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Seston Distribution and Phytoplankton Production in a New, Eutrophic Reservoir subject to Artificial Mixing.

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by
Gordon Douglas Haffner, B.Sc.

- ABSTRACT -

Phytoplankton ecology of a new, artificially mixed Thames Valley Reservoir at Wraysbury, Buckinghamshire, was investigated during the period from late 1971 to early spring 1974. Biological, chemical, and physical aspects and their inter-relationships are discussed in reference to artificial mixing. Nitrates and phosphates were never limiting, and showed little fluctuation with phytoplankton growths. Although silicate concentrations decreased during vernal and autumnal diatom pulses of Stephanodiscus astraea (Ehrenb.) Grun. ≈ Stephanodiscus rotula (Kutz.) Hendey, dissolved silica seemed to be of secondary importance in limiting rates of growth or maximum yields.

Particular emphasis was placed on the interactions of the seston, in particular the ratio of productive to non-productive particles as determined by particle frequency-size analyses using Coulter Counter Models A and B with 100 and 200 µm. diameter aperture tubes. It was found by this method that non-productive particles strongly influenced the penetration of solar radiation. Although phytoplankton innocula from the River Thames were of little ecological importance, the turbid river water did alter the under water light ecology of the reservoir by changing the ratio of productive to non-productive particles. The suspension of non-productive particles was dependent on natural and artificial turbulence. Although the direct effects of mixing were the maintenance of vertically homogeneous temperature and oxygen distributions

and at most times vertically homogeneous phytoplankton populations, it was the indirect effects of mixing, the suspension of non-productive particles from the seston of the River Thames, which limited growth rates, and interacted with temperature and solar radiation to limit production in the highly eutrophic reservoir.

SESTON DISTRIBUTION AND PHYTOPLANKTON PRODUCTION IN A NEW, EUTROPHIC RESERVOIR SUBJECT TO ARTIFICIAL MIXING

CONTENTS

- INTRODUCTION -

Turbulence can affect the size, composition, time, and duration of phytoplankton pulses. Assessing the effects of turbulence on phytoplankton populations is difficult as ecological parameters are often inter-related and inter-dependent. Lund (1954, 1955, 1966, 1971) has reported that populations of Melosira italica (Ehrenb.) Kutz. (Subspecies subarctica O. Mull.) might increase and even dominate the phytoplankton under certain turbulent conditions. Similar conclusions were made for populations of Melosira islandica O. Mull. in Great Slave Lake, Canada (Lund, 1962). Talling (1965) found similar results for populations of Melosira nyassensis var. victoriae O. Mull. in Lake Victoria, Africa, and noted that the amount of incident light and the depth of the mixed water column determined the average available illumination for a circulating cell. The relationship of vertical mixing and algal production were discussed further by Talling (1957d, 1969a, 1970) and the importance of light penetration was emphasized.

Sargent and Walker (1948) associated phytoplankton populations in marine environments with eddies, as did Ketchum (1954a). Gran and Braarud (1939), however, noticed that an increase in the diatom flora of the Bay of Fundy corresponded with the onset of stabilization of the water column, and noted the importance of the mixing depth. This concept of the mixing depth was discussed more fully by Riley (1942, 1943) who generalized that the rate of increase in a phytoplankton population was a linear function of the reciprocal thickness of the turbulent zone. Turbulence (mixing) has many positive and negative effects on algal production which are dependent on the nature and situation of the phytoplankton.

The production capability of phytoplankton is affected by the maintenance of the algal species in vertically homogeneous suspensions. Sverdrup (1953) presented a theory relating mixing depth and algal production and found that production decreased logarithmically with depth as did light intensity. Similar conclusions were formed by McGill (1969) working on Thames Valley Reservoirs. Production would occur independently of the thickness of the mixed layer if there was an uneven vertical distribution of the plankton. The first increase of the phytoplankton was not associated with stabilization, but with the seasonal increase of the compensation depth.

Combined effects of mixing and turbidity on net photosynthesis and production were discussed by Bartsch (1959), Chandler (1940, 1942a), Chandler and Weeks (1945), Cushing (1959), Roy (1955), Ryther (1956), and Verduin (1951b, 1954). Measurement of light penetration is complex (Westlake, 1965) and often relative because of a failure to quantify turbidity in absolute units. Turbidity is usually expressed as parts per million or as mg. $l.^{-1}$ although it is not a measure of the weight or volume of suspended matter, and is often confused with light scattering (Talling, 1969a).

Eddy (1934) found that turbidity exerted a marked effect upon the length and magnitude of diatom blooms. Chandler (1942b) noted that diatoms composed a greater part of the phytoplankton populations of

Lake Erie when the average turbidity was in excess of 25 p.p.m. The general influence of turbidity on primary production was discussed by Chandler (1940). Phytoplankton pulses under conditions of high turbidity tended to be of short duration with relatively low maxima. Stephanodiscus and Cyclotella growths were associated with periods of high turbidity. Periods of low turbidity were associated with phytoplankton pulses of long duration with high maxima consisting of Asterionella, Synedra, Fragellaria, Tabellaria, and Melosira. Chandler (1940) had previously noted that periods of mixing and high turbidity were coincident in Lake Erie, and that inorganic material contributed from 50% - 90% of the turbidity. Similarly, the light conditions of Lake Balatan (Entz, 1964) were determined by the suspension of inorganic material by natural mixing. Daily (1938) indicated the turbidity of Lake Michigan fluctuated, as did Javornicky (1966) working on the Slapy Reservoir.

In some instances (considered to be rare by Talling (1960)) turbidity has been directly related to phytoplankton growths (Sauberer and Ruttner, 1941) in terms of self-shading. Pearsall and Ullyot (1934) noted a relation of light penetration to the abundance of phytoplankton in Lake Windermere. Maciolek and Kennedy (1964) related turbid conditions to a spring bloom in a mountain lake. According to Chandler (1940), however, the primary effects of light penetration are antecedent to the maximum standing crop.

The relationship of light and algal production can be formulated by mathematical models (Patten, 1968). These over-simplify the problem of production ecology in that organisms can adapt to specific sets of environmental parameters. The major production-depth integrals (Sverdrup, 1953; Talling, 1957b; Vollenweider, 1965) are similar in that net production is inversely related with the vertical attenuation of radiant energy. Talling (1971) expressed the combined effects of mixing and light penetration on production by comparing the depths of the mixing and euphotic zones. In both marine and freshwater environments the ratio of mixing : euphotic depth is a primary factor governing algal production. The mixing depth and euphotic depth are often inter-related (Lund, et al., 1963). The depth of the epilimnion is usually an index of the extent to which mixing can occur against a density gradient (Mortimer, 1952; Talling, 1963). The density gradient is dependent on solar radiation and the rates of warming of the upper layers (as heat is absorbed exponentially (Happey, 1970a, -b, -c)) which are in turn influenced by the amount of material held in suspension by mixing (Gessner, 1948). Turbulence has been investigated strictly as a physical phenomenon by McEwen (1929), Hinze (1959), Bye (1965), and Bowden (1970) among others. Because of the complexity it is not wise to generalize on the net interaction of the mixing and the euphotic depths, or on the resultant effects of this interaction on algal production. The utilization of solar energy has been discussed by Clarke (1939), Juday and Schomer (1935), and Forti (1965), but no attempt was made to relate the utilization to mixing.

Reports of algal growths as a response to nutrients released to the upper layers by mixing are common in the literature, although detailed knowledge of the response is still lacking (Bozniak and Kennedy, 1968; Findenegg, 1965b; Goldman, 1960, 1965). As expressed by Lund (1972), the factors of eutrophication might be known, but there is little understanding of the interaction of these and other factors.

Talling (1969) discussed growths of Nitzschia acicularis A. Cl. and other diatoms such as Melosira, Surirella, and Stephanodiscus as being a result of increased SiO_2 concentrations in the surface layers as a consequence of mixing. Happey (1970d) noted increases in SiO_2 in the hypolimnion of Abbots Pond, Somerset, during periods of restricted mixing. Nutrients such as SiO_2, PO_4, and NH_3 have been noted by Mortimer (1941, 1942) and Pearsall and Mortimer (1939) to be released under low redox potentials which were dependent on restricted mixing. Turbulence through the water column can maintain an oxidized microzone (Steel, 1972) which can act as a barrier to nutrient recycling. Tessenow (1964, 1966) has suggested that transfer of SiO_2 from sediment to water might be rapid without deoxygenation at the mud-water interface. Lund et al. (1963) reviewed the interaction of chemical and physical conditions on the standing crop in Lake Windermere in 1947, and emphasized the importance of suppression of turbulence and the formation of the pycnocline on nutrient recycling and availability. Hutchinson (1944) examined the relationship of nutrients and phytoplankton and has made a major review of the subject (Hutchinson, 1957, 1967).

The length of algal growth periods is often related to the supply of available nutrients (Riley, 1943; Lund, 1949, 1950). Lund (1950) had found that Asterionella formosa Hass. could reach its maximum standing crop after thermal stratification in Lake Windermere. Nutrient depletion resulted in the death of dividing cells, and renewed growth was dependent on cells at depths below the thermocline where light is insufficient to stimulate divisions. Resuspension of these cells to the euphotic zone is dependent on turbulence. This concept would somewhat support Pearsall's (1923) hypothesis that the real causes of diatom periodicity are operative in cold weather, but have no causal connection with temperature.

Ridley, Cooley, and Steel (1966) and Ridley and Symons (1972) had reservations on discussing the effects of artificial turbulence on algal production in Thames Valley Reservoirs. Artificial mixing was introduced to prevent or control thermal stratification (Ridley, 1969), and to maintain homogeneous oxygen distribution throughout the depths of the reservoirs. Ridley (1964) noted that reservoirs of only 10 metres in depth would be isothermal for the majority of the year, yet a 20 metre reservoir would stratify into a three layered system of epilimnion, thermocline, and hypolimnion. Such systems are similar to those discussed by Pearsall, Gardiner and Greenshields (1946) when control of phytoplankton production was chemically (copper sulphate) oriented.

Apparent effects of vertical mixing of the water mass in Thames Valley Reservoirs were a general decrease in phytoplankton production and delays in the spring maxima. <u>Stephanodiscus</u> <u>astraea</u> (Ehrenb.) Grun. was reported by Ridley (1970) to reach maxima of 100 $\mu g. l.^{-1}$ of chlorophyll-a in standing reservoirs, whereas Steel (1972) predicts a theoretical maximum of 70 $\mu g. l.^{-1}$ of chlorophyll-a in a mixed reservoir (Queen Elizabeth II) assuming light penetration is not significantly increased.

The mechanics of thermocline control are well discussed by Cooley and Harris (1954), and Haynes (1973) presented a review of artificial mixing in North America. Lund (1970) cautioned that thermal stratification is not always undesirable from the biological point of view as thermal stratification can, in some instances, reduce standing crops. Blelham Tarn is cited as an example since algal maxima were three times as large in this lake as in Lake Windermere in the 0 - 5 metre water column. The major reason for the low Windermere maxima was the sinking of cells through the metalimnion. Predicting the effects of either a mixed or stratified condition on phytoplankton production and standing crop should be carried out with caution.

A new reservoir of the Metropolitan Water Board (M.W.B.), subject to artificial mixing, was completed in 1970 at Wraysbury, Buckinghamshire. The reservoir was designed with jet inlets (See Figure 1) to prevent (control) thermal stratification by adding water with such energy so as to maintain the reservoir in a state of vertical and horizontal circulation (Ridley and Symons, 1972). Water extracted from the River Thames at Datchet can be jetted into the reservoir with reportedly sufficient momentum to 'stir' the entire basin. The pumping mechanism is capable of delivering $4.5 \times 10^5 - 9.0 \times 10^5$ m^3 (approximately 100 - 200 million gallons) of water a day into the reservoir. There are three auxillary pumps permanently mounted on the pierhead; each is capable of pumping 7.3×10^4 m^3 of water a day, and these may be used for maintaining internal circulation when water cannot be abstracted from the River Thames due to flow regulations (Gilson, 1971). In addition to the

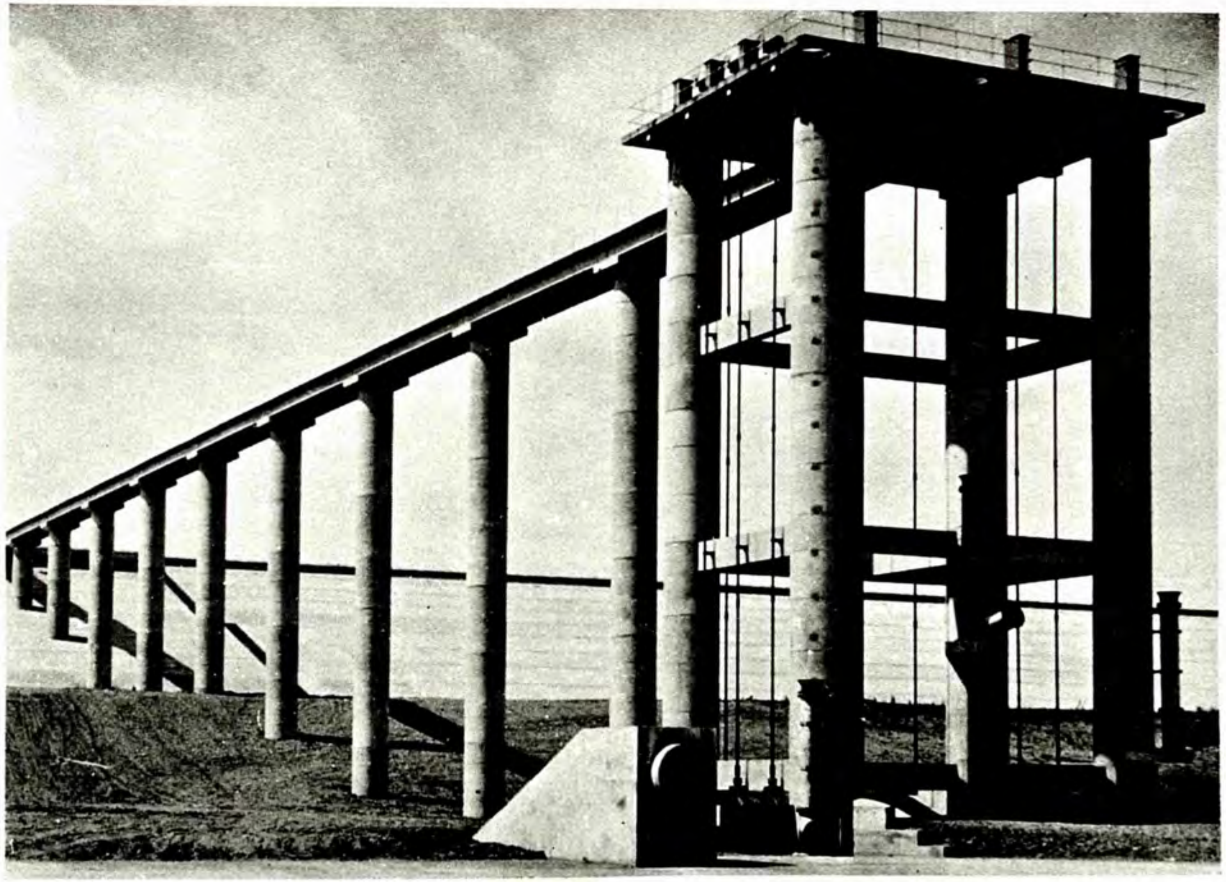


FIGURE 1. THE JET INLETS OF WRAYSBURY RESERVOIR

Reproduced with the permission of the Metropolitan Water Board jets there are two low velocity inlets used to permit sedimentation of the seston to occur at required times, without stopping the through-flow of the water. The choice of pumping mechanisms is a management decision of the M.W.B.

Wraysbury Reservoir has an approximate capacity of 3.5×10^7 m^3 at top water level (T.W.L.) of 21 metres. The water area is 2.8 km^2. The water is circulated by selective use of the jetting system which is aligned north and south of the Inlet Pier. The jets are in two sets of three, each set having jets at 45°, 22½°, and 0° inclination to the horizontal. A figure eight (Figure 2) is the theoretical circulation pattern. Wraysbury Reservoir was initially filled from King George VI Reservoir, and since March 1972 has been used as a through-flow reservoir. It is supplied directly from the River Thames. Because of usage as a supply reservoir, the water level fluctuated erratically throughout 1972 and 1973. General problems and consequences of replenishment in non-reservoir environments were discussed by Dickman (1963) and Findenegg (1965a) and have been taken into consideration in the Wraysbury system.

An investigation of phytoplankton productivity and production as a response to turbulence (artificial and natural) was initiated in October 1971 as part of a combined research project in association with the Metropolitan Water Board, Dr. J. H. Evans, and Mrs. D. Hardy. The latter researcher investigated the seasonal periodicity of nutrients and phytoplankton in the reservoir with special attention paid to the occurrence of certain algae. Intensive sampling routines involving physical and chemical analyses did not start until January 1972 and were carried through to the spring of 1974. A wide range

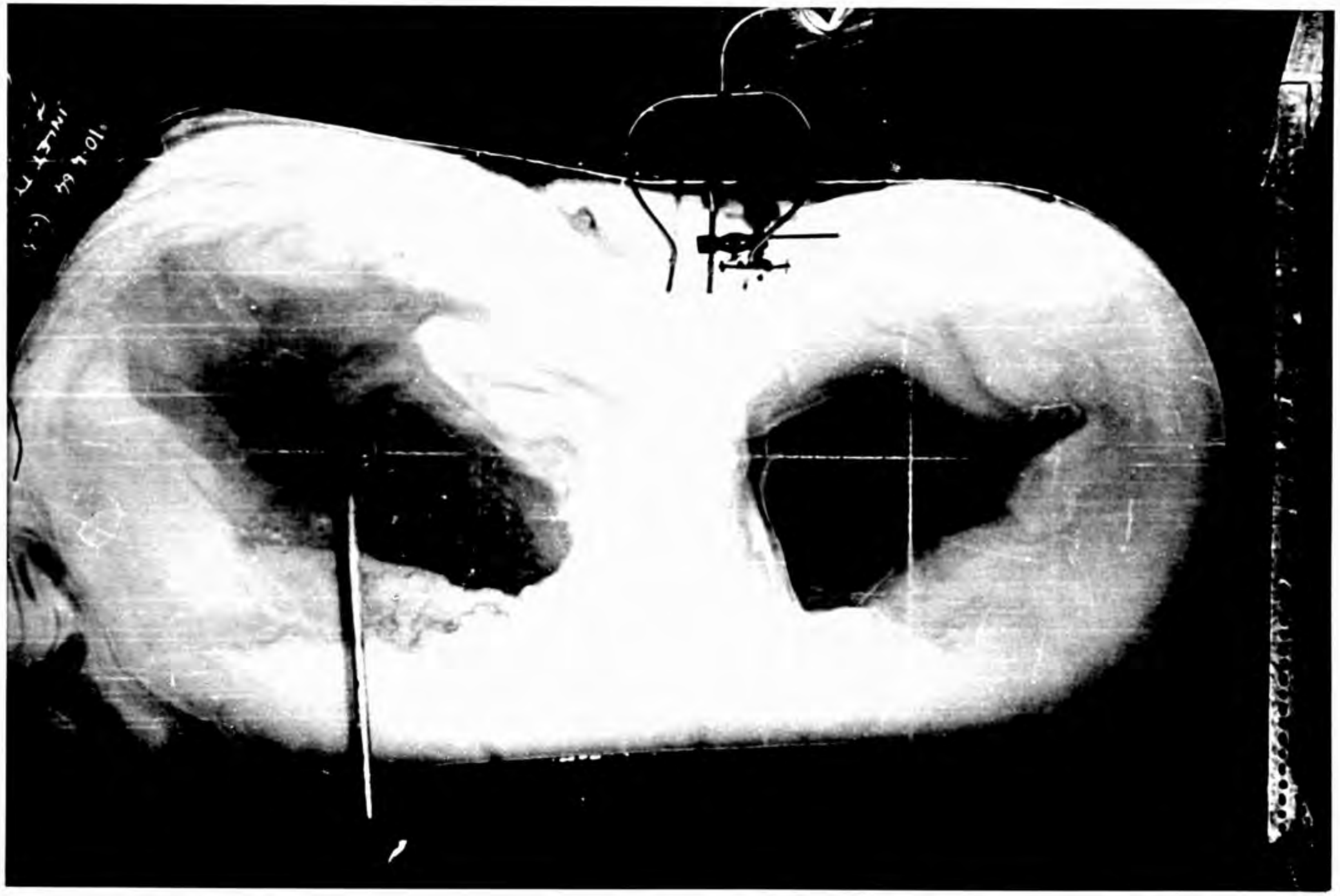


FIGURE 2. THE THEORETICAL CIRCULATION PATTERN IN WRAYSBURY RESERVOIR ON A SCALE MODEL

Reproduced with the permission of the Metropolitan Water Board of techniques were used to determine the quality, quantity and distribution of the standing crop. Dry weights, carbon, ash-free weight, chlorophyll-a, and direct counting methods were used in conjunction with particle frequency-size analyses (using a Coulter Counter) to assess algal production as a response to turbulence in a mixed supply reservoir. Work was carried out as a National Environmental Research Council research assistant in the Botany Department of Royal Holloway College, University of London, with Dr. J. H. Evans.

- METHODS -

A. Sampling Sites and Routines

A variety of sampling and experimental techniques were employed to investigate the effects of turbulence on phytoplankton production. Samples were collected twice weekly throughout 1972 and 1973 from a varying number of sampling stations on the reservoir. The first weekly collection was an intensive study of the water column at one sampling station (The Outlet Tower), and the samples were collected by the M.W.B. The second weekly collection was a more generalized survey of the reservoir by the research team of the Botany Department, using synoptic sampling methods. The depth samples were collected by a 1 litre Freidinger sampler. At least three stations (usually five) were sampled at three depths to obtain representative samples of the top, middle, and bottom of the reservoir. Physical data such as temperature and light penetration, and physico-chemical data such as dissolved oxygen were recorded during this second collection. During the summer of 1972 the synoptic sampling routines were concentrated at the Inlet Pier to determine the effects of jetting on general particle and phytoplankton distributions.

A total of nine sampling stations were used to investigate the spatial distribution of the seston in Wraysbury Reservoir. An aerial photograph (Figure 3) indicates the position of the nine stations. The major structures of the reservoir (the limnology towers, outlet

FIGURE 3. AERIAL PHOTOGRAPH OF WRAYSBURY RESERVOIR

Reproduced with the permission of the Metropolitan Water Board.

tower, and inlet pier) were specifically placed during construction for biological and engineering reasons. These structures were used as focal points for sampling. Six buoys were also set up as additional sampling stations at an early stage (March 1972) during the investigation. The buoys were sealed 230 litre drums anchored by a weight of 45 kg. and were placed with the help of the staff of the M.W.B. A detailed description of the sampling stations is given below.

1. The Inlet Pier:

This station is approximately 20 metres deep at T.W.L. Samples from this site are not expected to be representative of the reservoir as streams of river water from the jets or low velocity inlets might bias the samples. During the summer of 1972 an intensive study of the effects of jetting and resulting entrainment of water on particle distribution was carried out (Haffner and Evans, 1973). No samples were collected from this station during 1973.

2. Limnology Tower II (L II):

This station is 20 - 21 metres deep (T.W.L.), and was the most intensively sampled station during 1972 and 1973. Being in the center of the reservoir, 'piling up' problems of the wind blowing surface material across the reservoir were avoided, and this station was possibly the best vertically mixed station as it was just off the path of the theoretical circulation pattern. Light penetration, dissolved oxygen, temperature and productivity along with production experiments were localized at this station. A buoy was situated 10 metres from the tower as the precise sampling site to avoid tower influences.

3. Limnology Tower I (L I):

Located in the epicenter of the north circulation pattern, this station is 20 - 21 metres deep (T.W.L.). Although sampled occasionally in early 1972, no further observations were made at this site.

4. North West Corner:

Approximately 20 - 21 metres in depth, this station was not established until the spring of 1972 and it consisted of only an anchored buoy. To sample as nearly as possible the same water column, the boat was tied close to the buoy at all stations which were so designed. Occasionally temperature and oxygen profiles were determined here to compare with data collected at L II. This station was sampled during 1972 and 1973 at three depths only.

5. North East Corner:

This is the shallowest station at a depth of 15 - 16 metres (T.W.L.). Sampling procedure was similar to that of the North West Corner.

6. Central East Station:

Samples from this station were poorly representative of the reservoir since it is located directly opposite the Inlet Pier and is in the vicinity where the north and south circulation patterns separate (Figure 2). Approximately 20 - 21 metres deep (T.W.L.), this station was utilized only in 1972 to investigate particle distribution with respect to jetting regimes.

7. Outlet Tower:

At this, the deepest station investigated (21 - 22 metres), the water column was intensively sampled throughout 1972 and 1973. A tow rope was tied to the tower and the boat was allowed to drift 10 metres from the tower to avoid wall influences. In early 1972 a technique of repetitive column sampling and particle frequency-size analysis was used to investigate the accuracy of representation of a single sample at each depth. The Outlet Tower is in the epicenter of the south circulation pattern, a positionally important site. Weekly routine samples at vertical 2 - metre intervals were taken by the M.W.B. staff, and sub-samples provided to augment personally collected samples.

8. and 9. The South East and South West Corners:

These sampling sites were 20 - 21 metres deep and were sampled consistently through 1972 and 1973 in a manner similar to that employed for the North West and North East Corners.

B. Counting Procedures

Hutchinson (1953) has discussed the various types of distributions of organisms in their environments. He defined distributions which depended on random forces such as turbulence to approximate a Poisson series.

A good review of the types of distributions plankton might have was made by Ricker (1937). He suggested three types of distributions; a random, a bunched and a spaced distribution. Cassie (1959, 1963) referred to a bunched distribution as over-dispersion, and a spaced distribution as under-dispersion, thus relating these terms to the degree of departure from a random distribution. Cassie (1963) found that under-dispersion was a relatively unimportant phenomenon in plankton ecology, and that over-dispersion was the most common form of spatial heterogeneity. This conclusion is supported by Eddy (1927), Flint (1949), Anraku (1956), Cushing (1953), and Margalef (1958) though in some instances the heterogeneity might be a result of stabilization of the water column and not a plankton response to turbulence. When phytoplankton deviate from a random distribution the limits of confidence of an algal count cannot be applied with exactitude. The general effect of over-dispersion on sampling procedures is that a large number of samples are required to determine the number and distribution of organisms (Wieber and Holland, 1968). In such circumstances microscopic determination of composition and abundance is tedious and not always practicable (although samples can be combined but with loss of data on distribution). A more rapid method, which can be used in conjunction with the microscopic method, is that of particle size analysis (See Section C).

The problems of enumeration are similar to those of sampling. Colonial and filamentous forms result in a high degree of contagion. Precision of population determinations increases in proportion to the square root of the number of samples, and accuracy increases at a slow rate which is proportional to the number of counts.

Diverse methods of determining the frequency of phytoplankton have been developed. Ballantine (1953) compared different methods of estimating nannoplankton, and quite correctly warned of the effects of using fixatives, especially with Utermöhl's (1931, 1936) sedimentation technique. If allowance is made for the effects of fixatives, the sedimentation technique is extremely valuable, and the enumeration of phytoplankton as accurate as need be. Errors encountered can be minimal as compared with random error if the counting procedure of Lund, Kipling, and Le Cren (1958) is adhered to. This latter method was used to estimate the standing crop of phytoplankton in Wraysbury Reservoir using a modified sedimentation technique (Evans, 1973).

Phytoplankton studies are either general surveys or time-area studies in most instances (Holmes and Widrig, 1959). The former are often related to chemical, physical, and biological parameters; the latter are usually related to fluctuations in the phytoplankton. An intensive investigation of the effects of turbulence on phytoplankton production necessitates the combination of the two approaches.

Determination of algal species and numbers required that samples were fixed with Lugol's Iodine. Samples of three or more depths from the Outlet Tower were analysed in the Botany Department, Royal Holloway College, using the sedimentation and counting technique discussed above. These samples were routine weekly collections made by the M.W.B. Additional depths and extra sampling sites were included during periods of growth. The split tube technique of Evans (1973) was used with a Prior inverted microscope. This entailed covering the floor of the counting chamber using a 10x objective for larger forms and a 40x objective for the µ-plankton. Although oil immersion was possible for identification procedures, this was not of much success as the staining of organisms by Lugol's Iodine often made examination of the fine material difficult. Fresh material from net hauls was observed for most identifications. Centric diatoms of the River Thames and Wraysbury Reservoir were identified by a combination of light and electron microscopy and by the use of the scanning electron microscope.

River Thames samples were collected by dipping a plastic sample bottle into the river at the Datchet Intake. At most times, two or five millilitre aliquots were sedimented to obtain counts of approximately 100 individual units of the dominant species. Cells, filaments, and colonies were considered as individual units, and the initial counts in the counted sample were transformed to obtain standardization of counts in cells or other units per millilitre. Species represented by counts of fewer than 30 units $ml.^{-1}$ were listed as present in order to record their frequency and times of occurence. Owing to moderate production, the samples from the reservoir never had to be diluted, whereas river samples were at times diluted before enumeration.

C. Particle Size Analyses

The seston load of any body of water is composed of detrital particles of organic and inorganic material and productive particles. The nature and abundance of the latter are often determined by the methods discussed in the preceding section. Determinations of the composition and abundance of the entire seston and the interactions therein are few in limnological studies as a result of a basic lack of methodology. A promising approach to this problem is particle frequency-size analysis. Inman (1952) discussed the problem of measuring the particle size distribution of sediments, and noted the lack of a standardized approach. A possible method of particle size analyses is the use of a Coulter Counter.

In the past decade the Coulter Counter has been used to investigate phytoplankton populations in culture (Mahoney, Donovan and Robinson, 1962; El Sayeed and Lee, 1963; Parsons, 1965) and in freshwater and marine habitats (Sheldon and Parsons, 1966, 1967a, -b; Evans, 1967; McGill and Evans, 1967; Mulligan and Kingsbury, 1968; Parsons, 1969; Evans and McGill, 1970; Reynolds, 1973). The major criticism of using the Coulter Counter in most of these circumstances is that not only phytoplankton particles, but all particles regardless of nature and origin are counted. This has sometimes resulted in false estimations of phytoplankton abundance, (Reynolds, 1973).

Such a criticism is unjust. The Coulter Counter's major asset is that it does size and count all particles within the 'sensing' thresholds. Enumeration of phytoplankton is only possible in pure cultures or when the phytoplankton are a major proportion of the seston. Even in these circumstances the use of the Coulter Counter should be coupled with microscopical techniques. The precision of the Coulter technique to determine seston frequency-size distributions has been discussed by Haffner and Evans (1974a). Precision, and indeed accuracy, are dependent on the proper selection of aperture tubes, electrolyte concentration, and particle concentration. Kubitschek (1958, 1969) and Glover (1965) have outlined in detail the principles of the Coulter sizing and counting method and only a brief review of our technique is presented here.

A Coulter Counter consists of a mannometer and an electronic counting device. A current of a known resistance is passed through an aperture in the glass tube of the mannometer. In our own use of a Model A and B Coulter Counter (Industrial) samples to be analysed were at 20^{o}C, and NaCl was added to make a 0.5% electrolyte solution. Reasons for our choice of electrolyte solutions are discussed later See page 100). One-half millilitre aliquots are drawn up through the aperture by means of a vacuum pump. Particles which are much denser than the electrolyte solution result in a change in the resistance related to their volume as they enter the aperture tube. By means of measuring the change of electrical resistance the particles are 'sized'. There is a critical region about the aperture which can be considered as the sensing zone (Kubitschek, 1969), and the sample should be diluted to the extent that the probability of two or more particles being in the sensing zone at the same moment is low. Each resistance change is counted and sized as an individual particle, and there is no method by which the machine can distinguish the presence of two or more particles in the counting zone. In these circumstances two or more particles are counted as one large particle (coincidence error). Thus with high particle concentrations the Coulter Counter will underestimate the number and give a false particle size distribution of the sample. A coincidence correction is added to the counts in such circumstances, but is only applicable to 10% of the total count of particles in the range of aperture tube. Above this level the results become statistically unreliable.

The sizing technique is to adjust the current and threshold settings such that particles are counted in continuous size classes.

Changes in the magnitude of the current affect the sensitivity of detecting particles. A small current is more markedly affected by small particles than would be a large current. Changes in the threshold selects counts of particles in specific size classes. The Coulter Counter Model A has only a lower threshold setting, and particles are counted in a decreasing size range with increasing size of particle. The difference of counts between two successive size ranges is the number of particles in a particular size class. A Coulter Counter Model B has an upper and lower threshold, thus counts are directly made in distinct size classes. Eighteen size classes, covering the particle size range of 10 - 70,000 μm^3 were used in the investigation (See Table 1). Two aperture tubes, with 100 and 200 µm. diameters, were used to achieve analysis of this size range. An additional advantage of the two tube technique is that the smaller aperture tube can often cope with high particle concentrations of $\backsimeq$ 30,000/0.5 ml. There is a 'confidence limit' for Total Particulate Volume of 10^6 μm^3 (Evans and McGill, 1970) above which Total Particulate Volume can be related to biomass (See Figures 16, 17 and 18).

D. Synoptic Sampling Procedures and Total Particulate Volume

All samples from the river and from the reservoir were analysed by the Coulter technique using Models A and B. Total Particulate Volume (T.P.V.) (the cumulative sum of volumes of all measured size classes) was determined as an estimate of 'Biomass' (Evans and McGill, 1970). Weekly to fortnightly sample collections during

TABLE I

PARTICLE SIZE CLASSES OF THE SESTON

DIAMETER RANGE µm.		VOLUME RANGE μm^3 x 10^3		CORRESPONDING MINERAL SIZE
48.5 - 51.1		60 - 70	200 µm. aperture tube	
47.5 - 48.5		50 - 60		coarse silt
42.4 - 47.5		40 - 50		
38.5 - 42.4		30 - 40		
33.6 - 38.5		20 - 30		
27.6 - 33.6	100 µm. aperture tube	10 - 20		medium silt
24.2 - 27.6		7.5 - 10		
21.2 - 24.2		5.0 - 7.5		
17.9 - 21.2		3.0 - 5.0		
14.5 - 17.9		1.6 - 3.0		
11.5 - 14.5		0.8 - 1.6		fine silt
9.1 - 11.5		0.4 - 0.8		
7.2 - 9.1		0.2 - 0.4		
5.7 - 7.2		0.1 - 0.2		very fine silt
4.60 - 5.7		0.05 - 0.1		
3.6 - 4.6		.025 - 0.05		coarse clay
2.9 - 3.6		.001 - 0.025		medium clay

1972 and 1973 were designed to determine the general particle frequency-size distributions of all particle size classes of the reservoir at three depths representative of the top, middle, and bottom of the water column sampled. Usually five stations, Limnology Tower II, North East Corner, North West Corner, South East Corner, and South West Corner were sampled. On some occasions this was not possible as a result of adverse weather conditions and only three stations were sampled. The mean particle distribution of each size class for each depth was determined. An estimate of heterogeneity was made using a variance/mean ratio (Ricker, 1937) for each size class. It must be emphasized that a variance/mean ratio is only a comparative estimate of departure from a random distribution, and is selected only for its ease of use, and in order to present data on particle distribution in a simplified form. Ecological interpretations of the importance of such ratios are questionable.

During the summer of 1972 synoptic sampling and particle size analyses were combined to investigate the effects of jetting (Haffner and Evans, 1973). Sampling was confined to grid patterns in front of the inlet jets, centered about the swells on the surface caused by the momentum of the entering and entrained waters. The first grid system consisted of samples being collected at regular two metre intervals. A total of nine stations about each jet swell was sampled at three depths to determine the number of particles in the 0.05 - 70.0 x 10^3 μm^3 size range.

A second investigation using synoptic sampling methods was confined to the upper two metres. Samples were collected along a 12 x 5 metre grid at 2 metre intervals along the rows and at 5 metre intervals along the columns. A two metre rubber hose pipe (Lund, Kipling, and Le Cren, 1958) was used to collect samples which were analysed in the same manner as described above.

The third and final synoptic collection of samples in front of the Inlet Pier was designed to examine the direct effects of jetting on the phytoplankton. A five-by-five grid system was developed by taking two metre hose pipe samples at regular intervals. The grid extended from behind the jet swells to the Central East Buoy. Counts of *Aphanizomenon flos-aquae* (L.) (Ralfs.) were determined by counting procedures discussed earlier. Other phytoplankton components such as *Tribonema* spp., *Ceratium hirundinella* (O.F. Muller) Schrank, and *Eudorina elegans* (Ehrenb.) were also enumerated.

E. Chlorophyll-a Determinations (µg. l.$^{-1}$)

Standing crop of phytoplankton is often estimated by chlorophyll-a and many procedures of analysis have been discussed (Lorenzen, 1965, 1967; Manning and Juday, 1941; Krey, 1958; Talling and Driver, 1963). Spectrophotometric methods described by Golterman (1969) were used to determine chlorophyll-a as total pigment. Volumes of samples (varying with phytoplankton concentrations) were filtered using Whatman GF/C filters. The filter pads were placed in 100% acetone overnight in a dark refrigerator at 5°C. An extinction coefficient of 90 at 663 µm. was used to determine pigment concentrations on a Unicam 800 spectrophotometer. Results are relative, but are generally comparable.

F. Carbon, Dry Weight, and Loss-on-Ignition

Carbon was determined by two separate methods. Particulate carbon content was determined as a routine procedure of the Metropolitan Water Board, and results are reproduced with their kind permission. A wet oxidation method similar to A.P.H.A. (1955), and Strickland and Parsons (1960) was used. Filter pads were pretreated at 500°C for one hour. The dried residues on the filter pads were put in 100 ml. conical flasks and distilled water, 0.25N potassium dichromate and sulphuric acid were added quickly in a ratio of 1 : 1 : 5. The mixture was shaken, and heated at 105°C for one hour. After cooling, 30 ml. of glass distilled water were added and excess potassium chromate was determined by titration with 0.025 N ferrous ammonium sulphate using ferroin as the indicator. Filter pad blanks were determined for every set of samples. Strickland and Parsons (1960) considered oxidizable carbon to be within 10 - 20% of the true carbon content.

The second method to determine carbon was loss-on-ignition. Dry weight was determined by filtering one or two litres of sample through pre-ignited Whatman GF/C filter paper. The filter pads were sucked dry, placed in an oven at 95°C overnight (Myers, 1962). (Myers (1962) suggested temperatures just below 100°C to prevent spattering.). Pads were weighed and reheated until a constant weight (mg. $l.^{-1}$) was achieved. Filters and residues were then placed in a muffle furnace at 200°C for one hour, and 500°C for one hour, cooled in a dessicator and weighed. Data on dry weight and loss-on-ignition is presented in Appendix D.

G. Vertical Net Haul

The dry weight of single, weekly, coarse vertical net hauls is presented as a crude approximation of zooplankton abundance in Wraysbury Reservoir during 1972 and 1973. Dry weight was determined by procedures similar to those described previously. Sampling and analyses were done by the Metropolitan Water Board. Data is presented in Appendix D.

H. Conductivity and pH

A dionic water tester was used to measure conductivity (specific conductance). Results are expressed in µMhos. $cm.^{-1}$ at 20°C.

Hydrogen ion concentrations were determined using a direct reading bench pH meter (E.I.L. Model 23A).

I. Alkalinity (mg. $l.^{-1}$); Dissolved Silica (mg. $l.^{-1}$); Nitrate (mg. $l.^{-1}$) Phosphate (µg. $l.^{-1}$)

Alkalinity was determined as bicarbonate as in Mackereth (1963) with no modifications.

For comparative purposes (± 1.0 mg. $l.^{-1}$ SiO_2) a rapid method of silica determination was used (McGill, 1969). More sensitive techniques (± 0.1 mg. $l.^{-1}$ SiO_2) as outlined by Jorgensen (1953) might not be applicable as a result of interference by other chemicals. One ml. of 10% ammonium molybdate and 0.25 ml. of 25% sulphuric acid were added to 50 mls. of membrane-filtered sample. The solution was stirred and allowed to stand for ten minutes to permit colouring. The optical density of the solution was determined using an E.E.L. 601 filter with an E.E.L. absorptiometer. A calibration curve of silica concentrations versus O.D. was prepared using standard solutions of sodium silicate and silicic acid.

Nitrate was measured by evaporating 25 mls. of sample to dryness and adding 2 mls. of phenoldisulphonic acid to wet the residue. After colour development the solution was made up to 50 mls. with distilled water, and 2 mls. of 10% magnesium sulphate added, followed by the addition of sodium hydroxide until the magnesium hydroxide precipitated out. The resultant solution was filtered through Whatman number 42 paper, and the O.D. measured against reagent blanks with an E.E.L. 601 filter. A standard calibration curve was prepared using potassium nitrate.

Phosphate was measured by a method similar to that of Strickland and Parsons (1960) using ascorbic acid as the reducing agent to determine ortho-phosphate. Optical density was measured using an E.E.L. 609 filter. A standard calibration curve was made with solutions of potassium dihydrogen phosphate (See Golterman, 1969 for details of the method used).

J. Dissolved Oxygen and Temperature

A Q.M.I. (Quality Measuring Instruments) oxygen meter and a Mackereth oxygen probe were used to determine the percent dissolved oxygen - depth profile of Wraysbury Reservoir. An E.I.L. (Electronic Instruments Limited) oxygen meter and probe were used to measure dissolved oxygen for productivity experiments. The probe was inserted into the 250 ml. volumetric flasks used for productivity experiments and gently moved in a circulating manner. This gave readings in terms of percent saturation which was converted to mg. $l.^{-1}$ by using Mortimer's (1956) nomogram. Oxygen probes and meters were calibrated monthly.

Temperature was measured using a thermistor (Mortimer, 1953; Mortimer and Moore, 1953) and was determined at each depth from the surface to the bottom of the reservoir.

K. Solar Radiation and Light Penetration

Solar radiation (milliwatt hrs. $cm.^{-2}$) was obtained from the Meterological Station at Kew, and corrected to photosynthetically available energy by multiplying by 0.5 (Taylor and Kerr, 1941; Talling, 1957a; Strickland, 1958). Radiation data was transformed into units of cal. $cm.^{-2}$, and irradiance into units of cal. $cm.^{-2}$ $min.^{-1}$ to be more readily comparable with the general literature (Kimball, 1928; Poole and Atkins, 1936; Westlake, 1965). Such an approximation is possible as 1 mWhr. $cm.^{-2}$ = 0.86 cal. $cm.^{-2}$ (Meteorological Office, Bracknell).

Light penetration into Wraysbury Reservoir was measured by submersible photo-electric cells (Walker, 1948). Sangamo-Weston selenium cells in water-tight casings were connected back to back (positive of one connected to negative of the other) and balanced with a potentiometer (Bellinger, 1968). One cell was maintained in a horizontal unshaded position on the boat, the other lowered at one metre stages until 5% of complete attenuation was measured. The point of complete attenuation was predetermined by a surface reading using one cell only. Five percent was chosen as approximating complete attenuation as below this there is a non-linear relationship of light intensity and selenium response. Measurements were made on a galvanometer of low internal resistance. During use, the filter wells of the photocells were filled with water, and filters were added with caution to prevent the trapping of air bubbles. Light penetration was measured at least monthly.

Chance filters OB1, OG2, OY2, and OR2 were used. These filters have transmission maxima at 480, 530, 625, and 675 mμ respectively. The relative spectral response of selenium has a maximum between 560 - 580 mμ (Preston, 1950). A neutral density filter was used for a general estimation of the penetration of natural light minus ultraviolet effects. All filters were used with an opal diffusing glass which was usually placed on top of the filters. Under these conditions a linear response by the meter to changes in irradiation is expected (Lund and Talling, 1957).

As expressed by Smith (1968), and Smith and Tyler (1967) the vertical attenuation coefficient (extinction coefficient) is a function of the spectral response of the photoprocess and the spectral transmission of the water. For these reasons secchi disc determinations of transparency and attenuation of radiant energy are questionable (Atkins, Jenkins and Warren, 1954; Tyler, 1968) and more elaborate techniques using monochromatic light have been used (Tyler and Smith, 1967). Such methods do not, however, result in much information on the penetration and modification of natural light in bodies of water. Assuming the relative spectral response of selenium is approximately equal to all wavelengths of the photosynthetic spectrum, first order approximations of spectral transmission of the water can be made.

The attenuation of light with depth as measured by an upturned horizontal surface is defined as;

$$\varepsilon_{\lambda} = \frac{2.3}{z}\left(\log_{10} I_o - \log_{10} I_z\right)$$

which is the same as used by Poole and Atkins (1928), Sverdrup, Johnson, and Fleming (1942), and Graham (1966). The attenuation coefficient ε_{λ}(in units $m.^{-1}$) is the rate of change of light intensity from the surface (I_o) to depth z (I_z). In homogeneously mixed water, Hutchinson (1957) noted that plots of irradiance against depth are close to straight lines. The slope of the lines is not dependent on sun height, but is dependent on the distribution and the nature of the water and suspended particles (Atkins and Poole, 1952). As the attenuation coefficient is additive, (James and Birge, 1938),

$$\varepsilon_{tot} = \underset{\text{(water)}}{\varepsilon_{w}} + \underset{\substack{\text{(dissolved)}\\ \text{(material)}}}{\varepsilon_{d}} + \underset{\text{(particles)}}{\varepsilon_{p}}$$

suspended particles can affect a major proportion of the attenuation of light by scattering as compared with selective absorption (Jones and Wills, 1956). Selective absorption (molecular absorption by the water) might result in an increase in slope, but Westlake (1965) noted that this effect is unimportant when using selenium photocells as they are more sensitive to the more readily transmitted wavelengths. Dissolved material, particularly organic material, can in some instances markedly affect the attenuation of light (Ruttner, 1966) and result in 'colouring' of the water.

L. Productivity and Production Experiments

The rate of oxygen production and consumption was investigated at three or four depths using the light and dark bottle method. Special containers were designed to hold three light and three dark bottles at specific depths (Bellinger, 1968). Dissolved oxygen was measured using an E.I.L. Mackereth oxygen probe, and results were converted to mg. $l.^{-1}$ (See section J). Errors involved in this method are similar to those encountered in the Winkler method (Pratt and Berkson, 1954; Carpenter, 1964). Results are expressed as rates of oxygen production (mg. $l.^{-1}$ $hr.^{-1}$).

As for this investigation the rate of oxygen production at different depths was the only requirement, there was no need to have a constant algal suspension maintained for productivity experiments. Populations were too low to sample a depth and resuspend the sample at the same depth, and algal suspensions were usually prepared by mixing a tow net collection with Wraysbury water. Such a procedure was acceptable for productivity investigations as long as the original oxygen content was less than 100% saturation. Super-saturation levels tended to either exceed the range of the oxygen meter after a short exposure or over-emphasize respiratory oxygen leakage. The light and dark bottle technique of measuring primary productivity was used monthly in 1972 and seasonally in 1973.

Potash (1956) discussed the advantages of biological tests to determine the potential productivity of a lake or river. A bioassay technique was used during 1973 to test phytoplankton production at different depths. Transparent plastic bags (later (26/04/73) medicine flasks were substituted to avoid leakage problems) were half-filled with a phytoplankton suspension which was prepared as in the light and dark bottle experiments. The bags were suspended at three or four depths in the water column. The remaining mixture was returned to the laboratory and the phytoplankton counted by the sedimentation technique. If there was sufficient sample mixture, particle size distribution and chlorophyll-a concentrations were also determined. Though crude, such experiments can give an elementary insight which helps determine (though does not measure) some of the major parameters affecting production. Lund (1959b, 1970) discussed the values and disadvantages of the above and similar techniques of bioassay. Whipple (1896) used similar methodology to measure diatom growth rates. Bioassay is an extremely useful tool for both the phycologist and limnologist, but care must be taken to insure that one is not measuring an organism's affinity for closed containers.

- THE ALGAE OF THE RIVER THAMES AND WRAYSBURY RESERVOIR -

1971 - 1974

It was suggested by Uhlmann (1971) that bodies of water with long retention times and high nutrient loads do not exist. Wraysbury Reservoir has a moderately long retention time, with a mean in excess of two months through 1972 and 1973. The reservoir is directly fed from the River Thames and can at most times be considered to be hyper-fertilized. During this investigation particular emphasis was placed upon determining the effects of the river on the reservoir. As it was practicably impossible to study the two complex systems simultaneously in any detail, the influence of the river seston on the production of the reservoir was particularly studied. Data obtained from samples of the River Thames at Datchet were limited to phytoplankton counts, chlorophyll-a, carbon, total particulate volume, and particle size analyses. Detailed chemistry was not routinely done as this would duplicate work of an associated research project and thus only major nutrients were considered. The two systems will be discussed together in each section for comparability of biological, chemical, and physical parameters.

A. Phytoplankton Species of the River Thames and Wraysbury Reservoir

In any ecological study it is essential to correctly identify the organisms involved. For most species encountered this was not difficult as the algae of the Thames Valley have been investigated by Fritsch (1902, 1903, 1944), Rice (1938a, -b), Bellinger (1968, 1969), and McGill (1969). Such background work facilitated identifications. Problems do arise when discussing the centric diatoms of the River Thames and of the reservoir as a result of their modes of reproduction (Geitler, 1935) and morphological variation.

Identifications were made by consulting Huber - Pestalozi (1942), Smith (1950), Hustedt (1930), Prescott (1951), Cleve - Euler (1951) and Helmcke - Krieger and the Fritsch microfiche collection. These were not adequate, however, to determine the taxonomic groupings of the common centric diatoms which occurred in numerous forms. A large centric diatom of the reservoir is referred to as Stephanodiscus astraea (Ehrenb.) Grun. As reported by Bellinger (1968) several varieties are thought to exist. Although diameters were within the range reported by Hustedt (1930) of 30 - 70 µm. several smaller forms appeared. Valves were circular and radially punctate with high variability of pattern. Punctae were in uni- and multiseriate rows. Scanning electron micrographs (Figures 4 and 5) represent the common form of S. astraea "var. typica" found in Wraysbury Reservoir. A smaller form of Stephanodiscus astraea possibly var. intermedia Fricke. (Figures 6 and 7) was frequently present but not in as large numbers as was the former. The combination of the two forms resulted in a slightly skewed size distribution curve (Bellinger, 1967; Evans, 1974 personal communication).

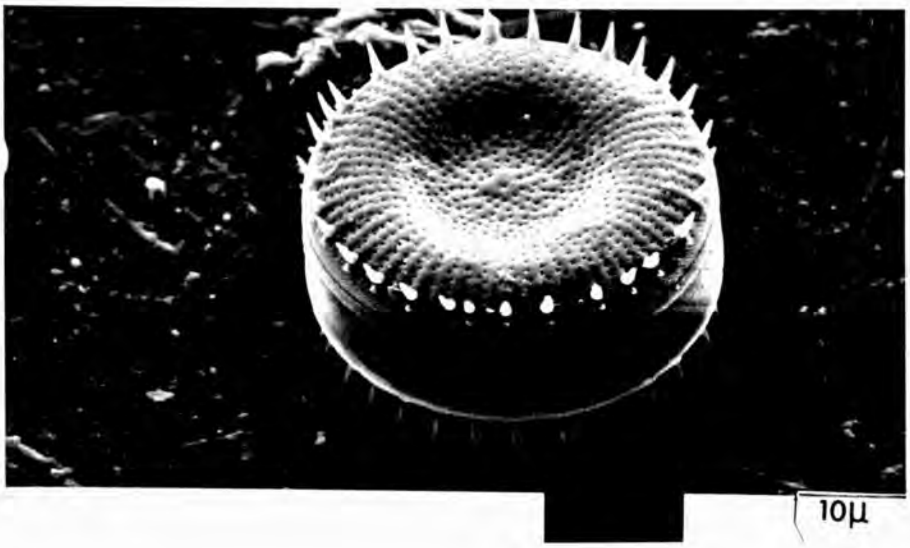


Figure 4. Scanning Electron Micrograph of *Stephanodiscus astraea* var. *typica* of Wraysbury Reservoir.

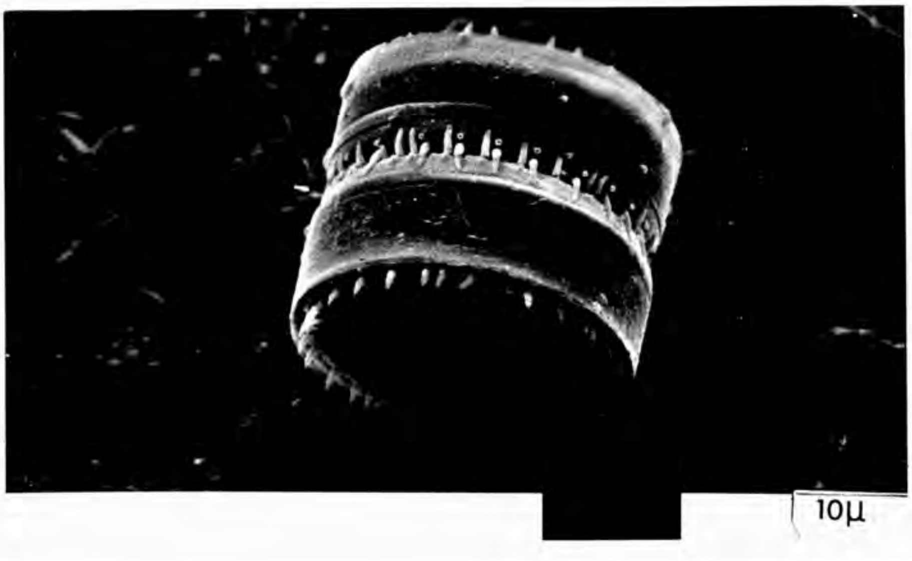


Figure 5. Scanning Electron Micrograph illustrating a doublet of *Stephanodiscus astraea* var. *typica* of Wraysbury Reservoir.

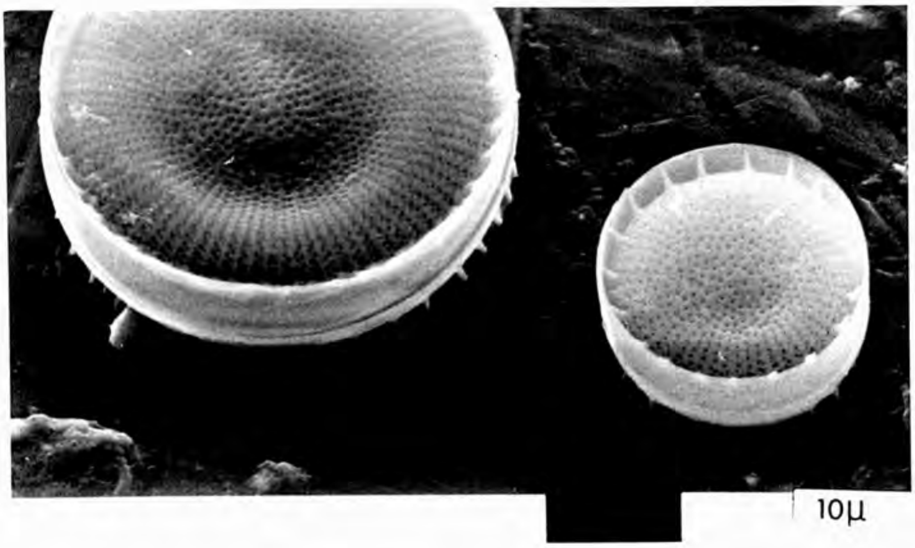


Figure 6. Two morphologically different forms of <u>Stephanodiscus astraea</u> of Wraysbury Reservoir. The larger was the most common, possibly var. <u>typica</u>; the smaller possibly var. <u>intermedia</u>.

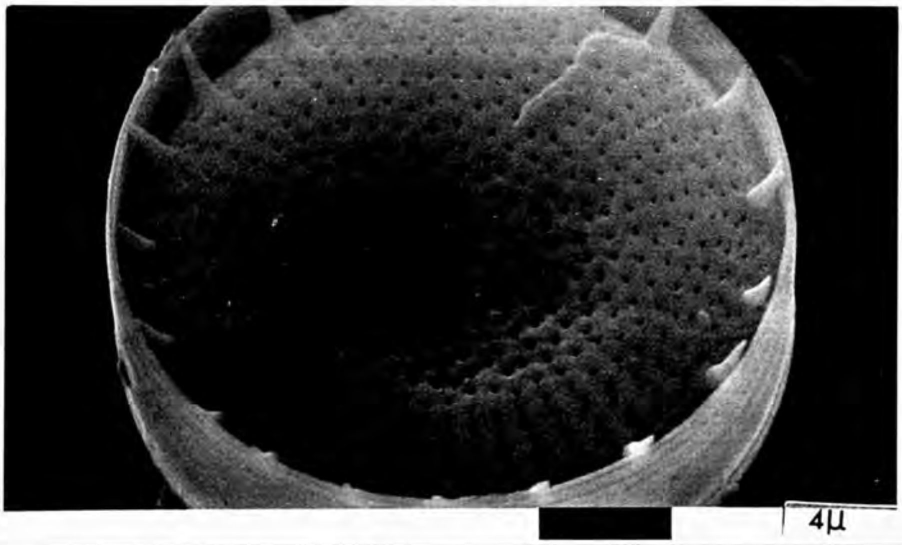


Figure 7. A valve view of <u>Stephanodiscus</u> <u>astraea</u> possibly var. <u>intermedia</u>.

Figure 8. Stephanodiscus astraea possibly var. incertus found in Wraysbury Reservoir in very low numbers.

Figure 9. The centrics of the River Thames, spring 1973, including various forms of S. astraea and S. hantzschii.

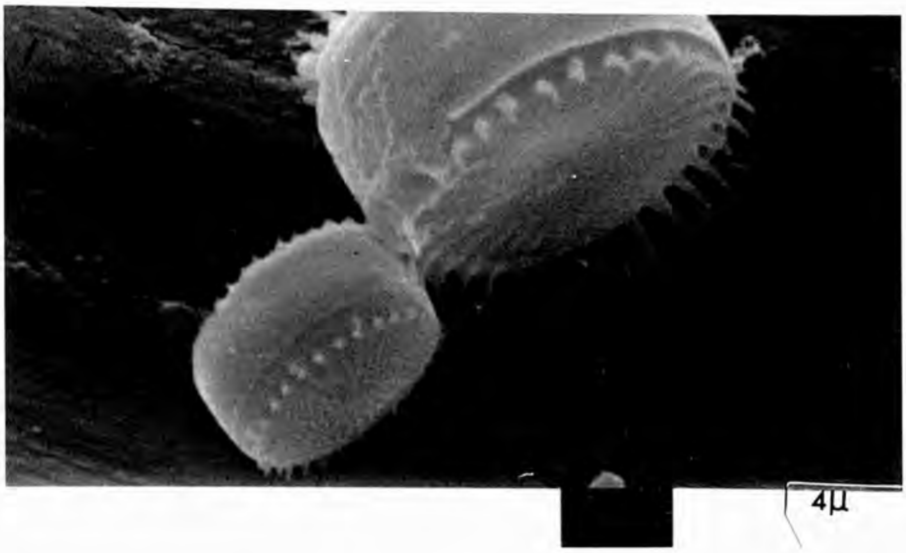


Figure 10. Stephanodiscus astraea (right) and Stephanodiscus hantzschii of the River Thames. Note the difference in the prominence of the spines.

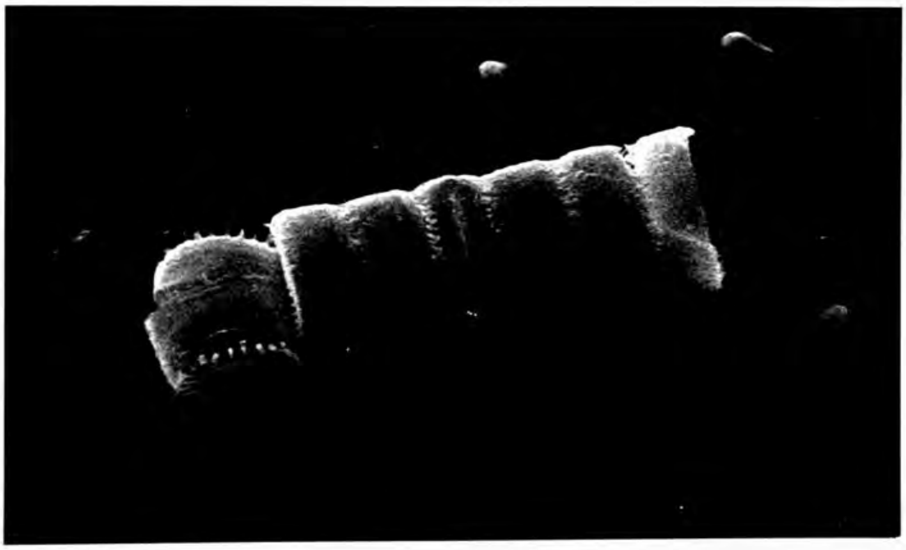


Figure 11. A chain form of Stephanodiscus hantzschii from the River Thames.

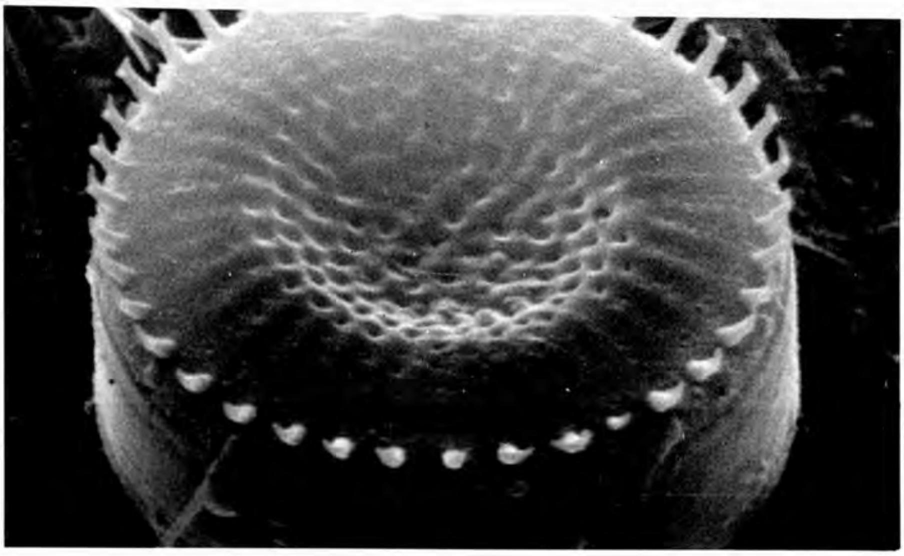


Figure 12. A possible form of Stephanodiscus dubius? Note the bifurcate spines are in line with the radial ridges.

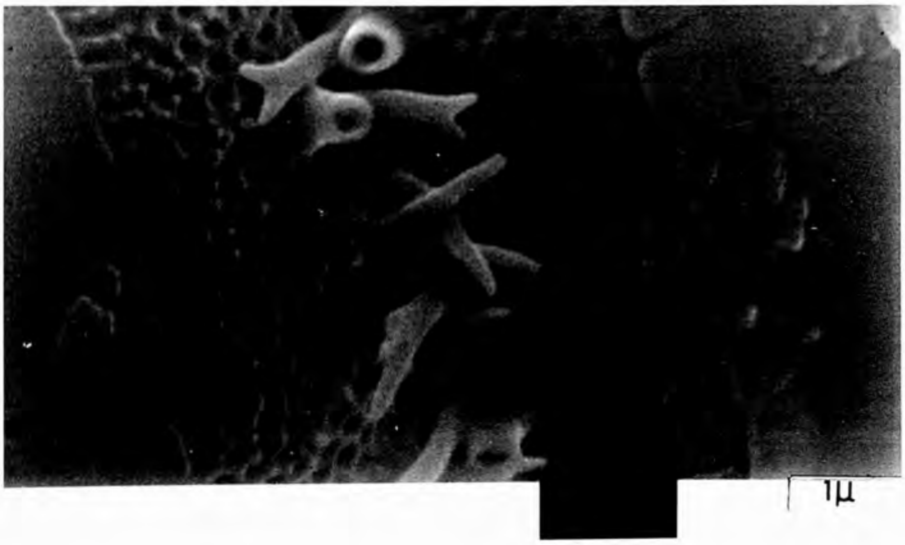


Figure 13. Bifurcate spines and mucilage pores of Stephanodiscus dubius? as in Figure 12.

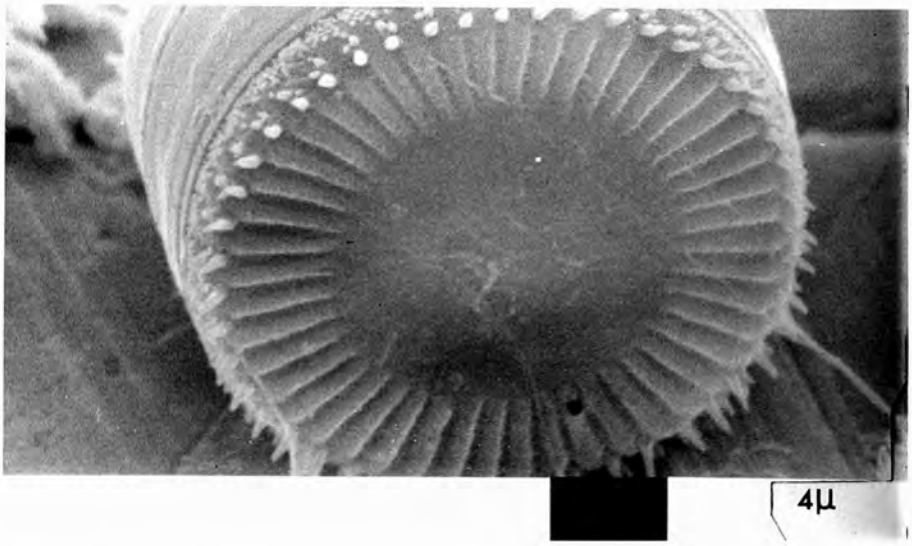


Figure 14. *Cyclotella* sp. of the River Thames illustrating the spines between the radial ridges and distinct peripheral ornamentation.

The common reservoir form of *Stephanodiscus astraea* was larger than other reported sizes (Gerloff and Gölz, 1944; Nauwerk, 1963; Anon., 1966; Sreenivasa and Duthie, 1973) perhaps as a result of the eutrophic environment (Margalef, 1969). Presence or absence of mucilage pores, prominence of spines, undulations of the valve faces added to the general taxonomic confusion. A less common form of *S. astraea* (Figure 8) found by scanning electron microscopy, has uniseriate rows of large punctae, and is similar to *Stephanodiscus astraea* var. *incertus* as described by Cleve - Euler (1951) though smaller in diameter.

Problems of reduction of cell size and formation of girdle bands have been discussed by Round (1972a, -b). Similar work (Hendey, Cushing and Ripley, 1954; Okuono, 1955; Hendey, 1959) has suggested that new terminology would have to be agreed upon in order to research the microstructure of diatoms. A detailed taxonomic study would be required to resolve the problems of the numerous morphological forms observed in the reservoir.

Centrics of the River Thames present the same problem. The most common form was *Stephanodiscus hantzschii* Grun. with valve diameters of 7 - 10 µm. Figure ~~9~~ 10 illustrates *S. hantzschii* beside a small form of *S. astraea* possibly "var. *typica*" considering the prominent spines and three seriate rows of punctae between each pair of spines. A chain form of *S. hantzschii* is seen in Figure 11.

Other River Thames centrics included a form of *Stephanodiscus dubius* ? (Fricke.) Hust. as determined by the prominence of spines (although bifurcate) in line with the radial ridges (Round, 1970). Figures 12 and 13 emphasize the presence of bifurcate spines. I know of no other centric diatoms with bifurcate spines except the marine centric Thalassiosira nordenskiöldi Cleve. Whether the presence or absence of bifurcate spines is a characteristic to delineate this particular morphological form into a distinct group is not known. A species of Cyclotella with spines between the radial ridges, and distinct peripheral ornamentation is illustrated in Figure 14.

It was not within the scope of this project to investigate any further the centrics discussed above. The larger S. astraea (Figures 4 and 5) and S. hantzschii (Figures 10 and 11) were the most important ecological forms occurring during the period of study, and were by far the most abundant. Both are recognizable by their valve diameters and prominence of spines. The remaining forms, although often not recognizable by light microscopy, were not sufficiently frequent to invalidate enumeration procedures.

B. The Phytoplankton Populations of the River Thames and Wraysbury Reservoir

The study of phytoplankton ecology in river environments includes many parameters (Kofoid, 1908; Butcher, 1932, 1945; Blum, 1956; Peabody and Whitton, 1968) as a river is a very dynamic ecosystem. Single weekly samples at the Datchet Intake are by no means indicative of the River Thames as a whole, and only represent the quality of water entering the reservoir. During 1972 and 1973 there were only two major phytoplankton growths in the River Thames. Stephanodiscus hantzschii was abundant during late May and early June 1972, and during late April and early May 1973. The first year's growth (1972) was dominated by S. hantzschii reaching a maximum number of 2.1×10^4 cells $ml.^{-1}$ (4.2×10^6 $\mu m.^3$ $ml.^{-1}$) (Figure 15). (Chlorophyll-a and carbon concentrations in the river (Figures 16 and 17) reached respective maxima of 1.79×10^2 $\mu g.$ $l.^{-1}$ and 8.4×10^3 $\mu g.$ $l.^{-1}$). In 1973 a growth of similar magnitude occurred of 3.0×10^4 cells $ml.^{-1}$ (6.0×10^6 $\mu m.^3$ $ml.^{-1}$). This second growth had chlorophyll-a and carbon concentrations of 2.0×10^2 $\mu g.$ $l.^{-1}$ and 9.0×10^3 $\mu g.$ $l.^{-1}$ respectively. Associated with S. hantzschii during this growth period was Nitzschia acicularis which reached a maximum of 1.0×10^3 cells $ml.^{-1}$ ($\simeq 10^5$ $\mu m.^3$ $ml.^{-1}$)and Asterionella formosa Hass. which was very low in numbers at 100 cells $ml.^{-1}$ (8.0×10^4 $\mu m.^3$ $ml.^{-1}$). These were the dominant diatom species of the River Thames phytoplankton during this investigation.

Flagellates were common throughout the study but contributed little to the total biomass as can be seen by the low carbon and chlorophyll-a values, and by the total particulate volume (Figure 18) recorded. The more frequently occurring forms were Cryptomonas ovata

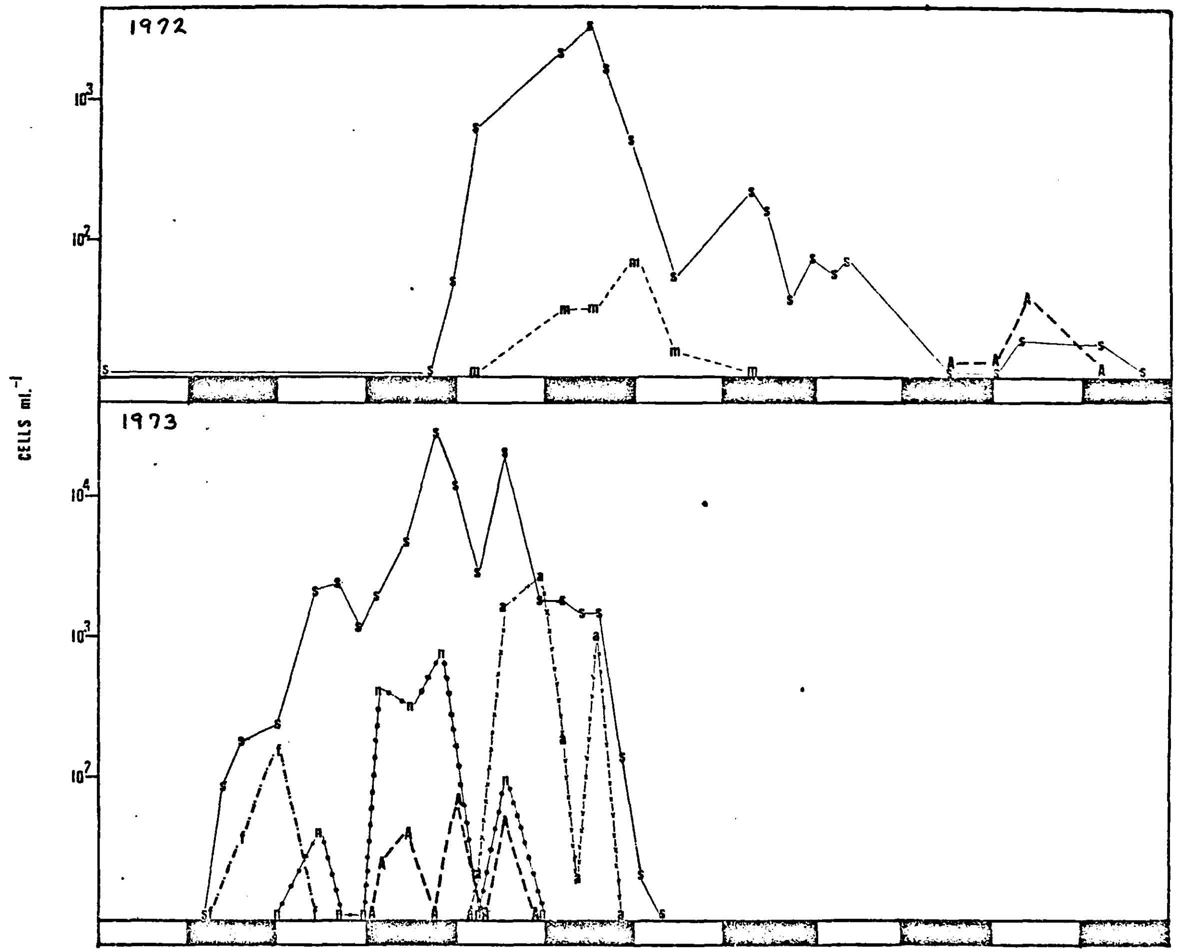


Figure 15. The phytoplankton of the River Thames 1972 - 1973. S——S Stephanodiscus hantzschii M----M Melosira varians; A--A Asterionella formosa; a-×-a Actinastrum spp.; n-●-n Nitzschia acicularis; f-·-f Flagellates.

Ehrenb., *C. curvata* Ehrenb. (Penard amend.), and *Rhodomonas minuta* var. *nannoplanctica* Skuja. Associated with this group were many unidentified green flagellates, the most common of which was *Chlamydomonas* spp.

Many other algal species were found, but contributed little to the total biomass of the inlet water from the river. This group includes *Scenedesmus* spp. *Melosira varians* Agardh., *Synedra ulna* (Nitzsch.) Ehrenb., *Synedra acus* Kutz., and *Nitzschia palea* (Kg.) W. Smith.

Wraysbury Reservoir was not greatly affected by the phytoplankton innoculum from the River Thames. During the periods of high chlorophyll-a, carbon, and total particulate volume of the River Thames (Figure ~~20~~ 18) there was apparently little or no influence upon the related parameters of Wraysbury Reservoir, supporting Ridley's and Symons' (1972) and McGill's (1969) observation that river innoculum does not directly affect the standing crop of the reservoir. Only *Nitzschia acicularis* appeared to be successful in that it increased slightly in numbers after being introduced into the reservoir. In May 1973 it reached concentrations of 200 cells ml.$^{-1}$ (2.0 x 10^4 µm.^{3} ml.$^{-1}$), which would not be accounted for by dilution unless some growth occurred while in the reservoir environment. The suspension of cells of *N. acicularis* in a bottle of Wraysbury water suspended at five metres depth indicated the ability of this organism to grow in the reservoir. Cells in a bottle near the bottom of the reservoir showed no signs of growth and there was a decrease in cell numbers (See Table V).

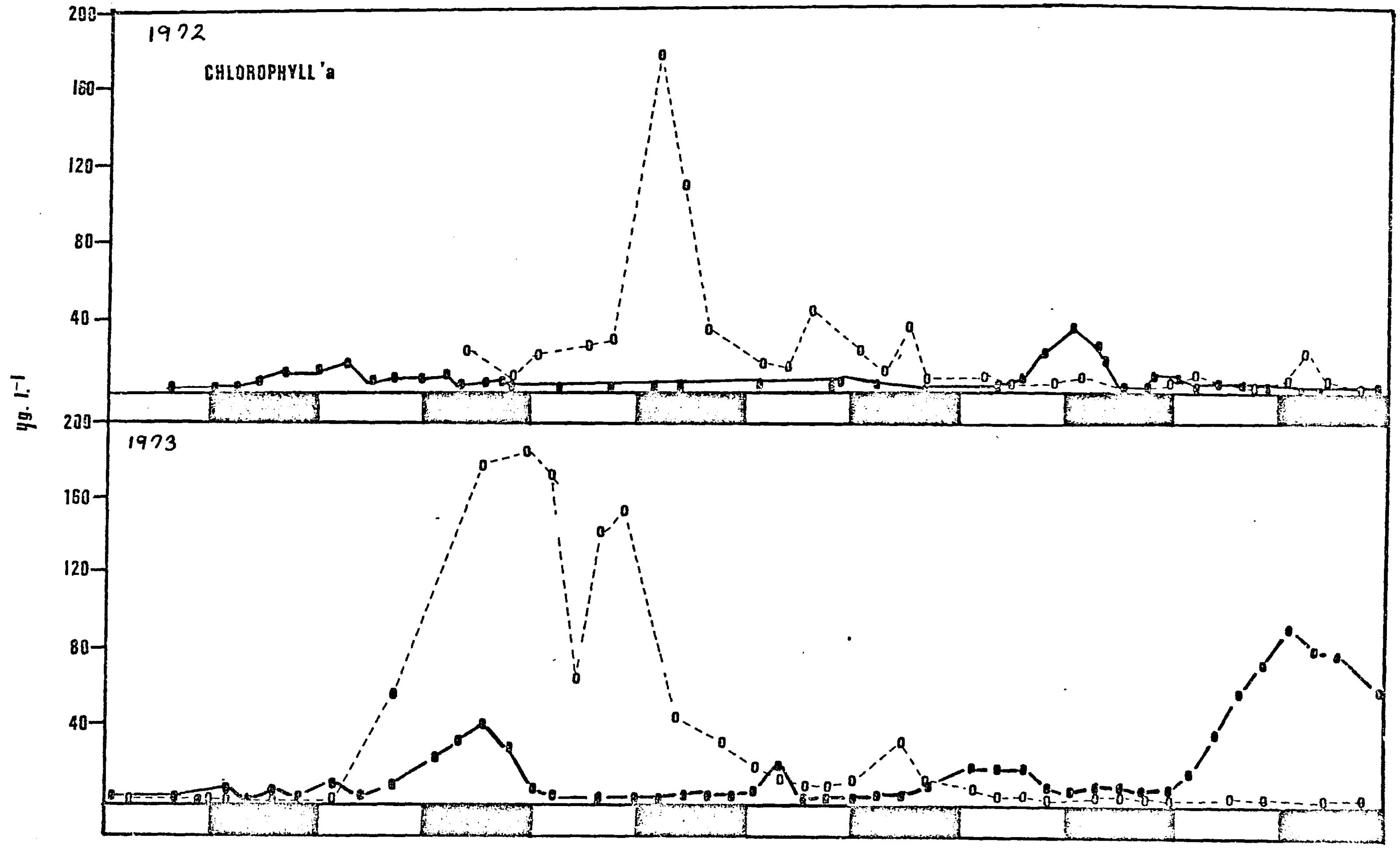


Figure 16. Chlorophyll a (μg. l^{-1}) of Wraysbury Reservoir ● and the River Thames O during 1972 - 1973.

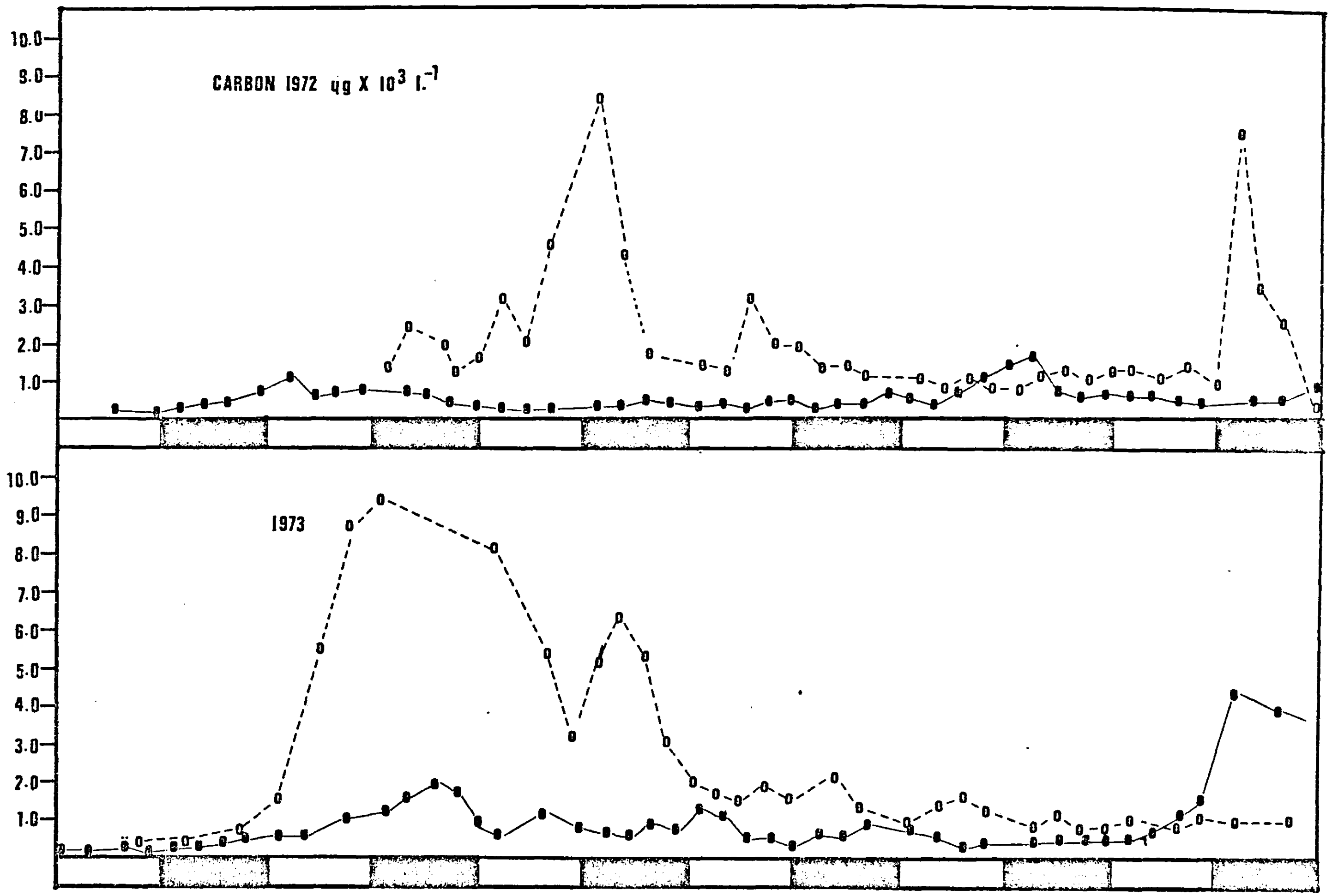


Figure 17. Carbon (µg. l^{-1} X 10^3) of Wraysbury Reservoir ● and the River Thames O during 1972 - 1973.

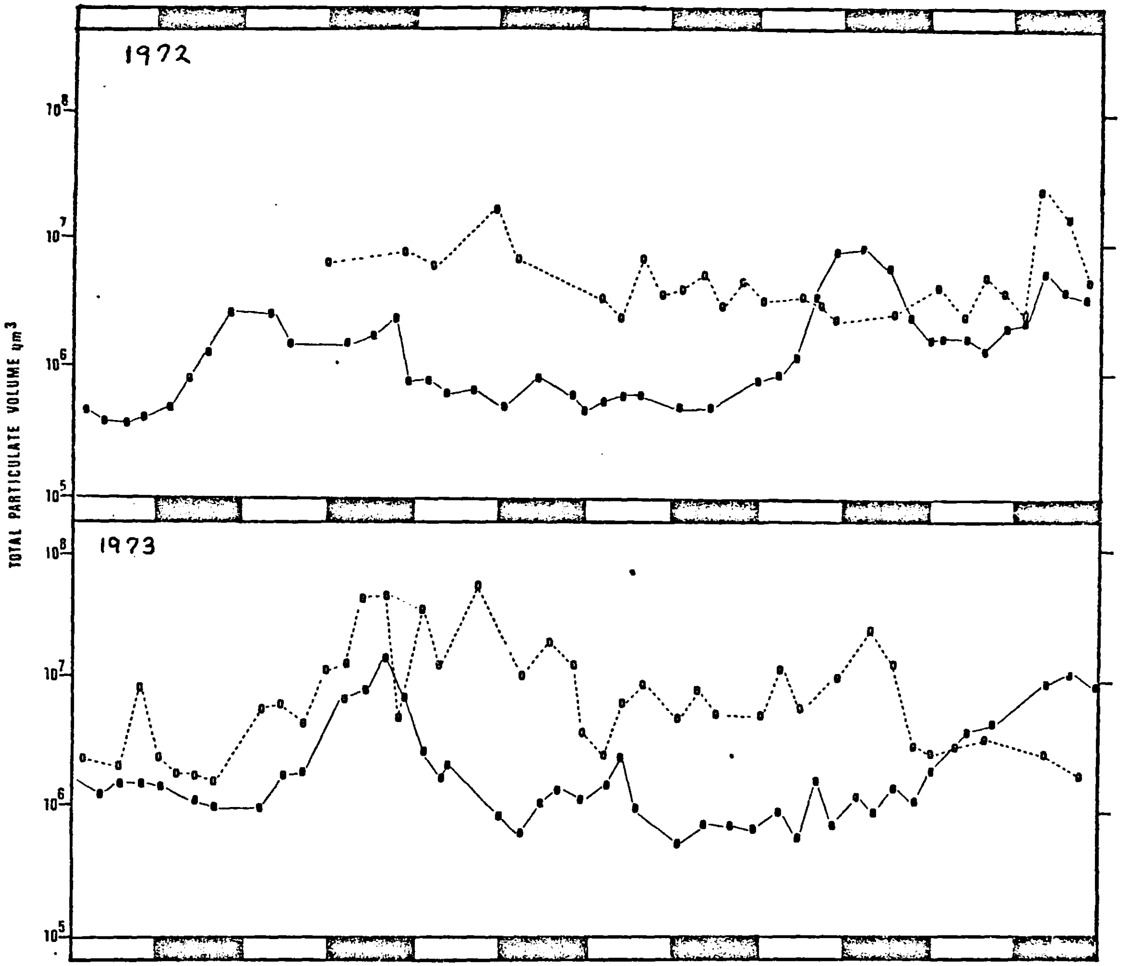


Figure 18. Total Particulate Volume ($\mu m^3 ml.^{-1}$) of the River Thames O and Wraysbury Reservoir ● during 1972 - 1973.

By far the most dominant organism of Wraysbury Reservoir was Stephanodiscus astraea (Figure 19). This species was originally derived from King George VI Reservoir (from which the Wraysbury Reservoir was initially filled) since it was present in Wraysbury before any river water was run in. S. astraea was common in both mud and volume samples during the late autumn and winter of 1971 - 1972, but was relatively unimportant in the river. The first observed growth of S. astraea was in February to early March 1972, and it reached a maximum of 200 cells $ml.^{-1}$ (2.5×10^6 $\mu m.^3$ $ml.^{-1}$). By the middle of March the growth ended. This was before jetting had occurred. It is quite possible that this growth was silica limited as the original dissolved silica levels of the reservoir were relatively low (≈ 2 mg. $l.^{-1}$) (See Section C). During July and August live cells were frequently found in mud samples, but seldom in volume samples.

In the middle of September 1972 a second pulse of the large centric was initiated. This pulse was slightly larger than the original spring growth, and extended over a longer period of time. A maximum of 400 - 500 cells $ml.^{-1}$ (5.0×10^6 $\mu m.^3$ $ml.^{-1}$) was achieved and chlorophyll-a, carbon, and T.P.V. levels were correspondingly higher than in the spring (Figures 16, 17, and 18).

Although there was a large decline in the population by the middle of October (probably due to sedimentation as jetting was stopped during the first week of October) many cells remained in suspension throughout the remainder of the autumn and the entire winter. These cells served as an innoculum for the growth in the spring of 1973. This growth was delayed in comparison with the original growth which had taken place the preceding spring. This delay might have been the

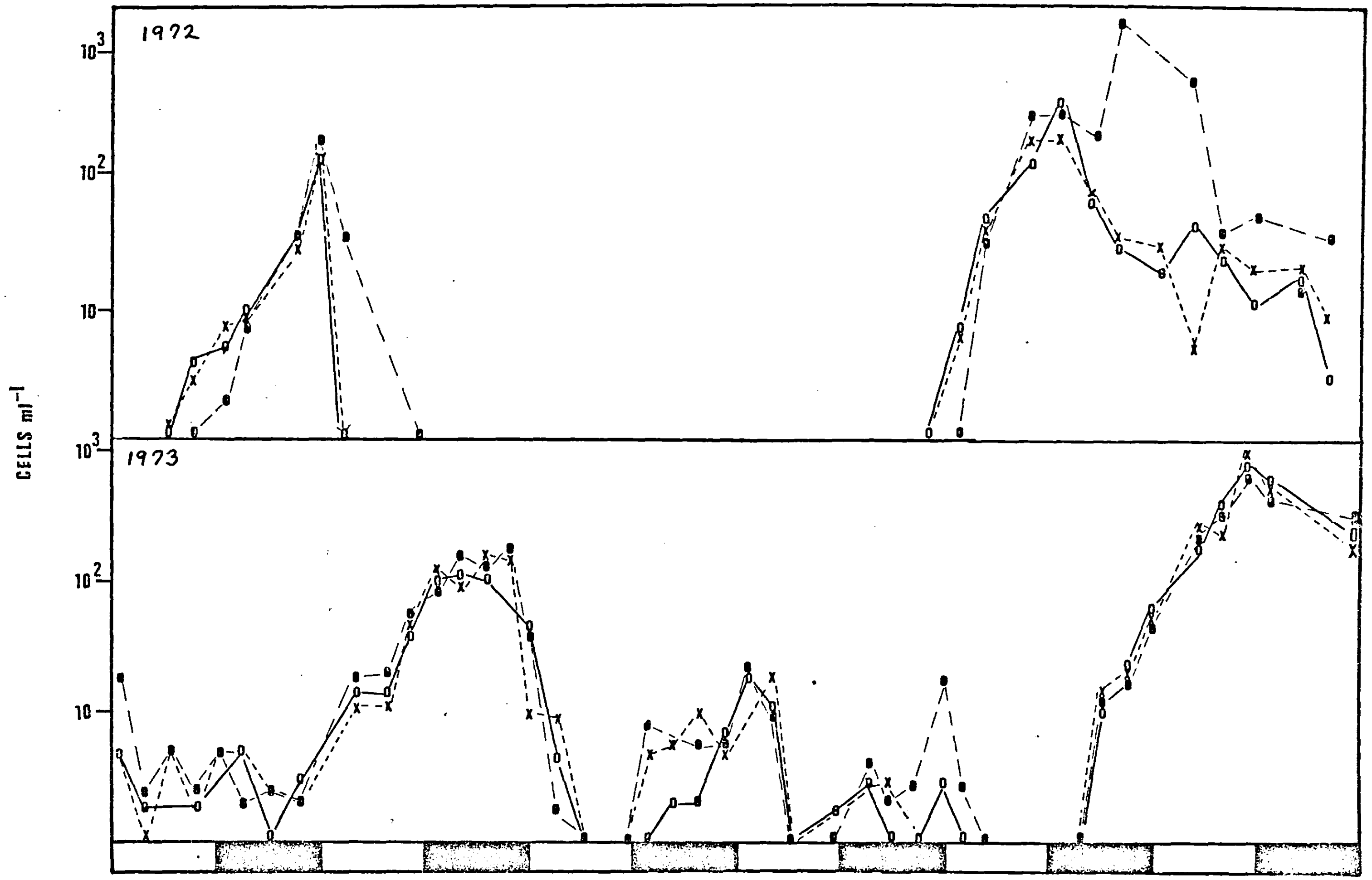


Figure 19. Stephanodiscus astraea (cells $ml.^{-1}$) at 3 depths in Wraysbury Reservoir during 1972 - 1973.

(O - 1 metre; X - 9 metres; ● - Bottom)

result of turbulence. Ridley (1970) noted a delay of up to a month in spring growths in supply reservoirs which could be a result of advective flow of water in from the river and eventually out to the filter beds. This delay is more fully discussed in the section on turbulence and phytoplankton production (Section D iv). The spring growth of 1973 reached a maximum standing crop of 200 cells $ml.^{-1}$ (5.0×10^5 $\mu m.^3$ $ml.^{-1}$) (40 $\mu g.$ $l.^{-1}$ chlorophyll-a; 2×10^3 $\mu g.$ $l.^{-1}$ carbon; and 2.0×10^7 $\mu m.^3$ $ml.^{-1}$ T.P.V.). Rapid warming of the water column (See Section on Solar Radiation, Appendix E) might have increased the rate of sedimentation so that the standing crop was reduced. the effects of sedimentation rates and other cropping factors on standing crop were discussed by Uhlmann (1971). Should the rate of loss of cells exceed the rate of reproduction, the standing crop will decline.

In early July 1973 there was a small pulse of S. astraea in the upper layers (above 5 metres) of the reservoir when there was a slight vertical temperature differential. Due to the small numbers and the short growth period it could not be determined if the growth was coincidental with the temperature differential or was resultant. During July and August live cells were frequently found in the mud and occasionally in the volume samples.

Since the complete volume of the reservoir had been replaced about twice or more in the summer period (4 months), many cells of S. astraea suspended in the water column from the spring growth are likely to have been removed or lost by advective flow as well as by sedimentation. The autumn innoculum is possibly dependent on living cells at the bottom of the reservoir. This is in agreement with Reynolds

(1973a) who had found very high sinking rates of Stephanodiscus astraea (particularly moribund cells) as compared with Asterionella formosa or Fragillaria spp.

The autumn growth of 1973 was delayed in comparison with the autumn growth of 1972, but was much higher in terms of standing crop. This population (1973) of S. astraea reached a maximum of 1.0×10^3 cells $ml.^{-1}$ (1.3×10^7 $\mu m.^3$ $ml.^{-1}$), with a chlorophyll-a level of 100 $\mu g.$ $l.^{-1}$; carbon of 7.8×10^3 $\mu g.$ $l.^{-1}$; and a total particulate volume of 1.0×10^7 $\mu m.^3$ $ml.^{-1}$. The close similarity between calculated algal volume and T.P.V. suggests that a large part of the volume of suspended particles in the reservoir were cells of Stephanodiscus.

During the first autumn growth in 1972, jetting was continued through September and into early October. In the second year jetting was stopped in early September (1973), and the low velocity inlets were used. Although there was a drop in water temperature, natural turbulence (wind induced) was not sufficient to re-suspend the large cells as sinking rates were too high in September and October 1973. This delay suggested that natural turbulence was sufficient to re-suspend the cells of Stephanodiscus later in the autumn. Re-suspension and vertical circulation of the large cells were delayed until November 1973 when wind induced turbulence was sufficient to suspend the cells throughout the winter. It is doubtful if loss of cells by outflow could have caused such a large delay, and probable that the timing of growths of S. astraea in Wraysbury Reservoir is dependent to a large extent on the interaction of turbulence and sinking rates.

Asterionella formosa was originally in the reservoir in very low numbers, and was not noted in sufficient numbers to determine the standing crop until after river input was initiated. Although two forms of *Asterionella* were present (similar to those described by Ruttner (1939) as var. *epilimnetica* and *hypolimnetica*) only the larger-celled form was present in substantial numbers. The first evidence of growth occurred slightly after the decline of the autumn *S. astraea* population (Figure 20). This growth was very small, reaching only 50 cells ml^{-1}, and might have been light and temperature or nutrient limited. Although not of any major importance in terms of water supply, this growth did suggest that whatever limited the growth of the preceding *Stephanodiscus*, it was not apparently nutrient limitation (Kilham, 1971). As did the large centric diatom, *Asterionella* remained in suspension during the winter. In the spring of 1973 *Asterionella* reached a maximum of 400 cells ml^{-1} (3.2×10^5 μm^3 ml^{-1}), but would not have contributed much to the total production of the reservoir at that time. During early July 1973, due to rapid warming of the upper layers of the water column and inconsistent jetting, a moderate temperature and hence density gradient occurred. This incipient thermocline was associated with a rapid growth of *Asterionella* in the upper five metres of the reservoir. Cell numbers reached a peak of 1.2×10^4 ml^{-1} (9.6×10^6 μm^3 ml^{-1}). Below this depth cell concentrations of 3.0×10^3 and 6.0×10^2 cells ml^{-1} were found at the middle and bottom depths respectively, and these cells were probably settling out from above the incipient stratification. Possible reasons for this sudden growth, and the generally more moderate growth of *Asterionella formosa* in Wraysbury Reservoir are discussed in association with the production experiments in Section D iv. The following autumn only a few cells (< 50 cells ml^{-1}) were found.

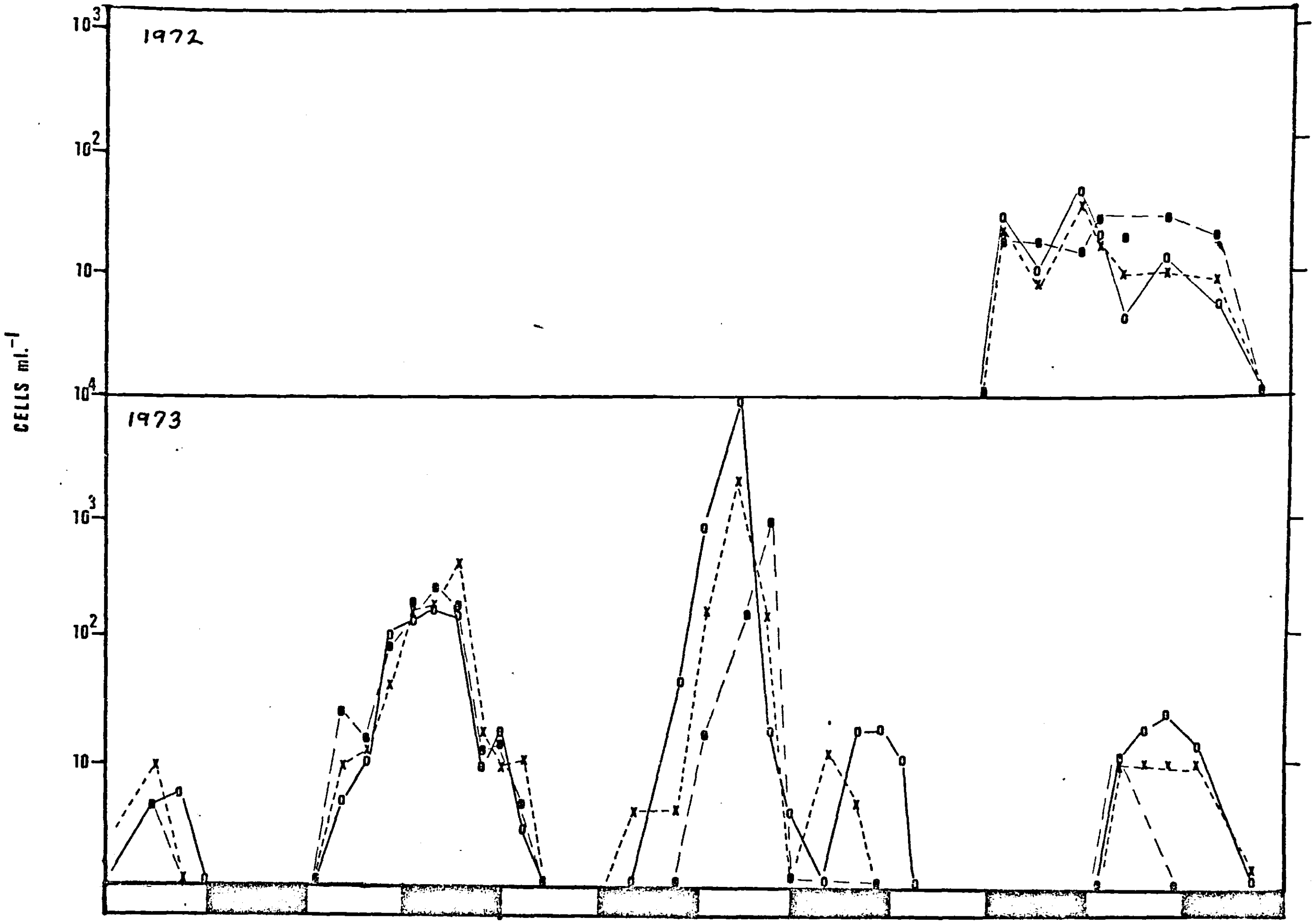


Figure 20. Asterionella formosa (cells ml.$^{-1}$) at 3 depths in Wraysbury Reservoir during 1972 - 1973.

(O - 1 metre; X - 9 metres; ● - Bottom)

Melosira granulata (Ehrenb.) Ralfs. was a common warm water form in the reservoir. Reynolds (1973) considered increased water temperatures to be instrumental in stimulating the growth of this diatom, but cautions that the alga might require substances or other conditions which are only available in the summer. Rodhe (1948) suggested that organic substances (perhaps similar to those sulphur containing substances discussed by Harvey (1939)) might be essential for growth of some diatoms, and mentions Melosira granulata and Stephanodiscus astraea as possible examples. Observations made by Rodhe suggested that these organisms are facultative mixotrophs. As Zajic and Chiu (1969) conclude that light stimulates heterotrophic growth by the formation of A.T.P. the production ecology of such organisms would be extremely complex.

M. granulata was present in low numbers during the autumn of 1971, but did not reappear until late August 1972 (Figure 21). Growth was relatively low and a maximum of 50 filaments ml^{-1} (1.5×10^5 μm^3 ml^{-1}) occurred in early October. By December the growth had dissipated, although a few filaments remained until April 1973.

The growth of the second summer was the largest, and reached its maxumum very quickly. It is possible that this growth was initiated in the quiescent areas about the Outlet Tower and Limnology Tower I. Sampling at Limnology Tower II, and at the four corner buoys revealed only small numbers of filaments, yet filament concentrations at the Outlet were such that the primary filters at Ashford (Middx.) were being rapidly blocked. The growth soon spread throughout the entire basin but rapidly declined as river input was changed from jetting to low velocity input and sedimentation rates increased.

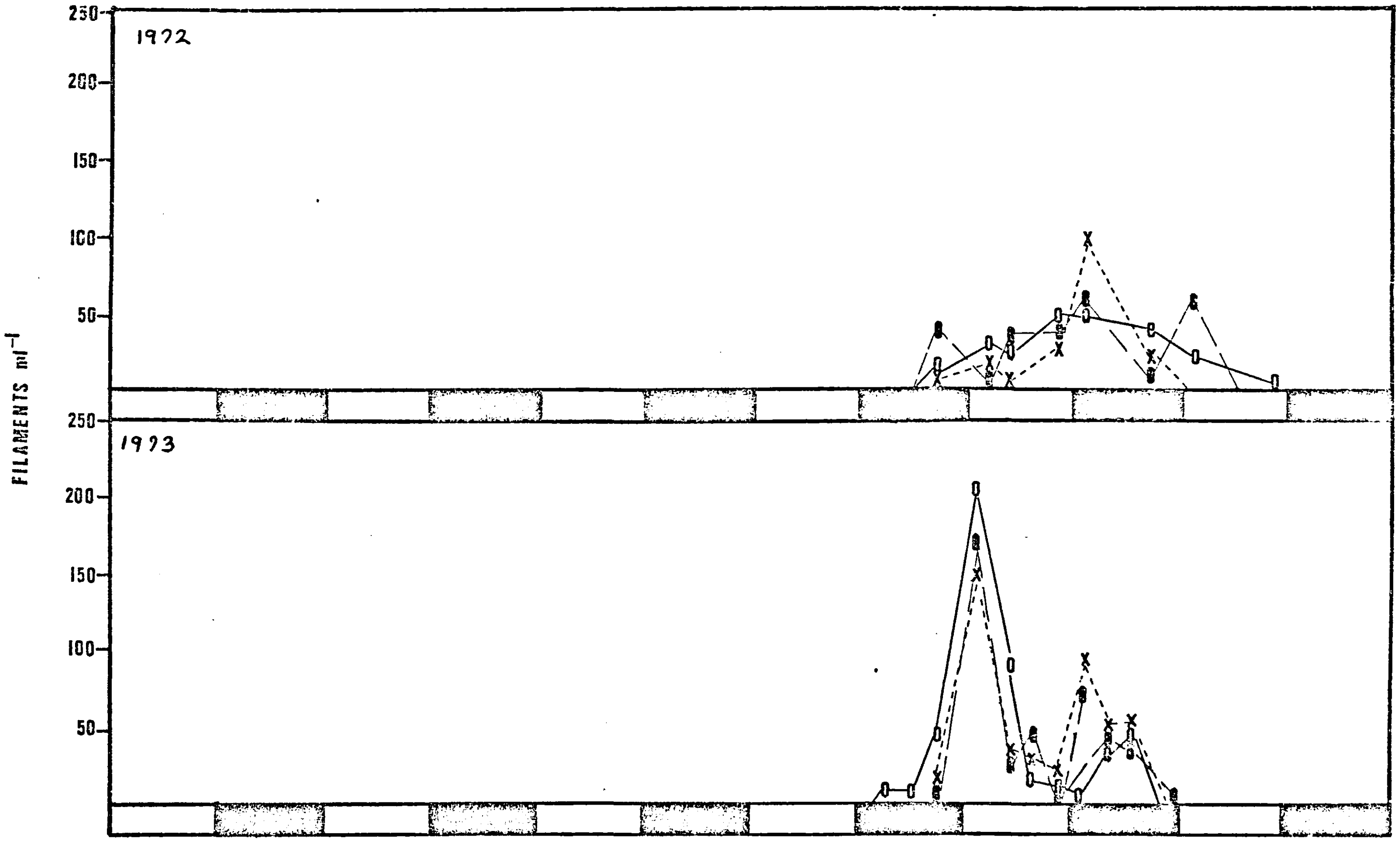


Figure 21. *Melosira granulata* (filaments ml.$^{-1}$) at 3 depths in Wraysbury Reservoir during 1972 - 1973.

(O - 1 metre; X - 9 metres; ● - Bottom)

During the first summer's growth (1972) the inlet jets were being used, and this artificial turbulence did not seemingly increase the production of *M. granulata*. The decline of the second summer's growth was coincident with the change to low velocity input. This second growth produced a maximum of approximately 100 filaments $ml.^{-1}$ (3.0×10^5 $\mu m.^3$ $ml.^{-1}$), and some filaments remained in the water column until December 1973 in very low numbers ($<$ 10 filaments $ml.^{-1}$). Some observations of possible physiological resting stages in *Melosira italica* subspecies *subarctica* have been made by Lund (1966) and similar observations for *Melosira granulata* have been made by Reynolds (1973). Cells of *M. granulata* with shrunken contents were not common in the reservoir and this might be a function of the aerobic microzone maintained by artificial and natural turbulence. *Melosira granulata* and *Stephanodiscus astraea* were frequently found living in mud samples. Both species are probably mero-planktonic, but *Stephanodiscus astraea* showed no distinct morphological differentiation. *Asterionella* was seldom found living in mud samples possibly as a consequence of low oxygen tensions, and lack of light (See Figures 27 and 28).

The summer periods were dominated by Cyanophyceae, including *Aphanizomenon flos-aquae* (L.) Ralfs., *Anabaena flos-aquae* (Lyngb.) Breb. with infrequent occurrences of *Microcystis aeruginosa* Kg. Cultured mud samples often produced growths of *Oscillatoria* sp., but this organism was never directly observed in reservoir samples.

Surface blooms were rare, and only occurred under very calm conditions. The slightest wind mixing often resulted in the homogeneous distribution of the algae and because of this, populations were generally

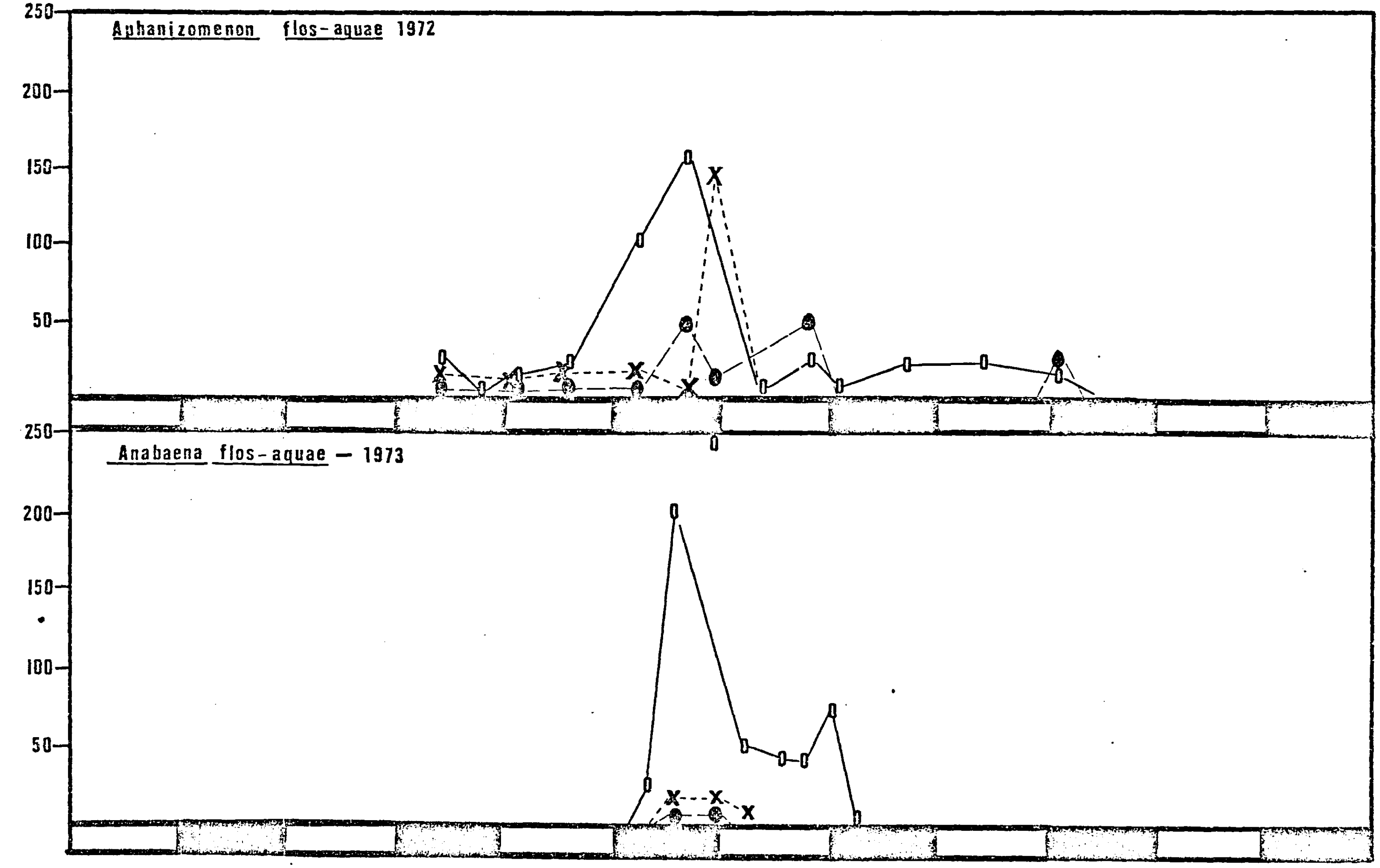


Figure 22. Dominant Cyanophyceae of Wraysbury Reservoir during 1972 (*Aphanizomenon flos - aquae*, trichomes ml.$^{-1}$) and 1973 (*Anabaena flos - aquae*, coils ml.$^{-1}$). Depths as in Figure 21.

low (Figure 22) with chlorophyll-a and carbons indicating a slight vertical heterogeneity (Appendices A and B) as shown in an increase in the range of the values of chlorophyll-a and carbon. Members of the Cyanophyceae can often control their own mixing depth by means of gas vacuoles (Smith and Peat, 1967a, -b) and this often results in surface blooms (Reynolds, 1971, 1972). As can be seen in Figure 24 the trichomes of *Aphanizomenon* and the filaments of *Anabaena* were vertically distributed at most times as a result of combined artificial and natural turbulence. No doubt mixing is an important parameter controlling their production (McGill, 1970), but the reason for the change of dominance of *Aphanizomenon flos-aquae* in 1972 to *Anabaena flos-aquae* in 1973 is unclear and other factors such as rates of warming of the water column and actual temperature must be considered (Hammer, 1964) as well as the amount of incident radiation. There was no indication of toxicity effects as standing crops were much too low (Heaney, 1971).

Another frequent summer form was *Tribonema* spp. (possibly three species existed; *Tribonema vulgare* Pasch., *Tribonema minus* (Wille) Hazen, and *Tribonema angustissimum* Pasch. as described in Huber - Pestalozi (1941)). This alga did not grow well, reaching a maximum of less than 100 filaments ml^{-1} (2.0×10^3 cells or $\lesssim 8.0 \times 10^5$ µm^3 ml^{-1}) in 1972 and 1973, and presents a peculiar problem to phytoplankton ecology of reservoirs. *Tribonema* has grown well in the only other mixed reservoir (Queen Elizabeth II) of the Thames Valley (McGill, 1969), but has not yet appeared in Wraysbury in significant numbers. This rarity of occurrence, coupled with its method of reproduction (by the requirement initially of a substratum, and by aplanospores) discouraged intensive study in this reservoir. Much more work is required to determine the effects of vertical mixing on this organism.

Of the many flagellates (mostly unidentified) present in both the river and the reservoir, Cryptomonas spp. (including C. curvata and C. ovata) and Rhodomonas minuta var. nannoplanctica were the most frequent and abundant. In late autumn of 1971 both genera were present in the reservoir, but Cryptomonas reached a higher standing crop at 150 cells $ml.^{-1}$ (6.0×10^4 $\mu m.^3$ $ml.^{-1}$) as compared with Rhodomonas with more cells (512 $ml.^{-1}$) but a lower volume (5.0×10^4 $\mu m.^3$ $ml.^{-1}$). Representatives of the two genera grew in the spring of 1972 but Rhodomonas reached a higher standing crop of 700 cells $ml.^{-1}$ (7.0×10^4 $\mu m.^3$ $ml.^{-1}$) as compared with 80 cells $ml.^{-1}$ (3.2×10^4 $\mu m.^3$ $ml.^{-1}$) for Cryptomonas. Both were present throughout the period of study, but neither exceeded 300 cells $ml.^{-1}$ during the remaining investigation of 1972 - 1973. Other flagellates were present and included Chlamydomonas, Carteria, and dinoflagellates such as Ceratium hirundinella (present only in the summer periods) and one or possibly more species of Gymnodinium (in autumn and winter periods only).

Desmids were infrequent as would be expected in such eutrophic conditions (Rawson, 1956), but nutrient levels might not be the only factors affecting their presence or absence. In the autumn of 1971 a population of Cosmarium botrytis (Bory.) reached a peak of 400 cells $ml.^{-1}$ (1.6×10^6 $\mu m.^3$ $ml.^{-1}$) but occurred sporadically in very low numbers after jetting.

Pediastrum boryarum (Turp.) Meneghini and P. duplex (Turp.) Meneghini were often found near the interstitial mud - water layer but rarely in the water column. Pediastrum was probably originally innoculated from King George VI Reservoir. Scenedesmus quadricauda (Chod.) G. M. Smith and S. acutus (Meyen) were frequent along with many other species of Scenedesmus (See Bellinger (1968) for a taxonomic revision of Scenedesmus in the Thames Valley) were common but not abundant in either the river or the reservoir during this investigation. There was little evidence of chytrid infections and it is doubtful if such infections affected the standing crop of any of the previously mentioned species.

Zooplankton abundance was estimated in dry weight per vertical net haul. As zooplankton populations were low, grazing was relatively unimportant. This data is presented in Appendix D. The reason for the low zooplankton populations might be the lack of organic detritus (Duncan, 1974 personal communication) and might increase as the level of organic detritus increases with the age of the reservoir.

C. Major Nutrients and Related Chemical Factors

Figure 23 outlines the levels of PO_4-P, NO_3-N and SiO_2-Si in the reservoir during 1972 and 1973. As Wraysbury was initially filled from King George VI Reservoir, a storage reservoir, the nutrient load was relatively low as compared with that of the River Thames. The filling of Wraysbury occurred in the late spring of 1971, and SiO_2-Si was low in King George VI Reservoir as a result of a vernal diatom growth. Phosphate and nitrate concentrations were high as compared with those of most natural bodies of water (Lund, 1949, 1950; Hughes and Lund, 1962; Hutchinson, 1944, 1957).

In late March 1972, River Thames water was jetted into the reservoir. From this date onwards, Wraysbury was an active supply reservoir with a more or less continuous input and outflow. Nutrients increased in concentration until the basin was in equilibrium with the inflowing river water by June 1972. The change in nutrient concentrations might have had an effect on the flora of the reservoir (Reynolds, and Allan, 1968) considering the consequential rarity of desmids such as Cosmarium, Pediastrum, and Staurastrum which were frequent in 1971.

C (i). River Thames Nutrient and Chemical Analyses:

Both vernal diatom growths of the River Thames at Datchet were probably SiO_2 limited, similar to those reported by Kowalczewski and Lack (1971) and Lack (1971). Swale (1963, 1964) noted that growths of Stephanodiscus hantzschii require slowly flowing water ($<.5$ Km. hr.$^{-1}$) and recorded a maximum of 4.0×10^4 cells ml.$^{-1}$, similar to the maxima recorded in 1972 and 1973 in the River Thames. The high chlorophyll-a, carbon, and T.P.V. suggest the rich production potential of Thames water, and emphasize the low phytoplankton production in the reservoir. Despite the more or less constant nutrient and biological nature of the river water, reservoirs of the Thames Valley vary in total production capabilities. Production is often lower in the reservoir environment than in the river environment.

River nutrients such as phosphate, nitrate, and soluble carbonate (expressed as alkalinity) were high (See Table II). The hydrogen ion concentration, and conductivity were indicative of a good supply of available nutrients. Although trace elements were not directly measured, bioassay (Section D (iv)) indicated that none were limiting, and Lund and Talling (1957) have suggested that some nutrients (potassium, calcium, magnesium, and sulphate) are unlikely to reach limiting concentrations.

Possible effects of flood rainfall, flow, tributaries, and industrial and urban effluents can probably account for the wide range of nutrient concentrations in the river. Despite the wide range, all nutrients excluding SiO_2 are probably abundant. It is sufficient to state here that nutrient depletion, such as with SiO_2 during the vernal growths, was quickly compensated for, and high nutrient levels returned rapidly.

The double pulse of S. hantzschii in the spring of 1973 (See Figure 15) was probably an artifact of rainfall diluting numbers, and increasing the river flow. Rainfall could only affect the reservoir in any major nutrient sense indirectly via the River Thames and the inlet regimes.

TABLE II

River Thames Nutrients and Chemistry

1972 - 1973

	Mean	Range	Comments
P - PO_4 (μg. $l.^{-1}$)	137.0	73 - 215	
N - NO_3 (mg. $l.^{-1}$)	6.7	5.0 - 11.0	
SiO_2 (mg. $l.^{-1}$)	8.5	$<$ 1.0 - 20.0	fluctuated with *S. hantzschii*
pH	8.2	7.8 - 8.8	
$CaCO_3$ (mg. $l.^{-1}$)	206	111 - 242	
Conductivity (μMhos.)	567	550 - 600	

C. (ii) - (v): Wraysbury Reservoir Nutrient and Chemical Analyses

C. (ii). SiO_2 Availability:

Silicon is available to diatoms in the forms of silicates and silicic acid (King and Davidson, 1933). Silicates are probably the most important nutrients as Wraysbury Reservoir supports mainly diatom growths. Low silica concentrations probably limited the original S. astraea growth in early spring, 1972. This population reached only a low standing crop of about 200 cells $ml.^{-1}$ and declined rapidly. Even after river input there was no second pulse when SiO_2 was introduced from the River Thames at concentrations of 10 mg. $ml.^{-1}$. This might have been a result of low numbers of living cells, and the inability of the artificial turbulence to overcome the sedimentation rate which was increasing, partly as a result of the warming of the water column (Figure 26). With high phosphate levels, and good light penetration (Figure 28), SiO_2 depletion resulted in the death of reproducing cells. Only those cells at or near the bottom of the reservoir could act as innoculum for a later growth.

Van Landingham (1964) generalized that diatom maxima were more correlative with water temperature and dissolved nutrients than with the time of year. This agreed with Kilham's (1971) hypothesis that declining silica concentrations might influence the sequence of seasonal succession, and this appeared to be the reason for the failure of a second vernal growth after the innoculation of water rich in silica into the reservoir. Kilham reported that the genus Stephanodiscus was very efficient at utilizing silica and the diatom often achieved

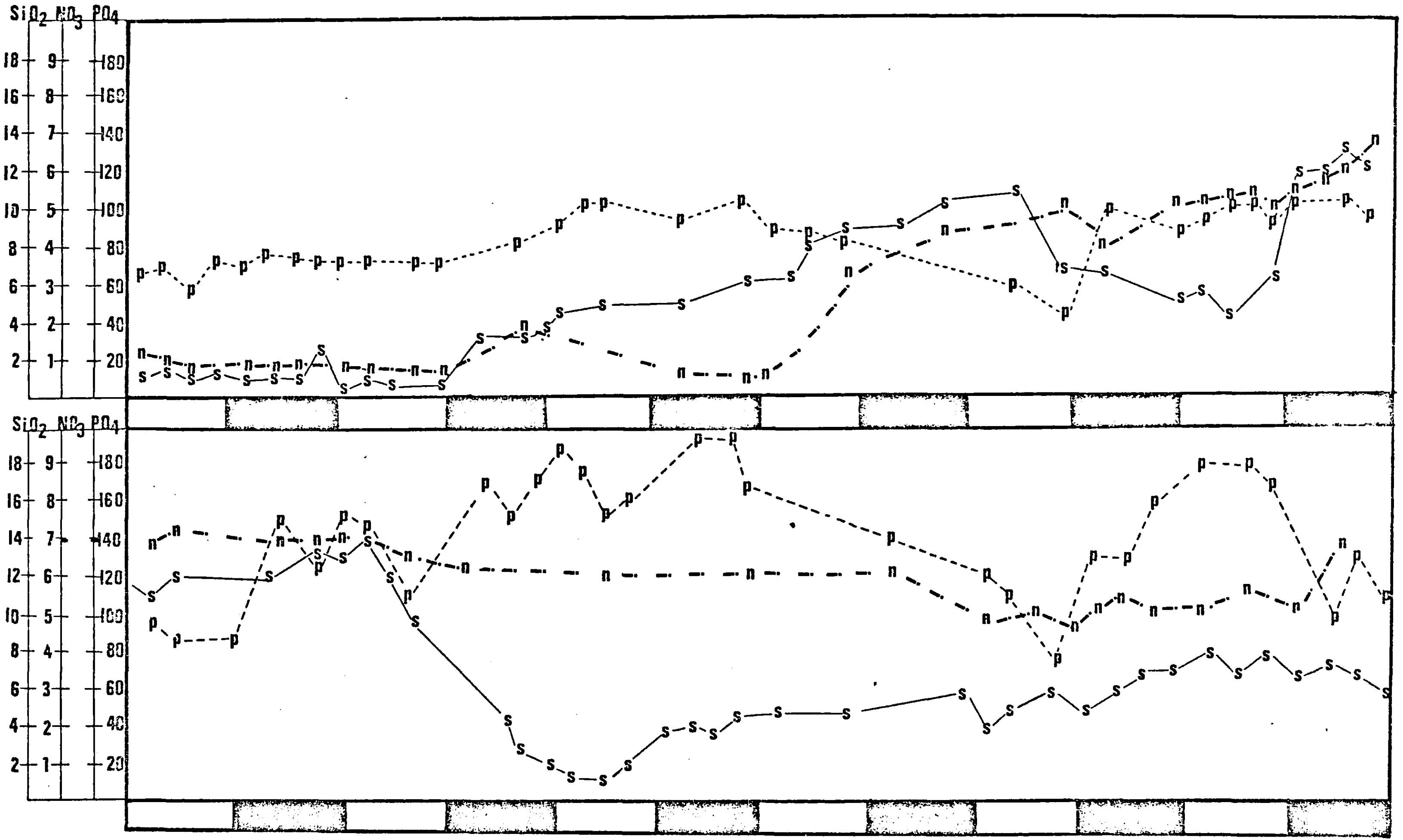


Figure 23. Major nutrients of Wraysbury Reservoir, SiO_2 S S; PO_4 P P; NO_3 N N; during 1972 - 1973.
Expressed as Column Means.

dominance at SiO_2 concentrations of 0.6 mg. $l.^{-1}$. Assuming the SiO_2 was completely utilized in the water column in spring 1972, an assumption quite plausible as a result of the high phosphate levels, even the silica-rich river innoculum could not sufficiently raise the available SiO_2 concentrations before the water column was too warm to support a significant standing crop.

The assimilation and utilization of silica was studied by Jorgensen (1950, 1952, 1953, 1955a, -b, 1957) and by Lewin (1953, 1954, 1955a, -b) and both concluded that the assimilation could vary within and between species. Lund (1950) made similar observations of diatom periodicity and silica availability, and noted that some of the variations in silica content were a result of interaction with other nutrients, phosphate in particular. Silica content is often inversely proportional to the number of cells (Jorgensen, 1955a) although some diatoms such as Asterionella cannot produce cells containing low amounts of silica (Hughes and Lund, 1962a); this is probably true of Stephanodiscus astraea which was heavily silicified (perhaps as a response to high phosphate levels) (See Figures 4 and 5). Such a large diatom, an efficient utilizer of silica, would use large amounts of SiO_2. McGill (1969) estimated that 4 mg. $l.^{-1}$ of SiO_2 in Queen Elizabeth II Reservoir could produce 10^6 cells $l.^{-1}$. Light conditions, available nutrients, and temperature would be temporarily optimal in Thames Valley Reservoir for growths, but such a large maximum was never achieved in the deep stirred reservoirs. Happey (1970d) supported McGill's estimate when she suggested that 10^6 cells of Stephanodiscus rotula (Kutz.) Hendey (small form of S. astraea)? required 0.5 - 0.73 mg. $l.^{-1}$ SiO_2. During the present investigation the

SiO_2 content of S. astraea was found to vary widely between 1.0 - 5.0 mg. $l.^{-1}$ for 10^6 cells, and approaches the estimate of Einsele and Grim (1932) of 8.5 mg. SiO_2 for 10^6 cells of Stephanodiscus astraea of much larger volumes. This large variation could be a result of the large size distribution of the cells ($7.5 \times 10^3 - 20.0 \times 10^3$ μm^3) in the reservoir. The influence of the underwater light climate of the reservoir on slowing the growth rates of the diatom might result in increased silica content (Jorgensen, 1955a) per cell.

Once advective flow was initiated, the SiO_2 concentrations ranged from 2.0 - 16.0 mg. $l.^{-1}$. It is doubtful if SiO_2 was directly a limiting resource factor from this time onwards (Figure 23). River innoculum and possible recycling despite the oxidized microzone (Tessenow, 1964, 1966) maintained high SiO_2 concentrations. Recycling of SiO_2 in aerobic conditions is questionable, but is probably unimportant in that rates of assimilation would exceed rates of nutrient release from the bottom. [Note, however, that 16.3 - 49 mg. Si per 100 g. of dried reservoir mud were found between March 21 and December 12, 1939 (33rd. Annual Report, Metropolitan Water Board, 1940; p.46).]

Another possible source of silica was suggested by Cheng and Tyler (1973) and Edwards and Lise (1973); that silica was attached to tryptonic particles. In bodies of water with a high pH, there would be a tendency for the bound silica to become dissolved.

As the original 1972 growth of S. astraea was initiated at 2 mg. $l.^{-1}$, it is doubtful if limiting concentrations were directly achieved after river input. Even the largest growth of S. astraea in Wraysbury to date was declining before silica depletion. (Compare Figures 19 and 23). It is apparent that the growth rate of S. astraea was held in check and the population gradually decreased. Light limitation (including self shading) and temperature effects possibly were the parameters suppressing the growth of the population. Even in a turbulent mixed water column there is one consistent force affecting particle distribution and that is gravity. A reduced growth rate and a steady sinking rate influenced the size of the standing crop more than nutrients. Even in the later phases of this growth (January, 1974) SiO_2 did not drop below 1 mg. $l.^{-1}$. A silica budget was not made for the reservoir as a result of the complexity of the problem and sampling routines required.

C (iii). P - PO_4 Availability:

Phosphates were initially high in Wraysbury, and never showed signs of limiting growth. Although some fluctuations occurred (Figure 25), once equilibrium with the river was established, phosphates had a mean concentration of 100 µg. $l.^{-1}$ with a range of 40 to 180 µg. $l.^{-1}$.

The role of phosphorus was discussed by Stumm and Stumm - Zollinger (1972); Goldberg, Walker, and Whisenand (1951); and Weaver (1969). Even when not limiting, phosphate concentrations can change the flora of a body of water (Lund 1959b), but this probably was not the only cause of the change in flora at Wraysbury Reservoir before and after jetting. Lund (1950) and Mackereth (1953) noted that phosphates were limiting for Asterionella formosa at levels less than

1 µg. l.$^{-1}$. Similar concentrations were reported by Ignatiades (1969) to limit spring diatom growths in the lower Saronicas Bay (Aegean Sea). As the values in the Thames Valley are 10 - 100 times these values, it seems unlikely that phosphates might limit growth.

C (iv). NO_3 Availability:

Nitrates increased in Wraysbury Reservoir at the time of input of river water. Lund (1950) reported that Tabellaria, Fragillaria and Asterionella could utilize NO_3 at concentrations below 0.1 mg. l.$^{-1}$. Nitrate levels of Wraysbury were again 10 - 100 times this amount with a mean of 6 mg. l.$^{-1}$ and a range of 1 mg. l.$^{-1}$ to 11 mg. l.$^{-1}$. The gradual increase in NO_3 suggests that originally concentrations were low as supplied from King George VI Reservoir, and gradually built up from the River Thames. The oxidized layer at the bottom of the reservoir would act as a nutrient barrier to reduced substances underneath it; hence the bottom is a nutrient sink, which might have delayed the equilibrium of the river and reservoir water. This oxidized zone in itself does not explain the gradual increase in NO_3 which was slower than would be predicted by dilution. Mud samples in early 1972 were unobtainable using an Eckmann bottom grab as little settlement, hence nutrients, had accumulated.

Only by the summer of 1972 were mud samples obtainable. The large amount of particulate matter from the river which settles out is illustrated by comparing the T.P.V. of the river with the T.P.V. of the reservoir during 1972 and 1973 (Figure ~~20~~ 18). Only during growths of S. astraea were total particulate volumes greater in the reservoir than in the river. If rapid filling in of the basin can be considered as 'ageing', reservoirs in the Thames Valley 'age' rapidly in comparison with many natural lakes. This 'filling in' effect might affect nutrient balance by increased reduction.

C (v). Alkalinity, pH, and Conductivity:

Conductivity was approximately 500 µMhos with a range of 470 - 560 µMhos suggesting high ionization of salts. Hydrogen ion concentrations were generally constant, pH was approximately 8.2 with a range of 7.7 - 8.4. Alkalinity, measured as $CaCO_3$, was high at $\simeq$ 200 mg. $l.^{-1}$ as would be expected owing to the chalk basin the River Thames flows through in part. There was plenty of available dissolved CO_2 in the water but this fluctuated diurnally and seasonally.

All measured nutrients excluding SiO_2 were abundant, and did not limit phytoplankton production in the reservoir. Only before being used as a supply reservoir did SiO_2 limit production, and possibly in 1973 - 1974 did SiO_2 exert an indirect effect on algal production. Bellinger (1968) and McGill (1969) both found that nutrient supply was generally adequate in reservoirs.

Gardiner (1941) suggested a means of estimating gross production of diatoms by the rate of silicon depletions. The Barn Elms Reservoir in 1938 had a growth of _S. astraea_ reaching 3.0×10^3 cells $ml.^{-1}$, and _Asterionella formosa_ preceded this growth reaching approximately the same cell concentration. Neither population responded to nutrient enrichment or replenishment. At that time phosphorus and silica were at approximately the same concentrations as they were during 1971 - 1974, yet such large crops were not produced in Wraysbury Reservoir. Nor could the crops produced be directly related to nutrient utilization alone, suggesting that additional factors were affecting the Wraysbury populations. The enrichment is such that control measures would be costly should the production potential of the water be achieved.

D. Physical and Physico-chemical Factors

D (i). Dissolved Oxygen and Temperature:

The use of a Mackereth oxygen probe facilitated dissolved oxygen determinations. Figure 25 illustrates the dissolved oxygen profiles of Wraysbury Reservoir during 1972 and 1973. In the first year (1972) the isopleths ran vertically indicating the homogeneity of the water column with some indication of the photosynthetic activity of Aphanizomenon flos-aquae in the upper layers during the summer, and a rapid drop in dissolved oxygen in later July. The vernal diatom growth was not sufficient to alter the oxygen profile, and the autumn growth indicated a tendency for greater photosynthetic activity near the surface despite artificial mixing.

In the second year, however, the isopleths illustrated that 1973 had higher oxygen demands. Isopleths, though vertical in the spring and early summer indicating homogeneity, tended to be horizontal in the later summer suggesting a vertical heterogeneity. The spring diatom growth resulted in a continuous oxygen gradient as did the late autumn growth. A quick outburst of Asterionella formosa during the first week of July was confined to the upper five metres as a result of a temperature discontinuity with depth (Figure 26). This was reflected in the dissolved oxygen profiles.

Below five metres during the second summer there was a distinct oxygen gradient to the bottom which lasted from May until August 1973. No doubt this resulted from the high oxygen demand of the mud of the reservoir brought on by rapid, uneven warming of the water column and

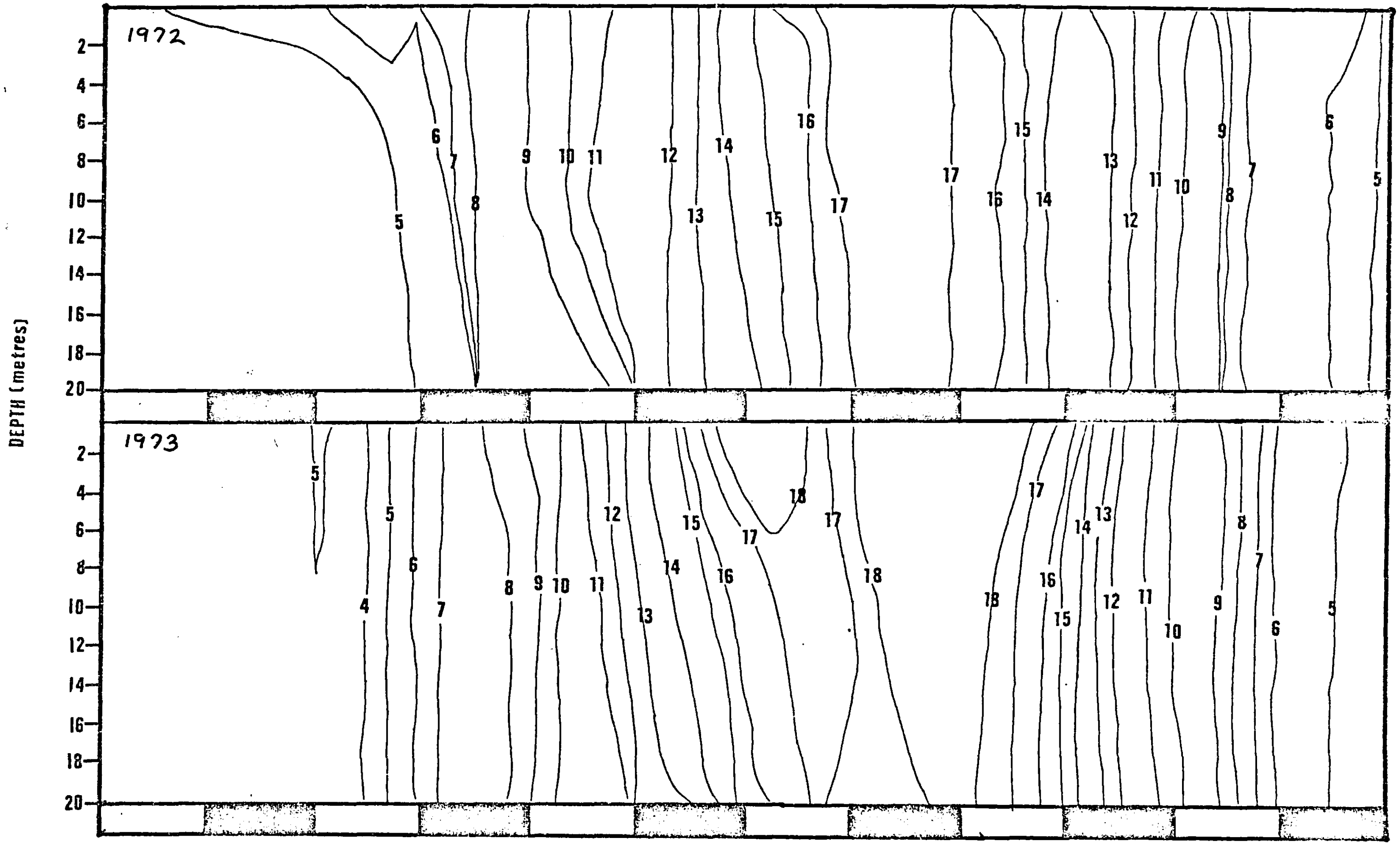


Figure 24. Temperature – depth profile of Wraysbury Reservoir during 1972 – 1973. (°C.)

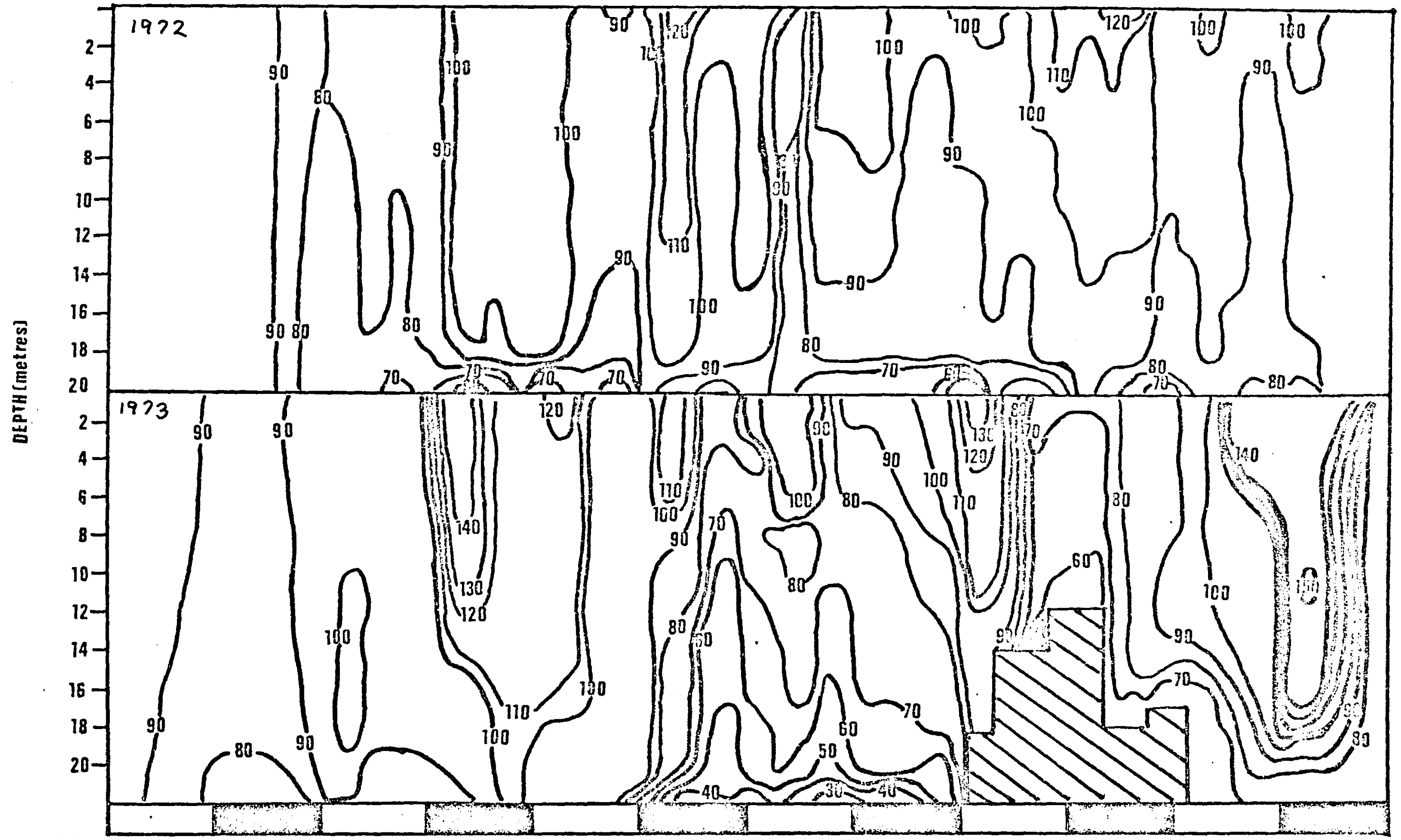


Figure 25. Dissolved oxygen (percent saturation) - depth profile of Wraysbury Reservoir during 1972 - 1973.

the resultant restricted vertical mixing. As water temperatures increased there was rapid sedimentation of organic and inorganic particles from the river and reservoir.

In 1972 the summer was cool and cloudy. As this was the first summer in which Wraysbury was a supply reservoir, small amounts of bottom sediment had accumulated. In general, the bottom was well oxidized, but after a full year of sedimenting river seston and three moderate diatom growths in the reservoir, the oxygen demand increased rapidly. Although some evidence of reduction in the mud samples was found, this was a transient feature and was often confined below the mud-water interphase. Oxygen demand by the mud emphasized the periods of high productivity; the oxygen isopleths are crowded together as a result of the low dissolved oxygen content of the water. A growth by Melosira granulata at the end of the summer of 1973 is emphasized by this high oxygen demand by the mud. This was a small growth (See Section B) in comparison with the subsequent growth of Stephanodiscus astraea, but in terms of the oxygen profile would appear to be as intensive and productive because of the dramatic alteration of the oxygen content of the water. Dissolved oxygen of the reservoir was generally 90% saturation.

A direct effect of mixing was the maintenance of isothermal conditions (Figure 24). During the second summer there was a slight temperature gradient forming an incipient thermocline as a result of rapid warming of the water column due to climatological conditions and erratic artificial mixing. At all other times the reservoir was isothermal.

Rates of warming and cooling might have an influence on the periodicity and duration of phytoplankton growths, and actual temperature can directly affect production. *Stephanodiscus* spp. are possibly eurythermal (Happey, 1969d; Reynolds, 1973b). Temperatures at the start of spring and autumn growths varied between 5°C (Spring, 1972) and 15°C (Autumn, 1972) which supports this concept. *Asterionella formosa* is also eurythermal, but the situation might be more complex as populations of this diatom have been described as having both warm (*epilimnetica*) and cold (*hypolimnetica*) varieties (Ruttner, 1937) which can be differentiated by size. As mentioned before, the larger form tended to dominate, and probably it was populations of this particular diatom which were responding to different sets of ecological conditions as there was no major cell size variation between the summer and winter growths.

Hammer (1964) discussed the effects of temperature on blooms of *Aphanizomenon flos-aquae* and *Anabaena flos-aquae* in lakes of Western Canada. He noted that *Aphanizomenon* tended to bloom at 24°C and was found at a wide range of temperatures. According to Hammer, *Anabaena flos-aquae* appeared to have a limited temperature range of 15°C to 20°C and bloomed at $\simeq$18°C. Thses results were supported in the present work in terms of presence or absence of these species in Wraysbury Reservoir. *Aphanizomenon* was present throughout the year except the winter, and *Anabaena* was confined to the summer period. As neither species 'bloomed' in Wraysbury, it was not possible to make more detailed observations.

One of the most important effects of water temperature is its influence on sedimentation. Standing crops of phytoplankton are dependent on the disparity between reproductive rates and rates of loss. The major cropping factor during growths of S. astraea was sedimentation; as grazing and dilution factors (including loss of cells by advective flow (Brook and Woodward, 1956)) were small. As indicated in Figure 19, there is a large increase in cell numbers at the bottom of the reservoir at the end of each growth. Although sedimentation and mixing can directly affect the size of standing crop by loss of cells, indirect effects of mixing and sedimentation are often ignored. Other non-productive particles in suspension can affect the reproduction rate (Murphy, 1962) and a loss of non-productive particles by sedimentation can increase reproduction rates as light penetration is increased. Temperature and related density changes strongly alter the ratio of productive and non-productive particles in suspension, and so affect the production potential of the reservoir.

D (ii). Light Penetration:

The vertical attenuation of radiant energy can determine the rate of photosynthesis and growth of phytoplankton populations (Strickland, 1958; Jitts et al., 1964). Absorption properties of clear water were discussed by Smith and Tyler (1967) and absorption properties of more productive water were discussed by Birge and Juday (1929). Westlake (1965) made a critical review of the measurement of irradiance and transmission of under-water radiation, and noted that the absorption coefficient of water (ξ_w) is small in comparison to the total attenuation coefficient. Whitney (1938a) estimated ξ_w to be approximately 0.03. Generally the red wavelengths are absorbed and the blue ones transmitted (Whitney, 1938a, 1941a). Suspended matter, both organic and inorganic in nature, is responsible for the greater part of the scattering of light (Atkins, 1932; Atkins et al., 1954). The scattering produced by fine particles affects the short wave (Blue end of the spectrum) radiation more than the remainder. Water with suspended fine material acts like yellow filters because of high attenuation at both ends of the visible spectrum, and partially as a result of the colour of the suspended and dissolved materials. Angular scattering of red, green, and blue light by suspended particles was studied by Atkins and Poole (1954). They found that there was little difference between the scattering of red and green light, and that particles less than 0.1 µm. diameter did not produce significant amounts of scattering.

Jerlov (1951) reached similar conclusions that the scattering produced by suspended particles was only slightly dependent on the wavelengths of light, but found that particles less than 1.0 µm. were of little importance in scattering light. Burt (1955a, -b) concluded that the cause of extinction of light energy in Chesapeake Bay was particles less than 2 µm. in diameter, and that extinction was not closely correlated with diatom growths. The relationship of light scattering and particle diameter suggests that particles can be considered as spheres (Le Grand, 1939). The spherical surface area of particles can be determined with some degree of accuracy by particle size analyses, assuming the particles are randomly orientated (Haffner and Evans, 1974b).

Figure 26 illustrates the penetration of light using blue, green, yellow, red and neutral density filters in Wraysbury Reservoir. Also presented is the depth of the euphotic zones as determined by Talling's (1971) relationship:

$$Z_{eu} = \frac{3.7}{\epsilon_{min}}$$

where Z_{eu} is the euphotic depth, and ϵ_{min} is the minimum attenuation coefficient.

Blue was the least penetrating wavelength. This implied that a high number of small particles (<2 µm. in diameter) were constantly present in the water. Filtering of the water through a membrane filter (pores = 0.45 µm.) removed this optical effect of the water, and blue light was transmitted as well as green or yellow. Apparently particles between 0.45 and 2 µm. in diameter have large effects on the attenuation of radiant energy in the reservoir.

A comparison of phytoplankton counts (Figures 21 and 24), carbon, and chlorophylls (Figures 18 and 19) with light penetration suggests that light penetration is not constantly correlated with standing crop in Wraysbury Reservoir. Small and Curl (1968), Atkins and Parker (1951), Atkins and Jenkins (1953), and Riley and Schurr (1959) have been able to relate light penetration with chlorophyll-a in different environments, but Talling (1971) noted that the relationship of chlorophyll concentrations with the vertical attenuation coefficient in Lake Windermere was a transient phenomenon which did not hold after the autumn overturn. Haffner and Evans (1974b) studied the relationship of light attenuation and total particulate volume (T.P.V.) and total particulate surface area (T.P.S.A.) over the particle size range of

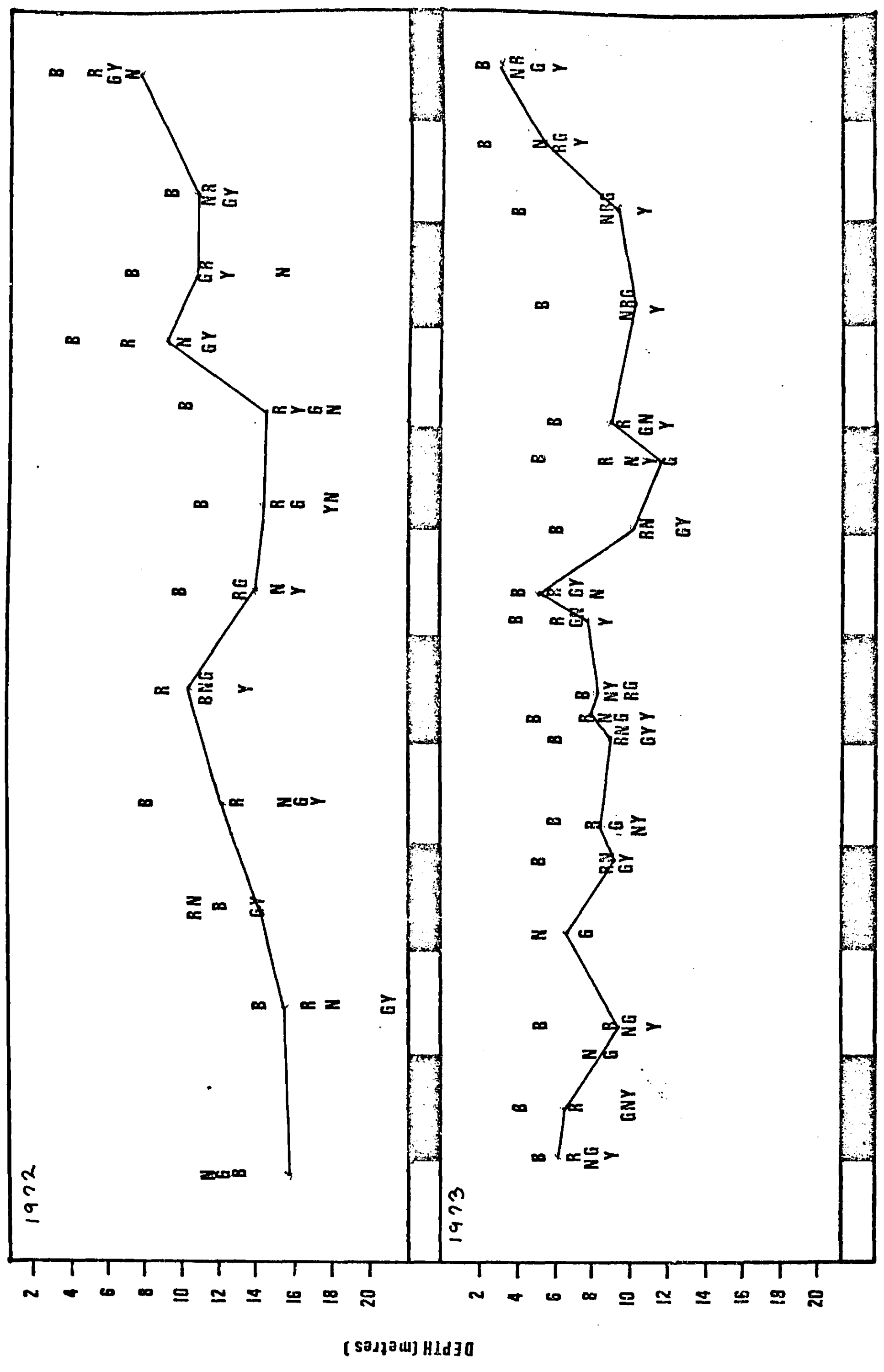


Figure 26. Light penetration, spectral modification, and the euphotic zone in Wraysbury Reservoir during 1972 - 1973.

$10\ \mu m^3 - 70.0 \times 10^3\ \mu m^3$ and found that T.P.S.A. was more constantly related to the vertical light attenuation then was T.P.V.

Determinations of T.P.V. can be related to biomass in reservoir environments (Evans and McGill, 1970) within certain conditions (T.P.V. $> 10^6\ \mu m^3$). Strathmann (1967) had suggested that the amount of organic carbon could be estimated from the cell volume (though see Williams, 1964), and it is by this association that the seston volume in terms of T.P.V. can be used to estimate biomass. Steele and Baird (1961b, 1962a, -b, 1965) discussed the associations of carbon and chlorophyll, and particularly noted that carbon values varied with detrital organic material. Weber and Moore (1967) found that 15.8% of the seston of the Little Miami River, Ohio, was organic matter, thus in such an environment T.P.V. would overestimate standing crop. Even though T.P.V. is a good determination of the volume of suspended particles, and is a much more sensitive method of determining seston load, its failure to be closely related to the vertical attenuation of natural light would suggest that previous relationships of light penetration and carbon, chlorophyll, or other measures of biomass are tenuous because of the influence of detrital material.

It was found by Haffner and Evans (1974b) that T.P.S.A. was closely related to the attenuation of the blue waveband and ε_{min}. A poor correlation was found between T.P.V. and the attenuation of all measured wavelengths. As the attenuation coefficient of the blue wavelengths was closely related to T.P.S.A. this supported the conclusion that small particles influenced the penetration of radiant energy (Atkins and Poole, 1954; Bartsch, 1959). Photosynthesis is, however, more affected by total photosynthetic energy available than by the quality available as a result of spectral modification with depth. For this reason, and for the ability to have long path lengths, ξ_{min} was selected as the better parameter to study the interaction of particle distribution and light penetration. Particles below 2.0 µm. in diameter and water colour accounted for 0.18 of the attenuation coefficient in Wraysbury Reservoir (See Haffner and Evans, 1974b).

Determining particle distribution with a Coulter Counter has been shown by Haffner and Evans (1974a) to be a very precise method. Analyses of water samples proved to be quick, and made a synoptic sampling technique possible. In addition, the frequency distribution of particles of different size classes (Table I) can be determined. This technique has been applied to investigating sampling errors resulting from particle distribution in the reservoir, and , most importantly, has been used as a basis for studying phytoplankton distribution and seston interaction. It is also possible to measure the effects of turbulence on phytoplankton production particularly in terms of the effects of turbulence on light penetration. Jerlov (1955) reported that scattering was proportional to the square of the diameter of a particle, and Paasche (1960) concluded that area of a phytoplankton individual was closely correlated with its production potential; thus surface area is an important dimension in phytoplankton production ecology. Although the direct effect of turbulence is the maintenance of particles in vertically homogeneous suspensions, the indirect effect of turbulence on production is the effect of these suspended particles (productive and non-productive) on light penetration.

D (iii). Particle Distribution in Wraysbury Reservoir:

There are three major forces which affect particle distributions in the reservoir. They are natural mixing, artificial circulation by inlet jetting, and sedimentation. A further factor which must be considered involves the biological control of buoyancy in both diatoms (Gross and Zeuthen, 1948; Lund, 1959a) and in blue-green algae (Reynolds, 1971, 1972) which might influence the effective mixing depth (the depth to which the phytoplankton are actually mixed). The range of carbon and chlorophyll-a concentrations with depth presented in Appendices A and B indicate that this fourth point is not of direct significance in Wraysbury Reservoir. Figure 27 illustrates in isopleth form the distribution of T.P.V. with depth during 1972 and 1973, and suggests that there are only a few points of heterogeneity in the vertical plane. The most marked period of vertical heterogeneity was associated with the growth of *Asterionella formosa* in early July 1973, and its resultant sedimentation. The other periods of heterogeneity might have been due to the sedimentation of dying cells as they occurred only at the time of, and slightly after the maximum standing crops of *S. astraea*. In Figure 27 it is worthwhile to note that not only are growths distributed throughout the reservoir, but they occur and dissipate extremely rapidly. Only the winter growth of 1973 did not follow this pattern.

A comparison of Figure 27 with Figures 16 and 17 (carbon and chlorophyll-a concentrations) supports Evans' and McGill's hypothesis (1970) that T.P.V. is closely related to biomass in Thames Valley Reservoirs, and can be used with accuracy when combined with microscopic techniques to determine phytoplankton standing crop and to

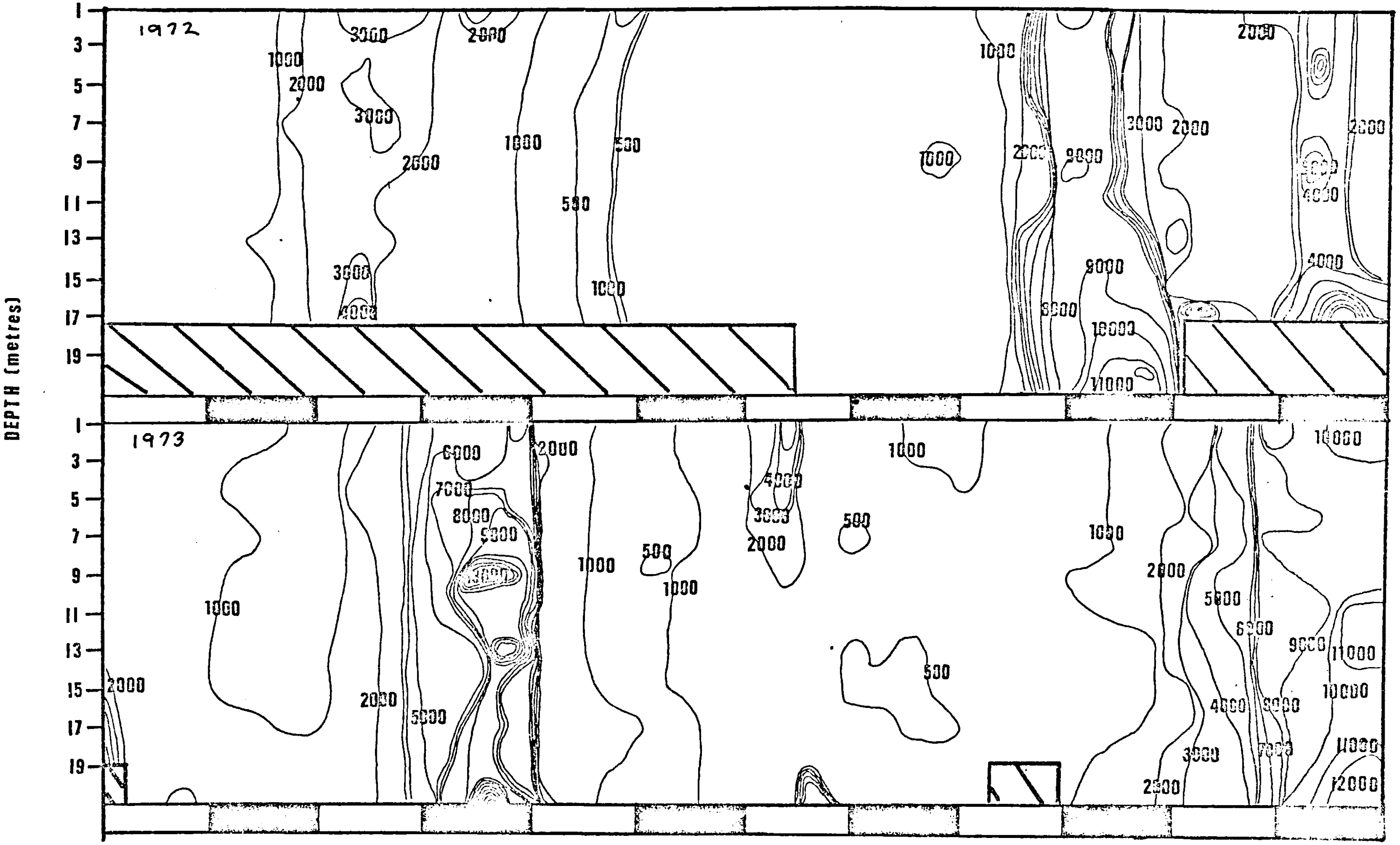


Figure 27. Total Particulate Volume ($\mu m^3\ ml.^{-1}$) - depth profile of Wraysbury Reservoir during 1972 - 1973.

estimate production. The sedimentation rate of Stephanodiscus astraea was more rapid in the spring of 1973 than in the autumn and winter of 1972 and 1973 as sinking rates were significantly affected by temperature. In spring 1972, there was a rapid decline of the population, not because of an increase in temperature, but probably because of a lack of SiO_2.

The rapid increase in temperature in the spring of 1973 resulted in increased sinking rates despite artificial and natural turbulence. One of the first points of vertical heterogeneity in the spring of 1973 was a build up of material at nine metres depth reaching a T.P.V. of 1.3×10^7 μm^3 ml^{-1}. This was possibly the maximum depth to which wind energy was penetrating, and only artificial mixing was maintaining cells in suspension or, this depth represents a critical zone of production of cells. The latter is unlikely as the major increase in standing crop occurred before this build up of material at a particular depth. A rapid piling up of material at the bottom is evident in Figure 27.

Autumn growths tended to be more homogeneous probably as a result of an increase in natural turbulence. Although sedimentation was evident in October 1972, it was not as sharp as in the following spring. This autumn growth of 1972 was earlier than the following year, possibly because artificial mixing was continued through the summer and into the autumn of 1972. This mixing stirred up cells from the bottom and, coupled with a decrease in temperature during September, with good light penetration, the cells of S. astraea stayed in suspension and grew rapidly. Artificial mixing was stopped in early October 1972 and the cells sedimented out as the water temperature was still above

10°C. Sedimentation was not as fast as in the following spring as lower temperatures and increased natural mixing maintained some cells in suspension until the vernal growth.

In late August 1973 artificial mixing was stopped before any significant change in water temperature occurred, and the autumn growth of 1973 was dependent on decreased temperatures, and on an increase in natural turbulence. The two parameters did not suffice until the middle of December when S. astraea reached a maximum of 10^3 cells $ml.^{-1}$. This was the largest standing crop recorded in Wraysbury Reservoir and approached the size of populations of S. astraea (3.0×10^3 cells $ml.^{-1}$)reported by Gardiner (1941) in Barn Elms Reservoir. Sedimentation was not noted until early 1974, and then sedimentation was a slow process ocurring throughout January and early Febuary 1974. Limited light penetration, decrease in total radiation (See Appendix E), and low temperatures (5 - 6°C) reduced the rate of carbon assimilation as noted by the decline in percent dissolved oxygen in December. The resultant effect of this was a reduction in the reproductive rate, and, as sedimentation continued at approximately the same rate, the standing crop slowly declined. Apparently the combined effects of turbulence and temperature can in part explain the periodicity and duration of the vernal and autumnal growths. Questions still remain about the dominance of S. astraea when Asterionella formosa is present and able to grow in Wraysbury water (as in July, 1973), and as to why the maximum production potential of the water was not reached.

Relevant to these questions is a consideration of the indirect effects of turbulence upon production. These indirect effects involve the maintenance and distribution of non-productive particles in the water column. The main and ultimate source of these particles is the

River Thames, and their distribution is dependent on the mixing regime (Jerlov, 1953). Weekly samples of the River Thames at Datchet were taken to determine the seston load entering Wraysbury from the River Thames. Figure 18 presents the T.P.V's of the river during 1972 and 1973. These are generally higher than the reservoir figures, and give an estimate of the amount of allochthonous material sedimented out in the reservoir. In view of the high number of particles present, the two tube technique was used to extend the range of particle size analyses for river samples. General seasonal particle frequency-size distributions (range of 10 μm^3 - 4.0 x 10^4 μm^3) for the river during 1972 and 1973 ~~is~~ are presented in Figures 28a and 28b. These frequency-size curves are weekly means for each size class during one particular season. The seston load did not vary greatly from one season to another during the progress of the work. During the spring of 1972 and 1973 there is a shouldering in the 200 μm^3 - 800 μm^3 range as a result of growths of S. hantzschii. Also of particular interest is the low frequency-size distribution of river particles in the autumn of 1973 before and during the growth of S. astraea in the reservoir. This near constancy of particle frequency-size distribution in the river in 1972 and 1973 is associated with the lack of flood rainfall during this period, as one would expect there to be an increase in the seston load during the rainy season of a "normal" winter. A slight flood response occurred in December 1972, and the river was very turbid reaching particle concentrations of 3.0 x 10^4 particles 0.5 ml^{-1} in the 10 - 25 μm^3 size class, as compared with the seasonal mean of 3.0 x 10^3 particles 0.5 ml^{-1}. The flood pulse was short in duration and did not affect the overall shape and position of the seasonal size distribution curve, but did have a large

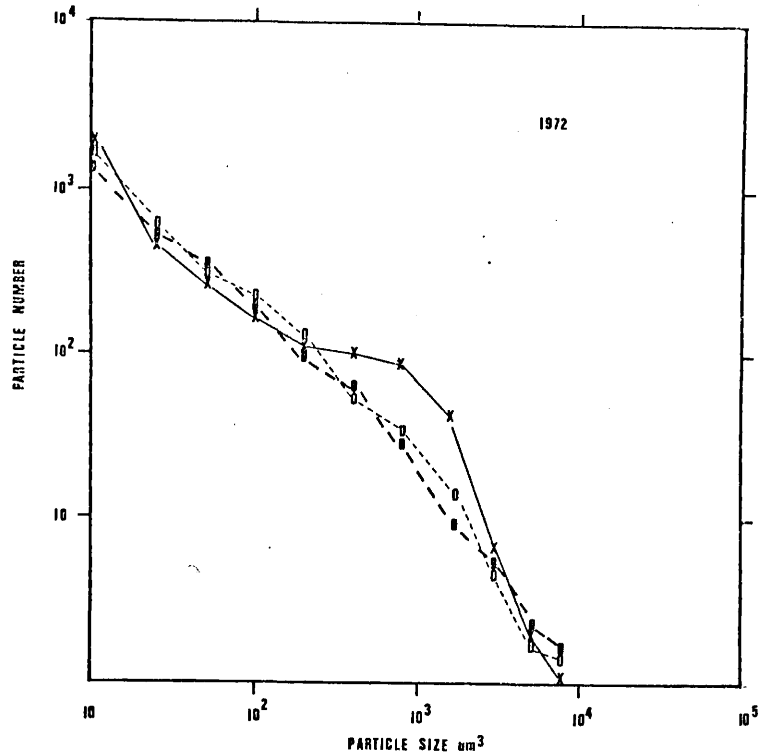


Figure 28a. 1972

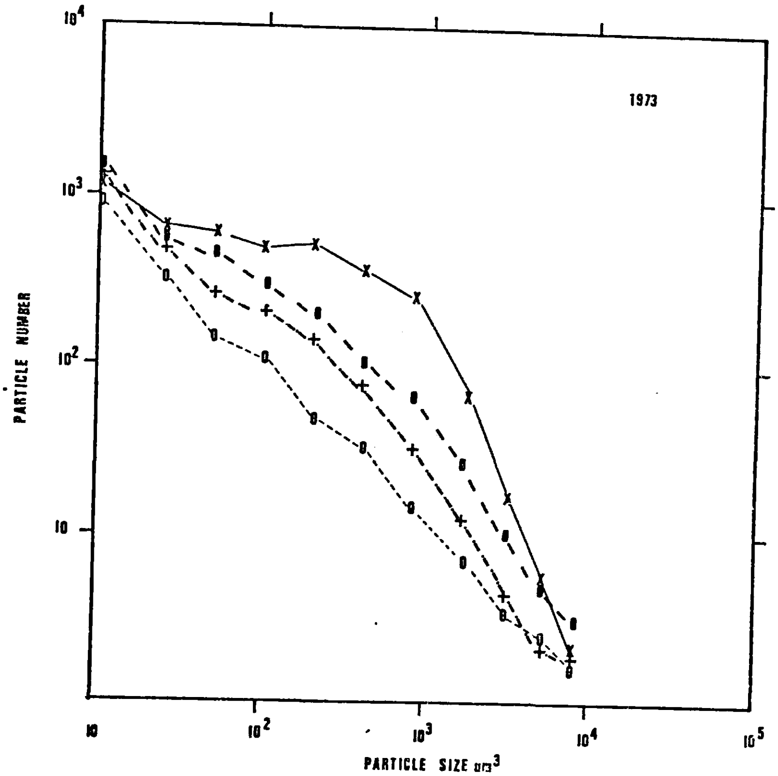


Figure 28b. 1973

X - Spring; ● - Summer; O - Autumn; + - Winter.

Figures 28a and 28b. Seasonal particle frequency - size distributions of the River Thames at Datchet. (Particles 0.5 ml.$^{-1}$).

effect on the attenuation of radiant energy in Wraysbury Reservoir (Figure 26) (See Haffner and Evans, 1974b).

Haffner and Evans (1973) suggested that particle size analyses could, under certain circumstances, determine the physiological state of diatom populations. Dead or moribund cells of the large S. astraea tended to plasmolyse more readily, and once the cell membrane ruptured the frustule broke up into the corresponding valves and girdles. As plasmolysis occurred, however, electrolyte penetrated the frustule and plasmolysis was electronically recorded.

The use of a Coulter Counter to size and enumerate turgid cells of S. astraea assumes that the electrolyte solution (0.5% NaCl) in which the particles were suspended, does not itself plasmolyse a healthy cell. If such plasmolysis did occur, this would result in inaccurate sizing of cells, and frequency-size distributions would be meaningless; though total particulate volume would remain accurate. A brief comparison of the relationship of particle counts in the 10.0×10^3 µm³ - 20.0×10^3 µm³ size class (Figure 29b) with the counts of cells of S. astraea by visual methods (Figure 19) would suggest that healthy cells of S. astraea do not plasmolyse. It is necessary, however, that more rigorous tests are included before frequency-size data can be analysed more critically for any one species in any particular habitat. Selection of the concentration and type of electrolyte is important.

To determine if the source of plasmolysis was a natural characteristic of the population, or a result of the 0.5% electrolyte solution, the osmotic pressure of S. astraea was determined by placing

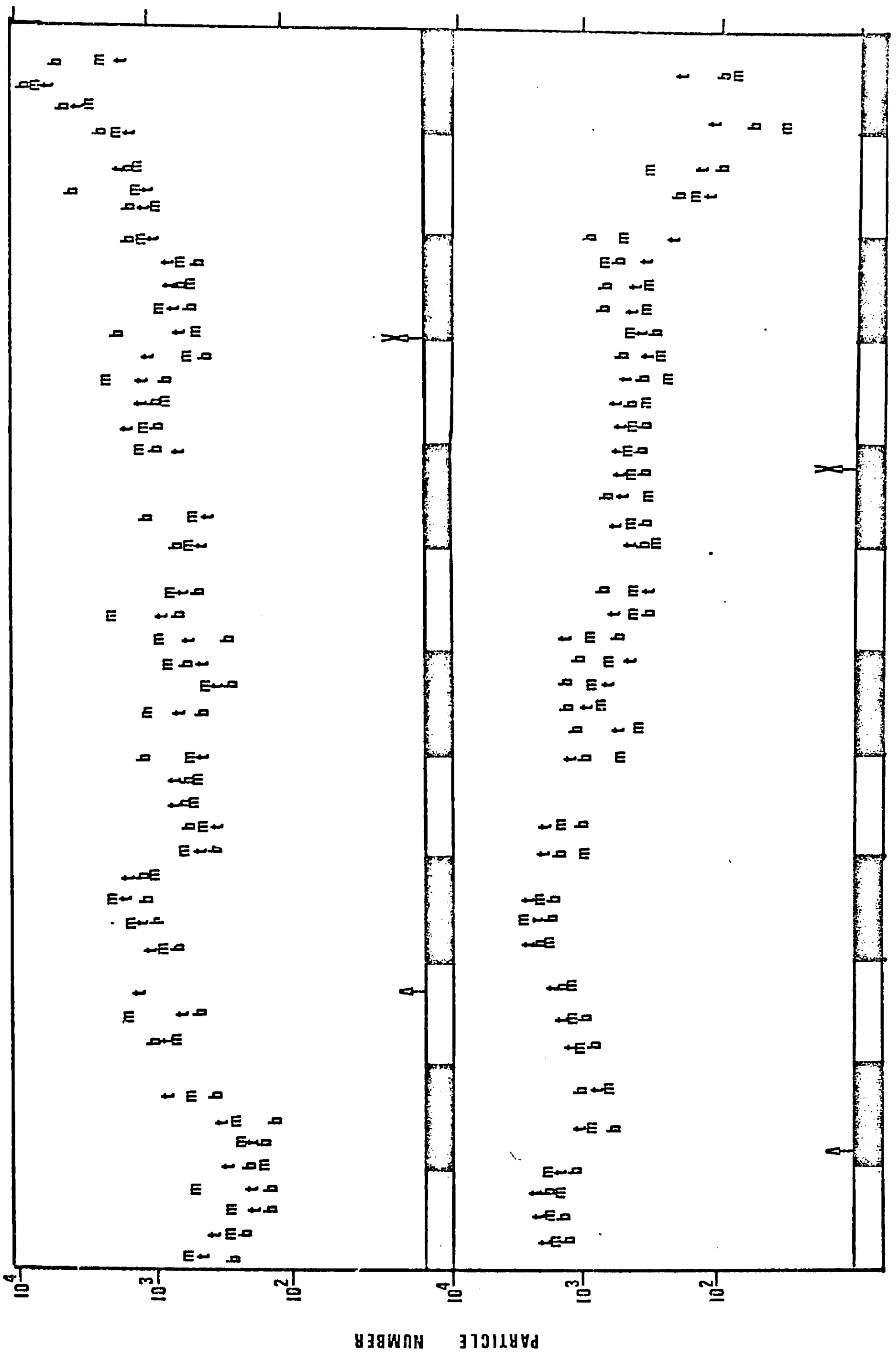


Figure 29a. Particle (50 μm^3 - 100 μm^3) concentrations in Wraysbury Reservoir during 1972 - 1973.

(Particles 0.5 $ml.^{-1}$) (↑ Beginning and ✱ end of jet input.).

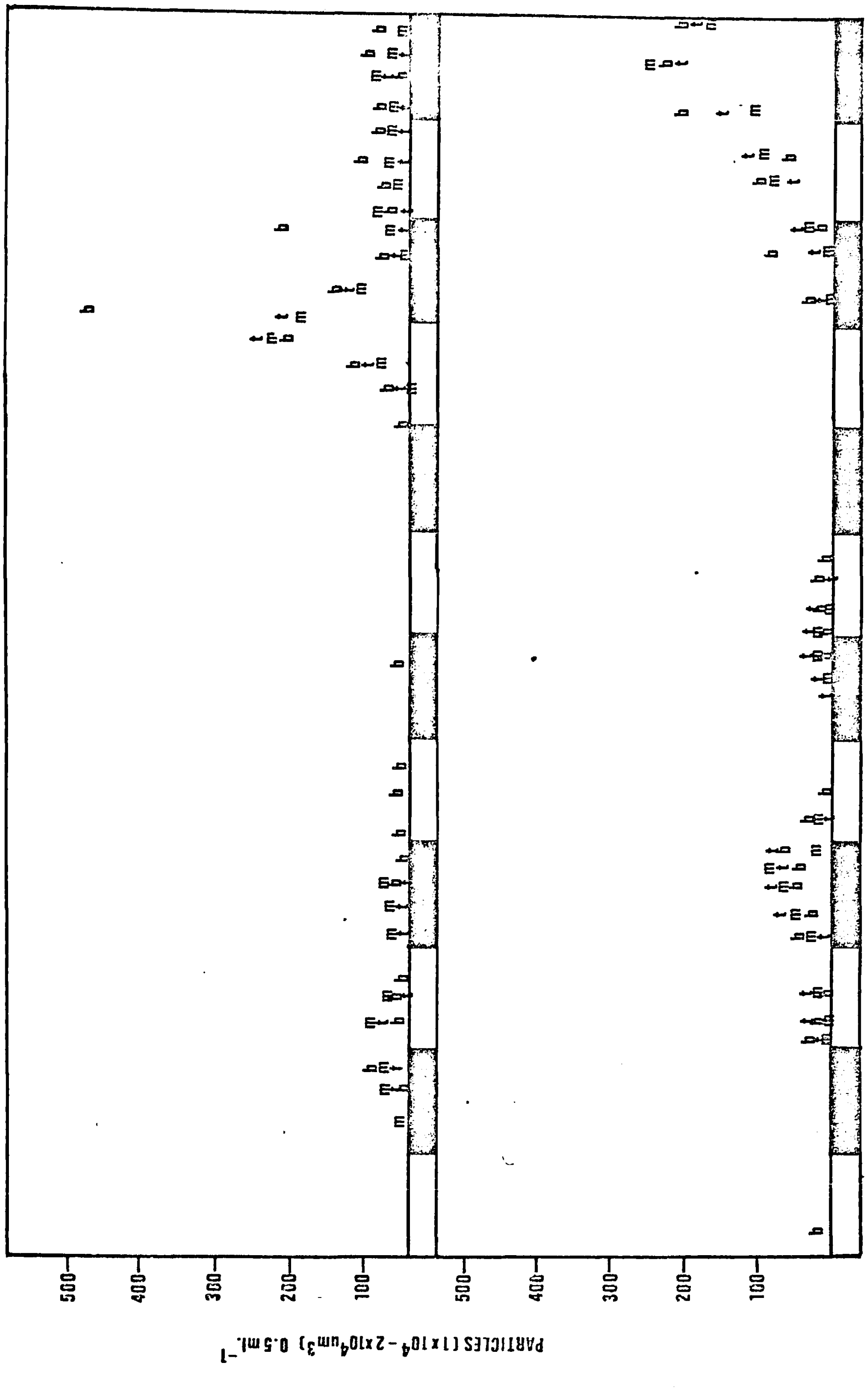


Figure 29b. Particles (1.0 x 10^4 μm^3 - 2.0 x 10^4 μm^3) of Wraysbury Reservoir during 1972 - 1973.
(Particles 0.5 $ml.^{-1}$).

cells in solutions of varying salt concentrations for one-half hour. This time interval was the maximum time required for particle size analyses over the entire range of the aperture tube (200 μm.) used. A control, and salt concentrations of 0.1%, 0.5%, 1.0%, 2.0%, 4.0% and 5.0% were used, each repeated in triplicate. The control was a natural population from Wraysbury Reservoir. Estimations of numbers of plasmolysed cells in test samples were determined by the microscopic counting method discussed previously (Methods, Section B). Results are expressed in Figure 30 as the percent of the mean number of turgid cells in the electrolyte solutions to the mean number of turgid cells in the control. From Figure 30 it would appear that a 1.5% - 2.0% (0.26 M - 0.34 M) solution of NaCl is required to effectively initiate plasmolysis of healthy cells of S. astraea in the Thames Valley. This is beyond the range reported by Guillard (1962) and Ubeleis (1957) of 0.10 M - 0.19 M for plasmolysing diatoms of natural freshwater, and S. astraea of the Thames Valley has an uncommonly high osmotic pressure $\simeq$ 0.30 M NaCl.

Although a salt (NaCl) concentration of 0.5% (5.0 x 10^3 mg. $l.^{-1}$) is extremely high and unnatural, it has a molarity of approximately 0.09 M and thus even the diatoms investigated by Guillard and Ubeleis would not be effectively plasmolysed at that salt concentration. Still it is not wise to generalize that a 0.5% concentration is always safe to use. The chloride concentrations of the River Thames and the Thames Valley Reservoirs are frequently above 40 mg. $l.^{-1}$ (M.W.B. reports 42 - 45) and the phytoplankton of the area have perhaps adapted to the high salt concentrations. It is possible that 0.5% electrolyte solutions will plasmolyse cells of Stephanodiscus frequenting oligo-

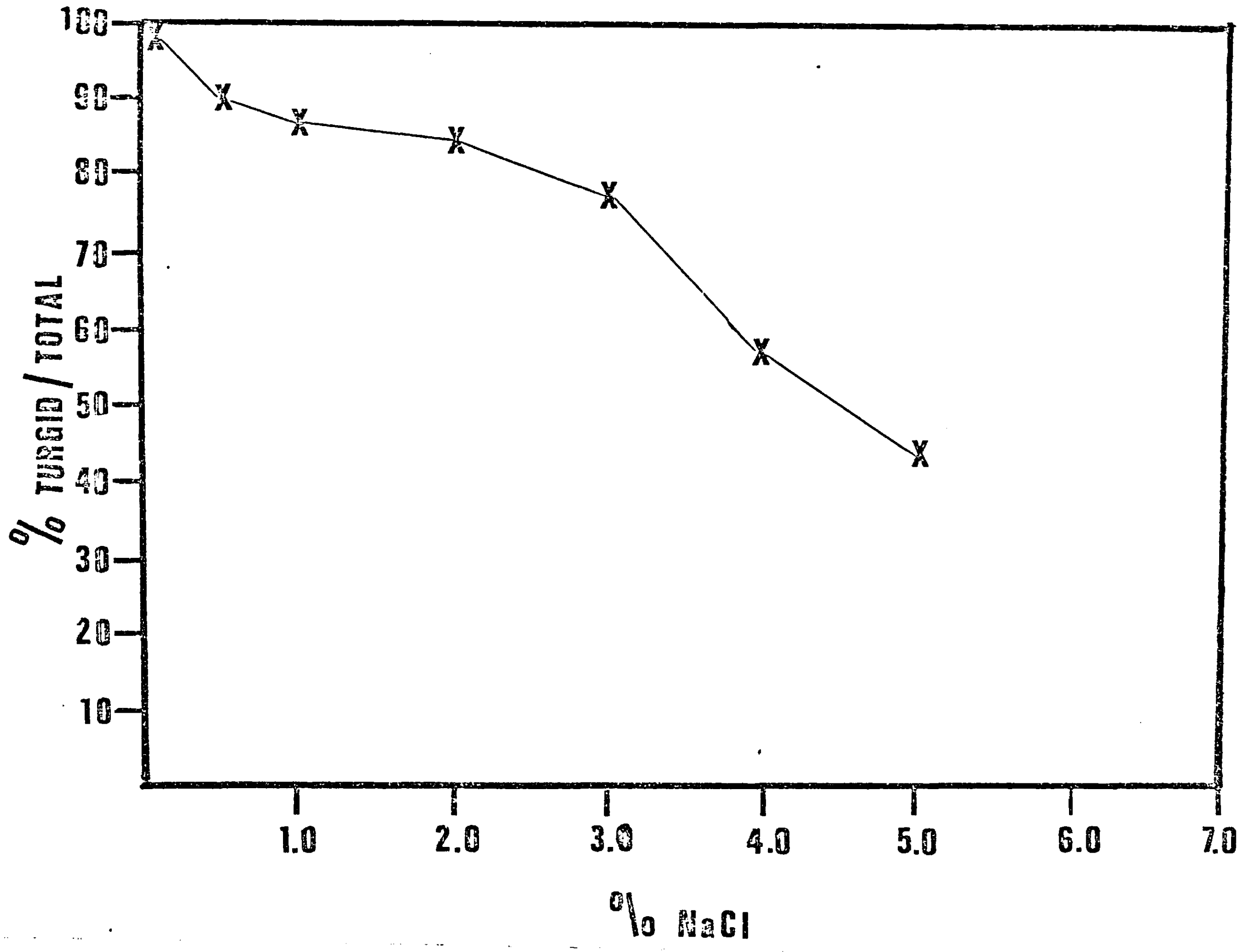


Figure 30. Plasmolysis of Stephanodiscus astraea of Wraysbury Reservoir in varying concentrations of electrolyte (NaCl).

and meso-trophic waters. In such circumstances a 0.1% electrolyte solution might suffice, but in the Thames Valley a 0.1% salt solution is possibly too low as any change in the natural salt levels caused by rainfall, effluents etc. could alter the electrical resistance between the two electrodes of the Coulter Counter, and affect the calibration of the machine.

Plasmolysis might occur during particle size analysis, therefore this was tested by repeated analyses on the same sample of Wraysbury water containing S. astraea. Figure 31 illustrates repeated runs of frequency-size analyses over one hour on a sample containing S. astraea. Only the overall size range of 5.0×10^2 µm^3 - 30.0×10^3 µm^3 was considered as another diatom, M. granulata, was also present in a smaller size class. The peak in the 10×10^3 - 30.0×10^3 µm^3 size range is stable, and there is no evidence of plasmolysis. A slight increase in the 10.0×10^3 - 20.0×10^3 µm^3 size class might be a result of mechanical breaking up of doublets by the stirring of the sample.

As demonstrated in the above data, a healthy uni-algal population of S. astraea gives a sharp, distinct peak in the 10.0×10^3 - 20.0×10^3 µm^3 size class. As plasmolysis is a transient feature, the presence or absence of shouldering, the degree of shouldering, and the size or position of secondary peaks is difficult to determine, and requires an intensive sampling routine. Determining the mean particle frequency-size distribution of the reservoir by analysing particle distributions at five stations of the reservoir at three depths often results in the smoothing out of the particle size distribution curve for the reservoir as a whole. Only in extreme circumstances of high concentrations of plasmolysed cells will these features be apparent.

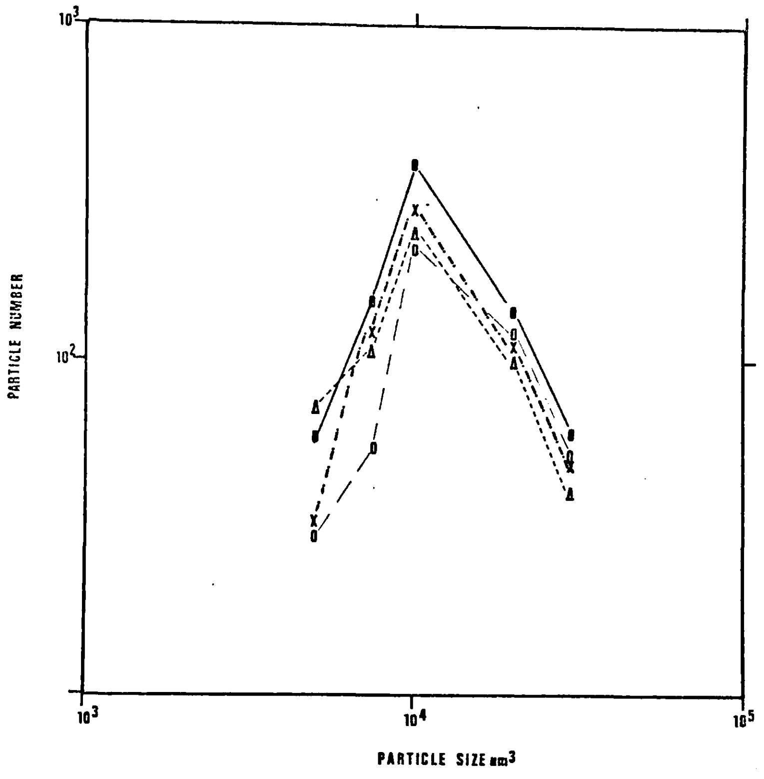


Figure 31. Repetitive analysis of sample containing S. astraea. Note sharp distinct peak in the 1.0 x 10^4 - 2.0 x 10^4 μm^3 size class.

(O - 1/4 hr.; X - 1/2 hr.; ● - 1 hr.; △ original).

The growths of S. astraea in the spring of 1973 and autumns of 1972 and 1973 were of sufficient numbers to demonstrate the occurrence of shouldering and secondary peaks. Figures 32a, 32b, and 32c are arranged to illustrate the mean particle frequency-size distributions of the reservoir before, during and after the crop maxima as determined by chlorophyll-a, carbon, and T.P.V. Particle size distributions were determined at one and nine metres, and one metre above the floor of the reservoir at five stations. On all three occasions particle frequency-size distributions revealed little or no indication of secondary peaks during the growth phase. At the time of the maximum standing crop there is some sign of secondary peaks in the bottom sample during both autumn periods. During the population decline secondary peaks are more common at all depths, and are much more intense (see in particular the particle size distribution of 17 January, 1974). The spring growth of 1972 did not have as marked an occurrence of plasmolysis probably because of the high sinking rates. From these figures it would appear that there is a tendency for a secondary peak to occur in the $3.0 \times 10^3 - 5.0 \times 10^3$ μm^3 size class. This might represent the size class that the frustules occupy once plasmolysis has occurred to the critical extent where they do break down into their component parts. Although there seems to be a relation between population growth, maxima, and decline and the occurrence of shouldering and secondary peaks in the size analyses, more intensive work is required before diatom populations can be precisely monitored and structured by such a method.

A further use of particle size analyses is in the determination of seston sedimentation. Figure 33a shows the sedimentation of particles

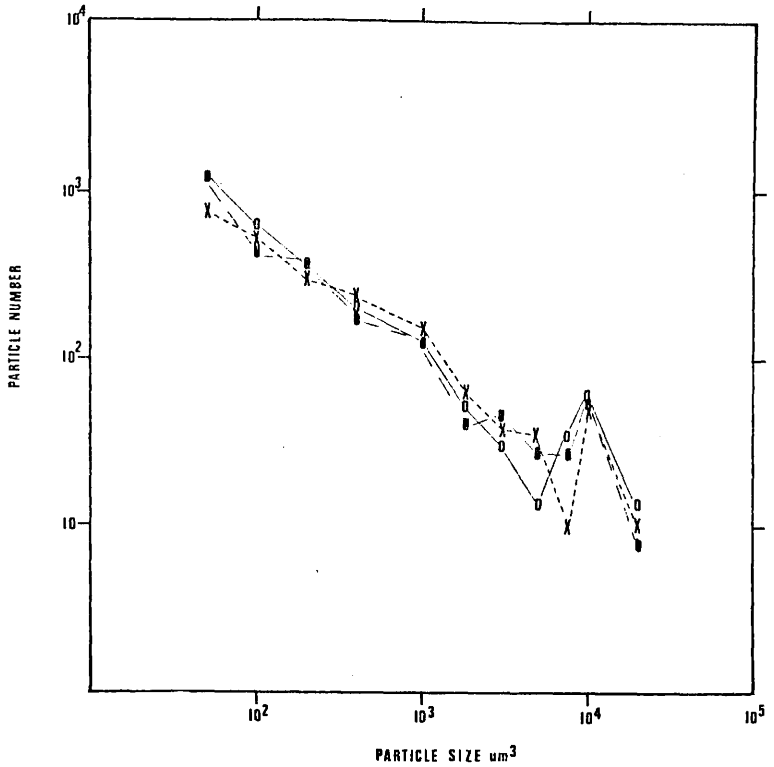


Figure 32a. September 19, 1972

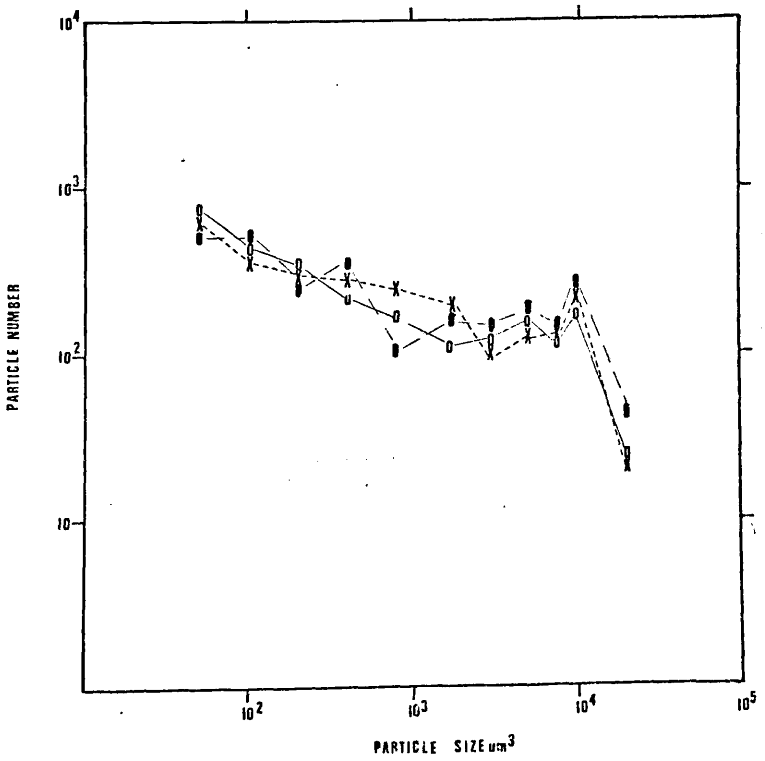


Figure 32a. October 3, 1972

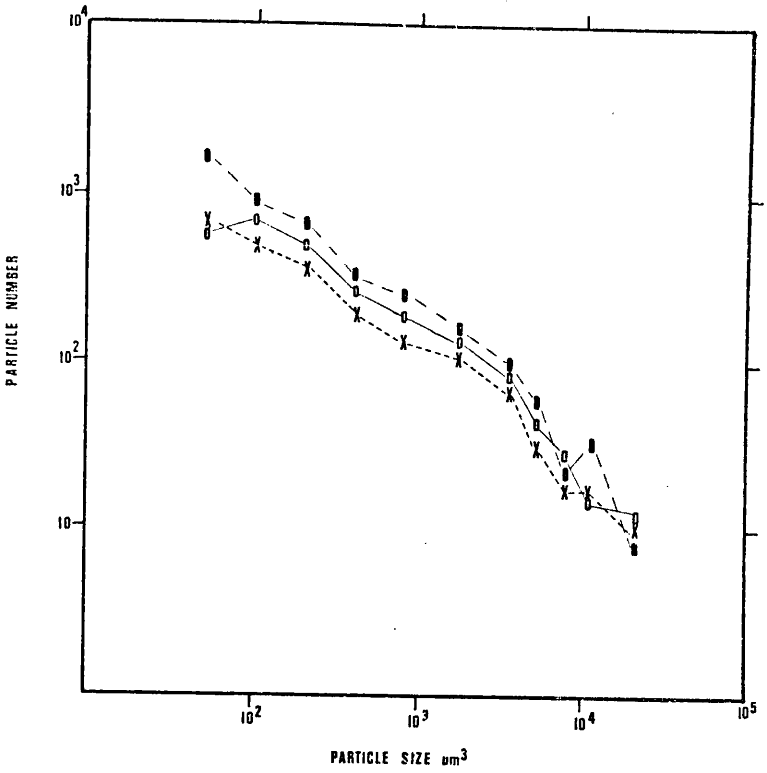


Figure 32a. October 19, 1972

Figure 32a. Particle frequency - size analysis at 3 depths before during, and after the autumn maximum (1972) of *Stephanodiscus astraea.* Note that shouldering is evident at the time of the maximum.

(O - 1 metre; X - 9 metres; ● - Bottom)

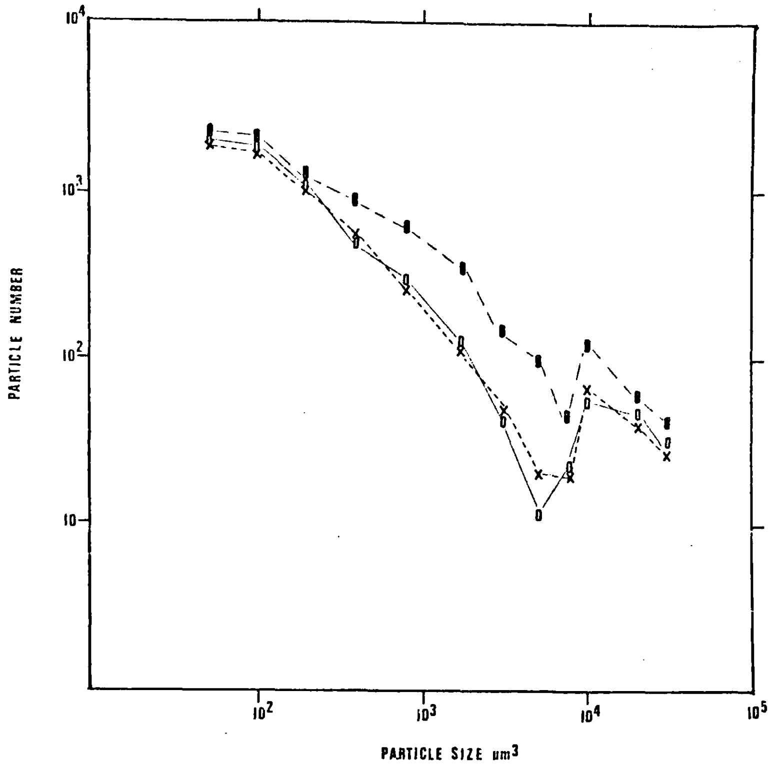


Figure 32b. April 12, 1973.

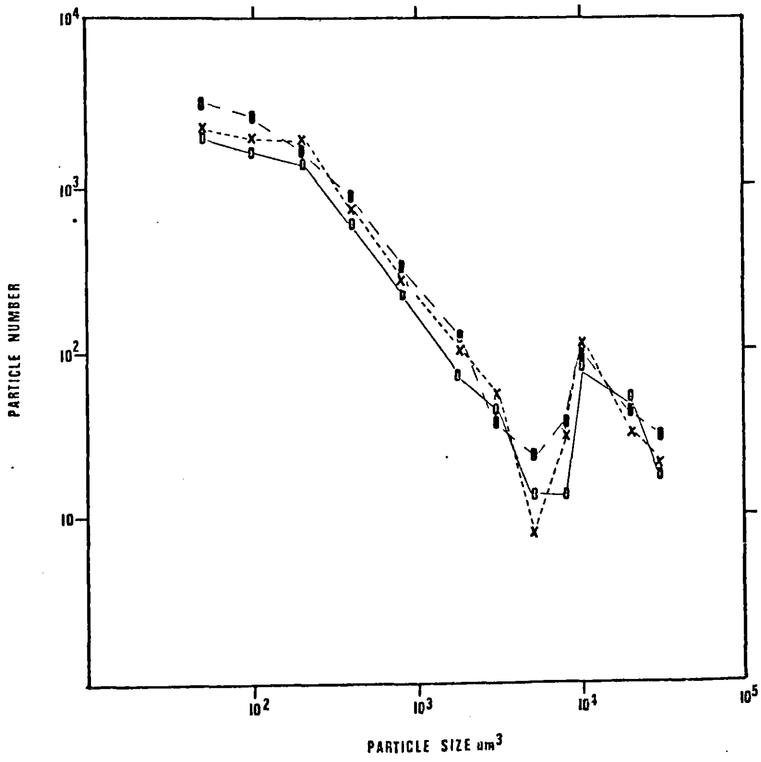


Figure 32b. April 19, 1973.

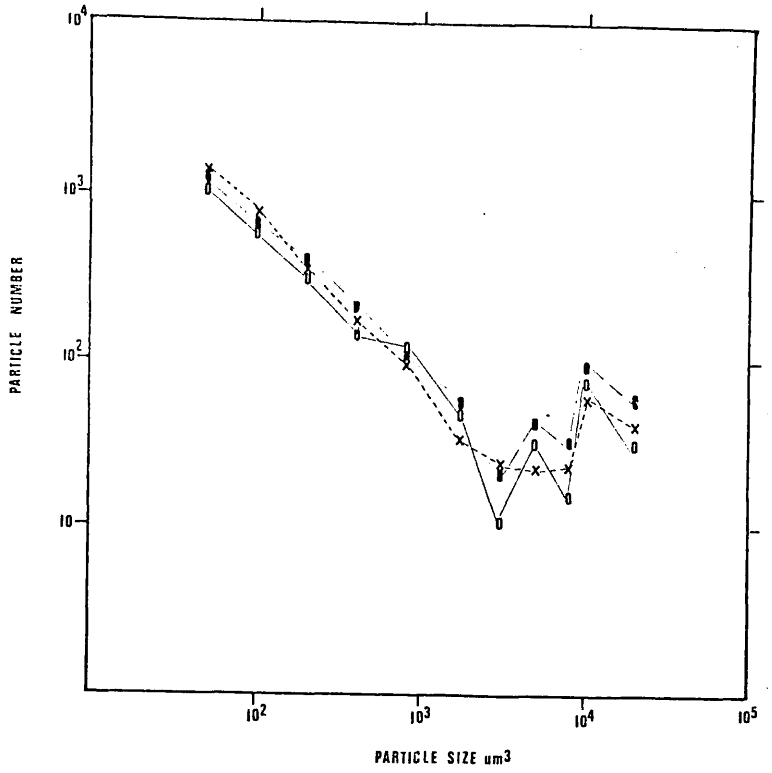


Figure 32b. April 26, 1973.

Figure 32b. Particle frequency - size distribution at 3 depths before, during, and after the maximum standing crop of S. astraea . Note the shouldering after the maximum standing crop. Depths as in Figure 32a.

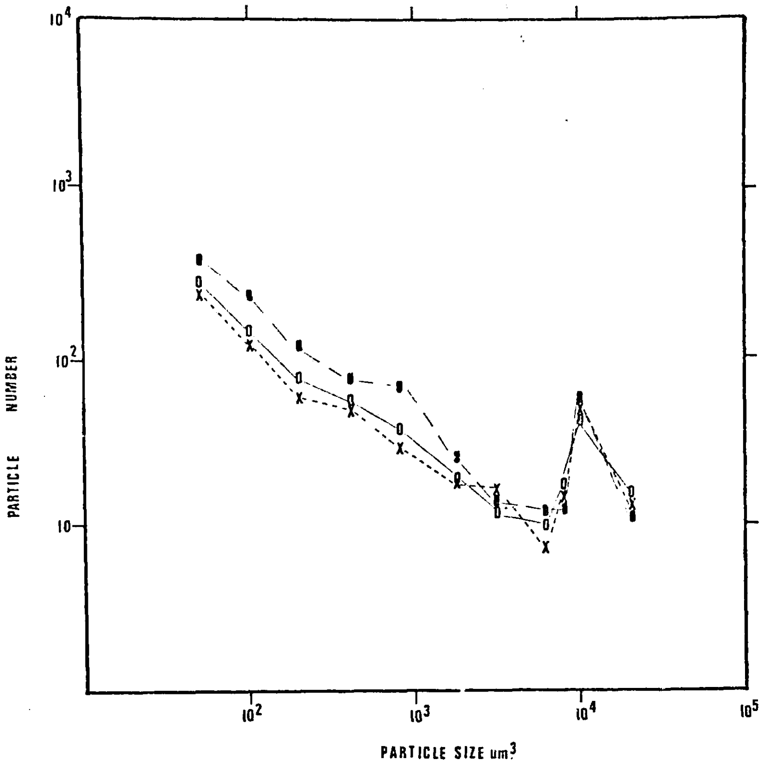


Figure 32c. November 1, 1973

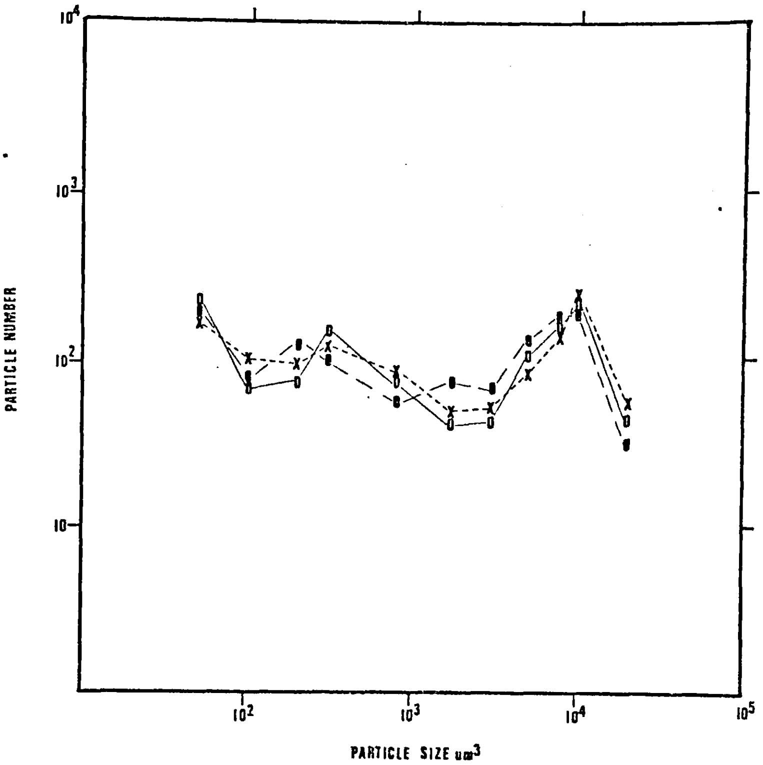


Figure 32c. December 13, 1973.

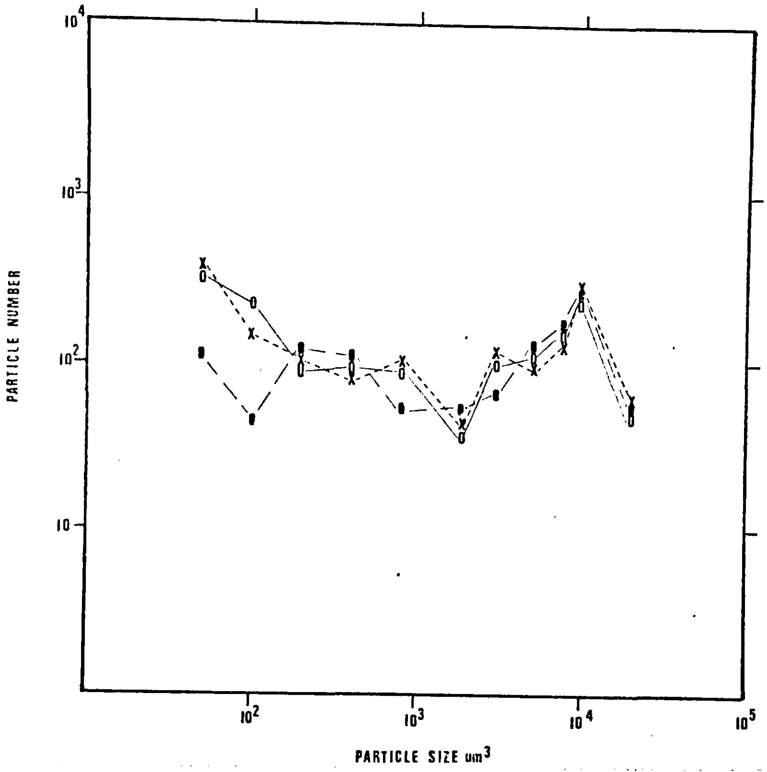


Figure 32c. January 17, 1974.

Figure 32c. Particle frequency - size distribution at 3 depths in Wraysbury Reservoir before, during and after the maximum standing crop of _S. astraea_. Note the shouldering after the maximum standing crop.

introduced from the River Thames in early December 1972 (on December 14 and 20 and February 2, 1973). Sedimentation was slow as a result of natural turbulence and low temperatures. Later, in April 1973 (Figure 33b), during a growth of S. astraea, sedimentation of the seston is increased by a rise in temperature, and a decrease in natural turbulence. Even the large centric diatom showed signs of decreasing in number. Again note the occurrence and shifting of the secondary peaks in chronological order.

Particle distribution was determined for ten size classes with a total range of 50.0 - 20,000 μm^3. The vertical disturbution of particles in the 50 - 100 μm^3 and $1.0 \times 10^4 - 2.0 \times 10^4$ μm^3 size classes in the reservoir at three depths are presented in Figures 29a and 29b respectively. These indicate that at most times of the year these particles are homogeneously distributed with depth. The number of particles in the $1.0 \times 10^4 - 2.0 \times 10^4$ μm^3 size class correspond to the numbers of cells of S. astraea. When there are few or no cells present in the water there is no record of any counts of particles in this size class. The maximum size of detrital particles of any quantitative significance was $3.0 \times 10^3 - 5.0 \times 10^3$ $\mu m.^3$ (see Figures 28a and 28b). Counts above this size class in reservoir samples corresponded mainly to S. astraea. Non-living material of such a large size would sink rapidly despite artificial mixing. The homogeneous mixing of cells of S. astraea is apparently a function of cell physiology (Lund, 1959a) as well as the physical mixing processes. This concept is supported by the observation that cells of the much smaller S. hantzschii, with reportedly low sinking rates (Swale, 1964), sank to the bottom after being innoculated from the river, despite

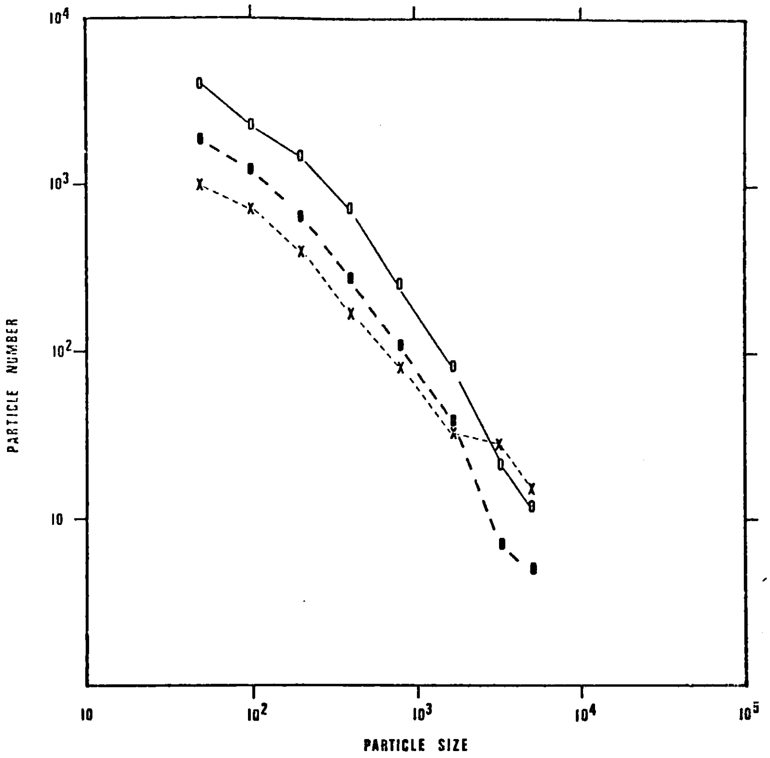


Figure 33a. Illustrating the sedimentation of particles despite low temperatures and natural mixing during the winter of 1972 - 1973.

(O - 14/12/72; ● - 20/12/72; X - 12/2/73).

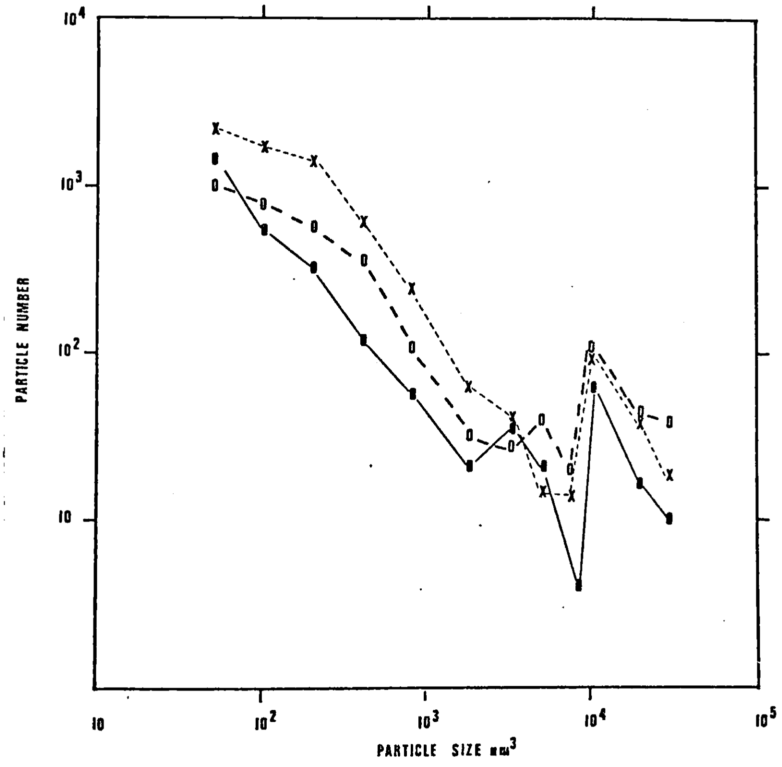


Figure 33b. Sedimentation of detrital and productive particles during April 1973.

(X - 19/4/73; O - 26/4/73; ● - 30/4/73) mixing of the water column. S. hantzschii was usually innoculated when the reservoir was warm (May - June) and sedimentation high (see Figure 33b). It would appear that they are not adapted to the physical features of the reservoir, particularly that of reduced turbulence.

Figure 29a illustrates the number of particles 0.5 ml^{-1} in the 50 - 100 μm^3 size class. Interestingly, the number of particles at depths representative of the top, middle, and bottom of the reservoir is fairly constant. The large increase in December 1972 reflected the influence of the River Thames' high seston load which had resulted from high rainfall (Appendix E). In the autumn of 1973 there was a gradual decline in particles of this size class as the river was unusually clear (Figure 28b) and the low velocity input was permitting sedimentation. Light penetration in the reservoir became more dependent on productive particles than on non-productive particles as a result of this decline in concentrations (see Section D (ii)).

Horizontal distribution of particles at five stations was determined at three depths for the ten size classes (Figures 34a and 34b; Appendix F). It would be expected that the particle distribution of a mixed reservoir would be random and approach a Poisson distribution of variance = mean. As Wiebe (1970) has indicated, there is a tendency for the variance : mean ratio to approach unity with decreasing particle numbers. This suggests that the ratio is not entirely independent of the mean.

Various forces interact with mixing and particle distribution might deviate from random. Changes in the ratio of natural and artificial mixing, changes in the efficiency of mixing as a result of temperature fluctuations, the nature and shape of the particles, and the influence of objects such as towers and the inlet pier all interact; the true particle distribution of the reservoir results from all these possible interactions.

Seager (1972) investigated the circulation in the northern half of the reservoir at 10 metres depth using drogues. A circuit was completed in approximately 16.5 hours under steady inflow of 5.8 m^3 sec^{-1} (110 m.g.d.) which compared well with the M.W.B.'s model studies (Figure 2). Current speeds were highest after issue from the jet, and when near the jets' influence at the end of one circulation. Thus entrainment was a major factor of circulation. The currents of the reservoir were shown to have velocities below the lower threshold of a conventional current meter.

As water currents could not be directly assessed due to the complexity of the mixing phenomenon (see Bye, 1965), the only method available to study mixing was by particle distribution assuming mixing (natural and artificial) was the primary factor. Samples were collected at five stations at three depths and were analysed by the Coulter Counter. Variance :mean ratios were determined for all size classes on each occasion. These ratios are presented in Figures 34a and 34b for particles of 50 - 100 μm^3 and $1.0 \times 10^4 - 2.0 \times 10^4$ μm^3 size classes respectively. The latter size class is well distributed though some degree of contagion (variance > mean) is noticed. From this it can be concluded that the counts of S. astraea presented in Figure 19 are presented as representative of the reservoir as a whole, and the cells are vertically and homogeneously distributed.

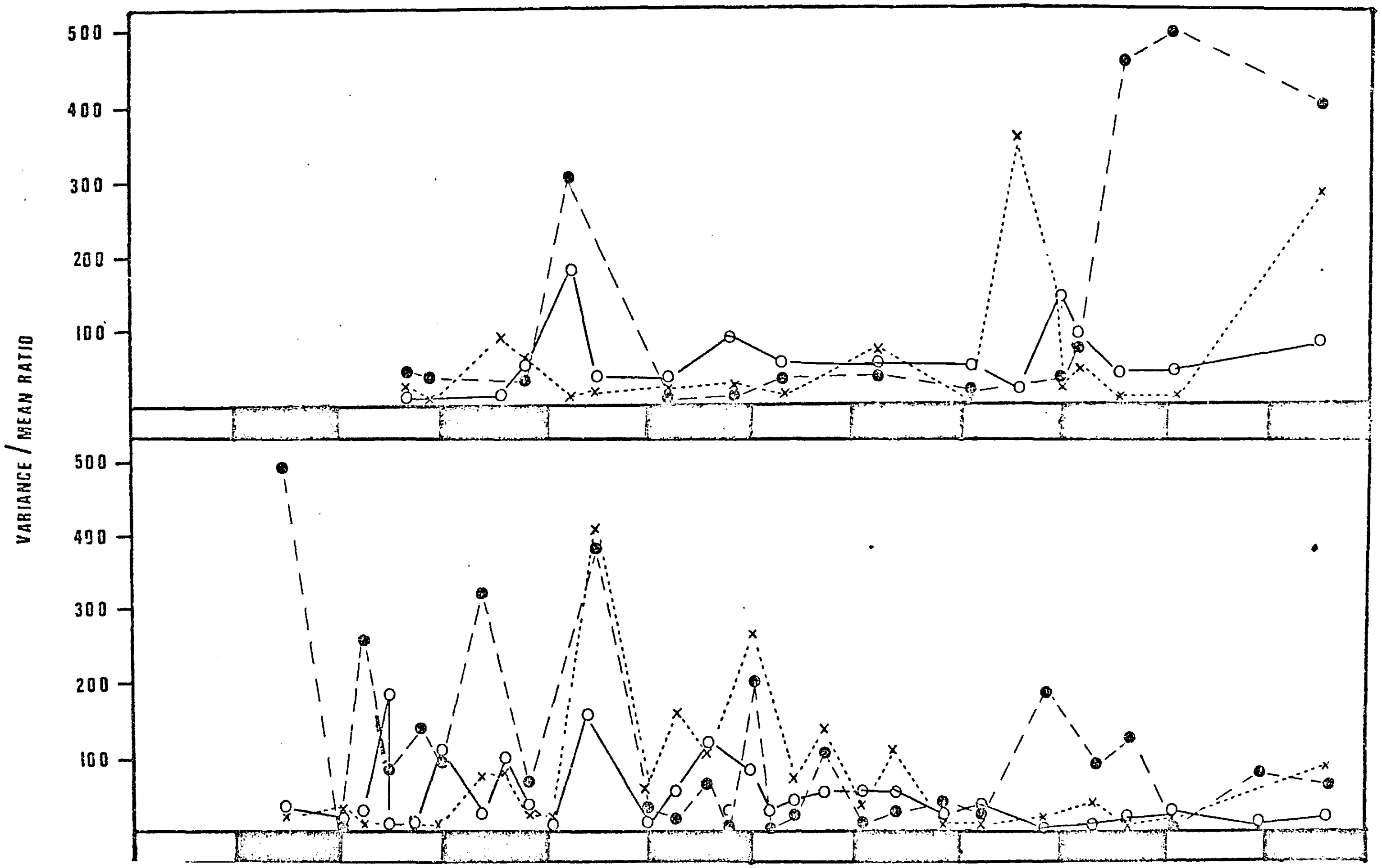


Figure 34a. Variance - Mean Ratios of particles 50 μm^3 - 100 μm^3 illustrating horizontal and vertical particle distributions in Wraysbury Reservoir as determined by Synoptic Sampling and Particle Frequency - Size analyses.

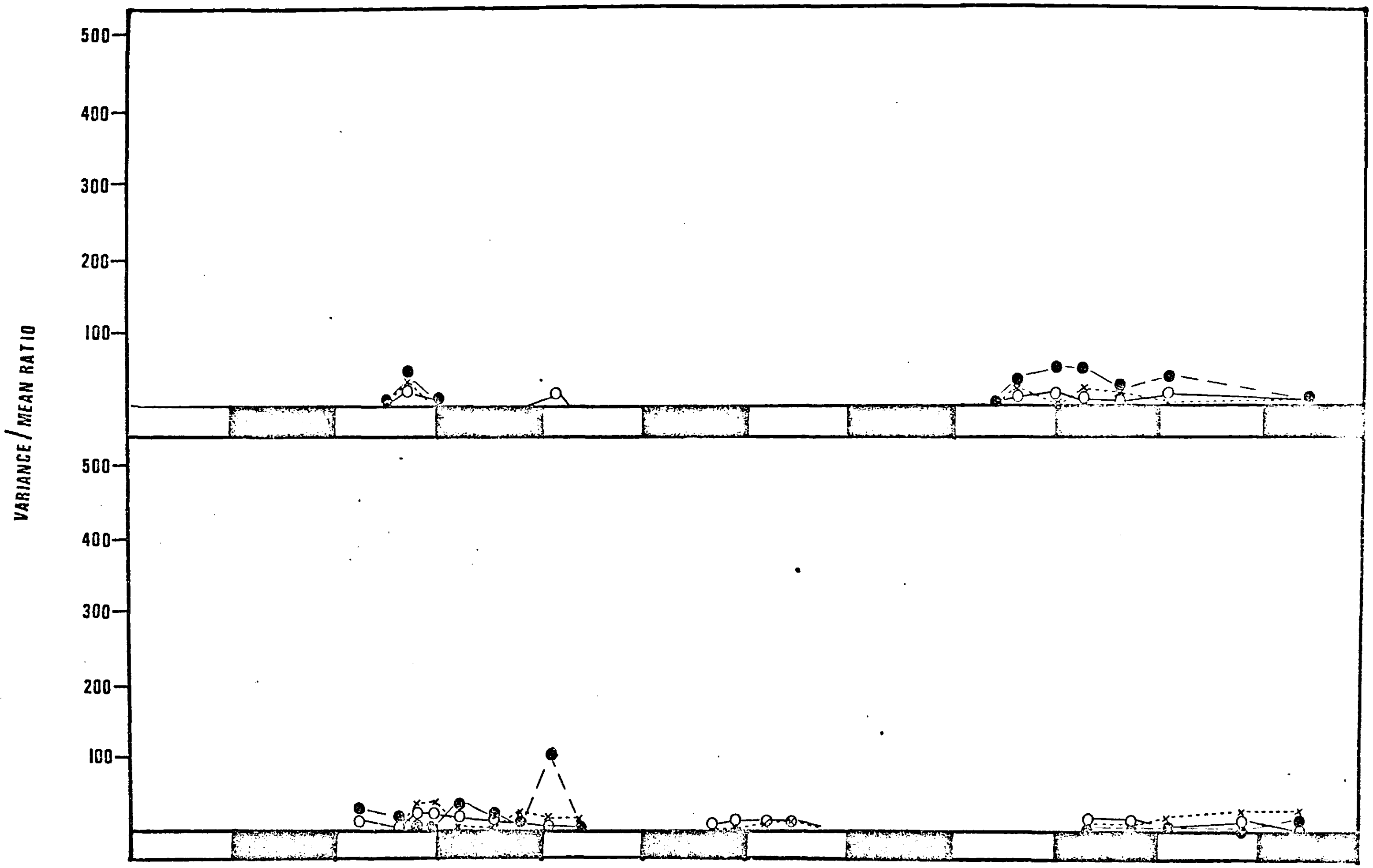


Figure 34b. Variance - mean ratios of particles (1.0 x 10^4 μm^3 - 2.0 x 10^4 μm^3) illustrating the vertical and horizontal distribution of productive particles (<u>S. astraea</u>) in Wraysbury Reservoir during 1972 - 1973.

The particles of the 50 - 100 μm^3 size class indicate a much higher amount of contagion, particularly at the bottom of the reservoir during periods of maximum natural mixing. These small particles are assumed to be the most affected by mixing, and their distribution is assumed to be representative of the 'mixed state' of the reservoir. The high degree of contagion at the bottom during the winter might be a function of inaccurate depth sampling due to the rocking of the boat by wind and waves, plus the stirring up of particles from the bottom of the reservoir by the wind. To elucidate further the problem of contagion near the bottom requires an alternative sampling method.

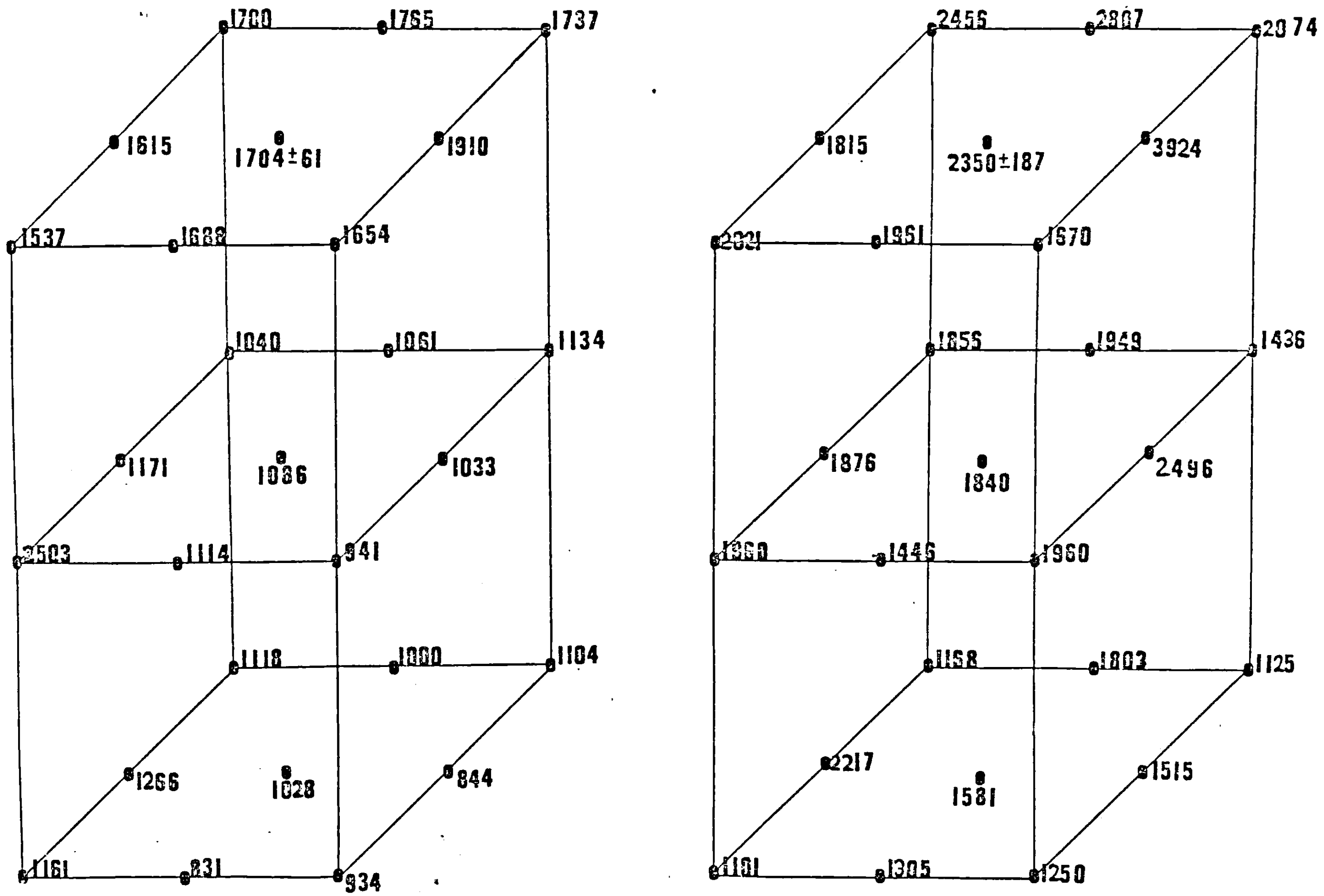
Seager (1972) commented that short circuiting of the circulation pattern could occur under certain wind conditions. This short circuiting was observed before storms when wave interference patterns outlined the circulation pattern. The normal circulation pattern would bend in the direction of the wind. Although Seager noted wind effects in the upper two metres, strong winds could penetrate much deeper depending on the temperature distribution in the water column. The shallow depth of wind mixing noted by Seager is possibly associated with the season of his experiments (August).

Wraysbury Reservoir is seldom completely homogeneously mixed at any one time. Appendix F presents the particle distribution (variance/mean) for the ten particle size classes (50 μm^3 - 3.0×10^4 μm^3) and in general supports this conclusion. Over-dispersion is the common distribution of all particles of the seston.

A study of the spatial heterogeneity encountered near the Inlet Pier was carried out in the summer of 1972. The river seston is usually composed of high numbers of small particles - silts, clays, and decomposed organic matter which often results in the high turbidity of the water. By determining the distribution of these particles after inlet into the reservoir, the mixing pattern of the river and reservoir water could be determined. This mixing pattern can influence and determine the particle distribution of the reservoir.

The results of the first grid pattern (see Method, D) are illustrated in Figure 35. These grids were positioned about the surface jet swells created by the 22½° and 45° jets when these were issuing water at $5.8\ m.^3\ sec.^{-1}$. At this jetting intensity, river samples taken at Datchet indicated that 8.5×10^3 particles per 0.5 ml. were entering the reservoir. Determination of particle concentrations at various stations reflects the dilution of the river water by reservoir water, and hence gives an indication of the amount of mixing. Reservoir water had approximately 1.0×10^3 particles per 0.5 ml.

Figure 35 illustrates two aspects of jetting. Particle concentrations tended to decrease with depth which suggested that river and reservoir water mixed only when the river water had lost its momentum at the jet swells; little mixing occurred before this. The second point is that particle concentrations increased in the direction of the wind, particularly in the upper metres, and the wind effect decreased with depth. This supports Seager's (1972) concept - the effects of wind mixing are limited to the upper metres, at least during the summer. Even so, Seager might have underestimated wind effects. As discussed by Steel (1972) the vertical mixing effects of wind are increased in isothermal conditions. Thus the theoretical mixing pattern of Figure 2 is not entirely representative of the upper ten



NORTH JET **SOUTH JET**

Figure 35. Particle Distribution (50 μm^3 - 7.0 x 10^4 μm^3) about the Jet Swells.

metres of Wraysbury Reservoir, and it is these ten metres which are the most important when considering phytoplankton production (Figure 28).

A variation of the synoptic sampling routine involved the use of a two metre hose pipe (Lund and Talling, 1957) to sample sixty stations from the inlet pier across the reservoir in a five by twelve station grid. Mixing was determined as above, and wind direction is illustrated by an arrow. River and reservoir particle concentrations were similar to the previous values. Figure 36 indicates once again wind can strongly influence particle distribution, as particle numbers increased in the direction of the wind. Even the particle distribution of the north jet swell was elongated in the direction in which the wind was blowing.

The sampling of five stations at three depths during the two year study indicated that large particles, $1.0 \times 10^4 - 2.0 \times 10^4$ µm^3. (*S. astraea*) were vertically and horizontally homogeneously distributed. It is tempting to hypothesize that autochthonous particles of the reservoir have a greater tendency to be homogeneously distributed, than the allochthonous material of river origin. This might be true if all particles behaved similarly but owing to their buoyancy mechanisms the blue-green algae which occurred in the reservoir do not mix as well as other particles such as the large diatom *S. astraea*. A synoptic sampling routine, again with a two metre hose pipe, was used to determine the distribution of *Aphanizomenon flos-aquae*. Enumeration of trichomes was by the microscopic technique as discussed in Methods Section B. Other phytoplankton species present were in too low numbers to be of use in determining their distributions.

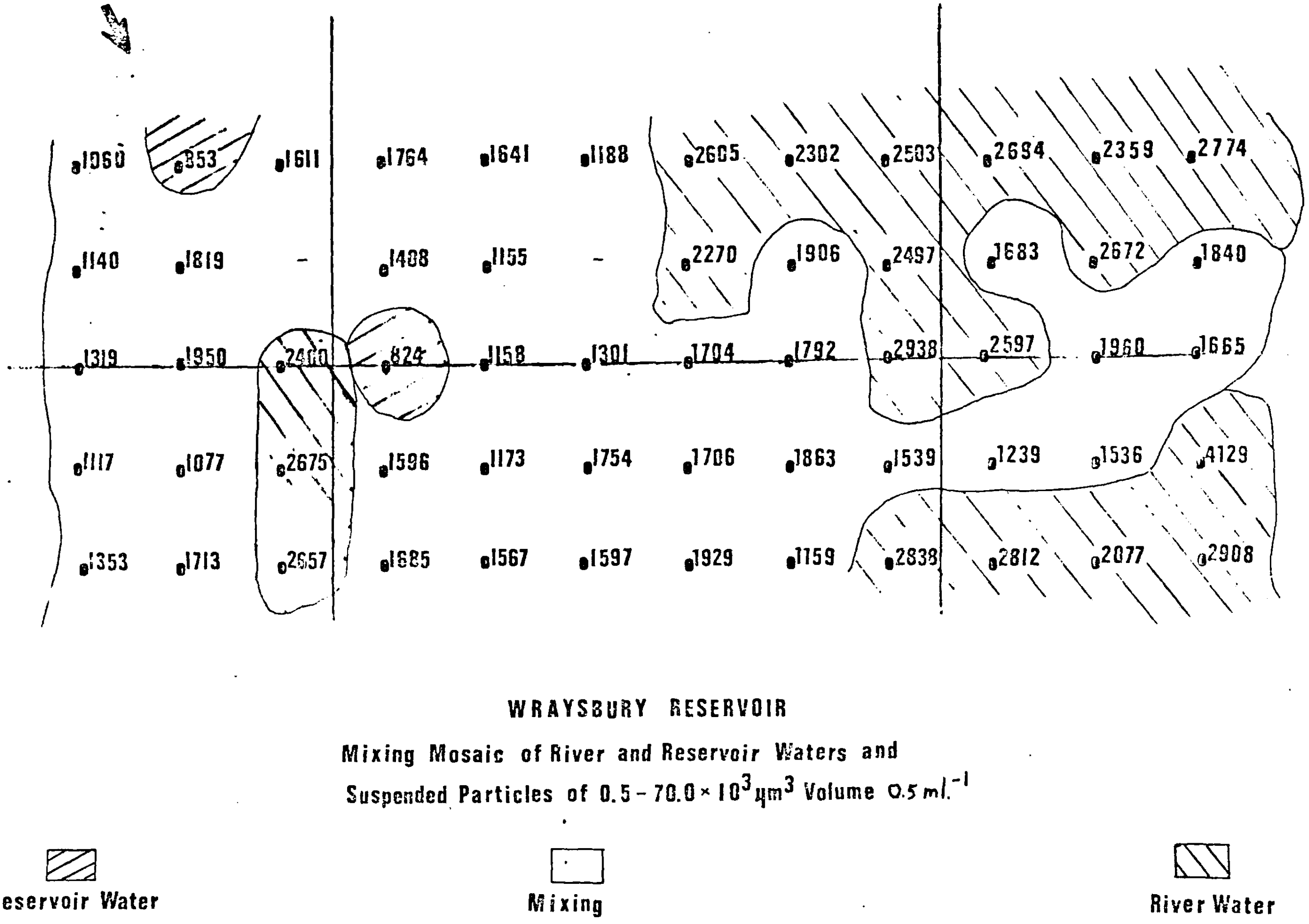


Figure 36. Particle distribution and the mixing of river and reservoir water. Note the effects of wind.

TABLE III

Horizontal Distribution of <u>Aphanizomenon</u> <u>flos-aquae</u> (trichomes $ml.^{-1}$) at the <u>Inlet Pier</u>

7 July 1972

	112	129	* (Central East Buoy)	17	
92	118	145		360	111
163	206	150	(Limnology * Tower II)	420	12
73	12	0		26	4
195	* (North Inlet Jet)	217		* (South Inlet Jet)	150

Table III illustrates that the distribution of Aphanizomenon flos-aquae is erratic. This is possibly because of difficulties in counting clumping organisms (the bundle sheath of trichomes) and/or the entrainment effects of jetting combined with patches of river water. The latter is likely to be the most important factor since counting error alone is unlikely to account for such discrepancies. Buoyancy mechanisms complicated the effects of mixing, and mixing 'depth' should be applied to the species in question. Figure 24 (and chlorophyll-a distributions in Appendix A) illustrates that both Anabaena flos-aquae and Aphanizomenon flos-aquae can overcome the effects of mixing on calm days and maintain themselves in the upper metres. Wraysbury Reservoir phytoplankton communities are reflective of the stability of the water column (see Moss, 1969a, -b), and diatom communities are generally more adapted to the mixed isothermal conditions.

Flagellates were not sufficiently frequent to allow reliable assessment of their distribution. Cryptomonas and Rhodomonas, however, can apparently maintain themselves in the upper ten metres.

D (iv). Turbulence, Phytoplankton Production, and Productivity in the Reservoir:

Turbulence has direct and indirect effects on phytoplankton production and productivity. The direct effects have been extensively studied (Lund, 1954, 1955, 1966; Talling, 1957b, 1971; Vollenweider, 1965; Steele, 1965; and Steel, 1972a). These direct effects are the maintenance of phytoplankton in the water column and the resultant homogeneous vertical distribution of the organisms. In such situations predictions of phytoplankton production have been made. Steele (1965), however, noted the importance of detritus in such predictions, and Murphy(1962) tried to determine the effects of detritus by using a base turbidity attenuation coefficient (based on the work of Jones and Wills (1956)). Murphy assumed, probably as a result of a lack of precise methodology, that basal turbidity was constant, but as discussed by Chandler (1940), Verduin (1954), and Talling (1971) this is not true. Turbulence can re-suspend and/or maintain non-productive particles in the water column (Hunt, 1954). These particles can, in some instances, greatly influence light penetration, and hence be of primary importance when considering the production and productivity of a body of water. Steel (1972) considered the influence of detrital particles on phytoplankton production by introducing an 'extinction depth' which is the product of the vertical attenuation coefficient as caused by detrital particles and the depth of the basin. It is essential, however, to know the ratio of non-productive and productive particles before the production of any two environments can be compared.

Table IV is a summary of productivity experiments (oxygen production, mg. $l.^{-1}$ $hr.^{-1}$) in Wraysbury Reservoir as determined by the light and dark bottle method. Productivity is low in winter and high in summer as a result of temperature and solar radiation. The vertical profile of productivity indicates that marked oxygen production is usually limited to five metres and above. Only on one occasion, June 29, 1972, was theresignificant oxygen production below five metres. This might be related to the observation that June had the highest daily average solar radiation that year (Appendix E), combined with moderate light penetration. Stephanodiscus astraea, which is considered to be

TABLE IV

Rate of Net Oxygen Production (mg. $l.^{-1}$ $hr.^{-1}$) at Different Depths

(Wraysbury Reservoir 1972 - 1973)

DATE	DEPTH 1 METRE	DEPTH 5 METRES	DEPTH 9 METRES	DEPTH BOTTOM
27/01/72	0.7	-	0.9	0.9
16/02/72	0.7	-	0.0	0.0
21/03/72	0.3	-	0.5	0.1
20/04/72	0.8	-	0.8	0.8
16/06/72	3.1	-	0.2	0.2
29/06/72	4.3	3.9	2.9	1.1
13/07/72	2.9	1.1	0.5	0.0
24/08/72	5.8	2.5	0.9	0.3
12/09/72	1.1	0.3	0.0	0.0
27/10/72	0.6	-	0.0	0.0
28/11/72	0.5	-	0.2	-0.2
14/12/72	0.1	-	0.0	0.0
26/04/73	0.3	-	0.1	0.0
14/06/73	2.5	-	0.1	0.0
02/08/73	5.3	-	0.0	0.0
06/09/73	4.2	0.5	0.0	0.0
18/10/73	6.4	1.6	0.3	-0.6
13/12/73	5.2	2.0	1.1	0.0

a deep water diatom (Chandler, 1942b; Van Landingham, 1964), does not show significant oxygen production at or below nine metres depth. This is consistent with the depth of the euphotic zone as shown in Figure 28 and agrees well with general theories on photosynthesis in diatoms (Barker, 1935).

In Table IV it is interesting to note that only on two occasions was there a net loss of oxygen, suggesting there is not much respiration. This is confirmed as the oxygen concentrations in the dark bottles changed very little during these investigations.

From these productivity experiments it would appear that S. astraea has a very wide range of light saturation values (I_k ; Talling, 1957b) varying from 0.007 cal. $cm.^{-2}$ $min.^{-1}$ (5 K ergs $cm.^{-2}$ $sec.^{-1}$) to 0.030 cal. $cm.^{-2}$ $min.^{-1}$ (20 K ergs $cm.^{-2}$ $sec.^{-1}$). (Similar results were obtained by Steel (1972, 1974 personal communication).) This suggests that the organism is adapted to mixing, going through zones of high and low light intensity. It might also be concluded that S. astraea can be considered as a facultative shade species. Temperature does not seem to affect the light saturation values directly, and other factors such as the amount of chlorophyll-a, rates of mixing, and the general physiological state of the cells interact to determine the actual I_k. The value of 5 K ergs $cm.^{-2}$ $sec.^{-1}$ is consistent with Talling's (1957a) approximation of I_k for Melosira italica subspecies subarctica of 3.0 K ergs $cm.^{-2}$ $sec.^{-1}$ which in ecological terms is considered to be a shade species (Talling, 1957a; Lund, 1971).

Should culturing of Stephanodiscus astraea have been successful, production and productivity experiments might revealed much more information on the ecology of the reservoir. As remarked by Lund (1971) when comparing the growth of three desmids in Lake Windermere, a standard is required. Lund compared growth rates of the desmids with that of *Asterionella formosa*. Since the large centric, *S. astraea*, was not successfully cultured there was no method available to compare growth rates except in the more general sense of positive and negative growth rates; any absolute comparison would only reflect the affinities of the organisms for culturing. An added complexity is the interpretation of production data as applied to the true ecological situation (Rodhe, 1940; Myers, 1962). The growth rates of organisms (measured as change of cell or filament numbers) presented in Table V are not idicative of the real growth rates involved (Hughes and Lund, 1962; Cushing, 1959, 1962). They serve only to express what change in numbers occurred when mixed phytoplankton in Wraysbury water was suspended at different depths. Whipple (1896) used a similar technique to measure growth rates in uni-algal cultures.

Some of the results shown in Table V suggest that cells of *S. astraea* can survive when suspended at different depths for periods of up to two weeks. For example, in November and December 1973 there is no indication of a decrease in cell numbers. Only on the 22nd. June, 1973 was there a significant decrease in numbers of *S. astraea* at all depths, and this might well have been a failure to compete with *Asterionella formosa* which usually showed a higher growth rate as in June, 1973. The general tendency of low positive growth rates might merely be a result of cells already in the process of separation at the start of the experiment, and the restriction of further growth by containment of cells in bags or in bottles. The observation of live

TABLE V

Production Experiments

Expressed in Growth Rates ($K = \frac{\log N_t - \log N_o}{t}$)

DATE	SPECIES COMPOSITION	DEPTH 1 METRE	DEPTH 5 M.	DEPTH 9 M.	DEPTH 15 M.	BOTTOM
08/03/73-15/03/73	S. astraea	+0.04	-	0.00	-	0.00
	A. formosa	-0.04	-	-0.12	-	-0.16
	Chlorophyll-a µg. $l.^{-1}$	-	-	-	-	-
	T.P.V. μm^3 $ml.^{-1}$ x 10^6	-	-	-	-	-
15/03/73-22/03/73	S. astraea	-0.12	-0.12	-	+0.06	+0.03
	A. formosa	+0.06	+0.02	-	-0.03	-0.03
	N. acicularis	0.00	+0.06	-	-	-0.01
	Chlorophyll-a	-	-	-	-	-
	T.P.V.	11.0	8.0	-	7.0	6.4
26/04/73-03/05/73	S. astraea	-0.02	-	0.00	-	+0.04
	A. formosa	+0.09	-	+0.01	-	-0.14
	N. acicularis	+0.05	-	-0.02	-	-0.17
	Chlorophyll-a	29.0	-	-	-	33.0
	T.P.V.	-	-	-	-	-
19/06/73-22/06/73	S. astraea	-0.26	-	-0.26	-	-0.26
	Anabaena flos-aquae	+0.02	-	-0.50	-	-0.82
	A. formosa	+0.12	-	-0.14	-	-0.04
	Chlorophyll-a	-	-	-	-	-
	T.P.V.	-	-	-	-	-

TABLE V continued -

DATE	SPECIES COMPOSITION	DEPTH 1 METRE	DEPTH 5 M.	DEPTH 9 M.	DEPTH 15 M.	BOTTOM
05/07/73- 12/07/73	S. astraea	-0.10	+0.10	+0.11	0.00	0.00
	A. formosa	+0.01	0.00	0.00	-0.01	-0.01
	Anabaena flos-aquae	-0.10	-0.30	-0.30	-0.30	-0.30
	Chlorophyll-a	173.0	118.0	93.0	97.0	97.0
	T.P.V.	-	-	-	-	-
11/10/73- 18/10/73	S. astraea	+0.10	-	0.00	-	0.00
	Melosira granulata	+0.03	-	0.00	-	-0.01
	Chlorophyll-a	-	-	-	-	-
	T.P.V.	8.6	-	5.4	-	3.3
01/11/73- 15/11/73	S. astraea	+0.03	+0.03	0.00	-	-
	A. formosa	+0.56	-0.04	-0.04	-	-
	M. granulata	-0.02	-0.02	-0.03	-	-
	Chlorophyll-a	-	-	-	-	-
	T.P.V.	8.1	8.0	7.5	-	-
15/11/73- 29/11/73	S. astraea	0.00	-	0.00	-	0.00
	A. formosa	+0.07	-	-0.01	-	-0.01
	Chlorophyll-a	161.0	-	144.0	-	140.0
	T.P.V.	16.0	-	12.0	-	12.0
29/11/73- 13/12/73	S. astraea	+0.20	+0.10	+0.10	0.00	0.00
	A. formosa	0.00	-0.01	-0.01	-0.01	-0.01
	Chlorophyll-a	-	-	-	-	-
	T.P.V.	-	-	-	-	-

cells in the bottom sediments with very little or no change in the appearance of chromatophores suggests that cells of *S. astraea* might survive for at least six months without light.

If *Stephanodiscus* spp. is a deep water form as discussed by Chandler (1940) and Verduin (1954), it would initially appear that the results of Happey (1970d) with *S. rotula* in Abbots Pond, and Reynolds (1971) with *S. astraea* in the Shropshire Meres would be inconsistent as these bodies of water are relatively shallow. Closer observation of the data presented by Verduin (1954), Chandler (1940), Happey (1970d), and Reynolds (1973) indicate that in all circumstances the cells of *Stephanodiscus* were experiencing light-dark mixing as would the cells of *S. astraea* in Wraysbury Reservoir, and cells of *S. hantzschii* in the River Thames. If nuclear division was dependent upon periods of dark (Fogg, 1965), one might hypothesize that the rate of light-dark mixing, combined with temperature and radiation could determine the production capabilities of *Stephanodiscus*. This would also suggest that *S. astraea* can grow at high or low light intensities by adjusting its metabolism (expressed as a change in I_k) to the rate of mixing and degree of light penetration. It would appear that *S. astraea* (& *S. rotula*) and *S. hantzschii* are usually restricted to optically deep waters (see also Baily, Watts, and Lund, 1973).

Combined effects of mixing and temperature, though exerting some effect on I_k, influence maximum production by maintaining the cells of *S. astraea* in the water column. Tessenow (1966) had noted that the onset of stratification prevented a growth of *S. astraea*, but it is not known if there still existed a favourable light-dark mixing regime.

As the euphotic depth often corresponds to the depth of the epilimnion, this is probably not so.

As indicated by the negative growth rates in Table V it appears that *Asterionella* formosa cannot grow below five metres. The remaining living cells suspended below five metres have a shrunken discoid type of chromatophores. Lund (1949) has commented on this phenomenon, and noted that cells of *Asterionella* die quickly in conditions of low light and low oxygen tensions. Thus the innoculum for the autumn growths was lower than for *S. astraea*. Spring growths are affected by loss of cell production due to mixing below five metres depth. It is possible that cells with the shrunken discoid chromatophores do not recover soon enough to fix sufficient carbon to grow before they are mixed below this depth. Reproductive rates would be adversely affected, and, in addition, a higher death rate would be incurred. The growth rate of any organism is not dependent on its cell reproductive rate alone, but also upon its ability to survive. A potential increase in number does not always result in a large population despite low cropping. This is a basic problem of applying mathematical models to biological problems. The adaptedness and adaptiveness of organisms vary, and although the maximum standing crop of one organism can be successfully predicted by a formula, that of another organism cannot be predicted, or even that of the same organism with one ecological or physiological parameter slightly changed.

Asterionella formosa would appear to be an organism adapted to a specific set of environmental parameters and requirements. When these conditions are met, as in July 1973 in Wraysbury, a large population (10^3 cells $ml.^{-1}$) can develop. The large growth in Wraysbury was probably influenced by the restricted artificial mixing, high solar radiation, and a slight temperature discontinuity at 5 metres depth. *Stephanodiscus astraea* would appear to be more adaptive, and can respond to a wider set of conditions, but the response is slow and less marked. However, optimum conditions (such as during November - December 1973) can be responded to rapidly.

One of the most important facets of the combined effects of solar radiation, temperature, and turbulence on phytoplankton production is the role of non-productive particles. This is particularly true, for example, of Wraysbury Reservoir. Non-productive material from the River Thames is constantly introduced into the reservoir. Artificial and natural mixing combine to suspend many of the small non-productive particles (usually below 5.0×10^3 μm^3.) in the water column until (as with the chemistry of the reservoir) an equilibrium is achieved (Figure 29a). This equilibrium is reflected by the constant (and often maximum) depth of the euphotic zone (Figure 28) which changes most dramatically when the river seston load alters or with growths of *S. astraea*. The first growth of *S. astraea* (spring 1972) was probably SiO_2 limited, the second (autumn 1972) and third (spring 1973) growths were probably limited by sedimentation with restricted mixing and higher temperatures. The fourth growth of autumn 1973 was probably more affected by self-shading and low solar radiation. At the time of the maximum standing crop (13/12/73) the minimum vertical attenuation coefficicient was 0.9 ln units metre^{-1}. As Wraysbury has a near constant absorption coefficient (including particles of 2.9 µm. and under) approximating to 0.18, $\varepsilon_{min.}$ can be partitioned into

$$\varepsilon_{min.} = 0.18 + \varepsilon_q + \varepsilon_p$$

where ε_q is that part of the vertical attenuation coefficient related to non-productive particles, and ε_p is related to the size and number of productive particles.

ε_q can be interpolated from Haffner and Evans' (1974b) relation of $_{\text{min.}}$ and T.P.S.A. by adding the surface area of all particles under 5.0×10^3 µm^3, and was found to be 0.22 ln units $m.^{-1}$ (at this time, though it has varied between 0.10 - 0.70). Thus ε_p was 0.5 ln units $m.^{-1}$, and accounted for only slightly over one half of the total minimum vertical attenuation coefficient.

With low available solar radiation (Appendix E) and a relatively high amount of self-shading, the growth of S. astraea in December 1973 was held in check despite adequate nutrients (SiO_2 on 13/12/73 was 5.5 mg. $l.^{-1}$) and adequate turbulence. Numbers of cells declined gradually and the population was finally dissipated by early February 1974. Concentrations of SiO_2 did not go below 1 mg. $l.^{-1}$, and though near limiting concentrations, there was no sign of nutrient deficiency.

Although Talling's (1971) discussion of the effects of the ratio of the euphotic depth and mixing depth is generally applicable, the rates and the indirect effects of mixing are just as important when determining the nature and the size of a phytoplankton growth in nutrient rich environments. The distribution of phytoplankton not only affects their production, but can influence their temporal succussion (Margalef, 1958). Adaptation to distribution by changes in concentrations of pigments and numbers of photosynthetic enzymes (Jorgensen and Steemann Nielson, 1965) can occur. Mommaerts (1973) has shown the response to changing environmental conditions, particularly turbidity and nutrients in the sea, by production, and Goldman, Mason, and Wood

(1963) have discussed effects of light inhibition because of phytoplankton distribution. Any parameter, such as mixing, which can influence all these interactions is much too difficult to study comprehensively in any one piece of work. Artificial mixing does not in itself inflence phytoplankton production in Thames Valley Reservoirs. It is the interaction and interdependence of mixing and other ecological parameters which combine to produce a distinct response by the phytoplankton.

- SUMMARY -

1. The biology of the phytoplankton of a Thames Valley Reservoir which is artificially mixed is described from late 1971 to early 1974 in terms of biological, chemical, and physical interactions.

2. The morphological variation of some Thames Valley centric diatoms was investigated by use of light, transmission, and scanning electron microscopy. Several morphological varieties of *Stephanodiscus astraea* are thought to exist. The dominant species of the River Thames is *Stephanodiscus hantzschii*, while *Stephanodiscus astraea* var. *typica* dominated the phytoplankton of Wraysbury Reservoir.

3. A change in the flora of the reservoir was associated with a change in nutrient conditions when the River Thames water was innoculated. Only the original spring growth of *Stephanodiscus astraea* was probably nutrient limited when SiO_2 concentrations dropped below 1 mg. l.$^{-1}$. Any other nutrient effects on phytoplankton were probably secondary.

4. Although the direct effect of artificial mixing was the maintenance of homogeneous distributions of temperature and dissolved oxygen, the phytoplankton were often well mixed through the water column. The latter is particularly true of vernal and autumnal diatom growths, but two species of the Cyanophyceae, *Aphanizomenon flos-aquae* and *Anabaena flos-aquae* tended to 'control' their mixing by buoyancy mechanisms, but total production was limited.

5. An intensive study was made of the indirect effects of artificial mixing on phytoplankton production in Wraysbury Reservoir. These indirect effects of mixing were the suspension of non-productive particles and the resultant effect of these suspended particles on the turbidity of the reservoir.

6. The development of ecological implications of particle frequency-size distributions by the Coulter Counter were presented. It is by this method that seston interaction was studied. For Wraysbury Reservoir it was found that:

a. The major source of non-productive particles is the River Thames, and these particles tended to decrease the production potential of the reservoir. Particle concentrations in the reservoir reflect those in the River Thames. As there was little fluctuation in seasonal particle concentrations of the River Thames the concentration in Wraysbury Reservoir remained more or less constant. The latter point is reflected in the maintenance of a somewhat constant euphotic depth.

b. Particle frequency-size analyses can be used, by recording plasmolysis, to determine the presence of dying or moribund cells in a diatom population. It must be emphasized that this procedure must be carried out with caution, but was particularly successful in Wraysbury Reservoir as detrital particles seldom exceeded 5.0 x 10^3 μm^3. The large Stephanodiscus astraea (approximating 10.0 x 10^3 μm^3) formed a disjoint particle size distribution, and shouldering and secondary peaks were not influenced by detritus.

c. The cumulative volume of particle size analyses (T.P.V.) can represent 'biomass' but can also represent amounts of detritus. This latter point can be used to determine basal detrital levels.

d. An accurate partitioning of the vertical attenuation coefficient is possible by studying seston interaction with the Coulter Counter. At Wraysbury Reservoir the minimum vertical attenuation coefficient can be partitioned into;

$$\varepsilon_{\text{min.}} = \underbrace{\varepsilon_w + \varepsilon_s}_{0.18} + \underbrace{\varepsilon_q}_{0.10-0.70} + \underbrace{\varepsilon_p}_{0.0-0.5}$$

where ε_w = attenuation as a result of molecular absorption

ε_s = attenuation of dissolved substances and particles under 2.9 µm. in diameter

ε_q = attenuation by non-productive particles ($>$ 2.9 µm. in diameter)

ε_p = attenuation by productive particles ($>$ 2.9 µm. in diameter).

It was noted that ε_q was the most variable but, as a result of a somewhat constant load of non-productive particles in suspension, basal particle turbidity tended to be about $\varepsilon_q = 0.20$

e. Rapid analyses of samples yielded data on particle distribution in vertical and horizontal planes. Combined with synoptic sampling the size and distribution of a phytoplankton population can be quickly and accurately determined.

7. Stephanodiscus astraea (Ehrenb.) Grun. ≃ Stephanodiscus rotula (Kutz.) Hendey was the dominant phytoplankton species. Possible

reasons for the success of *S. astraea* were:

a. Survival through extended periods (six months) of darkness

b. Adapted to light-dark mixing, perhaps by having a wide range of light saturation values to adapt to the rates of mixing and the changing ratio of euphotic : mixing depths.

c. Appears to be eurythermal, thus unlike *Melosira granulata*, can take advantage of correct mixing - light regimes at anytime of year, particularly when the water temperature is low, sinking rates are low, and mixing more efficient.

Asterionella formosa, although eurythermal, did not adapt well to the mixing regimes, perhaps as a failure to recover from extended phases of darkness. When mixing depth was altered by incipient stratification *Asterionella* grew extremely well.

Aphanizomenon flos-aquae and *Anabaena flos-aquae* could exert some control over their own mixing depth, but not enough to achieve maximum production potential.

8. The water of the Thames Valley has high production capabilities, but mixing can reduce actual production primarily by influence on light penetration and utilization. It is the interactions of mixing with other ecological parameters and their interdependencies which affect phytoplankton production. Generalizations on the effects of mixing are at best tentative.

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APPENDIX A

Chlorophyll'a' (Total Pigment) µg./l. - 1972

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
18/01/72	1	2.48	-	
01/02/72	1	2.41	-	
08/02/72	3	3.4 ± 0.17	3.2 - 3.5	
16/02/72	4	6.0 ± 0.30	5.8 - 6.3	
23/2/72	4	11.3 ± 0.20	10.8 - 11.5	*S. astraea*
29/02/72	9	14.7 ± 2.60	14.8 - 19.0	growth
08/03/72	9	19.0 ± 4.00	12.0 - 24.0	
15/03/72	9	8.0 ± 2.00	5.0 - 10.0	
21/03/72	9	10.0 ± 4.00	6.0 - 14.0	
29/03/72	8	9.8 ± 0.60	9.0 - 11.0	
10/04/72	8	7.8 ± 1.00	6.0 - 9.0	
17/04/72	9	7.0 ± 1.00	6.0 - 8.0	
24/04/72	4	6.7 ± 1.00	6.0 - 7.0	
01/05/72	4	2.0 ± 0.50	1.1 - 2.2	
08/05/72	5	1.8 ± 0.40	1.2 - 2.2	
15/05/72	4	1.2 ± 0.10	1.2 - 1.3	
22/05/72	3	3.00	1.9 - 3.8	
05/06/72	5	3.0 ± 1.00	2.1 - 3.3	
12/06/72	6	3.8 ± 1.40	1.8 - 5.6	

APPENDIX A continued -

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
19/06/72	5	2.3 ± 0.80	1.0 - 3.1	
26/06/72	6	2.0 ± 1.60	0.5 - 4.7	*Aphanizomenon*
03/07/72	10	4.7 ± 3.30	0.5 - 12.0	*flos-aquae*
10/07/72	11	1.2 ± 0.30	0.8 - 1.5	
17/07/72	11	2.2 ± 0.80	0.7 - 2.4	
24/07/72	1	0.90	-	
31/07/72	11	2.3 ± 1.30	0.7 - 4.8	*Aphanizomenon*
07/08/72	6	2.0 ± 0.60	1.4 - 2.6	*flos-aquae*
14/08/72	9	2.1 ± 1.00	0.8 - 3.9	
21/08/72	6	4.1 ± 1.00	2.7 - 4.9	*Tribonema*
28/08/72	6	3.6 ± 0.80	2.7 - 4.6	spp.
04/09/72	6	3.9 ± 0.50	3.2 - 4.4	
11/09/72	6	5.3 ± 0.40	4.7 - 5.6	*S. astraea*
18/09/72	10	11.5 ± 1.50	10.7 - 13.0	
25/09/72	11	24.2 ± 4.50	16.2 - 29.5	Settling out of *S. astraea*
02/10/72	11	37.0 ± 12.0	29.0 - 66.0	
09/10/72	11	28.0 ± 15.0	10.0 - 46.0	
16/10/72	11	7.1 ± 0.40	3.7 - 7.6	
23/10/72	5	8.5 ± 0.50	8.1 - 9.3	
30/10/72	5	10.0 ± 0.50	9.5 - 10.6	
06/11/72	5	8.8 ± 0.80	7.9 - 9.7	
13/11/72	10	8.1 ± 0.60	7.5 - 8.9	
20/11/72	5	5.5 ± 1.00	4.5 - 6.4	

APPENDIX A continued -

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
27/11/72	5	5.7 ± 0.50	5.1 - 6.0	
11/12/72	3	5.1 ± 1.20	4.1 - 6.4	
18/12/72	3	4.5 ± 0.10	4.3 - 4.7	
27/12/72	1	0.60	-	

APPENDIX A continued -

Chlorophyll'a' (Total Pigment) µg./l. - 1973

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
03/01/73	1	2.60	-	
08/01/73	1	0.70	-	
18/01/73	1	1.10	-	
22/01/73	1	1.80	-	
29/01/73	5	1.8 ± 0.20	1.7 - 2.1	
05/02/73	3	1.6 ± 0.50	1.2 - 2.2	
12/02/73	12	2.3 ± 0.40	1.8 - 2.7	
19/02/73	5	2.6 ± 0.40	2.2 - 3.9	
26/02/73	4	3.2 ± 0.30	3.0 - 3.6	
05/03/73	4	3.9 ± 0.40	3.4 - 4.2	
12/03/73	4	5.5 ± 0.30	5.2 - 5.9	
26/03/73	6	13.6 ± 1.70	12.6 - 16.4	*S. astraea*
03/04/73	12	25.0 ± 5.00	16.0 - 29.0	
09/04/73	12	34.0 ± 5.00	27.0 - 43.0	
16/04/73	12	43.0 ± 1.00	42.0 - 44.0	
24/04/73	12	31.0 ± 4.00	25.0 - 40.0	
30/04/73	6	9.9 ± 5.30	4.9 - 20.0	
07/05/73	4	6.8 ± 0.90	5.6 - 8.2	
21/05/73	4	11.7 ± 0.20	10.2 - 13.8	
29/05/73	4	4.3 ± 0.80	3.5 - 5.7	
04/06/73	6	4.0 ± 1.50	3.0 - 4.8	

APPENDIX A continued -

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
11/06/73	6	5.8 ± 2.40	2.7 - 9.3	
18/06/73	8	5.7 ± 0.90	4.6 - 7.3	
25/06/73	9	4.3 ± 1.90	2.9 - 8.6	
02/07/73	8	8.5 ± 2.50	5.2 - 10.3	*Asterionella formosa*
09/07/73	8	21.0 ± 17.0	5.0 - 55.0	
16/07/73	10	4.0 ± 2.10	2.3 - 9.3	
23/07/73	12	4.5 ± 7.00	1.0 - 22.0	*Anabaena flos-aquae*
30/07/73	12	2.4 ± 1.30	1.4 - 6.0	
06/08/73	12	5.7 ± 1.80	3.1 - 9.2	
13/08/73	12	5.3 ± 5.10	2.0 - 17.0	
20/08/73	12	10.9 ± 8.60	5.0 - 29.0	*Melosira granulata*
03/09/73	4	20.0 ± 2.00	18.0 - 23.3	
10/09/73	10	8.8 ± 3.50	7.0 - 8.0	
17/09/73	10	7.2 ± 0.40	4.9 - 8.8	
24/09/73	10	5.5 ± 0.40	4.9 - 5.8	
09/10/73	11	10.6 ± 2.10	9.2 - 15.7	
15/10/73	11	11.0 ± 1.00	9.7 - 13.2	
22/10/73	8	8.7 ± 0.50	8.2 - 9.7	
29/10/73	6	10.8 ± 0.40	10.0 - 11.2	
05/11/73	5	18.5 ± 2.00	17.4 - 19.9	
12/11/73	12	39.9 ± 3.00	34.0 - 43.0	*Stephanodiscus astraea*
19/11/73	11	61.0 ± 7.00	45.0 - 71.0	
26/11/73	5	75.0 ± 2.00	73.0 - 78.0	

APPENDIX A continued -

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
03/12/73	5	91.0 ± 8.20	81.0 - 101.0	*Stephanodiscus astraea*
10/12/73	5	85.0 ± 6.00	75.0 - 91.0	
17/12/73	3	80.0 ± 6.00	-	

APPENDIX B

Carbon µg./l. - 1972

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
18/01/72	1	341	-	
01/02/72	1	239	-	
08/02/72	3	377 ± 30	352 - 412	
16/02/72	9	400 ± 30	351 - 438	
23/02/72	4	439 ± 66	344 - 600	
29/02/72	9	769 ± 44	740 - 841	
08/03/72	9	1109 ± 105	981 - 1243	*Stephanodiscus astraea*
15/03/72	9	625 ± 38	557 - 663	
21/03/72	9	729 ± 210	487 - 986	
29/03/72	8	867 ± 74	757 - 946	
10/04/72	8	802 ± 42	738 - 855	
17/04/72	9	776 ± 93	646 - 918	
24/04/72	9	541 ± 133	356 - 631	
01/05/72	10	461 ± 45	403 - 518	
08/05/72	5	394 ± 82	261 - 473	
15/05/72	5	290 ± 23	254 - 312	
22/05/72	5	336 ± 94	213 - 413	
05/06/72	5	355 ± 51	294 - 412	

APPENDIX B continued -

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
12/06/72	5	430 ± 148	215 - 582	*S. hantzschii* in river
19/06/72	4	500 ± 117	366 - 652	
26/06/72	12	499 ± 121	419 - 747	
03/07/72	10	437 ± 357	216 - 1216	*Aphanizomenon flos-aquae*
10/07/72	11	462 ± 77	357 - 620	
17/07/72	11	373 ± 102	237 - 496	
24/07/72	5	265 ± 154	133 - 482	
31/07/72	11	526 ± 124	401 - 627	*Aphanizomenon flos-aquae*
07/08/72	11	371 ± 60	277 - 450	
14/08/72	11	384 ± 199	242 - 886	*Tribonema* spp.
21/08/72	11	427 ± 42	369 - 484	
28/08/72	11	651 ± 196	508 - 1151	
04/09/72	10	501 ± 24	475 - 540	
11/09/72	5	417 ± 39	379 - 487	
18/09/72	11	728 ± 48	666 - 783	
25/09/72	11	1092 ± 52	991 - 1214	*Stephanodiscus astraea*
02/10/72	11	1400 ± 147	848 - 1465	
09/10/72	11	1693 ± 326	1242 - 2250	
16/10/72	11	773 ± 65	662 - 875	
23/10/72	5	611 ± 74	492 - 587	
30/10/72	5	712 ± 31	671 - 746	
06/11/72	5	616 ± 71	544 - 723	
13/11/72	11	633 ± 78	584 - 824	

APPENDIX B continued -

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
20/11/72	5	540 ± 43	491 - 601	
27/11/72	5	479 ± 43	446 - 534	
11/12/72	3	583 ± 3	580 - 585	
27/12/72	1	970	-	

APPENDIX B continued -

- Carbon µg./l. - 1973

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
03/01/73	1	331	-	
08/01/73	1	435	-	
18/01/73	1	403	-	
22/01/73	1	352	-	
29/01/73	6	417 ± 27	389 - 460	
05/02/73	3	440 ± 64	386 - 511	
12/02/73	4	448 ± 51	392 - 509	
19/02/73	12	418 ± 44	369 - 534	
26/02/73	5	581 ± 39	593 - 604	
05/03/73	4	525 ± 14	504 - 538	
12/03/73	4	646 ± 60	597 - 731	
26/03/73	4	1073 ± 113	918 - 1164	*Stephanodiscus astraea*
03/04/73	6	1299 ± 48	1218 - 1368	
09/04/73	12	1640 ± 75	1595 - 1756	
16/04/73	12	1902 ± 131	1674 - 2076	
24/04/73	12	1696 ± 97	1521 - 1873	
30/04/73	12	1015 ± 134	807 - 1187	
07/05/73	6	858 ± 80	753 - 967	
21/05/73	4	1198 ± 458	809 - 1814	*Aphanizomenon flos-aquae*
29/05/73	6	864 ± 124	685 - 1039	
04/06/73	6	767 ± 218	587 - 1173	

APPENDIX B continued -

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
11/06/73	8	772 ± 359	592 - 1259	
18/06/73	10	913 ± 288	657 - 1636	
25/06/73	8	781 ± 193	501 - 1100	
02/07/73	8	1272 ± 766	609 - 2672	*Asterionella formosa*
09/07/73	10	1150 ± 947	491 - 3081	
16/07/73	12	661 ± 249	402 - 1138	
23/07/73	12	662 ± 519	385 - 1470	
30/07/73	12	460 ± 199	272 - 961	
06/08/73	12	680 ± 128	485 - 864	
13/08/73	12	676 ± 495	274 - 1506	
20/08/73	12	910 ± 595	356 - 2663	*Melosira granulata*
03/09/73	12	828 ± 204	553 - 1257	
10/09/73	10	600 ± 228	385 - 1102	
17/09/73	10	397 ± 121	208 - 552	
24/09/73	10	422 ± 75	331 - 608	
09/10/73	10	543 ± 116	393 - 754	
15/10/73	11	560 ± 80	491 - 736	
22/10/73	7	671 ± 118	443 - 570	
29/10/73	6	500 ± 50	457 - 623	
05/11/73	6	525 ± 59	497 - 623	
12/11/73	12	882 ± 60	789 - 970	
19/11/73	11	1273 ± 66	1177 - 1301	

APPENDIX B continued -

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
26/11/73	4	1561 ± 33	1512 - 1581	*Stephanodiscus astraea*
14/12/73	4	1811 ± 102	1701 - 1872	

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APPENDIX C

Total Particulate Volume μm^3 x 10^3 ml^{-1} - 1972

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
04/01/72	9	476 ± 118	222 - 609	
10/01/72	9	388 ± 89	297 - 553	
18/01/72	9	375 ± 38	343 - 445	
25/01/72	9	461 ± 72	367 - 627	
03/02/72	9	472 ± 35	412 - 522	
09/02/72	9	778 ± 136	637 - 1070	)
18/02/72	9	1538 ± 228	1340 - 2028	) <u>Stephanodiscus</u>
23/02/72	9	2794 ± 153	2547 - 2960	) <u>astraea</u>
09/03/72	9	2784 ± 546	1813 - 3486	)
16/03/72	9	1615 ± 292	1096 - 1898	- end of growth
04/04/72	3	1743 ± 38	1699 - 1767	- river input
12/04/72	8	1958 ± 527	1541 - 2045	)
18/04/72	3	2442 ± 512	1971 - 3000	) <u>Aphanizomenon</u>
24/04/72	3	740 ± 252	555 - 1029	) <u>flos-aquae</u>
02/05/72	3	714 ± 284	516 - 1040	)
09/05/72	3	604 ± 105	494 - 705	
15/05/72	3	732 ± 211	512 - 934	
21/05/72	3	530 ± 48	487 - 581	
30/05/72	3	487 ± 207	327 - 722	
12/06/72	3	887 ± 202	709 - 1108	) <u>S. hantzschii</u>
22/06/72	4	580 ± 201	372 - 803	) in River Thames
27/06/72	3	421 ± 165	266 - 594	

APPENDIX C continued -

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
03/07/72	3	492 ± 294	286 - 830	
10/07/72	3	543 ± 96	434 - 630	200 m.g.d. input
17/07/72	9	570 ± 169	299 - 811	100 m.g.d. input
31/07/72	12	495 ± 155	207 - 656	
10/08/72	4	456 ± 104	384 - 576	
29/08/72	4	792 ± 203	560 - 941	
05/09/72	3	805 ± 321	550 - 1107	
12/09/72	3	1396 ± 278	1097 - 1649	*Stephanodiscus astraea*
19/09/72	9	3637 ± 1506	2754 - 7584	
26/09/72	10	8437 ± 512	7570 - 9194	
03/10/72	9	8668 ± 2477	3134 - 11030	Sedimentation
10/10/72	5	6428 ± 2387	4846 - 11000	
19/10/72	8	2444 ± 236	2192 - 2609	
27/10/72	8	1846 ± 504	1481 - 22089	
30/10/72	3	1754 ± 370	1377 - 2166	
09/11/72	3	1826 ± 382	1411 - 2165	
16/11/72	8	1601 ± 250	1382 - 14044	
23/11/72	5	2002 ± 376	1734 - 2591	
30/11/72	7	2301 ± 1801	1234 - 6332	River detritus
07/12/72	9	4616 ± 1179	3734 - 4726	
14/12/72	5	3480 ± 195	3198 - 10934	
20/12/72	3	3504 ± 3115	1462 - 7090	

APPENDIX C continued -

Total Particulate Volume $\mu m.^3 \times 10^3\ ml.^{-1}$ - 1973

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
08/01/73	8	1365 ± 228	1110 - 1858	
15/01/73	5	1509 ± 355	1258 - 2086	
22/01/73	4	1570 ± 329	1232 - 2004	
29/01/73	4	1445 ± 131	1256 - 1558	
12/02/73	8	1101 ± 224	798 - 1378	
18/02/73	6	909 ± 147	688 - 1058	
05/03/73	3	931 ± 159	758 - 964	
12/03/73	6	1722 ± 610	1278 - 2934	*S. astraea*
19/03/73	5	2049 ± 1124	2080 - 2788	
03/04/73	5	6737 ± 1117	5258 - 8092	
09/04/73	11	7884 ± 2357	4892 - 13830	
24/04/73	10	7953 ± 1938	6200 - 10772	
30/04/73	8	3024 ± 2112	990 - 4472	Sedimentation
07/05/73	10	1746 ± 627	1048 - 2004	
29/05/73	6	802 ± 172	586 - 1082	
05/06/73	3	639 ± 297	350 - 944	
11/06/73	6	1130 ± 364	890 - 1852	
18/06/73	6	1438 ± 384	918 - 1842	
25/06/73	6	1261 ± 114	1094 - 1420	
02/07/73	6	1767 ± 928	1066 - 3480	*Asterionella*
09/07/73	8	2422 ± 1474	1256 - 5518	

APPENDIX C continued -

DATE	N	MEAN ± STANDARD DEVIATION	RANGE	COMMENTS
16/07/73	6	894 ± 332	558 - 1468	
30/07/73	9	553 ± 155	310 - 740	
06/08/73	8	719 ± 150	502 - 926	
13/08/73	9	856 ± 385	352 - 1590	
20/08/73	7	737 ± 398	396 - 1600	
03/09/73	8	932 ± 319	606 - 1474	
10/09/73	6	593 ± 104	398 - 690	
17/09/73	7	478 ± 140	290 - 628	
24/09/73	6	701 ± 142	510 - 886	
01/10/73	3	1144 ± 182	992 - 1346	
08/10/73	7	914 ± 237	686 - 1348	
15/10/73	8	1118 ± 363	758 - 1280	
22/10/73	7	1226 ± 207	894 - 1322	*S. astraea*
29/10/73	9	2145 ± 307	1732 - 2268	
12/11/73	8	3923 ± 622	2940 - 4594	
19/11/73	7	4452 ± 701	3770 - 5572	
03/12/73	6	8958 ± 271	4662 - 12694	
10/12/73	7	10838 ± 815	9662 - 12108	
04/01/74	1	8000	-	
28/01/74	1	2217	-	
05/02/74	3	1700 ± 150	1532 - 2226	

APPENDIX D

Dry Weights, Loss-on-Ignition, and Vertical Net Hauls**

DATE	DRY WEIGHT mg. l^{-1}			LOSS-ON-IGNITION µg. l^{-1}			VERTICAL NET HAUL mg.
	TOP	MIDDLE	BOTTOM	TOP	MIDDLE	BOTTOM	
07/12/71	4.4	-	1.6	300	-	100	-
14/12/71	1.6	-	1.5	500	-	900	-
10/01/72	1.6	-	-	700	-	500	-
18/01/72	2.0	-	0.2	800	-	200	-
03/02/72	0.6	-	0.5	100	-	500	-
08/03/72	1.4	-	0.7	-	-	-	-
28/03/72	1.8	1.2	2.2	1600	900	1200	-
04/04/72	2.2	2.0	2.4	2200	1700	2333	-
17/04/72	1.3	-	24.3‡	900	-	2300	-
01/05/72	2.3	2.3	2.4	1100	1000	1400	-
08/05/72	2.3	2.2	2.2	900	800	700	-
12/06/72	2.5	-	2.0	200	-	150	-
13/07/72	4.0	2.2	2.0	2000	800	900	-
10/08/72	2.0	1.1	2.0	-	-	-	-
20/09/72	8.0	8.2	8.4	8000	7000	7110	-
16/10/72	2.7	-	2.4	400	450	450	-
06/11/72	3.0	-	1.4	100	-	100	-
20/11/72		2.2*			500*		57.0
27/11/72		1.7*			450*		30.4
04/12/72		2.0*			-		-
11/12/72		6.0*			450*		9.2

APPENDIX D continued -

DATE	DRY WEIGHT mg. l^{-1}			LOSS-ON-IGNITION µg. l^{-1}			VERTICAL NET HAUL mg.
	TOP	MIDDLE	BOTTOM	TOP	MIDDLE	BOTTOM	
18/12/72		5.1*			-		92.8
27/12/72		1.2*			-		107.4
02/01/73	3.0	-	1.7	150	-	80	-
03/01/73		3.1*			-		33.3
08/01/73		2.4*			-		19.7
18/01/73		2.8*			-		24.4
29/01/73		3.4*			-		35.4
01/02/73		8.0*			180*		-
05/02/73		2.3*			-		56.4
12/02/73		2.2*			-		20.4
15/02/73		3.0*			200*		-
19/02/73		2.3*			-		35.0
22/02/73		5.1*			380*		-
26/02/73		2.4*			-		25.0
05/03/73		2.4*			-		26.0
12/03/73		2.2*			-		23.0
26/03/73		4.0*			-		26.0
28/03/73		1.2*			580*		-
03/04/73		3.9*			-		26.0
09/04/73		6.2*			-		34.0
12/04/73	6.7	7.4	7.0	3400	3600	3211	-
16/04/73		6.1*			-		78.2
24/04/73		6.5*			-		211.0

APPENDIX D continued -

DATE	DRY WEIGHT mg. l^{-1}			LOSS-ON-IGNITION µg. l^{-1}			VERTICAL NET HAUL mg.
	TOP	MIDDLE	BOTTOM	TOP	MIDDLE	BOTTOM	
30/04/73		3.0*			-		83.0
07/05/73		2.2*			-		205.0
21/05/73		3.9*			-		473.0
23/05/73	3.2	3.7	2.0	600	100	100	-
29/05/73		3.6*			-		306.0
04/06/73		3.2*			-		239.0
11/06/73		3.6*			700*		112.0
18/06/73		4.1*			-		353.0
21/06/73	3.4	2.1	3.0	210	130	180	-
25/06/73		3.1*			-		204.0
28/06/73	6.0	5.3	6.0	400	340	260	-
02/07/73		4.3*			-		332.0
09/07/73		4.4*			-		143.0
16/07/73		2.6*			-		261.0
19/07/73	4.1	2.9	3.1	200	200	200	-
23/07/73		4.0*			-		170.0
30/07/73		1.0*			-		114.0
06/08/73		2.4*			-		89.0
09/08/73	2.3	2.2	1.8	700	900	700	-
13/08/73		3.1			-		153.0
20/08/73		2.7*			-		< 100.0‡
30/08/73		3.9*			-		< 100.0‡
03/09/73	5.5	-	5.8	200	-	290	-

APPENDIX D continued -

DATE	DRY WEIGHT mg. l^{-1}			LOSS ON IGNITION µg. l^{-1}			VERTICAL NET HAUL mg.
	TOP	MIDDLE	BOTTOM	TOP	MIDDLE	BOTTOM	
10/09/73		2.4*			-		≤ 20.0
17/09/73		2.1*			-		105.0
24/09/73		2.2			-		< 30.0
01/10/73		2.8*			-		< 20.0
04/10/73	6.6	5.8	5.7	600	560	560	low
12/10/73	5.7	4.7	4.2	-	-	-	-
15/10/73		2.5*			-		low
22/10/73		2.8*			-		121.0
29/10/73		2.7*			-		71.5
05/11/73		2.0*			-		29.6
12/11/73		2.4*			-		29.0
19/11/73		6.3*			-		26.8
26/11/73		9.2*			-		41.8
03/12/73		12.2*			-		125.0
10/12/73		9.7*			-		41.5
04/01/74	6.0	6.2	6.0	3000	3100	6000	-

** Vertical Net Haul data is provided with the permission of The Metropolitan Water Board.

* Combined depth samples

‡ Possible fault in sampling or analytical procedures

APPENDIX E

Solar Radiation and Rainfall (Monthly averages)

	DATE	TOTAL RADIATION mWhr. cm.$^{-2}$	TOTAL ILLUMINATION Klux. hrs.	TOTAL RAINFALL mm.
1972	January	61.8	81.2	53.5
	February	86.1	114.9	44.5
	March	261.0	327.2	49.9
	April	311.6	388.7	40.6
	May	444.6	554.5	26.0
	June	449.9	558.8	15.2
	July	441.9	553.8	27.7
	August	397.9	500.9	14.3
	September	251.3	326.7	26.5
	October	173.0	251.7	18.3
	November	89.1	110.7	57.5
	December	59.7	74.6	66.8
1973	January	56.1	71.8	13.3
	February	132.0	158.0	13.9
	March	260.9	322.7	11.1
	April	330.1	408.3	58.6
	May	413.0	530.8	54.0
	June	536.0	688.7	69.4
	July	436.1	558.8	49.6
	August	440.9	556.9	39.4
	September	371.5	474.4	66.7

APPENDIX E continued -

	DATE	TOTAL RADIATION mWhr. cm.$^{-2}$	TOTAL ILLUMINATION Klux. hrs.	TOTAL RAINFALL mm.
1973	October	159.6	197.5	37.7
	November	98.6	118.1	24.2
	December	66.1	78.5	51.8

APPENDIX F

Seston Distribution in Wraysbury Reservoir during 1972 - 1973
as expressed by Variance : Mean Ratios -A: At one metre depth

Volume Class x 10^3 μm^3	23/03/72	18/04/72	25/04/72	09/05/72	16/05/72	23/05/72	06/06/72	22/06/72	10/07/72	08/08/72	05/09/72	19/09/72	29/09/72	03/10/72	19/10/72	02/11/72	20/12/72
20.0	1.3	0.3	-	-	-	-	-	-	-	-	-	0.6	0.7	0.6	2.7	0.9	-
10.0	4.9	0.3	-	-	9.0	-	-	-	-	-	-	3.2	6.1	2.3	0.4	7.8	-
7.5	0.3	0.1	-	0.17	0.3	-	-	0.6	5.4	0.6	-	24.3	7.9	0.6	2.6	4.3	-
5.0	1.3	0.1	-	0.11	8.0	8.0	-	7.0	1.6	0.7	-	5.7	20.6	3.5	10.7	11.1	1.7
3.0	0.6	0.5	1.2	0.26	5.0	17.0	0.8	0.4	2.1	0.4	2.8	6.3	24.8	8.7	20.5	3.1	2.8
1.6	4.7	3.6	0.6	8.1	17.0	36.0	9.0	8.0	37.0	38.0	4.4	6.0	44.8	9.6	1.5	16.4	1.3
0.8	49.0	1.5	5.6	24.8	20.0	21.0	11.0	38.0	9.0	15.0	18.3	0.1	5.0	9.5	47.0	9.4	13.7
0.4	522	21.0	19.6	31.2	53.0	12.0	16.0	9.0	10.0	12.0	8.9	5.2	19.6	19.4	31.4	53.2	16.5
0.2	173	50.3	8.8	13.4	33.0	5.0	7.0	15.0	16.0	11.0	13.6	0.02	31.3	16.2	140.6	146.0	12.5
0.1	37.0	2.4	45.0	16.1	328.0	15.0	40.0	90.0	55.0	60.0	40.9	0.1	44.0	40.0	48.2	14.2	16.0
0.05	17.1	12.4	54.0	185.1	40.0	57.0	-	-	-	-	52.8	14.5	147.5	91.4	40.0	44.5	83.0

APPENDIX F continued -

Seston Distribution in Wraysbury Reservoir during 1972 - 1973
as expressed by Variance : Mean Ratios -A: At one metre depth

Volume Class x 10^3 μm^3	15/02/73	01/03/73	08/03/73	16/03/73	22/03/73	28/03/73	12/04/73	19/04/73	26/04/73	03/05/73	10/05/73	31/05/73	07/06/73	14/06/73	21/06/73	28/06/73	05/07/73
20.0	-	-	3.0	0.6	0.7	7.6	8.3	0.3	3.6	3.5	6.0	-	-	-	-	2.3	1.4
10.0	-	-	1.0	0.8	4.3	1.5	16.7	4.1	0.4	7.2	0.6	-	-	-	3.0	4.6	2.9
7.5	-	-	0.3	0.2	8.7	24.0	1.5	23.1	16.0	5.3	1.1	-	-	-	2.3	8.1	31.0
5.0	2.7	4.0	1.0	0.3	0.8	1.4	0.75	16.0	14.0	2.2	13.1	1.8	0.1	1.2	2.4	6.7	44.0
3.0	1.3	2.0	1.3	2.4	6.1	11.4	9.3	1.8	81.0	1.2	4.9	0.8	1.9	0.3	16.0	2.9	10.2
1.6	10.8	4.0	3.3	3.1	3.5	2.2	16.2	4.8	23.0	16.0	3.5	4.0	11.0	4.7	13.0	46.0	15.4
0.8	4.5	4.4	4.2	1.0	11.0	23.0	21.0	0.5	13.0	11.3	3.4	2.6	6.9	3.8	38.0	80.0	19.0
0.4	19.3	9.0	5.0	8.6	50.6	-	48.0	9.8	13.0	0.14	2.0	13.0	116.0	8.2	24.3	108.0	42.0
0.2	9.1	7.4	3.4	13.2	13.6	-	33.4	22.4	12.0	18.2	76.0	50.0	141.0	16.0	14.2	118.0	15.6
0.1	32.6	3.3	7.9	34.0	2.4	45.9	4.7	1.9	41.0	2.0	173.0	215.0	36.6	46.3	11.3	185.0	41.7
0.05	36.0	15.5	29.0	186.0	5.6	115.3	33.8	100.9	37.0	1.4	160.0	11.4	51.6	125.0	20.0	81.0	17.6

APPENDIX F continued -

Seston Distribution in Wraysbury Reservoir during 1972 - 1973
as expressed by Variance : Mean Ratios -A: At one metre depth

Volume Class x 10^3 μm^3	12/07/73	19/07/73	03/08/73	08/08/73	22/08/73	06/09/73	27/09/73	11/10/73	18/10/73	01/11/73	29/11/73	13/12/73
20.0	7.0	-	-	-	-	-	-	2.0	1.5	1.0	6.3	2.6
10.0	8.0	-	-	-	-	-	-	0.1	1.0	0.6	11.0	6.0
7.5	5.4	3.3	0.4	-	5.7	2.1	-	1.8	1.0	18.0	5.0	6.0
5.0	28.0	14.9	1.6	12.5	17.0	3.7	1.2	0.7	0.2	10.0	11.0	19.0
3.0	3.6	4.6	2.1	1.6	2.5	3.3	2.2	1.4	0.8	5.3	53.0	25.0
1.6	2.6	14.6	6.9	1.5	2.6	5.4	1.2	1.3	1.0	9.4	6.8	21.0
0.8	9.9	16.4	36.4	1.7	5.2	7.3	4.1	3.9	1.7	2.8	15.0	1.0
0.4	12.2	6.3	10.1	10.2	3.2	13.0	4.0	5.1	7.7	0.7	14.0	38.0
0.2	8.0	0.4	0.3	17.2	7.1	16.0	23.0	1.0	5.4	8.9	3.0	17.0
0.1	16.0	6.4	63.0	19.4	20.0	24.0	14.0	6.0	18.0	0.7	19.0	59.0
0.05	46.0	52.0	54.6	54.8	27.9	30.0	1.0	6.5	21.0	21.0	17.0	18.0

APPENDIX F continued -

Seston Distribution in Wraysbury Reservoir during 1972 - 1973
as expressed by Variance : Mean Ratios -B: At nine metres depth

Volume Class x 10^3 μm^3	23/03/72	29/03/72	18/04/72	25/04/72	09/05/72	16/05/72	23/05/72	06/06/72	22/06/72	10/07/72	08/08/72	05/09/72	19/09/72	29/09/72	03/10/72	19/10/72	02/11/72
20.0	-	-	1.3	-	-	-	-	-	-	-	-	-	16.2	2.3	0.7	1.6	-
10.0	0.8	-	10.0	-	-	-	-	-	-	-	-	-	10.6	5.2	6.3	2.8	0.6
7.5	1.8	0.15	6.0	2.5	-	1.0	-	0.6	8.0	-	-	-	-	2.5	18.0	0.4	1.4
5.0	3.0	4.1	3.3	5.1	0.48	3.6	3.0	0.1	0.2	8.0	-	0.09	5.0	9.1	23.1	0.1	1.4
3.0	1.0	-	8.5	5.1	1.6	4.0	3.0	11.0	1.3	3.0	6.0	4.7	10.8	17.8	18.7	1.8	8.2
1.6	3.2	3.5	29.0	6.2	1.6	6.0	7.0	17.0	11.0	5.5	9.2	1.2	3.3	30.8	38.2	18.8	3.2
0.8	5.6	48.0	18.0	16.0	5.0	17.0	7.0	32.0	6.0	9.2	4.1	1.2	0.1	9.1	4.2	2.6	3.2
0.4	52.0	0.6	41.0	32.7	1.8	35.0	9.0	13.0	0.1	1.0	0.1	1.7	3.9	16.0	30.9	19.8	9.0
0.2	42.0	14.6	44.0	61.0	1.7	11.0	14.0	17.0	70.0	16.0	130.0	10.2	7.6	7.1	13.9	7.2	8.9
0.1	9.2	11.1	64.0	69.0	9.5	15.0	14.0	31.0	52.0	104.0	111.0	3.2	64.0	14.9	14.6	11.6	88.0
0.05	23.3	6.4	98.0	57.0	9.8	18.0	38.0	25.0	30.0	125.0	8.0	2.9	360.0	39.7	49.0	12.0	3.2

APPENDIX F continued -

Seston Distribution in Wraysbury Reservoir during 1972 - 1973
as expressed by Variance : Mean Ratios -B: At nine metres depth

Volume Class x 10^3 μm^3	20/12/72	15/02/73	01/03/73	08/03/73	16/03/73	22/03/73	28/03/73	12/04/73	19/04/73	26/04/73	03/05/73	10/05/73	31/05/73	07/06/73	14/06/73	21/06/73	28/06/73
20.0	-	-	-	0.3	0.3	2.6	7.2	4.9	9.8	6.8	0.9	-	-	-	-	-	-
10.0	-	-	-	0.2	0.1	6.0	3.9	13.9	7.4	6.2	0.2	5.8	-	-	-	-	2.0
7.5	4.0	-	4.0	0.3	0.5	2.5	6.4	1.8	14.7	5.1	1.7	2.0	-	0.4	0.52	3.0	6.6
5.0	0.3	0.7	1.0	1.3	0.6	2.9	1.0	7.2	36.0	3.2	0.3	4.0	1.0	2.2	0.18	3.3	9.9
3.0	1.2	4.0	0.3	0.2	0.2	3.4	5.5	2.4	39.0	25.0	12.0	7.0	0.6	2.4	1.5	2.0	16.0
1.6	2.5	2.0	0.3	3.0	2.7	3.2	23.6	3.1	18.0	34.0	2.6	19.0	5.4	8.9	32.9	16.6	23.0
0.8	7.9	4.6	3.6	0.8	3.9	4.8	13.7	6.1	15.7	6.6	2.2	2.2	5.5	29.4	46.0	11.2	26.0
0.4	3.7	6.7	2.2	1.3	3.1	11.7	12.9	9.9	45.7	12.0	0.2	109.0	100.0	13.1	139.0	13.7	44.3
0.2	86.0	2.8	4.7	2.0	4.0	14.2	67.0	19.4	32.0	15.0	1.4	209.0	7.0	54.1	157.0	41.1	92.0
0.1	111.0	15.3	20.5	4.9	15.0	5.5	16.8	17.9	65.0	23.0	5.1	434.0	54.9	11.9	225.0	43.5	144.5
0.05	280.0	28.0	19.1	8.6	11.0	4.4	3.4	77.4	69.0	31.0	11.1	423.0	55.0	162.0	122.0	25.0	276.0

APPENDIX F continued -

Seston Distribution in Wraysbury Reservoir during 1972 - 1973
as expressed by Variance : Mean Ratios -B: At nine metres depth

Volume Class x 10^3 μm^3	05/07/73	12/07/73	19/07/73	03/08/73	08/08/73	22/08/73	06/09/73	27/09/73	11/10/73	18/10/73	01/11/73	29/11/73	12/12/73
20.0	1.0	0.8	-	-	-	-	-	-	-	1.0	1.9	3.0	10.0
10.0	1.2	0.1	-	-	-	-	-	-	3.0	0.4	2.1	14.0	25.0
7.5	3.6	3.6	-	-	-	-	4.5	-	2.8	5.0	9.9	1.7	8.0
5.0	3.0	6.4	2.1	2.5	2.3	0.9	1.0	4.1	0.6	0.6	5.1	5.5	4.0
3.0	5.5	3.0	14.2	0.9	1.2	0.9	1.6	1.0	2.3	2.1	1.0	18.0	28.0
1.6	9.2	7.4	22.7	9.1	1.9	1.2	0.7	1.8	3.8	1.6	2.0	30.0	12.0
0.8	3.7	2.3	2.6	9.0	20.5	72.0	4.0	6.1	1.9	4.2	10.0	13.0	19.0
0.4	1.2	9.6	5.9	12.8	9.5	19.0	7.7	6.2	8.9	2.7	5.2	13.0	18.0
0.2	2.3	4.7	11.5	29.0	13.5	3.3	13.0	7.2	36.0	1.3	5.1	8.0	28.0
0.1	6.2	5.0	23.1	56.0	57.7	2.0	17.0	9.9	12.0	15.0	5.4	27.0	26.0
0.05	13.6	70.1	144.7	40.3	117.3	3.3	12.0	9.0	43.0	11.1	12.3	13.0	95.0

APPENDIX F continued -

Seston Distribution in Wraysbury Reservoir during 1972 - 1973
as expressed by Variance : Mean Ratios -C: At the Bottom

Volume Class x 10^3 μm^3	23/03/72	29/03/72	18/04/72	25/04/72	09/05/72	16/05/72	23/05/72	06/06/72	22/06/72	10/07/72	08/08/72	05/09/72	19/09/72	29/09/72	03/10/72	19/10/72	02/11/72
20.0	1.0	-	8.9*	-	-	-*	-	-	-	-	-	-	1.6	1.8	8.8	12.0	2.3*
10.0	1.7	1.3	46.0*	-	-	2.0*	-	-	-	-	-	-	12.2	53.1	51.4	2.4	43.0*
7.5	0.8	4.2	24.0	-	0.15	0.5*	3.0	-	-	-	-	-	6.7	9.9	16.7	1.2	1.0*
5.0	0.3	0.5	118.0	0.6	2.4	2.8*	0.5	0.8	9.9	2.5	-	-	3.4	32.4	24.5	7.6	102.0*
3.0	3.1	6.3	161.0	3.8	8.6	206.0*	1.3	1.1	4.3	13.0	3.0	0.5	8.3	36.8	3.0	12.0	140.0*
1.6	6.5	2.1	249.0	1.3	16.0	387.0*	4.0	3.0	51.0	31.0	13.0	0.5	6.8	3.4	31.8	18.1	279.0*
0.8	4.9	0.6	433.0	2.3	27.5	435.0*	0.3	2.1	20.0	20.0	6.0	3.7	4.7	27.4	0.9	51.8	165.0*
0.4	31.0	9.9	638.0	6.4	76.9	533.0*	15.0	0.1	8.0	17.0	21.0	0.5	4.9	13.8	50.1	64.7	212.0*
0.2	47.0	7.0	899.0	19.0	97.3	569.0*	1.9	17.0	11.0	130.0	28.0	27.2	3.7	58.4	7.4	198.0	314.0*
0.1	22.0	70.0	928.0	48.1	215.6	894.0*	30.0	37.0	-	-	-	44.3	3.5	190.9	19.2	320.0	362.0*
0.05	43.0	42.3	703.0	34.5	325.0	1849*	22.0	10.0	15.0	35.0	40.0	3.0	-	40.2	61.0	461.5	1971*

APPENDIX F continued -

Seston Distribution in Wraysbury Reservoir during 1972 - 1973

as expressed by Variance : Mean Ratios -C: At the Bottom

Volume Class x 10^3 μm^3	20/12/72	15/02/73	01/03/73	08/03/73	16/03/73	22/03/73	28/03/73	12/04/73	19/04/73	26/04/73	03/05/73	10/05/73	31/05/73	07/06/73	14/06/73	21/06/73	28/06/73
20.0	5.0	-	-	3.0	0.3	0.7	1.7	28.0	13.8*	1.3	103.0*	-	-	-	-	-	-
10.0	12.0	-	-	17.0	0.8	1.0	1.5	34.0	4.3*	8.4	104.0*	6.7	-	-	-	-	1.5
7.5	5.4	-	-	14.4	1.2	13.0	1.0	37.0	3.4*	2.2	75.0*	0.2	-	0.5	0.1	5.9	2.5
5.0	16.0	0.6	2.0	52.0	0.1	5.9	1.3	195.0	37.5*	10.3	126.0*	0.2	1.2	2.3	0.7	2.1	11.1
3.0	49.3	7.5	1.6	59.0	0.5	3.3	18.0	276.0	23.0*	6.0	146.0*	35.0	2.8	1.6	2.1	9.9	2.5
1.6	89.0	19.0	8.1	136.0	1.2	8.3	1.3	652.0	54.0*	24.0	393.0*	36.0	10.0	1.2	0.1	60.4	24.0
0.8	182.0	65.0	1.7	208.0	4.1	11.2	2.8	666.0	1.5*	9.7	411.0*	94.0	0.5	1.5	0.6	37.6	13.0
0.4	209.0	178.0	8.5	226.0	0.7	42.6	2.9	387.0	232.0*	3.7	664.0*	187.	12.1	2.4	2.5	19.1	48.0
0.2	304.0	251.0	5.9	248.0	19.3	86.6	1.7	174.0	373.0*	7.0	707.0*	288.	5.3	2.7	9.2	16.7	52.0
0.1	202.0	501.0	6.8	165.0	38.0	108.0	2.5	40.0	759.0*	36.0	658.0*	377.	42.0	5.3	24.3	5.7	165.0
0.05	400.0	648.0	3.5	262.0	79.0	145.4	99.7	327.0	1220*	66.0	917.0*	386.	28.5	16.9	74.0	3.4	201.0

APPENDIX F continued -

Seston Distribution in Wraysbury Reservoir during 1972 - 1973
as expressed by Variance : Mean Ratios -C: At the Bottom

Volume Class x 10^3 μm^3	05/07/73	12/07/73	19/07/73	03/08/73	08/08/73	22/08/73	06/09/73	27/09/73	11/10/73	18/10/73	01/11/73	29/11/73	13/12/73
20.0	1.3	0.8	-	-	-	-	-	-	-	1.5	1.9	7.0	12.0
10.0	1.0	0.7	-	-	-	-	-	-	1.4	0.4	0.6	10.0	12.0
7.5	1.0	1.5	3.6	-	-	2.7	0.2	-	1.0	1.0	3.0	1.1	1.0
5.0	1.7	2.7	4.2	0.9	0.3	1.5	0.3	-	0.2	3.3	3.0	7.4	4.4
3.0	4.3	6.9	8.5	0.6	1.7	8.8	2.3	4.6	8.7	0.4	7.0	7.3	40.0
1.6	4.3	5.6	13.5	3.2	9.3	11.0	1.2	36.0	3.1	11.7	9.0	11.6	16.0
0.8	0.7	4.4	14.0	11.2	6.3	11.0	4.7	1.0	0.4	1.0	1.0	8.5	34.0
0.4	2.8	16.0	20.3	6.5	12.0	21.0	11.0	28.0	8.5	65.0	3.1	5.3	26.0
0.2	4.8	5.4	28.1	12.6	11.0	9.1	8.1	22.0	7.8	7.8	1.6	14.0	11.0
0.1	5.4	28.6	42.0	15.0	18.0	48.2	7.5	143.0	18.0	65.3	5.4	28.0	23.0
0.05	13.2	28.0	113.7	11.0	39.0	48.5	16.5	171.0	81.0	135.0	1.3	70.0	69.0

* Sample biased by disturbance of floor of reservoir.

DETERMINATION OF SESTON SIZE DISTRIBUTION WITH THE MODELS A AND B COULTER COUNTERS AND THE TWO TUBE TECHNIQUE

by G.D. Haffner and J.H. Evans

Botany Department, Royal Holloway College, University of London

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- ABSTRACT -

A preliminary investigation of the precision and accuracy of two Coulter Counter models and two different aperture tubes indicate high reliability in the range 100 to at least 10,000 particles $ml.^{-1}$ especially when the two-tube method is used.

In an investigation of phytoplankton distribution in a reservoir of the Metropolitan Water Board at Wraysbury, Bucks., extensive use is being made of two Coulter Counters, Models A and B. As a necessary preliminary, comparative analyses have been made of these two instruments, and of the two aperture tubes being most widely used (100 µm. and 200 µm.) in determining seston size distribution.

The application of the Coulter Counter to determine phytoplankton biomass has ranged from investigations with unialgal cultures (El Sayed and Lee, 1963) to studies of natural phytoplankton populations (Mulligan and Kingsbury, 1968; Parsons, 1969; Evans and McGill, 1970). Comparisons have been made between biomass determined with the Coulter Counter and by other standard techniques such as visual analyses, chlorophyll-a and carbon content (Parsons, 1969; Evans and McGill, 1970) as well as particulate nitrogen (Sheldon and Parsons, 1967). In these comparisons the authors have discussed the uses and limitations of the Coulter Counter Technique. The discrepancies reported by Reynolds (1973) between direct counts of ultraplanktonic marine flagellates and particle counts with a Coulter Counter Model A are only to be expected when a high proportion of the seston is non-algal.

There have so for been reported no detailed assessments of the counting precision of either the 100 µm. or the 200 µm. aperture tubes for determining seston frequency-size distribution. The relative amounts of such components of the seston as silts, fine sand, bacteria and the phytoplankton will vary both spatially and temporally so that there is not a constant pattern of seston frequency-size distribution.

Optical methods used to estimate seston frequency-size distributions have limited application to the problem of measuring variations in particle distributions as they are dependent on the nature of the particles. Burt (1956) used a ratio of optical density of samples at 400 and 600 µm as an indication of the coarseness and concentration of the suspended material and commented that the estimate of the concentration of suspended material depended on the particle size distribution of the sample. Scattering meters (Spilhaus, 1968) can be used to determine size-distribution of the seston but results are again dependent on the nature of the suspended particles. Thus optical estimates of seston frequency-size distributions are not directly comparable. The Coulter Counter is a more direct and independent measure of the particle frequency-size distribution in a sample. It is therefore essential to know the limits of precision and accuracy of this method of analysis, as well as the coincidence errors involved.

The overall size range of all particles in a body of water would usually be expected to exceed the capacity of one aperture tube. Mulligan and Kingsbury (1968) noted that larger colonial members of the phytoplankton exceeded the upper limit of the 100 µm. aperture tube used. An extension of the analysis range can be achieved by the two tube technique as described in the Coulter Manual (Anon., 1964).

Samples for comparison of aperture tubes were collected from the River Thames at Datchet throughout 1972. Both tubes were used to analyse the same sample. Samples were mixed by constant stirrings and maintained at 20°C during analysis. The electrolyte used throughout was 0.5% NaCl.

Samples for the comparison of Coulter Counter Models A and B were collected with a Freidinger Sampler from Wraysbury Reservoir. All samples were shaken and divided into two. One was analysed on a Coulter Counter Model B at the Biology Laboratory of the Metropolitan Water Board at Wraysbury, the other was analysed on a Model A at the Botany Department of Royal Holloway College.

The counting procedure of the Coulter Counter Model A is to count all particles within the upper and lower thresholds of the aperture tube used. Since only the lower threshold is adjustable particles are counted in progressively smaller size ranges. The difference in counts between successive size ranges is the number of particles in that size class. Counting and sizing by this instrument is strictly dependent on the temperature and the concentration of electrolyte in the sample. The Coulter Counter Model B counts all particles within the upper and lower thresholds in direct size classes as both upper and lower thresholds are adjustable. This model is not strictly dependent on the temperature and electrolyte concentration of the sample.

After the analysis of 18 samples there was found to be a correlation coefficient of 0.92 between the 100 and 200 µm. aperture tubes. The coefficient and relationship of the two tubes is illustrated in Figure 1. There was an abberation when particle counts were less than ten per 0.5 ml. due to electronic limitations as well as subsampling error (see Coulter Manual). The high correlation suggested that coincidence corrections for the 200 µm. aperture tube were accurate up to a particle concentration of 5×10^3 0.5 $ml.^{-1}$. At this particle concentration the coincidence error correction was 10% of the Coulter estimate using a 200 µm. aperture tube, and less than 5% using a 100 µm. aperture tube.

Kubitschek (1969) has discussed the relationship of coincidence correction to aperture volumes and particle concentration. For minimal coincidence error, and hence minimal coincidence correction, a 100 µm. aperture tube should be used; but in the range of 10 to 5.0 x 10^3 particles 0.5 $ml.^{-1}$ discussed above, a 200 µm. aperture tube will give reliable results.

A scatter diagram representation of the comparison of the Coulter Counter Models A and B revealed the close relationship of the two models using both the 100 (Figure 2) and 200 (Figure 3) aperture tubes. Both instruments had counting discrepancies at low particle concentration. At high particle concentrations the Coulter Counter Model A, due to its method of counting particles in an overall particle size range, was possibly undercounting when used in combination with the 200 µm. aperture tube. Counting in wide volume ranges resulted in high particle counts and increased the probability of coincidence error.

The lower counting accuracy of the Coulter Counter Model A and 200 µm. aperture tube might be a result of an underestimate of the coincidence error. Coincidence correction is usually based on a normal frequency-size distribution, whereas particle size distributions in aquatic environments tend to be a highly skewed and irregular log - normal distribution. Thus coincidence correction has limited use when applied to seston, especially when using the Coulter Counter Model A with a 200 µm. aperture tube. Coincidence error probability is directly related to the number of particles counted. The counting procedure of this Model is such that the coincidence correction cannot be applied to a specific size class but is applied indirectly by correcting in each successive size range. Although coincidence corrections in the Model A are related to the summation rather than to the interval of numbers of particles in the size classes the high correlation of the Coulter Counter Models A and B suggests that these errors are minimal and that the determination of seston frequency-size distributions by the Model A are precise if particle concentrations are well within the range of the aperture tube used.

The two tube technique is a good method of widening the range of seston analysis and the two tubes are interchangeable should coincidence error be a problem. The Coulter Counter Models A adn B are accurate when counting particles in moderate concentrations. High reliability can be maintained in a particle concentration range of 100 - 5,000 counts 0.5 $ml.^{-1}$ when using a 200 Um aperture tube.

- ACKNOWLEDGEMENTS -

The authors of this paper express their thanks to the staff of the Petropolitan Water Board at Wraysbury for their assistance, and for the use of the Coulter Counter Model B. They would also like to recognize a N.E.R.C. grant with which this work was made possible.

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Figure 1. The Relationship between the 100 and 200 µm. Aperture Tubes in Determining Seston size distribution. (Coulter Model A)

LEGEND FOR FIGURES

PARTICLE SIZE INTERVAL μm^3 x 10^3	DIAMETER RANGE µm.	SYMBOL
0.010 - 0.025	2.9 - 3.7	X
0.025 - 0.050	3.7 - 4.6	○
0.050 - 0.100	4.6 - 5.7	Ѧ
0.100 - 0.200	5.7 - 7.2	+
0.200 - 0.400	7.2 - 9.1	⌖
0.400 - 0.800	9.1 - 11.5	Δ
0.800 - 1.600	11.5 - 14.5	0
1.600 - 3.000	14.5 - 17.9	⊙
3.000 - 5.000	17.9 - 21.2	◆
5.000 - 7.500	21.2 - 24.2	⊘
7.500 - 10.000	24.2 - 26.7	⧫
10.000 - 20.000	26.7 - 33.6	◊

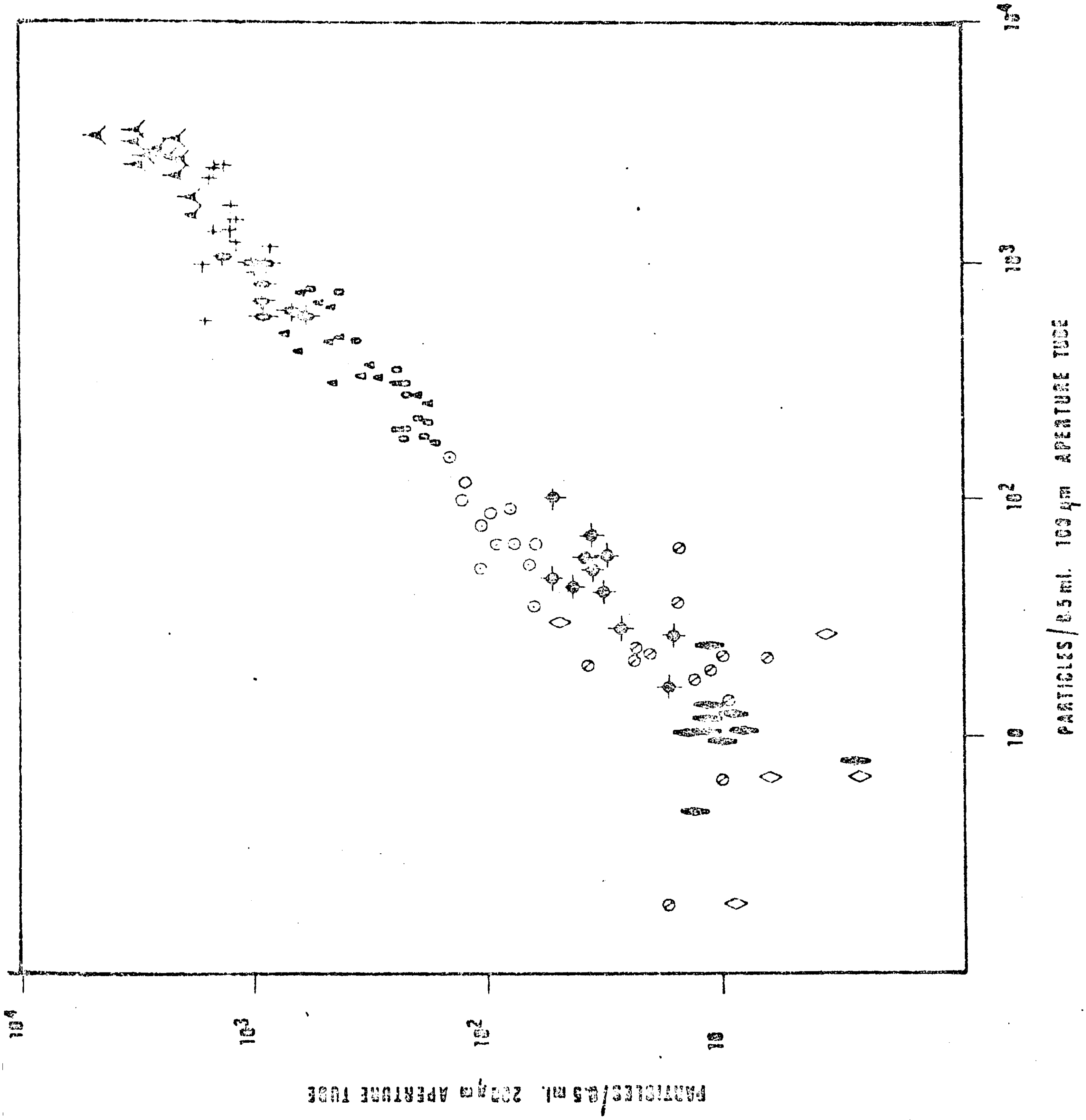
PARTICLES/0.5 ml. 100 µm APERTURE TUBE
10
10²
10³
10⁴
PARTICLES/0.5 ml. 200 µm APERTURE TUBE
10
10²
10³
10⁴

Figure 2. Scatter Diagram (Log-Log) Illustrating the Relationship of Coulter Counter Models A & B in Determining Seston Con-Centration (100 µm. Aperture Tube). Symbols as for Fig. 1.

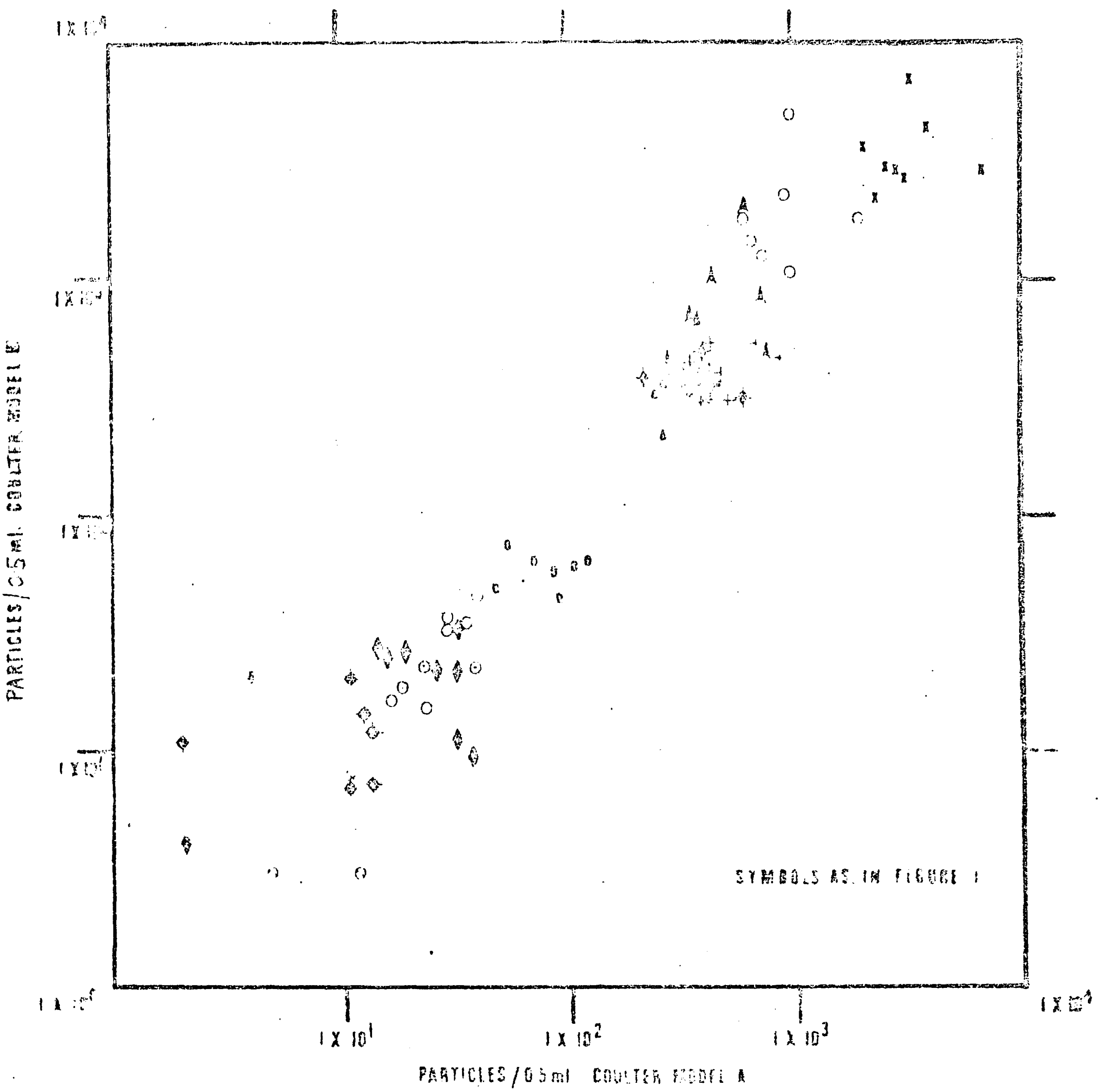

FIGURE 2 SCATTER DIAGRAM (LOG-LOG) ILLUSTRATING THE RELATIONSHIP OF COULTER MODELS A&B IN DETERMINING SESTON CONCENTRATION (100μm APERTURE TUBE).

Figure 3. Scatter Diagram (Log-Log) Illustrating the Relationship of Coulter Counter Models A & B in determining seston concentration (200 µm. Aperture Tube). Symbols as for Figure 1.

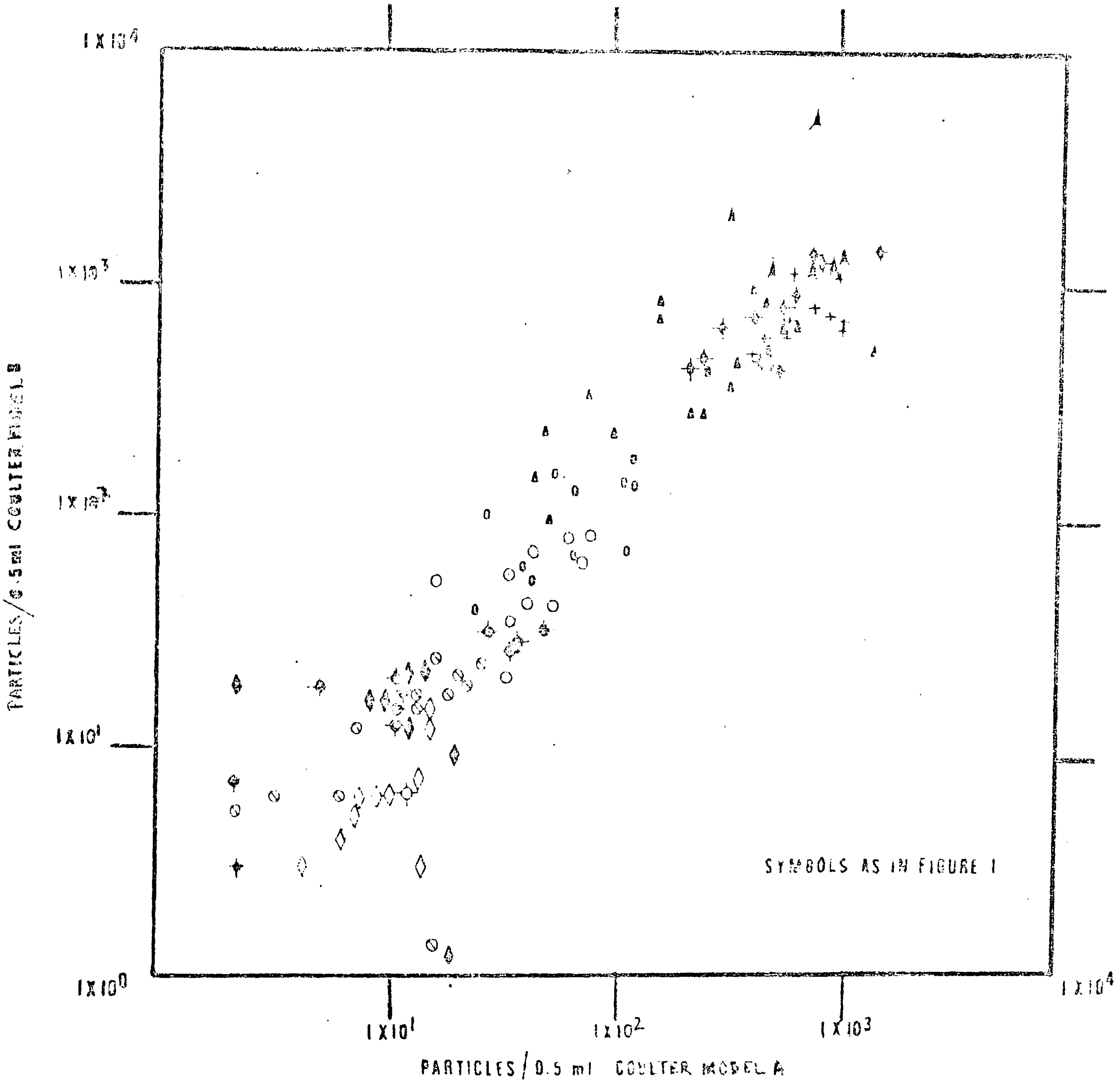

FIGURE 3 SCATTER DIAGRAM (LOG LOG) ILLUSTRATING THE RELATIONSHIP OF COULTER COUNTER MODELS A & B IN DETERMINING SESTON CONCENTRATION (200µm APERTURE TUBE)

RELATION OF LIGHT PENETRATION TO PARTICLE DISTRIBUTION IN VERTICALLY MIXED LACUSTRINE ENVIRONMENTS

by G. D. HAFFNER AND J. H. EVANS

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- ABSTRACT -

The penetration of natural light into a vertically mixed reservoir in the Thames Valley was compared with particle distribution as determined by a Coulter Counter. Attenuation coefficients determined using blue, green, yellow and red filters were correlated with Total Particulate Volume and Total Particulate Surface Area. While there was a low but acceptable correlation of light attenuation with Total Particulate Volume, there was a high correlation of light attenuation with Total Particulate Surface Area. Theoretical aspects of this correlation are discussed with reference to the moderate production of phytoplankton in vertically mixed reservoirs of the Thames Valley. The Coulter Counter can give absolute measures of turbidity resulting from suspended particles of a diameter exceeding 3.0 µm.

- INTRODUCTION -

The influence of suspended matter on light penetration in lacustrine and maritime environments has been investigated by many methods. Poole and Atkins (1928) discussed various methods of photo-electric measurement of light attenuation. Atkins, Jenkins and Warren (1954) presented the theoretical effects of particle size distribution on the spectral quality of penetrating light. More direct measurements were made by Jones and Wills (1956) who measured the effect of varying concentrations of mud suspensions on the attenuation of collimated light. The latter researchers attributed the non-linear relation of the attenuation coefficient and suspended matter to the nature and size distribution of the suspended material.

Riley and Schurr (1959) showed that in some instances light attenuation could be related to suspended photosynthetic organisms and were able to predict the attenuation coefficient from the chlorophyll-a concentration. This technique had limited success since chlorophyll-a is not in itself a consistently accurate measure of 'biomass' or number of planktonic organsims and extraction methods of chlorophyll-a are of questionable accuracy.

Recently Talling (1971) measured light penetration with photoelectric cells and compared the vertical attenuation coefficients with the concentrations of chlorophyll-a in Esthwaite Water. Although a direct relationship was found between the attenuation coefficient and chlorophyll-a concentration, Talling noted that after the autumn overturn this relationship did not hold. This change was tentatively explained as an effect of resuspended particles. Suspended silt can increase the optical density of water and limit the depth of the euphotic zone.

Steel (1972) discussed the relationship between vertical light attenuation and algal production, measured in terms of chlorophyll-a, during the spring diatom growth in Thames Valley Reservoirs which were subject to natural or artificial mixing. Suspended, non-productive particles were noted by Steel to be significantly limiting light penetration. Because of this, the relationship between light penetration and chlorophyll-a was not a direct one at all times.

Mackereth (1963) was able to directly relate the attenuation of light to dissolved carbon compounds such as humic acids in solutions apparently free of particles. To date, however, there has been no method presented which relates the attenuation of natural light directly to particle size and number.

Westlake (1965) surveyed some of the problems of measuring light penetration in water. The selection of the most meaningful attenuation coefficient was discussed by Talling (1971), and the use of the minimum attenuation coefficient (min.) was suggested. The coefficient is more dependent on particle size distribution than on the nature of the particles, hence should minimize the problem mentioned by Jones and Wills (1956). Additionally it has an advantage in that it can be used to measure particles' distribution to greater depths than most other wavelength bands of the visible spectrum. This augments the precision of determining the attenuation coefficient because the usable path length is thus increased to its possible maximum. Particle suspensions can thus be investigated in greater detail.

Particle suspensions have been investigated by means of light scattering meters (Jerlov, 1951; Spilhaus, 1968). Jerlov (1951) used a Tyndall meter to investigate particle distributions in the ocean, and noted that particles below 1 µm. had negligible effects on the scattering of light (however see Burt, 1955). Scattering meters are based on the assumption that suspended particles can be treated as spherical (Le Grand, 1939).

Steele (1965) commented that all the methods employed to measure particle distribution fail to distinguish between those particles which are non-productive (silts and clays etc.) and those which are productive, (primarily the phytoplankton component). The Coulter Counter can be used to detect and determine the biomass of phytoplankton populations in natural situations (Evans and McGill, 1970; Parsons, 1965, 1970; Sheldon and Parsons, 1967; Mulligan and Kingsbury, 1968), and to analyse seston frequency-size distributions (Haffner and Evans, 1973). This method of analysis can be used to distinguish productive particles from non-productive material.

MATERIALS AND METHODS

A. Particle Size Analysis:

A Coulter Counter is an electronic particle counter which can 'size' particles by measuring the change of electrical resistance between two electrodes. The sensing zone of a Coulter Counter is an aperture in a glass tube through which particles must pass to be counted. A change in the electrical resistance through this opening occurs when a particle enters into the critical aperture volume. Particles being counted by the Coulter Counter might be of irregular shapes but can be considered as spheres since the orientation of the particles as they pass through the sensing zone of the aperture tube is random. Using the two tube technique (Haffner and Evans, 1973) particles in a diameter range of 2.9 - 51.1 µm. can be measured.

If particles are assumed to be spheres (an assumption common to scattering meters and turbidity meters) a calculation of the Total Particulate Volume and Total Particulate Surface Area can be made. Inaccurate estimations will be made if the particles are porous, and therefore Coulter analysis should always be assisted by microscopic techniques. If a species of the phytoplankton of known shape is dominant a more exact area-volume transformation can be applied to that species. In the present work there was no requirement for specific area-volume transformations, and all particles were considered as spheres.

Theories on light scattering and absorption by suspended spherical particles have been applied to estimate size range, size distribution, and concentration of suspended material (Burt, 1955). Burt uses the Mie theory which introduces an effective area coefficient which he defined as a "dimensionless number by which the geometrical cross-sectional area of a particle must be multiplied in order to determine its effectiveness in removing or deflecting light....". Due to the large size of plankton (compared with the wavelengths of visible light) their effective area is constant with wavelength; thus no special coefficient is required. The Mie theory may be used for non-spherical particles with little error if the relative refractive index of the particles is less than 2.00. Burt has reported that the relative refractive indices of both organic and inorganic material were approximately 1.15.

It is thus possible to use the assumption that suspended particles might be treated as spheres. To avoid using an effective area coefficient the size range of particle analyses was kept to a minimum diameter of 2.9 µm. The two tube technique (100 and 200 µm. aperture tubes) was used when applicable to extend the size range of particle size analysis and/or to limit the probablilty of two or more particles being counted as one. Coulter Counter Models A and B were used with 0.5% NaCl as electrolyte.

B. Measurement of Light Penetration:

Balanced selenium photo-electric cells were used to measure light penetration in a vertically mixed reservoir of the Metropolitan Water Board at Wraysbury (Bucks.). The reservoir was mixed by the jetting in of water at a rate of 5.25 - 10.5 m^3 sec^{-1} [≙ 100 - 200 m.g.d. (million gallons day^{-1})]. This was to achieve homogeneous oxygen distributions. As a result of this jetting, the formation of a thermal discontinuity with depth was prevented, and the reservoir can be considered to be in a constant state of iso-thermal mixing.

During 1972 and 1973 water samples were collected with a Friedinger sampler and light penetration was measured. Samples were collected throughout the entire depth of the water column at two metre intervals at one station near the centre of the reservoir. A mean particle distribution for the water column was then determined down to the depth to which one per cent of the surface radiation penetrated.

'Chance' colour filters red, blue, green, and yellow were each used in combination with an opal diffusing glass. Attenuation coefficients (expressed as ln units m^{-1}) were calculated using each filter, and then compared with Total Particulate Volume and Total Particulate Surface Area. The attenuation coefficients (vertical extinction coefficients), for the sake of clarity, are defined here (as in Poole and Atkins, 1928) as determined by the percentage of natural underwater light falling on an upturned horizontal surface:

$$= \frac{2.3}{z} (\log_{10} I_o - \log_{10} I_z)$$

RESULTS AND DISCUSSION

Despite artificial mixing, particle distributions in the reservoir were not homogeneous with depth. Actual mixing was probably not uniform with depth. Particle sedimentation through the water column would also be a factor influencing the degrees of heterogeneity encountered. In the upper ten metres, however, particle distributions were found to be near homogeneous as a result of combined natural and artificial mixing. The attenuation of light to 1% of the surface value usually occurred at about ten metres depth.

Table 1 indicates that of the filters used, penetration only in the blue range was significantly correlated with Total Particulate Volume, and even this was correlated only at the 5% level of confidence. Total Particulate Surface Area, however, was closely correlated with the attenuation for all the filters. The best correlations were with the most absorbed wavelengths (blue) and the least absorbed wavelengths ($_{\text{min.}}$) usually measured with the yellow or green filter.

As would be expected, light penetration in aquatic environments is dependent more upon particle surface area than on particle volume. Previous relationships of particle suspensions and attenuation have been concerned with particle mass or volume (see Jones and Wills, 1956; Riley and Schurr, 1959). These relationships are dependent on monosized particle suspensions which might be rare in nature. The Coulter Counter is not limited in that respect as particles can be counted in successive size classes throughout the range of the aperture tubes.

Although the blue wavelengths had the best correlation with Total Particulate Volume and Total Particulate Surface Area, $_{\text{min.}}$ was selected as the more appropriate measure of particle suspensions. The reason for this is that the blue is quickly absorbed and cannot be used to estimate particle suspensions to great depths. The $_{\text{min.}}$ coefficient can be used to determine the euphotic zone and to correct for spectral modification (see Talling, 1971). Figure 1 illustrates the close relation of $_{\text{min.}}$ and Total Particulate Surface Area. The regression determined by least squares is:

$$\varepsilon_{\text{min.}} = 0.0402\ \text{T.P.S.A.} + 0.18$$

where T.P.S.A. has the units $10^5\ \mu m^2$. The regression 'constant' 0.18 is dependent on the dissolved substances and the effect of particles below 2.9 μm. in diameter. Thus the attenuation coefficient cannot be determined directly by particle size analysis alone. The entire particle size range, in particular the lower range, must be analysed and water colour known. Apparently a large proportion of the attenuation coefficient is determined by water colour and by the influence of extremely small particles. Continued work with smaller aperture tubes to extend the lower range of the Coulter Counter might elucidate this problem further. The above relationship suggests that water colour and effects of small particles are constant in short time periods.

Figure 2 illustrates the relation of Total Particulate Volume and min. The low correlation suggested that particle volume and related parameters such as carbon and perhaps chlorophyll were not reliable methods to be used for predicting the attenuation of light. Mullin, Sloan and Eppley (1966) found no direct relationship between cell volume or cell carbon and chlorophyll-a, and attributed this to the effects of temperature, light intensity, and nutrient supplu on the concentrations of chlorophyll-a. Cell carbon has been directly related to cell volume; thus it is probably a poor parameter which to relate to light attenuation.

The Riley and Schurr (1959) equation relating light attenuation and chlorophyll concentration is presented here as it defines an approximation of a volume-area transformation.

$$k = 0.04 + 0.0088C + 0.54C^{2/3}$$

k = Attenuation coefficient (ln. m^{-1})

C = Concentration of Chlorophyll (mg. m^{-3})

Though the equation is too specific for general use, since the phytoplankton must be mono-sized and in a particular physiological condition, it does emphasize the importance of determining the area-volume relationship of suspended particles.

Paasche (1960) noted that production capacity was correlated more with cell surface area than with cell volume. Coulter particle analysis using an area-volume relationship might be of use in determining the production capacity of natural populations.

As light attenuation is more closely related to particle surface area than particle volume, turbidity might better be expressed in terms of Total Particulate Surface Area rather than in terms of Total Particulate Volume, mass, or number. Production equations might then be modified as described by Murphy (1962). In his modification of Sverdrup's equation steps were taken to compensate for the attenuation of light by detrital particles. It is recommended, however, that the attenuation coefficient be that of natural penetrating light not of collimated light. Base turbidity can be determined by particle size analysis.

The ratio of productive material to non-productive is not constant as it is dependent on many varying parameters such as rainfall and turbulence. Nevertheless, to estimate primary production in a water column, this ratio must be known. A growth of any species in the phytoplankton population will increase the total particle surface area of productive material as compared to non-productive and light penetration will be directly affected.

In early September 1972, $_{\text{min.}}$ at Wraysbury Reservoir was determined as 0.288 m.^{-1} and such a low attenuation coefficient was found to be due to the low level of suspended matter. The natural colour of the water was low and approximately constant throughout the period Spring 1971 to the present. The Total Particulate Volume in September 1972 was 1.2×10^6 $\mu\text{m.}^3$ ml.^{-1}, and the Total Particulate Surface Area was 3.8×10^5 $\mu\text{m.}^2$ ml.^{-1}. At the end of September a moderate growth of

Stephanodiscus astraea (Ehrenb.) Grun. had results in an increase in Total Particulate Volume to 5.8×10^{6} μm^{3} ml^{-1} and Total Particulate Surface Area to 8.7×10^{5} μm^{2} ml^{-1}. The attenuation coefficient ($_{min.}$) was determined to be 0.511 m^{-1}. Thus the increase in Total Particulate Volume and Total Particulate Surface Area due to unialgal growth markedly affected light attenuation. It should be noted, however, that there was approximately a four times increase in Total Particulate Volume whereas Total Particulate Surface Area and $_{min.}$ merely doubled. This suggests the close relationship of Total Particulate Surface Area and light attenuation.

By middle December 1972 the phytoplankton had decreased to the extent where few species were known to exceed ten individuals per millilitre. Total Particulate Volume was moderately low (3.2×10^{6} μm^{3} ml^{-1}). At this time the River Thames had a high silt load, and water extracted from the river was being pumped into the reservoir. The fine silt particles contributed relatively little to the Total Particulate Volume, but had a large effect on Total Particulate Surface Area. The attenuation coefficient ($_{min.}$) was determined to be 0.92 m^{-1} indicating that the high concentration of small particles was definitely having an effect on light penetration and the depth of the euphotic zone.

In mixed lacustrine environments fine materials will tend to stay in suspension, and light penetration will be affected. If a large number of these particles are non-productive the production capacity of the water column will be limited.

The mixed reservoirs of the Thames Valley, such as Queen Elizabeth II and Wraysbury, have high suspended silt loads as a result of the artificial mixing. Although sedimentation does occur, a sufficient number of particles remain in suspension with the aid of natural and artificial mixing to limit light penetration. The moderate production of these reservoirs might well be an effect of limited light penetration.

Although non-productive material in these reservoirs might sometimes significantly affect single determinations of Total Particulate Volume, Evans and McGill (1970) have demonstrated Total Particulate Volume to be usually related to 'biomass' in such environments.

Many other methods of assessing particle distribution or concentration, such as turbidity meters and secchi discs, are not directly comparable from one situation to another. The Coulter Counter is an absolute measure of particle size distribution and concentrations. Results obtained by the latter method are comparable quantitatively and qualitatively.

- SUMMARY -

1. Light penetration is more closely correlated with Total Particulate Surface Area than with Total Particulate Volume as determined by a Coulter Counter.

2. Particle size analysis by a Coulter Counter is a precise and accurate method of determining the ratio of productive and non-productive material. A determination of particle volume and area by Coulter size analysis is absolute, and comparable in both temporal and spatial dimensions.

– ACKNOWLEDGEMENTS –

Our thanks are due to the Metropolitan Water Board for permission to work at the Wraysbury reservoir and for the cooperation of their staff, to the Natural Environmental Research Council for the award of a grant and to members of the technical staff of the Botany Department of Royal Holloway College who rendered invaluable assistance. We are most grateful to Dr. J. F. Talling of the Freshwater Biological Association for reading and constructively criticising the MS. before submission for publication although the authors must claim responsibility for any remaining errors.

TABLE 1

A Comparison (expressed as Correlation Coefficients) of Vertical Attenuation Coefficients (ln units m^{-1}) with Total Particulate Volumes (T.P.V.) and with Total Particulate Surface Area (T.P.S.A.)

$n = 17$

FILTER	T.P.V.		T.P.S.A.	
Red	0.2816	$p > 0.05$	0.6964	$p < 0.010$
Blue	0.4738	$p = 0.05$	0.7900	$p < 0.001$
Green	0.3134	$p > 0.05$	0.6760	$p < 0.010$
Yellow	0.2647	$p > 0.05$	0.6704	$p < 0.010$
$K_{min.}$	0.3947	$p > 0.05$	0.7346	$p < 0.001$

Figure 1 RELATION OF THE MINIMUM VERTICAL ATTENUATION COEFFICIENT (ln units $m.^{-1}$) AND TOTAL PARTICLE SURFACE AREA AS DETERMINED BY A COULTER COUNTER

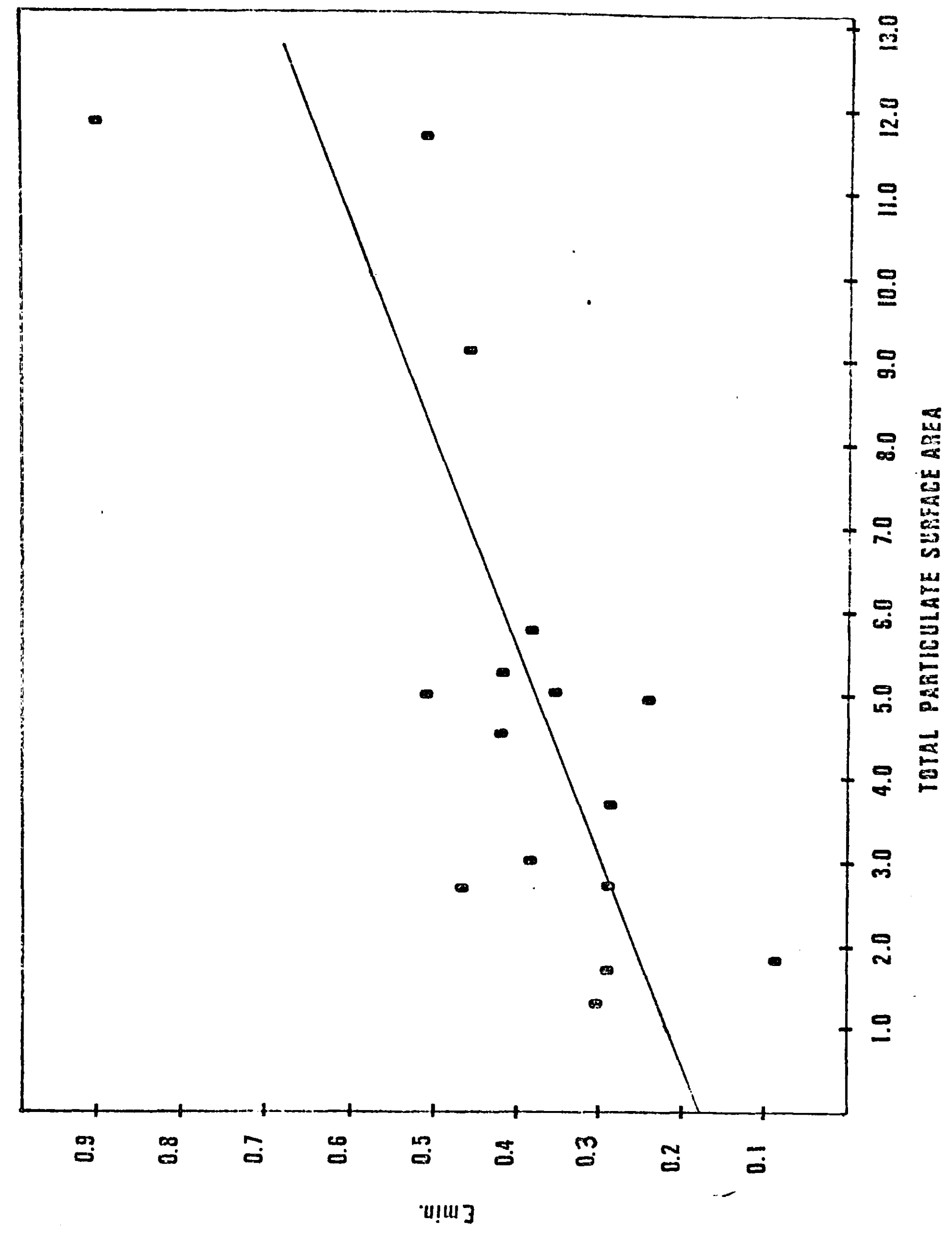
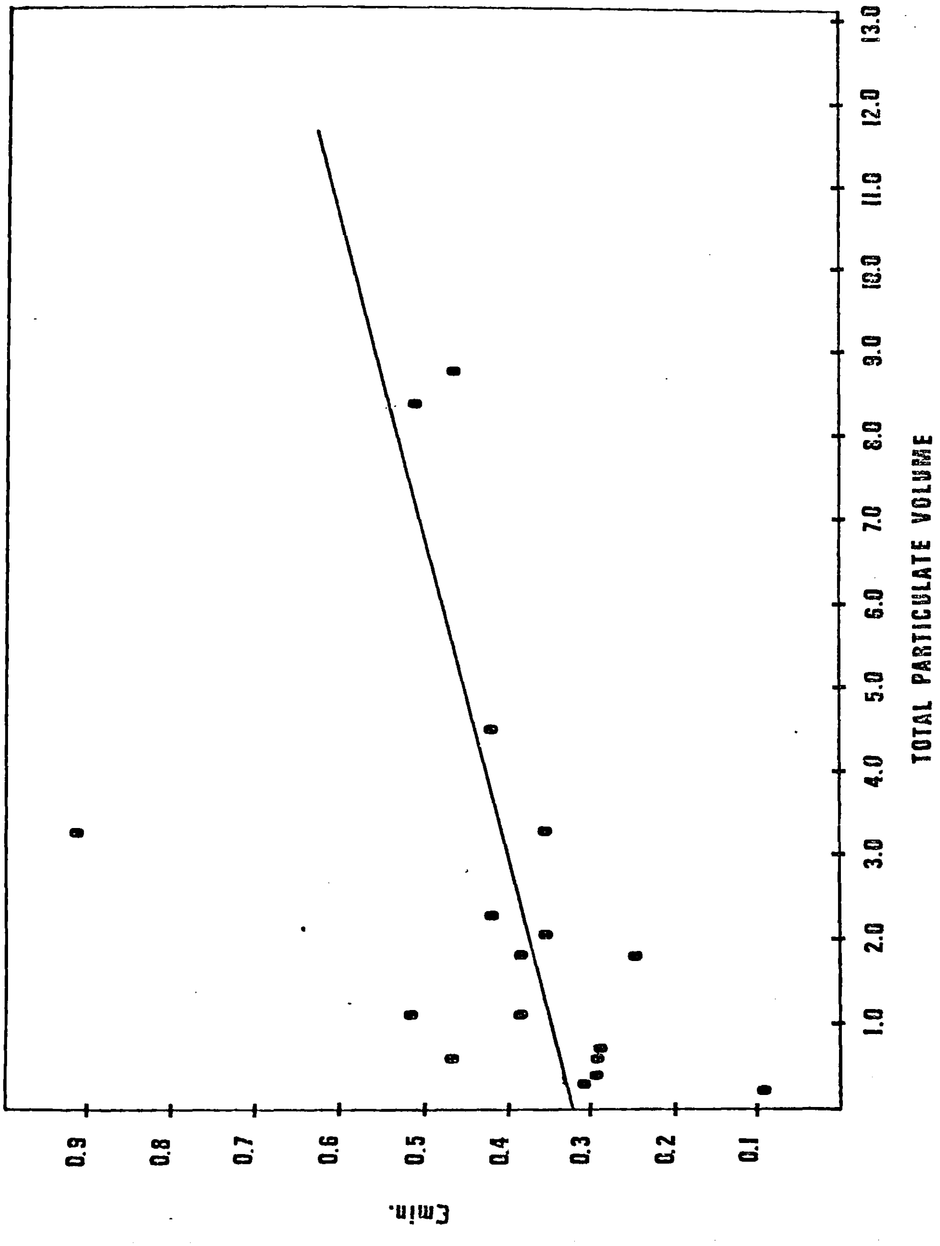

E min.
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
9.0
10.0
11.0
12.0
13.0
TOTAL PARTICULATE SURFACE AREA

Figure 2 RELATION OF THE MINIMUM VERTICAL ATTENUATION COEFFICIENT (ln units m^{-1}) AND TOTAL PARTICLE VOLUME AS DETERMINED BY A COULTER COUNTER


Cmin.
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
9.0
10.0
11.0
12.0
13.0
TOTAL PARTICULATE VOLUME

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