistrodesmus falcatus was found only occasionally in the River Thames.

Eudorina elegans showed lower requirements for nutrients (Figures 6.5,6.6,6.7).This may explain the reason why Eudorina elegans only found in the River Thames during the summer when nutrient concentrations was low.Higher light and temperature requirements of Eudorina elegans (see Chapter Four and Five) also could explain the occurrence of this species during the summer.

Centric diatoms other than those referred to Stephanodiscus ref.hantzschii were present in lower numbers during spring growth.These included Stephanodiscus rotula and smaller diameter cells which have been referred to Stephanodiscus rotula var.minutula as well as several unidentified species of smaller centric diatoms.

Previous investigator (Haffner,1974;Hardy,1977; Yallop,1980) have shown that the phytoplankton which flourish under river conditions generally did not produce extensive growth when river water was impounded.In this case Stephanodiscus ref.hantzschii ,dominant during the spring growth in the River Thames was not an important growing component of the reservoir plankton.This generalization was true during investigations in 1984 when Stephanodiscus rotula was dominant in the Wraysbury Reservoir.In 1984;when the investigation started on 2nd.April;Stephanodiscus rotula was dominant and reached a maximum number of 1051 cells per ml. However,during 1985 and 1986 Stephanodiscus rotula was reduced drastically to fewer than 30 cells per ml.

Other diatoms including Asterionella formosa, Nitzschia acicularis and several unidentified species of small centric diatoms were present in low numbers between March and April in the Wraysbury Reservoir.In the River Thames,the pennate diatoms of April included Nitzschia acicularis (which reached a maximum of about 500 cells per ml (April,1985)) and Navicula viridula,Nitzschia sigmoidea and Synedra spp. which

did not exceed 200 cells per ml during the period of this study. No marked autumnal growth of centric or pennate diatoms took place as recorded by Lack (1971) and Hardy (1977).

Melosira varians was represented by fewer than 200 cells per ml during March, April, May and June (1984 and 1985). However, during January and February (1986); it reached a maximum of 446 cells per ml in the River Thames. Aulacoseira granulata occurred during June to August (1986) in the River Thames but did not exceed 100 cells per ml. In the Wraysbury Reservoir; Melosira varians, Aulacoseira granulata and Aulacoseira granulata var. angustissima were recorded in low numbers (fewer than 200 cells per ml). However, as in the River Thames, they grow in different season. Melosira varians grew during the spring (March to April) whereas Aulacoseira granulata and Aulacoseira granulata var. angustissima grew during the late summer and autumn (August to November). This may have been due to light as temperature and nutrient requirements for both species were different. Melosira varians grew in low light and at a lower temperature with high nutrient concentrations in the spring compared to high light, high temperature and low nutrient concentrations during the late summer.

Asterionella formosa was present in low numbers between February to June in the River Thames. The maximum number of cells was 172(26 colonies) on 24th. June, 1986 with both large and small forms represented. In contrast Fritsch and

Rice recorded the winter appearance of Asterionella formosa. Lack (1971) found this genus was almost absent during his study.

Rhodomonas minuta could be found throughout most of the year with maximum numbers reaching 515 cells per ml on 29th.July,1986 in the River Thames and 1669 cells per ml on 4th.June,1986 in the Wraysbury Reservoir.

Cryptomonas spp. did not exceed 100 cells per ml during the study in the River Thames and the Wraysbury Reservoir.

Among Euglenophyceae,Trachelomonas volvocina was recorded during March,April,May,June and July with maximum number of 308 cells per ml in the River Thames.

The decline of the spring maximum of phytoplankton in temperate lakes is associated with an interaction of physical and biotic parameters.It is clear that reduction of nutrients in the photic zone of the epilimnion slows the growth of populations of the dominant as well as the rarer algae.Since diatoms are the dominant component of the phytoplankton and the spring maximum,after excessive growth, silica availability is a prime factor for suppression of growth.The reduction of silica concentrations to limiting levels (1 mg l^{-1}) occurred when Stephanodiscus ref.hantzschii reached a maximum number in 1984 in the River Thames (Figure 3.37).So distinct is the correlation between the observed decline of the diatom maximum with declining silica

concentrations and the experimental results from bioassays, that the relationship appears to be predominantly causal. Factors, such as of light intensity, temperature, nitrogen, phosphorus, zooplankton grazing and fungal parasitism do not appear to be instrumental in the decline. However, much more complex interactions of both physico-chemical and biotic factors undoubtedly exist in the seasonal succession of diatom populations when silica concentrations are not reduced to limiting levels for exponential growth.

As nutrient concentrations were reduced in the River Thames and the Wraysbury Reservoir, the diatom populations were succeeded by green algae (Chlorophyta). However, this occurred only for a short period during July when the concentrations of Chlorophyceae exceeded the Bacillariophyceae(69% Chlorophyceae and 16% Bacillariophyceae).

Members of the Chlorophyceae could be found during the summer. Scenedesmus quadricauda reached a maximum of 2804 cells (700 colonies) per ml on 8th. July, 1986 in the River Thames. In the Wraysbury Reservoir Scenedesmus quadricauda was found in low numbers (i.e. fewer than 40 cells (10 colonies) per ml. Scenedesmus acuminatus, reached a maximum of 1456 cells (268 colonies) per ml on 8th. July, 1986 in the River Thames. Pediastrum boryanum, Eudorina elegans and Actinastrum hantzschii appeared in quite high numbers during the periods of study (maximum number of 596 cells (44 colonies) per ml; 410 colonies per ml; 345 cells per ml; respectively). Chlamydomonas

spp.could be found throughout most of the year with a maximum number of 2,240 cells per ml on 5th.June,1985 in the River Thames.

Cyanobacteria (blue-green algae),Anabaena spp., Oscillatoria ref.agardhii were found occasionally in the River Thames during the autumn but in low numbers.Hardy (1977) found Anabaena flos-aquae and Aphanizomenon flos-aquae appeared only sporadically in the Thames and the counts did not indicate that rapid growth took place.Whereas Fritsch in 1902 recorded that only Microcystis progenita Raben. and M.marginata (Men.) Kirch. were present.However,in the Wraysbury Reservoir; Aphanizomenon flos-aquae,Oscillatoria spp.,Anabaena circinalis and Anabaena flos-aquae were found during the summer.Anabaena spp. reached a maximum number of 24,078 cells (291 filaments) per ml on 9th.July,1985.Whereas Aphanizomenon flos-aquae reached a maximum of 2,600 cells (36 filaments) on 22th.July, 1986 and Oscillatoria spp. reached a maximum of 1,210 cells (30 filaments) on 1th.October,1984.

Xanthophyceae,Tribonema vulgare was found throughout the year during 1984 in the Wraysbury Reservoir and reached a maximum number of 300 cells per ml on June 4th.However,in 1985 and 1986 it was present as fewer than 100 cells per ml between August and October.

The factors which influence species succession or periodicity can be grouped into three principle categories: allogenic,autogenic and sequential factors (Smayda,1980).

Allogenic factors are those environmental conditions over which the organisms have no direct control.Specific allogenic factors include: salinity (especially in the sea),temperature, light,turbulence and anthropogenic substances.Whereas autogenic factors are those environmental conditions which can be regulated to a significant degree by the phytoplankton themselves,or by other trophic levels.Specific autogenic factors include life cycle,nutrients,water quality,ectocrines and predation.It is apparent from these groupings that allogenic factors tend to represent physical environmental conditions,whereas autogenic factors represent biological processes and/or the environmental consequences of biological activity.However,allogenic and autogenic factors are not mutually exclusive since certain factors overlap these categories.For example,phytoplankton population density clearly influences the intensity and distribution of light within the water column,and light quality is further modified through the excretion of dissolved organic matter and soluble pigment residues liberated during grazing.

Introductions and translocation of populations by hydrographic disturbances,and the environmental modifications accompanying such disruptions,represent the principal sequential factor.

The fluctuations in the dominance of the phytoplankton,summarized in Figure 6.2 and 6.3 were amplified by the changes in the prominent species during the same

period, presented in Figures 6.1a and b. The data were based upon the concentrations of live, vegetative cells (number of cells per ml; $N_i ml^{-1}$), determined in the 1 metre column samples in the River Thames and from the mean of 21 metres column in the Wraysbury Reservoir. To afford comparability of specific crop sizes, they were plotted on identical natural logarithmic scales of specific cell volume ($N_i V_i$, where V_i is an approximation of mean individual cell volume of the given species).

6.2 ALGAL PIGMENTS

Phytoplankton growth can be estimated approximately but easily on the basis of chlorophyll a measurements. The results of measurements from 1984 to 1986 in the River Thames and Wraysbury Reservoir samples are given in Figure 6.1. Besides chlorophyll a, total solar radiation and temperature have been plotted. During the growimg season in all years, the chlorophyll a concentration reached >100 $\mu g\ l^{-1}$, with a maximum of 144 $\mu g\ l^{-1}$ in the River Thames. The concentration of chlorophyll a in the River Thames varied greatly during the period of observation. In general the lowest values were found during the winter months. Peaks of chlorophyll a concentration were found in spring, summer and autumn. The concentration of chlorophyll a reached 32 $\mu g\ l^{-1}$ (March, 1985) and 56 $\mu g\ l^{-1}$ (March, 1986) and then dropped to a level of 15 $\mu g\ l^{-1}$ and 30 $\mu g\ l^{-1}$ (1985 and 1986, respectively) two weeks later. There then followed a steady increase in concentration to a peak of 144 $\mu g\ l^{-1}$ on June, 1985 and of 128 $\mu g\ l^{-1}$ on July, 1986. A sudden decrease in concentration again occurred with the concentration drop to less than 4 $\mu g\ l^{-1}$, until August, when an increase resulted in a small peak of 12 $\mu g\ l^{-1}$. The concentration again decreased to its winter level except during December, 1985 a sudden increase in chlorophyll a concentration occurred. This might have been due to increasing rainfall which might have washed out benthic and epiphytic algae into the river.

The concentration of chlorophyll a in the Wraysbury Reservoir varied more or less in the same way as in the River Thames with generally the lowest values during the winter months and the peak values during spring, summer and autumn. However, the concentration of chlorophyll a was much lower than in the River Thames. The highest concentration of chlorophyll a in the Wraysbury Reservoir was only 48.1 $\mu g\ l^{-1}$ on 2nd. April, 1984 and did not exceed 25 $\mu g\ l^{-1}$ during 1985 and 1986. The lowest value of 0.5 $\mu g\ l^{-1}$ was found on 21st. January, 1986.

The comparison of the curves for chlorophyll a, temperature and radiation primarily shows a clear correlation between phytoplankton and intensity of irradiance and temperature. This result is comparable with the situation in the River Ruhr, a eutrophic, impounded tributary of the Lower Rhine (Musch, 1978) and in the River Rhine itself (Friedrich and Viehweg, 1984). A direct correlation between chlorophyll a concentration and the abiotic conditions (light and temperature) showed, that in general the growth of phytoplankton in the River Thames and the Wraysbury Reservoir were limited by light and temperature.

In the River Thames seasonal variations in chlorophyll a concentration closely followed the changes in cell numbers (Lack, 1971). This situation was also found during this study.

The spring peak of chlorophyll a was coincident with the spring bloom of phytoplankton, the highest concentration of

chlorophyll a occurring just after a cell density of 11,129 cells per ml in the River Thames and 2,305 cells per ml in the Wraysbury Reservoir (Figure 6.1).The peak of chlorophyll a in mid-summer was due to the bloom of diatoms and Chlorophyceae and again the peak occurred just after the maximum cell density.

6.3 TOTAL PARTICULATE VOLUME

Estimates of Total Particulate Volume determined with the Coulter Counter (Figures 6.4a and b) also showed the the lowest values during the winter months and peak values during spring,summer and autumn.Results obtained represent the the total seston present but as described earlier (see Chapter Two) during periods of dense phytoplankton populations,may accurately reflect the phytoplankton biomass (Evans and Mc Gill,1970;Haffner,1974).During March,April,May,June and July there was an increase in Total Particulate Volume in the River Thames and Wraysbury Reservoir.Total Particulate Volumes in the Wraysbury Reservoir were very low compared with those in the River Thames.Maximum Total Particulate Volumes were reached in May and June and coincided with the spring algal growth peaks.

CHAPTER SEVEN

GENERAL CONCLUSIONS AND SUMMARY

Growth of phytoplankton populations in nature and in culture have been investigated over a period of more than two years with reference mainly to species derived from the River Thames and the Wraysbury Reservoir.

From the investigations it was found that seasonal succession of phytoplankton populations occurred in the River Thames and the Wraysbury Reservoir.Algae were present throughout the year in the River Thames and the Wraysbury Reservoir with diatoms (especially Stephanodiscus ref. hantzschii) forming a large percentage of the populations. These results are comparable with those found by previous investigators (e.g.Fritsch,1902,1903;Rice,1938;Lack,1971; Haffner,1974;Hardy,1977;Bowles,1978;Yallop,1980 and Speller, 1984).

In this chapter,there is an attempt to relate observations on the growth of phytoplankton populations in cultures to the periodic changes that occur in the river and reservoir (nature) by drawing together data from the various aspects of this investigation.These include environmental factors (e.g.nutrients,light,temperature) and algal bioassay.

Seasonal periodicity,or succession of phytoplankton, that is changes in species composition and dominance through

time, is strongly influenced by the comparative dynamics of net specific population increase and the length of the time periods over which they apply (Reynolds, 1984). Many factors combine to determine where and when individual species are able to grow and increase; and all are required to be simultaneously satisfied before net increases in specific standing populations can be sustained (Reynolds, 1985). Seasonal variations in the relative performances of individual species depend upon consistent interspecific differences in their environmental requirements and the extent to which they can be satisfied by a changing external environment.

The hypothesis advanced at the outset of seasonal periodicity of phytoplankton in the River Thames and Wraysbury Reservoir during this study were environmental physical and chemical variables. Of physical variables, water temperature is one of the major environmental factor that affect phytoplankton populations growth. Water temperature, thermal stability and its influence on the underwater photic conditions, exerted an overriding mechanism selecting among the capacities of individual species to grow. From the study it is possible to distinguish among species which increase relatively rapidly at low temperatures (Stephanodiscus ref. hantzschii, Stephanodiscus rotula var. minutula, Asterionella formosa) and those which are more dependent upon higher water temperature (Scenedesmus spp., Eudorina elegans, Cyanobacteria (blue-green algae), e.g. Anabaena spp.). It is also possible to

distinguish among those whose growth is tolerant of relatively low light doses (Asterionella formosa, Stephanodiscus rotula) and those whose growth apparently requires significantly higher treshold (Eudorina elegans, Scenedesmus spp.). The present attempt to relate variations in phytoplankton characteristics of the physical environment recalls comparable early investigations (Findenegg, 1947).

The chemical variables, particularly nutrients, are also one of the major environmental factors that affect phytoplankton growth in nature and in culture. The influence of nitrogen, phosphorus and silica concentrations on the growth of phytoplankton populations have been investigated. The range of concentrations used in the experiments generally includes that found in natural waters.

In the studies of the influence of nitrogen concentrations on the growth of the phytoplankton in culture as described in Chapter Three; it was found that there is an optimum range of nitrogen concentrations most suitable for the growth of each phytoplankton species. The bearing of the experimental results on the interpretation of the occurrence of planktonic organisms in nature (River Thames and Wraysbury Reservoir) is discussed in relation to the nitrogen, phosphorus and silica concentrations observed in fresh waters.

The upper limits of concentrations of nitrogen, phosphorus and silica for optimum growth (in cell numbers per ml) of the phytoplankton populations studied are always higher

than the highest concentrations occurring in the River Thames and Wraysbury Reservoir. Therefore their growth is unlikely ever to be unfavourably affected by too high concentrations of nitrogen, phosphorus and silica for all phytoplankton species which have been studied. However, studies on the effect of nutrient concentrations on the growth rates of phytoplankton showed that the upper limit of concentrations of nitrogen, phosphorus and silica are always included in the concentrations found in natural waters. Therefore culture experiments might well indicate the concentrations which will encourage the growth of phytoplankton populations in nature. This information could be very useful in the water industry. It might be possible to maintain nutrient concentrations in the river and reservoir at the appropriate levels to discourage the growth of algae from becoming a nuisance.

Management of eutrophic water-bodies requires a knowledge of algal populations. Therefore predictions of growth in existing and proposed reservoirs are very important.

Bioassay tests using Scenedesmus quadricauda and Stephanodiscus ref. hantzschii were also carried out during this study. The results showed that the River Thames and Wraysbury Reservoir waters are potentially able to support considerable growths of Scenedesmus quadricauda and Stephanodiscus ref. hantzschii throughout the year. However, comparison of the results for the River Thames and Wraysbury Reservoir waters indicate clearly that growth of Scenedesmus

quadricauda and Stephanodiscus ref.hantzschii is less in the Wraysbury Reservoir.

Studies on the responses of phytoplankton populations in the River Thames and Wraysbury Reservoir waters were also carried out.Filtered,unfiltered and enrichment with phosphorus on the River Thames and Wraysbury Reservoir samples showed that addition of phosphorus alone stimulated the growth of phytoplankton in the Wraysbury Reservoir and in the River Thames.

Bioassay tests do not allow one to make precise predictions of how much of what will grow where and when. However,they appear to provide a tool for producing a general statement on potential algal quantity and quality for any water body.

Bioassay tests which are described in this study may provide information about the types of algae which will grow in a given test-water.Such information cannot be gained from inspection of chemical analyses alone.Bioassay tests also allowed a crude assessment to be made of the amount of algal material which a water has the potential to support.However,a comparison of bioassay results with growth which actually occurred shows that the bioassay tends to exaggerate what occurs in nature,that is the algal growth potential of a water body as revealed by the test is not often realized.

Appendix Table 1

NUTRIENT CONCENTRATIONS IN THE RIVER THAMES AND THE WRAYSBURY RESERVOIR DURING 1984 TO 1986.

DATE	RIVER THAMES			WRAYSBURY RESERVOIR		
	NO_3-N	PO_4-P	SiO_2	NO_3-N	PO_4-P	SiO_2
24.10.84	7.4	0.23	9.1	4.7	0.1	12
7.11.84	8.4	0.22	10.0	5.8	0.08	7
6.12.84	11.4	0.11	11.3	5.9	0.09	12
19.12.84	11.8	0.3	12.7	6.2	0.16	14
5.2.85	11.3	0.21	13.3	7.5	0.22	16
12.2.85	11.2	0.20	12.9	7.5	0.34	16
26.2.85	11.4	0.27	12.9	7.4	0.23	16
5.3.85	9.9	0.24	10.0	3.0	0.27	12
12.3.85	8.2	0.22	8.0	4.0	0.15	15
19.3.85	9.9	0.24	10.0	3.0	0.27	15
26.3.85	8.3	0.26	9.0	1.0	0.21	16
2.4.85	8.2	0.22	12.0	4.3	0.22	12
16.4.85	5.4	0.25	12.0	2.8	0.17	12
23.4.85	6.4	0.26	5.0	3.3	0.24	10
30.4.85	6.4	0.26	14.0	1.8	0.27	12
7.5.85	3.8	0.31	9.0	3.2	0.20	9
21.5.85	7.2	0.23	10.0	2.6	0.14	9
29.5.85	7.8	0.33	12.0	3.1	0.21	9
4.6.85	6.7	0.18	14.0	1.1	0.07	8
18.6.85	6.4	0.22	12.0	1.4	0.20	12
2.7.85	6.4	0.21	12.0	0.8	0.22	10
9.7.85	5.6	0.24	12.0	2.2	0.26	10
16.7.85	6.2	0.26	10.0	4.5	0.23	9.5
30.7.85	6.9	0.18	14.0	5.6	0.20	10
6.8.85	1.8	0.17	12.0	1.3	0.19	12
13.8.85	1.9	0.18	12.0	1.7	0.11	12
20.8.85	2.2	0.16	14.0	1.6	0.09	12
28.8.85	5.6	0.15	14.0	2.2	0.13	10

Appendix Table 1 (Continued)

3.9.85	1.8	0.31	12.0	1.2	0.12	12
22.10.85	6.0	0.29	12.0	4.2	0.23	10
29.10.85	7.0	0.31	7.0	4.1	0.19	10
5.11.85	8.4	0.24	8.0	6.5	0.28	16
12.11.85	11.4	0.21	10.0	-no data available-		
19.11.85	11.2	0.21	8.8	-no data available-		
26.11.85	13.2	0.21	9.0	7.8	0.26	16
3.12.85	11.5	0.23	7.0	7.9	0.27	16
10.12.85	6.2	0.23	5.0	7.5	0.27	16
14.1.86	7.6	0.21	5.0	3.9	0.09	12
21.1.86	6.4	0.19	4.0	5.6	0.23	14
28.1.86	5.4	0.18	6.0	4.5	0.19	16
4.2.86	4.9	0.33	7.7	4.0	0.19	16
18.2.86	5.4	0.16	7.7	3.33	0.17	12
4.3.86	3.6	0.24	5.0	2.74	0.22	16
18.3.86	5.9	0.23	3.6	7.6	0.20	12
8.4.86	5.4	0.14	2.5	5.9	0.18	12
15.4.86	5.4	0.14	2.0	6.6	0.19	8
22.4.86	6.9	0.12	2.9	6.2	0.09	10
29.4.86	5.0	0.12	4.0	3.8	0.15	10
6.5.86	2.6	0.07	1.43	3.9	0.005	8
13.5.86	4.5	0.01	1.27	2.7	0.09	10
20.5.86	4.2	0.09	1.54	2.88	0.10	12
27.5.86	6.5	0.06	5.26	7.6	0.06	10
3.6.86	7.8	0.03	5.3	7.7	0.07	11
10.6.86	8.4	0.20	2.86	6.2	0.14	9
17.6.86	3.0	0.16	4.35	5.0	0.13	10
24.6.86	2.8	0.17	7.0	5.9	0.15	10
8.7.86	1.87	0.21	4.0	5.2	0.15	10
15.7.86	4.2	0.23	5.6	6.2	0.16	8
22.7.86	7.1	0.23	3.85	6.4	0.23	10
29.7.86	6.4	0.20	6.3	5.4	0.17	10
12.8.86	2.3	0.21	5.9	2.2	0.19	10
19.8.86	1.5	0.28	5.9	4.4	0.17	7
2.9.86	4.6	0.17	4.0	4.5	0.17	10
9.9.86	5.0	0.19	5.0	4.3	0.17	6

Appendix Table 2

CHLOROPHYLL a CONCENTRATIONS IN THE RIVER THAMES AND THE WRAYSBURY RESERVOIR DURING 1984 TO 1986.

DATE	RIVER THAMES (Chlorophyll a $\mu g\ l^{-1}$)	WRAYSBURY RESERVOIR (Chlorophyll a $\mu g\ l^{-1}$)
19.3.84	-	43.6
2.4.84	-	48.1
16.4.84	50	7.1
30.4.84	-	3.1
14.5.84	51	9.2
14.6.84	24	5.5
18.6.84	10	1.6
9.7.84	17	2.3
6.8.84	13	4.1
20.8.84	14	1.7
3.9.84	6	3.1
1.10.84	11	5.4
15.10.84	8	2.1
29.10.84	10	1.5
5.11.84	8	0.9
5.12.84	24	1.0
5.2.85	9	0.6
12.2.85	10	1.2
19.2.85	5	0.9
26.2.85	9	1.5
5.3.85	6	0.8
12.3.85	9	1.1
19.3.85	14	2.7
26.3.85	25	3.1
2.4.85	31	5.7
16.4.85	16	1.3
23.4.85	72	5.4

Appendix Table 2 (Continued)

30.4.85	76	2.5
4.6.85	72	2.2
11.6.85	26	0.6
2.7.85	16	1.8
9.7.85	21	12.5
16.7.85	22	1.2
30.7.85	5	0.9
6.8.85	7	1.5
13.8.85	8	4.1
20.8.85	5	11.8
28.8.85	4	2.5
3.9.85	5	1.5
17.9.85	12	2.0
22.10.85	8	1.8
29.10.85	4	1.1
5.11.85	2	0.6
3.12.85	4	1.0
10.12.85	32	-
17.12.85	54	-
14.1.86	14	1.9
21.1.86	10	0.5
28.1.86	8	0.9
4.2.86	14	0.8
18.2.86	8	1.0
4.3.86	6	1.1
18.3.86	12	3.0
8.4.86	32	7.3
15.4.86	36	2.2
22.4.86	16	2.2
29.4.86	44	1.1
6.5.86	32	4.9
13.5.86	84	0.83
20.5.86	56	15.5
27.5.86	8	0.6

Appendix Table 2 (Continued)

3.6.86	96	1.9
10.6.86	102	6.4
17.6.86	104	0.7
24.6.86	48	2.2
8.7.86	32	0.6
15.7.86	100	0.7
22.7.86	128	2.6
29.7.86	30	2.2
12.8.86	12	3.5
19.8.86	2	2.0
2.9.86	8	3.7
9.9.86	4	2.0

Appendix Table 3

RESULTS OF BIOASSAYS ON THE RIVER THAMES SAMPLES USING *Stephanodiscus hantzschii* AS TEST ORGANISM.

DATE	INOCULUM (Cells ml^{-1})	MEAN COUNT (Cells ml^{-1})		CHLOROPHYLL *a* ($\mu g\ l^{-1}$)	
		TEST	CONTROL	TEST	CONTROL
25.2.85	220	12,592	10,101	25	20
26.3.85	197	21,620	11,500	43	20
24.4.85	205	20,239	9,867	40	20
8.5.85	203	15,096	8,521	30	20
15.5.85	200	7,916	11,555	16	30
11.6.85	180	12,204	12,650	24	30
16.7.85	198	5,122	8,459	10	20
22.8.85	200	5,750	17,280	12	30
3.9.85	200	4,120	12,351	8	20
22.10.85	220	20,126	15,161	40	30
26.11.85	206	26,180	13,500	52	30
10.12.85	201	18,510	12,200	37	20
14.1.86	200	12,300	10,156	25	20
18.2.86	198	19,600	11,950	39	20
18.3.86	201	20,215	15,510	40	30
22.4.86	200	28,156	10,971	56	20
20.5.86	204	6,520	11,191	13	22
24.6.86	198	7,780	13,100	15	26
22.7.86	200	8,513	12,200	17	24
19.8.86	200	10,120	12,102	20	24

Appendix Table 4

RESULTS OF BIOASSAYS ON THE WRAYSBURY RESERVOIR SAMPLES USING *Stephanodiscus hantzschii* AS TEST ORGANISM.

DATE	INOCULUM (Cells ml^{-1})	MEAN COUNT (Cells ml^{-1})		CHLOROPHYLL a ($\mu g\ l^{-1}$)	
		TEST	CONTROL	TEST	CONTROL
25.2.85	200	16,367	10,101	30	20
26.3.85	200	26,940	11,500	50	20
24.4.85	198	12,500	9,867	20	20
8.5.85	186	6,562	8,521	10	20
15.5.85	207	3,152	11,555	10	30
11.6.85	196	8,520	12,650	20	30
16.7.85	200	9,236	8,459	20	20
22.8.85	210	4,320	17,280	10	30
3.9.85	218	26,500	12,351	50	20
22.10.85	201	35,450	15,161	70	30
26.11.85	200	41,200	13,500	80	30
10.12.85	204	44,650	12,200	90	20
14.1.86	199	27,900	10,156	60	20
18.2.86	200	35,300	11,950	70	20
18.3.86	200	48,200	15,510	100	30
22.4.86	204	15,300	10,971	30	20
20.5.86	200	8,500	11,191	17	22
22.7.86	201	5,110	12,200	10	24
19.8.86	218	11,500	12,102	23	24

Appendix Table 5

RESULTS OF BIOASSAYS ON THE RIVER THAMES SAMPLES USING *Scenedesmus quadricauda* AS TEST ORGANISM.

DATE	INOCULUM (Cells ml^{-1})	MEAN COUNT (Cells ml^{-1})		CHLOROPHYLL a ($\mu g\ l^{-1}$)	
		TEST	CONTROL	TEST	CONTROL
25.2.85	500	164,701	331,910	30	66
26.3.85	500	70,896	160,786	14	32
24.4.85	510	53,996	210,961	12	42
8.5.85	500	208,762	29,836	40	8
15.5.85	498	151,673	231,356	30	46
11.6.85	502	190,824	201,919	38	40
16.7.85	500	56,667	219,350	6	44
22.8.85	500	85,746	200,121	16	40
3.9.85	510	139,563	157,910	18	36
22.10.85	500	156,713	239,310	31	48
26.11.85	500	565,741	215,231	113	43
10.12.85	500	687,742	199,346	138	38
14.1.86	498	250,951	176,216	50	35
18.2.86	500	813,371	213,798	164	41
18.3.86	500	497,346	289,415	94	52
22.4.86	500	220,115	287,831	44	43
20.5.86	500	390,117	203,461	58	30
24.6.86	500	51,131	310,965	10	62
22.7.86	500	191,317	379,330	34	70
19.8.86	500	276,600	450,300	54	80

Appendix Table 6

RESULTS OF BIOASSAYS ON THE WRAYSBURY RESERVOIR SAMPLES USING *Scenedesmus quadricauda* AS TEST ORGANISM.

DATE	INOCULUM (Cells ml^{-1})	MEAN COUNT (Cells ml^{-1})		CHLOROPHYLL a ($\mu g\ l^{-1}$)	
		TEST	CONTROL	TEST	CONTROL
25.2.85	500	85,451	272,400	17	55
26.3.85	493	8,040	229,563	2	46
24.4.85	520	12,056	227,378	2	45
8.5.85	556	13,711	248,101	3	50
11.6.85	589	18,857	219,620	4	44
16.7.85	435	180,110	249,573	32	50
22.8.85	500	90,920	285,634	18	56
3.9.85	521	96,420	223,200	19	42
22.10.85	561	87,561	185,996	17	37
26.11.85	550	327,000	210,911	64	40
10.12.85	500	250,000	176,110	50	35
14.1.86	498	220,101	90,111	44	18
18.2.86	551	89,100	36,866	18	7
18.3.86	486	131,002	147,500	26	28
22.4.86	500	180,186	215,121	36	43
20.5.86	521	122,210	213,786	24	40
24.6.86	586	147,560	301,911	30	60
22.7.86	482	51,910	256,901	10	51
19.8.86	493	95,101	236,300	19	46

Appendix Table 7

LEGEND

GROWTH ASSESSMENTS

VG	Very Good
G	Good
M	Moderate
P	Poor

PHYTOPLANKTON

Steph	Stephanodiscus
Mel	Melosira
Ast	Asterionella
Fra	Fragilaria
Nitz	Nitzschia
Scen	Scenedesmus
Ank	Ankistrodesmus
Cry	Cryptomonas
Ana	Anabaena

Appendix Table 7

OBSERVATIONS ON 'UNTREATED' RIVER THAMES SAMPLES.

DATE	GROWTH ASSESSMENT	DOMINANT ORGANISMS	CHLOROPHYLL a ($\mu g\ l^{-1}$)
25.2.85	G	Steph, Mel, Nitz, Nav	189
26.3.85	M	Steph, Nitz, Mel,	82
24.4.85	G	Steph, Nitz, Nav, Ast	125
8.5.85	VG	Nitz, Steph, Mel, Scen	127
15.5.85	VG	Nitz, Steph, Scen	277
11.6.85	VG	Scen, Chlam, Steph	287
16.7.85	VG	Scen, Chlam, Steph, Ank	262
22.8.85	G	Scen, Chlam, Eud, Ank	221
3.9.85	G	Scen, Chlam, Ank	186
22.10.85	G	Mel, Ast	272
26.11.85	G	Cry, Steph	190
10.12.85	VG	Steph, Nitz, Scen	291
14.1.86	VG	Steph, Nav, Scen	221
18.2.86	M	Steph, Mel	192
18.3.86	G	Steph, Nitz, Fra	221
22.4.86	VG	Steph, Nav, Ast	98
20.5.86	VG	Steph, Nitz	218
24.6.86	G	Scen, Chlam, Fra, Steph	220
22.7.86	G	Scen, Steph, Ank	281
19.8.86	G	Scen, Chlam, Ank, Eud	122

Appendix Table 8

LEGEND

GROWTH ASSESSMENTS

VG	Very Good
G	Good
M	Moderate
P	Poor

PHYTOPLANKTON

Steph	Stephanodiscus
Mel	Melosira
Ast	Asterionella
Fra	Fragilaria
Nitz	Nitzschia
Scen	Scenedesmus
Ank	Ankistrodesmus
Cry	Cryptomonas
Ana	Anabaena

Appendix Table 8

OBSERVATIONS ON 'UNTREATED' WRAYSBURY RESERVOIR SAMPLES.

DATE	GROWTH ASSESSMENT	DOMINANT ORGANISMS	CHLOROPHYLL a ($\mu g\ l^{-1}$)
25.2.85	M	Nitz, Steph, Ast	42
26.3.85	M	Ast, Steph	72
24.4.85	P	Steph, Mel, Fra	12
8.5.85	G	Steph, Nitz	86
15.5.85	G	Nitz, Ast	150
11.6.85	G	Nitz, Steph	114
16.7.85	G	Steph, Mel	120
22.8.85	G	Mel, Ana	101
3.9.85	M	Steph, Nitz, Scen	92
22.10.85	M	Scen, Ank	87
26.11.85	M	Scen	65
10.12.85	M	Scen, Ank	77
14.1.86	G	Steph, Nitz, Ank	156
18.2.86	M	Nitz, Steph, Ast	42
18.3.86	G	Steph, Ast	121
22.4.86	G	Ast, Mel, Steph	154
20.5.86	VG	Steph, Cry, Scen	124
24.6.86	G	Steph, Cry, Scen	105
22.7.86	G	Ana, Mel, Steph	189
19.8.86	G	Ana, Mel, Scen	160

Appendix Table 9

THE RELATIONSHIP BETWEEN CHLOROPHYLL a AND UNDERWATER LIGHT ATTENUATION IN THE RIVER THAMES

Chll.a X	11.5	13.5	40	51	49	16	5	9	5	2
E Y	1.11	1.5	1.71	1.87	2.72	1.84	2.11	1.49	1.3	1.43

Chll.a X	30	11	11	9	32	45	88	73	7	6
E Y	1.44	1.23	1.53	1.22	2.4	3.7	2.58	4.33	2.2	1.4

$\Sigma X = 514$ $\quad \Sigma Y = 39.11$ $\quad n = 20$

$\bar{X} = 25.7$ $\quad \bar{Y} = 1.96$ $\quad XY = 1284.75$

$\Sigma X^2 = 24737.5$ $\quad \Sigma Y^2 = 90.10$

$\Sigma X^2/n = 1236.9$ $\quad \Sigma Y^2/n = 4.51$

$$m = \frac{\Sigma XY - n\bar{X}\bar{Y}}{\Sigma X^2 - n\bar{X}^2}$$

$$c = \frac{\bar{Y}\Sigma X^2 - \bar{X}\Sigma XY}{\Sigma X^2 - n\bar{X}^2}$$

$$r = \frac{\Sigma XY - n\bar{X}\bar{Y}}{[\Sigma X^2 - n\bar{X}^2]^{\frac{1}{2}}[\Sigma Y^2 - n\bar{Y}^2]^{\frac{1}{2}}}$$

$Y = 0.024x + 0.64$

$r = 0.71$

Appendix Table 10

Seasonal variations of temperatures, and total particulate volume in the River Thames and the Wraysbury Reservoir during 1984 to 1986.

DATE	RIVER THAMES		WRAYSBURY RESERVOIR	
	Temp. (°C)	T.P.V ($X\ 10^6 \mu m^3 ml^{-1}$)	Temp. (°C)	T.P.V ($X\ 10^6 \mu m^3 ml^{-1}$)
19.3.84	-	-	4.7	8.58
2.4.84	6.9	8.29	5.1	18.92
16.4.84	11.1	27.93	5.7	6.11
30.4.84	14.3	24.73	7.9	5.70
14.5.84	14.0	31.78	9.8	1.74
14.6.84	12.1	27.31	12.0	4.30
18.6.84	19.8	15.11	19.6	1.18
9.7.84	19.0	7.67	18.6	0.62
6.8.84	20.0	3.03	20.0	1.13
20.8.84	19.5	3.57	19.3	0.90
3.9.84	19.6	2.54	19.3	0.50
1.10.84	17.0	1.06	14.9	1.10
15.10.84	12.5	1.67	13.6	0.74
29.10.84	3.8	1.05	2.7	0.45
5.11.84	11.7	5.30	11.9	0.32
17.12.84	9.0	8.5	8.3	0.21
5.2.85	4.5	2.83	4.8	0.72
19.2.85	2.6	3.32	2.2	0.95
26.2.85	4.5	6.96	4.0	0.51
5.3.85	3.5	3.59	3.3	0.82
12.3.85	4.5	2.48	4.0	0.58
19.3.85	4.8	1.61	4.5	0.87
26.3.85	4.6	2.32	4.6	0.78
2.4.85	6.2	5.67	6.1	1.17
16.4.85	8.7	6.14	8.4	0.91
23.4.85	9.3	20.11	9.0	1.98
30.4.85	11.5	20.62	10.1	0.62

Appendix Table 10 (Continued)

7.5.85	11.0	27.0	10.9	0.69
21.5.85	12.8	31.8	12.5	0.58
29.5.85	16.1	13.5	13.7	0.67
4.6.85	18.4	15.3	14.7	0.6
18.6.85	15.5	13.8	15.1	0.7
25.6.85	15.9	12.1	15.5	0.67
2.7.85	18.3	3.8	16.1	2.61
9.7.85	20.7	11.9	16.9	0.77
16.7.85	19.7	19.1	17.4	3.62
30.7.85	18.1	5.9	18.1	3.19
6.8.85	16.6	5.2	17.8	0.54
13.8.85	16.7	3.1	16.7	1.66
20.8.85	17.9	3.5	17.9	0.96
28.8.85	16.8	2.2	17.4	0.72
3.9.85	16.3	3.4	17.4	0.51
17.9.85	-	-	16.9	0.49
22.10.85	11.7	1.1	15.4	0.37
29.10.85	10.4	1.2	10.2	0.21
5.11.85	8.9	1.1	8.6	0.61
26.11.85	5.5	1.7	5.2	0.3
17.12.85	9.4	3.6	8.9	0.5
14.1.86	5.9	9.0	6.7	1.9
21.1.86	7.3	6.0	6.5	1.2
28.1.86	4.1	5.6	5.3	1.2
4.2.86	3.9	5.9	5.2	1.6
18.2.86	2.5	4.1	2.8	0.97
4.3.86	3.1	5.9	1.5	1.3
18.3.86	8.2	7.2	3.9	1.2
8.4.86	6.9	7.9	6.0	1.6
15.4.86	8.3	12.8	6.1	0.9
22.4.86	9.4	15.2	6.9	0.3
29.4.86	12.5	12.8	7.5	0.3
6.5.86	12.9	31.3	9.1	0.4
13.5.86	13.6	31.6	9.9	2.6
20.5.86	14.9	11.0	11.6	2.1
27.5.86	15.3	6.6	12.3	2.0

Appendix Table 10 (Continued)

3.6.86	14.9	20.9	9.9	0.56
10.6.86	15	25.6	13.3	0.80
17.6.86	19.8	25.0	14.9	0.30
24.6.86	20.0	23.6	16.2	0.5
8.7.86	19.6	20.4	18.3	0.5
15.7.86	21	21.9	19	0.4
22.7.86	19.7	28.7	19.2	0.8
29.7.86	18.5	31.5	19.2	0.9
12.8.86	17.5	15.9	18.3	0.9
19.8.86	17	2.5	18.2	0.8
2.9.86	14.5	2.5	16.8	2.2
9.9.86	15	1.6	14	2.1

Appendix Table 11

The growth of Stephanodiscus ref.hantzschii under different relative light intensities,photoperiods and temperatures.

DAY / Temp.(°C)	0	5	7	14	21	28
	Cells ml^{-1}					
10	250	614	1,094	11,520	15,200	12,650
20	250	1176	2,697	72,402	58,688	51,021
25	250	433	910	4,105	13,493	3,205

Temp.(°C)	Growth rates (ln day^{-1} units)				
10	0	0.18	0.21	0.27	0.25	0.14
20	0	0.31	0.33	0.40	0.26	0.19
25	0	0.11	0.18	0.20	0.19	0.09

Light (Wm^{-2})	Cells ml^{-1}				
20	250	679	1,249	9,509	20,537	16,647
40	250	1,236	2,707	58,940	22,910	3,103
60	250	1,012	1,901	29,144	16,508	1,772
80	250	614	1,164	4,722	13,494	1,012

Light (Wm^{-2})	Growth rates (ln day^{-1} units)				
20	0	0.20	0.23	0.26	0.21	0.15
40	0	0.32	0.34	0.39	0.22	0.09
60	0	0.28	0.29	0.34	0.20	0.07
80	0	0.18	0.22	0.21	0.19	0.05

Appendix Table 11 (Continued)

Photoperiods		Cells ml^{-1}				
24 hr.l	250	1,680	3,828	84,210	20,200	5,011
12 hr.l:12hr.d	250	1,236	2,707	58,940	22,910	3,103
16 hr.l: 8hr.d	250	691	1,176	11,940	13,600	8,420

Photoperiods		Growth rates (ln day^{-1} units)				
24 hr.l	0	0.38	0.39	0.42	0.21	0.11
12 hr.l:12hr.d	0	0.32	0.34	0.39	0.22	0.09
16 hr.l: 8hr.d	0	0.20	0.22	0.28	0.19	0.13

Appendix Table 12

The growth of Scenedesmus quadricauda under different relative light intensities, photoperiods and temperatures.

Day / Temp. (°C)	0	5	1 7	14	21	28
	Cells ml^{-1} X 10^4					
10	0.2	0.45	0.70	4.85	20.61	10.8
20	0.2	0.86	1.97	26.8	29.4	12.71
25	0.2	1.50	4.3	62.5	48.9	26.9
Temp. (°C)	Growth rates (ln day^{-1} units)					
10	0	0.16	0.18	0.23	0.22	0.14
20	0	0.29	0.32	0.35	0.24	0.15
25	0	0.40	0.44	0.41	0.26	0.18
Light (Wm^{-2})	Cells ml^{-1} X 10^4					
20	0.2	0.47	0.82	5.1	22.6	10.9
40	0.2	0.91	2.01	27.2	30.2	13.2
60	0.2	1.62	4.6	67.7	54.5	32.3
80	0.2	2.2	7.1	97.9	73.2	50.4
Light (Wm^{-2})	Growth rates (ln day^{-1} units)					
20	0	0.17	0.20	0.23	0.23	0.14
40	0	0.30	0.33	0.35	0.24	0.15
60	0	0.48	0.51	0.44	0.27	0.20
80	0	0.42	0.45	0.42	0.28	0.18

Appendix Table 12 (Continued)

Photoperiods	Cells ml^{-1} X 10^4					
24hr.l	0.2	1.21	5.2	55.3	26.1	9.5
12hr.l:12hr.d	0.2	0.91	2.01	27.2	30.2	13.2
16hr.l: 8hr.d.	0.2	0.85	1.8	20.2	18.1	3.0

Photoperiods	Growth rates (ln day^{-1} units)					
24hr.l	0	0.36	0.47	0.40	0.23	0.14
12hr.l:12hr.d	0	0.30	0.33	0.35	0.24	0.15
16hr.l: 8hr.d	0	0.29	0.31	0.33	0.21	0.09

Appendix Table 13

The growth of Eudorina elegans under different relative light intensities, photoperiods and temperatures.

Temp. (°C) \ Day	0	5	7	14	21	28
	Cells ml^{-1}					
10	0.095	0.156	0.206	0.896	4.2	1.57
20	0.095	0.269	0.386	2.7	6.4	2.6
25	0.095	0.313	0.48	6.5	17.7	8.4

Temp. (°C)	Growth rates (ln day^{-1} units)				
10	0	0.09	0.11	0.16	0.18	0.10
20	0	0.12	0.20	0.24	0.21	0.12
25	0	0.23	0.23	0.30	0.25	0.16

Light (Wm^{-2})	Cells $ml^{-1} \times 10^4$					
20	0.098	0.13	0.14	0.395	0.43	0.22
40	0.098	0.16	0.24	2.695	2.5	1.99
60	0.098	0.2	0.32	5.3	4.9	3.9
80	0.098	0.24	0.46	3.9	2.96	1.9

Light (Wm^{-2})	Growth rates (ln day^{-1} units)					
20	0	0.06	0.05	0.10	0.07	0.03
40	0	0.1	0.13	0.24	0.15	0.11
60	0	0.18	0.22	0.26	0.16	0.11
80	0	0.14	0.17	0.28	0.19	0.13

Appendix Table 13 (Continued)

Photoperiods	Cells ml^{-1} X 10^4					
24hr.l	0.08	0.18	0.23	1.07	1.88	1.0
12hr.l:12hr.d.	0.08	0.31	0.51	1.1	2.74	1.23
16hr.l: 8hr.d.	0.08	0.38	0.68	2.59	6.9	3.5

Photoperiods	Growth rates (ln day^{-1} units)					
24hr.l	0	0.12	0.14	0.17	0.14	0.07
12hr.l:12hr.d.	0	0.2	0,25	0.18	0.16	0.09
16hr.l: 8hr.d.	0	0.27	0.29	0.24	0.20	0.11

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