THE DIATOM ECOLOGY AND PALAEOECOLOGY OF SHALLOW LAKES SUBJECT TO EUTROPHICATION: THREE EXAMPLES FROM THE ENGLISH MIDLANDS.

by

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So our love of the valley is like a river, a love that runs on and on and is passed from one of us to the next in line. Through this love, we all hold on to our piece of immortality, and while the valley lives there will be a piece of every man that will never die.

John Bailey.

ABSTRACT

Lowland England abounds with shallow lakes subject to different levels of eutrophication. In the absence of long-term water chemistry records, palaeolimnology provides an alternative means of assessing the onset and extent of the nutrient enrichment process at a site. The diatoms preserved in lake sediments are extremely sensitive indicators of both past nutrient levels and of eutrophication-related changes in macrophyte-phytoplankton interactions. However the success of diatom-based palaeoecology depends upon a sound knowledge of the taxonomy, environmental requirements, and taphonomy of contemporary diatom communities.

This thesis has focused on aspects of the diatom ecology, taphonomy and palaeolecology of three, small (<22 ha.), shallow (<3 m), alkaline lakes of contrasting nutrient and macrophyte status in the English Midlands. These lakes, Tween and Clifton Ponds and Groby Pool, were monitored on a monthly basis (Jan-Oct) for key water chemistry parameters. At the same time samples were collected from the diatom plankton and periphyton and in turn compared with the diatom assemblages which accumulated in sediment traps and at the sediment surface. The small centric diatoms that were found in these lakes were initially difficult to identify using the light microscope (LM), and a scanning electron microscope (SEM) study of the 'problematic' forms revealed considerable ecophenotypic and life-cycle related morphological plasticity. However with careful LM analysis it was possible to confidently distinguish between the different species in the samples. The ecological studies revealed strong associations between the presence or absence of submerged macrophytes and the seasonality and relative competitiveness of planktonic and periphytic diatom species. The relationship between the present-day diatom communities and the diatoms found in the traps and surface sediments of the lakes was relatively good, although there were some problems related to the dissolution of delicate forms. The timing of surface sediment sampling was found to be a critical factor affecting the sedimentary representation of species associated with different periods of the year.

The eutrophication histories of Tween Pond (approx. last 30 yrs) and Groby Pool (approx. last 250 yrs) were inferred by comparing the fossil diatom record with the available historical records of lake disturbance, changing catchment land-use and submerged plant communities. The available modern data were used to assist in this process and using a simple life-form based approach it was possible to reconstruct past changes in the relative competitiveness of phytoplankton and submerged plants in both lakes. In Tween Pond the diatom stratigraphy clearly traced the dramatic increase in nutrient loading and the loss of submerged plants from the lake following the diversion of the Erewash in 1972. Similarly, in Groby Pool it was possible to identify the much slower transition from a mesotrophic, diverse plant dominated state to a eutrophic, tall plant dominated situation. The implications of this study are discussed in relation to modern numerical methods of reconstructing past nutrient loadings.

To Lilly Sayer

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CHAPTER ONE

INTRODUCTION

Eutrophication

The ecological characteristics of lakes are intimately dependent upon the supply of dissolved substances derived from inflowing streams, upwelling groundwaters and atmospheric fallout. In terms of autotrophic production, the most important of these substances are the 'plant' nutrients phosphorus (P) and nitrogen (N). These are scarce relative to the other materials required for plant growth and their abundance in the water has been found to be closely related to phytoplankton and submerged plant productivity. P in particular is thought to be the overriding importance for the phytoplankton (Reynolds, 1987) and bioassay experiments have shown that it is the main limiting resource (Schindler, 1977; Schelske, 1984). The relationship between P and phytoplankton biomass has also been explored using simple regression models which also indicate a very close relationship, particularly with chlorophyll *a* (Dillon & Rigler, 1974; Vollenweider, 1975; 1976). However in P-rich lakes, N is often the critical limiting nutrient (Reynolds, 1984; Moss *et al.*, 1994) and diatom growth is often limited by silica (Lund, 1964). Thus P is not always the overriding nutritional regulator of the phytoplankton.

The stimulation of plant productivity due to enhanced nutrient loading that is not balanced by equivalent release in the outflow, is known as eutrophication (Ellis, 1989). At the geological timescale subtle changes in lakewater nutrient concentration will occur due to climatically-induced changes in the intensity of catchment erosion and progressive siltation (Reynolds, 1984). Natural vegetation has evolved mechanisms which conserve nutrients and there are typically minimal losses to leaching and erosion in pristine, forested catchments (Borman & Likens, 1967). However clearance of the primaeval forest by man since at least neolithic times disturbed this delicate balance and as the forest was progressively removed the land started to leak nutrients into freshwaters (Fritz, 1989; Moss, 1996). The intensity of this proccess has accelerated in modern times with the development of large-scale, arable agricultural systems and the application of N and P-based fertilisers. N in particular is readily leached from the soil (largely as soluble NO_3) and washed into streams, rivers and eventually lake ecosystems, while P compounds are less soluble and less easily removed. However P is often supplied to lakes in other ways, via sewage, farm and industrial effluents. Thus all but the most isolated of English lakes have been affected by eutrophication to a lesser or greater degree. In response to a perceived need to quantify the progression of eutrophication at a given site, several trophic status classification schemes have been developed, the most widely accepted of which is that of the Organisation for Economic Cooperation and Development (OECD, 1982) as given in table 1.1.

Trophic category	Mean P (μg l^{-1})	Mean Chl *a* (μg l^{-1})	Max Chl *a* (μg l^{-1})	Mean SD (m)	Min SD (m)
Ultra-oligotrophic	≤4	≤1	≤2.5	≥12	≥6
Oligotrophic	≤10	≤2.5	≤8	≥6	≤3
Mesotrophic	10-30	2.5-8	8-25	6-3	3-1.5
Eutrophic	35-100	8-25	25-75	3-1.5	1.5-0.7
Hypertrophic	≥100	≥25	≥75	≤1.5	≤0.7

Table 1.1. OECD class boundaries for different lake trophic status categories (OECD, 1982). Chl *a* = chlorophyll *a*. SD = Secchi disc depth.

The effects of eutrophication are diverse and depend to a large extent on lake morphometry. In deep lakes submerged macrophytes can only grow in littoral areas and the symptoms of eutrophication are usually expressed in the form of increased phytoplankton growth (Moss, 1990). The resulting decline in water clarity leads to a reduction in amenity and aesthetic value and in lakes used for water supply, elevated algal production much increases the costs of water treatment. If large bloom-forming populations of cyanophytes (blue-green algae) prevail in summer the water may become smelly as the algae decays in the margins and toxins released as result of this process can be harmful to mammals if swallowed in sufficient quantities. In natural, oligotrophic upland tarns and lochs, organic material derived from increased phytoplankton crops may threaten the survival of rare fish such as char (*Salvelinus alpinus* L.) and whitefish (Corogonids) by causing deoxygenation in the hypolimnion (Moss, 1988b).

In shallow, non-stratifying lakes the effects of eutophication are in many ways more complex. This is because there is no clear differentiation between littoral and profundal regions and usually macrophytes are able to grow in all areas. Also in contrast to deep lakes, internal nutrient loading is likely to be important in addition to the external load (Marsden, 1989; Søndergaard *et al.*, 1992; Kristensen *et al.*, 1992; Phillips *et al.*, 1994). The effects of nutrient enrichment in shallow lakes has been extensively studied in the Norfolk Broads, a series of shallow man-made lakes formed by the flooding of peat diggings in medieval times (Lambert *et al.*, 1960). The Broads are interconnected to a large extent by rivers and dykes and so are particularly susceptible to eutrophication.

Moss (1987); Moss (1989) and Phillips (1992) describe three distinct phases in the eutrophication history of the Broads as gleaned from palaeolimnological and historical ecological studies. Before the turn of the century most of the Broads are thought to have been naturally fertile, clearwater marl lakes, harbouring a diverse arrangement of submerged and floating plants in the open water (particularly low-growing *Chara* and *Najas* spp.), with a gradual transition to dense reedswamp in the margins (dominated by *Phragmites*, *Schoenoplectus* and *Typha* spp.). This clearwater, diverse, low-growing plant dominated state is termed phase I in the Broadland literature and a few of the most isolated Broads are still in this less disturbed state. Between the mid to late nineteenth century and the first half of this century, the Broads started to become enriched by agricultural run-off and mains sewage effluent and were able to support much larger phytoplankton populations. This resulted in the loss of many of the nutrient intolerant, low-growing plant species and their replacement by massive, 'choking' stands of a few tall, fast growing species such as *Potamogeton pectinatus* L. and *Ceratophyllum demersum* L. (phase II). These plants were best adapted to grow towards the better illuminated water surface and the result was a substantial reduction in aquatic plant diversity. By the 1960s, submerged plants were eliminated from most of the Broads which had become turbid, barren environments dominated by dense populations of phytoplankton (phase III). The fringing reedswamp also started to recede at around this time (Boar *et al.*, 1989) and the transition to phytoplankton dominance had several undesirable effects. The loss of macrophytes resulted in a drastic reduction in the available living and breeding habitat for fish and invertebrates and favoured dominance by a few highly resilient, turbid water species such as small cyprinid fish (particularly roach (*Rutilus rutilus* L.)), oligochaete worms and Chironomid larvae (Moss, 1983; Phillips, 1992).

There is growing evidence to suggest that the submerged plant (phases I and II) and phytoplankton (phase III) dominated states represent alternative stable equilibria (fig. 1.1.), each preserved by a partucular set of buffering mechanisms (Scheffer, 1989; Moss, 1989; Moss, 1990; Moss, 1996). The plant dominated clear water stage is thought to be stabilised by; (i) direct N uptake by the plants and enhanced denitrification in the sediments within the plant beds (Moss, 1990; Van Donk *et al.*, 1993; Meijer *et al.*, 1994); (ii) the provision of refuges for Cladoceran zooplankton within the 'underwater forest' so that they can avoid predation by zooplanktivorous fish by day and move out of the plant beds to graze down the phytoplankton at night (Timms & Moss, 1984; Schriver *et al.*, 1995) and; (iii) the provision of suitable hunting habitat for pike (*Esox lucus* L.) and piscivorous perch (*Perca fluvialtilis* L.) which reduce the population size of juvenile zoolanktivorous fish (Moss, 1990). Thus for a lake to switch from phytoplankton to submerged plant dominance, these stabilising mechanisms must be overcome. This is

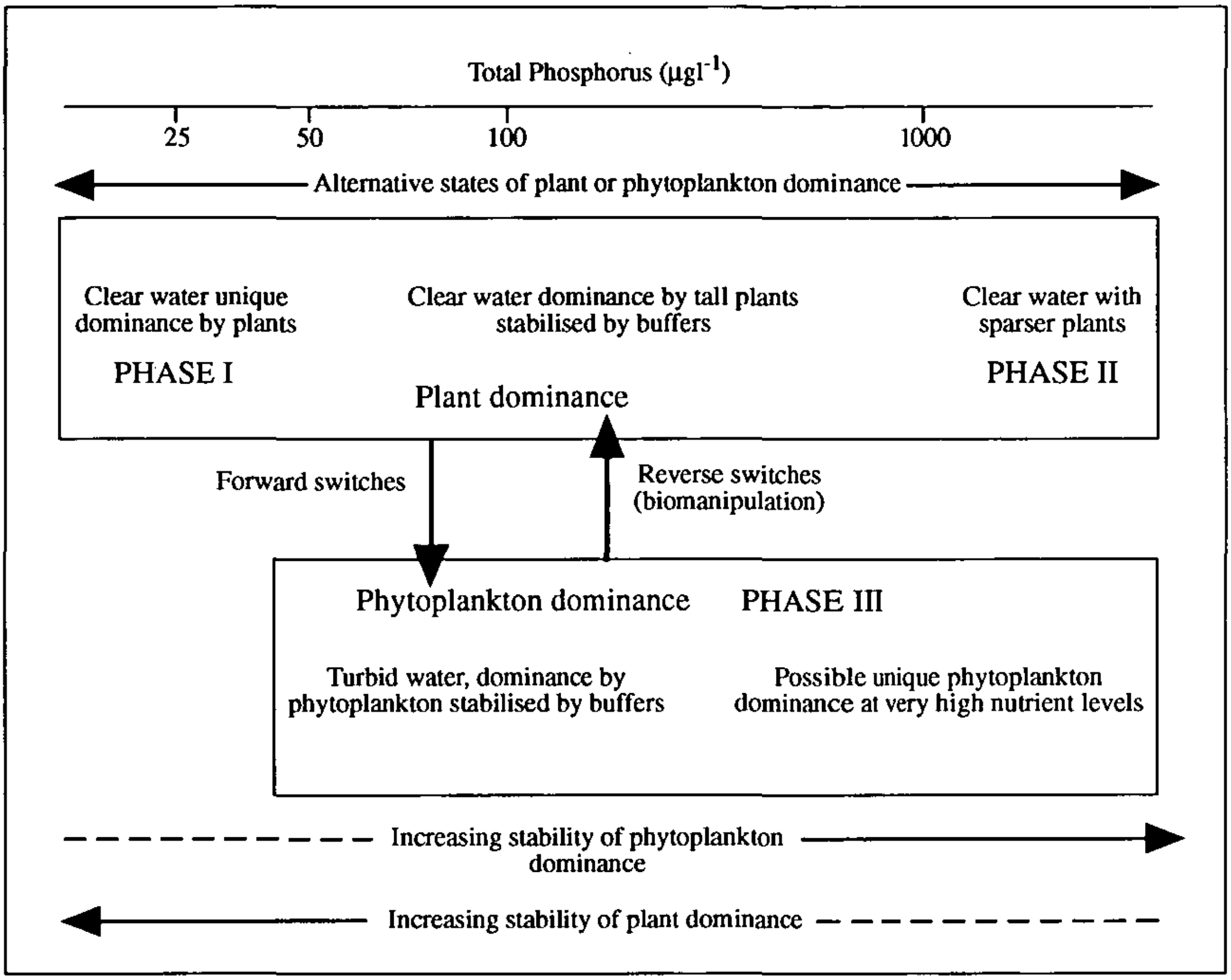


Fig. 1.1. The response of shallow lakes to eutrophication (after Moss, 1996).

made easier as nutrient concentrations increase, but the available evidence suggests that additional switch mechanisms are necessary (Balls *et al.*, 1989; Irvine *et al.*, 1989). Potential de-stabilising mechanisms include mechanical and herbicide damage, changes in fish populations induced by disease or stocking practices and destruction of the zooplankton grazing potential by organochlorine poisoning (Stansfield *et al.*, 1989; Moss, 1996).

In turn once the phytoplankton dominated state has been established it is preserved by another set of buffers. These include the shading out of plant propagules early in the year by large phytoplankton populations and the removal of 'top-down' control over the phytoplankton due to; (i) the loss of available plant refuges for the Cladoceran zooplankton; and (ii) the development of fish populations skewed towards the dominance of small cyprinid zooplanktivores (Perrow *et al.*, 1994). In deep lakes, dominated by point-source nutrient inputs, nutrient diversion alone has been an effective technique for restoring the clear water state (Bengtsson *et al.*, 1975; Edmondson, 1979). However in shallow lakes this simple approach has often been unsuccessful in terms of the permanent restoration of macrophyte communities and clear water. This is because of continued nutrient loading from diffuse and internal sources and reduced flushing which has often been shown to favour the prevalence of cyanophytes (Moss *et al.*, 1986; Perrow *et al.*, 1994). Thus restoration of the macrophyte dominated state by nutrient diversion alone is less likely and sediment removal may be necessary to reduce internal loading (Moss *et al.*, 1986). In reaction to the problems of this nutrient orientated approach, recent restoration strategies are focusing on biomanipulation techniques which attempt to increase the numbers and size of the Cladoceran zooplankton by the provision of artificial refuges (Moss, 1989; Irvine *et al.*, 1990) and the temporary removal of zooplanktivorous fish (Moss *et al.*, 1991; Lauridsen *et al.*, 1994; Meijer *et al.*, 1994). The long-term success of these approaches is presently being evaluated. In a five year study of four biomanipulated lakes in the Netherlands and Denmark (Meijer *et al.*, 1994) all lakes returned to a clear water state in the first two years resulting in the re-colonisation of submerged plants. However in the third year it was evident that two of the lakes were deteriorating and possibly returning to phytoplankton dominance. Thus it would appear that other factors may restrict complete recovery of some biomanipulated shallow lakes.

Palaeolimnology and eutrophication studies

The effective management of a eutrophic lake requires data on past conditions so that it is possible to establish; (i) the natural, or pre-disturbance nutrient state; and (ii) the timing, magnitude and rate of important eutrophication-related changes (Smol, 1992; Dixit *et al.*, 1992). However with the exception of a few intensively monitored sites, long-term water chemistry data are rare (Bailey-Watts *et al.*, 1990; Talling & Heaney 1988) and even data sets which span over fifty years may post-date many major nutrient fluxes (Anderson, 1994a). In the absence of water chemistry data covering the relevant time period, the lake manager must use other data sources. The possible sources include; (i) space-for-time substitution (i.e. comparing the chemical and biological status of affected lakes with adjacent, unaffected lakes) (Moss, 1983); (ii) hindcasts using export coefficient models (e.g. Johnes & O'Sullivan, 1989); (iii) water quality predictions from old algal samples (Battarbee, 1981), historical macrophyte records (e.g. Palmer *et al.*, 1992) and herbarium epiphytic diatoms (van Dam & Mertens, 1993) and; (iv) palaeolimnological reconstructions. The most reliable approach to reconstruction is to use a combination of the above methods and to use all available data sources.

Palaeolimnology is the most widely used and potentially most useful means of estimating past water chemistry conditons and trends in the effects of eutrophication. The sediment archive which accumulates in lakes contains a diverse array of geochemical and biological indicators which can be used to explore past changes in lake trophic status, including invertebrate remains such as Chironomids (Walker, 1987) and Cladocerans (Stansfield *et al.*, 1989) and phytoplankton remnants, including fossil pigments (Leavitt *et al.*, 1989) chrysophytes (Sandgren, 1991) and diatoms (Battarbee, 1978). The most effective and widely used of these indicators are diatoms which have been at the forefront of palaeolimnological studies of the eutrophication process. They are taxonomically diverse and different species often have strong habitat and water chemistry preferences. Moreover they are usually abundant in lake sediments and are known to respond rapidly to environmental perturbations which makes them ideally suited to pollution monitoring and environmental change studies (Reid *et al.*, 1995).

Until relatively recently, most diatom-based studies were concerned with defining qualitative trends in trophic status. These studies essentially fit into three categories; (i) indicator species approaches; (ii) simple index approaches; and (iii) diatom absolute abundance approaches. The indicator species approach has been most widely used and relates different species replacements in the sediment record to trophic changes using modern autoecological data (Battarbee, 1978; Haworth, 1980; Engstrom *et al.*, 1985; Fritz, 1989; Anderson *et al.*, 1990; O'Sullivan *et al.*, 1991). Index methods include the Centrales to Pennales (C/P) ratio (Nygaard, 1956) and the Araphidineae to Centrales (A/C) ratio (Stockner & Benson, 1967; Stockner, 1971:1972). However both the C/P and A/C ratios have been criticised for their lack of robustness and narrow applicability (Brugam, 1979; Agbeti, 1992). Approaches (i) and (ii) usually rely upon diatom relative frequency analysis, but an alternative means of inferring lake trophic status is provided by diatom accumulation rates and inferred diatom palaeoproduction changes (Anderson, 1994b). However due to variable sediment deposition patterns, even in small basins it is usually necessary to calculate a basin average from several cores (Anderson, 1989; 1990a) and this is extremely time consuming. This approach is also subject to error because it can not always be assumed that diatom production is directly related to total phytoplankton production, particularly under conditions of Si-limitation and when there are significant eutrophication-related shifts in phytoplankton competition.

The techniques described above are useful for inferring qualitative aspects of a lake's enrichment history and for answering questions such as, 'has the nutrient status of a lake changed and in what direction'? However, these approaches are not capable of addressing questions such as, 'how much have nutrient concentrations increased and what were pre-disturbance nutrient concentrations?' which necessitate numerical estimates of trophic variables. The develop an inference model capable of answering these questions involves a two-step process, whereby a predictive equation, or 'transfer function' is established and then applied to the fossil record. Usually transfer functions are constructed from a modern 'training set' consisting of the diatom remains found in recently deposited sediments and corresponding water chemistry data from a large number of lakes in a given region (Dixit *et al.*, 1992). Response models capable of solving these two steps are of two major types. The first of these attempts to quantify the diatom-trophic status relationship using a multiple linear regression approach (Agbeti & Dickman, 1989; Whitmore, 1989) by relating trophic variables (i.e. P, chlorophyll *a*) to different diatom indicator groups. This method has been successful applied, but unlike similar models used to reconstruct lakewater pH it has not been used to provide actual, quantitative values of trophic parameters. It also has an inherent theoretical disadvantage in that it assumes linear responses of diatoms to environmental parameters, when the fundamantal laws of community ecology relating to the species niche (i.e. Shelford's tolerance laws) indicate that organisms respond to aspects of their environment in a unimodal way ((Agbeti, 1992; Pianka, 1978).

The second more recently developed method uses the techniques of canonical correspondence analysis (CCA) and weighted averaging (WA) calibration and regression, which have been designed to more closely couple inference models with ecological theory (ter Braak & van Dam, 1989). These techniques assume a unimodal, or 'Gaussian' relationship between diatoms and environmental parameters (cf. Gauch & Whittaker, 1972) and for this reason they are theoretically superior to the multiple linear regression models (Birks *et al.*, 1990a). Prior to the development of a WA transfer function it is necessary to know if the environmental parameter to be reconstructed (e.g. total phosphorus (TP)) has a significant influence on the diatom distributions in the training set. This is achieved using CCA, a direct-gradient ordination method which can be used to explore underlying trends in the data. Thus if TP is found to be explain a substantial portion of the species variance, a diatom-TP transfer function can then be produced using WA (Line & Birks, 1990). WA is a simple approximation of the 'maximum likelihood' (ML) approach to calibration and regression, the rationale of which is that at a given level of an environmental parameter, taxa with have optima close to that level will be most abundant (ter Braak, 1987). Thus a simple way of estimating the past level of a given parameter is the average of the optima of all the species present in a fossil sample, weighted by their relative abundance (Birk *et al.,* 1990a). The WA method has recently been advanced by incorporating a partial least squares (PLS) approach and this new technique, WA-PLS (ter Braak & Juggins, 1993) improves on WA because it more fully utilises the residual correlations between taxa and unmodelled, or 'nuisance' variables (Korsman & Birks, 1996)

The majority of early advances in the use of WA-based diatom transfer functions have been made in the reconstruction of pH as part of the Palaeoecological Investigation of Recent Lake Acidification (PIRLA I and II) (Charles & Smol, 1990) and Surface Waters Acidification Programe (SWAP) (Stevenson *et al.,* 1989; Birks *et al.,* 1990a). More recently however, regional training sets have been put together to produce transfer functions capable of inferring trophic variables such as chlorophyll *a*, Secchi disc depth and in particular TP (Agbeti, 1992; Hall & Smol, 1992; Anderson *et al.,* 1993; Jones *et al.,* 1993; Fritz *et al.,* 1993; Reavie *et al.,* 1995a; Bennion *et al.,* 1996). The performance of a TP transfer functions is usually reported in terms of the root mean square error of prediction (RMSE) and the r^2 correlation coefficient of determination between measured TP concentrations in the data set and TP concentrations inferred from the model. However, because RMSE will be underestimated if it is based solely on the original training set (i.e. from which the model was derived), computer-intensive cross-validation techniques such as jackknifing and bootstrapping (Efron, 1982; Efron & Gong, 1983) are usually employed to generate independent test sets from the original data set, such that RMSE (i.e. $\mathrm{RMSE}_{[\mathrm{boot}]}$, $\mathrm{RMSE}_{[\mathrm{jack}]}$) can be more realistically estimated (Bennion *et al.,* 1995). The r^2 values for the observed-diatom inferred TP relationship is usually relatively high (i.e. typically r^2=>0.7) and in a recently amalgamated data set (Bennion *et al.,* 1996) an r^2 value of 0.91 was attained indicating that these models are potentially highly effective tools for reconstructing TP from the fossil diatom record. These models can also be validated in the field if long-term monitored water chemistry data is in existence and diatom-inferred water chemistry predictions can be compared with actual chemical data. This type of calibration exercise has been undertaken at Mondsee, an Austrian pre-Alpine lake, where a diatom-TP transfer function was found to accurately track directional trends in the TP history of the lake with a relatively close agreement between diatom-inferred and actual TP values (Bennion *et al.,* 1995). Thus it is apparent that diatom-TP transfer functions represent robust tools for inferring past TP concentrations from the sediment record. However, there are limitations associated with this approach and it is not always possible to be sure that modelled predictions are accurate. The error envelope associated with modelled predictions is usually quite large, much limiting the ability of these models to infer subtle changes in TP concentrations, particularly at the lower end of the trophic scale. These errors are undoubtedly related to the multivariate relationship between diatoms and their environment and the extreme inter-annual variability of TP concentrations.

Modern diatom studies

There have been many recent advances in diatom-based palaeolimnology, the most important of which has probably been the development of WA transfer functions. However, to improve these models and more fully realise their limitations, there is a requirement for modern calibration studies focusing on; (i) diatom taxonomy and systematics; (ii) the ecology of living diatom communities; and; (iii) the specific depositional and taphonomic processes affecting the representation of living populations in the sediments of a lake. These types of study are in many ways essential to the development of more precise and ecologically relevant techniques for palaeo-trophic status reconstruction from shallow lakes (cf. Davis & Smol, 1986).

(i) diatom taxonomy

The taxonomy of the diatoms is still to a large extent in a state of disarray and there remains some considerable confusion over the recognition and classification of common forms (Round *et al.*, 1990). Uncertainty is in many ways most intense, amongst the small centric forms (particularly *Stephanodicus*, *Cyclostephanos* and *Cyclotella* referred to in this thesis as 'cyclostephanoid' forms (cf. Theriot *et al.*, 1987)) which are often prolific in shallow eutrophic-hypertrophic lakes (Anderson, 1990c; Håkansson & Meyer, 1994). This is because these genera exhibit high levels of taxonomic diversity, with splits between different species frequently based on very subtle characters, many of which can only be confidently identified with the scanning electron microscope (SEM) (Bailey-Watts, 1988; Stoermer *et al.*, 1987). There is evidence to suggest that many cyclostephanoid forms are polymorphic (Håkansson & Bailey-Watts, 1993). This seems to be related to both (i) the effects of environmental factors on the make-up of the valve (i.e. ecophenotypic plasticity) (Geissler, 1986; Theriot, 1987; Theriot *et al.*, 1988); and (ii) natural morphological variation associated with diatom life-cycles (Hickel & Håkansson, 1987; John & Economou-Amilli, 1991; Kling, 1992). Thus the correct and consistent identification of many cyclostephanoid forms with the light microscope (LM) represents a severe challenge and is largely impossible with the inverted microscope as traditionally used in phytoplankton ecology. Unfortunately this has resulted in the grouping of many species which undoubtedly occupy quite different units of environmental space (cf. Håkansson & Regnéll, 1993). Thus as suggested by Kiss & Padisák, (1990) and Anderson, (1990c), where high densities of a variety of cyclostephanoid forms occur, electron microscope studies (i.e. SEM, TEM) should ideally supplement and confirm the identifications made with standard LM equipment.

(ii) diatom ecology

Usually it is a lack of modern ecological data which imposes the most important constraints on the interpretation of the fossil diatom record and in many studies ecological information for particular species is either lacking, or of poor quality. Planktonic diatom seasonality in shallow lakes is often similar to that experienced in deep lakes and late winter-spring is often the dominant period for diatom production when the water is cold, well mixed and nutrients are plentiful (Reynolds, 1984; Reynolds, 1987). However while chlorophytes and cyanophytes often dominate the plankton of deep lakes in summer and autumn, diatoms are sometimes dominant throughout the entire year in shallow lakes, as is frequent the case in eutrophic, lowland rivers (Köhler, 1994; Kiss *et al.*, 1994). Unfortunately the specific ecology of many of the centric planktonic species which dominate in shallow lakes is currently poorly understood, largely due to taxonomic problems and species 'lumping'. WA-transfer functions are beginning to more accurately characterise the nutrient demands of these forms, however there is minimal available information concerning the relative responses of different species to other important parameters factors such as light, Si-availability, salinity and turbulence. This problem is even more acute for periphytic diatoms, many of which have poorly defined habitat requirements and nutrient tolerances. Thus there remains considerable scope for studies investigating the ecology of shallow lake diatom communities.

(iii) diatom taphonomy

In palaeolimnology it is a fundamental uniformitarian assumption that the diatom assemblages found in lake sediments accurately reflect past diatom communities. Moreover it is usually assumed that lake sediment diatom assemblages afford an integrated, annual 'average' indication of the diatoms which grow in a lake (cf. Battarbee & Charles, 1987). The degree to which these assumptions are likely to hold true is related to the relative importance of; (i) sedimentation processes, outflow, grazing and dissolution losses, breakage and allochthonous, or re-worked sediment inputs; and (ii) physical mixing, sediment transport processes and bioturbation (fig. 1.2.). The first set of taphomonic processes are concerned with the thanatocoenose (death assemblage) -taphocoenose (fossil assemblage) transition and affect the degree to which contemporary diatom communities are deposited, permanently incorporated and accurately reflected in the sediment. The second set of processes affect the distribution of diatoms in the sediments of a lake and the resulting degree of sedimentological noise. These processes (i.e. both i and ii) are likely to range in importance from lake to lake as related to size, depth, morphometry, exposure and chemistry (Davis & Smol, 1986).

Unfortunately, studies which have been directly concerned with diatom taphonomy and the formation of the sediment record are relatively scarce. The importance of diatom losses have been considered in some studies (Jewson *et al.*, 1981; Reynolds & Lund, 1988; Barker, 1992; Barker *et al.*, 1994; Anderson, 1994a,b), just as others have considered the importance of allochthonous and re-worked inputs (Bejens & Denys, 1982; Battarbee & Flower, 1984). However rarely have these types of investigations been conducted in small, shallow, freshwater lakes subject to eutrophication. Sediment trap studies in deep lakes indicate that there is frequently relatively close agreement between seasonal fluxes in planktonic diatom abundance in the water column and resulting inputs to the sediment (Reynolds *et al.*, 1982; Trimbee & Harris, 1984). However the efficiency with which planktonic diatom populations are permanently buried in sediments (i.e. after dissolution and decomposition) is rarely considered (Anderson, 1994b). Moreover in shallow environments with abundant submerged plants, periphytic diatoms are often dominant and the degree to which these populations are accurately represented in sediments is largely unknown.

Physical mixing, sediment transport processes and bioturbation usually result in the partial homogenisation of assemblages from different sources and seasons and this space and time 'averaging' is beneficial to the palaeoecologist attempting to reconstruct responses of the total lake system to mean annual environmental changes. However the averaging process is almost always incomplete as diatoms are usually retained close to their source such that deep-water cores typically underrepresent the periphytic forms which dominate in littoral areas (Earle *et al.*, 1988; Anderson, 1989). The assessment of diatom deposition patterns has been the subject of several studies (Dixit & Evans, 1986; Earle *et al.*, 1988; Anderson, 1990a,b,d) and it is now recognised that a single sediment core is often insufficient to characterise the responses of all diatom communities to environmental changes. However these types of studies have not as yet been undertaken in small, shallow lakes. Moreover there is at present minimal knowledge of the temporal representativity of sediment samples and the way in which recent diatom populations and indeed diatom blooms are recorded in sediment samples collected during different periods of the year.

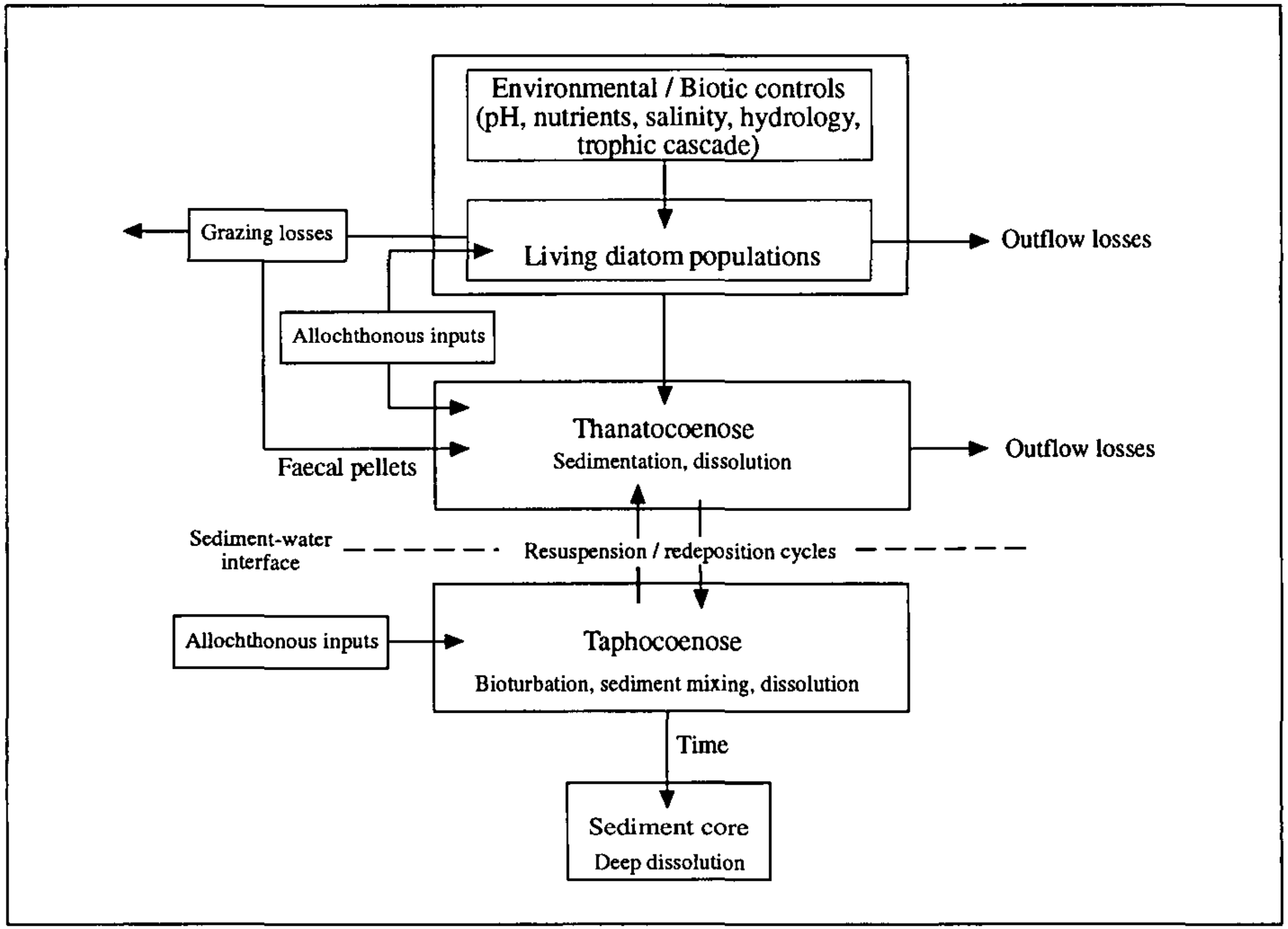


Fig. 1.2. The taphonomic processes affecting diatom representation in lake sediments (adapted from Anderson & Battarbee, 1994).

Introduction to the study sites

This thesis focuses on three shallow lakes in the English Midlands. These lakes Tween and Clifton Ponds and Groby Pool are similarly small (<25 ha.) and shallow (<3 m), but are very different in terms of their age, nutrient status and ecology. The sites are compared in detail in chapter four.

Tween and Clifton Ponds (plates 1.2, 1.3) are modern lakes (<30 yrs), which form part of the Attenborough Ponds SSSI complex (fig. 1.3.), a 221 ha. interconnected system of gravel-pit lakes excavated since the 1930s in the valley of the River Trent to the south of Beeston on the Nottinghamshire Derbyshire border. There are presently seven abandoned lakes in this complex, these being Beeston, Works, Duck, Tween, Church, Clifton and Coneries Ponds and work is on-going in the Erewash pit. The complex receives water from the R. Erewash, a highly polluted industrial river which drains a catchment of approximately 213 km^2. Land-use in this catchment is a mixture of urban, industrial and arable components and surface geology is predominately Coal Measures which consist of Shales and Mudstones with numerous coal seams. The R. Erewash enters the Attenborough Ponds complex in Coneries Pond. There are two outflows where water is conveyed to the R. Trent. These are in the eastern part of Coneries Pond (major outlet) and the north-eastern part of Duck Pond (subsidiary outlet). The Ponds fall into two main groups in terms of their water chemistry; (i) those presently linked to the R. Erewash (i.e. Coneries, Tween, Duck and Works Ponds) which are consequently, turbid hypertrophic, highly riverine environments; and (ii) those lakes which are mostly isolated from the R. Erewash (i.e. Church, Beeston and Clifton Ponds) and are mildly eutrophic, largely groundwater fed lakes. Presently Clifton Pond is the only lake which supports submerged plants.

In contrast to Tween and Clifton Ponds, Groby Pool (plates 1.4, 1.5, fig. 1.4.) is an ancient lake (>700 yrs old) and probably dates to at least early medieval times. It is found on the south-western edge of Charnwood Forest in Leicestershire and is also a SSSI site. The lake has one major inflow, one subsidiary inflow and one outflow. The Slate Brook is the dominant inflow and drains a small (approximately 8.5 km^2), rural, catchment in which land-use consists predominately of pasture with woodland and arable as sub-dominant components. Approximately 5% of the catchment consists of former granite quarries and surface geology is dominated by Pleistocene till on the upper slopes and Mercian mudstone on the mid-lower slopes. There are also outcrops of PreCambrian slate and diorite, one of which occurs on the south-eastern edge of the Pool. The Pool is eutrophic, but like Clifton Pond it supports dense beds of submerged plants and clear water.

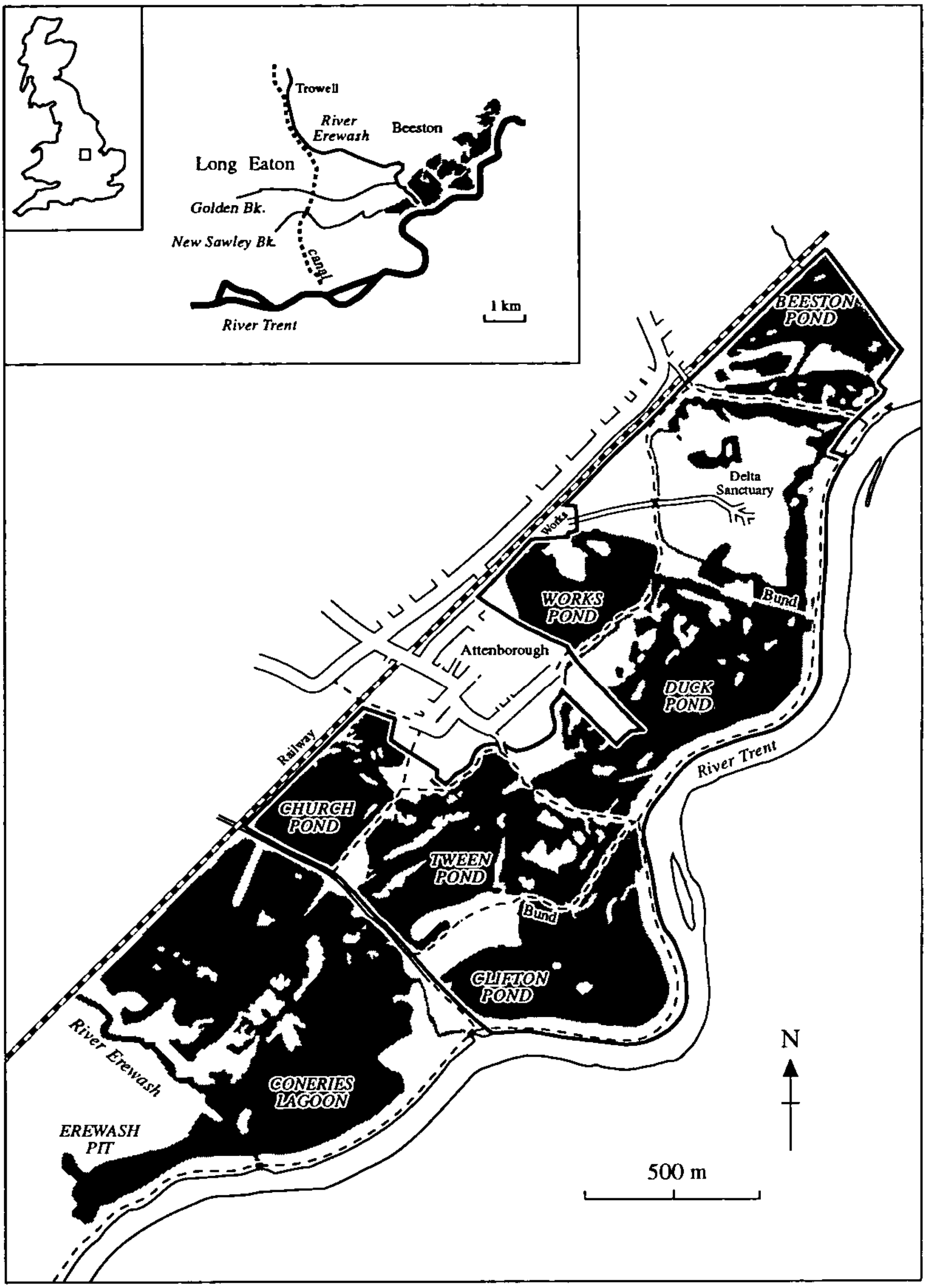


Fig. 1.3. The location of Tween and Clifton Ponds in the Attenborough Ponds SSSI.

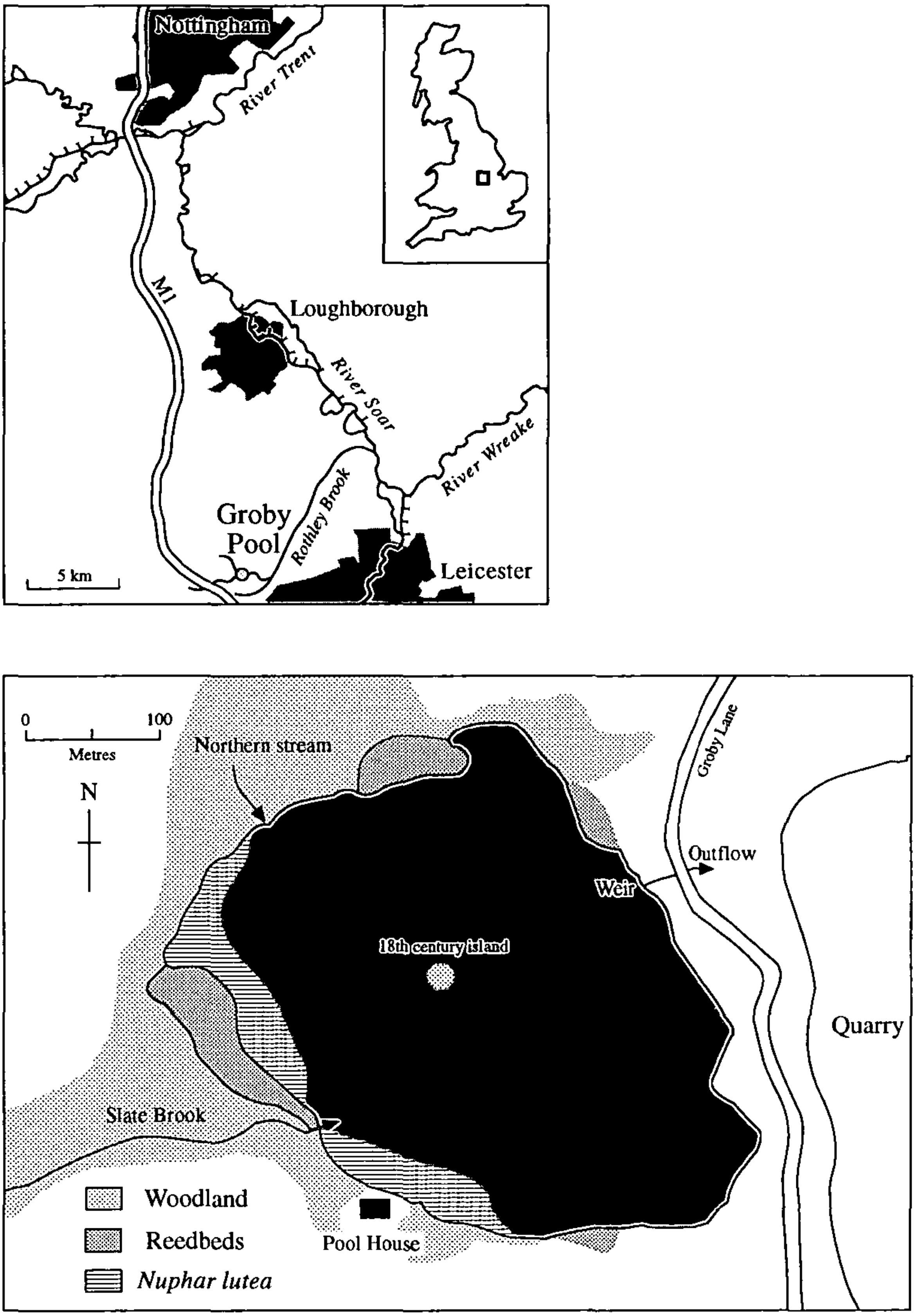


Fig. 1.4. The location of Groby Pool.

Plate 1.1. Brilliant summer fieldwork!

Plate 1.2. Tween Pond, early spring 1993 with Radcliffe-On-Soar power station in the background.

Plate 1.3. The northern corner of Clifton Pond, summer 1993.

Plate 1.4. Groby Pool, spring 1995 viewed from the northeast.

Plate 1.5. The western edge of Groby Pool, summer 1995.

Thesis aims

It is clear that modern studies into diatom taxonomy, ecology and taphonomy are crucial to the improved understanding and more accurate interpretation of the fossil diatom record (cf. Davis & Smol, 1986). Unfortunately these types of studies have rarely been undertaken in the shallow, fertile lakes which are so common in lowland England. The recent application of quantitative techniques of palaeo-trophic status reconstruction to shallow lake diatom stratigraphies represents a major advance. However to more fully realise the potential of this approach there is a requirement for more contemporary diatom studies. In this context this thesis has two major aims.

(1) The first of these is to achieve an increased understanding of the taxonomy, seasonality, habitat preference and representation in the sediments of diatom communities in three chemically and ecologically contrasting shallow lakes. These lakes, Tween and Clifton Ponds and Groby Pool have been chosen to represent a productivity gradient from mildly eutrophic to hypertrophic conditions.

(2) The second major aim of this study is to use the results of the above studies to assist in the interpretation of the fossil diatom record from two of these lakes, Tween Pond and Groby Pool. These lakes are SSSI sites and possess abundant historical evidence of changes in aquatic plant communities and shifting catchment land-use and disturbance. This data provides an excellent opportunity for exploring the different factors which have shaped the diatom record preserved in the sediments from these lakes. Thus efforts are made to compare the fossil diatom record with known historical changes, to more fully explore the eutrophication histories of Tween Pond and Groby Pool. In this respect, this thesis adopts a holistic, 'open minded' approach to trophic status reconstruction and attempts to tease as much environmental information from the sediments as possible, highlighting some of the potential limitations associated with quantitative nutrient reconstructions.

Thesis outline

The sampling protocols and field and laboratory methods used in this thesis are detailed in chapter two. Major taxonomic problems in this study were associated with the identification of the small centric diatoms and chapter three considers the taxonomy and morphological plasticity of the dominant and 'problematic' centric forms collected from the three study sites. In chapter four the study sites are compared and the results of the modern ecological and taphonomic studies are described and discussed. In chapter five the recently documented history of Tween Pond is described and by comparing the diatom record with known changes in the ecological history of the lake, the factors which have shaped the fossil diatom record are explored. The eutrophication history of Groby Pool is the subject of chapter six and again the available historical data in the form of old macrophyte records and documented changes in catchment land-use are compared with the diatom signal from a sediment core. These data are then used to provide an insight into eutrophication-related changes in nutrient status and phytoplankton-macrophyte interactions over the last 250 years. The major findings of chapters four, five and six are discussed in chapter seven which focuses on the use of diatoms in reconstructing historic changes in phytoplankton-macrophyte interactions and the inherent limitations of using a purely nutrient orientated approach to reconstruction. In chapter eight the significance of this thesis is summarised and a more holistic approach to diatom-based trophic history reconstruction for shallow lakes is advocated.

CHAPTER TWO

METHODOLOGY

This chapter considers the different sampling approaches and methodologies used in this study and discusses the different technical and interpretive methods which were employed. It is divided into two parts, the first concerning itself with the methods used in the modern studies into diatom taxonomy, ecology and taphonomy and the second with those methods employed in the palaeo-trophic reconstruction status process.

Modern diatom studies

Introduction

The accurate characterisation of the nutrient chemistry and phytoplankton dynamics of a lake requires that a regular sampling interval is maintained (Harris, 1986; Hanna & Peters, 1991). This is because sampling a nutrient resource (e.g. PO_4), or biological parameter (e.g. chlorophyll *a*) at too infrequent intervals leads to severe misrepresentation of its true flux. In small, meso-hypertrophic shallow lakes, as in other lake types, inter-annual changes in nutrient resources, phytoplankton biomass and the abundance of different phytoplankon species are marked. This is due to rapid fluctuations in external (i.e. catchment) and often internal nutrient inputs, differential nutrient uptake and the non-equilibrium nature of pelagic environments which results in rapid shifts in the prevalence of different species (Reynolds, 1984). Thus most studies concerned with seasonal aspects of shallow lake phytoplankton ecology have adopted a weekly, bi-weekly and at minimum a monthly sampling interval. However while temporal variability is usually marked in shallow lakes, spatial patchiness tends to be much reduced due to; (i) the small water area; (ii) intense water circulation; and often (iii) rapid flushing rates. This means that a single sample station is usually sufficient for nutrient and phytoplankton studies in small, bathymetrically simple shallow lakes.

Experimental details

The three study sites are small (<25 ha.) and shallow (<3 m) and it is likely, as indicated above, that properties of the water column are relatively similar in different parts of the profundal zone. Thus a single deep water site, away from feeder stream inputs was chosen for studying aspects of the phytoplankton ecology and water chemistry of the lakes. The main aims (cf. thesis aims) of the modern monitoring part of this study were to broadly characterise the seasonality and environmental requirements of the diatom communities found in the three shallow lakes and to estimate how well these communities were represented in accumulating sediments. In the light of these aims it was decided that lake water should be collected from each lake on a monthly basis during the main part of the diatom growing season (i.e late winter-late autumn) for the determination of major nutrient chemistry, pH and electrical conductivity (EC), phytoplankton biomass (as chlorophyll *a*) and planktonic diatom dynamics. This strategy was appropriate logistically as it enabled this study to fit into the existing protocol of the River Erewash catchment management programme (Petts *et al.*, 1995). Periphytic diatoms are often important primary producers in shallow lakes and are frequently dominant in the sediments, particularly if a lake posseses abundant plant macrophytes. The importance of the periphyton in the three shallow lakes was assessed by collecting monthly samples of the diatoms attached to submerged and emergent plants (the epiphyton) and rocks (the epilithon) in the margins. As one of the essential aspects of this study was to link the modern diatom populations to the fossil record sediment traps were also installed in the lakes. These were located in close proximity of the water chemistry sites and were emptied at the same time as the monthly sampling.

In Tween and Clifton Ponds monthly samples were collected between late January and late October, 1993 and in Groby Pool over the same time period in 1995. Lake water for water chemistry, chlorophyll *a* and planktonic diatoms was collected in sterile, pre-rinsed 500 ml polyethylene 'Pet' bottles and approximately 3 l was stored in the fridge at 4°C. The planktonic diatom water samples were preserved by the addition of 10% formalin and made up to a concentration of around 3%. Water chemistry samples were immediately coarse filtered using 9.0 cm, 11 μm Whatman™ No. 1 filter papers. If water chemistry and chlorophyll *a* analyses could not be undertaken within a few days the water bottles were deep frozen at -20°C. In Tween and Clifton Ponds planktonic diatoms were also sampled with a 53 μm plankton net. These nets, although still used to characterise the plankton of lakes have recieved much criticism for biasing both quantitative and qualitative phytoplankton studies as they tend to underestimate the density of nanoplanktonic forms which are smaller than the net mesh size (Wetzel & Likens, 1991). In Clifton Pond during late summer the tiny planktonic form *Cyclostephanos tholiformis* (mean diameter 4.8 μm, see chapter three) was prevalent in the lake water samples (>50%), while it was of minor significance in the tow (<5%) which was dominated by the chain-building species *Aulacoseira granulata* var. *angustissima* (fig. 2.1.). The latter form was never abundant in the Clifton Pond sediment trap and it can be assumed that it was selectively collected in the tow in preference to *C. tholiformis*. Thus results derived from the plankton net tows were disregarded in this study.

Water chemistry

pH, conductivity and Secchi-disc depth

pH and electrical conductivity (EC) were measured in the field using Whatman™ electronic probes to an accuracy of +/- 0.1 pH and +/- 10 $\mu S\ cm^{-1}$ respectively. These were pre-calibrated in standard solutions. The transparency of the water was estimated with a Secchi disc which provides a simple means of estimating the turbidity resulting from phytoplankton activity and loadings of suspended solids. The disc was lowered through the water and when it disappeared a Secchi disc depth measurement was taken. This was repeated three times and the mean of these values was taken.

Nutrients

Nutrient chemistry in Tween and Clifton Ponds was carried out as part of the River Erewash catchment management project (Petts *et al.*, 1995). In an effort to determine the effects of the polluted R. Erewash on nutrients and heavy metal concentrations in the ponds a large number of parameters were measured on a monthly basis between October 1992 and September 1993 from eight sampling stations in six of the Ponds and at twenty-five locations along the length of the River Erewash and its tributaries.

Nitrate (NO_3), phosphate (PO_4) and chloride (Cl^-) concentrations were measured in the water chemistry laboratory, Geography Department, Loughborough University, by Mr. Stuart Ashby. Analyses were performed using a Chem lab Auto-analyser. Silicate (SiO_2) was measured by Inductively Coupled Plasma Atomic Emission Spectroscopy (ICPAES) using a Perkin Elmer P400 machine in the environmental chemistry laboratory, Department of Mineral Resources Engineering, Nottingham University under the supervision of Dr. Brian Atkin. In Groby Pool TP, nitrate (NO_3) and silicate (SiO_2) were measured on a monthly basis between January and October 1995 and on three occasions (spring, summer and autumn) from the Slate Brook inflow stream. Analyses were performed at the Geography Department, Birmingham University by Mr. Andrew Moss.

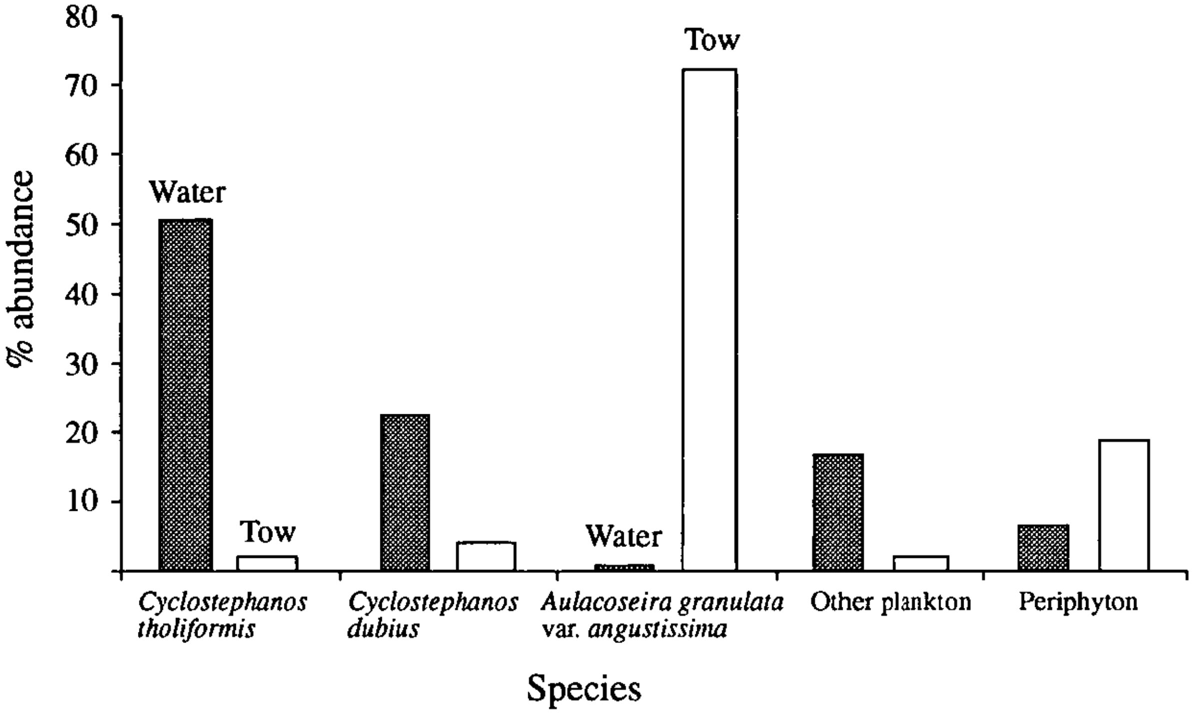


Fig. 2.1. The dominant diatoms found in of a 'spot' water sample and a plankton net sample collected from Clifton Pond (27/7/93).

Periphyton

The life-form classifications as used in this study are summarised in table 2.1. The term benthic as used here, refers to the epilithic, epipsammic and in particular epipelic forms associated with the lake bed. Epilithic diatoms were collected from submerged rocks in littoral areas on two occasions from each of the study lakes in late summer and autumn. This was achieved by gently washing off loosely attached sediments and then removing the thin biofilm from these 'clean' rocks with a penknife. Rocks with heavy growths of filamentous algae or thick mud deposits were avoided wherever possible. Epiphytic diatoms attached to submerged and emergent plants were sampled in early-mid-summer and towards the end of the growing season by breaking off a small piece of stem or leaf. It has been shown that different plant species do not select for different epiphyte communities in meso-eutrophic lakes (Eminson & Moss, 1980), thus samples were taken randomly from different species and one sample was used to represent the entire lake.

	Life-form	Definition
Plankton		
	euplanktonic	always planktonic
	tychoplanktonic	can be periphytic or planktonic
Periphyton		*attached to* :-
	epiphytic	plants
	epipelic	mud or silt
	epipsammic	sand
	epilithic	rocks

Table 2.1. The life-form classification as used in this study

Macrophytes

On each field trip during the summer and autumn the extent and diversity of the submerged plant stands was assessed. In both Clifton Pond and Groby Pool the water was extremely clear during the plant growing season and under these conditions it was possible to make a visual assessment of the macrophyte flora. Large areas of each lake were searched and samples of all different species were collected by hand, or with a small rake. Plants were identified using standard guides (Haslam *et al.*, 1975) with the assistance of Dr. Max Wade.

Chlorophyll *a*

The procedure for calculating chlorophyll *a* follows that of Wetzel & Likens (1991). Water samples were filtered through Whatman™ 9.0 cm, 1.2 μm GF/C glass fibre filter paper on, or within 24 hours of the day of collection using a water suction pump. The filter papers were then carefully folded, transferred into petri-dishes and immediately frozen at -20°C to help rupture the algal cells and improve the extraction of photosynthetic pigments. On removal from the freezer, filter papers were ground vigorously in 10 ml of 90% alkaline acetone, added in stages to a ceramic tissue grinder containing a small amount of silver sand. This was completed as quickly as possible (<45 seconds), after which time the extract was transferred into a stoppered centrifuge tube and stored for a few moments in the fridge. The tubes were then centrifuged at 3000 rpm for 5 minutes and the extract was transferred into glass cuvettes.

Pigment concentrations were measured using an Hitachi 0-1100 series spectrophotometer. Absorption was calculated at 750 nm (turbidity) and 665 nm (750o, 650o) and then samples were acidified by adding 0.1 ml of 1N HCl and allowed to rest for 5 minutes. This process degrades chlorophyll to phaeophytin and allows chlorophyll *a* to be corrected for phaeopigments. Absorption was then re-measured at 650 nm and 750 nm (750a, 650a) and chlorophyll *a* was calculated using equation 1 (Lorenzen, 1967).

eq. 1: $\text{chlorophyll } a\ (\mu\text{g l}^{-1}) = (k)\,(f)\,[(665o-750o)-(665a-750a)](v)/(V)\,(Z)$

where k is the absorption coefficient of chlorophyll *a* (11.0), f is the factor to equate the reduction in absorbency to initial chlorophyll concentrations (2.43), v is the volume of extract in ml, V is the volume of water filtered in l and Z is the length of light path through the cuvette in cm (1 cm) (Wetzel & Likens, 1991). The extraction process was repeated three times.

Sediment traps

Theoretical considerations

The main use of sediment traps in lake environments has been to estimate the production rates and loss to the sediment of various organic and inorganic materials washed into lakes and produced in the water column. In this respect traps have been concerned with; (i) estimating phytoplankton sinking losses (Livingstone & Reynolds, 1981; Reynolds & Wiseman 1982; Reynolds *et al.*, 1982); (ii) the recruitment of bloom-forming blue-green algae from overwintering spores (Trimbee & Harris, 1984); (iii) inputs of pollen to the sediment from fluvial and aerial catchments (Bonny & Allen, 1984); (iv) geochemical exchanges between the water column and sediment (Dillon *et al.*, 1990) and; (v) the relative importance of different sediment redistribution processes (Hilton, 1985).

The design and dimensions of sediment traps has varied considerably (Bloesch & Burns, 1980; Gardner, 1980). This is because of methodological problems relating in particular to the process of sediment resuspension. Resuspension can result in two specific types of problems in trapping studies, in that; (i) turbulence generated in and around the trap can remove particles already deposited in the trap; and (ii) resuspension and recirculation of material from the mud-water interface means that traps collect both primary and secondary (recycled) matter. Investigations into the effects of turbulence on sediment trap particle retention indicate that the aspect ratio (AR) of the trap (height:mouth opening diameter) is a critical factor. Laboratory experiments have revealed that in shallow, low AR traps, turbulent water around and created by the trap can penetrate the contents, causing resuspension of particles deposited during weaker currents (Staresinic *et al.*, 1978). Using oil droplets to determine flow Reynolds coefficients, Lau (1979) developed a relationship between AR and turbulence in cylinders and found that deep-sided traps (AR>10) were required to maintain an undisturbed water layer above the contents of a 10 cm diameter cylinder at a typical lake current velocity of 30 cm sec^{-1}. These results have been confirmed by trapping experiments in Lake Erie (Bloesch & Burns, 1980) and in Oyster Pond, Massachusetts (Gardner, 1980) and it is now recognised that deep traps with an AR exceeding of at least 4-5 do not permit resuspension of once deposited sediment and as such make the most efficient collection devices.

However under turbulent water conditions in shallow wind-stressed lakes and in deep lakes during overturn, the water column is frequently loaded with particles entrained by wave-action and turbulence at the mud-water interface (Søndergaard *et al.*, 1992; Kristensen *et al.*, 1992; Lemmin & Imboden, 1987; Gálvez & Niell, 1992). Under these conditions traps collect both primary and secondary resuspended matter (Davis, 1968; Hilton, 1985) and this means that high AR traps will overestimate the net downward particle flux. Experiments with both high (>10) and low (<0.25) AR traps in Lough Neagh, N. Ireland have revealed that high AR traps overestimate net particle accumulation by a factor of 10, whereas very low AR traps intercept material at a rate comparable to natural sediment accumulation. (Flower, 1991). However AR was observed to have little influence on the relative abundance of the dominant diatoms deposited in the traps. Thus where quantitative estimates of particle fluxes are required it is probable that low AR traps are most effective, while AR is less critical in qualitative studies.

Apparatus and methods

The main requirements of the sediment traps in this study were to; (i) record qualitative changes in planktonic and periphytic diatom communities and; (ii) to make comparisons between the relative scale of diatom recruitment to the traps both between sample intervals and between sites. Quantification of the total downward sediment flux was not a requirement of this study so it was not necessary to use high AR traps (cf. Bloesch & Burns, 1980). However exceptionally low AR traps (i.e. <1) are difficult to sample without disturbing the settled material. Thus intermediate AR (approximately 1.3) traps were chosen. These 'tub' type traps were cylindrical, made from polyethylene (height 13.7 cm, internal diameter 10.2 cm, aperture 81.7 cm^2) and tapered very slightly towards the top (plate 2.1.) In both Tween and Clifton Ponds, two of these traps were employed, one of which was sampled monthly (tub trap I) and the other of which was sampled at the end of the study period (tub trap II). In Groby Pool in addition to the intermediate AR tub traps, two high AR, 'tube' type traps were also used (plate 2.2.). These were made from clear plexi-glass tubing (height 40 cm, internal diameter 3.4 cm) and had an AR of approximately 11.8. Again one of these traps was sampled monthly (tube trap I) and the other was not sampled until the traps were finally removed from the Pool at the end of the study period (tube trap II). The aperture of each trap was supported around 50 cm above the lake bed in plastic holders, fixed to the base of plastic drain pipes which in turn slotted on top of the uprights of a rigid dexion™ frame (plate 2.1.). This system was probably adequate to prevent the traps from tilting during rough weather conditions. Retrieval of the traps was relatively simple and involved lifting the pipe slowly up through the water, fixing a protective lid on the trap, gently uncoupling it from its holder, after which point a new trap was installed.

The traps were then stored in the fridge (4°C) for a few hours, after which time the volume of sediment was measured and transferred into beakers without disturbing periphytic algae and invertebrates attached to the trap walls. The sediment was then left to settle before the supernatant was drained off using a water suction pump, after which it was transferred into

Plate 2.1. The 'tub' traps and supporting apparatus.

Plate 2.2. A 'tube' trap.

pre-weighed 60 ml containers, which were re-weighed for the calculation of total wet mass. The sediment was then homogenised and sub-samples were removed for the calculation of percentage dry mass, percentage organic matter and percentage carbonate (see palaeolimnological methods). The total dry mass of material collected in the traps was estimated by multiplying the total wet mass of material caught in the trap by percentage dry mass.

Efficiency of the traps

The interpretation of the results derived from sediment traps is never a straightforward process as it is impossible to be absolutely sure of the retention efficiency of a trap, with a given AR in different lake environments. This is particularly so in small, eutrophic, shallow lakes where trapping studies are rare. In theory if material is resuspended from sediment traps particle collection rates should be inversely related to exposure time, as the longer the trap is exposed the greater is the opportunity for material to be lost. Thus if internal resuspension of entrapped material was significant in the tub traps it might be expected that the cumulative quantity of material caught in trap I would significantly exceed that caught in trap II. However it is apparent that the total quantity of dry material collected in traps I and II was relatively similar (i.e. within an order of magnitude) in the three lakes (table 2.2.). Thus it seems unlikely that significant quantities of sediment are resuspended from the tub traps. This hypothesis is also supported by a comparison between the efficiency of the tub and tube type traps in Groby Pool. It is apparent that the tub traps caught a much greater quantity of material both in terms of dry mass and volume, but per area collection rates (g [DM] cm^{-2} day^{-1}) were relatively similar (again within an order of magnitude) for the two trap types (table 2.3.). Thus as high AR traps have been shown to prevent internal resuspension it can be assumed that the tub traps operate in a similar way.

	Tub trap I cumulative DM (g)	Tub trap II total DM (g)
Tween Pond	85.4	56.0
Clifton Pond	37.8	58.7
Groby Pool	17.3	18

Table 2.2. The cumulative total dry mass (DM) collected in tub trap I (sampled monthly) and the total DM collected in tub trap II (sampled at the end of the field period) in the three study lakes.

	Tub trap I (cumulative)	Tub trap II (total)	Tube trap I (cumulative)	Tube trap II (total)
Mass (g $[DM]^{-1}$)	17.3	18.0	2.5	4.7
SM Collection rate (mg [DM] cm^{-2} day^{-1})	0.81	0.84	1.08	1.97
Volume (ml)	328	150	37	52

Table 2.3. The mass (g [DM]), volume (ml) and per area collection rate (mg [DM] cm^{-2} day^{-1}) of sedimenting material (SM) collected in the tub and tube traps (cumulative total estimated for tub trap I and tube trap I and total for tub trap II and tube trap II) operating in Groby Pool.

Diatom preparation

Initially both periphyton and plankton samples were transferred into glass beakers. It was not necessary to quantify the diatoms found in the periphyton and so random quantities of plant material (both modern and dried herbarium macrophytes) and of the epilithic biofilm removed from rocks were processed. However quantification of diatom densities in the plankton and in the sediment (i.e. from the traps and cores) was a necessity. Thus fixed quantities of lake water (usually 1 l) and sediment (usually 0.1 g equivalent dry mass as calculated from eq. 2) were placed into the beakers. The lake water was left to settle for at least one day, after which time the supernatant liquid was siphoned off with a water pump to leave 50 ml of concentrate.

eq. 2: Wet equivalent = (0.1) (100/% DM)

The techniques used for digesting and cleaning the material and preparing microscope slides followed quite closely those suggested by Battarbee (1986), with some modifications as designed by Barker (1990). The sediments of the three study lakes were typically low in carbonates (i.e. usually <15%) so there was no need to treat samples with hydrochloric acid (HCl) as is often necessary in carbonate-rich saline lakes. However organic matter did have to be removed and this was achieved by oxidising the sediment at 80°C for approximately one hour with 30% hydrogen peroxide (H_2O_2). The H_2O_2 was removed from the material by rinsing it four times with de-ionised water, allowing at least one day as a settling interval before the supernatant was lifted off using a water suction pump (Barker, 1990). In some clay-rich sediments the supernatant remained coloured for several days and high densities of tiny centric forms were found in suspension, seemingly bound to the very fine clay particles. Thus a much longer period (up to one week) was used as a settling interval and where this was insufficient the samples were centrifuged four times at 1200 rpm for five minutes. The centrifuge method was been found to cause damage to some delicately silicified diatoms and for this reason the overnight settling method was used wherever possible. After all traces of H_2O_2 had been rinsed from the material it was diluted to a volume likely to yield the appropriate final density of valves, homogenised and a fixed quantity of solution (usually 0.8 ml) was evenly strewn onto 18 mm glass coverslips using a micro-pipette, and left to evaporate at room temperature. The coverslips were then mounted in warm Naphrax™ onto microscope slides for LM examination. The preparation of material for the SEM was exactly the same as described above with the exception that a random quantity of material was dried onto 10 mm coverslips affixed to aluminium stubs and sprayed with gold-palladium.

Microscopy and taxonomy

Identifications were made with a Zeiss 'Axioscope' LM at x1000 magnification using differential interference contrast. Due to difficulties experienced in confidently identifying some of the small, centric planktonic diatoms with the LM alone, the SEM was used to study the morphological characteristics of a range of species as found in the seasonal samples (chapter three). The SEM used was a Leica Stereoscan 5380 operating at a voltage of 10-30 kV. The dimensions (i.e. diameter, depth) of selected diatom species were estimated using the LM eye piece graticule (to an accuracy of +/- 0.5 µm) and in the case of *Stephanodiscus* cf. *medius* with the SEM. The main taxonomic reference sources used for standard identifications were Krammer & Lange-Bertalot (1986; 1988; 1991a; 1991b), Patrick & Reimer (1966; 1975) and Germain (1981). A wide range of additional material was consulted to assist in the recognition of the small, centric forms that were encountered (see chapter three). The papers of Håkansson (1986), Theriot *et al.*, (1987), Stoermer *et al.*, (1987), Håkansson & Kling (1989), Håkansson & Kling (1990), Kling (1992), Håkansson & Bailey-Watts (1993) and Clarke (1994) were of particular use in this respect. The terms used to describe morphological features are typically those of Ross *et al.*, (1979) and the authorities for all the taxa mentioned in this thesis are given in appendix 1.

LM counting procedures

The accurate characterisation of the density, frequency and diversity of species present in a given modern-day or fossil sample depends upon the establishment of a reliable approach to enumeration with the LM. Reliability increases as the quantity of individuals encountered increases, but after a critical point the above parameters achieve a state of relative stability. Lund *et al.*, (1958) revealed that at the 95% confidence level an accuracy of +/- 10% is achieved once 400+ individuals have been encountered with the inverted microscope and similar results have been derived by Battarbee (1986) and Barker (1990). The same type of exercise was undertaken in this study for a sediment sample from Clifton Pond (fig 2.2.). As in the above studies percentages were erratic up until 250-300 valves had been encountered and relative stability in the relationship between the dominant species was apparent only after 350-400 valves. However the total number of species found in the sample continued to increase substantially, even after 450 valves indicating that more valves would have to be counted to accurately characterise species diversity.

This study was concerned with characterising species relative abundance, as opposed to searching for rare species and assessing species diversity. Thus in normal circumstances 500+ valves were counted in the sediment trap and core samples and 300+ in the less diverse plankton and periphyton samples. Low diatom concentrations in the lower parts of the cores from both Tween and Clifton Ponds and in a mid-part of the core from Groby Pool meant that it was not always possible to find 500+ valves on the slide under these circumstances the diatoms were counted in ten randomly selected transects. However where this produced less than 250 valves the sample was usually eliminated. The strategy for dealing with fragmented diatoms was simple and a diatom was usually only included in the count if over half of the central valve area remained. In the case of some easily broken araphidinean forms ends were counted and the total was divided by two. The number of valves that were counted in each of the samples in this study are given in appendix 2.

Diatom concentrations

The estimation of diatom concentrations (valves g $(DM)^{-1}$) is essential to help in the interpretation of trophic status reconstructions derived diatom relative frequency data (Battarbee, 1978). There is often a close relationship between diatom crop size and inputs to the sediment (Reynolds *et al.*, 1982; Trimbee & Harris, 1984), hence diatom concentrations can offer direct evidence of changes in the diatom productivity of a lake. Recent studies have also shown that in some lakes diatom concentrations in the sediments are positively correlated with chlorophyll *a* in the overlying water and thus afford a

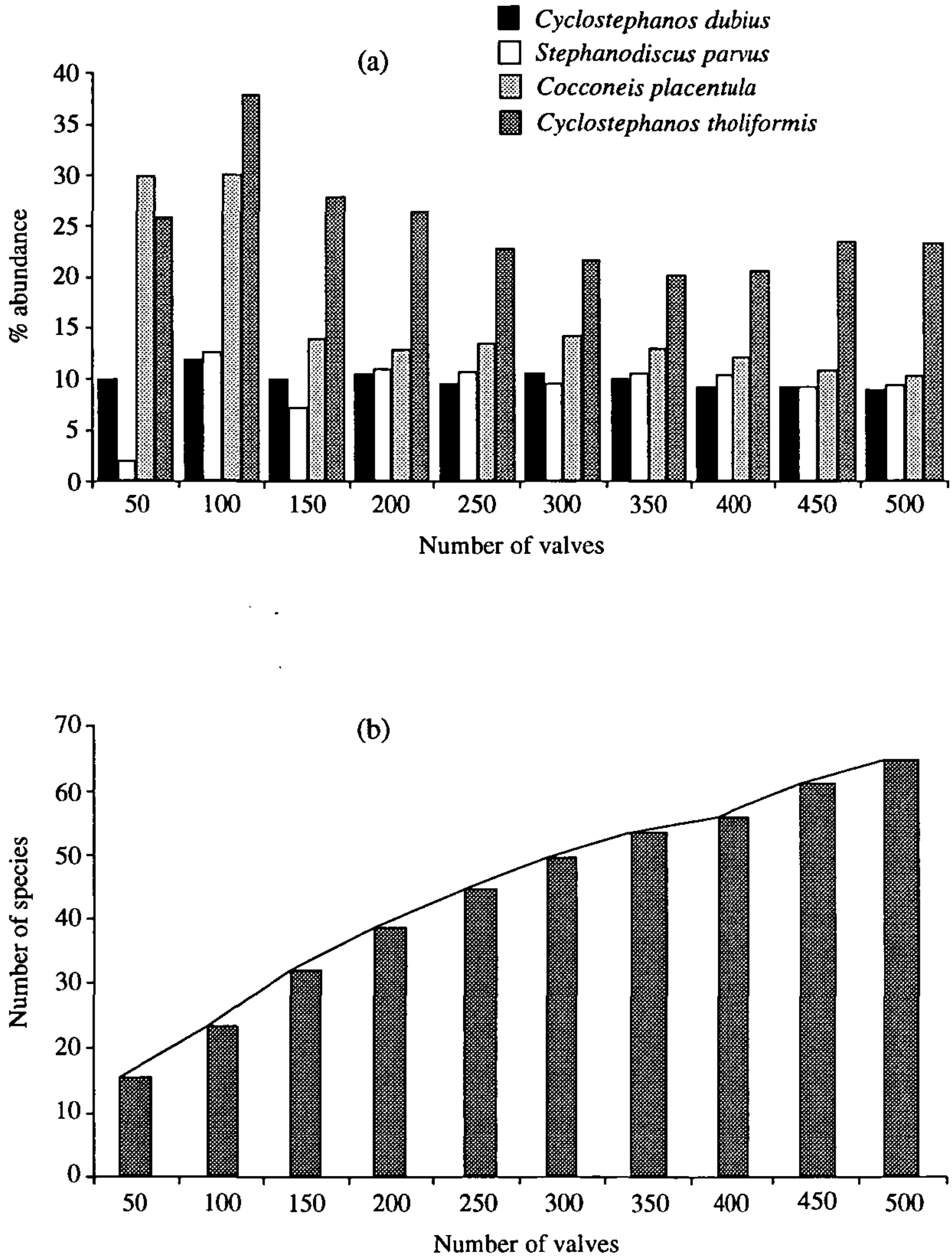


Fig. 2.2. The effects of count size on (a) species relative abundance; and (b) the number of different species encountered (CP193, 0-2 cm).

potentially useful means of assessing historic changes in overall phytoplankton productivity (Whitmore, 1991). However permanent grazing, outflow and diagenetic losses (Anderson, 1994b; Anderson & Battarbee, 1994; Reynolds & Lund, 1988), allochthonous inputs (Beyens & Denys, 1982) and indeed heterogeneous sedimentation patterns (Anderson 1990b) may distort the relationship between contemporary diatom production and cell sedimentation. Thus diatom concentrations must be interpreted with caution.

There are currently three methods that are used to estimate diatom concentrations in lake sediments; (i) the aliquot method (Battarbee, 1986); (ii) the evaporation tray method (Battarbee, 1973); and (iii) the microsphere method (Battarbee & Kneen, 1982). The aliquot method was used in this study for reasons of simplicity and abundance was estimated using equation 3:

eq. 3: $$\text{No. of valves g}^{-1} = (H/h)\,(n)\,(d)$$

where H is the total area of the coverslip, h is the proportion of the coverslip that was enumerated, n is the number of valves enumerated in h and d is the dilution factor. The major assumption of the aliquot technique is that there is a random distribution of diatoms on the coverslip, such that the quantity of diatoms found in the sample area h can be used to accurately predict the quantity found on the entire coverslip H. This assumption has been challenged due to the common observation that diatoms tend to be concentrated in the middle of the coverslip (Eaton & Moss, 1966; Battarbee, 1973). However the aliquot and microsphere methods have been found to produce similar abundance estimates in other studies (cf. Barker, 1990), thus it is probable that the aliquot method can be used to derive reliable results. Internal consistency was maximised in the present study by selecting mid-coverslip transects (typically <5).

Palaeolimnological techniques

Introduction

Lake sediments contain a diverse array of indicators which can be used to identify trends in lake water chemistry and ecology over a range of timescales. However before environmental trends can be identified, decisions must be made concerning where to core in a lake, and how many cores to take. The majority of studies concerned with reconstructing trends in lake trophic status have been based on a single sediment core taken from the deepest part of the basin. This is usually a sensible decision as sediment transport processes tend to focus sediments towards deep water (Davis & Ford, 1982; Hilton, 1985;

Hilton *et al.*, 1986) such that sediment accumulation rates are much faster in these areas. Thus temporal resolution is often greatest in deepwater profundal cores. The representivity of a single core has been the concern of several studies (Dixit & Evans, 1986; Engstrom & Swain, 1986; Earle *et al.*, 1988; Anderson, 1989; Anderson 1990a,b,d; Anderson *et al.*, 1994) and in small, bathymetrically simple lakes it has been shown that the same ecological trends are usually expressed irrespective in all cores from a lake (Earle *et al.*, 1988; Anderson, 1989). However due to heterogeneous sedimentation patterns several cores may be required to accurately characterise rates of sediment accumulation and indeed diatom palaeoproduction (Anderson, 1989; Anderson, 1994b).

The main aims of the palaeolimnological part of this study were to identify trends in the eutrophication histories of the three study lakes and not to construct sediment or microfossil budgets. Thus a single core methodology was adopted. The cores (<1 m) were taken from deeper areas, close to the monitoring sites using a mini-Mackereth compressed air piston corer (Mackereth, 1969). In Tween and Clifton Ponds two cores were retrieved in July 1993 from deep, flat-bottomed areas away from gravel islands and likely areas of sediment disturbance. The bathymetry and sediment stratigraphy of Groby Pool has been studied by David (1991) and cores from the Pool were taken in April 1995 from deep water close to the site of a ^{210}Pb dated master core which was retrieved from the the lake in 1987. The Mackereth cores were extruded in an upright position, sliced into 1-2 cm intervals and each sub-sample was transferred into plastic petri-dishes and stored in the fridge at 4°C. In addition to the Mackereth cores, short cores (<50 cm) were also collected so that the most recent lake deposits could be sampled. These were taken from all the lakes in the Attenborough Ponds SSSI in February 1995 and in a transect across Groby Pool in October 1995. A Hongve drop corer (Wright, 1990) was used in the initial Attenborough Ponds survey and a Glew drop corer (Glew, 1991) was used to collect all the other samples. The upper part of the cores were extruded in the field, transferred into sterile plastic bags or jars and again immediately placed in the fridge.

Dating

To establish the timing of important stratigraphic changes sediment cores must be accurately dated. The most widely used methods for dating cores over the short timescale relevant to recent trends in lake trophic status (i.e. the last 150 yrs) are the lead-210 (^{210}Pb) and caesium-137 (^{137}Cs) techniques (Engstrom *et al.* 1985). ^{210}Pb is a naturally occurring radio-isotope with a half life of 22.26 years and is the residual of the decay of the parent isoptope radium-226 (^{226}Ra) (Appleby & Oldfield, 1983; Oldfield & Appleby, 1984). ^{137}Cs is an artificial fallout radio-isotope resulting from nuclear weapons testing. It was first detected in the atmosphere in 1954 and maximum fallout occurred when thermonuclear weapons testing reached its peak in 1963. ^{137}Cs deposition then declined until a second peak in 1986 associated with the Chernobyl nuclear reactor accident. Using this method dates are attained by matching theoretical ^{137}Cs fallout against the distribution of ^{137}Cs in the sediment (Pennington, 1974). The resolution of the ^{210}Pb and ^{137}Cs techniques is limited by bioturbation (i.e. the actions of benthic invertebrates and bottom feeding fish) and wind-induced sediment resuspension which can destroy much of the integrity of the sediment record in shallow lakes (Anderson & Odgaard, 1994).

The core TP193 from Tween Pond was dated using the ^{137}Cs technique and for this purpose twelve 4 cm bulked sediment samples were dried at 20°C for 2 days and a fixed dry mass (8.3 g) from each sample was ground into a fine powder and transferred into air tight plastic containers which were taken to Nuclear chemistry, Loughborough University. ^{137}Cs concentrations (relative counts sec g^{-1}) were measured using a Packard Intrinsic Germanium Detector connected to a multi-channel analyser driven by Maestro II software by Dr. Peter Warwick. In Groby Pool core GR95B was dated by cross-correlation to a master core (core 24, David, 1991) dated using the ^{210}Pb, ^{137}Cs techniques. The cores were matched using their percentage organic matter profiles and pollen influx data provided by David (1991). The potential for core correlation in basins where lithostratigraphic trends are repeatable is highlighted by Anderson (1986) and Anderson & Rippey (1994).

Loss-on-ignition

The loss-on-ignition (LOI) technique is used to approximate the organic matter and carbonate content of lake sediments as weight loss after high temperature ignition (Dean, 1974). In most lakes there is a very close relationship between LOI estimated organic matter and the organic carbon content of sediments (Mackereth, 1966; Dean, 1974) and in sediment trapping experiments organic carbon deposition has been found to be closely related to phytoplankton biomass (Bloesch & Sturm, 1986; Porcalová, 1990; Baines & Pace, 1994). Thus where organic carbon is predominantly autochthonous, fluxes in the organic matter content of a sediment core may be used to hindcast broad changes in biological activity resulting from eutrophication. Lacustrine carbonates may be formed as a result of four processes (Kelts & Hsü, 1978); (i) clastic input from the erosion and transport of allochthonous carbonates; (ii) production of calcareous materials as part of living organisms (e.g. chlorophytes and charophytes); (iii) primary inorganic precipitation and sedimentation, and; (iv) post-depositional changes or early diagenetic reactions. The relative importance of these sources is lake specific, but again if carbonates are thought to be largely biogenic, the sediment record may be used predict eutrophication related changes such as increased phytoplankton photosynthesis (Anderson, 1989).

LOI derived organic matter and carbonate estimates were made on all the sediment trap and sediment core samples in this study. Initially a fixed volume of wet sediment was homogenised and transferred into pre-weighed crucibles (a) which were then immediately re-weighed (b) using an Ohaus Galaxy TM110 electronic balance calibrated to the nearest 1×10^{-4} g. The sediment was then oven dried at 60°C for two days and weighed once more (c) and percentage dry mass was estimated using equation 4. The dried samples were then placed in the furnace at 550°C for two hours, allowed to cool in a dessicator, re-weighed (d) and percentage organic matter was estimated using equation 5. The furnace was then heated to 950°C and the samples were ignited for a further one hour and weighed for a final time (e) after which carbonate was estimated from equation 6. Equations 5 and 6 express the results as percentages of dry mass.

eq. 4: $\%\,\mathrm{DM} = (c\text{-}a/b\text{-}a)\,(100)$

eq. 5: $\%$ organic matter $= 100\text{-}[(d\text{-}a/c\text{-}a)\,(100)]$

eq. 6: $\%$ carbonate $= (d\text{-}e/d\text{-}a)\,(100)$

CHAPTER THREE

The taxonomy and morphological plasticity of centric planktonic diatoms found in the three shallow study lakes.

This chapter presents the results of a detailed taxonomic study into the dominant and 'problematic' centric, planktonic diatoms encountered in the three study lakes. In particular it focuses on those taxa which challenged the existing taxonomic literature and proved difficult to classify consistently using LM. It includes both LM and scanning electron microscope (SEM) observations and highlights how detailed observations with the SEM allow for much more accurate and reliable identifications with the LM. In the literature it is evident that LM illustrations of small centric species are rarely included in SEM studies, such that it is often difficult for the ecologist to be sure of how a newly described, or re-defined species or variety appears with the LM. Thus for each of the species descibed with the SEM, several LM illustrations are also provided. In the first part of this chapter the potential sources of morphological plasticity in the centric diatoms which proliferate in eutrophic lakes are discussed. Then in turn all the dominant, or 'problematic' centric forms encountered in this study are described and discussed.

Intraspecific morphological variability

One of the main reasons for the misidentification and grouping of species in the Thalassiosiraceae is the high level of intraspecific morphological variability, particularly amongst the small, centric cyclostephanoid species (e.g. *Stephanodiscus*, *Cyclotella* and *Cyclostephanos*) which tend to be dominant in eutrophic lakes. Håkansson & Bailey-Watts (1993) have shown that *Stephanodiscus hantzschii* exhibits at least five natural morphotypes in Loch Leven, Kinross and the same level of polymorphism is probably evident in other small centric forms. It is also well known that small centric species vary in their morphology between lakes and in the same lake over time and this heterogeneity affords many problems for the ecologist and palaeoecologist, particularly as different species often look extremely similar with the LM.

The high levels of morphological variability observed in many small centric forms might possibly be explained in three ways, namely that it reflects; (i) the effects of environmental factors on the development of the valve (i.e. ecophenotypic plasticity); (ii) different stages in the life cycle of a single species; and (iii) real genetic variation between different, sexually incompatible species. If the latter is found to be the case following some degree of testing of hypotheses (i) and (ii) then it may be valid to establish a new diatom species, or indeed diatom genera. Unfortunately insufficient consideration of hypotheses (i) and (ii) has been the source of much taxonomic confusion.

The valve morphology-environment relationship

It is well known that living diatom populations are extremely sensitive to fluctuations in the chemical composition of the aquatic environment. This is demonstrated by distinct temporal and spatial changes in diatom community structure, but may also be reflected by alterations in the morphological structure of different species (Schmidt, 1979). The dependence of valve morphology on environmental factors has been inferred from studies of natural populations and has also been revealed under culture conditions.

The demonstration of the valve morphology-environment relationship is perhaps most likely in polluted (i.e. hypertrophic lakes, lakes receiving industrial waste) environments where populations are often exposed to high levels of and abnormal interactions between a range of nutrient cations, anions and heavy metals etc. In a sediment core from Hamilton Harbour (Lake Ontario), Yang & Duthie (1993) found some unusual and apparently 'underdeveloped' terratological forms of *Stephanodiscus niagarae* and *Stephanodiscus parvus* coincident with anthropogenic disturbance. The increased occurrence of these forms was believed to be related to either intense competition for silica or the effects of heavy metal pollution on the morphology of diatoms in the harbour.

The importance of environmental control over cell morphology in the cyclostephanoid group has also been demonstrated by exploring the relationship between different taxonomic characters and environmental variables in a large number of lakes using principal components analysis (PCA). Using this approach for *S. niagarae* and *Stephanodiscus alpinus* it has been shown that valve silicification is quite closely related to trophic status parameters (e.g. Secchi disc depth, chlorophyll *a*) (Theriot & Stoermer, 1982; Theriot *et al.*, 1988) and Theriot (1987) has shown that cell silicification in *S. niagarae* is dependent upon both cell size and the silicon : phosphorus (Si:P) ratio, with larger valves being more heavily silicified regardless of environmental conditions and more heavily silicified valves developing at higher Si:P ratios.

Laboratory studies have shown that the structure of the cell wall in many cyclostephanoid forms is heavily dependent on environmental conditions, with morphological changes in response to factors such as salinity (Geissler, 1982; 1986) and nutrient levels such as TP

(Krankemann, 1974) and NO_3 (Randig, 1974). Thus it is apparent that the environment which a lake presents to a diatom species is closely related to its resulting morphological expression. This is problematic for taxonomists who prefer to classify species on the basis of stable characters which do not vary significantly between different populations.

Life cycle changes in centric diatoms

Life cycle studies of centric diatoms in natural populations are rare due to sampling difficulties and the long duration of these cycles (i.e. between 2-5 years (Jewson, 1992a)). Sexual reproduction is gametic and fertilization results in the development of an auxospore which is generally thought to be an organic zygote (Round, 1982). The trigger for the onset of sex is probably an environmental cue (i.e. nutrient stress, low light levels), affecting cells below a minimum size threshold. In a complete life cycle study of a large *Stephanodiscus* species from Lough Neagh, Jewson (1992b) found that sexual cells appeared with the replenishment of N in late summer. Auxospores were then apparent in low numbers (no more than 1% of the population) for the next 3-4 weeks giving rise to initial cells which were about 2-2.5 times the diameter of the parent cells. Over the next two years through frequent analysis of the size distribution of the population, it was possible to follow the vegetative development of this cohort through several asexual divisions (approximately 21 during the entire 3 year cycle) until there was a return of the sexual phase at a size threshold of below 50% of maximum diameter. The progressive (although occasionally sudden) reductions in cell diameter that occurred with asexual division, were associated with important changes in the morphological construction of the diatom cells. In particular the position and number of marginal and valve face fultoportulae which are traditionally important taxonomic characters, were found to be extremely variable.

This dependence of cell morphology on life cycle stage has been demonstrated for a number of other cyclostephanoid species, including *Cyclotella distinguenda* (John & Economou-Amilli, 1991), *Cyclostephanos dubius* (Hickel & Håkansson, 1987) and *Stephanodiscus hantzschii* (Kling, 1992) and potentially in the *Cyclotella kuetzingiana* 'group' (Teubner, 1995). Hickel & Håkansson (1987) examined morphological variation in populations of *C. dubius* and distinguished two distinct morphotypes on the basis of size range and costae density. Morphotype I was smaller (4.9-22.5 µm) with a coarse structure (9-12 costae/10 µm). In contrast, morphotype II was much more finely silicified (12-18 costae/10 µm), often with shorter costae, and was found to have a larger size range (11.2-35 µm). Morphotype II was assumed to represent an earlier stage in the life cycle of the same species as morphotype I (i.e. *C. dubius*) and as with the two morphotypes of

C. distinguenda identified by John & Economou-Amilli (1991) both expressions in their extreme form were found to differ markedly in appearance, such that it would be easy for the unenlightened ecologist to mistake them for quite different species with both the LM and SEM.

In a pioneering study, Kling (1992) was able to isolate and grow the polymorphic *S. hantzschii* in clonal culture for one year. Over this period changes in valve morphology were observed during different life cycle phases (i.e. lag, exponential, stationary and death). At the onset of exponential growth, high abundances of an occluded form developed which had a skin-like sheet over the valve face and an underdeveloped rimoportula. In this early stage, cells were frequently heterovalvate with one valve occluded and the other having an open, well developed structure. This was followed by finely structured valves with open areolae, typical of *S. hantzschii* var. *hantzschii* where no central annulus was present and then by extremely weakly silicified valves often with a clearly defined central annulus as characteristic of *S. hantzschii* var. *tenuis* (cf. Håkansson & Stoermer, 1984). This latter form was found to be dominant in both old and 'dead' cultures. Thus very different morphological structures were associated with the growth of this one species and comparable growth related polymorphism is probably apparent for many other cyclostephanoid forms.

The centric planktonic diatoms in the three study lakes

The centric diatoms which were found in the modern plankton and sediment trap studies are listed in table 3.1. This table also gives the distribution of these species in the three study lakes, the ecological implications of which are considered in chapters four, five and six. The most diverse centric flora was found in Tween Pond, where the majority of the small centric, planktonic forms commonly encountered in shallow eutrophic-hypertrophic environments were present as major or minor taxa. Those species which were either difficult to identify with the LM, or dominant in any one sample from the three study lakes are considered in detail in the discussion which follows. In some cases specimens from other shallow eutrophic lakes are included to help assess potential levels of ecophenotypic plasticity. The additonal sites which are referred to in this study are Girton Pool, Notttinghamshire (SK 824 654), Grafham Water reservoir, Bedfordshire (TL 150 680), Letheringsett 'Small' Pond, N. Norfolk (TG 063 387) and Baconsthorpe castle moat, N. Norfolk (TG 121 382). These lakes are all eutrophic, 'plantless' waterbodies with diverse planktonic diatom floras.

	Modern distribution		
Species	Tween Pond	Clifton Pond	Groby Pool
Pelagodictyon tenue	1	3	3
Pelagodictyon fritzii	1	3	2
Stephanodiscus parvus	1	1	1
Stephanodiscus cf. *medius*	1	1	3
Cyclostephanos tholiformis	2	1	3
Cyclostephanos dubius	3	1	3
Cyclotella atomus var. *atomus*	1	3	4
Cyclotella atomus var. *gracilis*	1	3	4
Cyclotella sp. 1	3	3	3
Cyclotella meneghiniana	1	3	3
Cyclotella radiosa †	4	3	4
Cyclotella pseudostelligera	2	3	3
Aulacoseira granulata var. *angustissima* †	3	3	3
Aulacoseira aff. *alpigena* †	3	4	4
Skeletonema potamos	1	3	4
Thalassiosira pseudonana	3	1	4
Thalassiosira guillardii	2	3	3
Thalassiosira weissflogii †	3	4	4

Table 3.1. List of the centric diatoms found in present-day samples from the three study lakes and their modern distributions. 1 = common taxa, 2 = minor taxa, 3 = rare taxa and 4 = not recorded. † = not discussed in this chapter.

Pelagodictyon tenue / Stephanodiscus hantzschii

This species is frequently associated with the top end of the trophic spectrum (Bennion, 1994) and its mass occurrence in the plankton or, in the sediment has usually been found to be associated with eutrophic-hypertrophic conditions (Håkansson & Stoermer, 1984). Thus it is crucial that it is recognised with certainty by aquatic ecologists and palaeoecologists concerned with eutrophication processes and not confused with other similar taxa.

In Tween Pond centrics seemingly diagnostic of the *S. hantzschii* complex were extremely abundant in the spring plankton and attained a population size of 69 x 10^5 cells l^{-1} on the 25/3/93 when it contributed to 44% of the plankton assemblage (chapter four). With the LM it appeared that two main morphotypes were present representing the nominate and "*tenuis*" forms described by Håkansson & Stoermer (1984) and discussed by Casper *et al.*, (1987). However after the emergence of published descriptions of the new genus *Pelagodictyon* and the extremely similar species *Pelagodictyon tenue* from the Norfolk Broads (Clarke, 1994), it was decided that more detailed work was required on the "*hantzschii*" type cells in Tween Pond.

Plates 3.1 **a,b** show a typical vernal plankton assemblage for Tween Pond with the co-dominance of a range of cyclostephanoid forms, including *S. hantzschii* type cells and *S. parvus*. In this sample, as in all plankton samples collected from Tween Pond during any season, there are essentially two *S. hantzschii* valve types present. In the descriptions which follow these will initially be referred to as forms A and B.

(i) form A

LM observations

This form has a diameter range in Tween Pond of 8-11.5. Valves are flat to very slightly undulate and appear to be much more coarsely silicified than form B, with a highly punctate appearance (plate 3.1 **c**). Interfascicles are not discernable in the valve centre and only become apparent as slightly raised ridges about half way across the valve face, where they end in a thick, pointed spine. The spines occur at the ends of all interfascicles except for one which ends in a much shorter tubule (resembling a broken spine). This represents the external opening of the rimoportula. The areolae are irregularly arranged in the valve centre and radiate out as single rows becoming bi to triseriate at the valve margin.

SEM observations

The SEM reveals form A to be 'underdeveloped' with a skin of silica obscuring the areolae (plates 3.1 **d,e**). On both the valve face and the mantle, the areolae are heavily occluded and appear as circular domes pitted with fissures and holes (plate 3.1 **f**). Internally, the areolae are also domed and close examination reveals them to be pitted with tiny pores in a 'flower' like pattern (plate 3.1 **g**). The marginal fultoportulae occur as short tubules directly below every 2-5 spines (plate 3.1 **f**). Internally these have three satellite pores (plate 3.1 **g**). The rimoportula appears as a small, shortened tubule (plate 3.1 **f**) and on the inside of the valve it is represented by a labiate process positioned diagonally relative to the mantle edge (plate 3.1 **g**)

This form has been identified as being associated with *S. hantzschii* in a number of previous studies. In the late winter-spring diatom maximum in Loch Leven Bailey-Watts

(1988) refers to it as a "stippled" form of *S. hantzschii* (figs 28-30). It is also illustrated by Håkansson & Stoermer (1984) (figs 2, 9, 11); Anderson (1990c) (figs 15, 16); Koyabasi *et al.*, (1985) (figs 24, 26) and Fritz (1989) (fig 1d). Importantly this form also appears to be identical to specimens which characterise the early life cycle stage of *S. hantzschii* figured in the culture studies of Kling (1992) (figs 3, 5a, 6) as described earlier.

(ii) form B

LM observations

This form is slightly larger than form A with a diameter range of 9-12.2 µm. It is much more delicately silicified and the interfascicles are much more clearly defined and often become sinuous as they approach the centre of the valve where they almost always combine to create a hyaline ring or 'annulus' (plates 3.1 **h,i**). In contrast to form A the areolae become tri to quadriseriate at the margin and are barely distinguishable in most valves. As in form A, the rimoportula appears as a short tubule in place of a spine.

SEM observations

The main difference between forms A and B is the nature of the fascicles. In form B the cribra of the areolae on the valve face consists of a system of short ribs or 'frets' in a 'fishnet' type of arrangement (plates 3.1 **j,k**). These frets surround the areolae which are flat, polygonally shaped and depressed into the basal siliceous layer of the valve face (plates 3.1 **l,m**), contrasting starkly to the system of domes apparent in form A. However, similarly to form A, it is possible to see tiny pores pitted into the areolae (plate 3.1 **m**). This fishnet arrangement has been described in small centric diatoms found in the Norfolk Broads and has formed the basis for the establishment of the new genus, ***Pelagodictyon*** (Clarke, 1994). Three new species have been described in this genus, ***P. tenue***, *Pelagodictyon fritzii*, and *Pelagodictyon spinosum*.. Form B would appear to be exactly the same as ***P. tenue*** (Clarke, 1994, figs 7-9). Again this form is flat and has marginal fultoportulae which occur beneath every 2-5 spines (plates 3.1 **j,k**). These have three satellite pores internally (plate 3.1 **m**). No valve face fultoportulae are found in any specimens of this type, which is the characteristic used by Clarke (1994) to differentiate ***P. tenue*** from the other two species in the genus.

In addition to the form of the areolae, the other main difference between form B and form A is the thickness of the basal siliceous layer. A comparison between plates 3.1 **m** and **n** shows that form A is composed of a much larger mass of silica than form B and the width of the valve edge would appear to be significantly thicker. In discussing the structure of

Pelagodictyon, Clarke (1994) estimates that per unit area of valve structure *Pelagodictyon* is about three times lighter in its construction than a *Stephanodiscus* type valve (i.e. form A). This is supported by observations on the structure of form B (i.e. *P. tenue*) which looks extremely fragile (plate 3.1 **m**) and often collapses when fresh material is air dried onto SEM stubs.

The relationship between form A (*S. hantzschii* type) and form B (*P.tenue* type).

There is considerable evidence for the existence of a close relationship between forms A and B and both have been found to co-occur in plankton samples taken from Tween Pond and in other shallow lakes in Norfolk (Sayer, unpublished data). The main difference between types A and B is in the make-up of the cribrum and the form of the areolae. However these characters must be used very cautiously for species or genus differentiation. Sieminska & Chudybowa (1979) established the new species *Stephanodiscus rugosus*, as a small (<10 µm), coarsely silicified, heavily occluded centric largely on this basis. The valve face of *S. rugosus* was constructed of irregularly positioned chunks perforated with 'slit' like openings representing the areolae. It was later decided that these special characteristics necessitated its transference to a new genus, hence *Pseudostephanodiscus* and *Pseudostephanodiscus perforatus* (=*S. rugosus*) (Sieminska, 1988). However on the basis of SEM studies of *Stephanodiscus. minutulus* and the type material of *Stephanodiscus hantzschii* Genkal & Håkansson (1990) decided that *P. perforatus* was probably a terratological or life cycle variant of *S. minutulus* and hence belonged to the latter genus. The authors also suggested that occluded valve expressions are a feature of many *Stephanodiscus* species. Thus considerable care must be exercised in using areolae morphology in taxonomy.

Kling (1992) illustrates valves extremely similar to forms A and B as belonging to different phases in the life cycle of *S. hantzschii* (fig. 26). Form A would appear to be extremely similar to the newly formed valves that have closed, externally occluded areolae and are characteristic of exponential population growth (e.g. figs. 3, 6). Alternatively form B appears similar to the mature and dead valves (e.g. figs 1, 2, 9, 10) with open areolae that characterise the lag and stationary phases in the growth cycle. Kling (1992) only shows one internal view of this valve type (fig. 2), however the morphology of the cribrum appears to be the same as in form B in the possession of depressed areolae separated by a 'net' like arrangement of frets. In the exponential growth phase Kling (1992) observed that cells were often heterovalvate (i.e one valve having occluded areolae and the other having well developed areolae). In a spring bloom sample collected from Tween Pond on 26/3/95 several similar heterovalvate cells have been observed with one valve possessing the form A structure and the other appearing extremely similar to form B (plates 3.1 **o,p,q,r**). It has also been possible to find one of these cells with the SEM. Plates 3.1 **q,r** show such a cell with a form B type at the top and what appears to be a form A valve underneath. This lower form A valve also has longer spines than those of form B, some of which fork at the ends. Thus it seems that forms A and B represent different stages in the life cycle of the same species as described by Kling (1992). The possible progression between forms A and B is evident if plates 3.1 **e,s,j** are viewed in sequence and it seems feasible that a form A valve could be transformed into a form B valve with the progressive loss of silica from the valve face.

The question remains as to which genetic entity the form observed here belongs (i.e. *S. hantzschii* or *P. tenue*?). In a detailed study of morphological variability in *S. hantzschii*, Håkansson & Bailey-Watts (1993) include several illustrations of both the nominate and '*tenuis*' forms of *S. hantzschii* and none of these appear to have the extreme 'net' like internal structure as described by Clarke (1994). Alternatively the valves in this study have areolae which are either domed internally or appear as rounded holes. Thus it remains possible that the form encountered here is a separate entity to *S. hantzschii* as described by Håkansson & Bailey-Watts (1993) and that it may be valid to make a separation between *P. tenue* and *S. hantzschii*. However it is also possible that the *Pelagodictyon* structure represents an ecophenotypical response to environmental factors, such as silica and other macro-nutrients. In this thesis both forms A and B are included under the species *P. tenue*, but it is recognised that further research is required to determine if this is indeed a valid species.

Stephanodiscus* cf. *medius

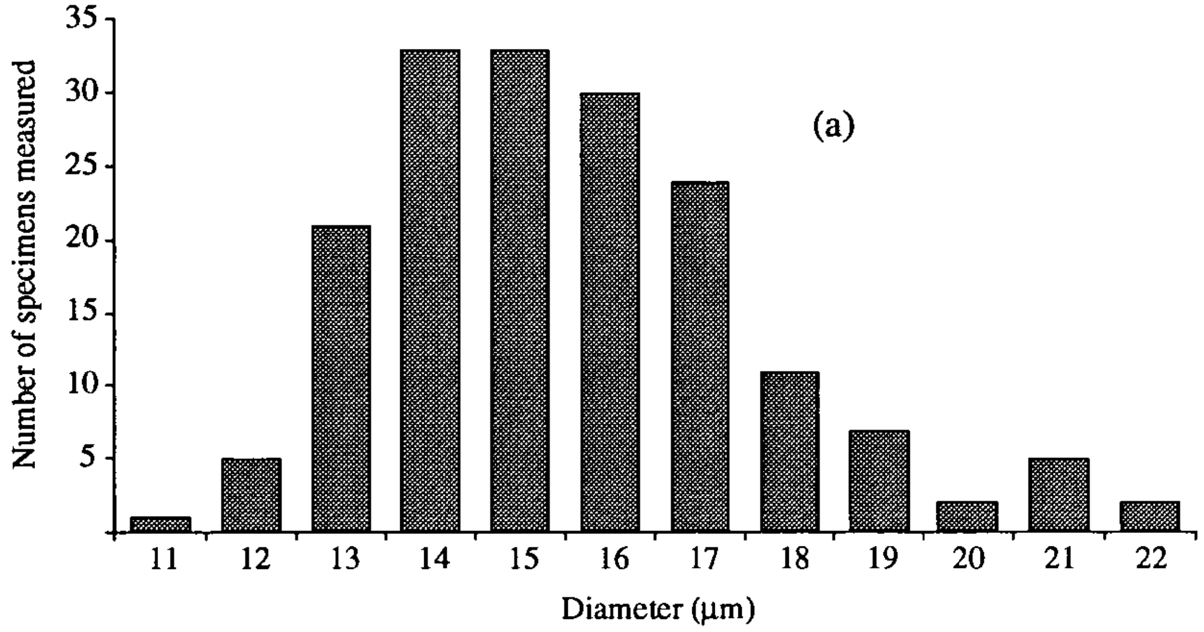
LM observations

In summer and autumn plankton samples from Tween Pond and to a lesser extent Clifton Pond, a large *Stephanodiscus* species was observed (plate 3.2 **a**). This form has a diameter range of 11-22 µm, with a mean of 15.7 µm (fig 3.1 a) and is characterised by having a pronounced concave/convex centre with relatively disorganised areolae. These become organised into uniseriate fascicles just outside the valve centre, which become biseriate between 80-90% of the way across the valve face. The interfascicles are relatively indistinct and structureless and appear slightly raised towards the valve margin where they may end in a short, but strong spine. In nearly all the valves which have been encountered of this form there are several interfascicles that are not tended by a spine.

SEM observations

It is only with the SEM that it is possible to discern the marginal and valve face fultoportulae in this form. Externally the marginal fultoportulae appear as relatively inconspicuous, short tubules directly beneath every 4th to 5th spine (plate 3.2 **b**). Internally these are always surrounded by three satellite pores (plate 3.2 **c**) and the number of marginal fultoportulae per valve is closely related to valve size (fig 3.1 b). This form usually has 1-2 and occasionally 3 valve face fultoportulae which are clearly evident internally and guarded by two satellite pores (plate 3.2 **d**). However even with the SEM it is difficult to discern these externally. The positioning of the valve face fultoportulae varies between the convex and concave valves. On the convex valves they are situated at the valve centre and on the concave valves towards the margin on the edge of the area of undulation. This form has a single rimoportula which takes the appearance of a relatively long tubule in place of a spine (plates 3.2 **b,e**). Internally, the rimoportula is sessile and positioned diagonally relative to the rim of the mantle (plate 3.2 **c**).

There are two *Stephanodiscus* species which appear to be closely related to this form. The first is *Stephanodiscus medius* as described by Håkansson (1986). This species has a diameter range of 6-33.8 µm and in contrast to the form described above the areolae form bi-triseriate fascicles at the margin and spines occur at the end of every interfascicle. Unfortunately Håkansson was not able to observe the detail of *S. medius* with the SEM, thus it was not possible to determine the fultoportulae morphology of this form. The second closely related form is *Stephanodiscus alpinus* as described by Theriot *et al.*, (1988) and Hickel & Håkansson (1993). This species has a diameter range of 7.5-33 µm and as in *S. medius* the areolae are arranged in bi-triseriate fascicles at the margin and again virtually all interfascicles are tended by a spine. In this species the valve face only has one fultoportula in contrast to the two and occasionally three found in the form described above. Thus there are distinct differences between the large *Stephanodiscus* encountered in Tween and Clifton Ponds and the two most similar species described in the literature. However as this form most closely resembles the LM illustrations of *S. medius* in Håkansson (1986) and is dissimilar to the very 'regular' appearance of *S. alpinus* with the LM and SEM, it is referred to as *Stephanodiscus* cf. *medius* in this study.



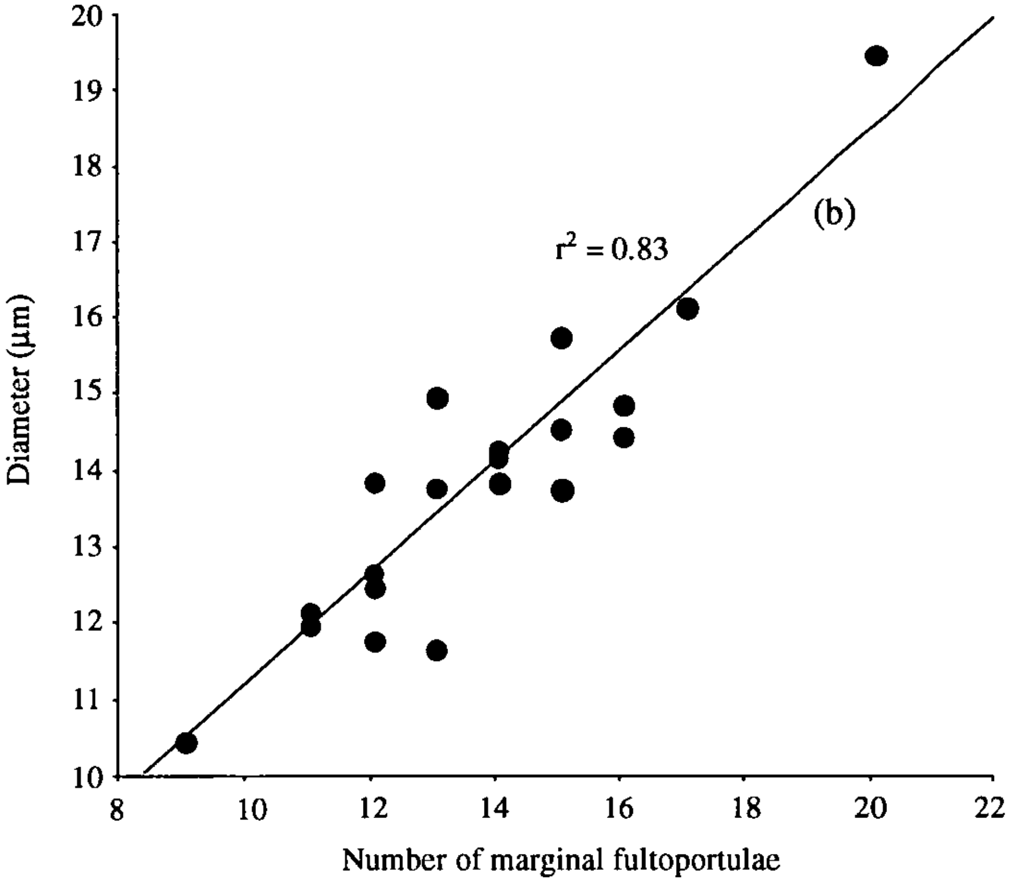


Fig. 3.1. The size distribution of *Stephanodiscus* cf. *medius* as determined with the LM (a) and the relationship between valve diameter and the number of marginal fultoportulae as determined with the SEM (b).

Cyclostephanos tholiformis

In spring and autumn plankton samples from Clifton Pond and to a lesser extent Tween Pond and Groby Pool, a tiny, finely structured cyclostephanoid form was found. Interestingly this same species was also relatively abundant on herbarium plant specimens dated 14/7/1896 and 6/1916 collected from Groby Pool.

LM observations

Using the LM this centric is most easily confused with *S. parvus*, however it is much more finely structured and fragile than the former and often smaller, occurring mainly in the size range 4-7 µm (plates 3.3 **a,b,c**). Valves range from being almost flat to being quite strongly undulate and valves with an undulate morphology are most common in the summer-autumn samples. This phenomenon also applies to *S. parvus* suggesting that environmental factors may exert an important influence over valve topography in these two species. The presence of a single valve face fultoportula and conspicuous and infrequent marginal fultoportulae which occur every 5-7 interfascicles are also clearly evident with the LM.

SEM observations

There were difficulties encountered in getting high resolution SEM pictures of this form, until a virtually pure stand was collected in a lake edge (into which the prevailing wind was piling up the algae) water sample from Clifton Pond on the 18/9/95.

With the SEM this form appears to be very similar to the two closely related *Cyclostephanos* species, *C. tholiformis* and *C. delicatus*. These two species are compared with the form encountered here (i.e. *Cyclostephanos* ?) in table 3.2. Plates 3.3 **d,e,f** show the detail of the areolae on the valve surface and on the mantle. In the valve centre these tend to be disorganised, circular to elongate holes, radiating out as uniseriate fascicles, becoming biseriate between 50% and 75% of the way across the valve face. This arrangement continues onto the mantle. Internally the areolae are very slightly domed in the valve centre becoming flattened and depressed into the valve towards the valve edge, where they become separated by short frets in a 'net' like arrangement as characteristic of species in the genus *Pelagodictyon* (Clarke, 1994) (plate 3.3 **g**). The close examination of the areolae reveals them to contain a series of tiny punctures (plate 3.3 **k**). The interfascicles occur as thickened ribs which become slightly raised towards the valve edge where they end in a short spine (plate 3.3 **i**). This also occurs internally and in many valves the interfascicles can be seen to branch on the mantle, creating a 'forked stick' type effect (plate 3.3 **h**). The marginal fultoportulae occur as shortened tubules beneath every 5-7 spines (plate 3.3 **i**) and internally these have two satellite pores (plate 3.3 **j**). This form has a single valve face fultoportula which is also tended by two satellite pores (plate 3.3 **l**). Unfortunately it has not been possible to locate the external opening of the rimoportula in the SEM investigations of this form, however internally the rimoportula is represented by a sessile labium (plate 3.3 **h**).

Håkansson & Kling (1990) suggest that *C. tholiformis* is different to *C. delicatus* in a number of respects (table), in that it possesses (i) a central annulus; (ii) regular, straight rows of areolae on the mantle; (iii) interfascicles that branch at the valve face/mantle junction (interfascicles do not branch on the mantle in *C. delicatus*); (iv) a tiny rimoportula that lies beneath a spine (as opposed to beside a spine in *C. delicatus*); and (v) marginal fultoportulae with two satellite pores (as opposed to three in *C. delicatus*). Thus in terms of the latter two characteristics, the form encountered in Clifton Pond would seem to be most closely aligned to *C. tholiformis* as opposed to *C. delicatus*. There are some differences between this form and *C. thoiliformis* however, in that valves are often flat and generally smaller than the size range quoted in Håkansson & Kling (1990) (table 3.2.). It is likely however that these differences are an ecophenotypical response to the particular set of environmental conditions present in Clifton Pond (Si-availability may be important in this respect). More typical valves of *C. tholiformis* have been collected in an autumn (17/8/95) water sample from Grafham Water reservoir, Bedfordshire (Plates 3.3 **l,m,n**) and SEM examination suggests that these valves are almost exactly the same as those found in Clifton Pond except that they tend to be larger (i.e >6 μm) and are nearly always strongly undulate. Thus the form described here is taken to represent *C. tholiformis*.

	Cyclostephanos tholiformis	*Cyclostephanos delicatus*	*Cyclostephanos* sp. ? (this study)
Diameter range (μm)	7-12	6-14	4-7
IF arrangement	slightly raised on valve face, branch on the mantle	slightly raised on valve face, do not branch on the mantle	slightly raised on valve face, branch on the mantle
Fascicles	uniseriate to about 50% across, then biseriate and triseriate at the margin	uniseriate to about 50% across, then biseriate and triserate/quadriseriate at the margin	uniseriate to about 70% across then biseriate to the valve margin
Occurrence of MF	every 4-5 spines, 2 satellite pores internally	every 4-6 spines, 3 satellite pores internally	every 5-7 spines, 2 satellite pores internally
Areolae ornamentation	circular-elongate holes	circular-elongate holes	circular-elongate holes.
Valve topography	fairly strongly undulate	fairly strongly undulate	flat to fairly strongly undulate
RP morphology	inconspicuous, lies beneath a spine on mantle. Internal sessile labia.	located beside a spine as an enlarged pore. Internal sessile labium.	? internal sessile labium.
VFP	usually 1 but can be up to 3. 2 satellite pores.	1 with 2 satellite pores.	1 with 2 satellite pores.

Table 3.2. Relationships between *Cyclostephanos* ? (i.e the form encountered in this study) and the two closely related *Cyclostephanos* species, *C. tholiformis* and *C. delicatus* as described by Håkansson & Kling (1990). IF=Interfascicle, MF=Marginal fultoportulae; RP=Rimoportula; VFP=Valve face fultoportula.

Stephanodiscus parvus

There remains considerable uncertainty in the literature as to the correct identity of *Stephanodiscus parvus* and of its relationship with other similar forms. The species was described by Stoermer & Håkansson (1984), but was more recently amended by Håkansson & Stoermer (1988) who retracted several of the initial illustrations. Particular confusion surrounds the relationship between *S. parvus* and *Stephanodiscus minutulus*. The main difference between literature descriptions of the two species is the pronounced valve face undulation observed in *S. minutulus*, compared to *S. parvus* which is generally supposed to be relatively flat (table). However Kobayasi *et al.*, (1985) studied material from four Japanese lakes containing cells in this group and observed a gradation of valve elevation/depression in the samples, suggesting that the two forms are conspecific. The distinction between these two entities is also debated by Håkansson & Kling (1990) who questioned whether valve undulation is a strong enough character for species differentiation. Valves in the *S. parvus/S. minutulus* group were abundant in plankton samples from Tween Pond, Clifton Pond and Groby Pool, particularly in the spring. The 'flat' valve expression tended to be dominant in these samples, although a continuum of valve undulation was observed and some strongly undulate valves were encountered in summer and autumn.

LM observations

This form is always small (typically 5-8 μm diamater), however there is considerable heterogeneity in its degree of silicification. Plates 3.4 **a,b,c,d,e** show typical valves found in the early season plankton of the three study lakes. In all three lakes, both strongly and feebly silicified valves are evident with some valves having a coarse punctate appearance, with thickened interfascicles and others having a very delicate appearance, a much higher interfascicle density and barely discernable areolae. The latter valve type is particularly abundant in the samples from Groby Pool and in some cases very closely resembles some of the larger valves of *C. tholiformis* found in Clifton Pond and some of the smaller valves of *P. fritzii* from Tween Pond. It is not possible to recognise different morphotypes with the LM because a continuum of continuous variation can be observed between the two extreme expressions described above. In nearly all the specimens from the three lakes, it is possible to discern a single off centre valve face fultportula and often an adjacent sibling cell depression.

SEM observations

The marginal fultoportulae occur at the end of every 2-5 interfascicles, directly beneath a short, strong spine (plate 3.4 **f**). Internally these are always tended by three satellite pores (plate 3.4 **g**). The single valve face fultoportula is very distinct and always has two satellite pores (plates 3.4 **g,h**). Internally the areolae are domed and are extremely similar to those found in the form A *S. hantzschii* type valves described earlier.

The major source of variability in populations from the three study lakes is in the external form of the areolae, the arrangement of the fascicles and the positioning of the rimoportula. There are basically two types of areolae structure which can be recognised. In the first type the areolae appear as irregularly shaped holes on the external valve face (plates 3.4 **i,j**). These are disorganised in the valve centre, forming biseriate fascicles 40-60% of the distance out from the centre and often become tri-quadriseriate at the margin (particularly in the Tween Pond populations). Alternatively in some valves (plates 3.4 **i,k,l**) the areolae are heavily occluded and appear as irregularly shaped fissures scattered across the valve face similar to the underdeveloped valves illustrated in Genkal & Håkansson, (1990). The occluded valve type is particularly abundant in the early season plankton samples from Groby Pool and Clifton Pond.

	Stephanodicus parvus +	*Stephanodiscus miutulus* Δ	*Stephanodiscus binatus f*
Diameter range (μm)	5-11	5-12	5-9
IF arrangement	slightly raised	slightly raised	slightly raised, occasionally branching at valve face/mantle junction
Fascicles	uniseriate to biseriate and occasionally triseriate at the margin	uniseriate to biseriate and occasionally triseriate at the margin	uniseriate to multiseriate at the margin (often >3 rows of areolae)
Occurrence of MF	every 3-6 spines, 3 satellite pores internally	every 2-5 spines, 3 satellite pores internally †	every 4-5 spines, 2 satellite pores internally
Valve topography	flat- quite undulate	undulate	undulate
RP morphology	single tubule occurring at the end of an interfascicle	single tubule in a marginal position	single conspicuous external tubule emerging very close to a spine giving impression of a 'paired process'
VFP	1 with 2 satellite pores	1 with 2 satellite pores*	1 with 2 satellite pores

Table 3.3. Relationships between the three small *Stephanodiscus* species *S. parvus*, *S. minutulus* and *S. binatus*. IF=Interfascicle, MF=Marginal fultoportulae; RP=Rimoportula; VFP=Valve face fultoportula. += as described by Stoermer & Håkansson (1984) and Yang & Duthrie (1993). Δ= as described by Round (1981) and Håkansson (1986). *f*= as described by Håkansson & Kling (1990). †= Håkansson & Kling (1990) suggest that *S. minutulus* has three satellite pores surrounding the internal openings of the marginal fultoportulae, however both Round (1981) and Håkansson (1986) have not commented on this. *= as suggested by Håkansson & Kling (1990) for a form they call *S.* cf. *minutulus*.

In the Tween Pond samples many of the valves appeared to be very similar to *Stephanodiscus binatus* as recently described by Håkansson & Kling (1990) (e.g. plate 3.4 **j**). The morphology of this form is described in table (3.3) which compares the characteristics of *S. binatus* with *S. parvus* and *S. minutulus*. The features which delineate *S. binatus* from the latter two species are; (i) the broad distance between the interfascicles (i.e. there is always room for over two rows of areolae); (ii) a conspicuous rimoportula which emerges next to a spine giving the impression of a 'paired process'; and (iii) the three satellite pores surrounding the internal projections of the marginal fultoportulae (Håkansson & Kling, 1990). In Tween Pond a high proportion of valves have broadly spaced interfascicles and a rimoportula which appears as a conspicuous tubule, emerging very close to a spine (plates 3.4 **j,m**) in contrast to a short tubule in place of a spine as characteristic of the more typical *S. parvus*/*S. minutulus* type valves. However unlike *S. binatus* (as already stated) there are always two satellite pores around the marginal fultoportulae. Thus although many of the valves in Tween Pond very closely resemble *S. binatus* it is not possible to confidently associate them with this species. Moreover it is also extremely difficult to separate the *S. binatus* type valves from the other *S. parvus*/*S. minutulus* type valves with the LM. Thus no attempt is made to recognise *S. binatus* as a separate ecological entity. Also because there is a clear gradation between the flat and undulate types it is assumed that the valves encountered in this study are more likely to belong to *S. parvus*, as opposed to *S. minutulus*. Thus all the forms described above are included under the *S. parvus* epithet in this study.

Pelagodictyon fritzii

Valves extremely similar to *P. fritzii* as described by Clarke (1994), were important in the plankton of Tween Pond, particularly during the spring. This form was also present in lesser abundance in plankton samples collected from Clifton Pond and Groby Pool.

LM observations

With the LM this form can be relatively easily distinguished from the other cyclostephanoid forms (plate 3.5 **a,b,c,d**). It is extremely finely silicified with between 15-20 interfascicles/10 μm and like the similarly delicate *C. tholiformis* it is very difficult to discern the areolae with the LM and the interfascicles appear as very fine ribs which are slightly raised near the mantle. These often become sinuous as they approach the valve centre and a large proportion of the valves have a central annulus. However unlike *C. tholiformis* this form is always flat and generally larger, occurring in the 8-11 μm diameter range. A slightly off centre valve face fultoportula is usually apparent and it is also often possible to see the marginal fultoportulae which occur beneath every 4-7 spines.

SEM observations

The critical taxonomic features which define this species can only be seen with the SEM (plates 3.5 **e,f,g**). The areolae are arranged in uniseriate fascicles in the valve centre, becoming biseriate between 60-75% of the distance to the mantle and as in *P. tenue* the areolae appear as irregularly shaped depressions surrounded by a network of frets. These 'zig-zag' within the fascicles, creating a 'fish net' like pattern. This arrangement is apparent in both internal and external views. The interfascicles appear as thin ridges which become slightly raised towards the mantle where they end in a short, blunt spine (3.5 **h**). The marginal fultoportulae occur as short, wide tubules directly beneath a spine. These are tended internally by two satellite pores (plate 3.5 **g**). The valve face fultoportula forms a conspicuous hole externally and internally it appears as a short tubule which is also surrounded by two satellite pores (plate 3.5 g).

The species encountered in this study agrees very closely with *P. fritzii* in all the respects described above, but there are differences concerning the external position of the rimoportula. In *P. fritzii* Clarke (1994) suggests that the rimoportula appears as a truncated spine in place of a spine, (although there are no SEM illustrations of the rimoportula). However in the form discussed here the rimoportula invariably takes the form of a small pore beneath a spine at the base of a thickened interfascicle (plates 3.5 **i,j**). Internally it is represented by a compact, sessile labium as in *P. fritzii* (plates 3.5 g). It seems likely that Clarke (1994) may have misjudged the positioning of the rimoportula in his descriptions of *P. fritzii* as the form examined in this study (particularly in Tween Pond) appears to be exactly the same as this species (Clarke pers. comm.).

The remaining source of confusion concerning the identity of this form is its relationship with the extremely similar species *Cyclostephanos invisitatus* as described by Theriot *et al.,* (1987). The major difference between *P. fritzii* and *C. invisitatus* as suggested by Clarke (1994), is the nature of the areolae. In *C. invivisitatus* the areolae are represented by small, rounded holes externally and internally by domed cribra in the valve centre, which become flattened in the biseriate region of the fascicles and on the mantle. However in *P. fritzii* as already mentioned the areolae appear as depressed polygons surrounded by short frets. The external expression of the rimoportula in *C. invisitatus* is exactly the same as that found in the *P. fritzii* type form in this study and according to both Kobayasi & Inoue, (1985) and Theriot *et al.,* (1987). It is represented by a small, dome shaped opening on the mantle beneath a spine. Thus it seems likely that the only difference between *P. fritzii* and *C. invisitatus* is the 'net like' arrangment of the areolae in *P. fritzii* and the more delicate silicification of this species compared to *C. invisitatus.*

The morphological variability of *P. fritzii* was assessed by LM and SEM investigation of populations from Girton Pool, Letheringsett 'Small' Pond and Grafham Water reservoir. In Girton Pool valves of *P. fritzii* are much larger than those found in all the other populations with a diameter range of 10-15 µm and a higher interfascicle density

(>22 interfascicles in 10 µm). The structure of the valves are extremely similar to those found in Tween Pond however (plate 3.5 **k,i**). In Letheringsett 'Small' Pond and Grafham Water reservoir valves with *P. fritzii* type areolae are dominant, however in each population valves are found which very closely resemble *C. invisitatus*, with the areolae appearing as small, circular punctures externally (plates 3.5 **l,m,n**). The occurrence of these valves suggests that *P. fritzii* is very closely related to *C. invisitatus* and that these forms may represent different life cycle phases or ecophenotypic responses within the same genetic entity. However further work is required to clarify the relationship between these species and in the light of this confusion the forms encountered in this study are all referred to as *P. fritzii*.

Cyclostephanos dubius

This species was an important component of spring and autumn plankton assemblages in Clifton Pond and was found as a rare species in Tween Pond and Groby Pool. The two life cycle morphotypes (I and II) described by Hickel & Håkansson (1987) were encountered.

In samples from Clifton Pond *C. dubius* has a size range of between 5-22 µm. With the LM the morphotype I valves of *C. dubius* appear strongly undulate and coarsely silicified (plates 3.6 **a**) with distinct, radiating interfascicles separating the fascicles of areolae in the outer part of the valve. These are usually tended by a short spine which is often difficult to see using the LM. The areolae are boldly formed and irregularly arranged in the valve centre giving the valves a highly punctate appearance. However in the fasciculate area of the valve the areolae are usually very difficult to discern. The morphotype II valves (plates 3.6 **b,c**) are weakly silicified and have a much higher interfascicle density than those of morphotype I. The areolae are much smaller, more organised and frequently form relatively distinct rows, often radiating out from a central annulus. In these valves it is sometimes possible to see the valve face fultoportulae (often several) which are arranged in a ring around the central area. These are invariably impossible to discern with the LM. The marginal fultoportulae in *C. dubius* are usually only visible with the SEM (plate 3.6 **d**).

With the LM, *C. dubius* is not easily confused with any of the other cyclostephanoid forms. The smaller, finer valves of *C. dubius* may sometimes resemble some of the larger more undulate valves of *C. tholiformis*. However the distinct, single valve face fultoportula, the clearly evident marginal fultoportulae and the much more delicate overall structure of *C. tholiformis* usually make it easy to separate from *C. dubius* in mixed populations.

Cyclotella atomus

This species was a common component of the summer plankton in Tween Pond, but was very rare in Clifton Pond and Groby Pool. The taxonomy of this species has recently been studied by Sabater & Klee (1990), Genkal & Kiss (1993) and Håkansson & Clarke (1996).

It is easily recognised with the LM and impossible to confuse with the other centric forms (plate 3.7 **a**). The valves are small (4.5-7 µm), slightly transversely undulate and always possess a single eccentrically positioned valve face fultoportula which is clearly evident in the unstructured, hyaline central area. The marginal alveolar chambers are defined by short costae, every 3rd to 5th of which appears markedly thicker than the others. These represent the internal positions of the marginal fultoportulae which can only be easily observed with the SEM.

In samples from Tween Pond where *C. atomus* is abundant a similar, but less common form is always found. This form has an overlapping size range and is similarly transversely undulate and also has a prominent valve face fultoportula which is clearly evident with the LM (plate 3.7 **b**). However the alveolar chambers are more clearly defined at the margin and the costae appear shorter. This gives the impression of a much clearer separation between the marginal and central parts of the valve. In samples from the Eastern European rivers systems Genkal & Kiss (1993) found two different expressions of *C. atomus* and have described *Cyclotella atomus* var. *gracilis* as a new variety. Although no LM illustrations have been provided of *C. atomus* var. *gracilis* it seems likely that it is the same as the form described here. Thus both *C. atomus* and *C. atomus* var. *gracilis* are recognised in this study.

Cyclotella sp. 1

This unidentified form was found as a rare component of the plankton in Tween and Clifton Ponds and Groby Pool.

With the LM it is very similar in appearance to *C. atomus* var. *gracilis* and has a large eccentrically located valve face fultoportula and a very definite narrow marginal ring of alveolae defined by short costae (plates 3.8 **a**). However this form was generally larger (7-9 μm) than typical valves of *C. atomus* var. *gracilis* and appears to have a higher costae density. Unfortunately insufficient time has been available to undertake an SEM investigation of this form, however an isolated valve found in Groby Pool is shown in plate 3.8 **b**.

Cyclotella pseudostelligera

Valves corresponding to *C. pseudostelligera* were found in moderate abundance in Tween Pond during the spring and very occasionally in Clifton Pond and Groby Pool.

Under the LM there were two distinct morphotypes of this species are apparent. These are given in plates 3.9 **a,b**. Morphotype I includes the more 'typical' *C. pseudosteliigera* valves found in Clifton Pond and Groby Pool. These are usually 6-9 μm in diameter and have a well defined central area containing the typical 'flower' like patterning. The central region is surrounded by costae and a ring of widely spaced marginal fultoportulae (6-10 per valve) are clearly evident. Morphoytpe II is found exclusively in Tween Pond and appears to be similar to large specimens of *Thalassiosira pseudonana*. Belcher & Swale (1977) describe a similar morphotype of *C. pseudostelligera* as collected from the River Wye and also indicate the similarity of this form to *T. pseudonana*. However in this study these two forms do not co-occur so this did not create a problem. Morphotype II is smaller (3-6 μm diameter), and in contrast to morphotype I there is no clear delineation of the central and marginal parts of the valve. The central area appears to be relatively featureless, but in many specimens it is possible to see sinuous valve markings. The marginal fultoportulae are clearly evident as in morphotype I and with the SEM these appear to have lateral protrusions (plate 3.9 **c**). In this study morphotype II was separated from morphotype I with the LM and is referred to here as *C. pseudostelligera* type 2.

Cyclotella meneghiniana

This species was abundant with *C. atomus* in summer plankton samples from Tween Pond, but was also occasionally encountered in Clifton Pond and Groby Pool.

In Tween Pond *C. meneghiniana* exhibits some considerable morphological plasticity. However it is not possible to separate different morphotypes due to the occurrence of a range of intermediate forms and what is obviously a continuum of subtle variation between extreme expressions of this species. Plates 3.10 **a,b,c** show the three major forms of *C. meneghiniana* as found in Tween Pond (i.e. types A, B and C). Valves with a type A morphology are small (5-10 µm diamater), appear relatively flat to slightly transversely undulate and have a conspicuous, off centre valve face fultoportula. There are similarities between form A and *C. atomus*, particularly in the lack of a clear separation between the marginal alveoli and the central part of the valve and the irregular distribution and length of the costae. However in contrast to *C. atomus*, the costae in this form taper inwards to a relatively sharp point and often reach further into the valve centre (plate 3.10 **a**). This form appears to be exactly the same as *Cyclotella cryptica* as recognised in the culture experiments of Reimann *et al.*, (1963). However the designation of *C. cryptica* as a distinct species has been questioned recently (Kling & Håkansson, 1988). The observations made here agree with those of Kling & Håkansson (1988) and suggest that *C. cryptica* is probably a morphotype of *C. meneghiniana*. In culture Reimann *et al.*, (1963) found that immediate post-auxospore cells in the *C. cryptica* isolate, very closely resembled *C. meneghiniana* thus it seems likely that *C. cryptica* type cells are formed as part of the life cycle of *C. meneghiniana*.

The form B valves tend to be larger (7-20 µm diameter) than those of form A and have a much higher costae density. There is a much clearer separation between the alveolar chambers on the margin and valve centre and there are often sinuous, 'wavy' valve markings which start at the bases of the alveoli and wind inwards. This form is very similar to a centric formerly known as *Cyclotella kuetzingiana* which has recently been found to be conspecific with C. meneghiniana. It also has a diameter range of 7-15 µm and also have well developed alveoli. However the costae density tends to be lower than in typical form B valves and the alveoli reach much further into the valve centre than in form B. Both forms B and C have between 1-3 valve face fultoportulae. As forms A, B and C are all believed to belong to the same genetic entity they are included under *C. meneghiniana* in this study, however the form A (*C. cryptica*) valves have been separated from the other types with the LM to improve the accuracy of cell volume estimates (chapter four).

Skeletonema potamos

This tiny, fragile diatom was an important component of the plankton of Tween Pond, particularly in the autumn, early winter period but was not encountered in either Clifton Pond or Groby Pool.

In both plankton and sediment samples cells of *S. potamos* are extremely finely silicified and are frequently collapsed on LM slides (plate 3.11 **a**). This species usually forms short chains, each containing 2-4 elongate cells, typically 6-12 µm in length and 2.5-4.5 µm in diameter. Each valve has 4-7 long 'tubes' positioned equidistant around the margin and these represent the external protrusions of the marginal fultoportulae (Belcher & Swale, 1978). With the SEM (plate 3.11 **b**) the marginal fultoportulae are clearly evident.

Thalassiosira guillardii

This species was a consistent minor species in the plankton of Tween Pond and was initially mistaken for relatively unstructured valves of *S. parvus*. The morphology of this species has been described in detail by Hasle (1978).

Under the LM the valves are small (5-12 µm diameter), flat and appear to be finely silicified with an unstructured central region and a ring of closely spaced tubules around the margin which represent the external openings of the marginal fultoportulae (plates 3.12 **a,b**). The number of marginal fultoportulae on each valve is highly variable (usually >10 but <30) and seems to be closely related to diameter, with larger cells having more marginal fultoportulae which are often much more tightly spaced.

With the SEM it is possible to see the detail of the external valve face which is either covered with irregularly spaced silica nodules in the heavily silicified specimens or pitted with tiny, closely spaced punctures in the more delicately silicied forms (plates 3.12 **c,d,e**). Externally the rimoportula is evident as a slightly elongated tubule in place of a marginal fultoportula. Internally the marginal fultoportulae occur as short tubular openings tended by four curved satellite pores and the rimoportula is represented by a compact labiate process (plate 3.12 **f**). In the descriptions of *T. guillardii* by Hasle (1978) this species is attributed with one valve face fultoportula, however in the specimens encountered from Tween Pond a valve face fultoportula is not always present.

Thalassiosira pseudonana

This tiny centric diatom was a dominant component of the Clifton Pond plankton in the spring. The important features of this species are again discussed by Hasle (1978).

This tiny species forms drum shaped cells, typically 4-5 µm in length and 2.5-4 µm in diameter. Under the LM it is usually found in girdle view and appears as a simple cylinder with short tubules which represent the marginal fultoportulae occasionally visible at the margin (plate 3.13 **a**). In valve view the central area is featureless and it is possible to see the marginal fultoportulae much more clearly. In contrast to *T. guillardii* these are more widely spaced and there are between 7-12 per valve. Even though *T. pseudonana* was extremely abundant in the spring plankton samples it was difficult to find this species with the SEM and it seems likely that it may have decomposed in storage or may have suffered during the air drying process. However it has been possible to take some SEM photographs of this species (plates 3.13 **b,c**). These reveal the external valve surface to be pitted with tiny holes as was apparent in *T. guillardii*. The rimoportula is also evident and occurs as a short, labiate protuberance mid-way between two marginal fultoportulae. This contrasts to the position of the rimoportula in *T. guillardii*.

Conclusions

The confident and reliable identification of the tiny centric diatoms which proliferate in eutrophic-hypertrophic lakes poses a difficult task. This is due to the combined effects of life cycle and ecophenotypic morphological plasticity which makes many species appear remarkably similar in their extreme form. Initially considerable difficulties were encountered in the present study and in the light of the SEM investigations many samples had to be re-assessed with the LM. However in the light of the SEM investigations it has been possible to make confident identifications with the LM. The validity of some of the species names which are adopted in this study are open to question. In particular, confusion surrounds the status of the two *Pelagodictyon* species *P. tenue* and *P. fritzii* and their relationships with the similar forms *S. hantzschii* and *C. invisitatus*. These problems need to be addressed in the near future and taxonomists need to work closely with ecologists and palaeoecologists so that taxonomic practices are standardised. It is undoubtedly the case that inaccurate identifications make much of the ecological data available for different species invalid and it is highly desirable that ecologists make greater efforts to include the most 'up to date' taxonomy in their studies.

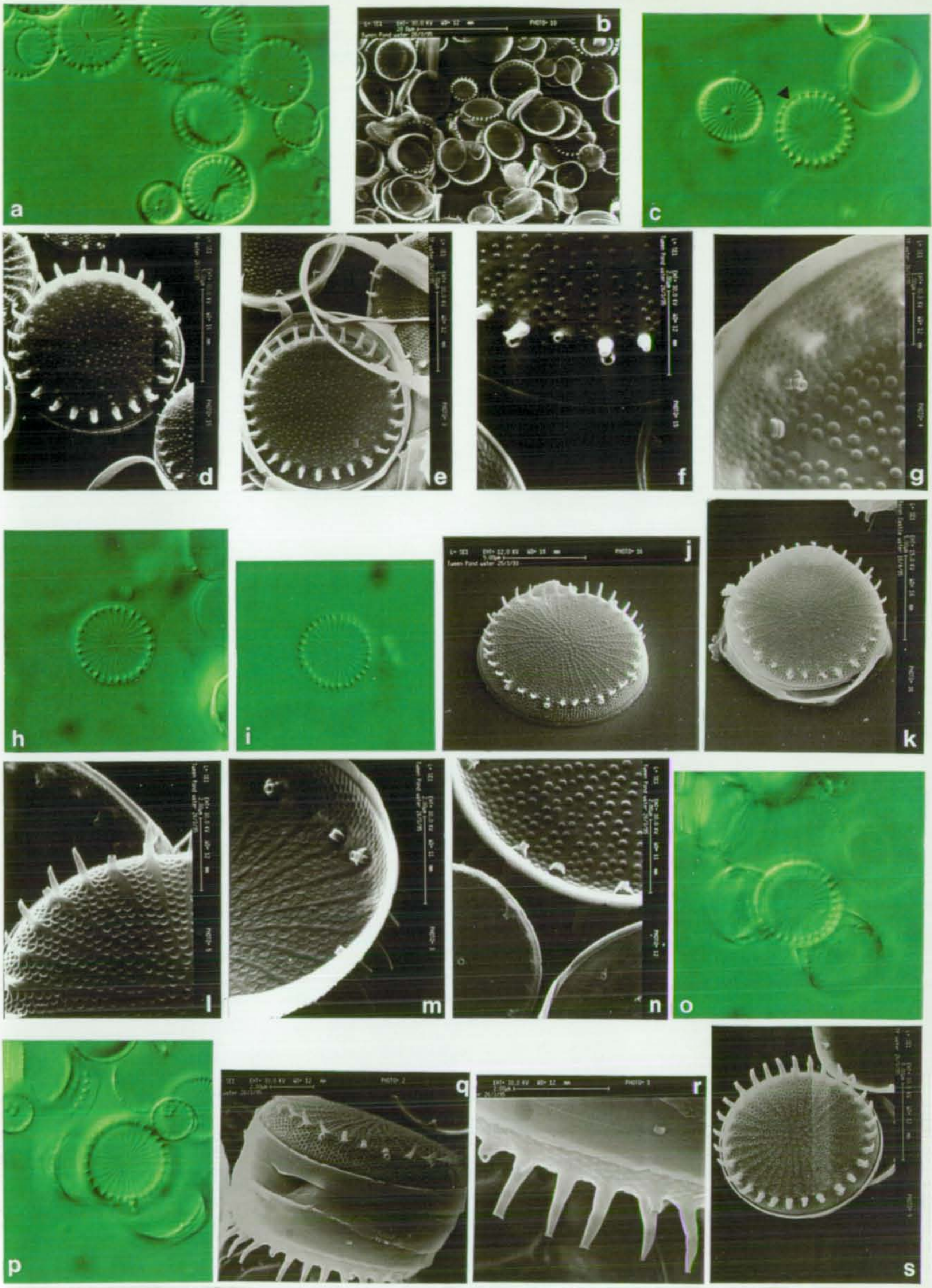


Plate 3.1. *Pelagodictyon tenue / Stephanodiscus hantzschii*. LM scale 1 mm = 0.85 µm, SEM scale bars given: **a**, **b** centrics in the spring bloom from Tween Pond; **c** form 'A' valve (rimoportula arrowed); **d,e** form A valves with occluded areolae; **f** form A valve showing marginal fultoportulae and rimoportula (arrowed); **g** internal view of form 'A' valve showing marginal fultoportulae with 3 satellite pores and internal opening of the rimoportula; **h,i** typical form 'B' valves; **j,k** form B valves showing 'fish net' arrangement of the areolae; **l** external view of form B valve showing detail of the areolae and the external opening of the rimoportula; **m** internal view of form B valve showing areolae as polygons depressed into the basal siliceous layer, surrounded by short frets; **n** internal view of from A valve, note thickness of the basal siliceous layer; **o,p** different focus on same specimen (**o**= form A, **p** = form B valve); **q** heterovalvate cell with the form B expression on top and form A expression underneath; **r** close up of form A valve in **q**; **s** external view of valve intermediate between forms A and B.

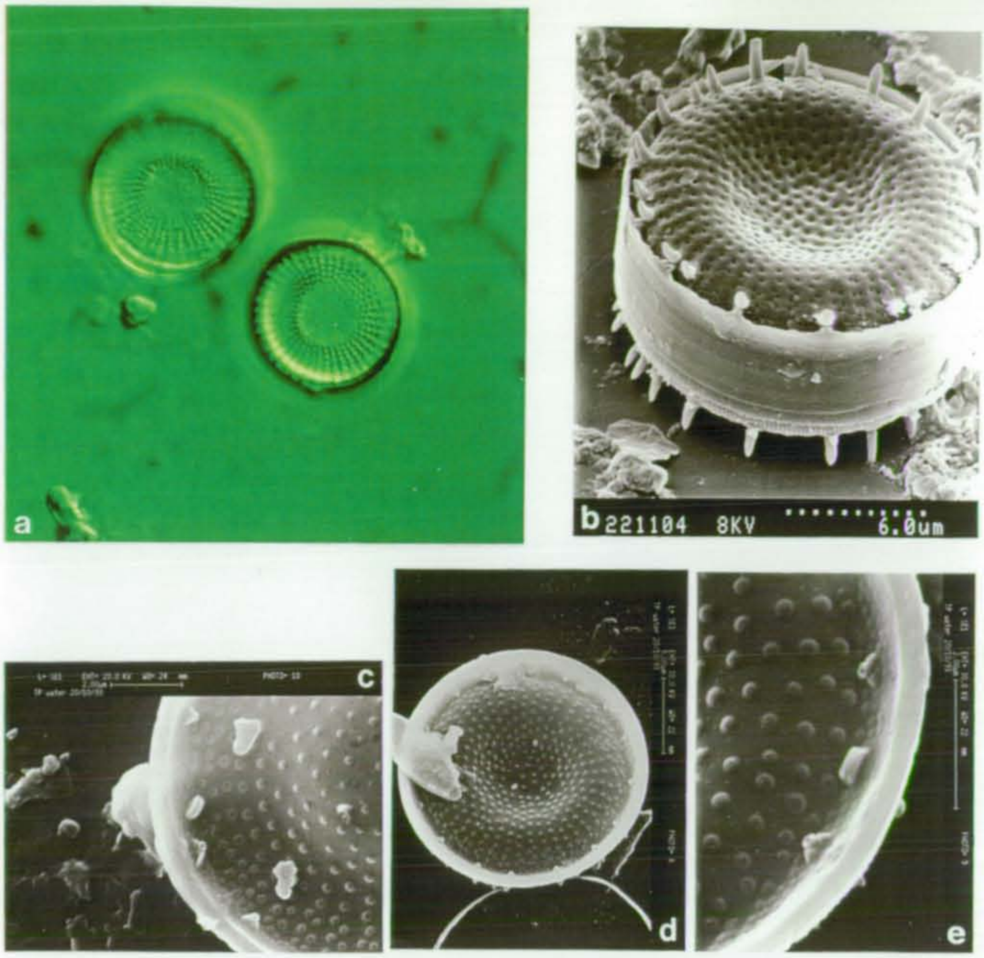


Plate 3.2. *Stephanodiscus* cf. *medius.* LM scale 1 mm = 0.85 µm, SEM scale bars given **a** two typical convex valves from Tween Pond; **b** external view showing irregular spination and the rimoportula (arrowed), **c** internal openings of the marginal fultoportulae with 3 satellite pores; **d** internal view of the valve face fultoportulae guarded by 2 satellite pores; **e** internal view showing internal opening of the rimoportula.

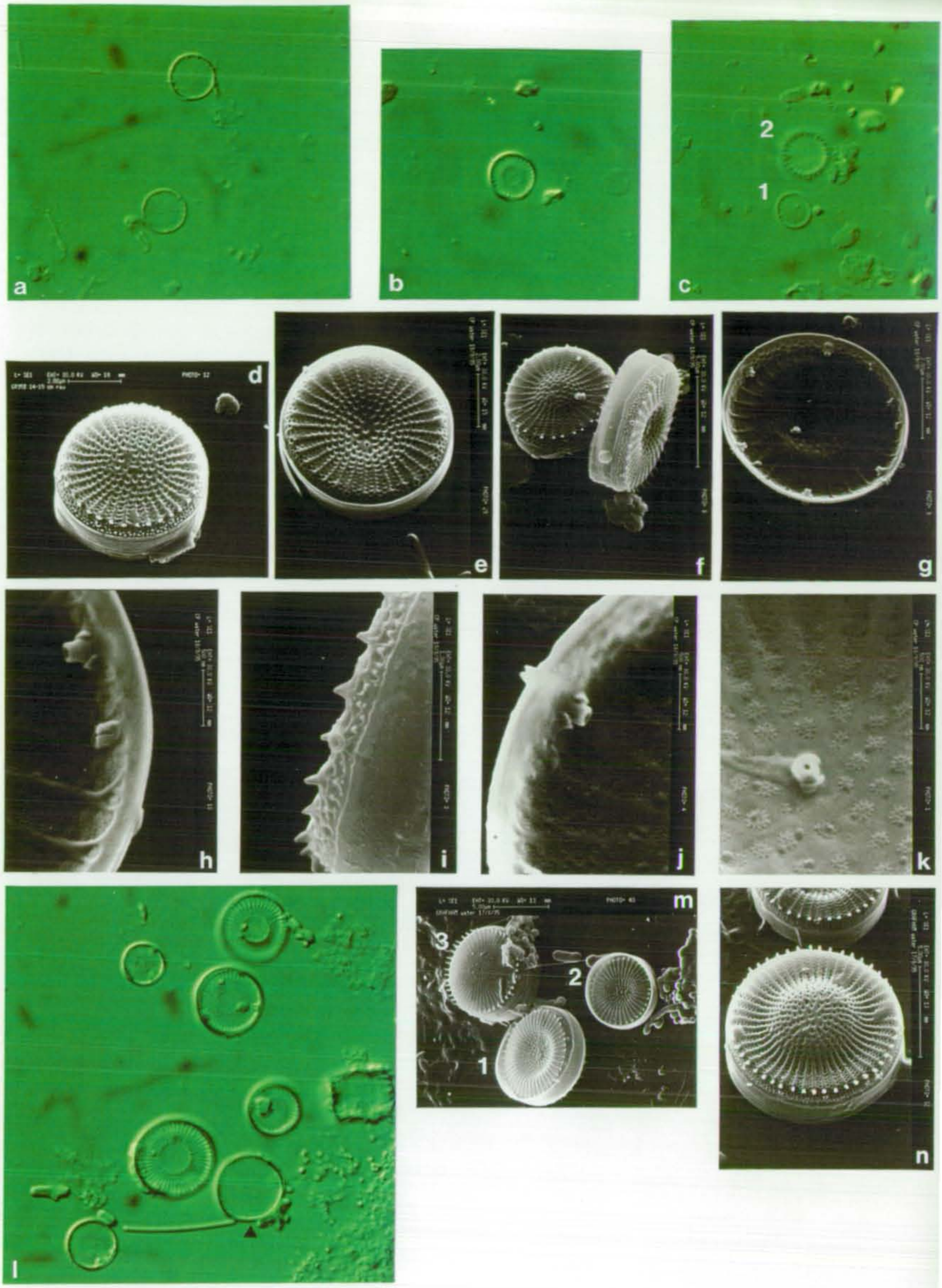


Plate 3.3. *Cyclostephanos tholiformis.* LM scale 1 mm = 0.85 µm, SEM scale bars given: **a,b** typical flat and undulate valves; **c** *C. tholiformis* (1) next to *S. parvus* (2); **d,e,f** external views showing variation in topography, the arrangement of the areolae, the marginal fultoportulae and the single valve face fultoportula; **g** internal arrangement of the areolae and the marginal fultoportulae; **h** the internal opening of the rimoportula and the branching of the interfascicles on the mantle; **i** close up of the external opening of the marginal fultoportulae and the marginal spines; **j** the internal openings of the marginal fultoportulae surrounded by 2 satellite pores; **k** internal opening of the valve face fultoportula with 2 satellite pores, note the tiny pores pitted into the flattened areolae; **l** large, undulate valves from Grafham Water reservoir next to a valve of *P. fritzii* (arrowed); **m** cells of *C. tholiformis* (1, 2) next to a cell of *P. fritzii* (3) from Grafham Water reservoir; **n** close up of an undulate valve from Grafham Water reservoir.

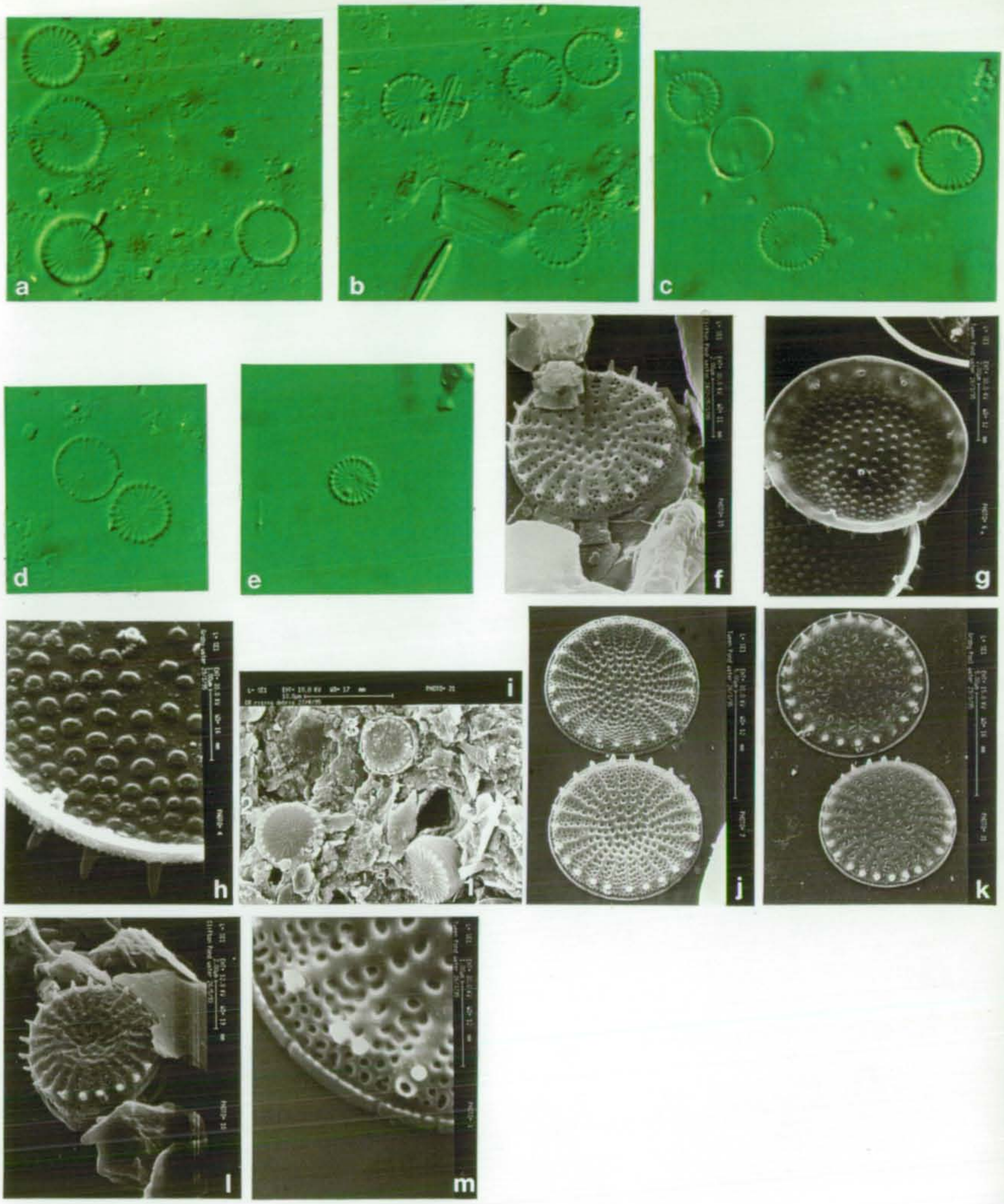


Plate 3.4. *Stephanodiscus parvus.* LM scale 1 mm = 0.85 µm, SEM scale bars given: **a,b,c,d,e** typical valves from Clifton Pond (**a,e**) and Groby Pool (**b,c,d**) showing variable levels of silicification; **f** external view giving detail of the areolae, the single valve face fultoportula and the marginal fultoportulae which occur beneath every 2-5 spines; **g,h** internal views showing the domed areolae, marginal fultoportulae with 3 satellite pores and the valve face fultoportula with 2 satellite pores; **i** valves in a 'FLAB' detachment from Groby Pool, valve 1 has open areolae and valves 2 and 3 have occluded areolae; **j** two valves with open areolae; **k** valves with occluded areolae; **l** occluded undulate valve; **m** external view of *Stephanodiscus binatus* type valve from Tween Pond showing rimoportula which emerges close to a spine.

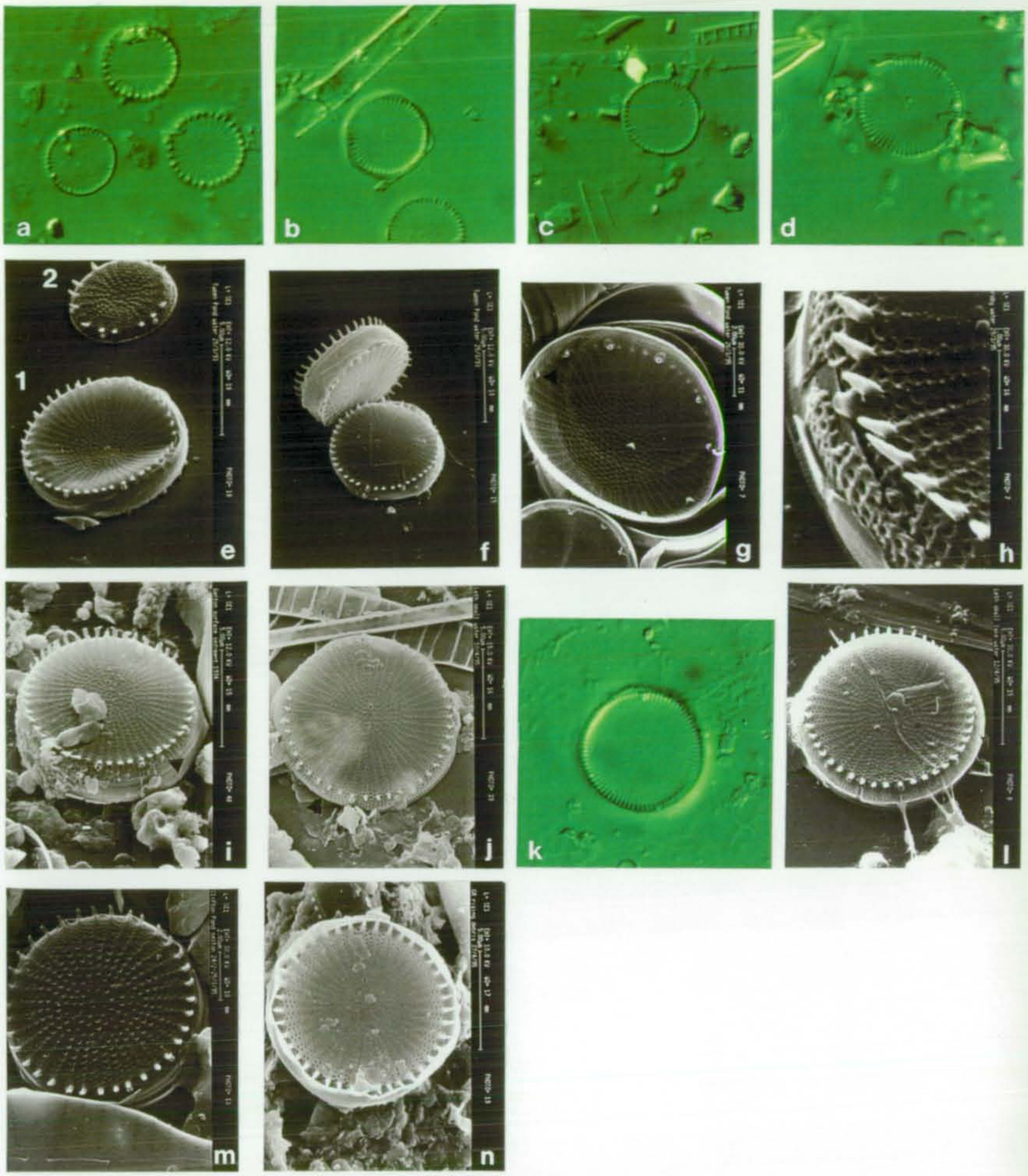


Plate 3.5. *Pelagodictyon fritzii* / *Cyclostephanos invisitatus*. LM scale 1 mm = 0.85 μm, SEM scale bars given: **a,b,c,d** valves from Tween Pond (**a**); Letheringsett 'Small' Pond (**b**); Groby Pool (**c**) and Girton Pool (**d**) showing variable size and silicification; **e** *P. fritzii* (1) next to a valve of *S. parvus* (2); **f** external and girdle views showing areolae, the thin interfascicles, the single off-centre valve face fultoportula and the marginal fultoportulae which occur beneath every 4-7 spines; **g** internal view showing the 'fish net' pattern created by the areolae, the marginal fultoportulae tended by two satellite pores, the valve face fultoportula with two satellite pores and the rimoportula (arrowed); **h** external opening of a marginal fultoportula beneath a short, blunt spine; **i,j** external opening of the rimoportula (arrowed); **k** large *P. fritzii* type valve from Girton Pool; **l,m,n** *Cyclostephanos invisitatus* type valves from Letheringsett 'Small' Pond (**l**), Clifton Pond (**m**) and Groby Pool (**n**) with areolae appearing as small, circular holes.

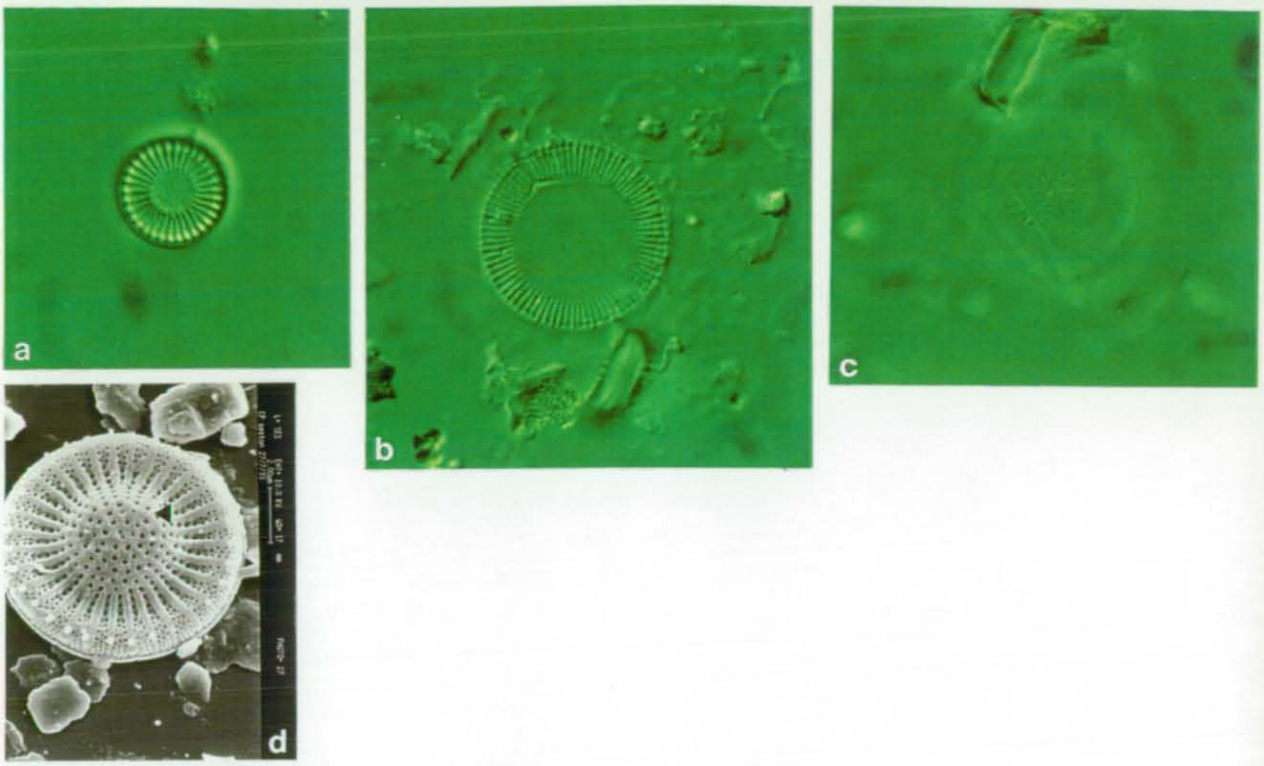


Plate 3.6. *Cyclostephanos dubius*. LM scale 1 mm = 0.85 µm, SEM scale bar given: **a** morphotype I valve; **b,c** different focus on morphotype II valve; **d** external view showing the distinct radiating interfascicles, the marginal fultoportulae and a valve face fultoportula (arrowed).

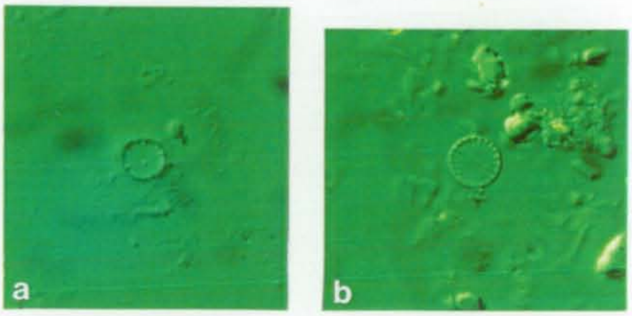


Plate 3.7. *Cyclotella atomus*. LM scale 1 mm = 0.85 µm: **a** typical valve of *C. atomus* from Tween Pond with single, bold valve face fultoportula and clearly defined costae; **b** valve of *C. atomus* var. *gracilis* with shorter costae and more obvious separation between the marginal and central parts of the valve.

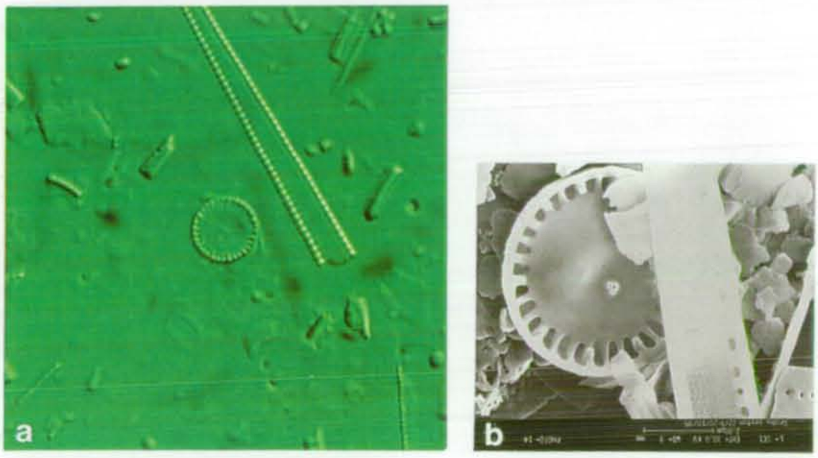


Plate 3.8. *Cyclotella* sp. 1. LM scale 1 mm = 0.85 µm, SEM scale bar given: **a** valves from Groby Pool; **b** internal view.

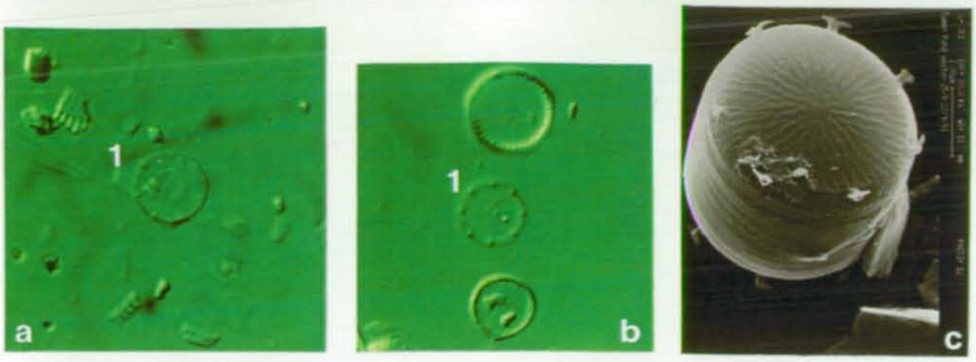


Plate 3.9. *Cyclotella pseudostelligera*. LM scale 1 mm = 0.85 μm, SEM scale bar given: **a** morphotype I valve from Groby Pool (marked 1); **b** morphotype II valve from Tween Pond (marked 1) with poorly defined central region; **c** cell of morphotype II from Tween Pond.

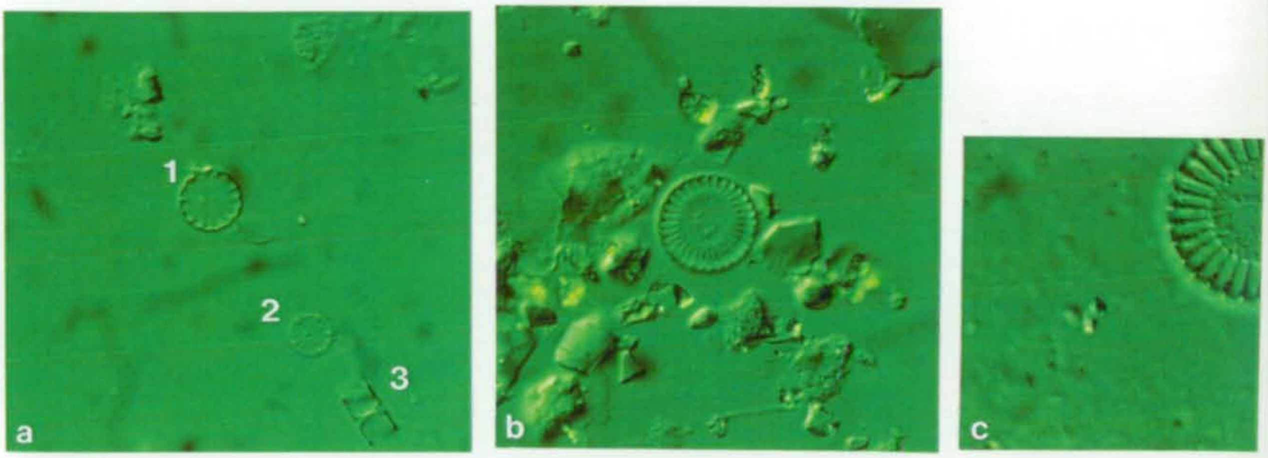


Plate 3.10. *Cyclotella meneghiniana*. LM scale 1 mm = 0.85 μm: **a** morphotype A valve (1) next to a valve of *C. atomus* (2) and two valves of *S. potamos* (3); **b** morphotype B valve showing the clear separation between the central and marginal regions; **c** morphotype C valve unfortunately cut in half!

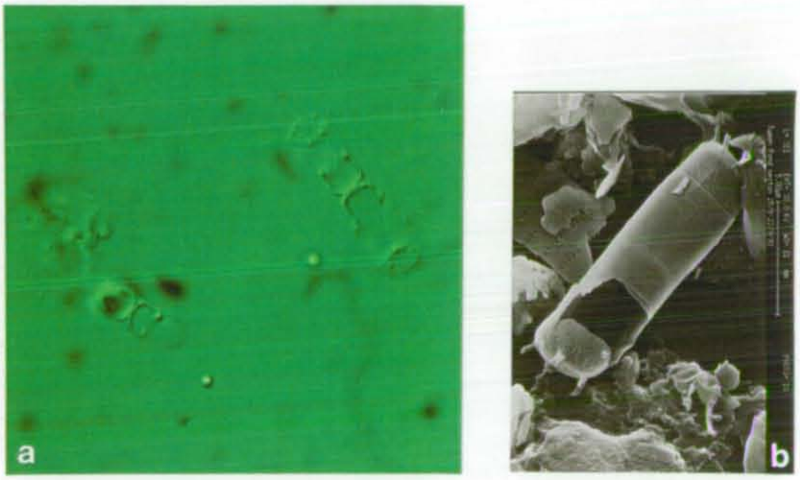


Plate 3.11. *Skeletonema potamos*. LM scale 1 mm = 0.85 μm, SEM scale bar given: **a** short, squashed chains from Tween Pond; **b** cell with external protrusions of the marginal fultoportulae clearly evident.

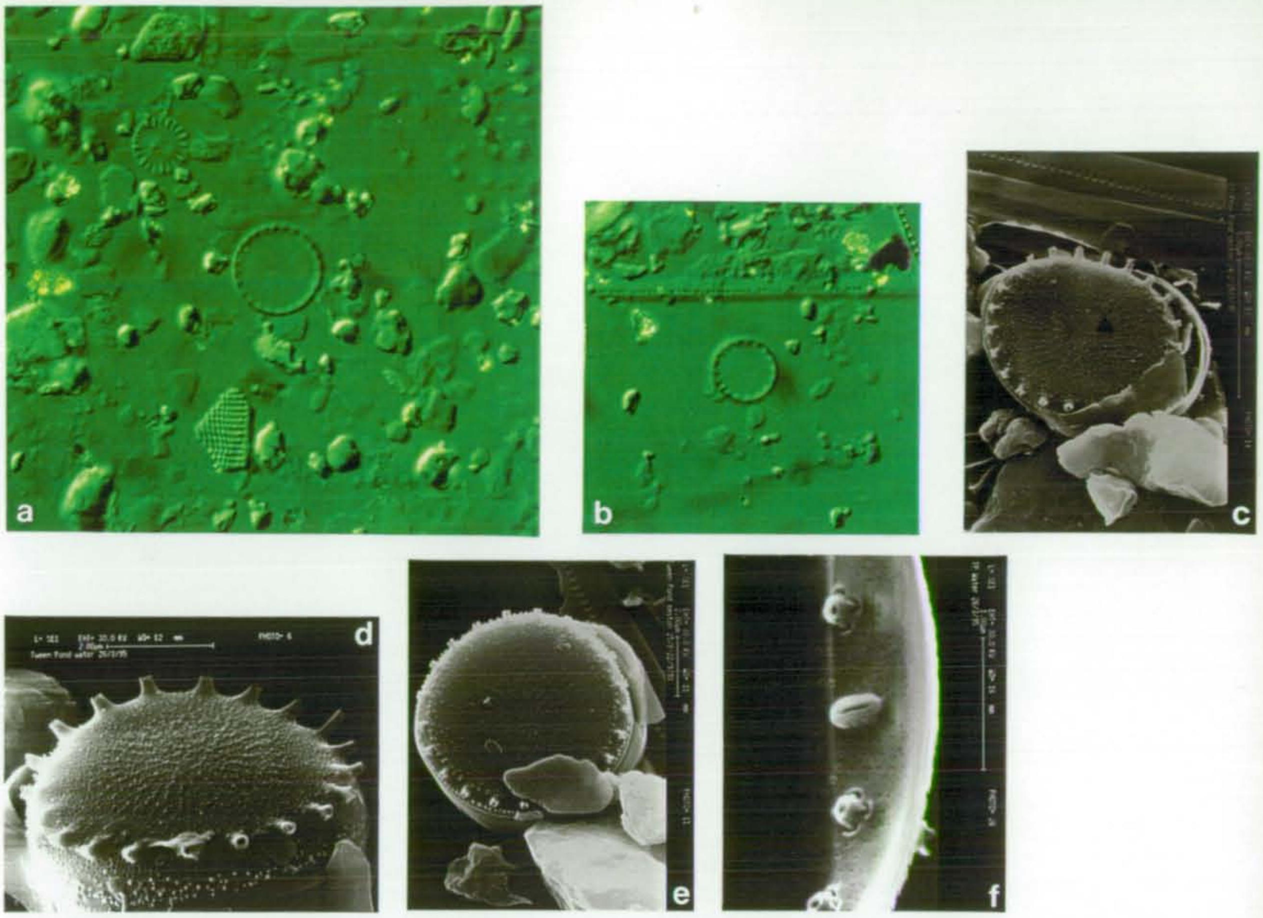


Plate 3.12. *Thalassiosira guillardii*. LM scale 1 mm = 0.85 µm, SEM scale bars given: **a,b** typical valves from Tween Pond showing the unstructured central area and closely spaced marginal fultoportulae; **c,d,e** detail of the valve surface and the marginal fultoportulae (valve face fultoportula arrowed in **c**); **f** internal view showing the marginal fultoportulae with 4 curved satellite pores and the rimoportula.

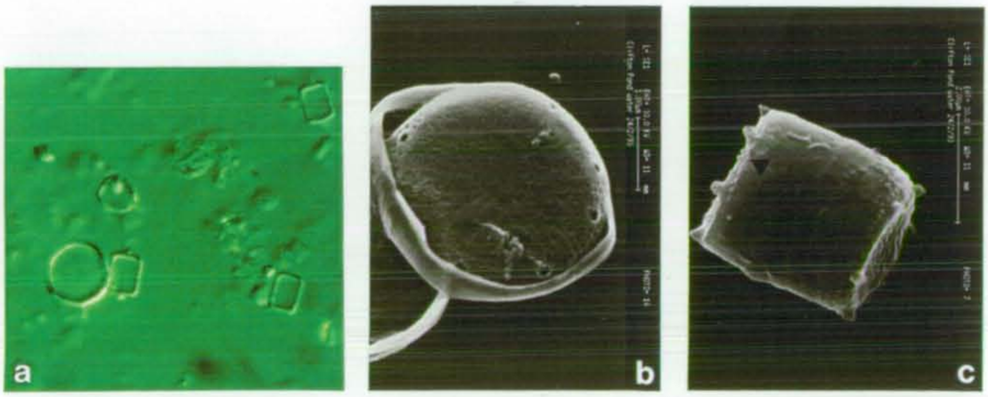


Plate 3.13. *Thalassiosira pseudonana*. LM scale 1 mm = 0.85 µm, SEM scale bars given: **a** typical, relatively featureless 'drum' shaped cells in girdle view; **b** external valve view showing the marginal fultoportulae and the valve surface pitted with tiny holes; **c** girdle view of a cell showing the external opening of the rimoportula (arrowed).

CHAPTER FOUR

Modern water chemistry, diatom ecology and diatom representation in the sediments.

Introduction

This chapter presents the results of the modern monitoring studies in the three shallow study lakes, Tween and Clifton Ponds and Groby Pool. The aim is to characterise the diatom ecology, seasonality, habitat preferences, and the representation of modern populations in the sediments of the three contrasting shallow lakes. In the first part of this chapter the major physical, chemical and biological characteristics of the three lakes are briefly summarised. Then in turn seasonal aspects of water chemistry, water clarity, phytoplankton biomass, macrophyte communities, diatom plankton and periphyton communities are described and compared. In the second part of this chapter the diatom communities collected in the modern periphyton and plankton are compared with the assemblages found in the sediment traps and in the surface sediments of the three lakes. These three sample types represent overlapping time-scales (i.e. daily, seasonal and annual) and by linking them together the degree to which modern diatom populations are represented in the sediments is considered. This process is taken a step further in Groby Pool where the representativity of a single surface sediment diatom assemblage is considered in the light of a transect of sediment samples collected from the lake. In the final part of this chapter aspects of the diatom ecology and taphonomy of the three study lakes are summarised.

The characteristics of the three shallow lakes

The morphometric, hydrological, chemical and biological attributes of the three study lakes are compared in table 4.1 and the positions of the sample sites are given in figs. 4.1 and 4.2. Morphometrically the lakes are very similar, all being small (<25 ha.), shallow (between <3 m) with gently shelving margins. However bathymetry is slightly more complex in Tween and Clifton Ponds due to the presence of gravel bars and several islands. Tween Pond and Groby Pool are both river-fed and hydraulic retention times are likely to be relatively short, perhaps in the order of a few weeks in Tween Pond and a few months in Groby Pool. However as Clifton Pond is isolated from river inputs, it probably has a much longer retention time of several months. This lake is highly stagnant in summer as groundwater levels are rapidly reduced and lake levels can drop by up to 1 m in droughted years (e.g. 1989, 1990, 1991). Alternatively in Tween Pond and Groby Pool, constant river inputs and regulated outputs (i.e. by weirs) maintain water levels within a relatively narrow range (i.e. around 40 cm).

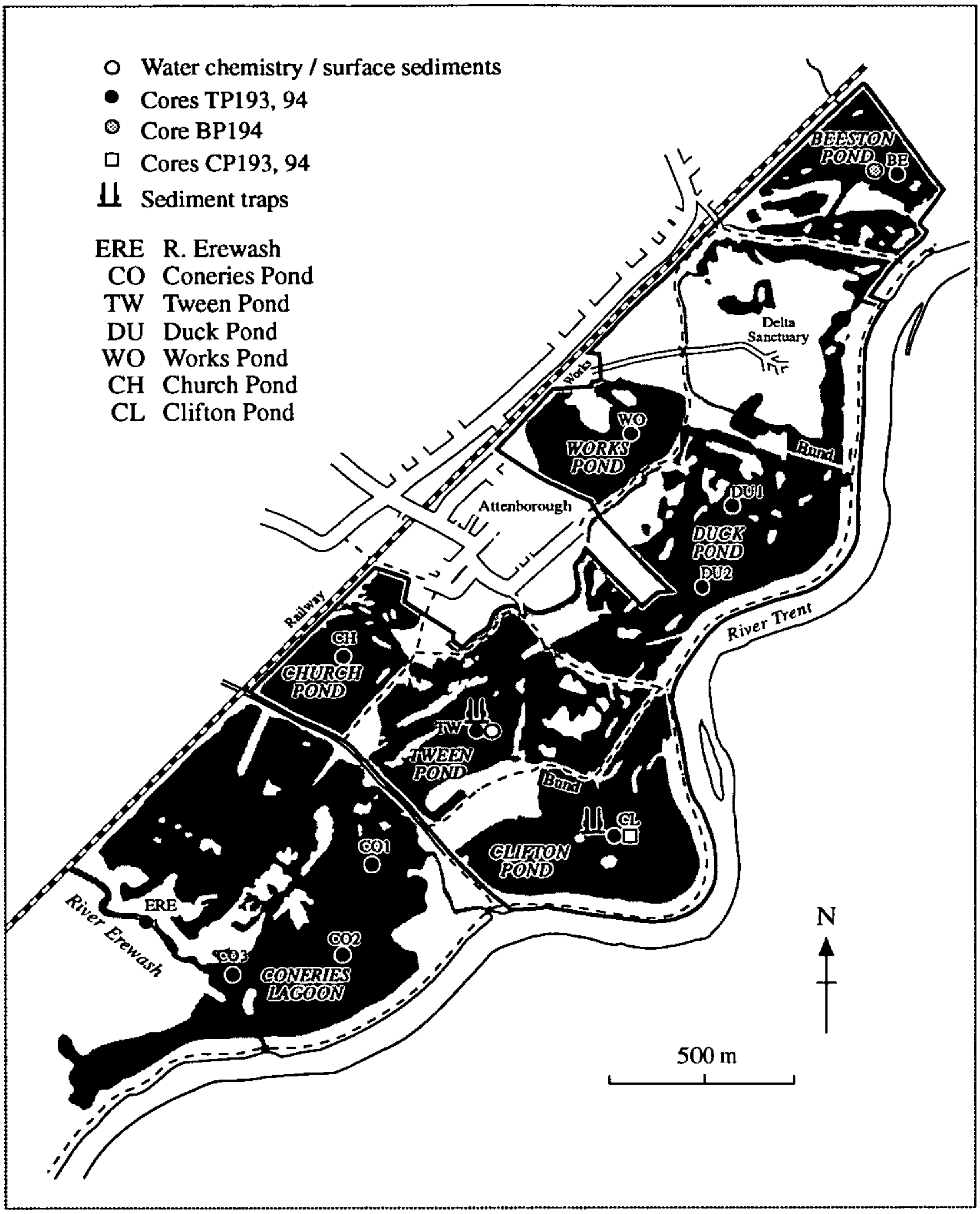


Fig. 4.1. Location of the sample sites in the Attenborough Ponds SSSI.

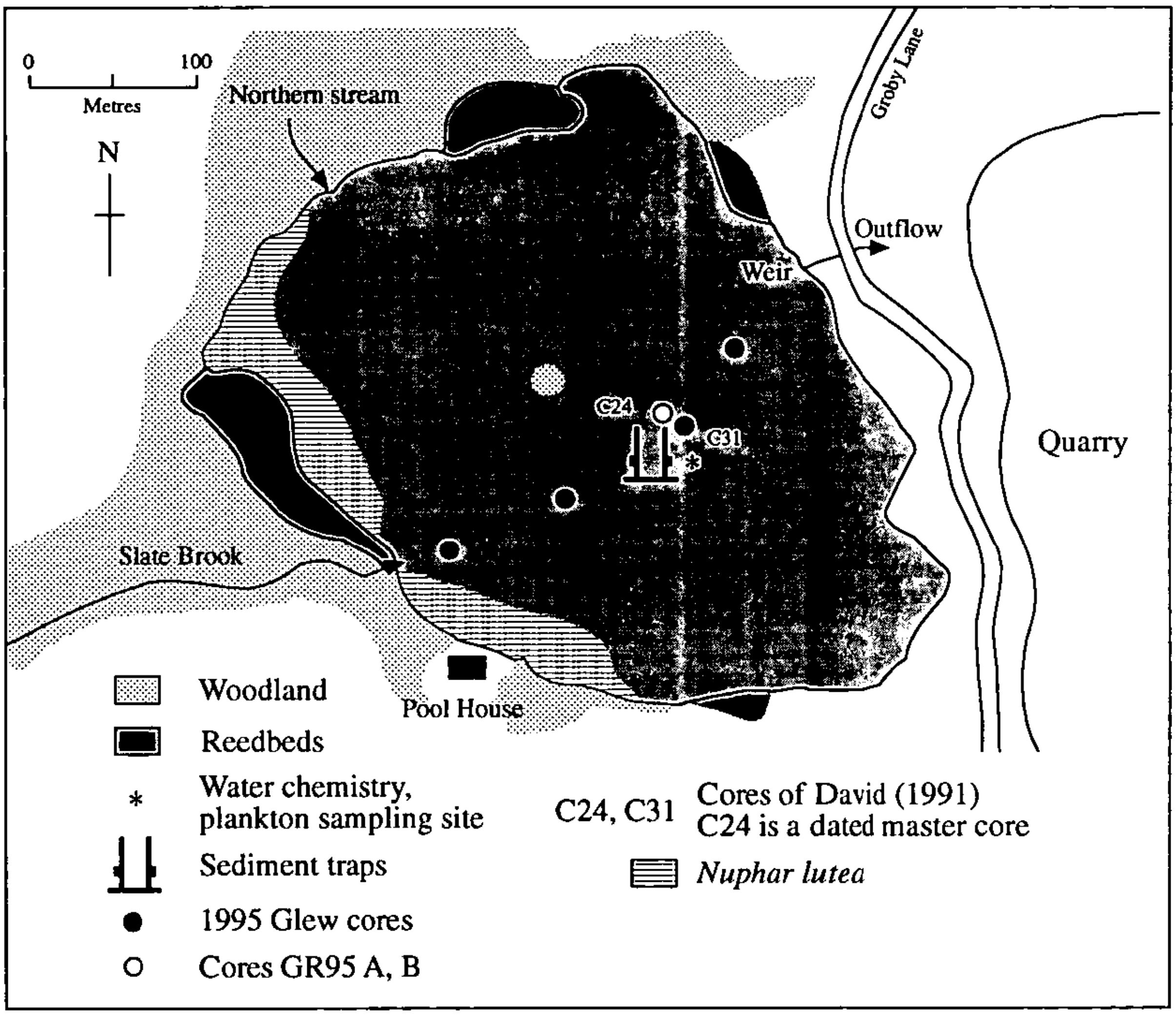


Fig. 4.2. Location of the sampling sites in Groby Pool.

The water chemistry of the three shallow lakes is markedly different. Tween Pond is the most polluted lake by far, receiving polluted inputs (sewage and industrial effluent) from the River Erewash via Coneries Pond. It is hypertrophic (OECD, 1982) and has extremely high concentrations of PO_4 and NO_3 with mean annual values of 1500 µg l^{-1} and 7.3 mg l^{-1} respectively. In contrast, isolated Clifton Pond has much reduced mean PO_4 (63 µg l^{-1}) and NO_3 (0.39 mg l^{-1}) concentrations despite a mere 5 m wide barrier between itself and Tween Pond and using OECD criteria it is classified as eutrophic. This eutrophic classification also applies to Groby Pool, which has mean TP concentrations of 240 µg l^{-1} and slightly higher NO_3 concentrations than Clifton Pond (0.5 mg l^{-1}). Mean pH is similar in Tween and Clifton Ponds at just over 8 and much lower than Groby Pool which has a very high Feb-Oct mean of 9. Electrical conductivity (EC) is extremely high in Tween Pond (1133 µS cm^{-1}) reflecting high dissolved salt (particularly chloride) inputs from industrial sources in the R. Erewash catchment. Similarly Clifton Pond also has a high mean EC (983 µS cm^{-1}), which probably results from two factors; (i) saline groundwater inputs from the R. Trent aquifer; and (ii) dry fall-out from the adjacent power station at Radcliffe-on-Soar. In Groby Pool EC is also higher than might be expected naturally (613 µS cm^{-1}) and all three lakes can be classified as oligosaline (Gasse *et al.*, 1987).

	Tween Pond	*Clifton Pond*	*Groby Pool*
National grid reference	SK 519 339	SK 520 336	SK 474 075
Area (ha.)	21	19	12
Water depth mean (m)	2	2	1.1
Nitrate (mg l^{-1})	7.41	0.39	0.49
Phosphate (µg l^{-1})	1591	63	nd
Total phosphorus (µg l^{-1})	†1980	†108	(†503) 240.6Δ
pH	8.2	8.4	9
EC (µS cm^{-1})	1133	983	613
Chloride	140.1	143.9	nd
Chlorophyll *a* (µg l^{-1})	40.7	7.0	3.9
Secchi disc depth (cm)	46	144*2	136*6
Submerged plants	absent	abundant	prolific
Ecological state	phase III	phase II	phase II

Table 4.1. Summary characteristics of the three shallow study lakes. Measurements were carried out from Oct-Oct, 1992/93 in Tween and Clifton Ponds (chlorophyll *a* measured from Feb-Oct) and from Jan-Oct, 1995 in (Groby Pool). *2 = Secchi disc visible on the bottom of the lake on 2 occasions *6 = Secchi disc visible on the lake bottom on 6 occasions. † = NRA data for 11/7/94. Δ = mean annual value obtained in this study.

Substantial nutrient concentrations in Tween Pond allow for much heavier phytoplankton development as inferred from mean chlorophyll *a* concentrations (40.7 μg^{-1}) than in Clifton Pond (7 $\mu g\ l^{-1}$) and Groby Pool (3.9 $\mu g\ l^{-1}$). In the latter two lakes a clear water state prevailed in summer and a Secchi disc could frequently be seen on the bottom. In contrast in Tween Pond the water was extremely turbid (mean Secchi depth = 46 cm) throughout the year. Both Clifton Pond and Groby Pool support dense beds of submerged macrophytes. Plant diversity is highest in Groby Pool, which may reflect its much greater age and hence the time available for the colonization and establishment of different species. The growth of emergent macrophytes is prolific around the littoral fringe of Groby Pool and in the more gently shelving margins of Clifton Pond, whereas in Tween Pond emergent plants are very sparse. In Clifton Pond and Groby Pool fish community structure is dominated by perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.) and tench (*Tinca tinca* L.). Alternatively in Tween Pond small roach (*Rutilus rutilus* L.) and bream (*Abramis brama* L.) are the most prolific fish (NRA, data).

Water chemistry in the Attenborough Ponds SSSI

Prior to the description and interpretation of seasonal changes in water chemistry in Tween and Clifton Ponds, it is initially necessary to discuss the relationships between the water chemistry of the R. Erewash and the entire Attenborough Ponds gravel-pit series (fig. 4.1, plate 4.1). The different Pond sites are briefly introduced at the end of chapter one. Essentially the R. Erewash and Ponds represent a river-lake continuum (cf. Köhler, 1994; Köhler & Nixdorf, 1984) and in those lakes which are directly connected to the R. Erewash (i.e. Coneries, Tween, Duck and Works Ponds) water chemistry is directly regulated by riverine inputs of dissolved and particulate materials derived from point (industrial and sewage effluents) and diffuse sources (urban and agricultural run-off) in the R. Erewash catchment. However the chemistry of the isolated lakes (Clifton, Church and Beeston Ponds) is regulated by aquifer inputs and also by the occasional overtopping of adjacent Ponds when the R. Erewash is in flood.

Water chemistry changes along the river-lake continuum and in the isolated Ponds (with the exception of Beeston Pond) are given in fig. 4.3 which provides annual mean values (Oct 1992-Sept 1993) for key chemical parameters (PO_4, NO_3, EC and SiO_2) and orders the eight Ponds sample sites (fig. 4.1) by degree of connectivity and isolation from the Erewash inflow (i.e. CO1). A site just up-stream of the Erewash inlet (ERE) is also included. There is a rapid down-continuum reduction in nutrients (PO_4, NO_3 and SiO_2) and EC which is accelerated after the Trent outflow site (CO3) with lowest values in Works Pond (WO). Isolated, Church (CH) and Clifton (CL) Ponds at the end of the

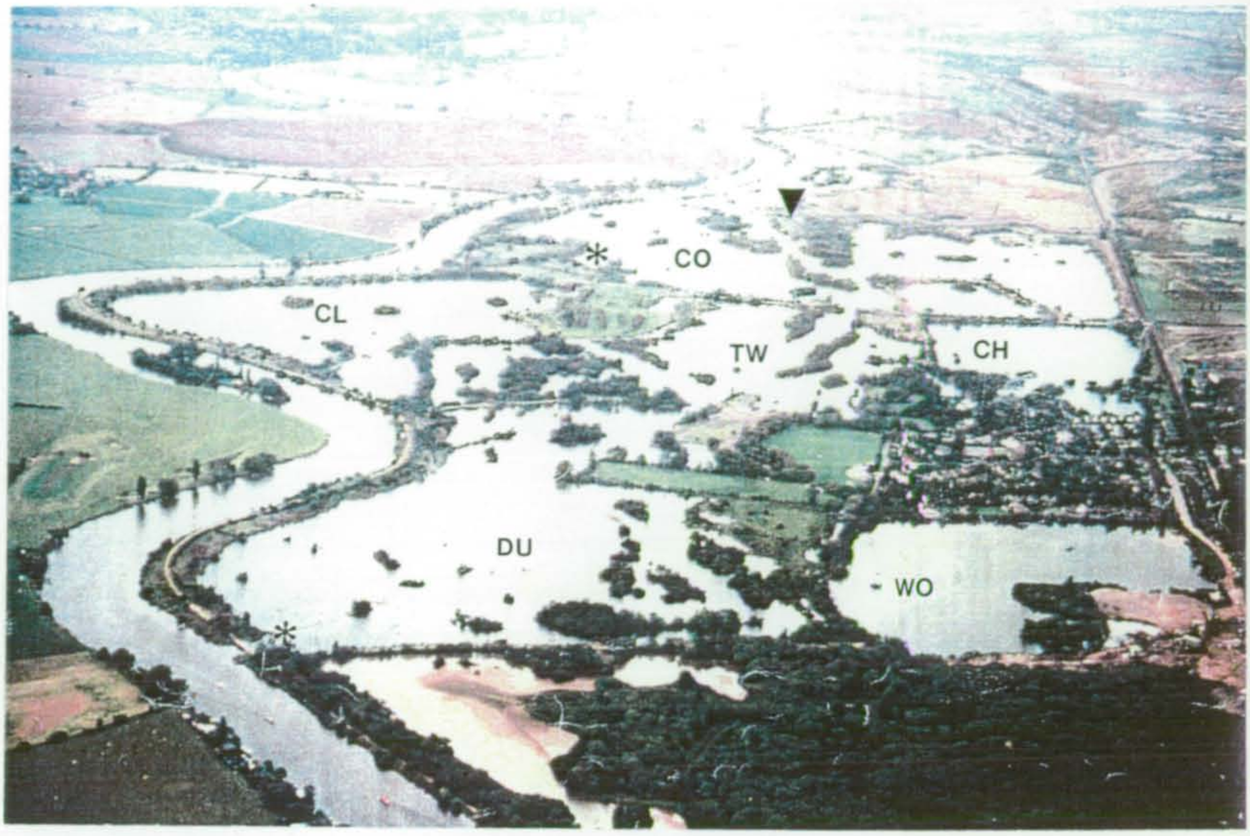


Plate 4.1. Recent aerial photograph of the Attenborough Ponds, SSSI. CO = Coneries Pond, TW = Tween Pond, DU = Duck Pond, WO = Works Pond, CH = Church Pond, CL = Clifton Pond. Erewash inlet arrowed. * = outlets.

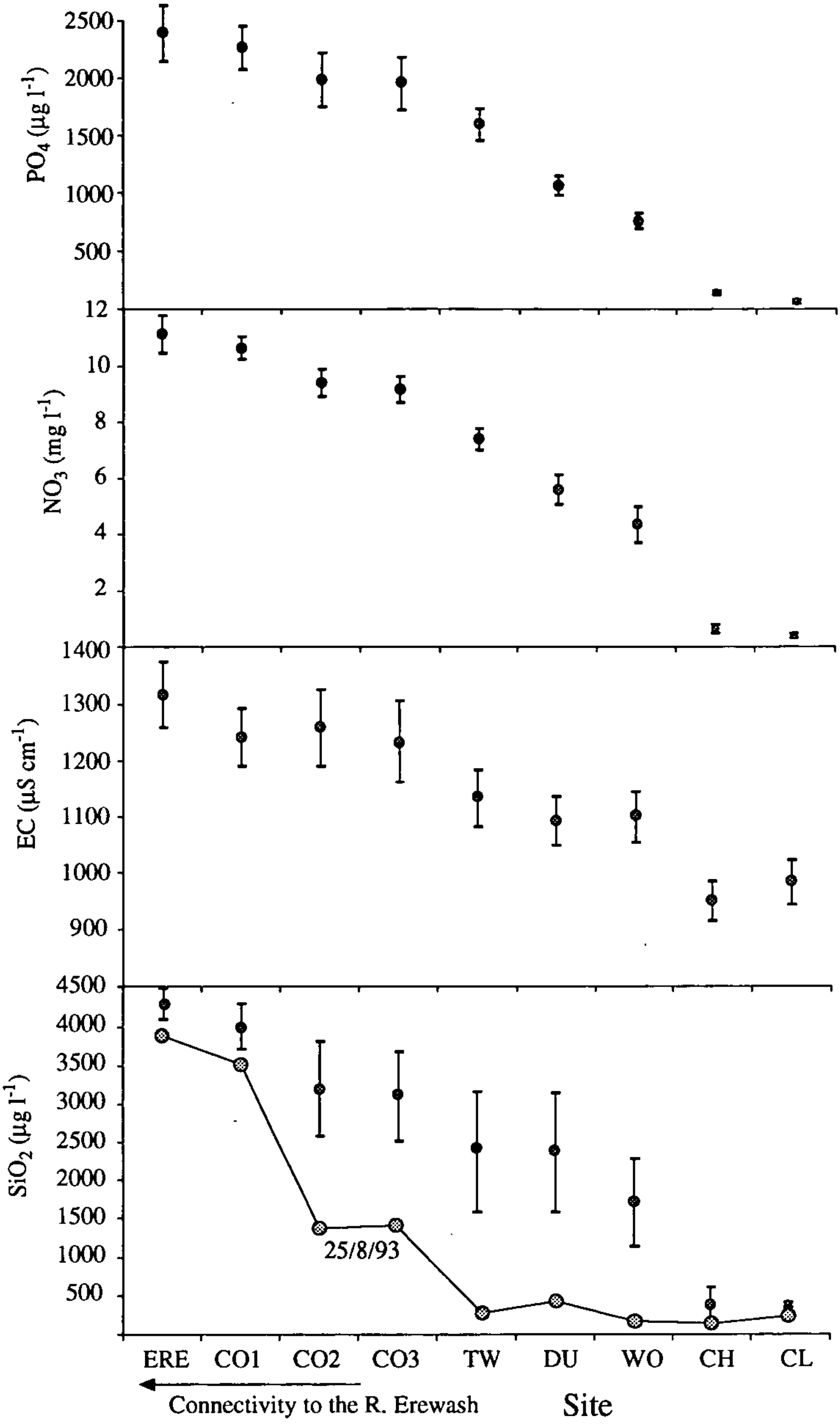


Fig. 4.3. Water chemistry changes across the Attenborough Ponds system (from the R. Erewash to Clifton Pond). Ponds are arranged by degree of connection to the R. Erewash. Water chemistry data expressed as annual means (with standard error bars) for Oct-1992-Sept-1993. SiO_2 is also given for the 25/8/93. Site codes are as in fig. 4.1.

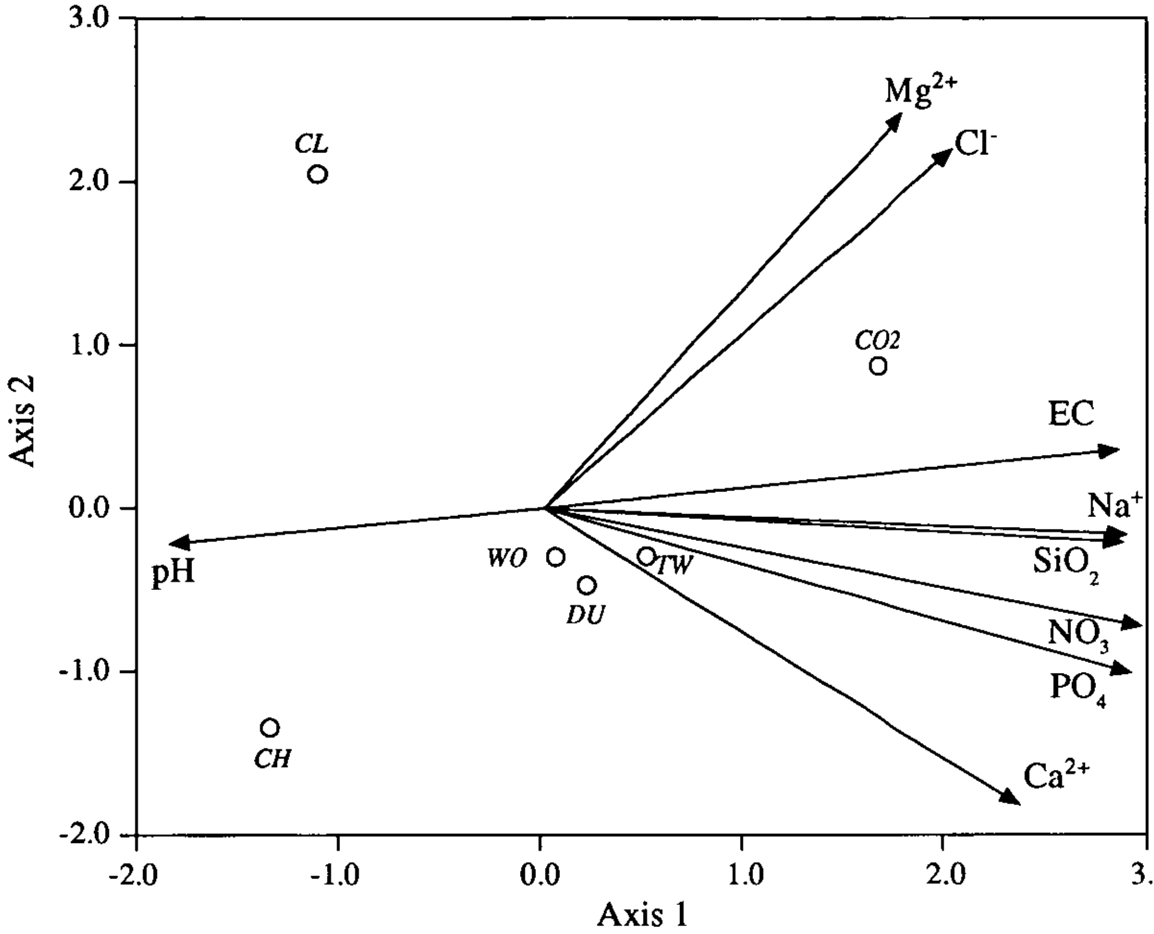


Fig. 4.4. PCA plot of the six monitored Attenborough Ponds sites and the available water chemistry data (expressed as 1993 annual means). Site codes as in fig. 4.1.

continuum are clearly separated from the connected lakes and have much reduced nutrient concentrations and lower EC. Elevated NO_3 and PO_4 concentrations in Church Pond compared to Clifton Pond are the result of a high water link (balancing pipe) with Tween Pond.

The relationships between chemical conditions in the Ponds has been further explored using principal components analysis (PCA). This was performed on mean annual values for eight chemical variables at six of the sites (fig. 4.4). With the exception of pH and SiO_2 all variables were log-transformed. Axes 1 and 2 together explain almost 90% of the variance in the data (table 4.2). Axis 1 is positively correlated with PO_4, NO_3, SiO_2, Na^+ and EC and negatively correlated with pH. Axis 2 is positively correlated with Mg^{2+} and Cl^- and negatively correlated with Ca^{2+}. The riverine sites, Tween (TW), Duck (DU) and Works (WO) Ponds form a distinct group suggesting similar chemical relationships. Alternatively Coneries Pond (CO2) and the two isolated Ponds Church (CH) and Clifton (CL) are outlier sites indicating unique chemical conditions. There is considerable co-variance in the data set and no single parameter has a significant independent influence on the site distributions.

	Eigenvalue	% Cumulative variance
Axis 1	0.715	71.5
Axis 2	0.183	89.8
Axis 3	0.05	98.3
Axis 4	0.013	99.7

Table 4.2. Eigenvalues and the cumulative percentage variance in a PCA of the 6 sites and 9 measured water chemistry variables.

Water chemistry seasonality

Monthly changes in PO_4, NO_3, SiO_2 Cl^- concentrations and pH and EC in the three study lakes are given in figs. 4.5, 4.6, 4.7. In Tween Pond, chemical values are compared with those in the R. Erewash (i.e. ERE in fig. 4.1) just below Toton sewage treatment works, some 500 m upstream of the Ponds and in Groby Pool with a site on the Slate Brook inflow stream some 400 m above the lake close to the main A50 Trunk road. Monthly monitoring is undoubtedly insufficient to characterise the full range of seasonal chemical variation in the lakes, however it is possible to make some broad conclusions about potential nutrient sources (i.e. external or internal), resource limitation and nutrient availability.

Tween Pond

In Tween Pond PO_4 and NO_3 concentrations exhibited a close directional association with the river. PO_4 was lowest in early Dec 1992 (600 $\mu g\ l^{-1}$) when values were very similar to the river, indicating rapid throughputs of water and minimal depletion of the external load by the phytoplankton. PO_4 concentrations then steadily increased throughout spring and summer and peaked in late August (2690 $\mu g\ l^{-1}$). The discrepancy between PO_4 in the R. Erewash and Tween Pond was maximised in the late winter-early summer period as discharge in the river declined and inflowing PO_4 was probably more efficiently translated into phytoplankton standing crops. The relationship between NO_3 concentrations in Tween Pond and the river was very similar to that of PO_4, with maximum difference in summer and comparable concentrations in winter. NO_3 (4.37-9.1 mg l^{-1} range) increased through the winter and then declined in spring and early summer, after which it was more variable. Both NO_3 and PO_4 were never severely depleted in Tween Pond and it seems unlikely that either of these nutrients limited phytoplankton production. However SiO_2 fell to very low values on two occasions (<200 $\mu g\ l^{-1}$), associated with phases of intense diatom production and there were probably times when it was completely exhausted. River inputs of this nutrient were relatively low and ranged between 3938-4731 $\mu g\ l^{-1}$. This may have been related to Si-depletion by riverine diatoms as has been observed in other lake-river systems (Köhler & Nixdorf, 1994). Rapid depletion of the SiO_2 inputs was particularly evident in late Aug (fig. 4.3) when there was a very rapid reduction in SiO_2 concentrations between the river inlet (3938 $\mu g\ l^{-1}$) and Tween Pond (218 $\mu g\ l^{-1}$). Thus it seems probable that SiO_2 was an important regulator of diatom growth in the lake. External nutrient supplies would appear to have been dominant for most of the year, however internal recycling (particularly of PO_4 and SiO_2) may have been important during wind-induced sediment resuspension events (cf. Søndergaard *et al.*, 1992; Kristensen *et al.*, 1992) and in summer when the highly organic sediments became warm and anaerobic (cf. Bailey-Watts *et al.*, 1989, Osbourne & Phillips, 1978; Marsden, 1989; Phillips *et al.*, 1994).

pH in Tween Pond (7.5-9.5 range) was highest during spring and summer. EC had a similar pattern to Cl^- and again values were closely related to those in the river. Minimum concentrations were encountered in winter 1992 (900 $\mu S\ cm^{-1}$, 93.49 mg l^{-1} respectively) as point-source inputs were diluted by diffuse catchment run-off and highest values were apparent in summer and autumn under lower flow conditions.

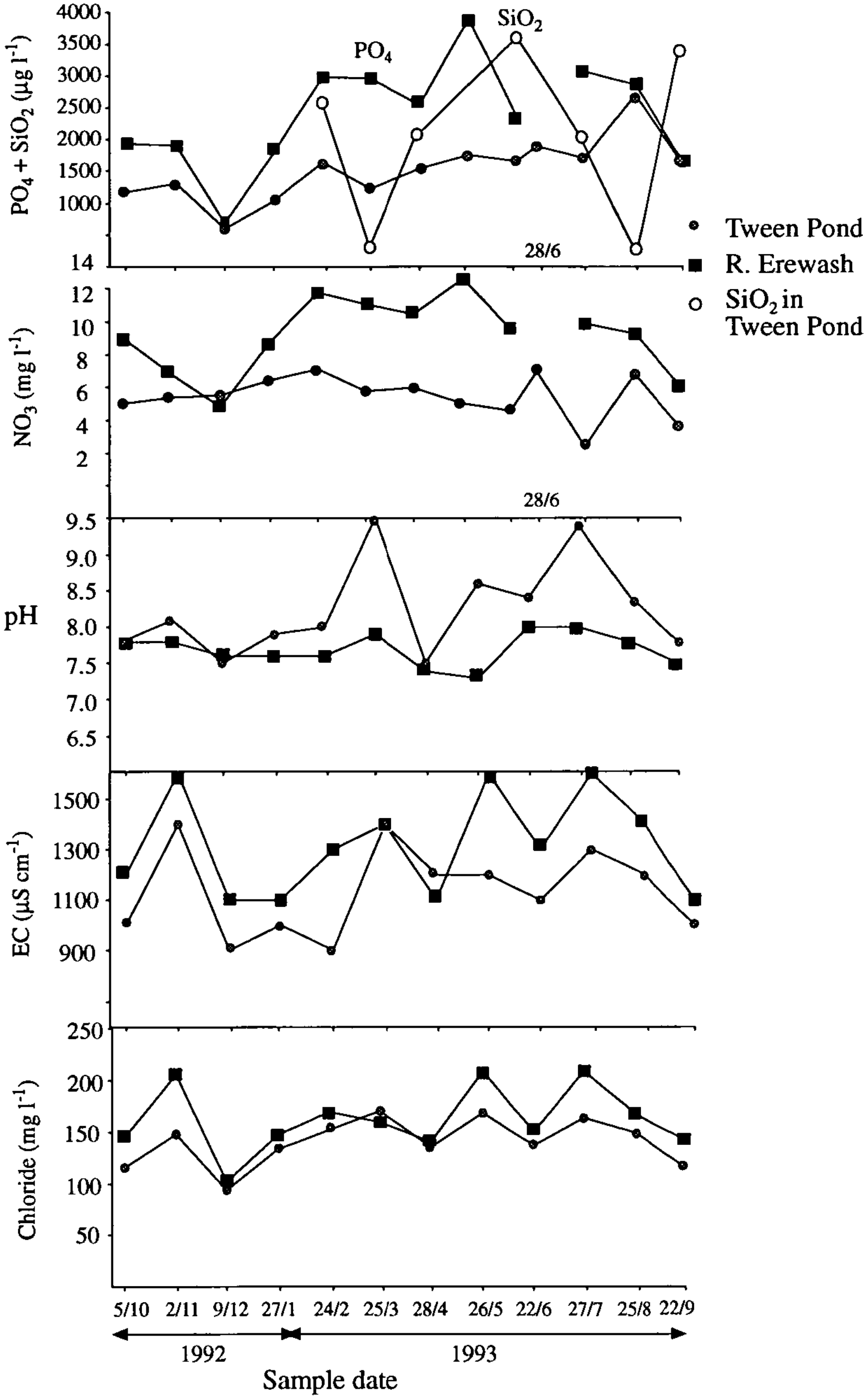


Fig. 4.5. Monthly water chemistry changes in Tween Pond (circles) and the River Erewash at the Ponds inlet (squares).

Clifton Pond

PO_4 concentrations were lowest in early winter 1992 (<30 $\mu g\ l^{-1}$) and highest in summer with a marked peak in late June (280 $\mu g\ l^{-1}$). This peak which occured when the lake was effectively isolated from the catchment may represent a period of internal release. NO_3 concentrations were also much reduced in early winter 1992, but significantly increased (as does PO_4 to a lesser extent) in early December 1992 (1500 $\mu g\ l^{-1}$). The latter event may be related to two factors; (i) ground-water replenishment; and (ii) possible overtopping of Tween Pond water under higher flows a few days previous. NO_3 concentrations then fell rapidly and remained low throughout the spring (<0.2 mg l^{-1}), before a renewed increase in summer and autumn. SiO_2 was extremely scarce and never exceeded 500 $\mu g\ l^{-1}$ suggesting that it may have limited diatom growth (cf. Kilham, 1975).

pH (7.7-9.1 range) did not exhibit a distinctive seasonal pattern, but lowest values were recorded in winter and highest values in late June and late July. EC had a range of 800-1300 $\mu S\ cm^{-1}$ and values were extremely variable between Oct-Feb and thereafter much more stable. In contrast to Tween Pond Cl^- did not closely follow the pattern of EC variation. Maximum values were observed in early winter 1992 (>155 mg l^{-1}) after which concentrations declined and oscillated between 130-150 mg l^{-1}.

Groby Pool

In contrast to Tween and Clifton Ponds TP was measured instead of PO_4. This revealed an interesting pattern with low values in late winter and spring (<200 $\mu g\ l^{-1}$). There was a marked peak in late May (448 $\mu g\ l^{-1}$) and concentrations in the lake were twice as high as those in the Slate Brook which is the major inflow stream (168 $\mu g\ l^{-1}$) suggesting internal P-release. P-translocation during the detachment of macro-algae from the sediment surface is a likely explanation for this (see macrophytes discussion below). TP concentrations declined below those of the Slate Brook in early July before a renewed steady phase of increase throughout August, September and October. In late October TP concentrations were much higher in the lake compared to the Slate Brook indicating that P-release was still potentially important. This may have been induced by sediment resusupension during strong winds (cf. Kristensen *et al.*, 1992) or possible release from decaying macrophyte tissues. NO_3 exhibited a clear seasonal pattern with highest concentrations in late winter (>1700 $\mu g\ l^{-1}$) associated with increased catchment run-off and then a dramatic reduction in spring, summer and autumn (<200 $\mu g\ l^{-1}$). NO_3 was plentiful in the Slate Brook during the latter period (>2000 $\mu g\ l^{-1}$) indicating that this reduction was due to uptake by phytoplankton and macrophyte populations and rapid depletion of the external load. It

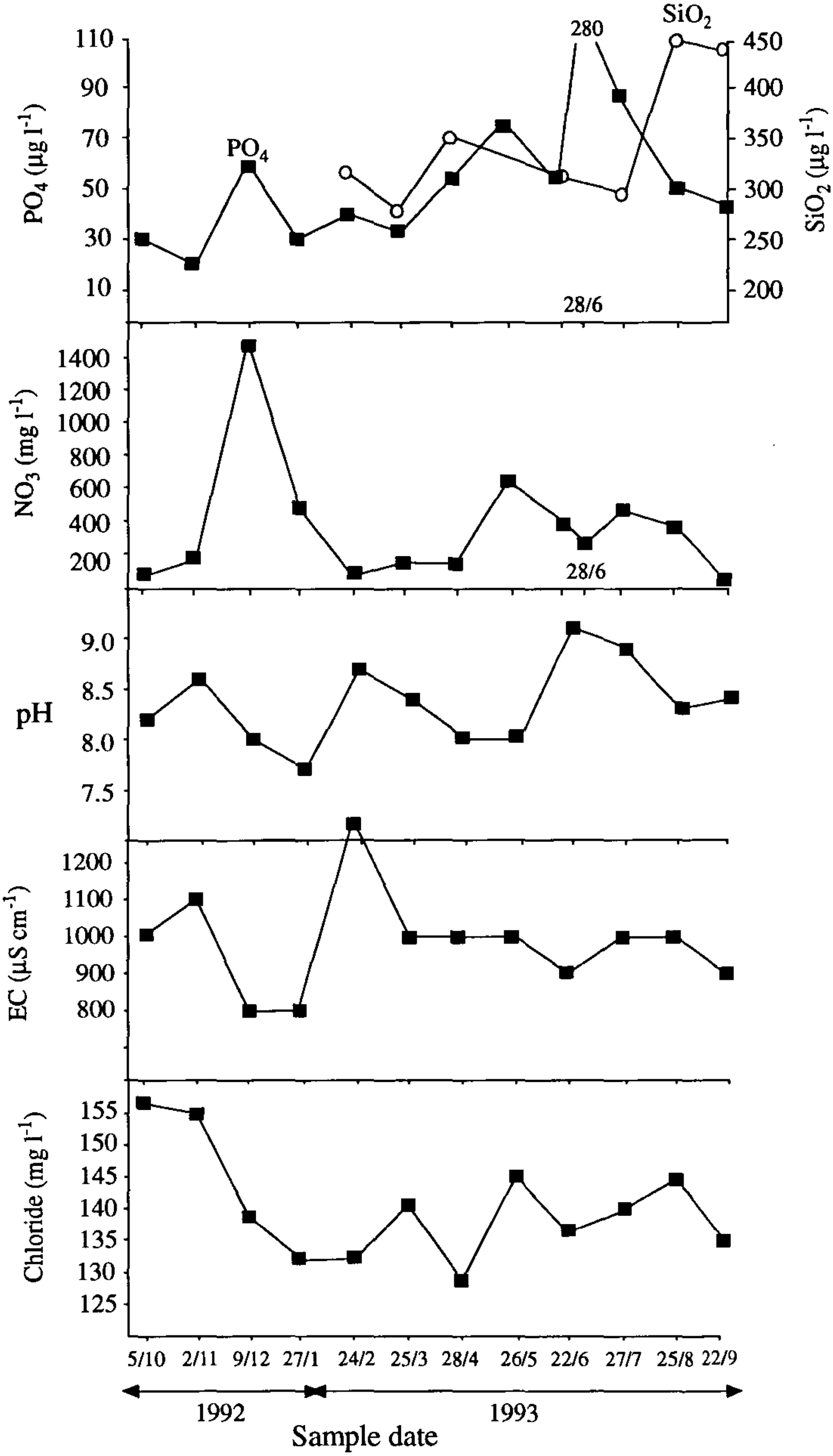


Fig. 4.6. Monthly water chemistry changes in Clifton Pond.

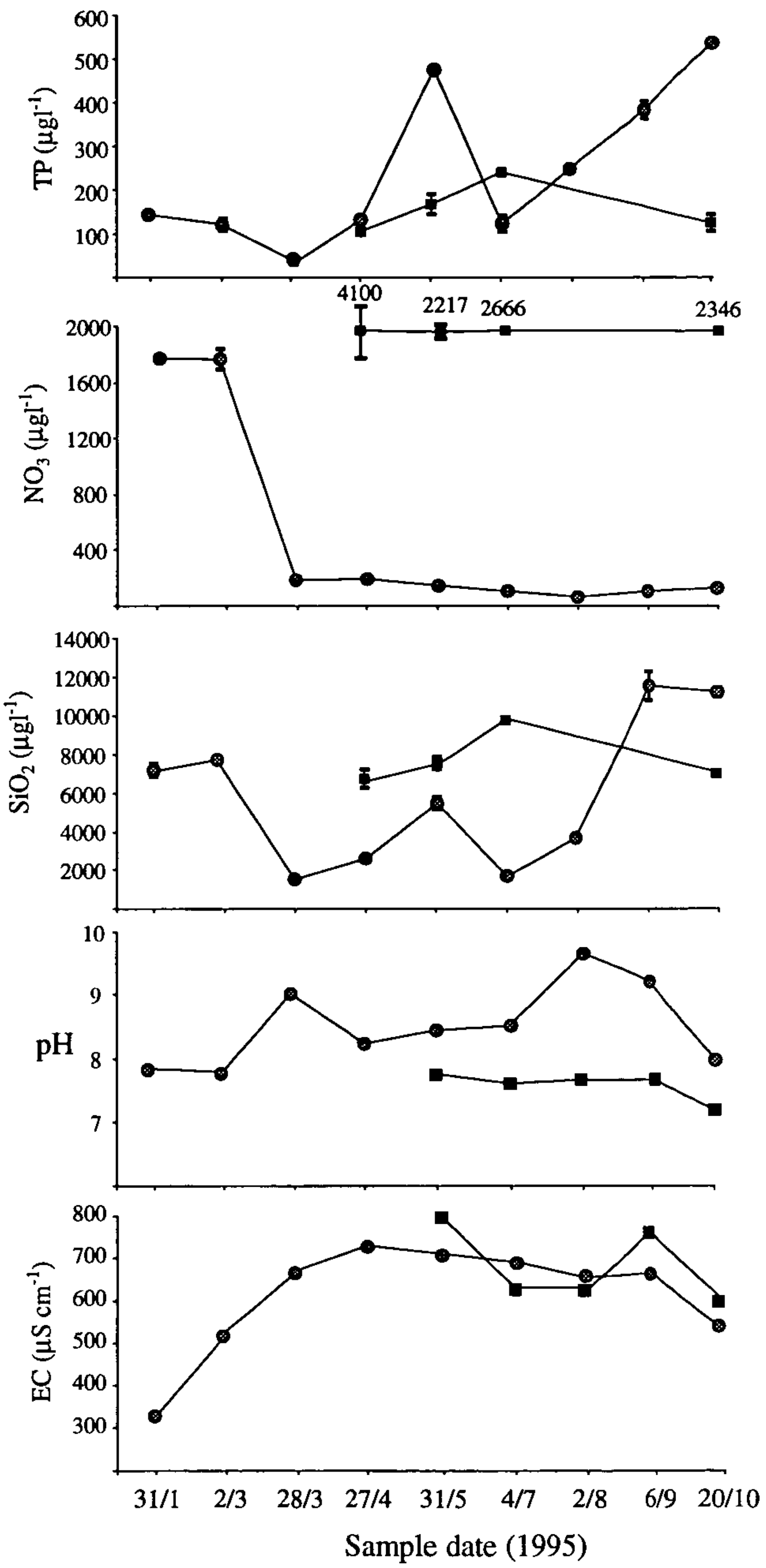


Fig. 4.7. Monthly water chemistry changes in Groby Pool (circles) and the Slate Brook (squares). Standard deviation errors bars are given for total phosphorus (TP), PO_4 and NO_3.

seems probable thererfore that NO_3 is an important limiting nutrient in this lake. SiO_2 was much more plentiful compared to Tween and Clifton Ponds and was never reduced such that it might have seriously restricted diatom growth. Minimum concentrations were detected in spring and autumn (<1800 µg l^{-1}) and peak concentrations occured in autumn-early winter (>11,000 µg l^{-1}). In early winter SiO_2 was more plentiful in the Slate Brook than in the Pool, again suggesting an internal input. The decay of plant matter at the sediment surface derived from the die-back of macrophytes is a likely source.

pH was high in Groby Pool and exceeded 9.0 in spring and autumn, with minimum values of below 8.0 in winter. EC exhibited a definite seasonal response and values increased througout winter and early spring to a peak of 730 µS cm^{-1} before a slow decline throughout summer and autumn.

Phytoplankton biomass and water clarity

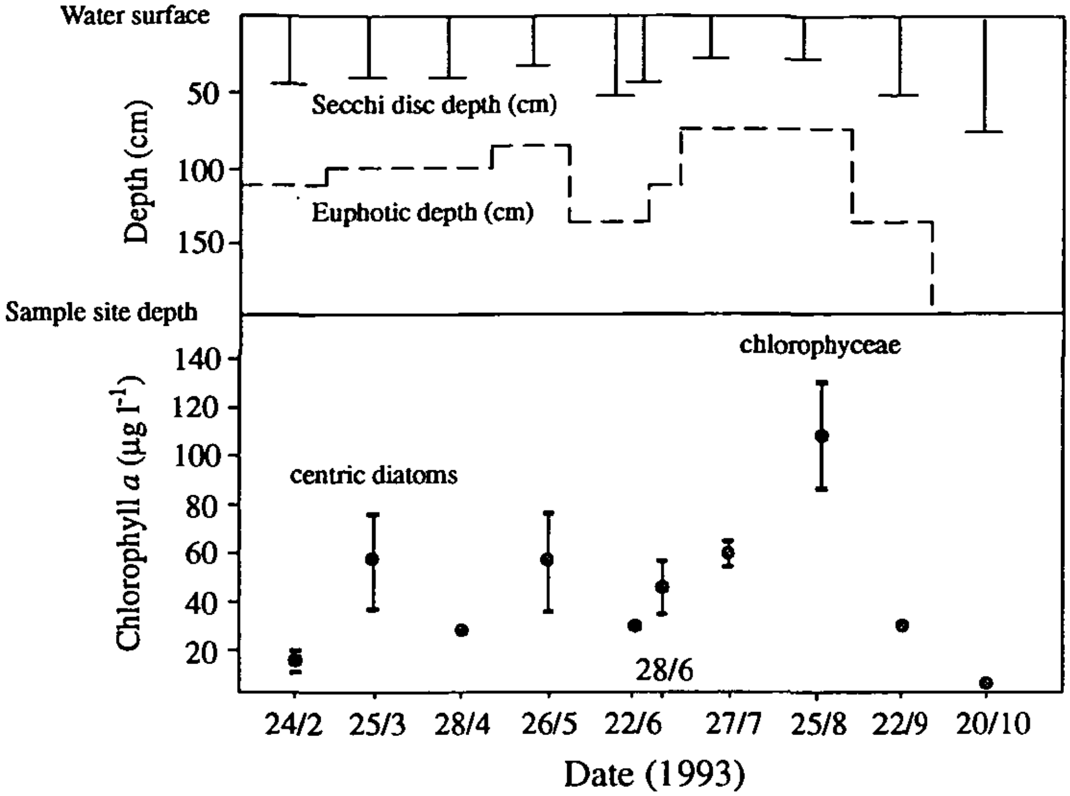
Monthly changes in chlorophyll *a* inferred algal biomass and water transparency measured as Secchi depth for the three studied lakes are given in fig. 4.8. The relationship between these two measurements was poor with the exception of Tween Pond (r^2=0.41). This is to be expected in shallow lakes where wind-induced mixing events (Kristensen *et al.*, 1992)) and the foraging activities of benthivorous fish (Meijer *et al.*, 1990; Havens, 1993) such as carp (*Cyprinus carpio* L.) and bream (*Abramis brama* L.) means that the water column is often loaded with particles resuspended from the sediment. Also more importantly in Clifton Pond and Groby Pool, the Secchi disc was frequently observed on the bottom in summer thus affording an inappropriate estimate of turbidity.

In Tween Pond chlorophyll *a* concentrations were high (40.8 µg l^{-1} mean) with peaks associated with centric diatoms in late March and chlorophytes in late August. Secchi-depth in Tween Pond was low (35-80 cm) and turbid conditions were prevalent throughout the Jan-Oct period. In contrast in Clifton Pond chlorophyll *a* concentrations were much reduced (6.6 µg l^{-1} mean) and with the exception of two bloom-forming episodes of centric diatoms (largely *Thalassiosira pseudonana* and *Cyclostephanos tholiformis*) and the cyanophyte *Anabaena spiroides* Klebahn in late Feb (13.7 µg l^{-1}) and late June (28.5 µg l^{-1}), phytoplankton biomass was low. The water was much less turbid than in Tween Pond (Secchi depth >70 cm) and there was shift to extremely clear water conditions in early summer as submerged plants became established and the Secchi disc was visible on the lake bed. However more turbid conditions prevailed in mid to late summer (<100 cm) prior to the return of very clear water in autumn-early winter. Phytoplankton biomass was similarly low in Groby Pool and sizeable chlorophyll *a* concentrations were only attained in late March (13.4 $\mu g\ l^{-1}$). The water was turbid in the late winter period due largely to high concentrations of suspended solids in the water column. However exceptionally clear water was evident throughout the April-October period, during which time the Secchi disc was visible on the bottom of the Pool.

The depth of light penetration is the critical factor controlling the depth distribution of phytoplankton and submerged plants (Spence, 1982). Phytoplankton photosynthesis takes place down to the point at which down-welling irradiance is reduced to 1% of that just below the water surface (i.e. the euphotic depth). However the colonisation depth for submerged plants already shaded by filamentous and epiphytic algae is probably considerably less than that for phytoplankton. Secchi-depth (Z_s) can be used to estimate euphotic depth (Z_{eu}) in a lake using simple equations and a Z_{eu}/Z_s value of 2.5 has been observed in shallow, Danubian lakes (Pelletier, 1984). Using this conversion to predict seasonal shifts in Z_{eu} in Tween Pond (dashed line) it is apparent that Z_{eu} exceeded water depth only in early winter. Thus a vast improvement in water clarity would be required to allow submerged plants to return in this lake and it is probable that 'self-shading' conditons were evident in the phytoplankton over much of the year. Alternatively in Clifton Pond and Groby Pool, Z_{eu} was considerably less than water depth throughout the growing season and as a result dense beds of submerged plants were able to grow in both these lakes.

The clear water submerged plant dominated state in shallow lakes is thought to be preserved by a range of homeostatic, or negative feedback mechanisms (chapter one) associated with the plants themselves (Moss, 1989; Moss, 1990). These include; (i) the reduction of N concentrations in the water both by direct uptake (luxury consumption) and enhanced denitrification in the sediments beneath the plant beds (van Donk *et al.*, 1993); (ii) the harbouring of large Cladoceran grazers which avoid predation by planktivorous fish during the day and migrate out of the plant beds by night to graze on the phytoplankton (Timms & Moss, 1984); (iii) the provision of hunting habitat for large perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) which control numbers of small (0+, 1+) planktivorous fish (Perrow *et al.*, 1994; Benndorf, 1990); and possibly; (iv) allelopathic effects (Wium-Anderson *et al.*, 1982). Substantial populations of large-bodied *Daphnia* spp. were observed amongst the littoral and open water plant beds in both Clifton Pond and Groby Pool and fish communities were dominated by perch and pike (NRA, data), thus it seems that buffering mechanisms (ii) and (iii) are very much in place and are preserving the clear water state. In Groby Pool NO_3 concentrations were very low in summer which indicates that mechanism (i) may also have been important. Mechanisms (i) and (ii) are directly associated with the ability of large Cladocera to control edible

(a)
Tween Pond



(b)
Clifton Pond

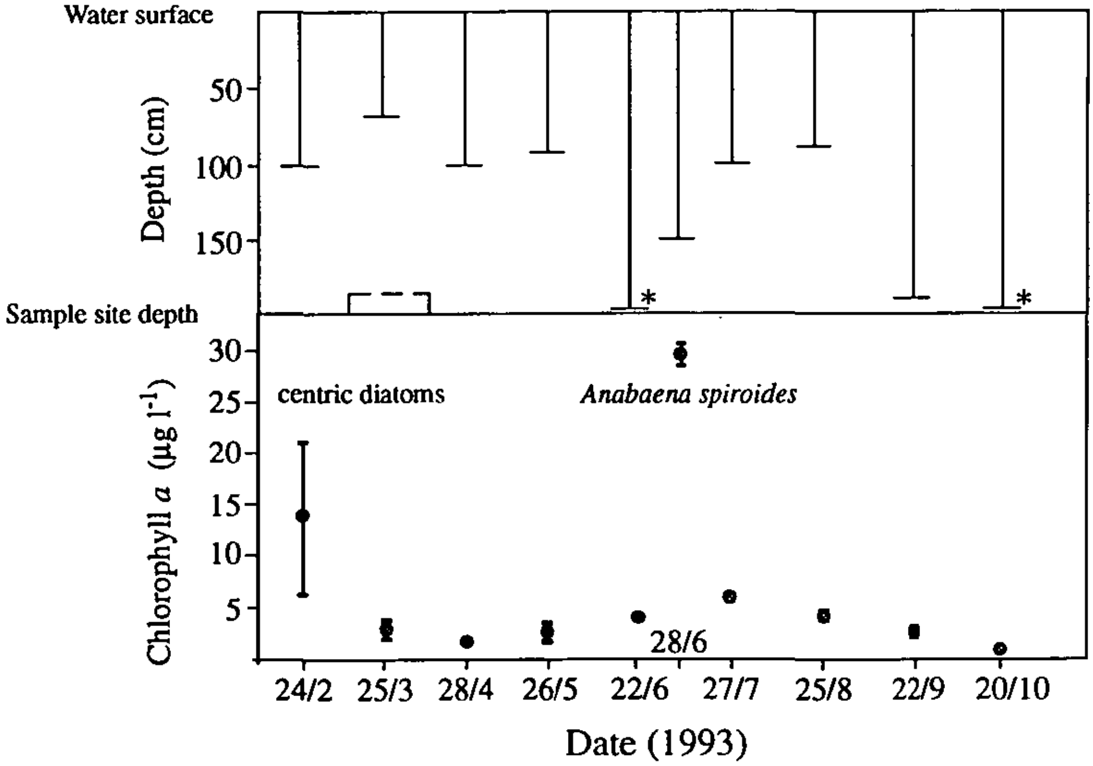
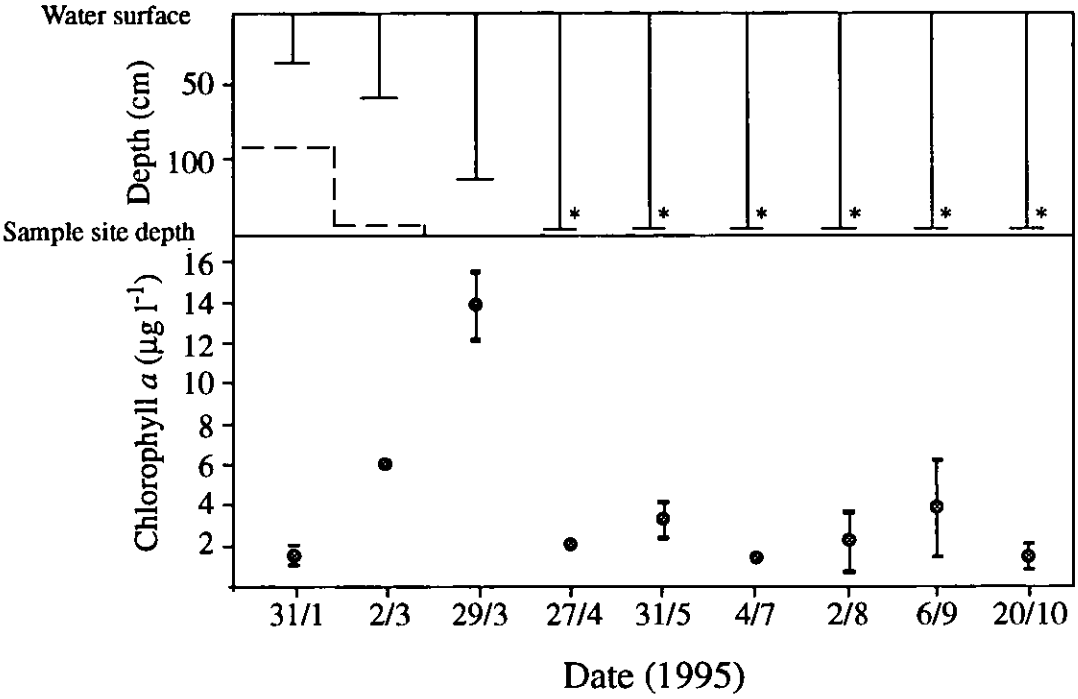


Fig. 4.8. Monthly changes in mean chlorophyll *a* concentrations(standard deviation error bars given) and Secchi disc depth in; (a) Tween Pond; (b) Clifton Pond; and (c) Groby Pool (overleaf)

* = Secchi disc visible on the lake bed


Water surface
Depth (cm)
50
100
Sample site depth
*
Chlorophyll a (μg l^{-1})
16
14
12
10
8
6
4
2
31/1
2/3
29/3
27/4
31/5
4/7
2/8
6/9
20/10
Date (1995)

(c)
Groby Pool

phytoplankton populations by intense grazing pressure. Infrequent flushing in Clifton Pond, as in other shallow lakes (Moss *et al.*, 1986) selects for the build-up of large populations of less edible cyanophytes in summer and the size of these populations will be under environmental rather than biological control (Moss *et al.*, 1991). Thus despite lower nutrient concentrations in Clifton Pond, it may be more susceptible to a future switch to turbid, phytoplankton dominated conditions if there is a permanent shift to the increased prevalence of cyanophytes.

Macrophytes

Year-round shading of the bottom sediments in Tween Pond does not allow for the successful colonisation of rooted submerged and floating leafed plants. However the shift to clear water conditions before the start of the growing season in Clifton Pond and Groby Pool allows dense crops of aquatic plants to thrive. In both lakes macrophyte growth was preceded by the widespread development of the bottom living filamentous alga *Cladophora* spp. (and to a lesser extent *Spirogyra* spp. in Clifton Pond) which grew to the water surface by mid-May. The initial growth of these species resulted in mass detachments of rising, intertwined mats of macro-algae and attached sediment which collected at the water surface creating an extensive scum layer (plate 4.2). This process was most prevalent in Groby Pool where a vast area of the water surface was covered with this material which was subsequently lost in the outflow. Although this annual 'lifting' phenomenon is frequently observed in shallow, enriched lakes and slow moving rivers (Moss, 1985; Bailey, 1992; Knott pers. comm.) its potential significance is little known. In N. USA these detachments are termed floating algal benthos (FLAB) mats and are often associated with over-wintering populations of the cyanobacteria *Lyngbya wollei* Farlow ex. Gomont (Speziale & Dyck, 1992) and other planktonic species such as *Oscillatoria* spp. (Czarnscki, pers. comm.) which become covered with epiphytic diatoms. The 'lifting' phase is thought to be the result of photosynthetically produced gasses which become entrapped in the mat and cause it to become positively buoyant. It seems likely that the same process may explain similar rising benthic mats in other aquatic habitats such as Antarctic lakes (Hambrook, pers. comm.), salt marsh pools (Malin, pers. comm.), shallow marine bays (Sundback, pers. comm.) and indeed in shallow, eutrophic lakes.

In Clifton Pond the first submerged plant species to colonize was *Potamogeton pectinatus* L. in late May and by mid-June this species had established itself as a dense monoculture over most of the lake. However the variable slope of the underwater terrain and the patchy distribution of suitable sediment conditions allowed for plentiful gaps in the plant canopy and the existence of bare areas of unshaded sediment. Other submerged plant species were found in the lake in July and August such as *Myriophyllum spicatum* L., *Zannichellia palustris* L., *Elodea nutalli* L. and *Callitriche truncata* L., but these occurred in small patches and were subdominant to *P. pectinatus*. In the shallow NE margins of the lake *Lemna minor* L., and *Lemna triscula* L. were abundant, but rooted floating plants were restricted to a small bed of *Nuphar lutea* L. in the opposing SW margins. The trophic ranking score (TRS) for the Clifton Pond submerged macrophyte community based on the classification scheme of Palmer *et al.*, (1992) is 9.8 which places the lake in the eutrophic category.

Plant colonisation in Groby Pool began in early May in the sheltered SW margins where there was a mixed assemblage dominated by *Potamogeton pusillus* L. and to a lesser extent *Ceratophyllum demersum* L. and *C. truncata*. A large bed of *N. lutea* also established itself in this area. In the open water, plant growth was sparse until June when *Potamogeton. pusillus* L., *Elodea canadensis* Michx. and *E. nutalli* started to form dense mixed stands reaching the water surface. By early July there was a closed canopy in all areas of the lake with the exception of the rocky SE shoreline. In littoral areas of less than 50 cm depth, *C. demersum* and *P. pusillus L.* were co-dominant with smaller, more patchy stands of *E. canadensis*, *E. nutalli*, *Z. palustris*, *C. truncata* and *Potamogeton crispus* L. Again profundal assemblages were dominated by *Elodea* spp. and *P. pusillus* which were associated with thick surface mats of scenescent *Cladophora* spp. and were much less diverse than in the shallower water. The TRS for the submerged macrophytes found in Groby Pool is 9.1, which like Clifton Pond places it in the eutrophic category of Palmer *et al.*, (1992).

Epiphytic diatoms

The surfaces of submerged plants in shallow macrophyte dominated lakes afford a vast potential niche for the colonisation of attached epiphytes. In eutrophic lakes different host plants are not thought to select for specific species assemblages as has been observed in oligotrophic environments (Eminson & Moss, 1980). Thus in eutrophic waters different diatom communities are probably more a reflection of environmental conditions and seasonality probably represents a more important dimension of variability, as opposed to differences between plants.

Epiphyte samples were collected from open water submerged plants in Clifton Pond and Groby Pool at the start and end of the growing season. In Clifton Pond samples were taken from *P. pectinatus* and in Groby Pool from *P. pusillus* and *C. demersum* (table 4.3). The most important epiphytic species in Clifton Pond were *Cocconeis placentula* and

Plate 4.2. Rising mats of sediment and filamentous algae in Groby Pool, May 1995.

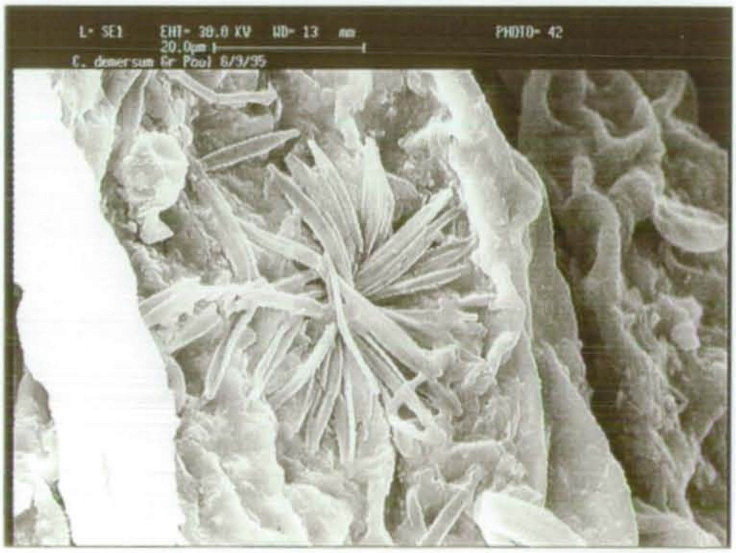


Plate 4.3. The epiphyte *Nitzchia paleacea* attached to the submerged plant *Ceratophyllum demersum*, collected from Groby Pool, 6/9/95.

Rhoicosphenia abbreviata, both of which reached maximum relative abundance towards the end of the growing season. In Groby Pool, *C. placentula* was also dominant in mid-summer but was displaced by *Nitzschia paleacea* in the autumn which formed beautiful, 'flower' like colonies on the plant surfaces (plate 4.3). This species was also prevalent in Clifton Pond in the spring. Thus despite contrasting chemical conditions in the two lakes a similar epiphytic flora prevailed.

Epilithic diatoms

Because of the abundance of gravel islands in Clifton Pond, the epilithic niche represents a potentially important diatom habitat. Similar potential exists in Tween Pond but turbid conditions may preclude the establishment of stable epilithic communities in all but the shallowest areas of the lake. In Groby Pool this life-form is also probably of reduced importance as suitable submerged surfaces are confined to a small area of exposed pre-cambrian rock in the SE margins of the lake.

Epilithic samples were collected from marginal rock surfaces on two occasions in each lake in spring and late summer-autumn (table 4.4). In contrast to the epiphytic samples, overlap between the epilithic assemblages in the three lakes was reduced, although *N. paleacea* was prevalent in late season assemblages in Clifton Pond and Groby Pool. There was an important component of seasonal variation in the epilithic niche and no one species was dominant in the two sample collections, with perhaps the notable exception of *Fragilaria capucina* var. *vaucheriae* in Tween Pond and *Fragilaria capucina* var. *perminuta* in Clifton Pond. The common forms *N. paleacea*, *R. abbreviata* and *C. placentula* were abundant on both plant and rock surfaces in Clifton Pond and exhibited the same seasonal response in each life-form. Similarly *N. paleacea* was also shared between habitats in Groby Pool and again had a comparable pattern of relative abundance, although interestingly *C. placentula* was not encountered in the epilithon in this lake.

	Clifton		Groby	
	P. pectinatus	*P. pectinatus*	*P. pusillus*	*C. demersum*
Species	28/6/93	25/8/93	4/7	6/9
Achnanthes minutissima	0.00	1.80	5.65	0.27
Amphora veneta	0.80	0.36	0.00	9.07
Amphora pediculus	0.00	3.96	3.53	0.00
Amphora spp.	0.80	0.72	0.00	1.10
Cocconeis placentula	27.89	43.88	32.51	8.79
Ctenophora pulchella	5.18	1.08	0.00	0.00
Fragilaria capucina var. *mesolepta*	0.00	0.00	1.41	0.00
Fragilaria fasciculata	4.78	1.44	1.41	0.55
Gomphonema clavatum	0.00	0.00	0.00	8.52
Gomphonema parvulum	0.80	1.08	2.83	0.82
Gomphonema spp.	1.99	1.08	1.41	0.00
Gyrosigma spp.	2.39	0.72	0.00	0.00
Melosira varians	0.00	0.00	0.35	1.37
Navicula capitoradiata	0.00	0.00	2.47	0.00
Navicula cryptotonella	0.00	0.00	2.12	0.00
Navicula gregaria	3.19	1.08	0.00	0.00
Navicula minima	0.00	0.00	10.95	2.20
Navicula spp.	2.39	0.72	2.47	0.27
Nitzschia amphibia	0.00	0.00	5.65	6.32
Nitzschia dissipata	1.99	2.16	0.71	0.00
Nitzschia fonticola	0.80	0.00	1.41	0.00
Nitzschia paleacea	9.56	1.80	16.61	59.34
Nitzschia supralittorea	1.59	0.72	0.00	0.00
Nitzschia spp.	5.18	0.72	0.71	0.55
Rhoicosphenia abbreviata	0.40	28.78	6.36	0.00
Cyclostephanos dubius	5.58	1.80	0.00	0.00
Cyclostephanos tholiformis	5.18	3.60	0.00	0.00
Stephanodiscus parvus	8.76	0.36	0.00	0.55
Stephanodiscus cf. *medius*	3.98	0.00	0.00	0.00
Other centric spp.	1.99	0.00	0.00	0.00
Other periphytic spp.	4.38	1.44	0.71	0.27

Table 4.3. Percentage abundances of epiphytic diatoms attached to submerged plant species in Clifton Pond and Groby Pool. * only species over 1% of assemblage relative abundance included.

Species	Tween		Clifton		Groby	
	28/4/93	27/7/93	28/4/93	27/7/93	29/3/95	6/9/95
Achnanthes minutissima	0.00	0.00	1.14	5.66	1.53	1.10
Achnanthes delicatula	0.40	0.80	0.29	2.94	0.00	1.47
Achnanthes lanceolata	0.00	0.40	0.00	1.36	0.00	2.21
Amphora pediculus	0.00	0.00	1.71	2.04	1.28	18.75
Amphora veneta	0.79	13.15	0.00	0.23	4.35	0.74
Cocconeis placentula	0.00	0.40	1.14	14.48	0.00	0.00
Cocconeis pediculus	0.00	0.00	0.00	7.01	0.00	0.00
Ctenophora pulchella	0.79	0.00	1.71	2.71	0.00	0.00
Diatoma moniliformis	0.00	0.00	5.14	0.00	0.00	0.00
Diatoma tenuis	4.37	0.00	0.57	0.00	0.00	0.00
Fragilaria capucina var. *perminuta*	0.00	0.00	30.57	11.09	0.00	0.00
Fragilaria capucina var. *vaucheriae*	11.90	6.37	0.00	0.00	0.77	0.00
Fragilaria fasciculata	1.19	0.40	1.14	0.68	2.56	0.00
Fragilaria ulna	7.54	0.00	0.00	0.00	0.00	0.00
Gomphonema minutum	0.00	0.00	1.71	4.52	0.00	0.00
Gomphonema olivaceum	0.00	0.00	6.86	2.04	0.77	0.00
Gomphonema parvulum	2.38	26.69	0.00	1.13	3.32	0.00
Melosira varians	19.44	0.00	0.00	0.23	0.00	0.00
Navicula capitata	0.00	2.39	0.00	0.00	0.00	0.00
Navicula cryptotonella	0.00	0.00	0.00	1.36	2.30	2.21
Navicula exilis	0.00	0.00	2.57	0.00	0.00	0.74
Navicula gregaria	4.37	0.00	1.71	0.68	0.00	0.00
Navicula lanceolata	3.97	0.00	1.14	0.00	0.51	0.00
Navicula minima	0.00	0.00	0.00	0.00	2.05	2.57
Navicula submenisculus	0.79	0.00	0.00	0.00	26.09	1.47
Navicula tripunctata + margalithii	0.79	0.40	0.00	0.23	3.07	0.00
Navicula spp.	1.19	0.40	0.00	0.23	0.77	0.37
Nitzschia amphibia	0.00	37.05	0.00	0.00	8.18	1.10
Nitzschia dissipata	0.00	0.00	4.29	2.04	1.28	0.00
Nitzschia fonticola	0.79	0.40	0.29	0.68	7.42	0.74
Nitzschia frustulum	0.00	1.20	1.71	0.90	0.51	0.00
Nitzschia inconspicua	0.00	0.00	2.29	1.13	3.84	10.29
Nitzschia liebetruthii	0.00	0.00	0.57	1.81	0.26	0.00
Nitzschia paleacea	0.40	0.00	28.29	0.00	0.00	50.74
Nitzschia spp.	4.37	0.40	1.71	0.23	3.07	2.57
Opephora olsenii	0.79	1.59	0.00	0.00	0.00	0.00
Rhoicosphenia abbreviata	0.79	3.19	2.57	28.73	1.53	0.37
Surirella brebisonii	12.70	0.00	0.29	0.23	0.26	0.00
Cyclotella atomus	3.97	0.00	0.00	0.00	0.00	0.00
Cyclotella meneghiniana	2.38	0.00	0.00	0.00	0.00	0.00
Pelagodictyon tenue	4.76	0.00	0.00	0.00	1.02	0.00
Stephanodiscus parvus	4.37	0.00	0.00	0.00	20.46	0.74
Other centric spp.	3.17	0.00	0.00	2.04	0.00	0.00
Other periphytic spp.	1.59	3.98	0.58	3.62	2.82	2.59

Table 4.4. Percentage abundances of epilithic diatoms attached to marginal rock surfaces in the three study lakes. * only species over 1% of assemblage relative abundance included.

Planktonic diatoms

The seasonal patterning and organisation of phytoplankton communities in lakes are thought to be controlled by interactions between two main groups of factors; (i) resource-induced stresses (i.e. light intensity, temperature, nutrients); and (ii) the frequency and strength of hydraulic mixing processes (Reynolds, 1987). These factors vary at a range of time scales and create a massive range of transient niches, resulting in interspecific competition between species with different morphological and physiological adaptations.

It is possible to discern broad categories of adaptive responses to seasonal shifts in environmental constraints, related to growth rates and the ability to tolerate resource-induced stresses (Reynolds, 1984). Using the evolutionary ecology ideas of MacArthur & Wilson (1967), Kilham & Kilham (1980) distinguish between r and K-selected species in phytoplankton communities. Those species with short regeneration times and the ability to exploit environments where resources are plentiful are r-strategists which tend to be small, with high surface area to volume ratios (SA:V). In contrast, K-strategists have much slower growth rates and are more tolerant of depleted resources. Typical r-selected species in shallow eutrophic lakes are small, centric diatoms and this explains their dominance in spring and often in autumn, when nutrients are abundant and the water is cold, intensely wind-mixed and turbid with suspended solids. In deep lakes as the water column becomes warmer and more stable in summer and as nutrients are depleted, K-selected species, such as cyanophytes may become prevalent (Reynolds, 1984), whereas in shallow lakes the transition to K-selected species may be interrupted, or prevented by sporadic internal nutrient loading, or rapid flushing which will again favour r-strategists which can best capitalise on the the freely available nutrients (Reynolds, 1984; Havens, 1991). Moreover in some shallow lakes the 'typical' phytoplankton succession may also be precluded by the growth of submerged and floating plants which select against phytoplankton development and channel the available resources into the periphyton during summer and autumn (Moss, 1990).

It is evident therefore that there is some degree predictability at the 'gross' level of which phytoplankton group (i.e. r-selected diatoms, or K-selected cyanophytes) will dominate during different parts of the year in shallow lakes. However the seasonality of the majority of diatom species found in shallow lakes is to a large extent poorly understood. This is particularly so with the small centric diatoms which often proliferate in eutrophic environments and it seems likely that taxonomic confusion has prevented detailed seasonal and ecological studies at the specific level (Anderson, 1990c; Clarke, 1992).

Planktonic diatom seasonality

Monthly shifts in diatom relative abundance in the water samples collected from the three study lakes are given in figs. 4.9, 4.10 and 4.11 and changes in diatom densities and centric diatom biovolume are given in figs. 4.12, 4.13 and 4.14. As cell size varies considerably between species, biovolume provides a potentially more reliable indication of cell carbon content (and hence biomass) than cell concentrations (Reynolds, 1984).

The biovolume of each of the centric species encountered in the study lakes was estimated using mean diameter and height measurements with the LM (typically over 20 specimens of each species were measured). In the absence of reliable height estimates for the unicellular centric species, cell volumes were estimated using the assumption that the height of each cell was approximately one half of its diameter (cf. Bailey-Watts *et al.*, 1989) (table 4.5). If a species was abundant in more than one lake separate biovolume estimates were made for each site. The dramatic size differential between some centric species is illustrated by a comparison of the large species *Stephanodiscus* cf. *medius* (1520 μm^3) and the tiny form *Thalassiosira pseudonana* (58 μm^3), the latter being able to fit into the space of the former some 58 times.

Site	*Species*	Mean size	Biovolume (μm^3)	Anderson (1994a)
Tween	*Stephanodiscus parvus*	d 6.1	89	135
	Stephanodiscus cf. *medius*	d 15.7	1520	2300
	Pelagodictyon tenue	d 9.95	387	740†
	Pelagodictyon fritzii	d 8.94	281	
	Cyclostephanos dubius	d 10.48	452	680
	Cyclotella meneghiniana (small)	d 6.2	94	
	Cyclotella meneghiniana (large)	d 10.7	481	
	Cyclotella atomus	d 4.65	40	85
	Cyclotella pseudostelligera 2	d 5.1	52	160
	Cyclotella sp. 1	d 4.8	43	
	Thalassiosira guillardii	d 6.5	108	
	Skeletonema potamos	l 8, d 3.5	77	
	Aulacoseira aff. *alpigena*	l 3, d 5	59	
Clifton	*Stephanodiscus parvus*	d 6.34	100	
	Cyclostephanos tholiformis	d 4.77	43	110
	Cyclostephanos dubius	d 9.2	306	
	Thalassiosira pseudonana	l 3.89, d 2.89	26	
	Aulacoseira granulata var. *angustissima*	l 12.3, d 4.25	175	
Groby	*Stephanodiscus parvus*	d 6.74	120	

Table 4.5. Biovolume of the common centric diatoms encountered in the three study lakes and a comparison with values obtained by Anderson (1994a). l = mean cell length, d = mean cell diameter. † = probably *Stephanodiscus hantzschii* in Anderson (1994a).

Tween Pond

In Tween Pond there were two main phases of planktonic diatom growth in spring and autumn with peaks of 156 x 10^5 cells l^{-1} and 281 x 10^5 cells l^{-1} in late March and late August respectively and much lower population densities in winter and late June (<10 x 10^5 cells l^{-1}). This same pattern was evident in the biovolume data, but the late August peak was less pronounced relative to that in late March due to the dominance of the small form *Skeletonema potamos* in the latter period.

The centrics *Stephanodiscus parvus*, *Pelagodictyon fritzii* and *Pelagodictyon tenue* were dominant in late winter-spring, the latter species occupying over 40% of assemblage relative abundance and the predominant portion of total centric diatom biovolume (265 x 10^7 μm^3 l^{-1}) in the late March peak. The contribution of these three species had declined by late May and there was an increase in the importance of *Stephanodiscus* cf. *medius*, *Cyclotella meneghiniana* and *Cyclotella atomus*. Planktonic diatoms were sparse in early summer and with the rise in cell densities in late July, the planktonic community largely consisted of *C. meneghiniana* and *C. atomus*, with much smaller percentages of those species which were common during the late winter-spring maximum. The late August peak in diatom cell densities saw a dramatic increase in the relative importance of *Skeletonema potamos* (>50%). This form was found to co-dominate the late summer-autumn plankton with *C. meneghiniana* and *C. atomus* with the additional importance of *S.* cf. *medius* in late Sept. The latter species was dominant in the late Oct sample (>60%) at which time *C. meneghiniana*, *C. atomus* and *S. potamos* had declined significantly. It is notable that in biovolume terms *S.* cf. *medius* was the prevalent planktonic form throughout the May-Oct period.

Clifton Pond

The early season peak in planktonic diatom growth in this lake occurred earlier in the year than in Tween Pond and a large population was present in early Feb (150 x 10^5 cells l^{-1}). The population that was achieved in late Feb (214 x 10^5 cells l^{-1}) was also in excess of the early season maximum in Tween Pond which occurred on the same day. However if the dimensions of these crops are compared using the biovolume data, it is apparent that despite higher cell densities, centric diatom biovolume (213 x 10^7 μm^3 l^{-1}) was almost half of that in Tween Pond (409 x 10^7 μm^3 l^{-1}). There was a marked decline in diatom abundance in late April (9.1 x 10^5 cells l^{-1}) and subsequently diatoms were comparatively sparse (despite minor resurgences in late May and late July).

The centric forms *Cyclostephanos dubius*, *Cyclostephanos tholiformis* and *Thallasiosira pseudonana* were dominant in late winter-spring and because the latter two forms are very small, *C. dubius* occupied the majority of total centric diatom biovolume. The competitive ability of *T. pseudonana* declined significantly in late April (<5%) and over the rest of the sample period *C. tholiformis* and *C. dubius* were the most prevalent forms. On those days when centric diatoms were very sparse, epiphytic forms dislodged from the submerged aquatic plants such as *R. abbreviata, C. placentula* and *N. paleacea* were significant in relative abundance terms.

Groby Pool

There was again one major phase of planktonic diatom growth in late winter. However the size of this early maximum was much reduced compared to the other study lakes with a peak of 27 x 10^5 cells l^{-1} in early March and a slightly lower density in late March (22 x 10^5 cells l^{-1}).

The plankton was partitioned between fewer dominant species and *S. parvus* was the predominant form accounting for 70% of the assemblage in both early and late March, while *P. fritzii* was also found to a much lesser extent (<15%). The former species was also dominant in terms of total centric biovolume which was also significantly reduced compared to the other two study lakes. There was a dramatic reduction in diatom densities in late April and true planktonic forms were very scarce subsequently (<5 x 10^5 cells l^{-1}). There were much higher percentages of non-centric forms associated with submerged plant beds after the spring, and in particular *Fragilaria capucina* var. *mesolepta* attained 52% in late August. Also as the plants were dying back in early Sept the epiphyte *N. paleacea* was washed into the plankton and accounted for 68% of sample relative abundance. The life-form of *F. capucina* var. *mesolepta* is problematic. Reavie *et al.*, (1995b) suggest it is periphytic, while Bennion (1995) indicates that it may be partly planktonic. It was sparse on the plant samples (<2%) and absent from the epilithic collections (tables 4.3, 4.4) and therefore was probably partly associated with the epipelic niche. In this study this species is considered to be tychoplanktonic.

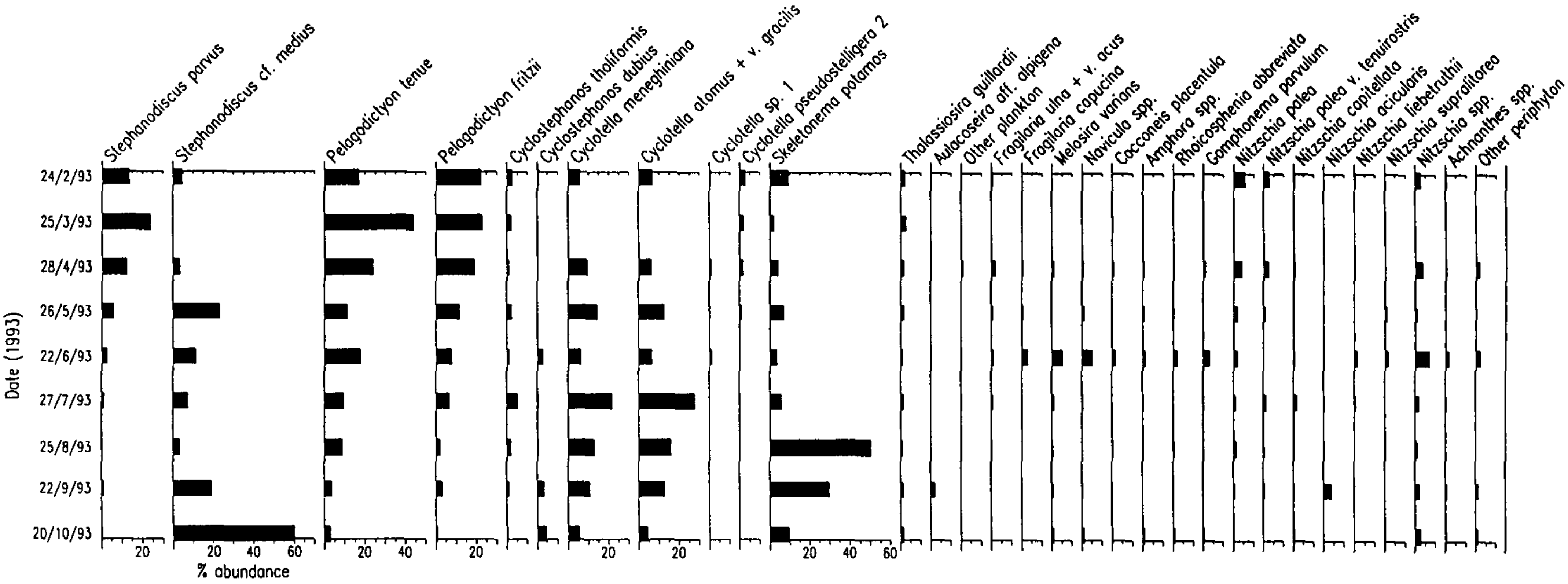


Fig. 4.9. Monthly changes in diatom assemblages found in the plankton of Tween Pond.

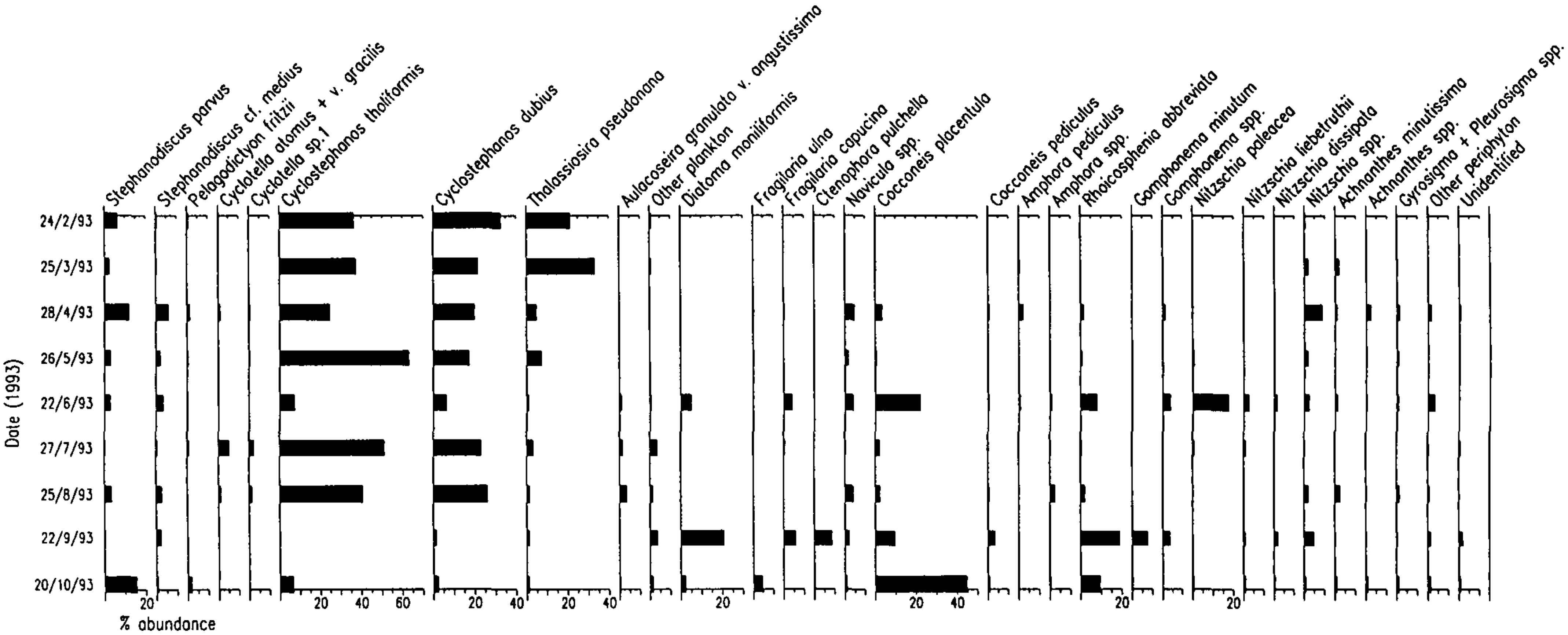


Fig. 4.10. Monthly changes in diatom assemblages found in the plankton of Clifton Pond.

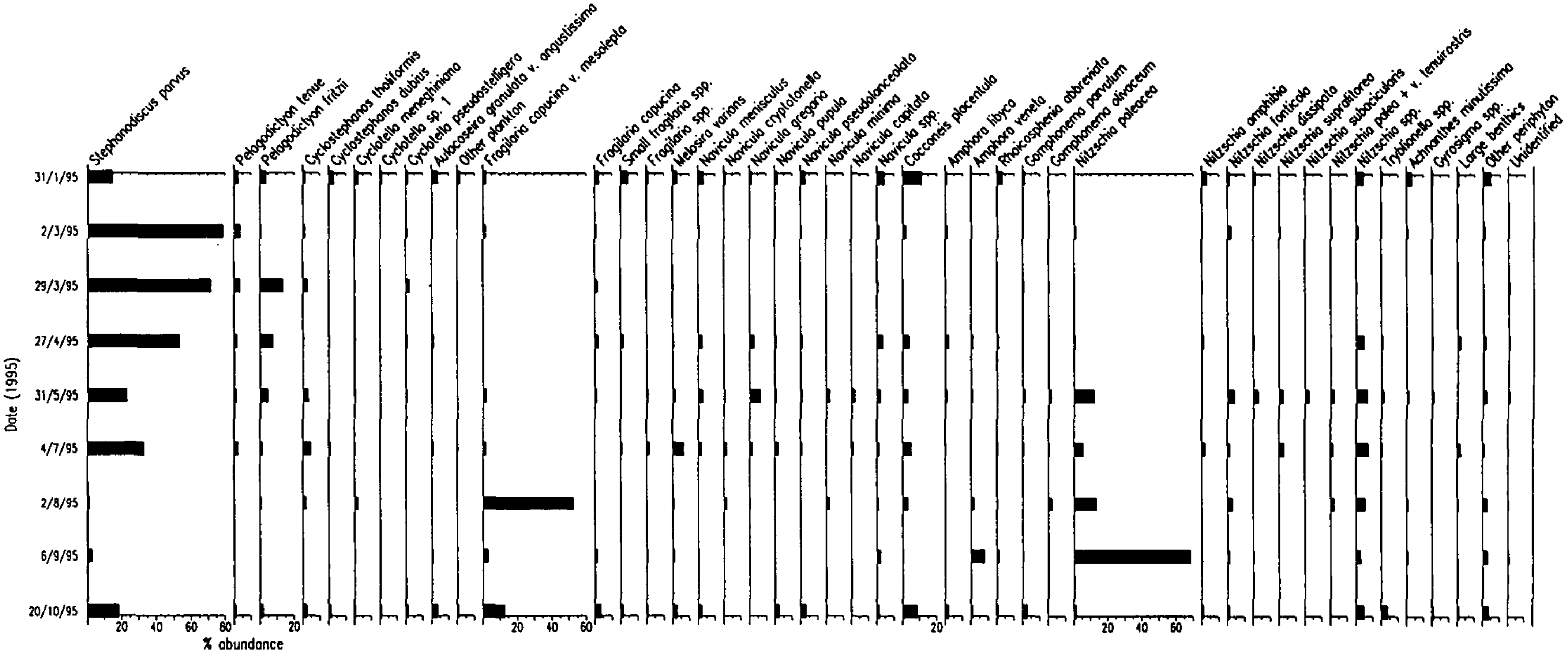


Fig. 4.11. Monthly changes in diatom assemblages found in the plankton of Groby Pool.

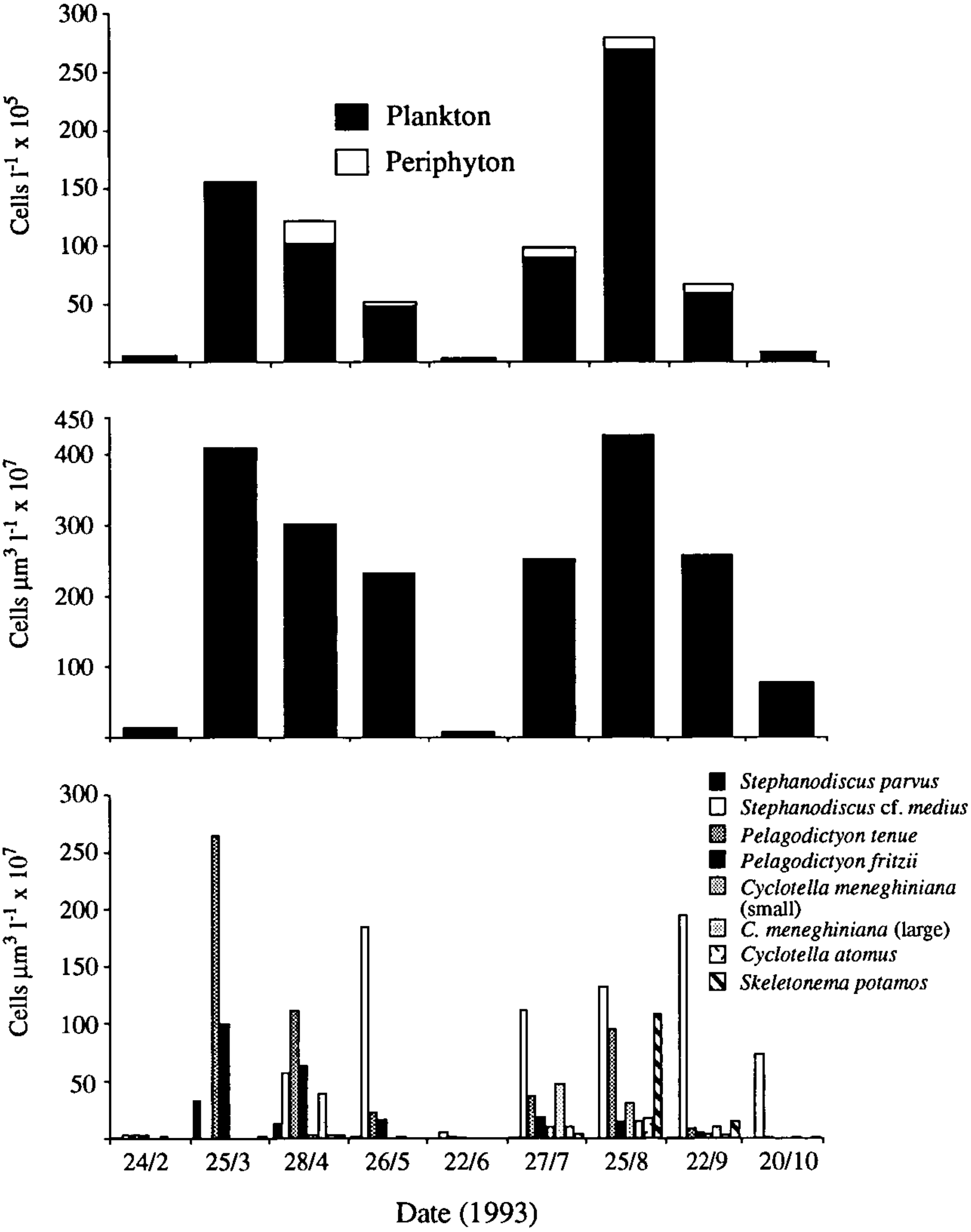


Fig. 4.12. Monthly changes in diatom abundance (cells l^{-1}) and diatom biovolume (μm^3 l^{-1}) in the plankton of Tween Pond.

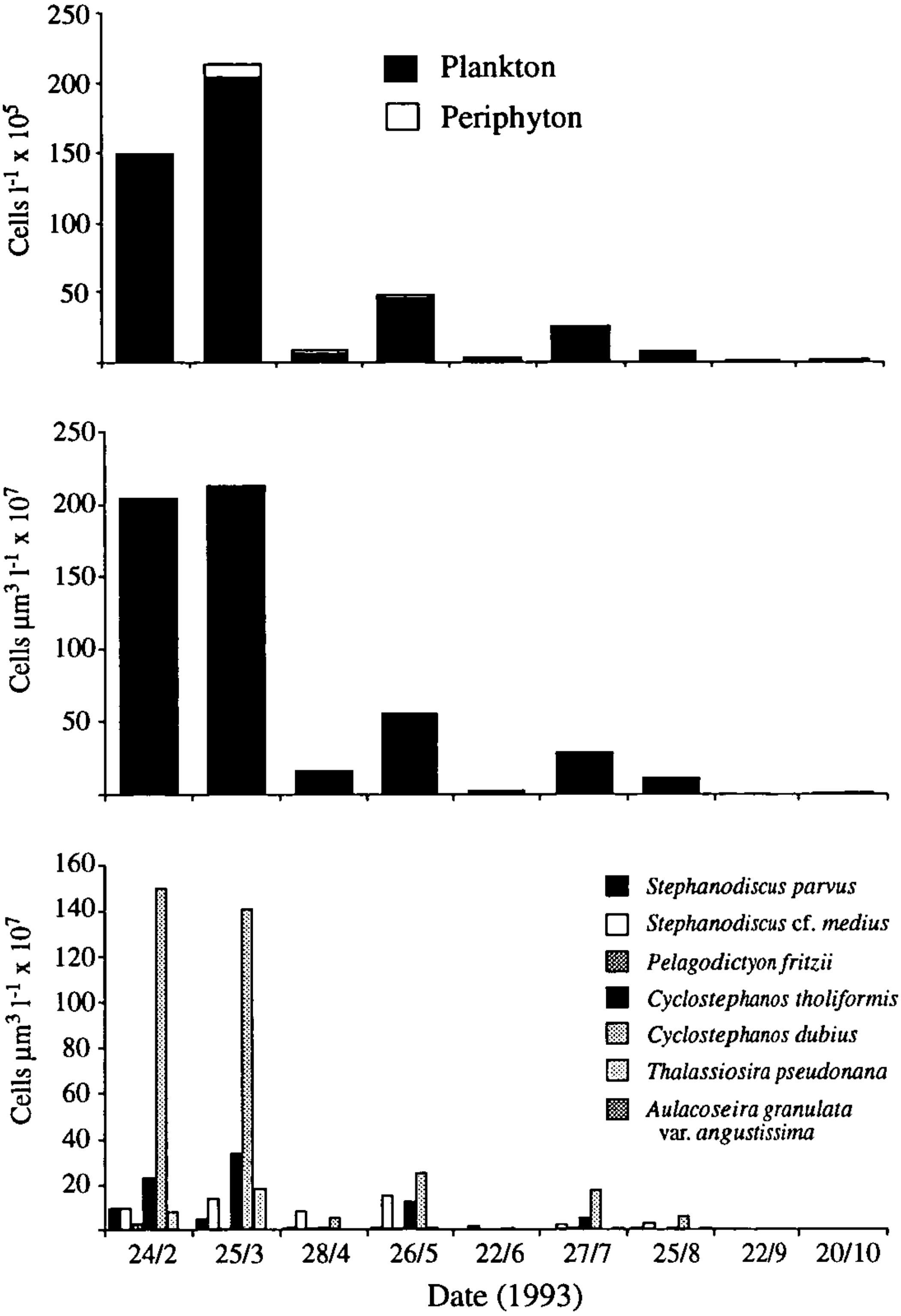


Fig. 4.13. Monthly changes in diatom abundance (cells l^{-1}) and diatom biovolume (µm^3 l^{-1}) in the plankton of Clifton Pond.

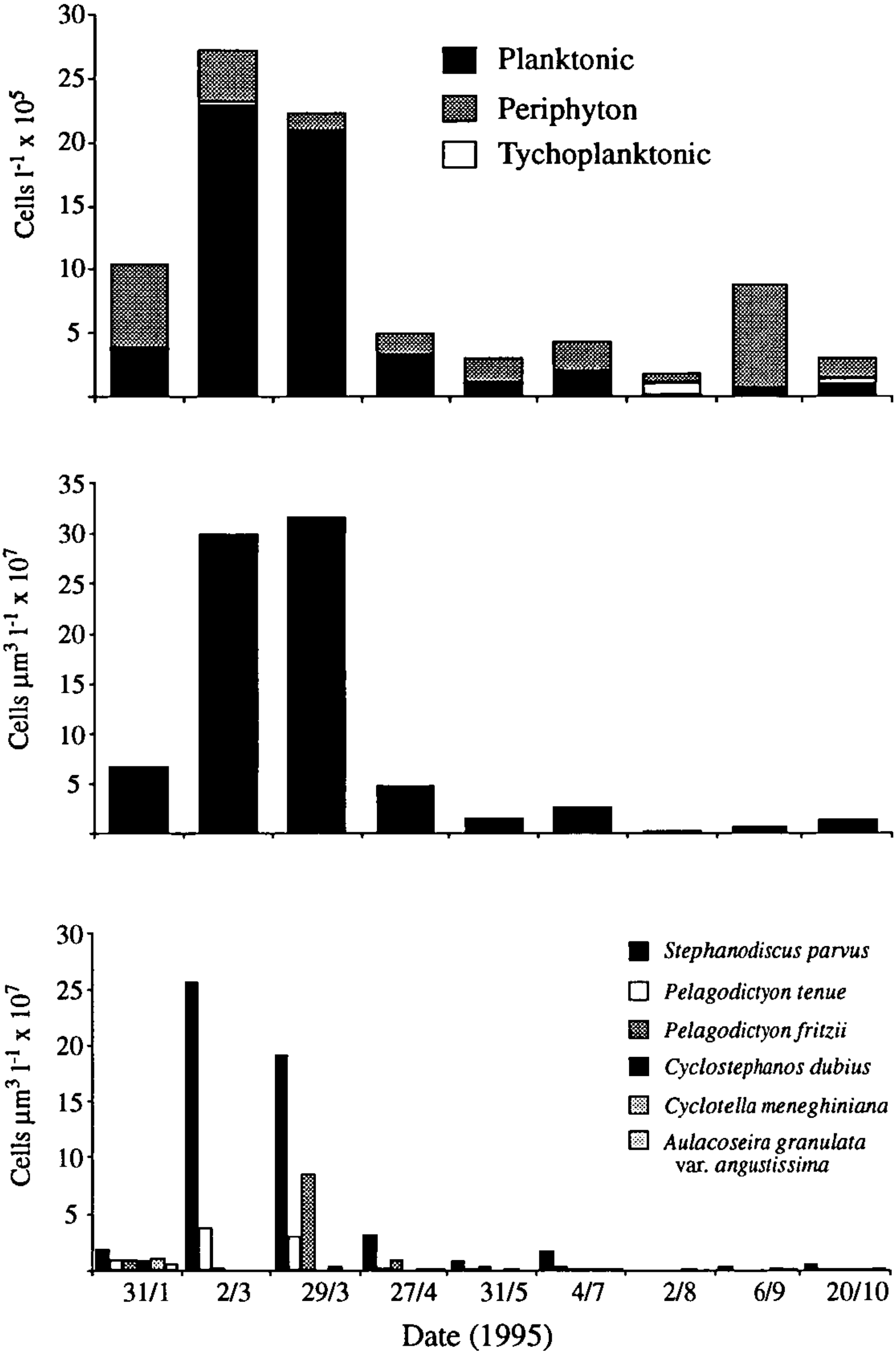


Fig. 4.14. Monthly changes in diatom abundance (cells l^{-1}) and diatom biovolume ($\mu m^3\ l^{-1}$) in the plankton of Groby Pool.

Sediment traps

In each of the three study lakes, two 'tub' type traps were installed at the start of the study period in late winter. One of these traps was sampled monthly (trap I) and the other at the end of the study period (trap II). In chapter two it was shown that the monthly sampled tub traps did not allow for the significant resuspension of once deposited material and hence must have substantially overestimated net particle accumulation rates. However this study was not concerned with quantifying net diatom losses, the major requirements being to; (i) track qualitative seasonal changes in the dominant diatoms in the lake as derived from both the plankton and periphyton; and (ii) estimate seasonal changes in the relative scale of planktonic and periphytic diatom inputs to the sediment, both between lakes and between sample intervals (chapter two).

Major characteristics of the monthly trap collections

The major characteristics of the trap I sediment collections in the three study lakes are compared in table 4.6. Monthly changes in rates of sediment (dry mass) accumulation, diatom concentrations and rates of diatom influx are given in figs. 4.15, 4.16 and 4.17. The organic matter and carbonate content of the monthly trap I collections are given in fig. 4.18.

	Tween Pond	*Clifton Pond*	*Groby Pool*
Mean monthly SM collection rate (mg [DM] $cm^{-2} day^{-1}$)	4.0	1.7	0.8
Mean monthly diatom influx rate (cells x $10^5 cm^{-2} day^{-1}$)	25.5	14.6	2.9
Total sample period diatom influx* % Plankton	88.7	89.3	25.2
Total sample period diatom influx* % Periphyton	11.3	10.7	74.8Δ

Table 4.6. Selected characteristics of the tub trap I catches in the three study lakes. SM = sedimenting material, DM = dry mass * = cumulative total diatom influx collected in all collection intervals in trap I. Δ = includes tychoplankton.

Tween Pond

The dominant primary sources of sedimenting material were probably phytoplankton growing in the lake. There were two major phases of sediment input into the trap in late

March-late May (>4.7 mg cm^{-2} day^{-1}) and late July-late Sept (>5.0 mg cm^{-2} day^{-1}). Least sedimenting material was collected in the early Feb-late March interval (<2.6 mg cm^{-2} day^{-1}). It was not possible to recognise an easily explainable seasonal pattern of organic matter sedimentation in this lake, although there was a marked increase in organic matter percentages during the period of elevated diatom production in late July-late August (>20%). The trap catches in Tween Pond were low in carbonate (typically <8%).

The seasonal pattern of diatom concentrations in the trap material closely followed that for sediment collection rates, suggesting that diatoms may have been the dominant source of sedimenting material. Thus diatom influx (which is the product of these two measures) also followed the same seasonal trend. However, due to lower diatom concentrations in the late summer-autumn period, influx was greatest in the spring with a marked peak, largely of planktonic forms in the late March-April settling interval (94 x 10^5 cells cm^{-2} day^{-1}) which accounted for 41% of total diatom influx into the trap during the study. Periphytic diatoms were never a major component of trap catches and accounted for just 11% of cumulative total diatom input.

Clifton Pond

The main sources of sedimenting material in this lake were probably phytoplankton remains in winter and spring with the additonal importance of macrophyte debris in the summer and autumn catches. Sediment collection rates and diatom influx to the trap were much reduced compared to Tween Pond (table 4.6). Highest quantities of sedimenting material were collected in late March-late May (>2.8 mg cm^{-2} day^{-1}) and to a lesser extent late June-late August (>1.8 mg cm^{2} day^{-1}). A marked peak in the organic matter content of the entrapped material was evident in the late Feb-late March interval (23%), associated with the sedimentation of the late winter diatom crop. However, percentages then declined and remained below 15% until late July-late August when plant matter became an important constituent of the trap catches and percentages remained high (>16%) for the rest of the study. There was a minor peak in carbonate percentages in the late June-late July interval (11%), but as in Tween Pond carbonate was not an important constituent of the trap catches.

Highest diatom concentrations in the sediment were achieved in late winter-spring and far exceeded those attained in Tween Pond. The influx of diatoms into the trap was closely related to diatom concentrations with an extremely high rate of influx in the late Feb-late March interval (76 x 10^5 cells cm^{-2} day^{-1}) which acccounted for 58% of cumulative total diatom input into the trap during the study. However influx was significantly reduced in the subsequent late March-late April interval and over the rest of the study period remained below 4.5 x 10^5 cells cm^{-2} day^{-1}. Planktonic forms accounted for the dominant part of the trap recoveries (89%) and periphytic diatoms were relatively insignificant (11%) in terms of total input into the trap.

Groby Pool

The major sources of primary sedimenting material were again probably phytoplankton in winter and spring and plant and filamamentous algae remains in summer and autumn. Even lower rates of sediment collection and diatom influx into the trap were evident (table 4.6). Most sedimenting matter was collected in late Jan-late March (>1.3 mg cm^{-2} day^{-1}) and lesser quantities were collected during spring, summer and autumn (<0.9 mg cm^{-2} day^{-1}). Until late summer, organic matter percentages were relatively high and stable (17-21%), but as the submerged macrophytes started to die back in the autumn-early winter period, there were considerable inputs of plant tissue into the traps and organic matter levels increased significantly (>25%). In contrast to the other two study lakes carbonate percentages were relatively high and there was a definite seasonal patterning with elevated levels in the early March-late March catch (>30%) and lower levels throughout the rest of the study period (<20%). This late winter maximum may have been the result of increased dissolved CO_2 uptake by phytoplankton (possibly planktonic diatoms) and thus enhanced biogenic carbonate precipitation, or possible increased inputs from the catchment.

Highest diatom concentrations in the sediment were achieved in late May-early August and diatom influx was also maximised (>4.3 x 10^5 cells cm^{-2} day^{-1}) in this period. Inputs of planktonic diatoms into the trap were highest in early March-late April. However periphytic and to a lesser extent tychoplanktonic forms became dominant after the spring and together were found to account for almost 75% of the diatoms recovered in the trap during the study.

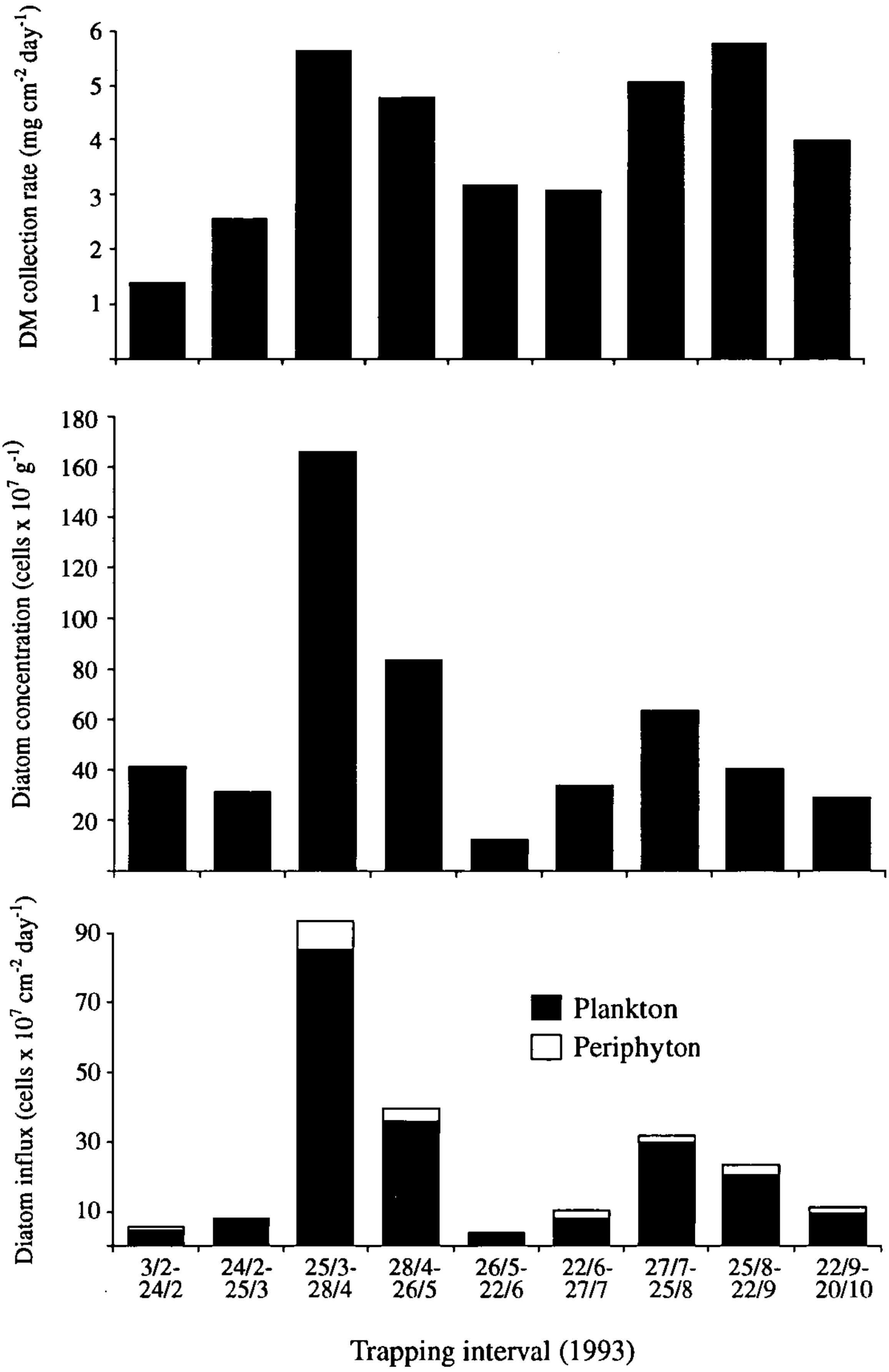


Fig. 4.15. Monthly changes in mean daily dry mass (DM) collection rates, diatom concentrations and daily rates of planktonic and periphytic diatom influx into trap I (sampled monthly) in Tween Pond.

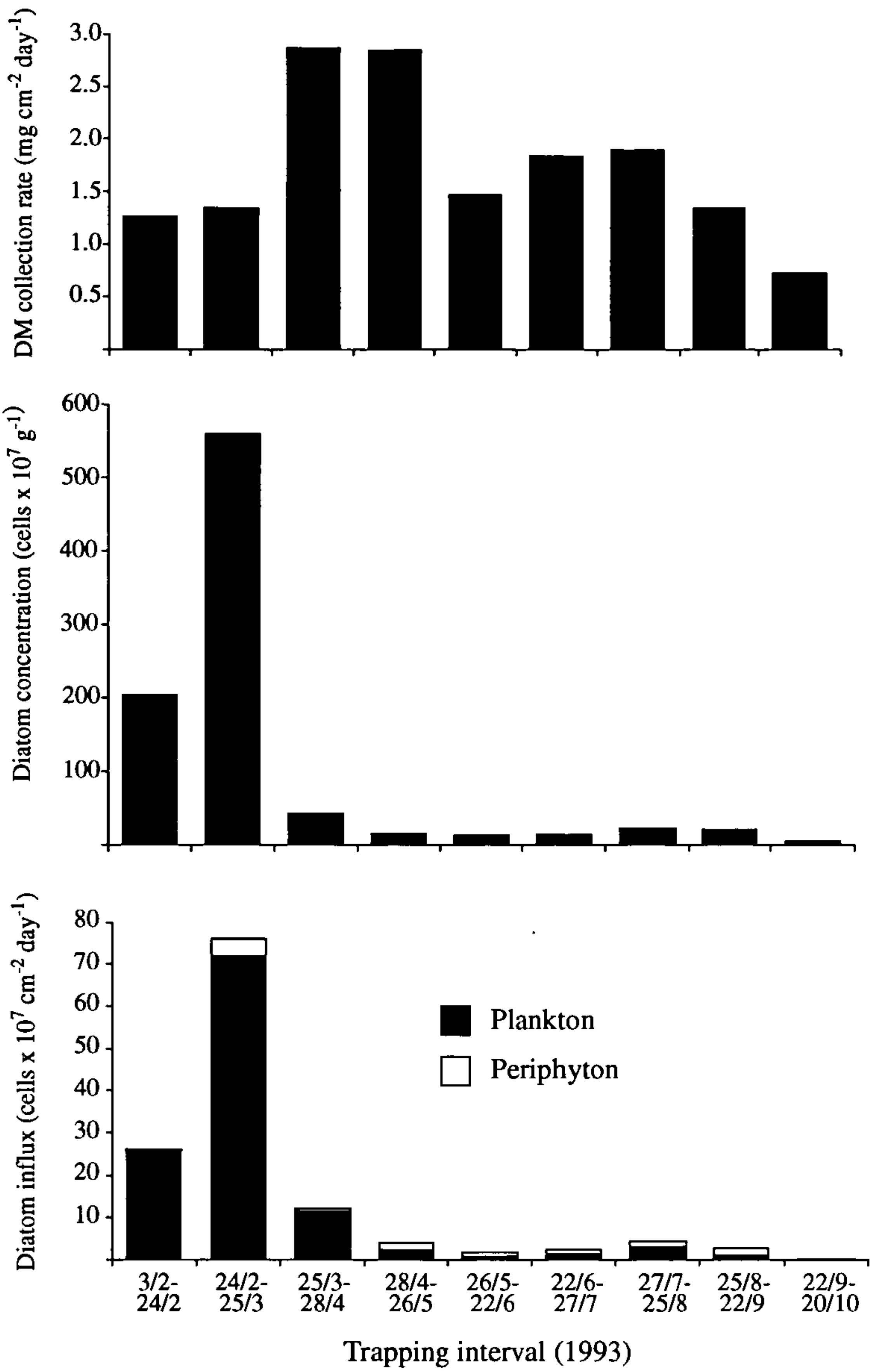


Fig. 4.16. Monthly changes in mean daily dry mass (DM) collection rates, diatom concentrations and daily rates of planktonic and periphytic diatom influx into trap I (sampled monthly) in Clifton Pond.

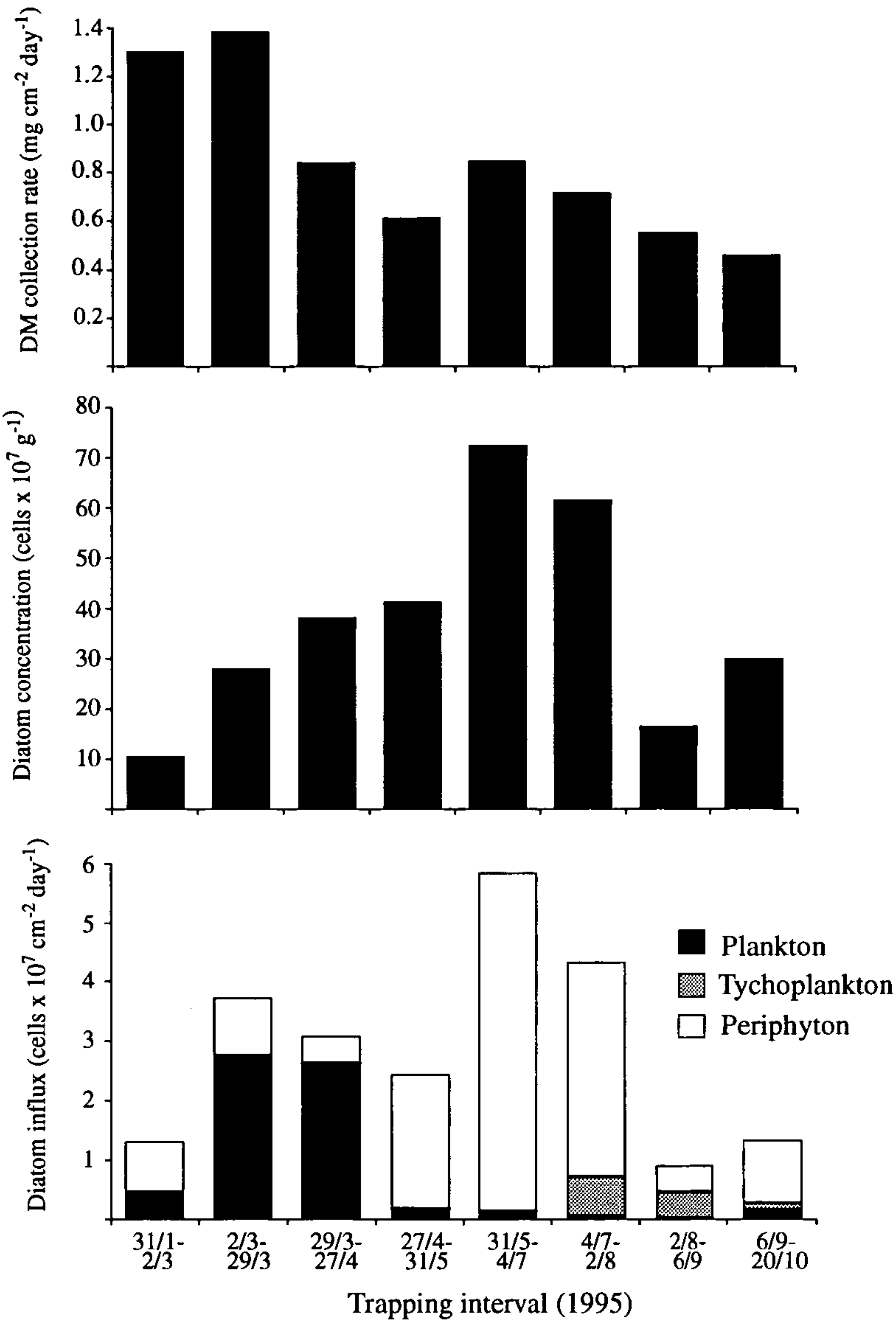


Fig. 4.17. Monthly changes in mean daily dry mass (DM) collection rates, diatom concentrations and daily rates of planktonic, tychoplanktonic and periphytic diatom influx into trap I (sampled monthly) in Groby Pool.

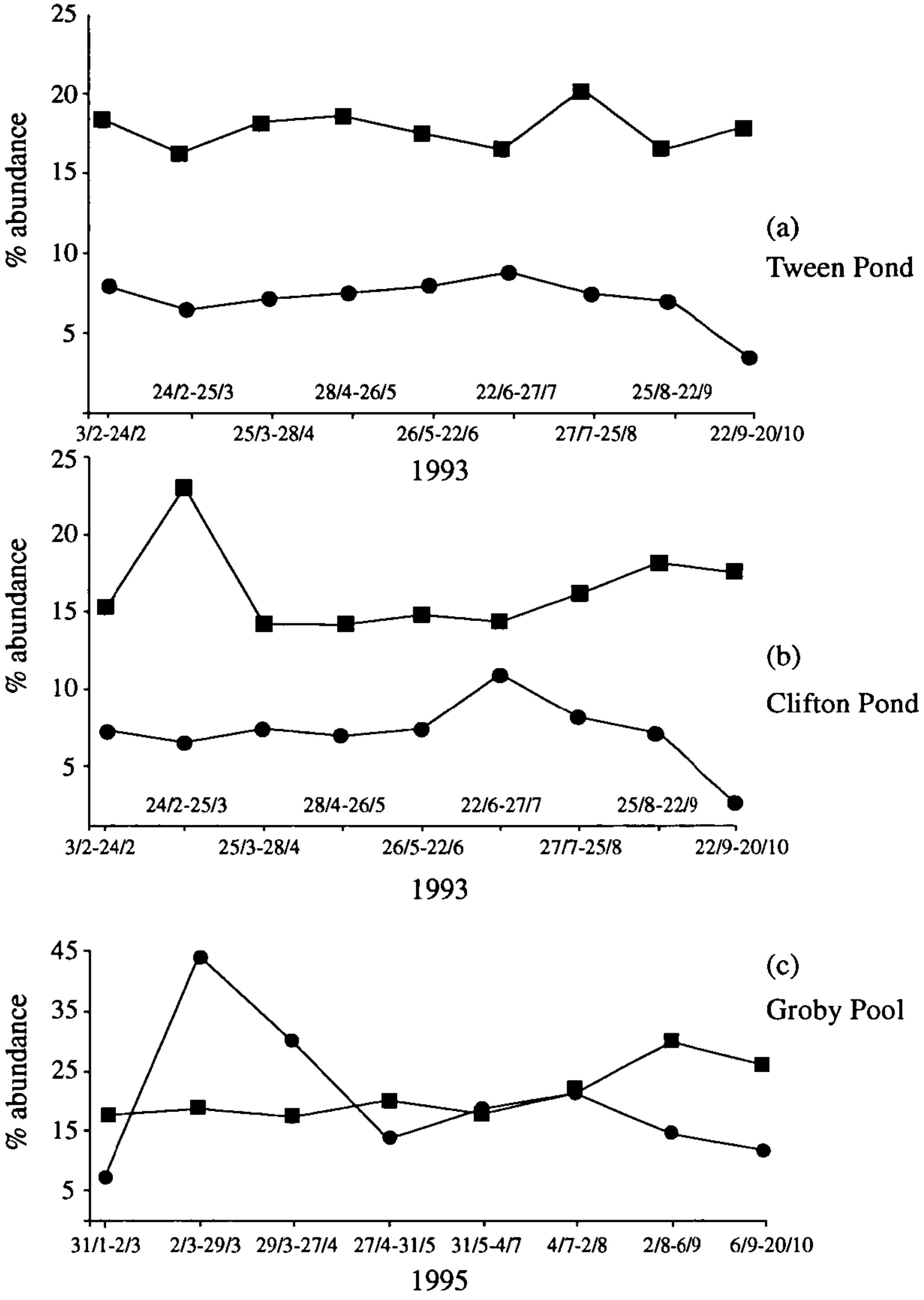


Fig. 4.18. Seasonal changes in the organic matter (squares) and carbonate (circles) content of the material collected in trap I (sampled monthly) in Tween Pond (a), Clifton Pond (b) and Groby Pool (c).

Relationships between modern diatom communities and surface sediment assemblages

The question of diatom representation in lake surface sediments is rarely addressed, but intuitively it would appear to be easily studied by comparing diatom samples from modern source communities in the plankton and periphyton, with the assemblages which accumulate in sediment traps and surface sediments. This approach has been successfully adopted by Haberyan (1990) and has also been used here. In the next part of this chapter the four sample types collected from the three lakes, i.e. (i) modern plankton and periphyton samples; (ii) trap I samples; (iii) trap II samples; and (iv) natural surface sediment samples are compared in turn. Unfortunately due to infrequent sampling, it has not been possible to estimate maximum diatom crops in the water column, so that the theoretical downward flux of planktonic diatoms could be predicted and quantitatively compared with the influx of planktonic diatoms into the trap. Thus the modern plankton and periphyton samples are compared with the trap I diatom assemblages (figs. 4.19, 4.20, 4.21) in a qualitative manner. The trap I, trap II and surface sediment assemblages are compared using percentage data as given in tables 4.7, 4.8 and 4.9 and fig. 4.23. To make the trap I diatom assemblages comparable to the other two samples types it has been necessary to calculate the theoretical relative contribution of each species to the cumulative total influx of diatoms into trap I during the entire study period (termed cumulative trap I).

There are obvious problems associated with comparing the modern plankton and periphyton assemblages with the trap I assemblage. This is because sediment resusupension may mean that non-contemporary species are incorporated in the sedimenting material. Moreover the cumulative trap I, trap II and surface sediment samples are not strictly comparable as they represent different time intervals and were collected in different ways. The natural surface sediment samples contain assemblages which accumulated over an unknown interval, whereas the trap samples were collected over a specific period. Moreover the sediment traps do not allow for the significant resuspension of entrapped material, while once deposited material is freely resuspended at the sediment surface. There are also problems associated with the use of percentage data to make comparisons between samples, as a proportionate increase in one species causes a proportionate decrease in the remaining ones. Thus if one species is superabundant, percentages of many other species are likely to be depressed. The importance of these problems are considered in the interpretation of the results.

Tween Pond

The late March-late May and late July-late Sept phases of increased diatom input into the trap (fig. 4.15) correspond very closely to periods when large diatom populations were encountered in the plankton (fig. 4.12). This supports the previously stated hypothesis that there were two phases of intensive planktonic diatom development in Tween Pond. While the largest planktonic diatom populations were evident in late summer, higher rates of diatom influx into the trap in spring suggest that this was the most important episode of planktonic diatom production. However this may have been the result of increased resuspension inputs during this period. The seasonal species succession in the trap (fig. 4.19) very closely mirrored that of the plankton (fig. 4.9) and those forms which were prolific in the water samples were also abundant in the sediment trap at approximately the same time. In early Feb-late May the trap was dominated by varying proportions of the species *S. parvus*, *P. tenue*, *P. fritzii*, *C. atomus*, and *S. potamos*. However *C. atomus* and *S. potamos* were much more abundant in the trap than they were in the plankton. These species have been found to grow most prolifically in the summer and autumn in eutrophic lakes and rivers (Kiss & Padisák, 1990; Kiss *et al.*, 1994) and it seems likely that a high percentage of the spring catches of these forms represented resuspended inputs. In the summer trap samples there was a switch to the increased importance of *S.* cf. *medius*, *C. meneghiniana* and *C. atomus*, while the small chain-forming centric *S. potamos* was the most prolific form in the late August-late Oct sediment trap catches (>26%). The post-spring sequence of events in the traps were very similar to those observed in the plankton.

The low abundances of periphytic diatoms in the traps (<25%) were to be expected given the absence of submerged plants from the lake and the shading of the sediment by dense phytoplankton crops. The only potential source habitat for periphytic forms in the lake was the epilithon and possibly the branches of overhanging trees. Those species which were common in the epilithon, *N. paleacea*, *Melosira varians* and *Gomphonema parvulum* (table 4.4) were present in very low percentages in the traps (<2%) and the small *Nitzschia* spp., *Nitzschia palea*, *Nitzschia palea* var. *tenuirostris* and *Nitzschia agnita* were the dominant periphytic forms. It is probable that a high proportion of the small *Nitzschia* spp. were derived from the River Erewash where they were have been found in considerable abundance in the epilithon and epipelon (Gell, unpublished data). However this may not mean that they were strictly allochthonous, as it is possible that inwashed populations (particularly *N. palea* and its *tenuirostris* morphotype) survived in a tychoplanktonic mode of existence for some time.

There was a remarkable similarity between percentages of the majority of the dominant and minor species in the cumulative trap I and trap II collections (table 4.7, fig. 4.22a,) and this confirms the hypothesis that the sediment already collected in the traps was not subject to significant resuspension. However there were more substantial differences between the two trap samples and the surface sediments. This was particularly evident for the tiny, chain-building centric *S. potamos* which achieved just 1% in the surface sample compared to 13% in the cumulative trap I assemblage and 25% in trap II. This species was found most abundantly in the plankton in late August when there was a very large population (50×10^5 cells l^{-1}). The surface sediment sample from Tween Pond was collected in July and this means that at this time the most recent input of this species to the sediment would have probably been some 9-10 months earlier. Thus it seems probable that these more recently growing diatom populations were better represented in the July sediment sample due to the reduced opportunity for the operation of decomposition processes (degradation induced by benthic invertebrates and resuspension-redeposition cycles) and Si-dissolution on recently sedimented populations. However it is also possible given the current, very rapid rate of sediment accumulation in Tween Pond (i.e. >2 cm yr^{-1}) that the July sediment sample represents significantly less than one years sediment build-up.

Clifton Pond

The pattern of planktonic diatom influx into the trap (fig. 4.16) closely followed monthly changes in the abundance of cells encountered in the water column (fig. 4.13) with a peak in early Feb-late March and much reduced inputs in the subsequent period. In this late winter peak the trap recoveries were dominated by the tiny centric form *T. pseudonana* (>50%) and to a lesser extent *C. tholiformis*, *C. dubius* and *S. parvus* (fig. 4.20). These species were also prevalent in the plankton during this period (fig. 4.10). *T. pseudonana* was rare in both the trap and plankton samples after the spring, but *C. tholiformis* and *C. dubius* were present in high relative frequencies, although they were sparse in the late Sept-late Oct interval. In early June dense beds of submerged plants had established themselves in the lake and there was a shift to the increased prevalence of periphytic forms in the trap collections. The species *R. abbreviata*, *C. placentula* and to a lesser extent *Amphora pediculus* became increasingly abundant in the trap catches, together accounting for over 45% of the assemblage in late August-late October. It is likely that *R. abbreviata* and *C. placentula* were transferred into the traps from the epiphyton as they were both found to be abundant on the submerged plant *P. pectinatus* (table 4.3). However *A. pediculus* was only a minor species (<4%) on the plants and was also relatively rare in the epilithon (<2%) (table 4.4) where it is often found (cf. Lee & Round, 1989) and so may have been derived from the epipelic life-form. Although these three periphytic forms were important in percentage terms, due to the much lower rates of diatom input into the trap after the spring they accounted for just 4% of the total quantity of diatoms recovered in the trap during the study.

The cumulative trap I diatom assemblage was significantly different to the trap II and July sediment assemblages (table 4.8, fig. 4.22b) due largely to the much higher relative abundance of *T. pseudonana* (53%) compared to the other two sample types (<9%). The major input of *T. pseudonana* into trap I was in late winter and one explanation for the much higher percentages of this species in this sample might be that the relative influx of this species was exaggerated due to frequent inputs of resuspended sediment. If this was the case then it might be expected that percentages of *T. pseudonana* in trap II would be much higher than in the surface sediment. However percentages were very similar in both these collections which makes this hypothesis less likely. An alternative hypothesis is that *T. pseudonana* was underrepresented in trap II and in the July sediment sample due to selective decomposition and dissolution. Evidence for this comes from the near complete loss of this species in re-examined sediment samples (i.e. for the SEM study) which were dominated by this form when freshly collected (see chapter three). Thus it would appear that *T. pseudonana* is very susceptible to dissolution. This is perhaps to be expected given the delicate silicification of this form and its high SA:V ratio (cf. Barker *et al.*, 1994). The recycling of SiO_2 from the sediments of shallow lakes is a common phenomenon in late spring-summer as the external load is depleted by spring diatom populations (Bailey-Watts *et al.*, 1989). Unfortunately it was not possible to establish the relative importance of internal and external sources of SiO_2 in this lake, but extremely low SiO_2 concentrations suggests that internal recycling may have been likely (chapter four). Thus the timing of the *T. pseudonana* maximum (i.e. just prior to Si-dissolution in spring/summer) and its tiny and delicate morphology may have favoured major diagenetic losses. High percentages of this species in the cumulative trap I sample make it difficult to compare the relative abundance of the other dominant species with the trap II and July sediment samples. However the same species were present, but in depressed percentages. This was particularly evident for the epiphytes *C. placentula* and *R. abbreviata.*

There were close similarities between the trap II and surface sediment samples and the dominant planktonic species were represented in extremely similar percentages. However there were important differences between percentages of the dominant periphytic forms *R. abbreviata* and *Gyrosigma* spp. The former species was present in the surface sample at just 3% compared to 12% in trap II. This could potentially be explained by the late season (i.e. post July) growth of this species in both the epiphyton and epilithon, such that the collection of the July sediment sample preceded its maximum abundance in the lake. Thus similarly to *S. potamos* in Tween Pond it is possible that there were increased opportunities for the degradation of this species in the sediments relative to those forms which were prevalent in spring and early summer. Also large benthic *Gyrosigma* spp. were rare in the cumulative trap I and trap II collections (<1%), but achieved 6% in the July sediment. This may mean that *Gyrosigma* spp. did not grow significantly in the traps and so was only introduced into the traps during resuspension events.

Groby Pool

There was a marked peak in planktonic diatom influx into the trap in early March-late April (fig. 4.17) coinciding with the maximum in planktonic diatom growth (fig 4.14), but after this period planktonic diatoms were of minor importance in the trap collections, reflecting much reduced growth in the water column. The small centric *S. parvus* was the dominant planktonic form in early Jan-late April and occupied over 59% of assemblages in the early March-late March and late March-late April trapping intervals (fig. 4.21) The epiphyte *C. placentula* (15%) was of additional importance in the late Jan-early March period, as was the centric form *P. fritzii* (8%) during early March-late April. In this late winter-spring period there was very close overlap between the sediment trap and plankton assemblages and the three dominant species mentioned above were present in the plankton in similar percentages (fig. 4.11). The high percentages of *C. placentula* in the Jan-early March trap collection suggests that a large portion of the material collected in this interval was probably resuspended sediment. In the late April-late May interval *N. paleacea* was prevalent (40%) and *S. parvus* was of much reduced importance (6%). The former species was abundant in both the epiphytic and epilithic samples in Sept (tables 4.3, 4.4), but during late April-late May it was probably epiphytic on the substantial growths of filamentous algae which were prolific in all parts of the Pool.

The luxuriant growth of submerged plants in summer and autumn and the onset of clear water conditions afforded a massive potential habitat for periphytic diatom colonisation in the Pool and over the rest of the study period (i.e. late May-late Oct) a range of periphytic forms were dominant, while planktonic forms were very sparse (<10%). The dominant epiphytes were *C. placentula*, *Amphora veneta*, *Nitzschia fonticola*, *Nitzschia amphibia*, *Achnanthes minutissima* and once again *N. paleacea*. These species were abundant in the submerged plant samples (table 4.3) and probably entered the trap attached to falling debris from the overlying plant canopy. In the late May-early July peak in diatom influx a small form of *N. meniscuslus* was dominant (16%). This species was not found on the submerged plants surfaces or attached to rocks in the margins (tables 4.3, 4.4) and it is assumed that it was probably associated with the epipelic habitat. Similarly *G. parvulum*, *G. minutum* and *N. supralittorea* were also abundant in the summer trap collections and were also rare in the plant collections, so again were probably associated with the epipelon. It is probable that these species and *N. menisculus* were actually growing on the sediment collected in the traps. The tychoplanktonic species *F. capucina* var. *mesolepta* was abundant in mid summer-early winter, achieving 43% in the early August-early Sept interval. This species attained high percentages in the plankton samples at around this time.

The cumulative trap I and trap II assemblages were extremely similar with comparable percentages for most of the major and minor species (table 4.9, fig. 4.22c). The only notable exception to this was the higher relative abundance of *N. paleacea* in the cumulative trap I assemblage (9%) compared to trap II (2%). The hypothesised influence of sample timing on the diatom assemblages found in surface sediment collections was investigated in the Pool by comparing two samples taken in April and Oct. There were some important differences between these two sediment samples with much higher percentages of *S. parvus* (44%) and lower percentages of *F. capucina* var. *mesolepta* (2%) and *C. placentula* (7%) in April compared to Oct (i.e. 24%, 10% and 13% respectively). These differences would again appear to be closely related to the time that the sample was taken, with higher abundances of *S. parvus* in April due to the recent peak of this species in March and higher abundances of *F. capucina* var. *mesolepta* and *C. placentula* in Oct as related to the increased abundance of these species in the lake in summer and autumn. Thus the same phenomenon observed in the other two study lakes was also evident in the Pool and for this reason the Oct sediment sample was much more similar to the cumulative trap I and trap II assemblages than the April sample.

Species	tub trap I (cumulative %)	tub trap II %	SS (July) %
S. parvus	12.39	8.85	6.65
S. cf. *medius*	5.21	6.54	12.43
P. tenue	11.79	12.56	20.67
P. fritzii	9.54	6.28	7.88
C. tholiformis	2.17	1.67	0.35
C. meneghiniana	8.89	7.05	19.26
C. atomus + *v. gracilis*	19.23	18.46	11.21
C. pseudostelligera 2	1.93	0.64	0.53
S. potamos	13.21	25.00	1.23
T. guillardii	3.25	2.69	1.75
G. parvulum	0.28	0.00	1.23
N. lanceolata	0.44	0.00	1.93
Navicula spp.	0.69	0.51	1.23
N. palea	1.30	1.92	2.80
N. palea v. *tenuirostris*	1.55	0.77	0.88
N. agnita	1.12	0.00	0.70
Nitzschia spp.	1.55	1.54	3.15
Plankton	89.34	63.12	61.13
Periphyton	10.66	36.88	38.87

Table 4.7. The relative abundance of the dominant species (>1% in any one sample) in trap I (percentage abundance of cumulative total diatom influx for the entire study period), trap II and in surface sediment samples (SS) collected in July (0-2 cm surface layer from core TP193) from Tween Pond.

Species	tub trap I (cumulative %)	tub trap II %	SS (July) %
S. parvus	5.74	5.81	8.87
S. cf. *medius*	1.52	3.82	5.47
P. fritzii	0.41	1.16	1.51
C. tholiformis	19.15	28.90	25.85
C. dubius	8.86	10.96	8.49
T. pseudonana	52.58	8.47	8.11
A. granulata v. *angustissima*	0.10	1.99	0.00
C. placentula	1.66	9.97	9.81
R. abbreviata	1.50	12.29	3.40
N. cryptotonella	0.20	0.00	1.70
N. gregaria	0.58	0.17	1.70
Navicula spp.	0.74	1.66	3.02
Nitzschia spp.	0.91	2.82	2.52
A. pediculus	0.63	1.66	0.57
Achnanthes spp.	0.15	1.66	1.70
Gyrosigma spp.	0.17	0.33	6.42
Plankton	89.34	63.12	61.13
Periphyton	10.66	36.88	38.87

Table 4.8. The relative abundance of the dominant species (>1% in any one sample) in trap I (percentage abundance of cumulative total diatom influx for the entire study period), trap II and in surface sediment samples (SS) collected in July (0-2 cm surface layer from core CP193) from Clifton Pond.

Species	tub trap I (cumulative %)	tub trap II %	SS (April) %	SS (Oct) %
S. parvus	20.26	28.62	43.71	24.36
P. tenue	0.47	0.50	3.10	0.54
P. fritzii	2.61	0.67	2.13	1.27
F. fasciculata	2.13	0.50	0.00	0.72
F. capucina v. *mesolepta*	5.98	6.66	2.32	10.00
Small *Fragilaria*	0.39	1.33	2.89	6.18
M. varians	2.45	1.66	4.84	5.09
C. placentula	4.36	3.16	7.16	13.27
R. abbreviata	2.49	5.82	1.16	2.00
N. menisculus	0.66	2.50	0.58	2.36
N. menisculus small	4.98	3.99	0.39	0.18
N. gregaria	1.18	2.66	0.39	1.27
N. pseudolanceolata	0.44	3.00	3.09	2.18
Navicula spp.	1.37	3.66	3.67	2.72
G. parvulum	4.65	2.33	0.39	1.09
G. olivaceum	1.70	2.00	0.00	0.18
G. minutum	2.01	5.66	0.00	0.00
N. paleacea	9.38	1.50	0.58	0.72
N. amphibia	2.24	1.16	0.00	0.54
N. fonticola	3.81	2.33	0.77	1.09
N. supralittorea	3.14	1.16	0.58	0.54
Nitzschia spp.	2.32	1.66	3.09	4.00
A. minutissima	2.21	4.16	0.19	0.00
A. veneta	1.57	0.33	1.55	2.18
A. pediculus	0.57	2.16	0.00	0.00
Surirella spp.	0.55	0.33	1.16	2.18
Plankton	25.23	30.62	54.16	29.78
Tychoplankton	5.98	6.66	2.32	10.00
Periphyton	68.79	62.73	43.52	60.22

Table 4.9. The relative abundance of the dominant species (>2% in any one sample) in trap I (percentage abundance of cumulative total diatom influx for the entire study period), trap II and in surface sediment samples (SS) collected in April, 1995 (the 0-1 cm surface layer from core GR95B) and October, 1995 (0-1 cm surface layer from Glew core) from Groby Pool.

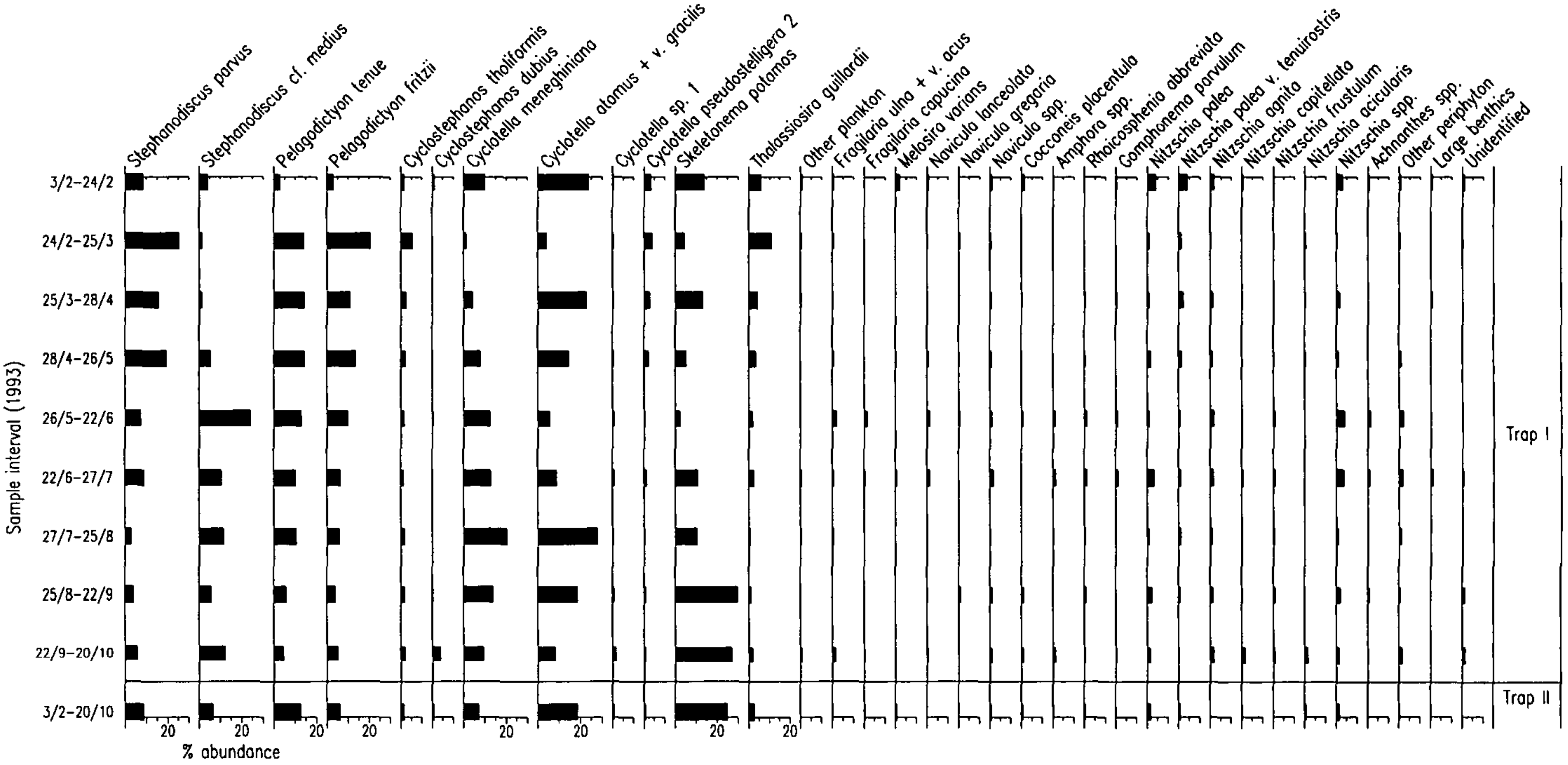


Fig. 4.19. Monthly changes in sediment trap I diatom assemblages collected in Tween Pond.

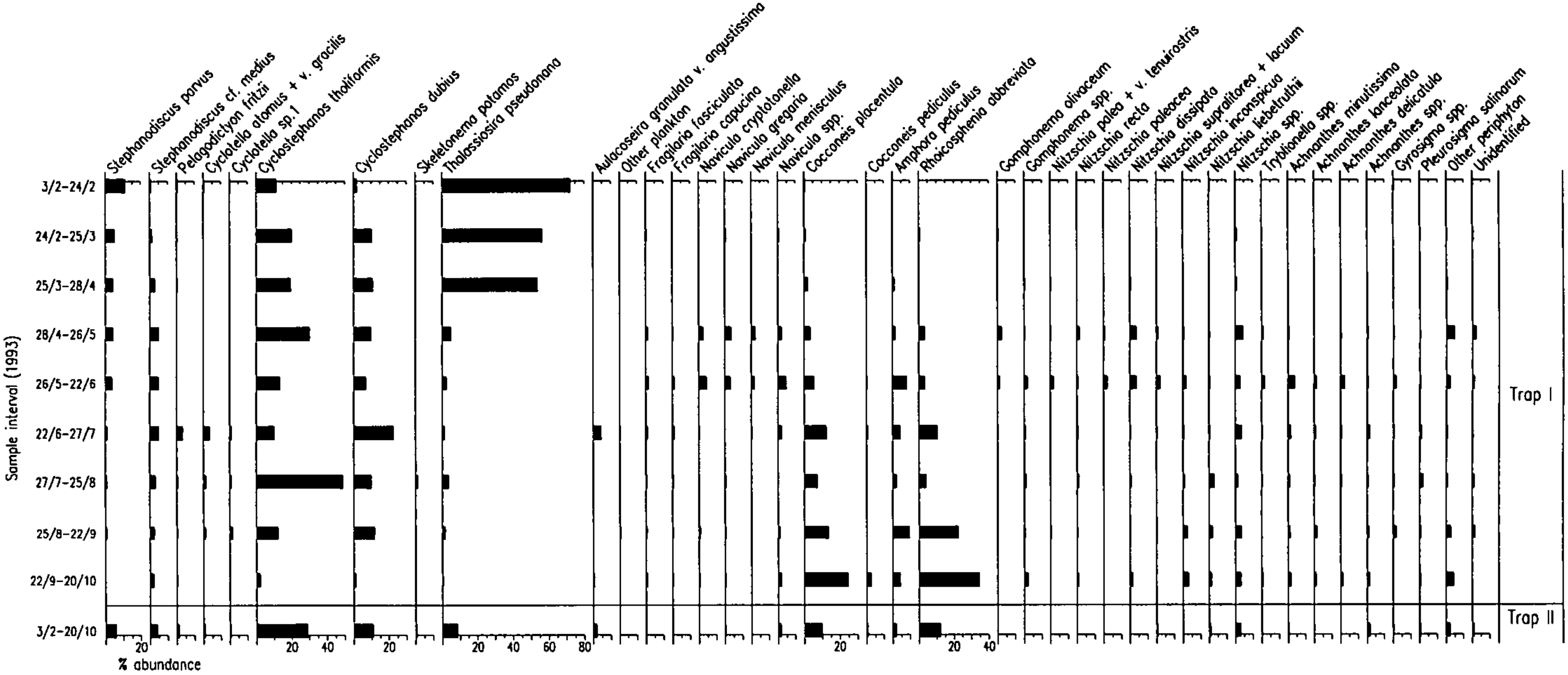


Fig. 4.20. Monthly changes in sediment trap I diatom assemblages collected in Clifton Pond.

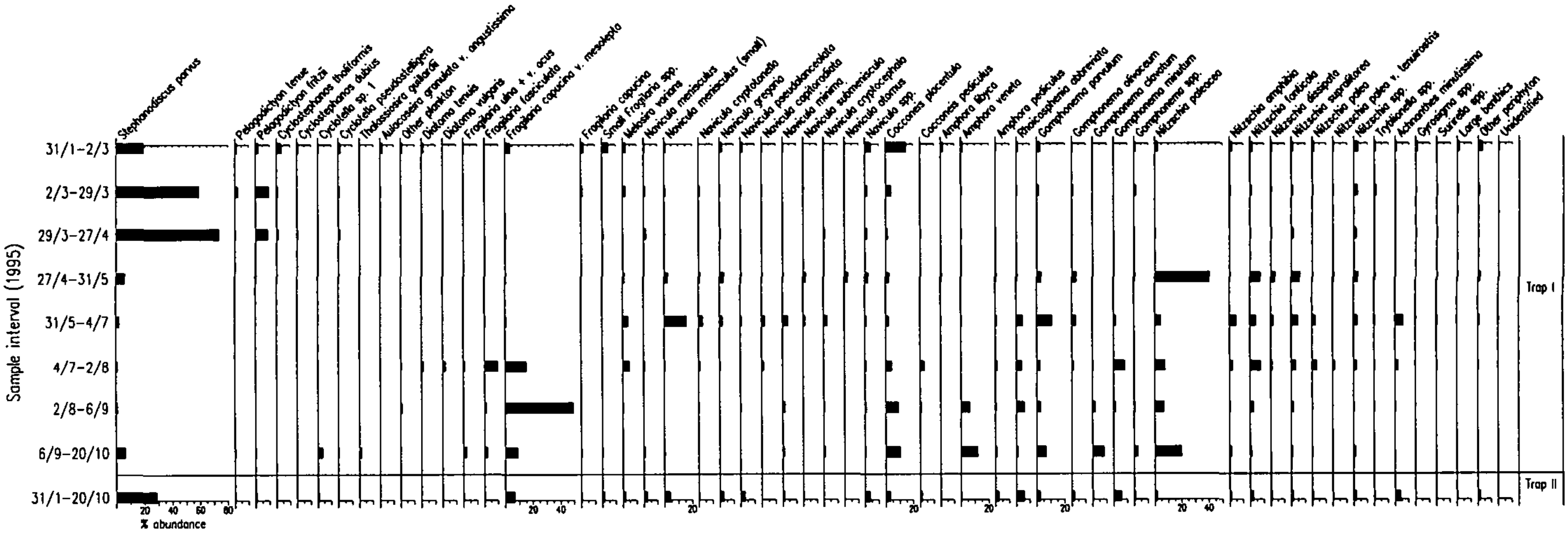


Fig. 4.21. Monthly changes in sediment trap I diatom assemblages collected in Groby Pool.

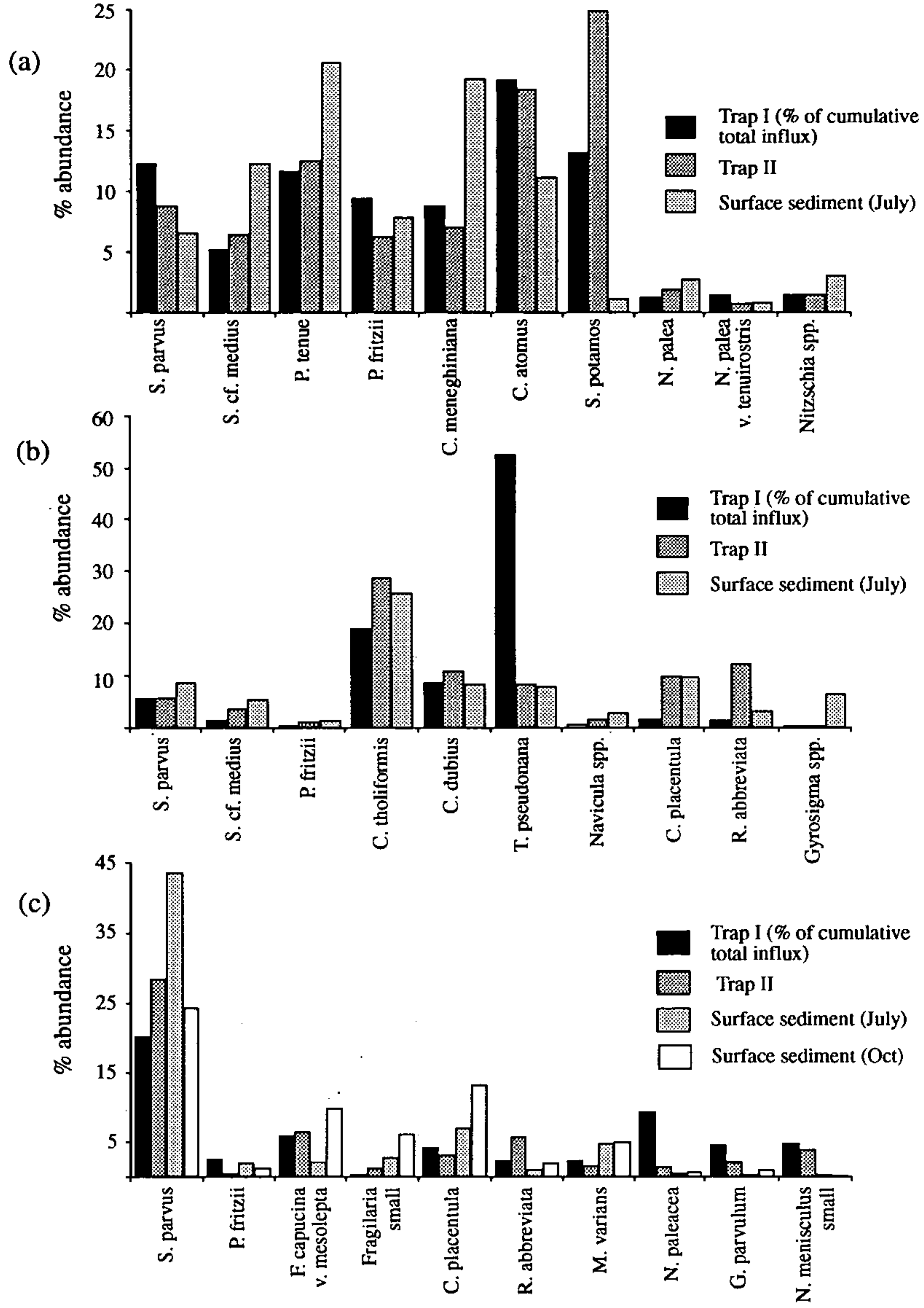


Fig. 4.22. Selected species relative abundance in trap I (percentage abundance of cumulative total diatom influx for the entire study period), trap II and in the surface sediments of the three study lakes; Tween Pond (a), Clifton Pond (b) and Groby Pool (c).

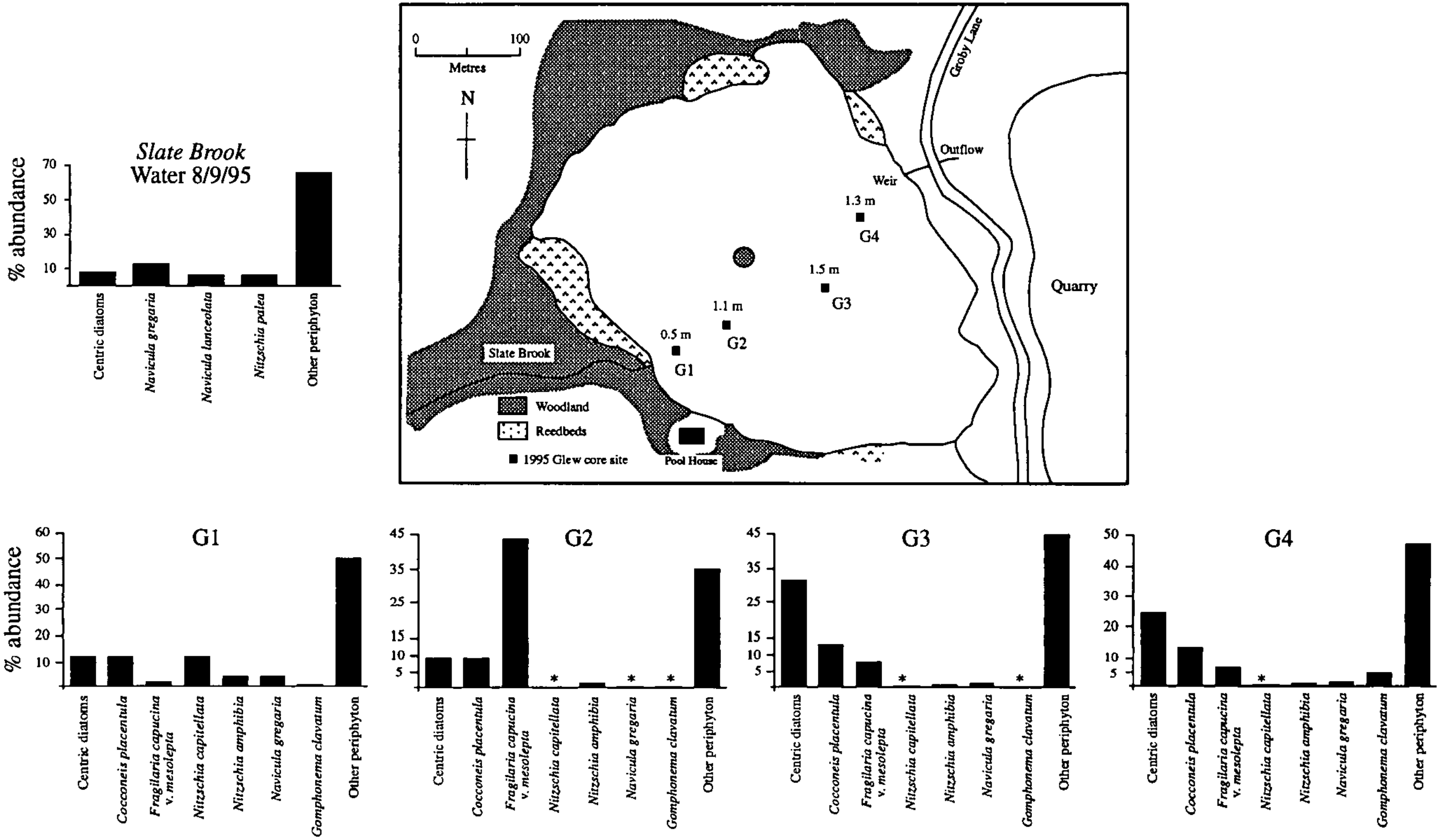


Fig. 4.23. Diatom assemblages in surface sediment samples collected in a transect across Groby Pool (Oct, 1995)
* = species recorded below 1% of sample relative abundance.

Conclusions

Environmental conditions

The hypertrophic gravel-pit lake Tween Pond was extremely turbid due to the presence of large phytoplankton populations (mean chlorophyll *a* = 46 $\mu g\ l^{-1}$) and high loadings of suspended solids. PO_4 and NO_3 concentrations were extremely high throughout the year and it is unlikely that these nutrients were limiting. In contrast SiO_2 was reduced to very low values on two occasions (<200 $\mu g\ l^{-1}$) due to rapid depletion of the external supply, and it is possible that this nutrient set an important limit on diatom production. Rapid flushing rates may also have exerted an important control over biomass, depending on the relationship between outflow loss and phytoplankton growth rates, but possibly the most important controls were light and temperature. The phytoplankton were probably largely 'self-shading' during calm weather conditions, when water temperature was suffucient for net growth. However photosynthesis may have been seriously restricted when water transparency was reduced due to the presence of high quantities of resuspended solids. This may have been an important factor in adverse weather and low chlorophyll *a* concentrations in winter may have been related to the effects of sediment resuspension on the light environment.

Phytoplankton biomass was much lower in Clifton Pond (mean chlorophyll *a* = 7 $\mu g\ l^{-1}$) and clear water conditions prevailed throughout much of the summer and autumn. Much lower concentrations of PO_4 and NO_3 were evident and these nutrients may have limited phytoplankton growth at times, although extremely low concentrations of SiO_2 (<0.5 mg l^{-1}) suggest that this was possibly the most important resource regulating diatom production. However in summer and autumn low phytoplankton and indeed diatom densities suggest significant zooplankton grazing and 'top-down' control. In Groby Pool phytoplankton biomass was again significantly lower than in Tween Pond (mean chlorophyll *a* = 4 $\mu g\ l^{-1}$) and the water was very clear in summer and autumn. TP and SiO_2 concentrations were relatively high, but NO_3 was massively depleted after the spring (<200 $\mu g\ l^{-1}$) indicating that it may have limited phytoplankton growth. Much reduced chlorophyll *a* levels in summer and autumn again suggest that plant-associated zooplankton (particularly Cladocera spp.) were very effective in controlling the phytoplankton.

Diatom seasonality

In Tween Pond there were major phases of planktonic diatom in spring and late summer-autumn and during both of these peaks small centric forms in the Thalassiosiraceae were dominant. However, different species were associated with these two maxima and whereas *P. tenue*, *P. fritzii* and *S. parvus* (often referred to as the *S. hantzschii* complex in phytoplankton studies) were most important in the spring, *C. atomus*, *C. meneghiniana* and *S. potamos* were prevalent in late summer-autumn. The proliferation of the *S. hantzschii* complex in late winter-spring has often been attributed to their rapid growth and superior light harvesting abilities (Reynolds *et al.*, 1994). However the dominance of different centric forms in the summer-autumn plankton indicates that there are other species with quite different adaptive strategies which are able to thrive at higher temperatures. The occurrence of large summer-autumn crops of centric diatoms is a common feature of many eutrophic, lowland rivers (Kiss *et al.*, 1994; Gosselain *et al.*, 1994) and turbid, riverine lakes (Köhler, 1994). The absence of submerged and emergent marginal plants in this lake and the permanently turbid conditions meant that there were minimal opportunities for periphytic diatom growth and so planktonic forms were dominant throughout the year.

The seasonal diatom succession was quite different in Clifton Pond and Groby Pool and significant planktonic diatom growth was restricted to the late winter-spring period and unlike Tween Pond there was no resurgence of the plankton in late summer. The colonisation of dense beds of submerged and floating macrophytes after May and associated clear water conditions allowed periphytic forms to thrive in summer-autumn and so in both these lakes there were two distinct phases of diatom production. Planktonic diatom communities in both these lakes were again dominated by small centric forms. The most diverse centric communtity was found in Clifton Pond where the species *T. pseudonana*, *C. tholiformis*, *C. dubius* and *S. parvus* were dominant. Alternatively in Groby Pool *S. parvus* was the prominent form. The sediment trap and periphytic diatom collections indicate that the the epiphytes *C. placentula* and *R. abbreviata* were the prevalent periphytic forms in Clifton Pond. These species were also important in Groby Pool in addition to the tychoplanktonic species *F. capucina* var. *mesolepta* and the epiphyte *N. paleacea.*

Sediment representativity

The degree to which the sediments of the three study sites accurately represented the modern diatom communities has been assessed by comparing the modern planktonic and periphytic diatom collections with the sediment trap and surface sediment samples.

The traps afforded relatively accurate estimates of changes in the seasonal behaviour of diatom populations in the three lakes. This was particularly evident for the small, centric species which were typically most abundant in the traps when they were most prevalent in the water column. Moreover seasonal changes in the relative competitiveness of different centric forms found in the water samples were relatively accurately represented in the traps and the same approximate monthly changes were evident. The degree to which the traps accurately measured seasonal changes in the importance of periphytic diatoms has been more difficult to assess. However most of the species found in the epiphyton and epilithon were also present in the trap collections. Thus it would appear that resuspended sediment inputs were insufficient to mask the seasonal pattern of primary sedimentation into the traps.

To relate the sediment trap samples to the surface sediment samples from the three study sites an influx weighted, cumulative trap I assemblage was estimated and compared with the trap II and surface sediment assemblages. There was generally good agreement between these three sample types and most of the dominant species in the trap I and trap II collections were also present in the surface sediment samples in comparable percentages. However the large population of *T. pseudonana* that developed in Clifton Pond during late winter was probably significantly understimated in the sediment, presumably due to selective dissolution. Moreover it is also apparent that there was a clear tendency for more recently sedimented species to be preferentially represented in the surface sediments of the three sites and again this was probably related to the reduced opportunities for the decomposition and dissolution of freshly deposited populations.

CHAPTER FIVE

The eutrophication histories of Tween and Clifton Ponds

This chapter focuses on the eutrophication histories of Tween and to a lesser extent Clifton Ponds in the Attenborough Ponds SSSI. The modern water chemistry, productivity and diatom ecology of these recently excavated gravel-pit lakes has been described in chapter four. The lakes were seriously disturbed in 1972 when the polluted River Erewash was diverted into the Ponds complex and the ecological trajectory of these lakes was significantly altered. The first part of this chapter focuses on the documented history of the Ponds complex and changes in pollution inputs, macrophyte status, hydrology and water chemistry are highlighted. Then the dating, lithostratigraphy and diatom biostratigraphy of sediment cores taken from Tween and Clifton Ponds are described. The environmental requirements of the diatoms found in the sediment cores are explored by studying the distributions of the dominant periphytic and planktonic diatom species in surface sediment assemblages from the Ponds. In the final part of this chapter the palaeoecological record from Tween Pond is compared with documented changes in the lakes ecological history. The reasons for alterations in the relative and absolute abundance of different diatom species in the sediment are discussed.

Site	Date of first extraction	Date of last extraction
Duck	1939	1960
Beeston (south)	1941	1951
Beeston (north)	1946	1950
Works	1929	1939
Tween	1959	1965
Church	1962	1965
Clifton	1964	1968
Coneries	1966	+
Erewash	+	+

Table 5.1. The dates of first and last extraction for the Attenborough Ponds. + = currently being excavated.

The history of the Ponds

The Attenborough Ponds SSSI consists of an interconnected series of gravel-pit lakes excavated largely between 1940 and the late 1960s (fig. 4.1, plate 4.1). The excavation history of the Ponds is given in table 5.1. On flooding these newly created lakes were colonised by a diverse set of submerged and floating plants growing in clear water (table 5.2). Emergent plant growth was also prolific and in most areas there was a succession from *Typha* and *Glyceria* spp. in the margins through to willow, ash and alder carr. The Ponds also developed into an important site for birds and in particular the common tern (*Sterna hirundo* L.) and the great crested grebe (*Podiceps cristatus* L.) and it was these bird communities which led to its official recognition as an important site for nature conservation (Britton, 1974).

However the natural succession that was progressing in and around the Ponds was interrupted in November, 1972 when the highly polluted River Erewash was diverted through the Ponds to allow gravel to be transported via barge from the area which is now the southern part of Coneries Pond. Previously the R. Erewash joined with the R. Trent at Barton lane and to achieve diversion through the Ponds this confluence was blocked off and a new outlet weir was opened up in the NE part of Duck Pond (fig. 5.1). The R. Erewash penetrated all parts of the Ponds complex on its route through to the R. Trent, but Church and Beeston Ponds were probably isolated during normal discharges. In 1980 there were a number of alterations to this arrangement and in an attempt to reduce Erewash flows into the connected Ponds, the Barton lane confluence was re-opened and its level was lowered to make it the dominant outlet (fig 5.1). The Duck Pond outlet weir was also raised at this time and flap gates were installed at both outlets to prevent backflows into the Ponds from the R. Trent. Thus the hydrology of the Ponds was significantly altered after 1980, with the bulk of Erewash water leaving the Ponds at the Barton Lane outlet. In an attempt to prevent the entry of Erewash water into Beeston and Clifton Ponds, earth bunds were also constructed in the early 1980s, however these Ponds still received river water during flood events.

Submerged	Floating
Potamogeton pusillus L.	*Polygonum amphibium* L.
Potamogeton crispus L.	*Nuphar lutea* L.
Potamogeton pectinatus L.	*Nymphaea alba* L.
Myriophyllum spicatum L.	
Myriophyllum verticillatum L.	
Elodea nuttallii L.	
Elodea canadensis Michx.	
Callitriche truncata L.	
Zannichellia palustris L.	
Hippuris vulgaris L.	
Utricularia vulgaris L.	

Table 5.2. Pre-1972 Submerged and floating plant records for the Attenborough Ponds SSSI (data source NCC; Britton, 1974).

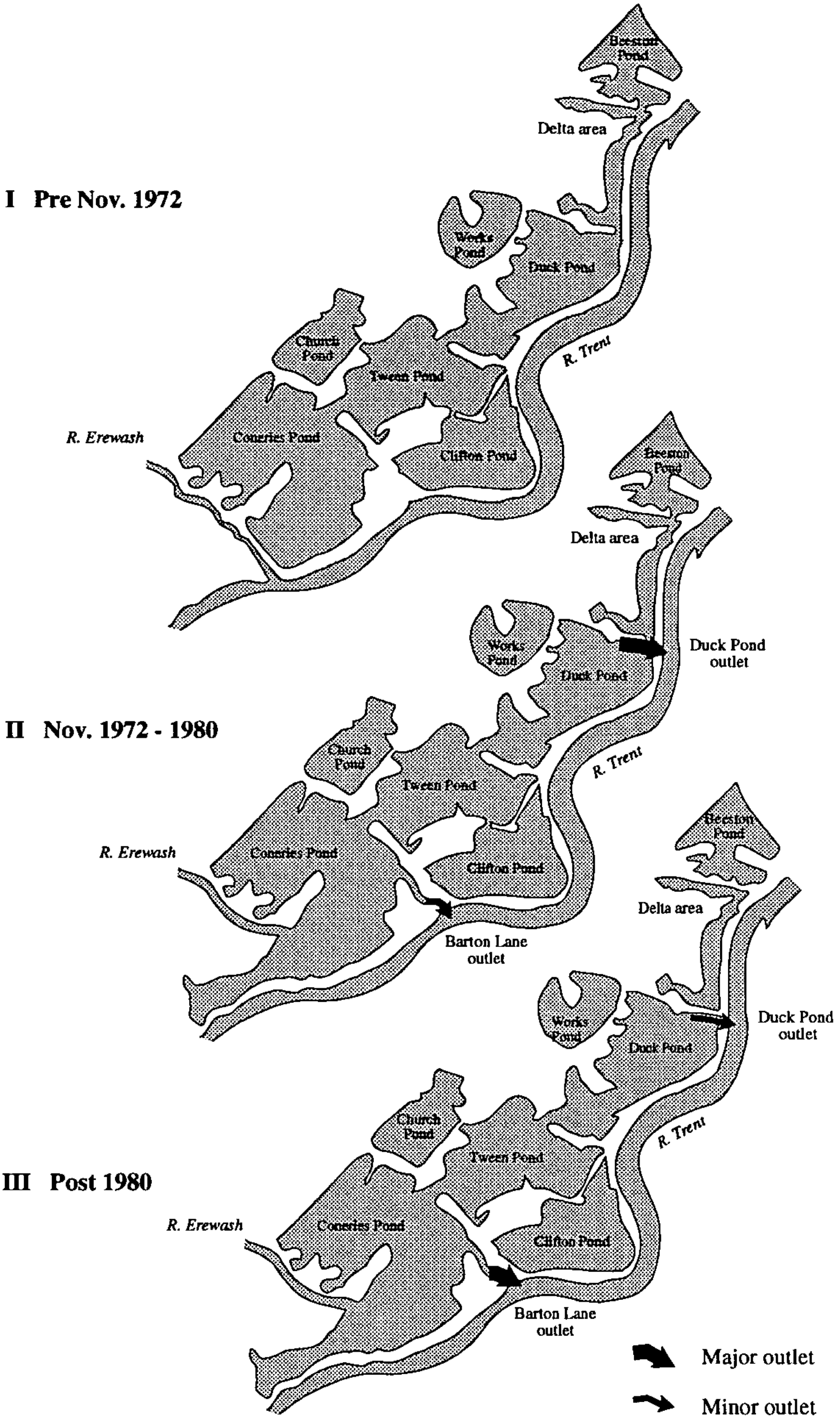


Fig. 5.1. Historical changes in the morphology and hydrology of the Attenborough Ponds SSSI.

Immediately after the Erewash diversion, the Institute of Terrestrial Ecology (ITE) were involved in an impact assessment project to record changes in the biological structure of the Ponds (Britton, 1974). Water chemistry sampling (NO_3, PO_4, NH_4, EC) started just two months before diversion in four of the Ponds (Coneries, Tween, Duck and Beeston)) and continued on a bi-weekly basis for a further year. The chemical data for Tween Pond are summarised in table 5.3. There were just three pre-diversion samples and these indicate that nutrient concentrations were relatively low and that EC was moderate. The initial post-diversion samples show an enormous rise in nutrient levels with NO_3, PO_4 and NH_4 increasing 14 fold, 13 fold and 19 fold respectively, indicating a shift from mildly eutrophic to hypertrophic conditions (OECD, 1982). If the pre and post diversion mean and maximum nutrient concentrations are compared, it is apparent that this difference was sustained over the next year. EC increased only slightly after the breach from 600 to 620 $\mu S\ cm^{-1}$ but reached 1040 $\mu S\ cm^{-1}$ in the following summer, a level most probably higher than was previously possible. Thus it is apparent that the chemical status of Tween Pond was severely altered by the diversion of the R. Erewash.

	NO_3 ($\mu g\ l^{-1}$)	NH_4 ($\mu g\ l^{-1}$)	PO_4 ($\mu g\ l^{-1}$)	EC ($\mu S\ cm^{-1}$)
Pre-diversion (mean)	400	117	40	527
Pre-diversion (max.)	500	150	50	600
Immediate post-diversion	7400	1340	960	620
Post-diversion (mean)	3955	812	675	795
Post-diversion (max.)	7500	2100	1200	1040
Nov 1972	500	100	50	510
Nov 1973	1400	400	330	880

Table 5.3. Summary pre and immediate post-breach water chemistry for Tween Pond (data source Britton (1974)).

Unfortunately the ITE did not collect any phytoplankton samples prior to the Erewash diversion so little is known of pre-disturbance phytoplankton densities and community structure. Phytoplankton sampling started in early May 1973 in Coneries, Duck and Church Ponds, all three of which exhibited a similar general seasonal pattern of cell abundance and species composition. In May and early June small chlorophytes were dominant and these were replaced by small centric diatoms in July and cyanophytes in late summer and autumn. The water was extremely turbid and no clear water phases were observed, largely because of high phytoplankton densities, with cell concentrations exceeding 400 x 10^6 cells l^{-1}.

The effects of the Erewash diversion on submerged plants would appear to have been quite dramatic. In the following July plant growth was very sparse in the connected Ponds and restricted to a few patches of *P. pectinatus* and *Z. palustris* in shallow marginal areas. The filamentous alga *Enteromorpha intestinalis* L. was abundant in Tween and Church Ponds and had taken over from the submerged plants. Thus it is apparent that the influx of river water had a profound effect on macrophyte communities in the Ponds. The only lakes to retain a stable plant dominated state after diversion were Beeston and Clifton Ponds. However, in 1976 there was a storm-induced pulse of urban sewage into Beeston Pond which led to the loss of its submerged plants. This event also affected the other Ponds to a lesser degree and a few years later Clifton Pond had also largely switched to phytoplankton dominance. The re-isolation of Clifton Pond in the early 1980s led to the re-colonisation of submerged plants in the mid-1980s, but similar measures in Beeston Pond have not allowed it to return to a plant dominated state (Lewis, pers. comm.)

Historical water chemistry data

Water chemistry data do not exist for the Ponds after 1973, however data are available for the R. Erewash at the inlet to the Ponds and approximately 8 km upstream at Trowell Bridge (fig. 4.1) for NH_4 and EC (1978 onwards at the inlet and 1970 onwards at Trowell) and PO_4 (1982 onwards at the inlet and 1974 onwards at Trowell). These data are displayed in fig. 5.2. It is apparent that the three water chemistry variables exhibit a similar inter-annual pattern of variation at both the Ponds inlet and at Trowell Bridge. This means that the Trowell data probably provides a reasonable indication of water chemistry trends at the inlet to the Ponds for the period before monitoring began at this site (i.e. the 1970s). In chapter four a good directional relationship was demonstrated between seasonal changes in nutrient concentrations and EC levels at the inlet and in Tween Pond during 1993. Thus it is equally probable that the long-term water chemistry data for the R. Erewash at Trowell accurately track historical shifts in chemical inputs to Tween Pond. As the Ponds were more directly connected to the R. Erewash prior to 1980 it is likely that the Ponds-Erewash water chemistry relationship was even stronger in the 1972-1980 period.

It is evident from fig. 5.2 that PO_4 had a quite complex pattern of variation between 1975-1993. PO_4 concentrations increased from 1975 to 1978 and then declined in 1979 and 1980, before a steady increase in the first half of the 1980s to an initial peak in 1986 (>5 mg l^{-1} at Trowell). Between 1986 and 1988 concentrations declined again and then ascended to a prominent peak in 1990 with values at the inlet and at Trowell of over 5 mg l^{-1}. The inlet peak of 5.6 mg l^{-1} in 1990 would translate to a PO_4 value of 4.9 mg l^{-1} in Tween Pond based on the modern relationship established between these two sites. EC

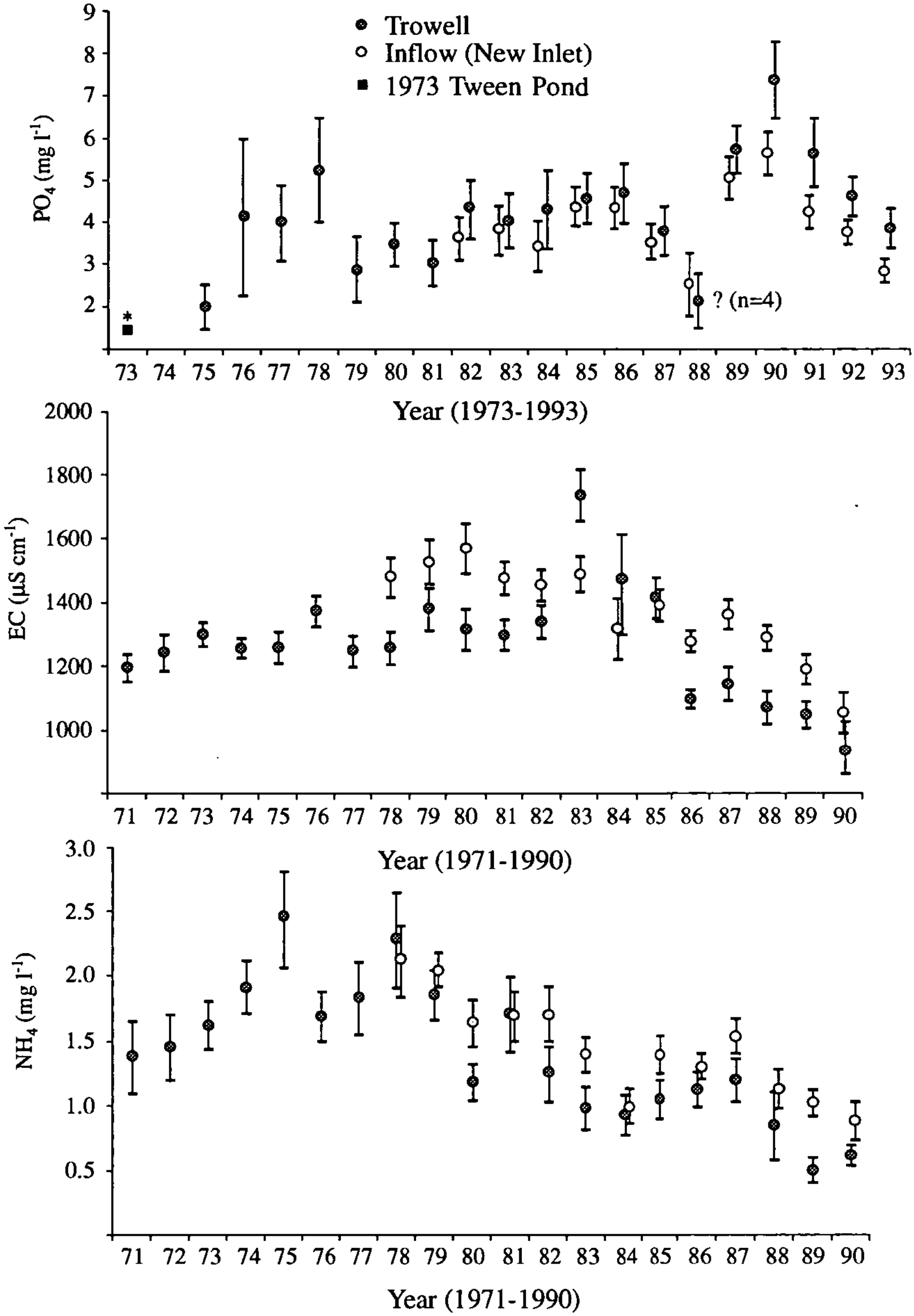


Fig. 5.2. Mean annual water chemistry data (PO$_4$, NH$_4$ and EC) for the River Erewash at Trowell (since 1971) and at the inlet to the Ponds (since 1978). Bars represent one standard error.

* = 1973 mean for Tween Pond from Britton (1974).

exhibited a gradual increase from 1971 to a peak in 1983 (1760 $\mu S\ cm^{-1}$ at Trowell) and then declined to minimum levels in 1990. NH_4 concentrations increased between 1971 and 1975 to a peak of 2.4 mg l^{-1}, fell in 1976 and increased again to a second slightly lower peak in 1978. In contrast to PO_4, NH_4 exhibited a steady decline between 1978 and 1990.

Sediment cores

Two short (<1 m) Mackereth sediment cores were collected from ythe deepest regions of Tween and Clifton Ponds and one core was collected from Beeston Pond (see fig. 4.1). In Tween and Clifton Pond the cores were collected in close proximity to the modern sampling sites. The cores were taken in two series in August 1993 (Tween and Clifton) and June 1994 (Clifton and Beeston).

The sediment core taken from Tween Pond (TP193) was 92 cm long, the upper 86 cm consisting of a dark, organic gyttja and the lowermost 6 cm of a mixture of fine lake sediments and coarse floodplain sands and gravels. In the cores (>70 cm) taken from Clifton (CP193, 94) and Beeston (BP194) Ponds, the upper 30-40 cm was again dark organic gyttja, below which there were alternating layers of river sands and gravels. The presence of river deposits at the base of the cores indicates that the entire lake sediment sequence was collected on each occasion.

Lithostratigraphy

In both cores TP193 and CP193 organic matter and carbonate profiles were generated and are given in fig. 5.3. In core TP193 organic matter levels steadily increase above the gravel-gyttja interface (86 cm) where percentages are relatively low (<9%) to 14.7% at 42-44 cm. There is then a slight decline and percentages remain relatively stable between 40-28 cm, above which there is a steady increase to a peak of 17.1% at 4-6 cm. The dominant source of organic matter above 68 cm (i.e. the post-breach sediments) is probably phytoplankton, but below this macrophyte inputs may be important. Levels of carbonate in TP193 are low, increasing from around 4% at the bottom of the core to an initial peak of 7.9% at 36-38 cm and then declining again between 36-24 cm to 5.8%. Above this levels increase rapidly and oscillate between between 6.5-8.5% to the surface. The experiments of Dean (1974) indicate that the removal of lattice water from clay minerals may account for up to 4% of loss on ignition between 550-950°C depending on clay content. Thus carbonate is barely detectable in the lower part of TP193. In core CP193 organic matter

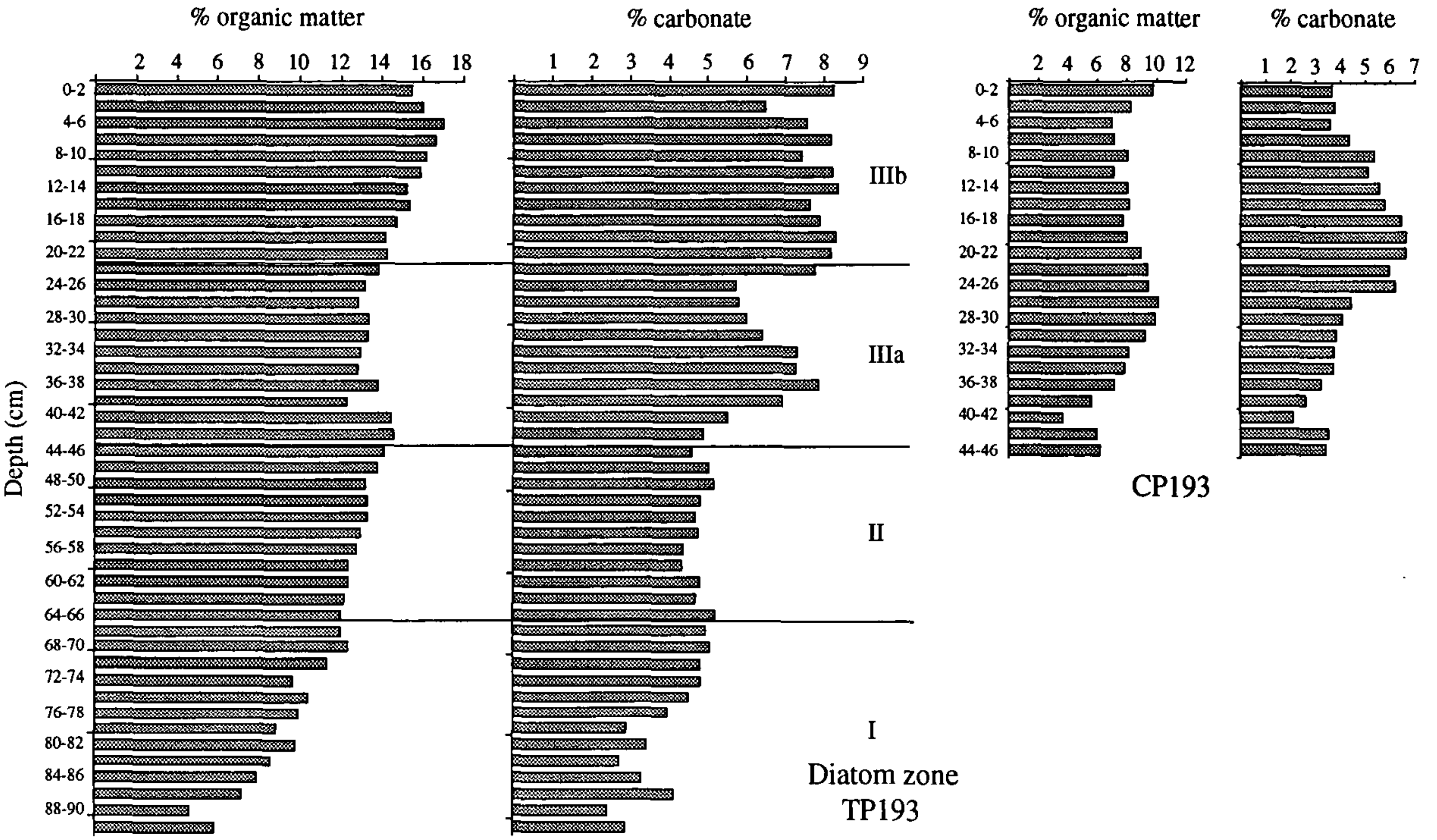


Fig. 5.3. Profiles of percentage organic matter and carbonate for core TP193 from Tween Pond and CP193 from Clifton Pond.

levels are moderate throughout the core increasing from 7.3% at the gyttja-gravel interface to a peak of 10.2% at 26-28 cm. There is then a steady decline until 6-8 cm, above which organic percentages increase to the surface (9.8%). Similarly to TP193 carbonate is a relatively unimportant mineral component, increasing from very low levels at the base of the gyttja to a maximum of 6.7% at 18-20 cm and then returning to low levels at the surface.

Dating

The sediment core TP193 from Tween Pond was selected for dating and given the recent age of this lake (i.e. date of last excavation 1965) ^{137}Cs analysis was the most appropriate dating technique. ^{137}Cs is a 'fall-out' radionuclide and maximum measured ^{137}Cs concentrations in the sediment can be used to mark depositional peaks associated with nuclear weapons testing in 1963 and the Chernobyl nuclear accident of 1986. The ^{137}Cs profile for TP193 exhibits a relatively well defined maximum at 24-28 cm which appears to be a marker for the Chernobyl event (fig. 5.4). ^{137}Cs then declines and there is a second peak at 76-80 cm which may represent the early-mid 1960s. These two stratigraphic markers locate the 1972 diversion between 57-72 cm and indeed the diatom record (fig. 5.5) suggests that it is represented by 67-68 cm. Using the two ^{137}Cs peaks and the theoretical position of 1972 it is possible to construct simple age-depth relations for the core (fig. 5.4). These indicate extremely rapid post-diversion rates of sediment accumulation with estimates of 3.0 cm yr^{-1} for 1972-1986 and 3.57 cm yr^{-1} for 1986-1993 and possibly a much slower pre-diversion accumulation rate of below 1.5 cm yr^{-1}. The very rapid post-diversion rate of accumulation means that each 2 cm sediment sample probably represents less than a year's sediment production. That the Chernobyl peak is seems to be clearly evident suggests that sediment resuspension-deposition cycles and bioturbation have not been sufficient to destroy the temporal resolution of the sediment record. However some mixing is indicated by the relatively slow decline in ^{137}Cs after the 1986 peak.

Diatom preservation

The preservation of diatoms in TP193 was generally good and few poorly silicified valves were encountered in the upper 72 cm of the core. However the two very delicately silicified centric diatoms *T. pseudonana* and *S. potamos* were frequently damaged and difficult to recognise with the LM. In chapter four it was shown that *T. pseudonana* is hightly susceptible to dissolution and this species in particular may have been significantly underestimated. Below 72 cm diatom concentrations were much reduced

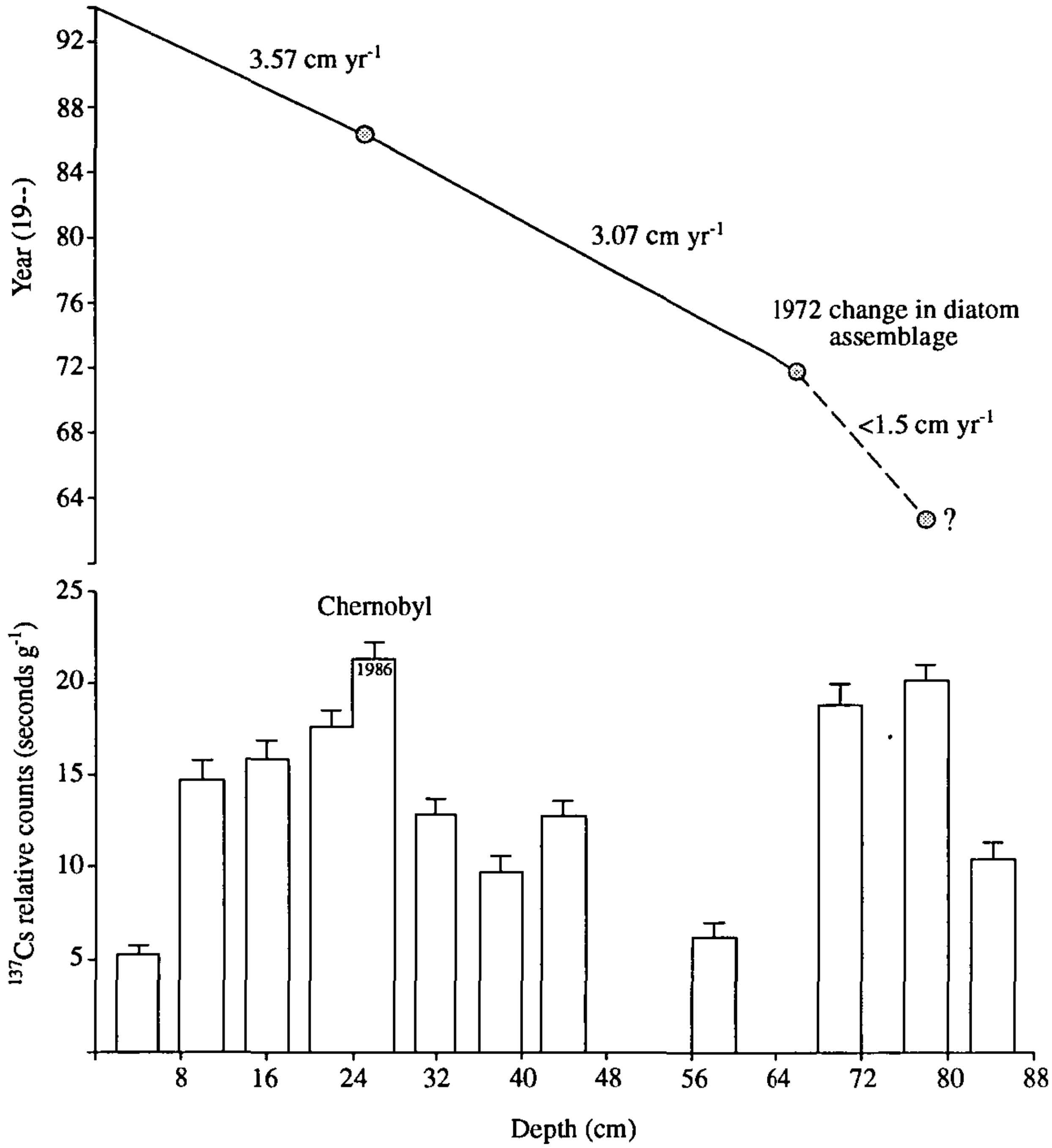


Fig. 5.4. ^{137}Cs distribution in core TP193 from Tween Pond (lower) and inferred age-depth relations (upper). Error bars represent one standard deviation.

* The change in the diatom assemblage associated with the 1972 Erewash diversion is used as a stratigraphic marker.

($<1 \times 10^7$ valves g^{-1}) and remaining valves were eroded and poorly silicified indicating dissolution. In CP193, 94 and BP194 just 6 to 8 cm of the upper sediments contained well preserved and abundant diatoms and below this there were few recognisable remains. Thus it has not been possible to reconstruct the ecological histories of these two presently isolated lakes.

It has been suggested that dissolution is minimal in the water column of shallow lakes (Reynolds, 1986) and so the most likely explanation for dissolution in these gravel-pits is probably upwelling groundwater reducing Si concentrations in the interstitial waters of the sediment. This process has been indicated as an important dissolution mechanism by Anderson (1994b) and may also explain the poor diatom preservation in the lower sediments of several river-valley reservoirs in southern England where early deposits lie close to the river aquifer (Sayer & Roberts, unpublished data).

Diatom biostratigraphy

The diatom record from TP193 (fig. 5.5) can be divided into three major zones (I, II and III) the upper of which is further divided into two sub-zones (IIIa and IIIb). These divisions are largely based on the groups generated by agglomerative clustering (i.e. CONISS). The zone and sub-zone boundaries are given approximate dates using the age-depth relationship constructed in fig. 5.4 and life-form data is largely derived from chapter four.

Zone I (72-68 cm; c. pre-1972) is representative of the pre-Erewash diversion sediments and consists of just two samples (68-70, 70-72 cm). Assemblages are co-dominated by planktonic and periphytic species. The dominant planktonic forms are *Stephanodiscus parvus* (>16%) and *Cyclotella. radiosa* (>8%), but as in other parts of the core the plankton is partitioned between several different species and *Stephanodiscus* cf. *medius*, *Cyclostephanos tholiformis*, *Cyclostephanos dubius*, *Cyclotella meneghiniana* and *Cyclotella atomus* are also present in reduced, but significant percentages. The periphytic component in these two samples is dominated by benthic *Gyrosigma* spp. (>18%) with the additional importance of the benthic form *Navicula pseudolanceolata*, *Navicula* spp., *Nitzschia* spp. and the epiphytes *Cocconeis placentula* and *Rhoicosphenia abbreviata*.

Zone II (68-46 cm; c. 1972-1979) represents the immediate post-diversion sediments. The initial two levels (66-68, 64-66 cm) probably incorporate some pre-diversion diatoms. The species *C. radiosa*, *S.* cf. *medius* and *Gyrosigma* spp. are present in moderate relative abundance in these samples, but are virtually absent from the rest of the zone suggesting that they were introduced by sediment mixing. At 66-68 cm *C. atomus* and *C. meneghiniana* replace *S. parvus* and *C. radiosa* as the dominant planktonic species and there is a significant reduction in *Gyrosigma* spp. (<4%). This level also sees the short-lived appearance of *Asterionella formosa* and *Aulacoseira granulata* var. *angustissima.* These species are very rare elsewhere and given the high temporal resolution of the core (i.e. >2 cm yr^{-1}) it is probable that their growth was restricted to a single season. In the post-diversion phytoplankton sampling (Britton, 1974) *Melosira (=Aulacoseira) granulata* var. *angustissima* was encountered in abundance in the summer plankton of the adjacent lakes, but *A. formosa* was rare. This is probably because it is a spring-adapted species (Maberly *et al.*, 1994) and so achieved its maximum abundance prior to the onset of sampling in May 1973.

There is a significant increase in *C. atomus* at 64-66 cm to 46% and *C. meneghiniana* also declines, while *C. dubius* becomes very rare. The dominant position occupied by *C. atomus* is further improved at 62-64 cm (>60%) and *S. potamos* and *T. pseudonana* make sizeable contributions for the first time. However *C. atomus* gradually declines in importance in the rest of the zone and is reduced to 27% at 46-48 cm. The sub-dominant planktonic species in zone II are *S. parvus*, *C. tholiformis* and *C. menghiniana*, while the small chain-forming centric *S. potamos* is temporarily important at 56-58 cm (11%) as is *Stephanodiscus hantzschii* at 54-56 cm (5%). The most prolific periphytic forms in this sub-zone are *Navicula lanceolata*, *Navicula* spp. and *Nitzschia* spp., while the epiphytes *C. placentula* and *R. abbreviata* are present in much reduced percentages compared to zone I. It is probable that a high proportion of these periphytic diatoms are allochthonous and derived from the River Erewash.

Sub-zone IIIa (44-24 cm; c. 1979-1987) is characterised by significant shifts in the dominant planktonic forms and *S.* cf. *medius* and *Pelagodictyton tenue* which are minor taxa in zone II beome more prominent. Similarly *S. parvus* also exhibits a positive response in the upper part of this sub-zone and achieves its maximum abundance (40%) at 28-30 cm. This species is also dominant at 24-26 cm where it co-dominates with *S.* cf. *medius* (25%). Alternatively *C. tholiformis* is less abundant in this sub-zone and both *C. atomus* and *S. potamos* are present in reduced percentages. The only planktonic species to maintain itself at relatively stable levels is *C. meneghiniana* which is a consistently important species (>11%). In the periphyton there are also some subtle species replacements with increases in the relative abundance of *Nitzschia palea* and the closely related morphotype *Nitzschia palea* var. *tenuirostris* in the lower half of the sub-zone.

Sub-zone IIIb (22-0 cm; c. 1987-1993) contains the same major species which are present in sub-zone IIIa but there are some subtle changes. In the lower two samples (16-18,

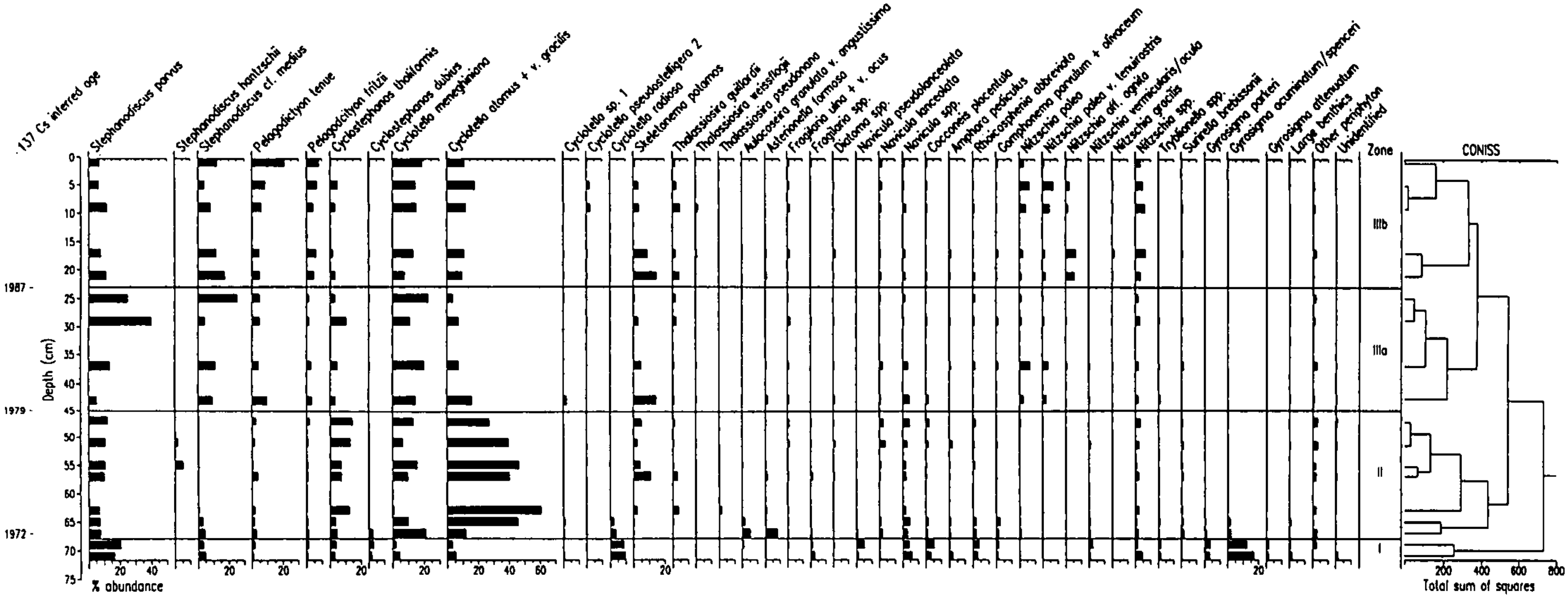


Fig. 5.5. Summary fossil diatom record for core TP193 from Tween Pond.

20-22 cm) there are increased percentages of *Pelagodictyon fritzii* (>4%) and *S. potamos* (>9%), while *S. parvus* returns to the lower levels it achieves throughout the major part of the post-diversion phase (<12%). There are also increased percentages of *Nitzschia* aff. *agnita* and *Nitzschia* spp. in these samples. In the upper three samples there is a decline in *S. potamos* and an increase in *P. tenue* which achieves a maximum of 21% in the surface sediment sample. The periphytic forms *N. palea* and *N. palea* var. *tenuirostris* are also of increased importance, whereas *N.* aff. *agnita* becomes rare.

Diatom concentrations and planktonic diatom biovolume

Estimates of diatom concentrations (valves g^{-1}), total planktonic diatom biovolume (cells μm^3 g^{-1}) and mean planktonic diatom cell volume (μm^3) for core TP193 are given in fig. 5.6. The cell volumes of the planktonic forms used in the above calculations are taken from table 4.5. Total planktonic diatom biovolume is thought to afford more reliable estimates of trends in planktonic diatom biomass than planktonic diatom concentrations which do not take into account cell size (Anderson, 1994a).

In the zone I sediments diatom concentrations are low (<6 x 10^7 valves g^{-1}) and then increase significantly in zone II to an initial post-diversion peak of 34 x 10^7 valves g^{-1} at 62-64 cm. Abundances then decline over the remainder of this zone but increase again in sub-zone IIIa (>17 x 10^7 valves g^{-1}). In sub-zone IIIb concentrations remain relatively high (>20 x 10^7 valves g^{-1}) and increase to a substantial peak at the sediment surface of 78 x 10^7 valves g^{-1}.

Total planktonic diatom biovolume is low in the zone I sediments (< 6 x 10^9 cells μm^3 g^{-1}), but significantly increases at 66-68 cm (27 x 10^9 cells μm^3 g^{-1}). However this increase is short-lived and there is a return to pre-diversion values in the second part of zone II related to the proliferation of the tiny form *C. atomus* (mean volume = 40 μm^3). In sub-zone IIIa there is a substantial increase in total planktonic diatom biovolume linked to higher abundances of the large centric *S.* cf. *medius* (mean volume = 1520 μm^3) and values remain relatively stable (18-26 cells μm^3 g^{-1}) in the initial three samples of this sub-zone, but increase further in the final sample (24-26 cm) to 61 x 10^9 cells μm^3 g^{-1}. Total planktonic diatom biovolume then fluctuates at relatively high levels in sub-zone IIIb and increases to a marked peak at the sediment surface (141 x 10^9 cells μm^3 g^{-1}).

The mean planktonic diatom cell volume calculations suggest three relatively distinct phases which correspond to the three major diatom zones; (i) an initial pre-diversion (zone I) phase of dominance by moderate sized cells (>350 μm^3); (ii) an immediate post-breach (zone II)

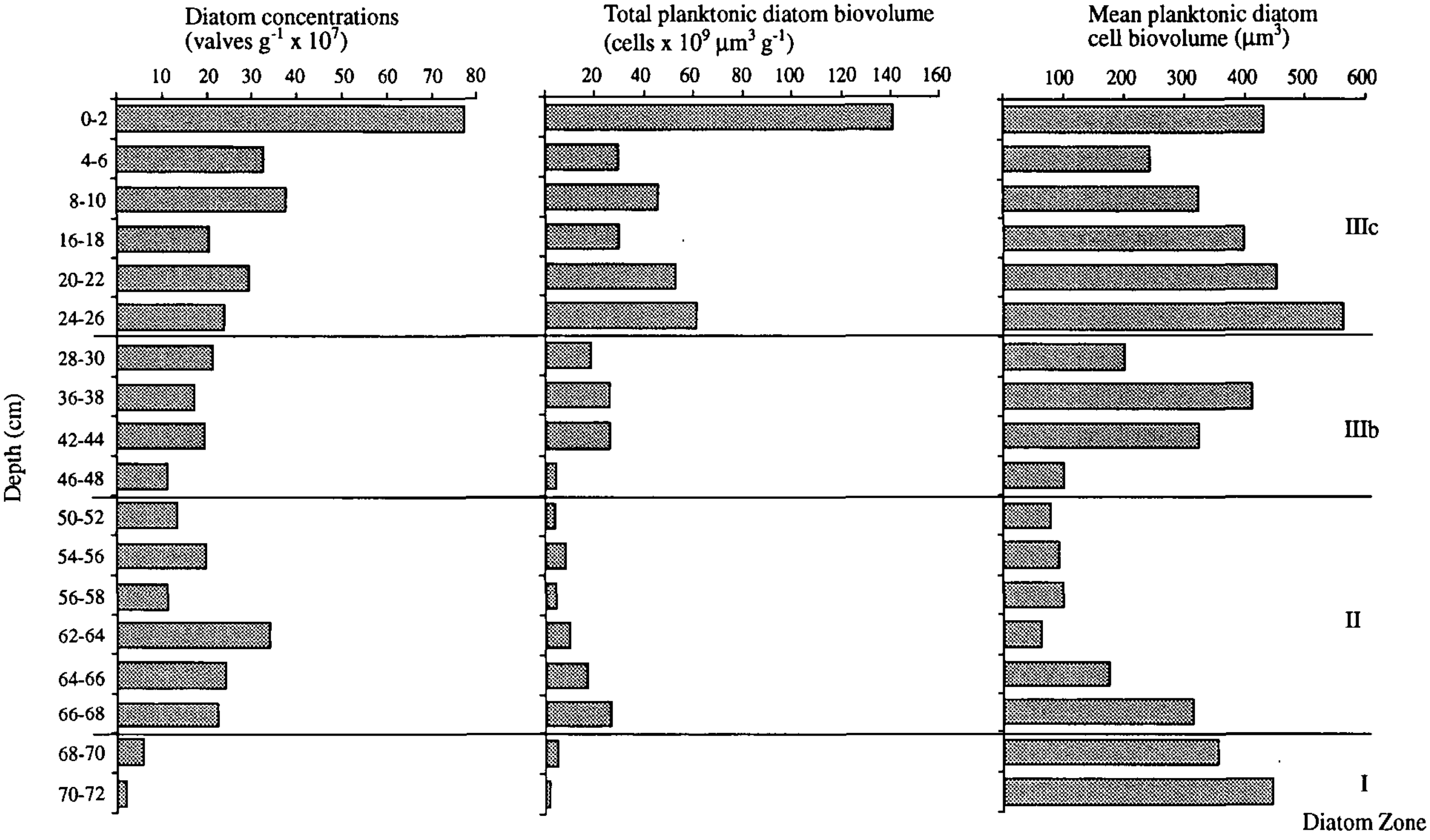


Fig. 5.6. Diatom concentrations, total planktonic diatom biovolume and mean planktonic diatom cell volume in the sediments of core TP193 from Tween Pond.

phase characterised initially by rapidly declining mean cell volume (66-68 cm, 64-66 cm) then stable, low mean cell volume in the upper four samples (<110 μm^3) and; (iii) a subsequent (zone III) return to the dominance of larger cells (200-570 μm^3).

Surface sediment assemblages in the Attenborough Ponds SSSI

Surface sediment samples were collected from the Attenborough Ponds complex in early 1995 from areas close to the the 1993 water chemistry sites (fig. 4.1). The diatom assemblages in these samples are shown in fig. 5.7 which orders the sites according to mean annual water chemistry data (fig. 4.3). The surface sediment samples for Clifton and Beeson Ponds come from the top of cores CP193 and BP194. Water chemistry data were not available for Beeston Pond and so this lake is given its most likely position in the river-lake continuum.

The only lake to support submerged macrophyte stands and clear water is Clifton Pond and this is reflected in the much higher percentages of periphytic diatoms in Clifton Pond compared to the other two isolated lakes (i.e. Church and Beeston Ponds). Periphytic forms are least important in Works Pond and then increase in relative abundance with proximity to the River Erewash reaching a maximum of over 50% in Coneries Pond. This trend can be related to the increasing input of riverine diatoms. Those periphytic species which are found in the connected lakes are *Navicula lanceolata*, *Cocconeis placentula* and a diverse set of *Nitzschia* species including *Nitzschia palea*, *N. palea* var. *tenuirostris*, *Nitzschia frustulum* and *Nitzschia amphibia*. These forms have been found in abundance in the epilithon and epipelon of the River Erewash (Gell, unpublished data) and this overlap suggests that they are transported into the lakes via the flowing wave of the river. It remains possible however that some of these species may survive and grow to some extent once they are introduced to the Ponds, particularly if they are capable of a tychoplanktonic existence as is possible for *N. palea* and *N. palea* var. *tenuirostris*.

Even with the possibility of allochthonous inputs it is possible to see some clear trends in the data set, with three distinct groups of assemblages. In the connected lakes (i.e. CO2, TW, DU2, DU1, WO) the dominant centric species are *S. parvus*, *S.* cf. *medius*, *P. tenue*, *P. fritzii*, *C. meneghiniana*, *C. atomus*, *S. potamos* and *T. guillardii* (group I). However in the isolated lakes (BE, CH, CL) the planktonic diatom community is very different and with the exception of *S. parvus*, the species which are listed above are rare. In Beeston and Church Ponds *C. dubius* and *C. tholiformis* are the prevalent forms and these lakes form a second distinct group (group II). These species are also important in Clifton Pond, but this lake would appear to stand apart from the other two isolated lakes due to the importance of

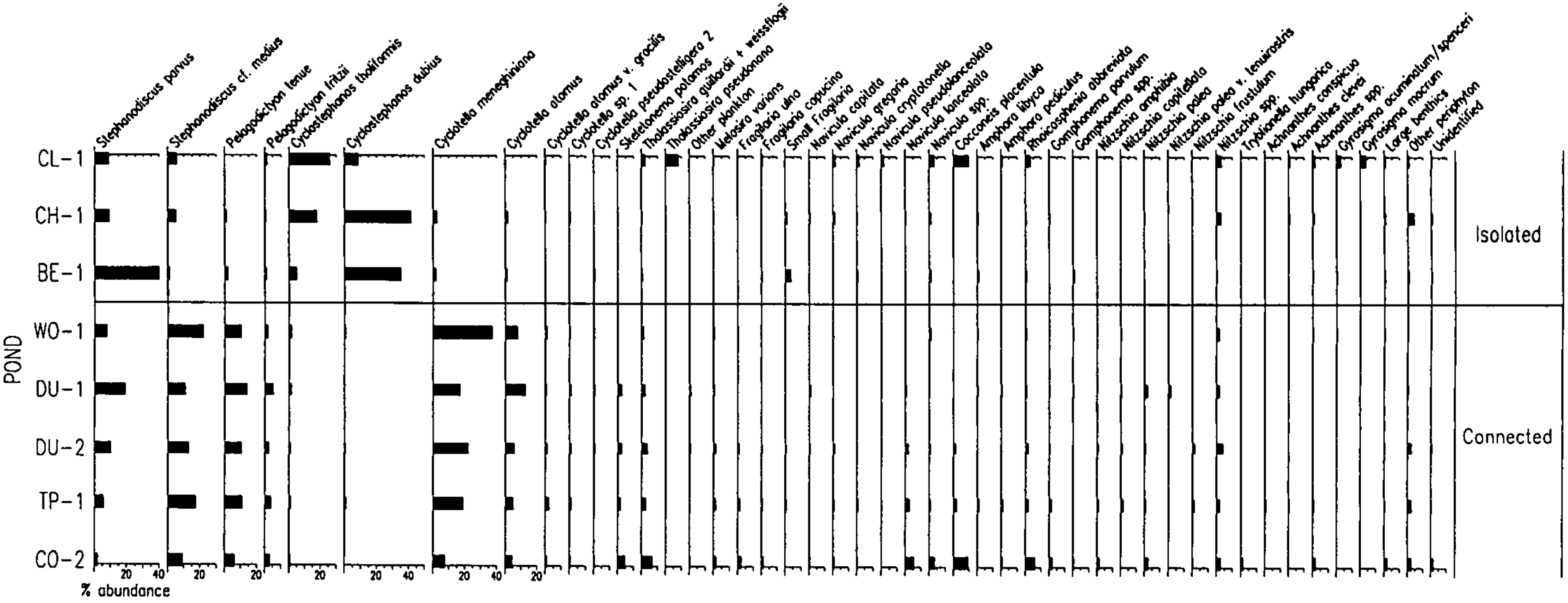


Fig. 5.7. Summary diatom diagram for the Attenborough Ponds SSSI surface sediment samples

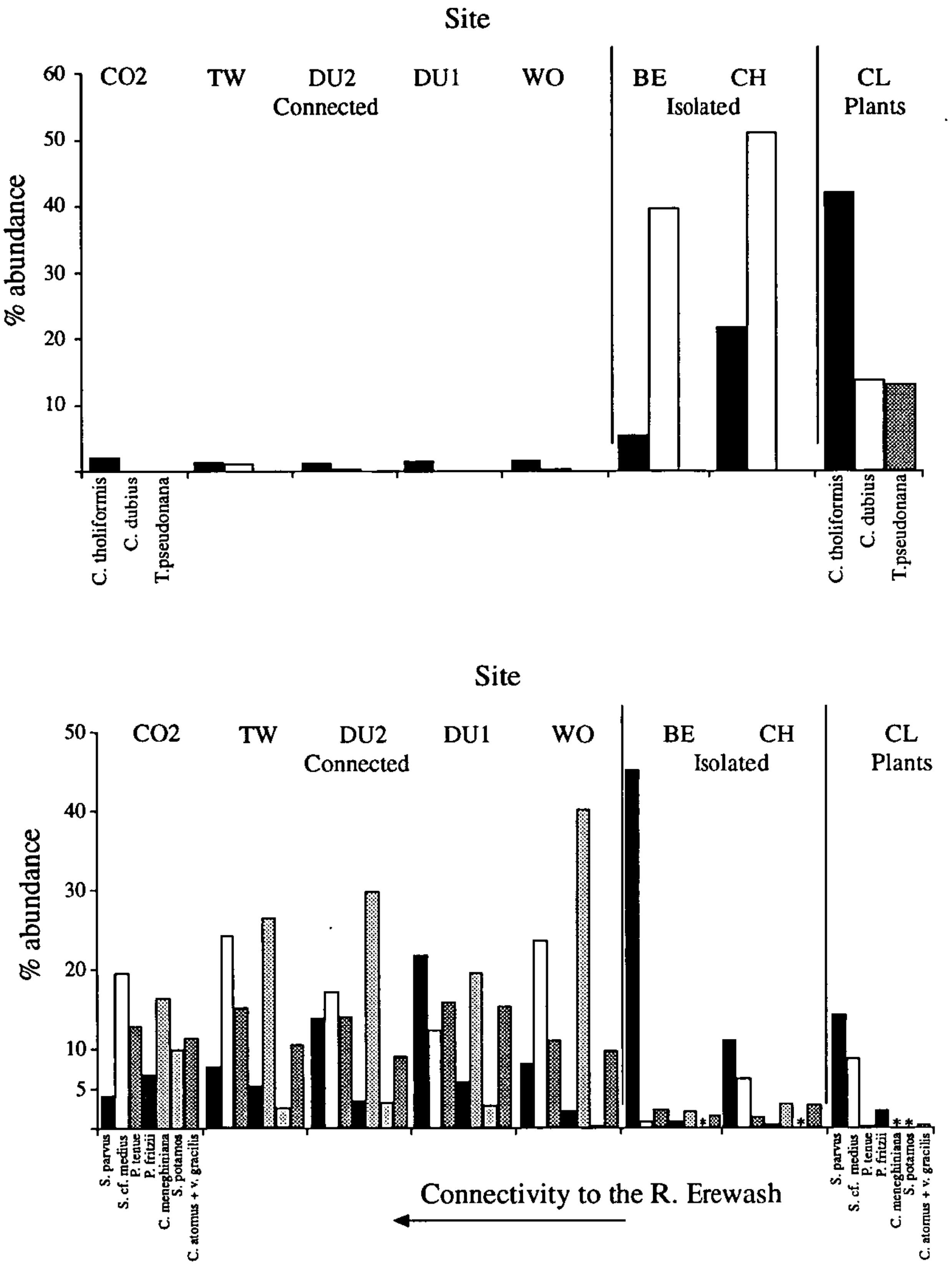


Fig. 5.8. Distribution of the dominant centric diatoms in the sediments of the Attenborough Ponds system expressed as percentages of the total plankton sum. Ponds are arranged by degree of connectivity to the R. Erewash. Site codes as in fig. 4.1.

the tiny centric *T. pseudonana* and high percentages of the epiphytes *C. placentula* and *R. abbreviata* and large benthic *Gyrosigma* spp (group III). These periphytic species are associated with the plant dominated state in Clifton Pond. Thus it is evident that the diatom assemblages clearly disinguish the river-connected sites from the isolated sites and between the alternative states of submerged plant and phytoplankton dominance.

The relationships between environmental conditions in the Ponds and centric diatom assemblages is best explored by eliminating the influence of allochthonous periphytic diatoms. Thus in fig. 5.8 the distributions of the dominant centric species are expressed in terms of their percentage contributions to the total plankton sum. The tiny centrics *T. pseudonana* and *C. tholiformis* are most abundant in Clifton Pond and would appear to favour less eutrophic conditions in the Ponds. Similarly *C. dubius* also seems to favour lower nutrient levels reaching high abundances in both Beeston and Church Ponds. Alternatively, *P. tenue*, *P. fritzii*, *S. potamos*, *T. guillardii*, *C. meneghiniana* and *C. atomus* appear to be better indicators of the highly eutrophic waters in the connected lakes, while *S. parvus* and to some extent *S.* cf. *medius* appear to have broader trophic tolerances and are found in both the isolated and connected sites. Unfortunately it is not possible to recognise clear nutrient-related responses amongst the centric forms in the connected lakes. This may be partly due to the inter-connected nature of Ponds system which means that the phytoplankton growing in one lake will drift into the next lake along the continuum. However it is also possible that this indicates the importance of other environmental factors in selecting for different combinations of species in the sediments such as Si-availability, salinity and light levels which are not linearly related to the R. Erewash water chemistry gradient.

Interpretation

The phase II to phase III transition

The seasonal diatom sampling in the three study sites (chapter four) has shown that in clear water, submerged plant dominated lakes (i.e. Clifton Pond and Groby Pool) there is a switch from plankton growth in late winter and spring to periphyton growth in summer and autumn. This seems to result in diatom assemblages in the sediment which are co-dominated by planktonic and periphytic forms. Alternatively in phytoplankton dominated lakes (i.e. Tween Pond) the absence of macrophytes and turbid water conditions means that there is minimal available habitat for periphytic diatom production and as a result assemblages are dominated by planktonic forms. The recognition of shifts in the competitive balance between phytoplankton and submerged plants requires that diatoms are grouped into different life-form categories so that the importance of different lake habitats can be assessed (cf. Moss, 1988a). In fig. 5.9 changes in the relative and absolute abundance of the different diatom life-forms in core TP193 are shown.

In the pre-diversion sediments from Tween Pond high percentages of benthic species (>35%) suggest clear water and minimal shading of the sediment by planktonic populations. Moreover high percentages of epiphytes (>13%) indicate the presence of submerged plants. Thus it is evident that the pre-1972 plant dominated state is clearly represented by the two pre-diversion sediment samples. The most prolific planktonic species in the pre-diversion sediments is *S. parvus.* This species is prevalent in the surface sediments of all the lakes in the Attenborough Ponds SSSI (figs. 5.7, 5.8) and does not appear to be a particularly good indicator of trophic status, at least in phase II and phase III lakes. However the co-dominant form *C. radiosa* (often referred to as *Cyclotella comta* in the literature (Håkansson & Regnéll, 1993)) is frequently found in the pre-eutrophication sediments of shallow lakes (Fritz, 1989; Håkansson & Regnéll, 1993) and can be associated with mesotrophic, to mildly eutrophic conditions and as such would appear to be a good indicator of lower nutrient levels and phase II conditons in Tween Pond prior to the diversion of the R. Erewash.

The reconstruction of the pre-1972 state in Tween Pond can be further refined using space-for-time substitution and by comparing modem diatom and water chemistry data for Clifton Pond with the available pre-diversion data from Tween Pond. This allows the potential of Clifton Pond as a pre-diversion analogue and restoration target to be evaluated. Unfortunately diatom dissolution (see preservation) restricted analysis to the upper 6 cm of CP193 (fig. 5.10). The dominant planktonic species in the surficial sediments from this core are *C. tholiformis*, *S. parvus* and *T. pseudonana,* although below 2 cm epiphytic and benthic forms dominate. Important planktonic species which are shared between the Clifton Pond surface sediment and Tween Pond pre-diversion sediments are *S. parvus,* *S.* cf. *medius* and *C. dubius* and notable differences are the rarity of *C. radiosa*, *C. atomus* and *C. meneghiniana* from Clifton Pond and the absence of *T. pseudonana* from the pre-breach sediments. Additional assemblage characteristics are compared in table 5.4 which reveals slightly higher plankton and epiphyte percentages, but much lower percentages of benthic *Gyrosigma* spp in Clifton Pond. Thus both samples have a generally similar life-form balance and the main difference appears to be in the presence or absence of particular species.

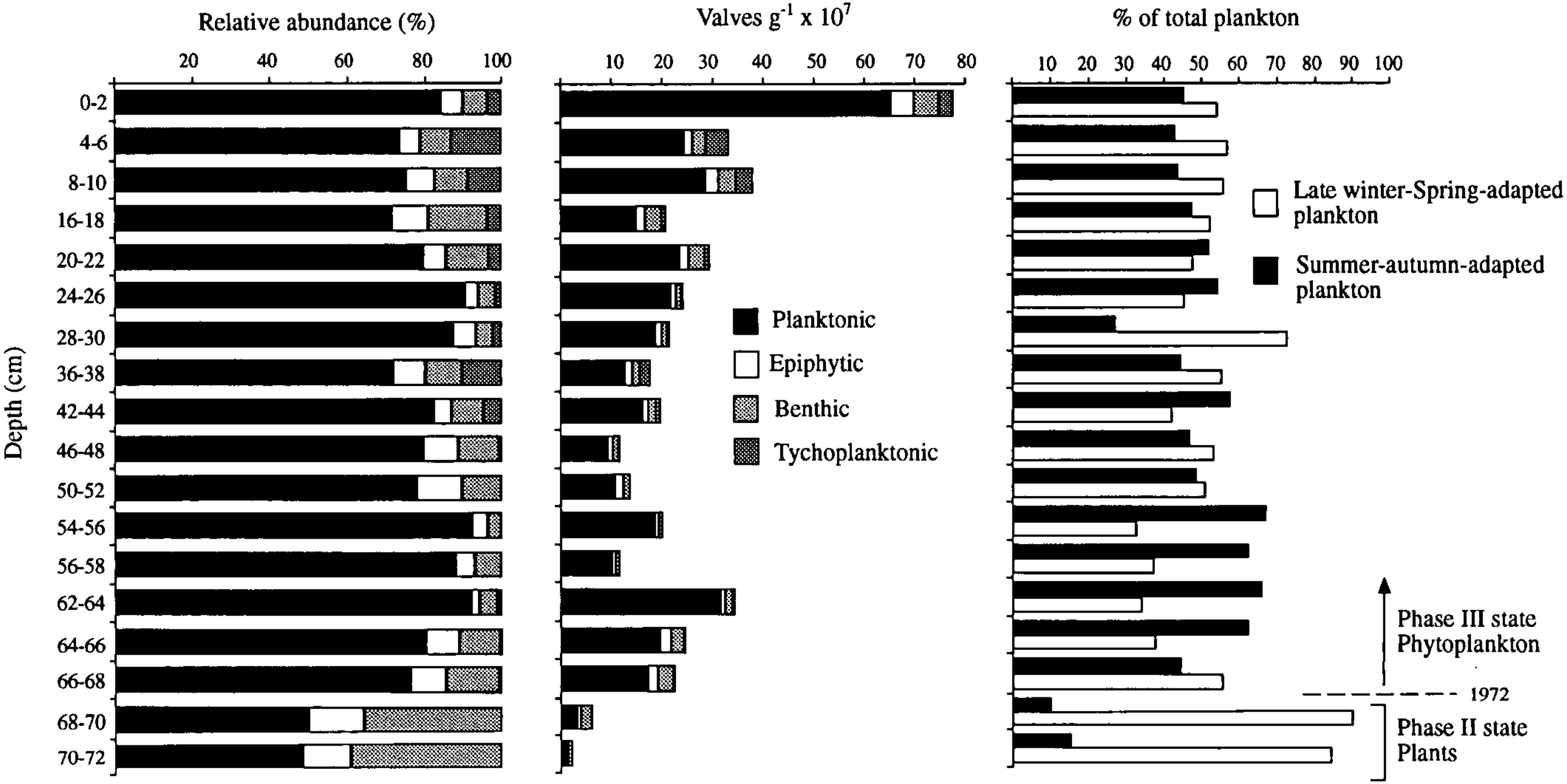


Fig. 5.9. Percentages and concentrations of different diatom life-forms and the balance between late winter-spring and summer-autumn adapted planktonic forms (expressed as percentages of the total plankton sum) in core TP193 from Tween Pond.

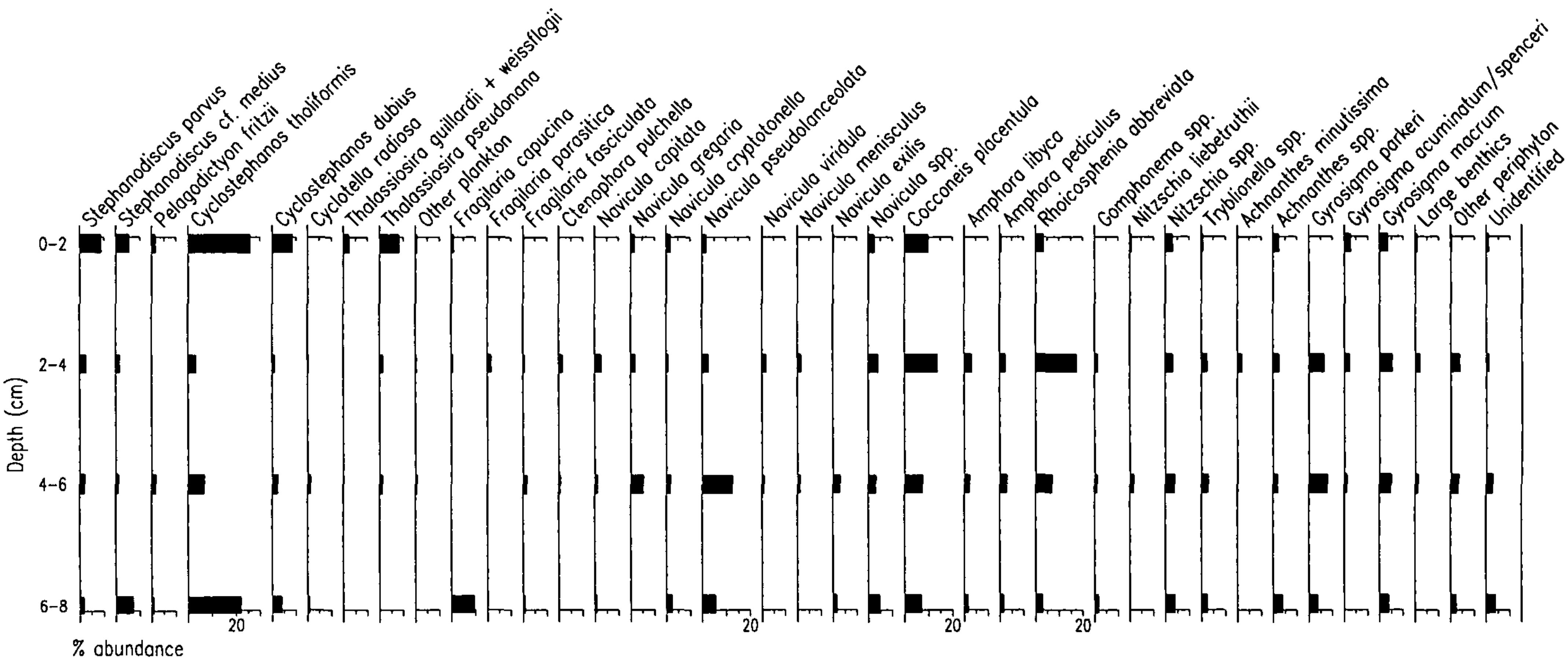


Fig. 5.10. Summary fossil diatom record for core CP193 from Clifton Pond.

	Valves $g^{-1} \times 10^7$	% Pl	% Epi	% Gy
Clifton Pond				
0-2 cm	23.5	61.2	20.6	6.4
Tween Pond				
68-70 cm	6.1	49.9	14.4	17.8

Table 5.4. The characteristics of modern surface sediments (0-2 cm) from Clifton Pond and pre-1972 (68-70 cm) sediments from Tween Pond. Pl = plankton), Epi = epiphytes, Gy = *Gyrosigma* spp.).

The available pre-diversion water chemistry for Tween Pond is compared with that of Clifton Pond in table 5.5. It is apparent that PO_4 and NO_3 concentrations are very similar such that Clifton Pond would appear to be relatively good analogue for pre-diversion nutrient conditions. However EC is much higher in present-day Clifton Pond than may have possible in Tween Pond in the pre-1972 period. This difference seems to be reflected in the modern diatom communities from Clifton Pond by the existence of indicators of raised salinity such as *Pleurosigma salinarum* and in particular *T. pseudonana*. The latter species is thought to have a relatively broad salinity tolerance (Belcher & Swale, 1977; Kiss, 1986) and it seems likely that its proliferation in the plankton of this lake is partly related to this aspect of its water chemistry. Thus while Clifton Pond would appear to be a good modern analogue for clear water conditions and low nutrient conditions in the pre-diversion period it is not a good analogue for salinity levels and this difference would appear to have left an imprint in the fossil diatom record.

	PO_4 ($\mu g\ l^{-1}$)	NO_3 ($\mu g\ l^{-1}$)	EC ($\mu S\ cm^{-1}$)
Clifton Pond (1993) n=12	63	390	983
Tween Pond (pre-Nov, 1972) n=3*	40	400	527

Table 5.5. Comparison of mean modern water chemistry for Clifton Pond with the available pre-diversion water chemistry data for Tween Pond. The pre-diversion data are derived from Britton (1974). *It is important to note that the pre-1972 means are based on just three values.

The switch from phase II to phase III conditions in Tween Pond was very rapid according to observations by the ITE and the Nottinghamshire Wildlife Trust (Lewis, pers. comm.) with very sparse submerged plant growth in the first summer following the influx of the R. Erewash. This would appear to be accurately reflected in core TP193 by an abrupt shift to planktonic diatom dominance (fig. 5.9) and a substantial increase in diatom concentrations at 66-68 cm (fig. 5.6), above which there is also a steady increase in organic matter percentages (fig. 5.3). In the post-breach sediments, the benthic and epiphytic life-forms are much restricted in percentage terms. However in several samples there are higher absolute abundances of benthic and epiphytic forms (fig. 5.9). This is undoubtedly related to the allochthonous inwash of periphytic diatoms found in the R. Erewash and its tributaries.

The switch from submerged plant to phytoplankton dominance in Tween Pond is also reflected by the altered seasonal preferences of the planktonic forms found in the diatom record. Using the seasonality data from the modern monitoring study (chapter four) in conjunction with literature sources, the different planktonic diatoms encountered in TP193 have been placed into two broad categories of seasonal responses; (i) late winter-spring adapted species, and; (ii) summer-autumn adapted species (table 5.6). In the pre-diversion sediments, species with survival strategies adapted to early season growth are dominant. This is to be expected given that prolific planktonic diatom production seems to be restricted to late winter-spring period in plant dominated, phase II lakes (chapter four). However in the post-diversion sediments, there is a balance between late winter-spring and summer-autumn adapted forms indicating that both periods of the year were probably important for diatom production as is often characteristic of phase III lakes (i.e. Tween Pond presently). The existence of an initial post-diversion situation of planktonic diatom growth throughout the year is confirmed by the 1973 phytoplankton monitoring in which large populations of centric diatoms were recorded over the June-August period (Britton, 1974). These populations were dominated by *Stephanodiscus astraea*, *Cyclotella meneghiniana* and *Melosira (=Aulacoseira) granulata* var. *angustissima*. The first of these species is probably synonymous with the form *S.* cf. *medius* in this study and it is likely that *C. atomus* is included under *C. meneghiniana*, these two species being very difficult to separate with the inverted microscope. These three summer-autumn forms were important in the immediate post-diversion sediments (i.e. 66-68 cm) and the other planktonic species encountered in this sample are largely spring bloom species which were probably abundant before the sampling began in May, 1973. Thus it seems likely that the early post-diversion diatom record accurately reflects the diatoms which were growing in the lake at this time.

Late winter-spring adapted species	Summer-autumn adapted species
Stephanodiscus parvus 3	*Stephanodiscus* cf. *medius* Δ
Stephanodiscus hantzschii 1,3	*Cyclotella meneghiniana* 5,6
Pelagodictyon tenue Δ	*Cyclotella atomus* 6, 8
Pelagodictyon fritzii Δ	*Cyclotella* sp.1 Δ
Cyclostephanos dubius 1	*Skeletonema potamos* 2,3,9
Cyclostephanos tholiformis Δ	*Aulacoseira granulata* var. *angustissima* 4
Cyclotella radiosa 1,6	
Cyclotella pseudostelligera type II Δ	
Thalassiosira pseudonana Δ	
Thalassiosira guillardii Δ	
Asterionella formosa 7	

Table 5.6. Different seasonal strategies amongst the planktonic diatom species found in the Tween Pond sediment stratigraphy. References: 1. Köhler (1994), 2. Kiss *et al.*, (1994), 3. Gosselain *et al.*, (1994), 4. Gómez *et al.*, (1995), 5. Rojo & Cobelas (1994), 6. Kiss & Padisák (1990), 7. Maberly *et al.*, (1994), 8. Genkal & Kiss, (1993), 9. Chang & Steinberg (1988). Δ = seasonality determined from this study only.

In Tween Pond both observational data and the diatom record suggest that the switch from macrophyte (phase II) to phytoplankton (phase III) dominanace was near instantaneous and involved the crossing of a critical system threshold. That the phase II/phase III transition tends to be rapid is suggested by studies in the Norfolk Broads. Moss & Leah (1982) revealed that the amount of weed removed for navigational purposes in Hickling Broad steadily declined between 1969-1974 such that there was no requirement for future plant harvesting and in all probability the Broad was largely devoid of plants in the open water. Thus it probably took some 5-7 years for the submerged plants to be completely eliminated from this lake, which is much slower than in Tween Pond. It seems likely that the rapidity of change is related to the cause of macrophyte loss. There are a range of potential switch mechanisms which have been postulated in the Broadland literature, including shading of the plant surfaces by filamentous and epiphytic algae (Phillips *et al.*, 1978) and the reduction of Cladoceran grazers because of poisoning by organochlorine pesticides (e.g. DDT) (Stansfield *et al.*, 1989) or rising salinities (Bales *et al.*, 1993). The latter two mechanisms were probably insignificant in Tween Pond, although it remains possible that the Cladocera were poisoned by another substance. However the first mechanism may have been significant and certainly large growths of filamentous algae were observed in the Ponds the summer after diversion (Britton, 1974). These growths in addition to the large phytoplankton populations which developed at the start of the growing season (May-early June) probably reduced the light available to the submerged plants precluding their growth in profundal areas.

Post-diversion changes in diatom assemblages

It is evident from the life-form data (fig. 5.9) that the diatom record from Tween Pond clearly reflects the loss of macrophytes from the lake in 1973. However, there are other diatom assemblage changes which are tracking subsequent alterations in the lake environment. The diversion of the River Erewash into the Ponds and the resulting loss of submerged plants would have resulted in a 'new' set of environmental conditions, selecting for different phytoplankton responses. In addition to enormous increases in nutrient concentrations and elevated summer EC, there would have been a shift from poorly flushed, to rapidly flushed, highly riverine conditions. The loss of macrophytes and of the refuges they provide for Cladoceran grazers (cf. Timms & Moss, 1984) would also have allowed for prolific summer phytoplankton growth, resulting in highly turbid conditions throughout most of the year. In nutrient-rich, lowland rivers it has been shown that nutrients are relatively unimportant in regulating phytoplankton biomass and community structure, more important factors being flushing rates and light and temperature regimes (Reynolds *et al.*, 1994; Gosselain *et al.*, 1994). This type of situation (as is presently the case, chapter four) has probably prevailed in Tween Pond since the Erewash diversion and it is likely that the enormous increase in nutrient concentrations after 1972 created an environment in which the phytoplankton were probably neither P or N-limited, although Si may have been an important restricting factor. The discussion which follows attempts to explain the major changes in the post-diversion fossil record and compares the major changes with the available environmental data.

The species which increase initially in the immediate post-diversion sediments are *C. meneghiniana*, *C. atomus*, *S. potamos* and *C. tholiformis*. The latter three forms are extremely small (mean cell volume = <80 μm^3) and as a result mean cell volume and total planktonic diatom volume estimates are low in the zone II sediments (fig. 5.6). Rapid flushing often favours, small forms with fast growth rates (Reynolds, 1989; Reynolds, 1994) and accelerated water through-puts after 1972 may have given *C. atomus*, *S. potamos* and *C. tholiformis* a competitive advantage over other larger centrics. Moreover, *C. meneginiana* is thought to be able to survive heterotrophically on the sediment surface (Lylis & Trainor, 1973) and may have been advantaged by 'opting out' of the flowing wave of water moving through Tween Pond. Phytoplankton studies in slow flowing, eutrophic, lowland rivers have often found *C. atomus*, *S. potamos* and *C. meneghiniana* to be common planktonic forms (Belcher & Swale, 1977; Belcher & Swale, 1978; Kiss *et al.*, 1994; Gosselain *et al.*, 1994; Clarke, 1995) and so it might be expected that these species should thrive in Tween Pond during the immediate post-breach period. Rapid flushing may also have affected the burial efficiency of different diatom populations in Tween Pond. In Hoveton Great Broad, Moss (1988a) found that the summer-adapted

Melosira (=*Aulacoseira*) spp. were grossly overrepresented in the sediments relative to the small cyclostephanoid species which were dominant in the spring. This was because rapid flushing in the early part of the year resulted in the removal of spring plankton populations before they could be incorporated in the sediments of the lake. Thus the overriding dominance of summer-autumn adapted planktonic species in several of the initial post-diversion sediments (fig. 5.9) may also be partly related to this aspect of the Tween Pond environment.

The onset of turbid, hypertrophic conditions and intense competition for light may have selectively advantaged *C. meneghiniana* over other species with higher light demands given its heterotrophic abilities. This species is also known to be indifferent to a broad salinity range (Rojo & Cobelas, 1995) and so was probably ideally suited to the post-diversion conditions. The autoecology of *C. tholiformis* is at present largely unknown as it is rarely identified in ecological studies. It was found in considerable abundance in the sediments of Marsworth reservoir (mean TP = 476 $\mu g\ l^{-1}$) by Bennion (1994) and was also prevalent in Clifton (mean $PO_4 = 63\ \mu g\ l^{-1}$) and Church (mean $PO_4 = 140\ \mu g\ l^{-1}$) Ponds. Thus it seems likely that this species may have a relatively broad tolerance of nutrients. Ecological data is more abundant for *S. potamos* and *C. atomus* and both these species seems to favour eutrophic/hypertrophic environments and like *C. meneghininana* are also tolerant of raised salinities (Belcher & Swale, 1978; Håkansson & Clarke, in press; Genkal & Kiss, 1993; Chang & Steinberg, 1988; Kiss *et al.*, 1994). Thus the appearance of the four 'new' post-diversion dominants can probably be best explained by a combination of, high P and N, elevated EC and rapid flushing.

The most distinctive species response in the post-diversion sedments is the progressive decline in both relative and absolute abundances of *C. atomus* (figs. 5.5, 5.6). This response curve suggests dynamic change and high levels of instability in the lake environment. An initial hypothesis put forward to explain this change was that *C. atomus* was responding to alterations higher up in the foodweb (i.e. biotic interactions) as the lake shifted from phytoplankton to submerged plant dominance. Phytoplankton and indeed diatoms are known to respond almost instantaneously to changes in water chemistry, but there will be lags in the adjustment of zooplankton and in particular fish communities to an external forcing. In the pre-diversion phase it is probable that fish communities were dominated by perch (*Perca fluvialilis* L.), tench (*Tinca tinca* L.) and pike (*Esox lucius* L.) as prevalent in Clifton Pond today. The typical response of shallow lake fish populations to eutrophication and macrophyte loss is a shift from a cyrinid-percid mixture, to dominance by cyprinids and in particular small, 0+ and 1+ roach (*Rutilus rutilius* L.) (Moss, 1989; Perrow *et al.*, 1994). At present bream (*Abramis brama* L.) and small roach are prolific in Tween Pond and the transition to this cyprinid dominated situation probably started soon after diversion, when macrophyte loss would have resulted in declining hunting and feeding habitat for perch, tench and pike. In theory the effect of such a shift in the fish community would be increased predation on large-bodied, plant-associated Cladocera as roach tend to be zooplanktivorous in their juvenile years (Timms & Moss, 1984) and this change might in turn have been expected to cascade down to the phytoplankton level, resulting in an increase in numbers of small, highly edible centric diatoms in summer and autumn. Thus it seems unlikely that 'top-down' effects caused the *C. atomus* reduction between 1972-1979 and for this reason 'bottom-up' control seems to be a more feasible explanation.

PO_4 data is available for Tween Pond in 1973 and for the R. Erewash at Trowell from 1975 onwards (fig. 5.2). If values for Tween Pond are predicted from current relationships between the lake, the inlet and Trowell, it is evident that PO_4 increased over the 1972-1978 from around 680 $\mu g\ l^{-1}$ to possibly over 3000 $\mu g\ l^{-1}$ in 1978. NH_4 also increased from 1972 to 1975 but was reduced in 1976, before a further increase from 1976 to 1978. In contrast EC remained relatively stable. It is possible that the progressive decline of *C. atomus* may have been related to increasing nutrient concentrations in the Pond and in the absence of any other information, this seems the most likely explanation. However it is difficult to find supportive evidence for this hypothesis as again there are no published data regarding the trophic requirements of this species relative to other eutrophic, centric forms. Moreover this species does not have an obvious distribution in the sediments of the Ponds complex (fig. 5.8).

The next major change in the diatom assemblage is at the zone II/zone III boundary (approx. 1979) with significant increases in valve concentrations and the return of mean cell volume to pre-breach levels (fig. 5.6). The important species shifts at the start of zone III are the increased contributions of *S.* cf. *medius* and *P. tenue* and the declining importance of *C. tholiformis* and *C. atomus*. There are some important water chemistry fluctuations which would appear to be synchronous with this event (fig. 5.2). NH_4 began to decline in the R. Erewash after 1978 as did EC after 1980 and PO_4 also began a short-lived decline in the R. Erewash at Trowell in 1978, however after 1981 concentrations started to increase again at both these sites. Thus it is possible that these changes may have been partly responsible for the increased relative competitiveness of *S.* cf. *medius* and *C. tholiformis.*

However the most likely explanation for the changes at the zone II/zone III boundary seems to be the alteration in the hydrology of the lake at this time. The outlet for the R. Erewash at Barton lane was constructed in 1980 (fig. 5.1) and this meant that under normal discharges a substantial portion of Erewash water flowed out into the Trent before it reached Tween presently) to plankton dominated assemblages and; (ii) the sudden appearance of significant percentages of summer adapted planktonic diatoms. These changes reflect the eutrophication-mediated transition from submerged plant to phytoplankton dominance and are as a result indirectly related to nutrient enrichment. In particular the increased abundance of summer-adapted centric species and the rapid reduction in the importance of benthic diatoms may have been the result of the removal of top-down control over phytoplankton growth and the onset of 'year-round' turbid conditions.

In most small lakes subject to eutrophication the fossil diatom record is interpreted as a direct response to changing nutrient levels and nutrient interactions. However in Tween Pond it is apparent that diatom-nutrient responses were often indirect and that other factors selected for the prevalence of different species in the sediment. In addition to the switch to phytoplankton dominance, changes in EC and hydrology were probably important in this respect and it is evident that the diatom record cannot be interpreted as a simple response to nutrients.

CHAPTER SIX

The eutrophication history of Groby Pool

This chapter focuses on the eutrophication history of Groby Pool. Modern water chemistry, productivity and diatom ecology data for this lake are given in chapter four. In contrast to Tween Pond which is just 30 years old and may never have attained a true stable, equilibrium state Groby Pool is a relatively ancient lake (>700 years old) and in the pre-1800s it is probable that it remained little disturbed. There is considerable evidence to suggest that at one time Groby Pool was the richest wetland habitat in Leicestershire. The aquatic plant flora of the Pool and surrounding marsh has been recorded in lyrical terms by botanists since the mid-18th century. In the 1886 'flora of Leicestershire' Groby Pool is described as, "perhaps the most remarkable botanical locality in the county. It has a flora almost peculiar to itself". This enthusiastic excerpt suggest that before the turn of the century the Pool was greatly valued by local botanists. However like many shallow lakes in lowland England it has suffered from nutrient enrichment in the present century, with associated damage to its aquatic plant communities. Recent aquatic plant surveys have revealed that the lake has lost many of the rare submerged and emergent plants species that it formerly supported (Primavesi & Evans, 1988) and at present it supports prolific, 'choking' annual growths of a few, highly competitive plants and thick mats of filamentous algae which cover large areas of the water surface in summer and autumn (Plate 6.1).

This chapter explores the eutrophication history of Groby Pool and compares the fossil diatom record with documented catchment land-use changes (David, 1991), old submerged plant records (Beresford, 1989) and herbarium epiphyte data. Initially the origins and history of the Pool, known changes in catchment land-use and previous palaeolimnological studies are discussed. Then the dating, lithostratigraphy and diatom biostratigraphy of sediment cores taken from the Pool are described and the available submerged and floating macrophyte records since the mid-eighteenth century are summarised. In the final part of this chapter the palaeoecological record from the Pool is compared with the other available data sources to try and reconstruct background ecological conditions, the pathway of trophic change and historic shifts in phytoplankton-macrophyte interactions.

The history of the Pool

The age and origin of Groby Pool has been the subject of recent debate and a range of hypotheses exist to explain its creation. Traditionally it has been assumed that the Pool occupies a natural depression, or a kettle hole (Woodward, 1984) and local guidebooks invariably refer to it as the largest natural sheet of water in Leicestershire (Stevenson, 1982). However the theory which has gained recent momentum is that it is an artificial lake, resulting from the damming of its two inflow streams (David, 1991). The derivation of the word Groby can be traced to the Gothic 'grouba' meaning 'pit', or 'hollow' and to the modern Danish words 'grob' and 'grop' which mean quarry. These references suggest that the parish was probably named after early quarrying in the locality and that the Pool itself is possibly a deliberately flooded quarry lake. The parish of Groby is recorded in the Domesday Book in AD1086, but there is no record of a lake. The first documented reference to such comes from an Inquisition Post Mortem in 1288 conducted on the estate of William de Ferrers which refers to two fish ponds and two associated water mills (David, 1991). Undoubtedly one of these ponds was Groby Pool and this suggests that the Pool dates to at least early medieval times.

The Close Rolls of 1371 mentions a 'fish pond called the Nere Mulnepol with the pond and cowail as long as broad as it used to extend, with the bayes and the elwhicce'. Mulnepol means mill pond and bayes are dams and Woodward (1984) suggests that the elwhicche may be an eel trap. Records of two fish ponds in the Ferrers estate continue until the mid 15th century after which time the smaller of the two ponds was infilled and the land was put down to pasture. The dam of this second pond is still visible in the landscape as an earthwork positioned at right angles to the Slate Brook in an area to the SW of the lake known as the 'Pool Tails'. In the 16th century Leland refers to Groby Pool as 'as faire and large a pole as lightely is in Leyrcestershire' (David, 1991). These words perhaps capture the importance of the Pool in the medieval landscape.

Historical land-use changes

The history of the Groby Pool catchment has been studied by David (1991) and is summarised here. In the medieval and early pre-modern periods a large amount of the ancient oak forest was felled. However, relative to other parts of Leicestershire considerable tracts of woodland survived and this was managed in the traditional way by rotational felling of 'coppice with standards' (Rackham, 1980). The pre-Enclosure map of the 'manner of Grooby' drawn up by Doherty in 1757 (Woodward, 1984), provides an excellent record of land-use at this time and from this it can be estimated that around 25% of the catchment was deciduous woodland, while the remaining land consisted almost entirely of pasture (fig. 6.1). In the post-enclosure period (i.e. post-1789) there was a broad movement away from arable cultivation towards permanent pasture over much of the Middle England landscape (Rackham, 1980). However this did not occur in the Groby catchment and it was in this period that large areas of pasture were ploughed up to make way for arable crops. It has been estimated that from at least 1860 onwards fields in the catchment were being cultivated with beans, corn and root crops and it is likely that there were arable fields during much of the period prior to this (David, 1991). The sales catalogue of the Bradgate estate for 1925 provides the first detailed post-Enclosure land-use record and from this it can be estimated that around 30% of the pastured area had become arable land by this time (fig. 6.1). In the Second-World War (1939-1945) additional land in the catchment was converted to arable and subsequently catchment land-use has probably remained relatively stable (David, 1991).

Previous palaeolimnological studies

The sediment stratigraphy of Groby Pool has been extensively studied by David (1991) who collected nearly forty short (mostly <1 m) cores from the lake between spring 1988 and summer 1989. Loss-on-ignition (LOI) profiles were established for twenty-nine of these cores and particle size, magnetic mineral and pollen analysis were performed on two central cores. The longest (>3 m) core (i.e. core 24) from the deepest part of the lake to the SE of the island was ^{210}Pb and ^{137}Cs dated. The uppermost sediments of the Groby cores have been found to consist of fine, black organic gyttja (*Limus detrituosus*) which grades down into a soft, light brown silty clay (*Argilla granosa*) that stiffens with depth. The thickest layers of organic gyttja (>100 cm) have been found in profundal cores from the area to the SE of the island and in littoral cores from the NW margins indicating higher sediment accumulation rates. Elevated accumulation rates in the NW littoral cores probably reflects localised inputs of organic debris derived from the annual die-back of emergent (*Typha* spp.), floating and submerged leafed macrophytes which are particularly prolific in this part of the lake (chapter four).

Sediment coring 1995

In June 1995 two parallel short cores were taken from deep water (>1.5 m) to the immediate NE of the sediment traps, close to the water chemistry sampling sites (fig. 4.1). The first of these cores, GR95A was 26 cm long and was collected with a Glew corer, and the second core, GR95B was 104 cm long and collected with a Mackereth corer. In GR95B the transition between the dark organic gyttja and the light brown silty clay occurred at approximately 77 cm. In both GR95A and GR95B the upper 10 cm of the gyttja was a dark, olive brown and slightly lighter in colour than the very dark brown sediment below.

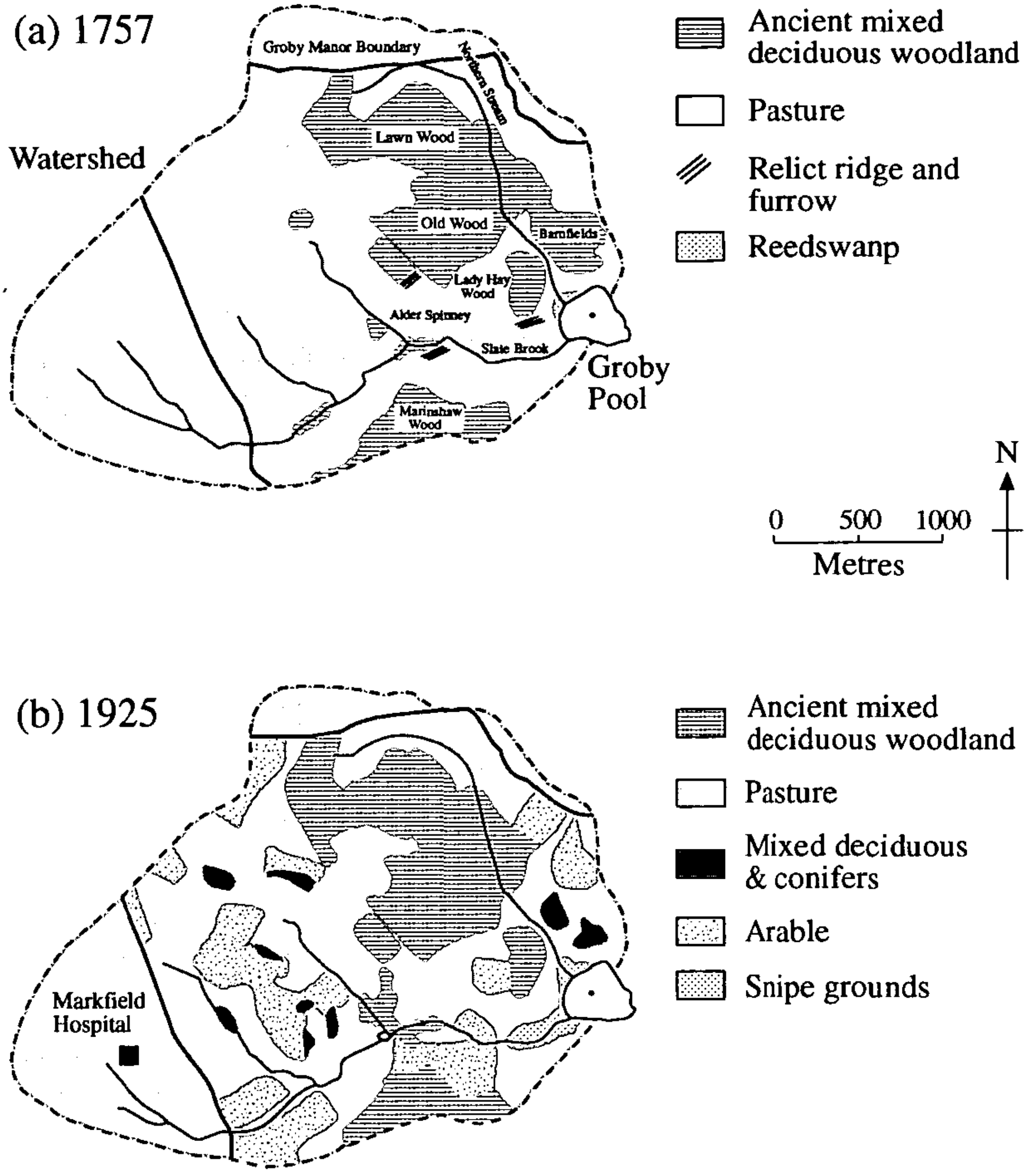


Fig. 6.1. Land-use in the Groby Pool catchment in; (a) 1757; and (b) 1925. The 1757 reconstruction is based on the field map produced by Doherty in the mid-eighteenth century and the 1925 reconstruction on the Bradgate Estate sale catalogue of that year (adapted from David, 1991).

* No accurate land-use data is available for the area outside the Groby Manor Boundary

Lithostratigraphy

Percentage organic matter and carbonate profiles for cores GR95A and GR95B are given in fig. 6.2. There are extremely close similarities between these two cores and so only the longer of the two, GR95B is described. In this core organic matter levels are relatively stable from 104-42 cm (9-11%), above which there is an increase to a temporary peak at 36-37 cm (12.9%). This is followed by a short lived decline and a renewed increase above 26-27 cm to a peak of 16.6% at the sediment surface. In many of the profundal cores analysed by David (1991) a similar pattern is evident, the most consistent feature being the rise in organic matter percentages above approximately 50 cm and relatively stable percentages below this level. In GR95B carbonate percentages are low and similarly stable (6-8%) in the lower part of the core. At 52-53 cm there is a relatively rapid increase to 10.3%, followed by a decline and comparatively stable levels between 45-22 cm. Percentages then increase rapidly to a maximum of 16.4% in the sub-surface sample.

Dating

It was not possible to undertake ^{210}Pb and ^{137}Cs analysis on core GR95B. However repeatability of the profundal organic matter signal in the Pool makes it possible to establish strong inter-core relationships between some sediment levels and as a result age-depth relations for this core have been established by correlating the organic matter profile of GR95B with the ^{210}Pb dated core 24 of David (1991). In GR95B the pattern of organic matter deposition is most similar to David's core 31 and unfortunately appears to be less strongly related to that of core 24. However core 31 has an extremely similar organic matter profile to core 24 and these two cores have also been correlated using pollen influx data, so it remains possible to establish age-depth relations for GR95B by transferring relationships between cores. Proposed correlations between GR95B and cores 31 and 24 are given in fig. 6.3. Between 15-60 cm there is a good match between the organic matter signal in GR95B and core 31, although above and below this part of the core reliable correlation is much more difficult. The rate of sediment accumulation is slightly slower in GR95B, relative to cores 31 and 24. In core 24 the mean accumulation rate for the upper 20 cm is around 0.44 cm yr^{-1} which means that approximately 3 cm of sediment will have accumulated since it was taken in 1988. This means that accumulation in GR95B is around 2-3 cm slower and so the same age-depth relations are theoretically transferable between these two cores.

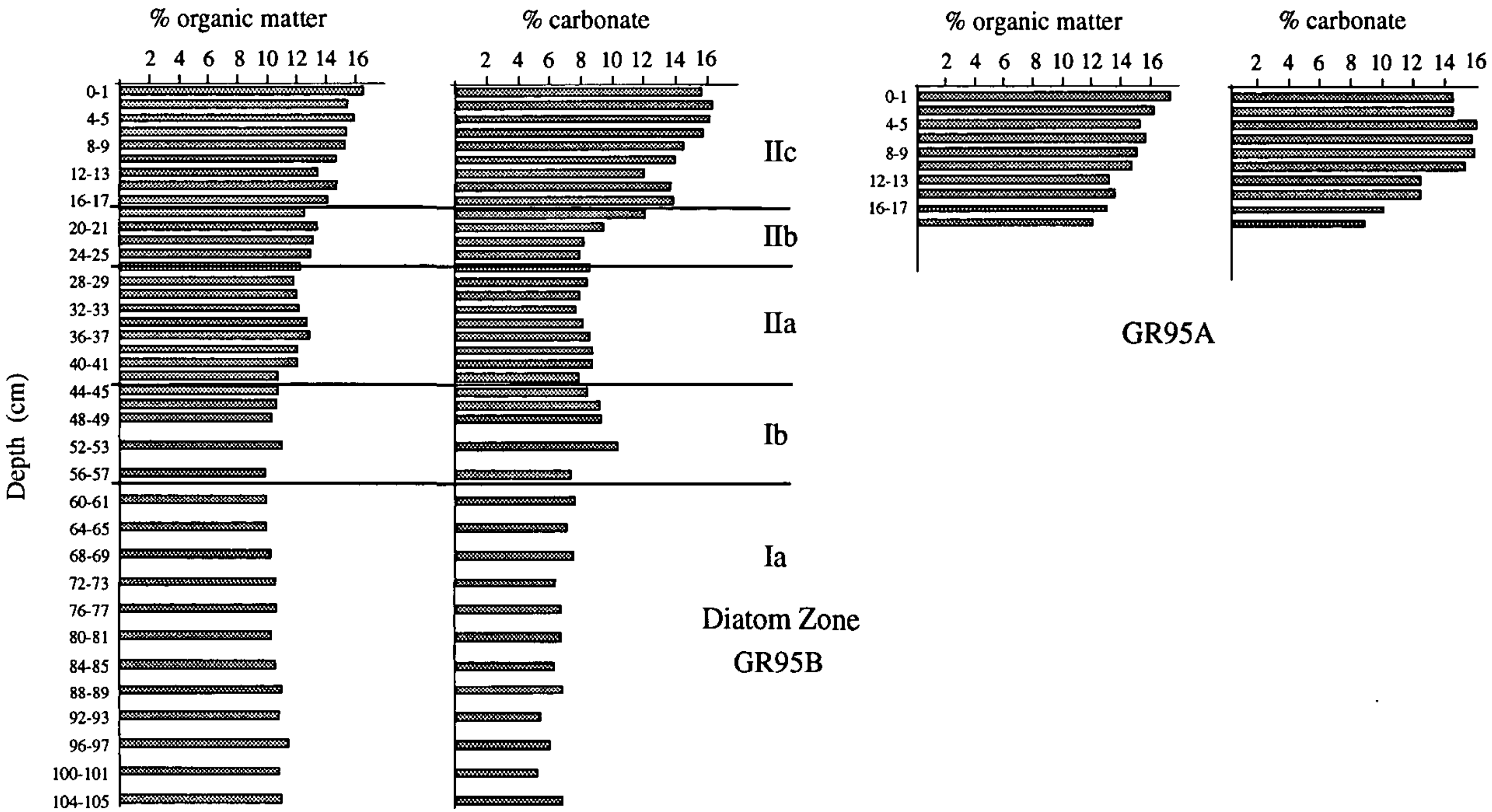


Fig. 6.2. Profiles of percentage organic matter and carbonate for cores GR95A and GR95B from Groby Pool.

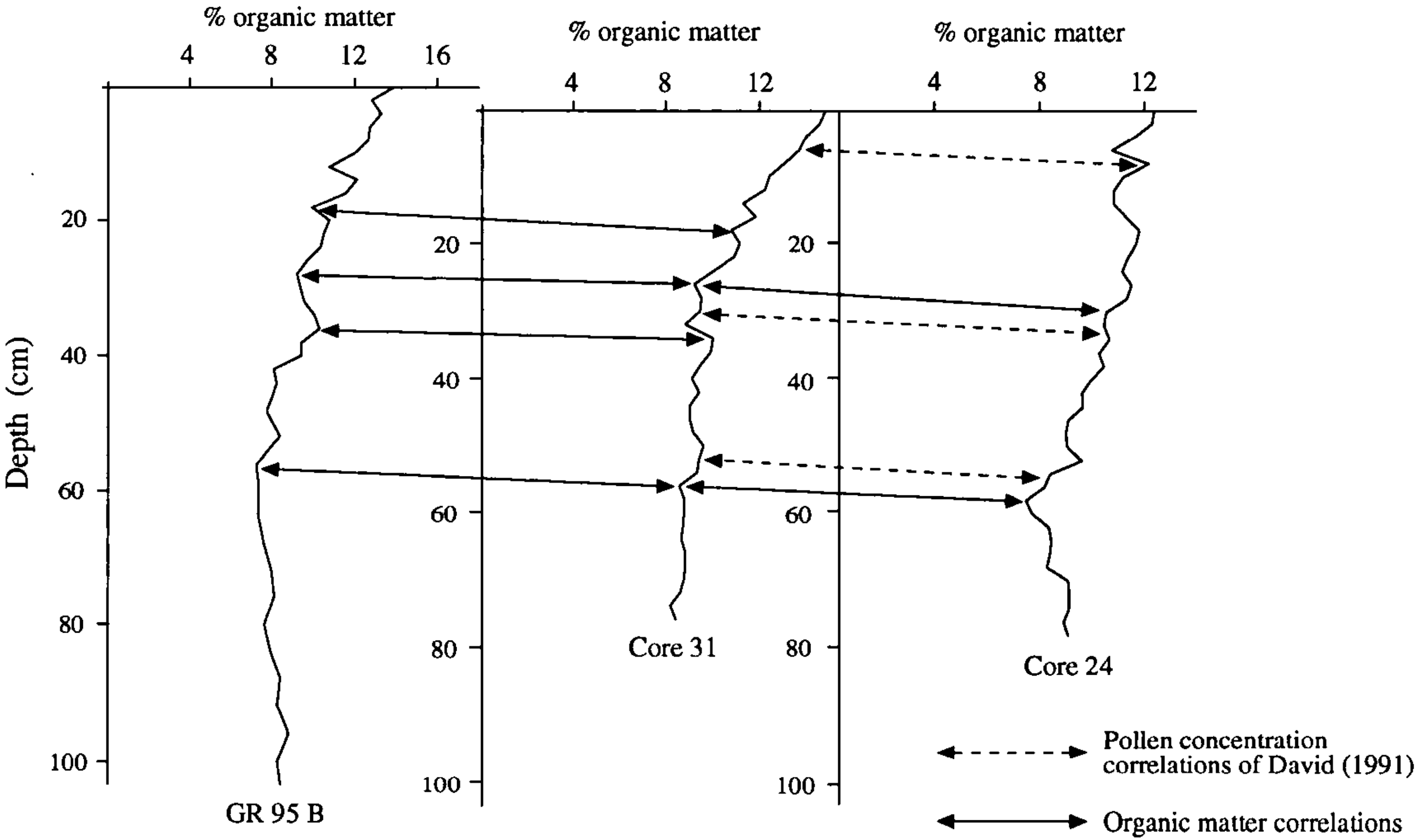


Fig. 6.3. The correlation of core GR95B with cores 31 and 24 (dated master core) from David (1991) using organic matter profiles and pollen concentration data.

Preservation

In core GR95B diatoms were generally well preserved with the exception of 42-57 cm where many valves were badly eroded and diatom concentrations were low (fig. 6.5) indicating a phase of diatom dissolution. This reduced the count to below 300 valves in the samples at 44-45 and 46-47 cm and as a result these levels were considered with caution in the interpretation. The dominant species in this part of the core were small *Fragilaria* spp. and the centric form *Cyclostephanos dubius*. Under the LM it appeared that *C. dubius* was more susceptible to erosion and several valves had poorly preserved marginal alveolar chambers. Thus it is probable that this species was underrepresented relative to the *Fragilaria* spp.

In Tween and Clifton Ponds dissolution in the lower parts of the cores was thought to be related to upwelling groundwater reducing Si concentrations in the interstitial waters (chapter five). However this is unlikely to apply to Groby Pool where there was excellent diatom preservation below 60 cm. Reynolds (1986) indicates that dissolution kinetics means that dissolution is unlikely in the water column of shallow lakes. Thus it is probable that there was a strong dissolution front at the mud-water interface. This may explain why dissolution appeared to be selective on the spring centric species *C. dubius* which would have been deposited in the sediment just prior to the major phase of Si-recycling in the summer months (chapter four).

Diatom biostratigraphy

The diatom record from GR95B (fig. 6.4) can be divided into two major zones (I and II) based on significant changes in the diatom assemblages. These zones can then be further sub-divided into sub-zones Ia and Ib and sub-zones IIa, IIb and IIc. The zone and sub-zone boundaries are largely based on those suggested by the agglomerative clustering program CONISS. The zone and sub-zone boundaries are given approximate dates based on correlations to the age-depth curve constructed for core 24 (David, 1991).

Sub-zone Ia (104-58 cm; c. pre-1750-1845) is dominated (>80%) by the small, chain-building *Fragilaria* spp., *Fragilaria brevistriata*, *Fragilaria pinnata*, *Fragilaria construens* var. *venter* and to a lesser extent *Fragilaria construens* var. *construens*. There are some important shifts in the balance between these species and in the lowest two samples *F. pinnata* dominates the assemblage achieving 55% at 103-104 cm and 47% at 96-97 cm. Above this level the three taxa are more equally represented. At 88-89 cm *F. pinnata* declines quite abruptly and is displaced by the epiphytic forms *Amphora veneta* (8%) and

Cocconeis placentula (7%). It then increases to a secondary peak of 42% at 72-73 cm, followed by a further decline. In this sub-zone *A. veneta* is absent from samples above and below 88-89 cm and *C. placentula* is of much reduced importance. The response of *F. construens* var. *venter* above 88-89 cm mirrors that of *F. pinnata*, with a peak in relative abundance at 72-73 cm (29%), but contrasts to *F. brevistriata* which continues to increase in relative abundance. While the other *Fragilaria* spp. exhibit important fluctuations throughout this sub-zone *F. construens* var. *construens* is found at stable, lower levels (<7%). The only planktonic form that is encountered in any abundance in Ia is the small centric form *C. dubius*. This species occurs at extremely low levels from 104-72 cm (<5%), but increases towards the top of the sub-zone, achieving 17% in the uppermost sample at 60-61 cm.

Sub-zone Ib (58-44 cm; c. 1845-1890) is again dominated by small *Fragilaria* spp. There are continued reductions in the share of the assemblage occupied by *F. pinnata* and the sub-dominant form *F. construens* var. *construens* throughout this sub-zone, and *F. brevistriata* which reaches a peak of 37% in the bottom sample (58-59 cm) also declines to 17% at the top of Ib. In contrast, *F. construens* var. *venter* increases in IIb from 17% at 58-59 cm to over 27% in the top two samples (46-47, 44-45 cm). The small centric *C. dubius* remains at relatively stable levels in this sub-zone (<17%) and is joined by *Aulacoseira granulata* var. *angustissima* in the samples at 48-49 cm (6%) and 46-47 cm (3%). The only other diatom species encountered in any abundance in this sub-zone is a small centric form tentatively assigned to the genus *Melosira* (i.e. *Melosira* sp. 1) which achieves 5% at 46-47 cm.

Sub-zone IIa (44-26 cm; c. 1890-1937) is characterised by the decline of *F. construens* var. *venter* and *F. brevistriata* and a sharp increase in the importance of *C. dubius*. While *F. construens* var. *venter* achieves 27% at 44-45 cm it attains just 10% at 42-43 cm and *C. dubius* which occupies 12% of the assemblage at 44-45 cm improves to 29% at 42-43 cm. The rapid reduction of *F. brevistriata* also continues at 42-43 cm (10%) and both this species and *F. pinnata* exhibit a similar response to *F. construens* var. *venter* and progressively decline throughout this sub-zone. The centric *C. dubius* increases to 29% at 42-43 cm and remains at stable high levels (>27%) from 43-28 cm. However in the top sample at 26-27 cm, the contribution of *C. dubius* is reduced to 19%. The plankton becomes partitioned between more species in this sub-zone and *C. dubius* is joined by the small centric *Stephanodiscus parvus*. This form attains 11% at 42-43 cm, but then declines in importance between 41-34 cm, before a renewed increase in the upper part of the sub-zone to 15% at 26-27 cm. The unidentified centric *Stephanodiscus* sp. 1 which is not recorded in zone I attains 11% at 40-41 cm, although it is of minor importance elsewhere (<3%). Also present in detectable amounts in IIa are *Cyclostephanos tholiformis* and

Pelagodictyon tenue. The tychoplanktonic form *Fragilaria capucina* var. *mesolepta* appears for the first time in this sub-zone and oscillates between 1-7% while the periphytic forms *C. placentula, Amphora pediculus* and to a lesser extent *Navicula capitata* are consistent minor taxa.

Sub-zone IIb (26-16 cm; c. 1937-1957) contains just four samples and is defined by the replacement of *C. dubius* by *S. parvus.* While *S. parvus* maintains its position at over 15% in this sub-zone, *C. dubius* declines to below 4% in the samples at 20-21 cm and 18-19 cm. There are minor increases in percentages of the tiny centric *C. tholiformis* (<3%) and *P. tenue* (<4%), but *F. capucina* var. *mesolepta* maintains itself at similar levels to IIa. Percentages of *F. pinnata, F. construens* var. *construens*, and *F. brevistriata*, are relatively stable, although there is a slight increase in *F. construens* var. *venter* in the samples at 24-25 and 22-23 cm (>9%). The epiphyte *C. placentula* increases throughout IIb attaining over 7% in the upper two samples (20-21, 18-19 cm), but a minor decrease is evident in the relative abundance of *A. pediculus.* A major defining characteristic of this zone is the appearance of *Nitzschia intermedia.* This species was present in the ultimate sample of sub-zone IIa (3%) and remains at similar levels in the lower two samples of IIb before rising to 6% at 20-21 cm and 12% at 18-19 cm. The life-form of this species is uncertain.

Sub-zone IIc (16-0 cm; c. 1957-1995) is characterised by a range of subtle, but important assemblage shifts. The centric form *S. parvus* maintains itself at stable dominant levels (15-26%) from 17-2 cm and then increases to a marked peak at the surface of 44%. *P. tenue* and *F. capucina* var. *mesolepta* also occur at relatively stable levels in this sub-zone, but *C. tholiformis* which was scarce in IIb increases to 9% at 12-13 cm, before returning to below 3% in the overlying samples. Also *Cyclotella* sp. 1 increases to over 3% in the bottom two samples (16-17 and 14-15 cm) and *A. granulata* var. *angustissima* reappears, rising to a peak of 6% at 4-5 cm, followed by a rapid decline. Important changes in the periphyton are also evident and *Melosira varians* which was rare below 17 cm increases throughout this sub-zone to 11% at 2-3 cm and *C. placentula* steadily increases, marginally outstripping *S. parvus* in the samples at 6-7, 4-5 and 2-3 cm where it exceeds 16%. The small *Fragilaria* spp., *F. construens* var. *venter, F. construens* var. *construens, F. pinnata* and *F. brevistriata* resume their decline in IIc and become rare species in the top 6 cm (<3%). This sub-zone is also characterised by minor increases in the benthic forms *N. capitata* and *Navicula pseudolanceolata* and the epiphytic species *Amphora veneta.* There is also a detectable increase in *Nitzschia* spp. while the epiphyte *A. pediculus* declines in importance.

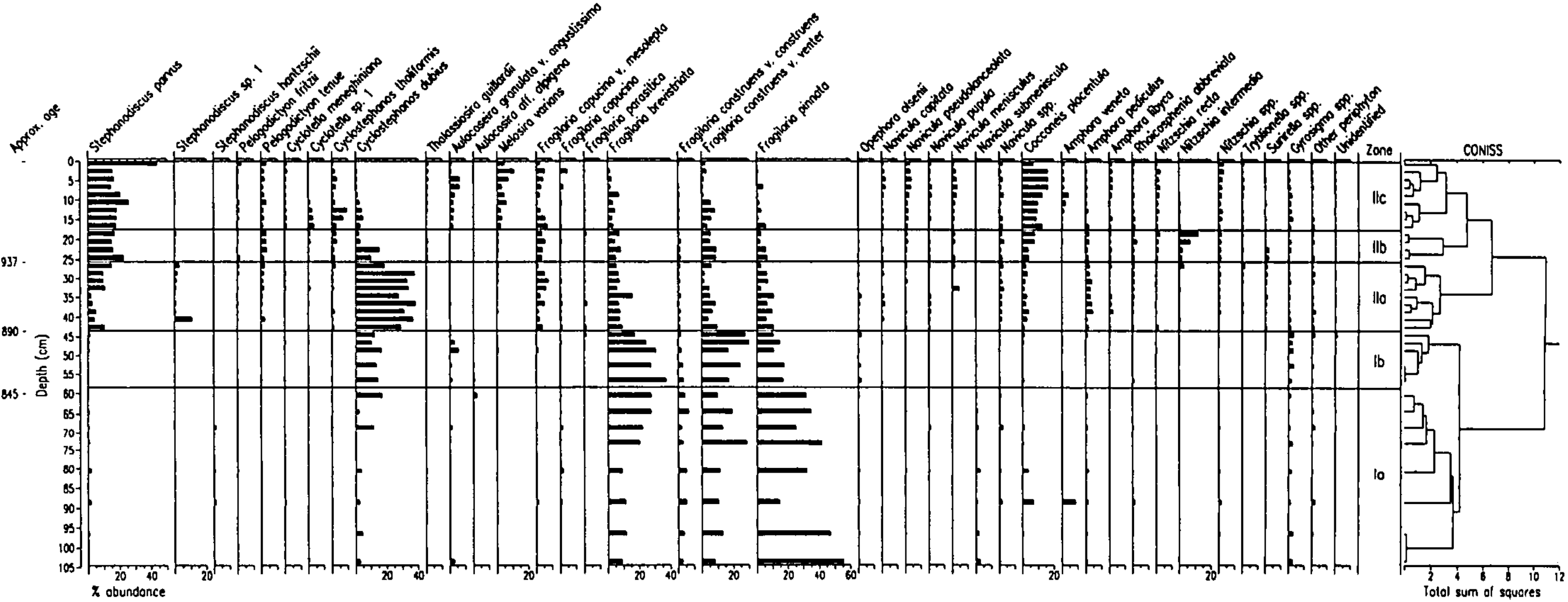


Fig. 6.4. Summary fossil diatom record for core GR95B from Groby Pool.

Diatom concentrations

Estimates of diatom concentrations (valves g^{-1}) for core GR95B are given in fig. 6.5. In the basal part of sub-zone Ia diatom concentrations are high and peak concentrations for the core are attained at 96-97 cm (26 x 10^7 valves g^{-1}). However in the upper three samples of this sub-zone (68-69, 64-65, 60-61 cm) concentrations fall to relatively stable, lower levels (11-12 x 10^7 valves g^{-1}). Low concentrations in sub-zone Ib (i.e. <4 x 10^7 valves g^{-1}) reflect dissolution losses and in this part of the core it is likely that diatom palaeo-production is severely underestimated. Abundances are also low in the initial sample of IIa (2 x 10^7 valves g^{-1}), but rapidly increase to a secondary peak of 25 x 10^7 valves g^{-1} at 36-37 cm, above which diatom concentrations fluctuate between 10-21 x 10^7 valves g^{-1} for the remainder of the sub-zone. In sub-zone IIb concentrations are relatively stable ranging between 7-12 x 10^7 valves g^{-1}, but steadily increase again in sub-zone IIc to 20-21 x 10^7 valves g^{-1} in the top three samples of the core.

Historic aquatic plant records

It is unusual to find detailed and continuous macrophyte records for lakes which span long periods of time (i.e. >100 yrs), but fortunately such a situation exists for Groby Pool. The plant communities in the lake have been recorded in four county floras (1850, 1886, 1933 and 1988) and the Pool is well represented in herbarium plant collections scattered around England. By utilising these twin sources of data, Beresford (1989) has prepared a detailed list of the emergent, submerged and floating leafed species found in the Pool since records began in the mid-18th century. Tables 6.1 and 6.2 are a synthesis of some of this data and incorporate some additional records from other recent surveys (1950-1990) and the results from chapter four. Table 6.1 lists the species found in the lake in four different time periods as defined by the temporal spacing of the four floras and table 6.2 lists the plants which were 'lost' and 'gained' between these intervals. It must be recognised that there are a number of problems associated with this type of data in that there are no reliable cover estimates (i.e. data is usually in the form of presence/absence) and it is usually impossible to define the exact timing of when individual species arrived or when they were eliminated from the lake. Moreover it is likely that species were overlooked particularly as most searches would have been made without a boat. Thus it is difficult to make reliable assessments of changes in macrophyte diversity. However despite these limitations this data provides an excellent and in many ways unrivalled insight into the effects that nutrient enrichment might have had on macrophyte communities in the lake.

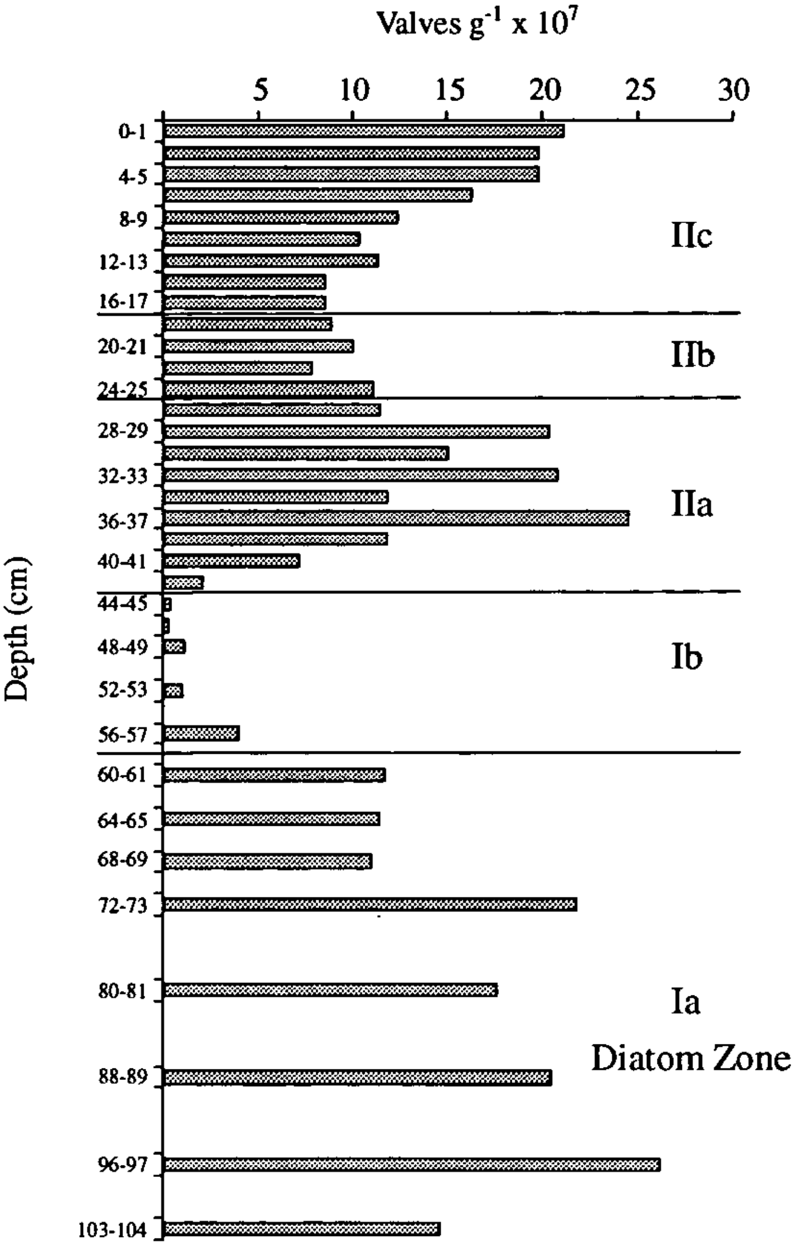


Fig. 6.5. Diatom concentrations in the sediments of core GR95B from Groby Pool.

The standing waters classification scheme of Palmer *et al.*, (1992) provides a means of relating different aquatic plant assemblages to trophic status. This classification is based on the occurrence of plant species in 1124 fresh and brackish standing water sites in Great Britain. TWINSPAN has been used to identify ten distinct site types on a trophic continuum ranging from oligotrophic and acid lakes in peat catchments, to eutrophic-hypertrophic lowland lakes and based on the frequency of occurrence of individual species in the ten groups, each plant has been assigned a 'DOME' ranking code. This indicates its distribution in the dystrophic (D or d), oligotrophic (O or o), mesotrophic (M or m) and eutrophic (E or e) categories with upper case letters indicating a greater degree of classification confidence than lower case letters. Trophic ranking scores (TRS) from 1-10 have also been given to each species. The DOME codes and TRS scores for the plants recorded in the Pool are listed in the two left hand columns of table 6.1.

Up until at least 1850 the Pool probably possessed a diverse arrangement of submerged and floating leafed aquatic plants and at least 17 different species are recorded in the lake between 1748 and 1850 (Table 6.1). The mean TRS for this period is 8.48 which places the lake in the mesotrophic (ME) class of Palmer *et al.*, (1992). The assemblage consists of a mixture of species with a range of TRS scores (i.e. 5.5-10), but many of the plants in this period (e.g. *Utricularia vulgaris* L., *Littorella uniflora* L. and *Potamogeton gramineus* L.) have low TRS rankings indicating that the lake was able to support a variety of species intolerant of nutrient-rich conditions. In particular *P. gramineus* is thought to rare in eutrophic waters (Preston, 1995) and *L. uniflora* which is common in infertile upland tarns, is generally associated with oligotrophic-mesotrophic sites (Palmer *et al.*, 1992).

Species	DOME	TRS	Pre-1850	1850-1900	1900-1950	1950-1990	1995
	classifications						
Utricularia vulgaris	OM	5.5	X				
Littorella uniflora	OMe	6.7	X				
Nymphaea alba	OMe	6.7	X	X			
Potamogeton gramineus	oME	7.3	X				
Potamogeton obtusifolius	oME	7.3			X	X	
Potamogeton perfoliatus	oME	7.3	X				
Callitriche stagnalis	omE	7.7				X	
Hippurus vulgaris	omE	7.7	X				
Eleocharis acicularis	ME	8.5	X				
Elodea canadensis	ME	8.5				X	Xf
Nuphar lutea	ME	8.5	X	X	X	X	XLa
Potamogeton crispus	ME	8.5			X	X	Xr
Potamogeton pusillus	ME	8.5				X	Xa
Ranunculus aquatilis	ME	8.5		X	X		
Ranunculus peltatus	ME	8.5		X	X		
Ranunculus trichophyllus	ME	8.5			X	X	
Lemna minor	mE	9				X	
Polygonum amphibium	mE	9	X	X	X	X	
Ceratophyllum demersum	E	10		X			Xa
Elodea nutalli	E	10				X	Xf
Lemna triscula	E	10	X				
Myriophyllum spicatum	E	10	X	X	X		
Oenanthe aquatica	E	10	X				
Potamogeton lucens	E	10	X	X			
Potamogeton pectinatus	E	10	X	X	X	X	
Ranunculus circinatus	E	10		X	X		
Zannichellia palustris	E	10	X	X	X	X	Xr
*Callitriche platycarpa**				X	X	X	
*Callitriche truncata**							Xf
*Ceratophyllum submersum**			X				
*Damasonium alsima**			X	X	X	X	
*Nymphoides peltata**					X	X	
Mean TRS			8.48	9.2	8.98	8.79	9.14
Mean TS (Holmes, 1995)			4.08	3.67	3.77	3.71	3.38
Total number of species			17	13	14	15	8

Table 6.1. Presence/absence of submerged and floating aquatic plants in Groby Pool at 50 year intervals since pre-1850 (see text) (after Beresford, 1989). Presence is noted by a cross. DOME = trophic tolerance (Dystrophic, Oligotrophic, Mesotrophic, Eutrophic) and TRS=Trophic Ranking Scores of Palmer *et al.*, 1992 (see text for explanation). * Species does not have a trophic ranking score. The cover values for the distribution of plants in 1995 are given as a (abundant), La (locally abundant), f (frequent), r (rare). The 1950-1990 list is compiled from NCC and English Nature sources.

The pre-1850 community has most overlap with TWINSPAN group 5a of Palmer *et al.*, (1992) which includes several slightly base-rich, mesotrophic lakes in Scotland and northern. England, including Windermere, Bassenthwaite and Esthwaite Water in Cumbria. Group 5a contains a number of species-rich sites characterised by *L. uniflora*, *Myriophyllum* spp., *Chara* and *Nitella* spp. and a range of *Potamogeton* spp. There are also strong similarities between the pre-1850 community and that found in some of the remaining, mesotrophic (i.e.<40 $\mu g\ l^{-1}$ TP) Norfolk Broads and many of the species recorded in Groby Pool at this time were also found in the Broads during the early part of the 19th century when they are thought to have been largely undisturbed, fertile marl lakes (Phillips, 1992). Thus Groby Pool was undoubtedly a mesotrophic, species-rich site in this period.

There are some important differences between the pre-1850 and 1850-1900 species lists. Of the nine species which are eliminated from the species list in this period five have TRS scores of below 8 and the mean TRS of the 'lost' species is 7.88 (Table. 6.2). Important losses are *U. vulgaris*, *L. uniflora*, *P. gramineus* and *Potamogeton perfoliatus* L. In total five plants are gained during this period, three of which are in the *Ranunculaceae* and the mean TRS for these 'new' species is 9.25, indicating that at some point in time probably after 1800, more nutrient intolerant macrophytes started to be out-competed by species which favour more eutrophic conditions. The mean TRS ranking for the 1850-1900 assemblage is 9.2 and this suggests that nutrient concentrations in Groby Pool were much higher than in the pre-1850 period.

Increased stability is evident when the macrophyte assemblages recorded in 1850-1900, 1900-1950 and 1950-1990 are compared. However there are some other important species replacements. In 1900-1950 three more species are no longer recorded, most important of which is the white water-lily *Nymphaea alba* L., which is usually found in mesotrophic sites (Palmer *et al.*, 1992). The niche left by this floating plant would appear to have been filled by the eutrophic indicator *Nymphoides peltata* L. (Holmes, 1995) which is one of four 'new' species recorded in the lake during this period. Interestingly the mean TRS score for the period is 8.98, which represents an apparent slight reduction in trophic status compared to 1850-1900. This is because the TRS scores of the 'new' species are lower than those which are eliminated from the list (table 6.2). However it seems unlikely that this represents a real improvement in water quality and a more realistic explanation is probably that the trophic tolerance characterisation of some species in the scheme is inaccurate. For example *Potamogeton crispus* L. is classified as a eutrophic species in the river water quality index of Holmes (1995), so in theory this plant should be given a TRS score of 10. Similarly *N. peltata* which is not given a TRS score in Palmer *et al.*, (1992) is also considered to be a eutrophic species in the river index of Holmes (1995) and if the mean TRS ranking score is re-calculated accordingly the 1900-1950 mean is 9.06.

Time interval	1850-1900	1900-1950	1950-1990
Species 'lost'	*Utricularia vulgaris* *Littorella uniflora* *Potamogeton gramineus* *Potamogeton perfoliatus* *Hippuris vulgaris* *Eleocharis acicularis* *Lemna triscula* *Oenanthe aquatica* *Ceratophyllum submersum*	*Nympaea alba* *Ceratophyllum demersum* *Potamogeton lucens*	*Ranunculus aquatilis* *Ranunculus peltatus* *Myriophyllum spicatum* *Ranunculus circinatus*
Mean TRS	7.88	8.9	9.25
Species 'gained'	*Ranunculus aquatilis* *Ranunculus peltatus* *Ceratophyllum demersum* *Ranunculus circinatus* *Callitriche platycarpa*	*Potamogeton obtusifolius* *Potamogeton crispus* *Ranunculus trichophyllus* *Nymphoides peltata*	*Callitriche stagnalis* *Elodea canadensis* *Potamogeton pusillus* *Elodea nutalli* *Lemna minor*
Mean TRS	9.25	8.1	8.74

Table 6.2. Macrophyte species changes in Groby Pool since pre-1850. Mean TRS = mean trophic ranking score of 'lost' and 'gained' species (see text for explanation).

There are 15 species listed as occurring in the Pool at various times during 1950-1990. Of the four species which are no longer listed three are meso-eutrophic *Ranunculus* spp. The species gained in this period include the highly competitive species, *Elodea canadensis* Michx and *Elodea nutalli* L. the eutrophic pondweed *Potamogeton pusillus* L. *Callitriche stagnalis* L. and the duckweed *Lemna minor* L. The mean TRS score for the species influx is again lower than that for the species which are eliminated from the list, so the TRS score for the period is slightly lower than in 1900-1950. In the 1995 survey (chapter four) some 9 species listed for 1950-1990 period were not found in the Pool (table 6.2). Plant communities in profundal areas were dominated by large stands of *Elodea* spp., with *P. pusillus* and *Ceratophyllum demersum* L. as sub-dominants and in the margins *P. pusillus*, *C. demersum* and *Callitriche truncata* L. were the most important species, with the occasional occurrence of *Zannichellia palustris* L. and *P. crispus*. In the shallow N and NW margins of the lake there was an extensive bed of *Nuphar lutea* L. from June-September, but other floating plants listed for 1950-1990 (i.e. *N. peltata*, *Polygonum amphibium* L. *Damasonium alisma* L. and *L. minor* were not observed to grow in the lake. Thus it appears that there have been some significant changes over the last few years and the species which survive today are all highly competitive species tolerant of eutrophic conditions, hence the mean TRS score of 9.14.

Thus important shifts have occurred in the macrophyte structure of Groby Pool since 1750. Up until perhaps 1850 there was a species-rich assemblage containing a mixture of low and tall growing species with a range of trophic tolerances. However by perhaps 1900 the more nutrient sensitive species had been eliminated and there was an influx of meso-eutrophic species in the *Ranunculaceae*. In recent times there have been further important changes and at present the lake has a typical shallow, eutrophic lake community with low diversity and dominance by a few prolific, tall growing species (particularly *Elodea* spp.).

Interpretation

The ecology of the small *Fragilaria* spp.

The pre-1900 sediments are dominated by *F. construens*, *F. pinnata* and *F. brevistriata* (referred to here as small *Fragilaria* spp.) and a knowledge of the ecology of these forms is essential to reconstructing the environmental history of the Pool. These species have commonly been found to dominate the sediments of several alkaline, oligotrophic-eutrophic lakes in England (Moss, 1988a; Moss, 1985; Bennion, 1995), North America (Koivo & Ritchie, 1978; Bradbury & Whiteside, 1980; Agbeti 1992); Minnesota (Brugam *et al.*, 1988) and Turkey (Roberts, *et al.*, unpublished) and have also often been associated with late-glacial sequences (Haworth, 1975; Marciniak, 1986). In the majority of these sites the four species listed above have been found to co-occur, often with the similar form *Fragilaria elliptica.*

There has been some considerable speculation regarding the life-form of the small *Fragilaria* spp. which often proliferate in shallow lakes, although they are usually associated with benthic and epiphytic habitats. In the Norfolk Broads small *Fragilaria* spp. are not thought to be truely epiphytic on submerged plant species, rather they have been associated with benthic habitats and the stable surfaces found at the bottom of marginal emergent macrophyte stems (Osbourne & Moss, 1977; Eminson, 1978; Moss, 1978; Moss, 1980; Moss, 1988a). The habitat preferences of the small *Fragilaria* spp. found in the lower part of GR95B have been investigated by an analysis of the diatoms 'attached' to five herbarium plant samples (fig. 6.6, table 6.3), four of which (i.e. collected in 1867, 1876, 1883, 1897) would probably have been growing in the Pool during the period of *Fragilaria* dominance. In two samples from leaves of the submerged macrophyte *M. spicatum* (14/7/1876 and 15/7/1897) *Fragilaria* spp. are absent and *C. placentula* is the

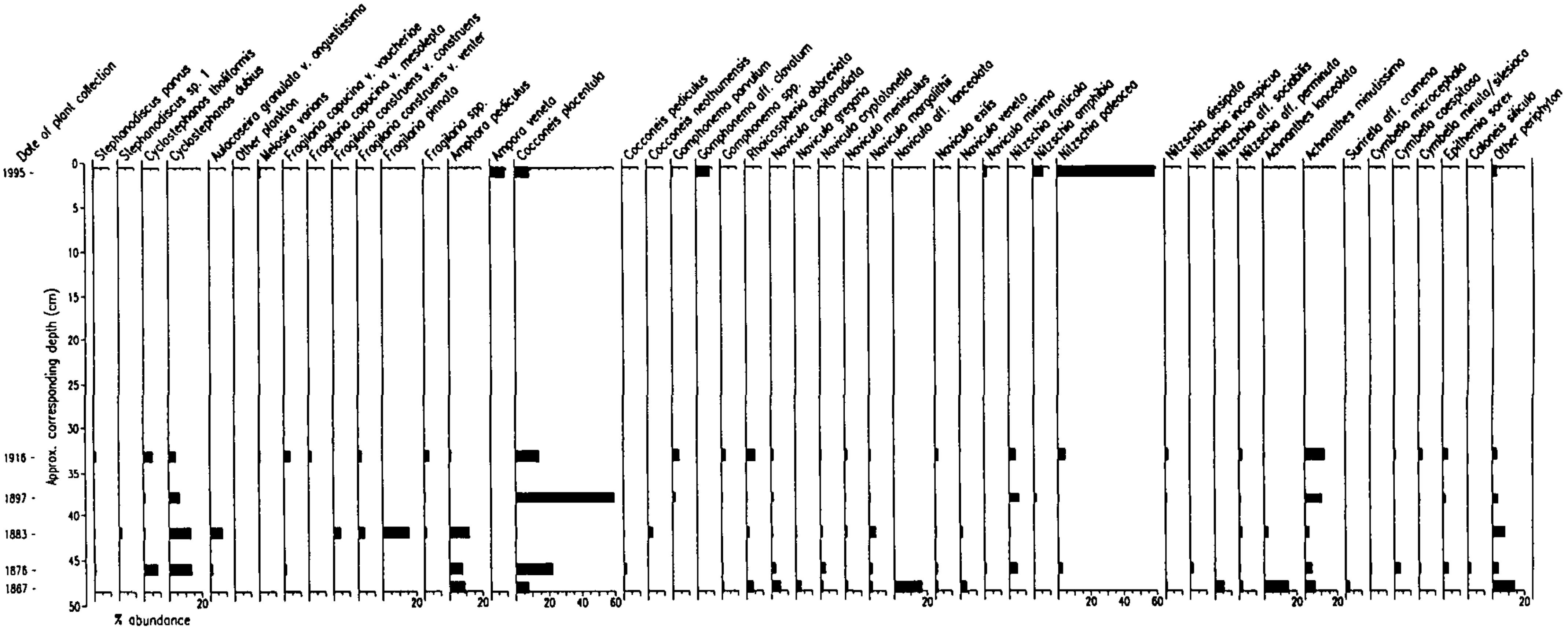


Fig. 6.6. Diatom assemblages found attached to modern and herbarium plants from Groby Pool.

most important epiphyte (table 6.3). The latter species is massively abundant on the 1897 specimen (plate 6.1), accounting for over 60% of the assemblage. However in a stem sample from the emergent rush *Eleocharis palustris* (7/1883), *F. pinnata* is the most abundant species (18%) and both *F. construens* var. *construens* and *F. construens* var. *venter* are found in significant quantities, while *C. placentula* is absent from surfaces of this plant. This suggests some degree of habitat specialisation amongst the epiphytic forms in the mid-late nineteenth century period and it seems probable that small *Fragilaria* spp. were only loosely associated with submerged macrophytes and that a more important habitat may have been provided by the extensive marginal beds of *Typha*, *Phragmites*, *Carex* and *Eleocharis* etc. Thus it seems likely that *Fragilaria* spp. require 'firm', stable surfaces to attach to and in the light of the above information they are assumed to have been largely derived from epipelic and to a lesser extent marginal macrophyte populations in the Pool.

Macrophyte species	Date of collection	Dominant diatoms
Ceratophyllum demersum (S)	9/1995	*Nitzschia paleacea*
Ranunculus peltatus (S)	6/1916	*Cocconeis placentula* *Achnanthes minutissima*
Myriophyllum spicatum (S)	7/1897	*C. placentula*
Eleocharis palustris (E)	7/1883	*Fragilaria pinnata* *Cyclostephanos dubius*
Myriophyllum spicatum (S)	7/1876	*C. placentula* *C. dubius*
Butomus umbellatus (S)	1867	*Navicula* aff. *lanceolata* *Achnanthes lanceolata*

Table 6.3. List of herbarium plant specimens examined for 'attached' diatoms and the dominant species found. (S) = submerged macrophyte, (E) = emergent macrophyte.

The dominance of small *Fragilaria* spp. in both oligotrophic late-glacial habitats and eutrophic lakes indicates that they have broad tolerances for plant nutrients. Thus perhaps a more important control over the abundance of species in this group is light climate. In mesotrophic-eutrophic, submerged plant dominated shallow lakes where populations of plant-associated *Daphnia* spp. maintain clear water, profundal sediments are often in the photic zone and under these conditions it is possible for highly competitive, benthic species to form dense colonial biofilms at the sediment surface. These types of lakes often support massive populations of small *Fragilaria* spp. and often larger benthic forms such as *Gyrosigma* spp. To this effect, in Blickling Lake, Norfolk (TG 177 293) thick layers of small *Fragilaria* spp. were observed growing in 'patches' on the surface sediment in spring

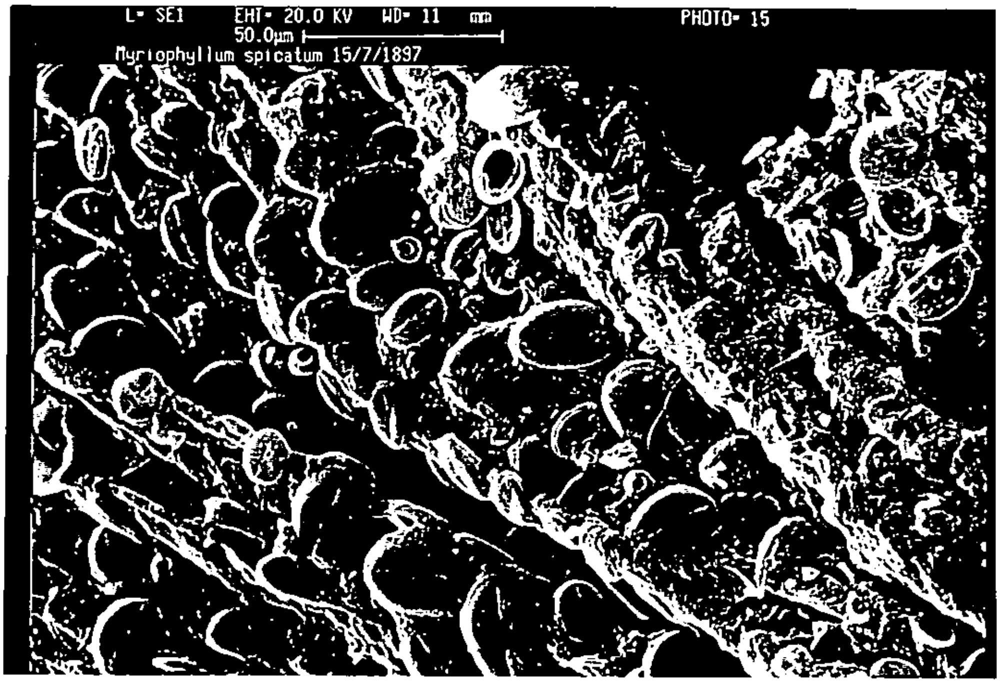


Plate 6.1. The epiphyte *Cocconeis placentula* attached to an herbarium specimen of the submerged plant *Myriophyllum spicatum* from Groby Pool, dated 15/7/1897.

and summer 1996 in very clear water. However it is possible for these species to dominate in turbid, plankton dominated lakes if they are extremely shallow (i.e. <1 m) and such a situation has been observed at Sawmill Pond, Norfolk (TG 222 344) (Sayer, unpublished data). Thus while these species seem to prefer shallow lakes with lower nutrient levels, they can survive in 'plantless', eutrophic lakes is they are so shallow that phytoplankton fail to shade the sediment and sufficiently sheltered from extreme winds so that mixing processes are not constantly resuspending the surface sediments and making them unstable.

Eutrophication history

The dominance of small benthic *Fragilaria* spp. in the pre-1800 sediments (i.e. below 75 cm) and the near absence of planktonic diatoms (figs. 6.4) suggests the existence of low ambient nutrient concentrations and possibly very clear water. Low nutrient concentrations are also suggested by the likely presence of the nutrient intolerant submerged plants, *L. uniflora*, *U. vulgaris* and *P. gramineus* and in particular the low-growing shoreweed *L. uniflora* indicates high water clarity and minimal overhead shading by phytoplankton populations, or tall growing macrophytes (Moss, 1990). There is temporary peak in epiphyte percentages at 88-89 cm, but apart from this epiphytic forms are relatively unimportant in the pre-1800 sediments. This might possibly be explained by one of two hypotheses; i.e. (i) that epiphyte development on the plants was minimal or; (ii) that aquatic plant biomass was low. The herbarium plant samples are useful in assessing the relative importance of these hypotheses. On herbarium specimens from the submerged plant *M. spicatum* collected in 1876 and 1897 (plate 6.1) it is apparent that there are substantial growths of the epiphyte *C. placentula*. These macrophytes would probably have been growing in the lake at the same time as the sub-zone Ib sediments were laid down. However *C. placentula* is barely represented in this part of the core. This suggests that epiphytic diatom abundances in the sediment may be more closely related to changes in aquatic plant biomass and as a result low macrophyte abundance may be the most likely explanation for the minimal representation of epiphytic diatom species in the pre-1800 sediments. Thus prior to 1800 the Pool was probably a naturally rich mesotrophic site similar to the 'phase I' Norfolk Broads (see chapter one), supporting a diverse collection of submerged and floating plants, but low macrophyte abundances. Under such conditions there would have been abundant gaps in the plant canopy and substantial areas of bare sediment suitable for the colonisation of benthic *Fragilaria* spp. in spring, summer and autumn.

Exactly when eutrophication processes started to affect the Pool is difficult to define. It is evident from the early plant records that there were probably important shifts in macrophyte species composition prior to 1850. The species *L. uniflora* was last collected in 1800 and *U. vulgaris* and *P. gramineus* are also not listed after this date and it is possible that they were not growing in the Pool after 1800. The transition between the light brown clay and the dark overlying organic gyttja occurs at 77 cm (c. 1795) in GR95B. In other cores from the Pool this transition is associated with a shift in the haematite/magnetite ratio and elevated percentages of fine-grained ferromagnetic material, indicating increasing soil erosion and the onset of arable agriculture in the catchment (David, 1991). The transfer of nutrients into the Pool in agricultural run-off might have been expected to increase the trophic status of the Pool, but there is no definitive evidence of this in the sediment record. The first potential eutrophication-related shift in fossil diatom assemblages is the rise in the relative abundance of the centric diatom *C. dubius* at 68-69 cm (c. 1815) which may indicate a shift towards the increased competitiveness of the plankton. However planktonic diatom concentrations did not increase significantly at this time (fig. 6.7) and the increase in *C. dubius* percentages is the result of lower concentrations of small *Fragilaria* spp. It seems unlikely therefore that there was a significant increase in planktonic diatom production. Thus while there may have been an increase in nutrient status in the early nineteenth century it is difficult to be certain.

Unfortunately diatom dissolution in the sub-zone Ib sediments (c. 1845 and 1890) and the probable underestimation of *C. dubius* make interpretation difficult. However it is possible that *C. dubius* was starting to become more prevalent in the second half of the nineteenth century. Potential evidence for this is provided by the large numbers of perfectly preserved cells of *C. dubius* found on herbarium plant specimens collected in this period (fig. 6.6). The increased intensity of the spring plankton bloom could have resulted in the rapid depletion of epilimnetic SiO_2 concentrations and conditions of Si-limitation after the spring. This may have resulted in intense internal recycling and the net release of SiO_2 from the sediments in late spring and summer as is a common phenomenon in eutrophic lakes (Bailey-Watts *et al.*, 1989). Thus dissolution itself may suggest that the lake was becoming more eutrophic. Elevated carbonate percentages in this sub-zone may provide additional support for this hypothesis (fig. 6.2). In chapter four it was shown that carbonate percentages were highest (>40%) in the spring sediment trap collections and this may indicate a close relationship between planktonic diatom production and carbonate precipitation. Thus increasing carbonate percentages in the core may also signal a stimulation of the diatom plankton. Perhaps the best indications of eutrophication-related changes during this period are provided by the historic macrophyte records and it is evident (tables 6.1, 6.2) that many of the rare, mesotrophic plant species which were recorded in the late eighteenth century and early part of the nineteenth century are not listed between 1850-1890. Moreover the plants which are added to the species list in this period are all highly competitive species which are able to survive in eutrophic, moderately turbid waters

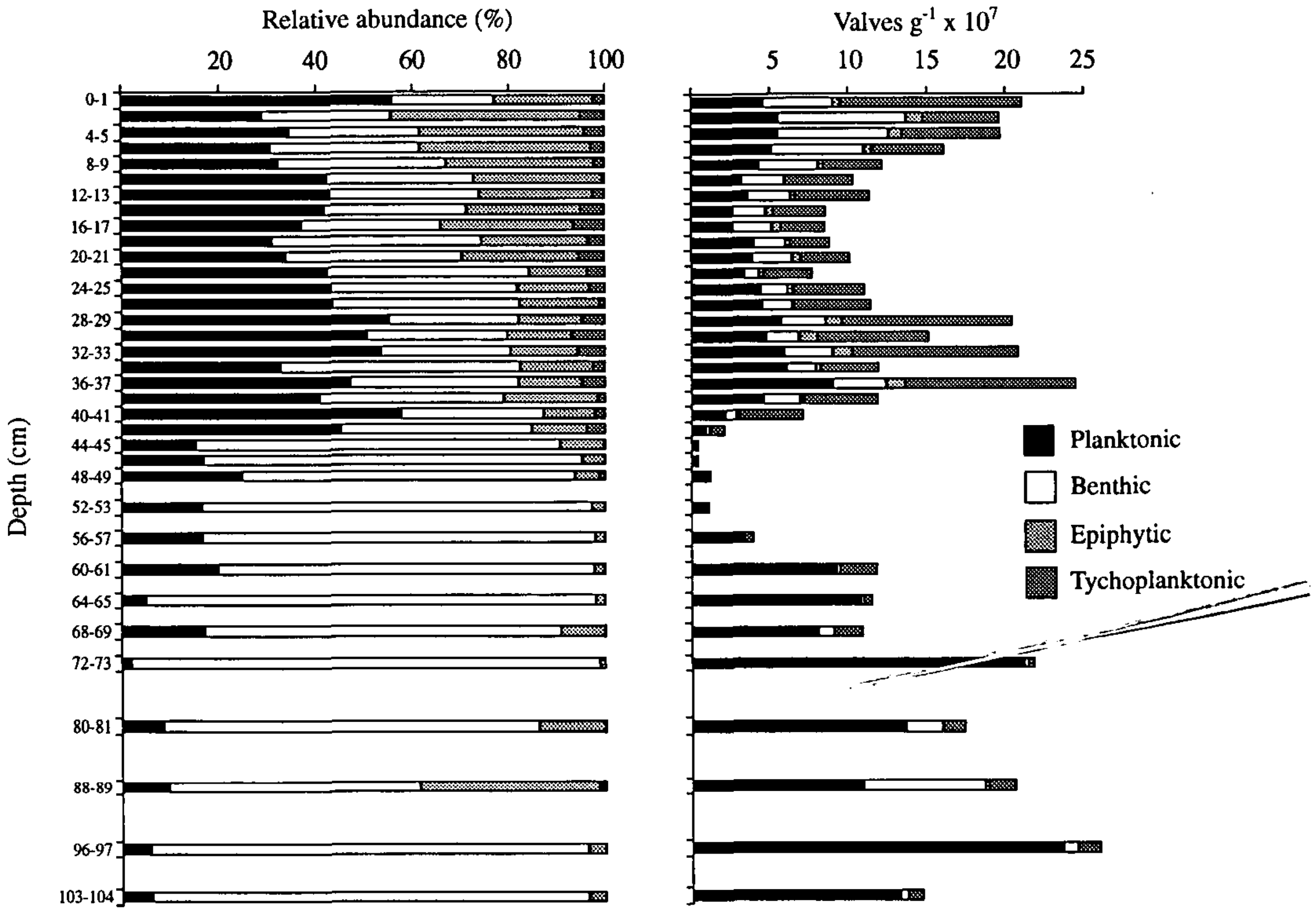


Fig. 6.7. Percentages and concentrations of different diatom life-forms in core GR95B from Groby Pool.

(Palmer *et al.*, 1992). Thus there is some strong evidence for nutrient enrichment in the second part of the nineteenth century.

The earliest, clear evidence of eutrophication in the fossil diatom record is at the start of zone II (c. 1890) where there is a dramatic shift towards planktonic diatom dominance (>40%) and the small, benthic *Fragilaria* spp. are replaced by *C. dubius* and to a lesser extent *S. parvus*. Planktonic diatom concentrations also increase dramatically in this sub-zone (fig. 6.7) and because diatom preservation is good it can be assumed that these data provide a more realistic estimate of changes in the intensity of diatom production. The shift towards assemblages co-dominated by planktonic and periphytic species suggests much larger planktonic diatom populations in the late winter-spring period and reduced water clarity. Thus it is possible that the small benthic *Fragilaria* spp. were 'shaded' out in the spring time and this may explain the sharp reduction in both the relative contribution and absolute abundance of benthic diatoms after 1890 (fig. 6.7). Nutrient enrichment is also suggested by the unimodal organic matter response (fig. 6.2) which clearly tracks the *C. dubius* curve. Thus it seems likely that the Pool had been seriously disturbed by at least the turn of the century and higher nutrient concentrations had probably shifted the lake from a phase I to a phase II state as is the case presently (chapter four). The explanation for enrichment was probably agricultural intensification and the conversion of pasture land to arable (see Historic land-use changes). Land-use reconstructions by David (1991) indicate that a substantial portion of the catchment was under the plough by the late nineteenth century and much of this land bordered the Slate Brook. Thus it seems likely that the late 19th century increase in nutrient loading was largely due to changing agricultural practices in the catchment and the transfer of readily leached plant nutrients from agricultural soils (probably largely soluble N and some particulate P (cf. Moss, 1988b)) into the Slate Brook and hence the Pool, via subsurface (throughflow) and overland flows.

The next major change in the diatom assemblage is marked by the start of sub-zone IIb (c. 1937) where *C. dubius* is replaced as the dominant planktonic form by *S. parvus*. The widespread distribution of *S. parvus* in the sediments of the Attenborough Ponds SSSI (fig. 5.8) clearly indicates that this species has a very broad tolerance for nutrients, whereas the more localised abundance of *C. dubius* in the isolated Ponds suggest that it is intolerant of extremely high nutrient levels. Moreover the transition from *C. dubius* to *S. parvus* dominance has been observed in other shallow lake eutrophication sequences (Anderson *et al.*, 1990; Håkansson & Regnéll, 1993). Thus it seems likely that this particular change represents an acceleration of the nutrient enrichment process in the Pool. That there may have been elevated phytoplankton productivity in the mid-part of this century is also suggested by the rise in carbonate levels above 22-23 cm to a subsidiary peak of 12% at 18-19 cm (fig. 6.2). There are a number of important disturbance events which may be responsible for the increased eutrophication of the Pool at this time. Artificial (< 1 ha.) fishing ponds (<1 ha.) were constructed in the middle reaches of the Slate Brook in 1925 and on the Northern stream just 100 m above the Pool in 1945 and soil disturbance may have resulted in increased nutrient inputs. Also as already mentioned additional land was cultivated during the Second World War and this may also have increased N concentrations in the Pool. However the most obvious and likely explanation is the installation of a small, private sewage treatment works on the Slate Brook at Markfield Hospital from around 1935 onwards (NRA, data). The form of treatment in this plant is unknown but it was operational until around the mid-1980s and must have significantly increased P inputs into the Pool.

The most significant change in sub-zone IIc is the shift towards by towards the increased prevalence of epiphytic diatoms and in particular *C. placentula*. Epiphytic diatom percentages and concentrations rise significantly in this part of the core (fig. 6.7) and this may reflect increases in macrophyte biomass. In eutrophic macrophyte dominated shallow lakes submerged plant communities typically consist of prolific stands of highly competitive plants adapted to produce a substantial portion of their photosynthetic biomass in the upper part of the water column (Phillips *et al.*, 1978; Moss, 1987; Moss, 1988b; Moss, 1989). Tall growth is a necessity in eutrophic waters where there is increased phytoplankton-induced turbidity and plants must compete for light at the start of the growing season. The submerged species present in the Pool in the later half on this century are all capable of growing to the water surface (i.e. particularly *Elodea* spp. *P. pectinatus*, *P. pusillus*, *C. demersum*) and the presence of these particular species suggests intense competition for light, reduced water clarity and phytoplankton biomass. Presently massive submerged plant stands are evident in the profundal zone such that it is difficult to see the bottom in most regions and it is probable that this phenomenon has been a feature of the lake for some decades. This may explain the rise in the importance of epiphytic diatoms after around 1940 as macrophyte biomass increased in the Pool and the continued demise of the small *Fragilaria* spp. in this period might also be linked to the stimulation of macrophyte productivity. The dense overhead canopy that is established by summer must severely restrict the amount of light available to benthic communities below. Thus the small *Fragilaria* spp. may have been 'shaded' out over the entire year.

There have probably been additional nutrient inputs into the Pool in recent decades. The A50 by-pass and M1 motorway were constructed in the early 1960s. These both traverse through the Slate Brook sub-catchment and resulting soil disturbance may have increased nutrient concentrations in the Slate Brook. Water chemistry data from an occasional sample in 1988 also targets the Slate Brook as the major nutrient source (table 6.5). TP and NO_3 concentrations in the Brook at the inlet to the Pool are very high, whereas the Northern feeder stream has slightly raised NO_3 levels but low, near background TP concentrations. By 1988 the treatment plant at Markfield Hospital was no longer functional. Nitrates from agricultural run-off could easily account for the levels in the Brook, but it is unlikely that this source could result in such high TP concentrations.

	Slate Brook inlet	Northern stream inlet	Pool outlet
EC ($\mu S\ cm^{-1}$)	540	470	460
NO_3 ($mg\ l^{-1}$)	15	5	3
TP ($\mu g\ l^{-1}$)	350	30	360

Table 6.4 Water chemistry for Groby Pool and its two inflow streams on 3/8/1988. Data source Leicestershire Ecology Unit.

Recent speculation by local conservationists has focused on the impact of wildfowl populations on P concentrations in the Pool and in particular the effects of increasing numbers of resident Canada geese (*Branta canadensis* L.). Annual winter wildfowl data are available from counts made by the Wildfowl at Wetlands Trust at Slimbridge (from 1960) and the Leicestershire and Rutland Ornithological Society (LROS) (from 1969) (fig. 6.8). There were just a few breading pairs of this bird in the early 1960s. However the population started to increase thereafter and by the mid-1970s a large colony of approximately 200 birds was established. Numbers have continued to increase to the present day and on the 15th of September, 1991, some 398 birds were counted by the LROS. The effects that the guano input of these geese might have on ambient nutrient concentrations in the Pool is difficult to quantify. In Hickling Broad, Norfolk excreta from a winter roost of over 50,000 black-headed gulls (*Larus ridibundus* L.) was found to account for daily TP concentrations in the lake of over 100 $\mu g\ l^{-1}$ in the summer when it started to decompose at the sediment surface (Moss & Leah, 1982). Thus it is possible that birds can have a significant influence on TP concentrations if they are present in sufficient numbers. If it is assumed for instance that the daily TP excreted by a Canada goose is ten times higher than that for a black-headed gull (i.e. a gull=40 mg day^{-1} (Gould & Fletcher, 1978)), then it can be calculated that 400 Canada geese input 160,000 mg (400 mg x 400 birds) of TP each day. If this mass is then diluted into the approximate volume of the Pool (12 ha. area x 1 m = 120 x 10^6 l) it can be estimated that each day 400 Canada geese would add 1.3 $\mu g\ l^{-1}$ of TP to the Pool. This is a very approximate value, but suggests that the resident Canada geese have a minor effect on nutrient concentrations compared to feeder stream inputs. Also unlike gulls which contribute 'new' TP from outside of a lake, Canada

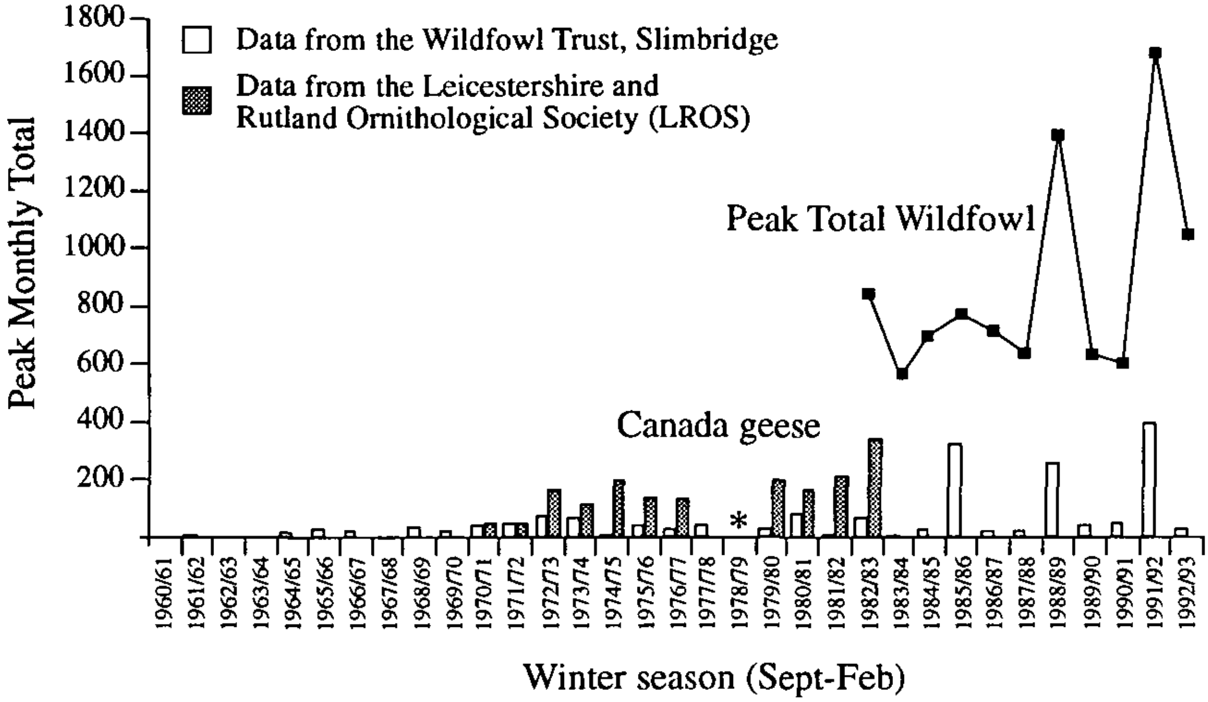


Fig. 6.8. Winter numbers of Canada geese at Groby Pool, 1960-1993.

geese largely recycle TP which is already present (i.e. in the plant biomass). Thus it is likely that the other additional sources of P input to the Pool and local farms may be important in this respect..

Conclusions

Predicted eutrophication-related changes in the macrophyte and phytoplankton status of Groby Pool since 1750 are shown in fig. 6.9. Prior to 1800 it seems likely that the Pool had suffered only minor disturbance. The historic macrophyte records suggest that a typical, diverse mesotrophic, shallow lake aquatic plant flora was evident, consisting of a mixture of low and tall growing macrophyte species. The *Chara* and *Nitella* swards which have been so important in defining the phase I state in the Norfolk Broads have not been recorded at Groby Pool. These highly developed algae prefer nutrient poor, calcium-rich waters and it may be that natural geochemical conditions in the Groby catchment preclude the growth of these species in the Pool. The phase I concept is applicable however, in that the Pool possessed a 'unique', species-rich flora (Moss, 1996).

Important changes in diatom assemblages after around 1890 indicate that the phase I state had been de-stabilised. The nutrient sensitive aquatic plant species had mostly been eliminated by this time and increasing percentages and concentrations of planktonic diatoms (particularly *C. dubius*) suggest a marked increase in the intensity of the spring planktonic diatom bloom. This may have resulted in insufficient light for benthic diatom populations early in the year and may account for the rapid decline in the importance of the small *Fragilaria* spp. The development of large plankton populations is indicative of a phase II trophic state (Moss, 1989; Philips, 1992) and it seems most likely that this state-change was the result of elevated nutrient concentrations in the Pool linked to arable cultivation in the Slate Brook sub-catchment (David, 1991; David & Roberts, 1990). Epiphytic diatoms which were sporadically important in Phase I become a consistently dominant component of fossil diatom assemblages from around the 1940s onwards and increase in abundance towards the top of the core, signalling increasing summer macrophyte biomass, another characteristic feature of the phase II state. Also at this time *C. dubius* is replaced as the dominant planktonic diatom by *S. parvus.* These two changes seem to be related to the beginning of sewage effluent inputs to the Slate Brook from a small, private hospital treatment plant. This direct cause-effect relationship suggests a marked acceleration of nutrient enrichment at this point in the Pool's history.

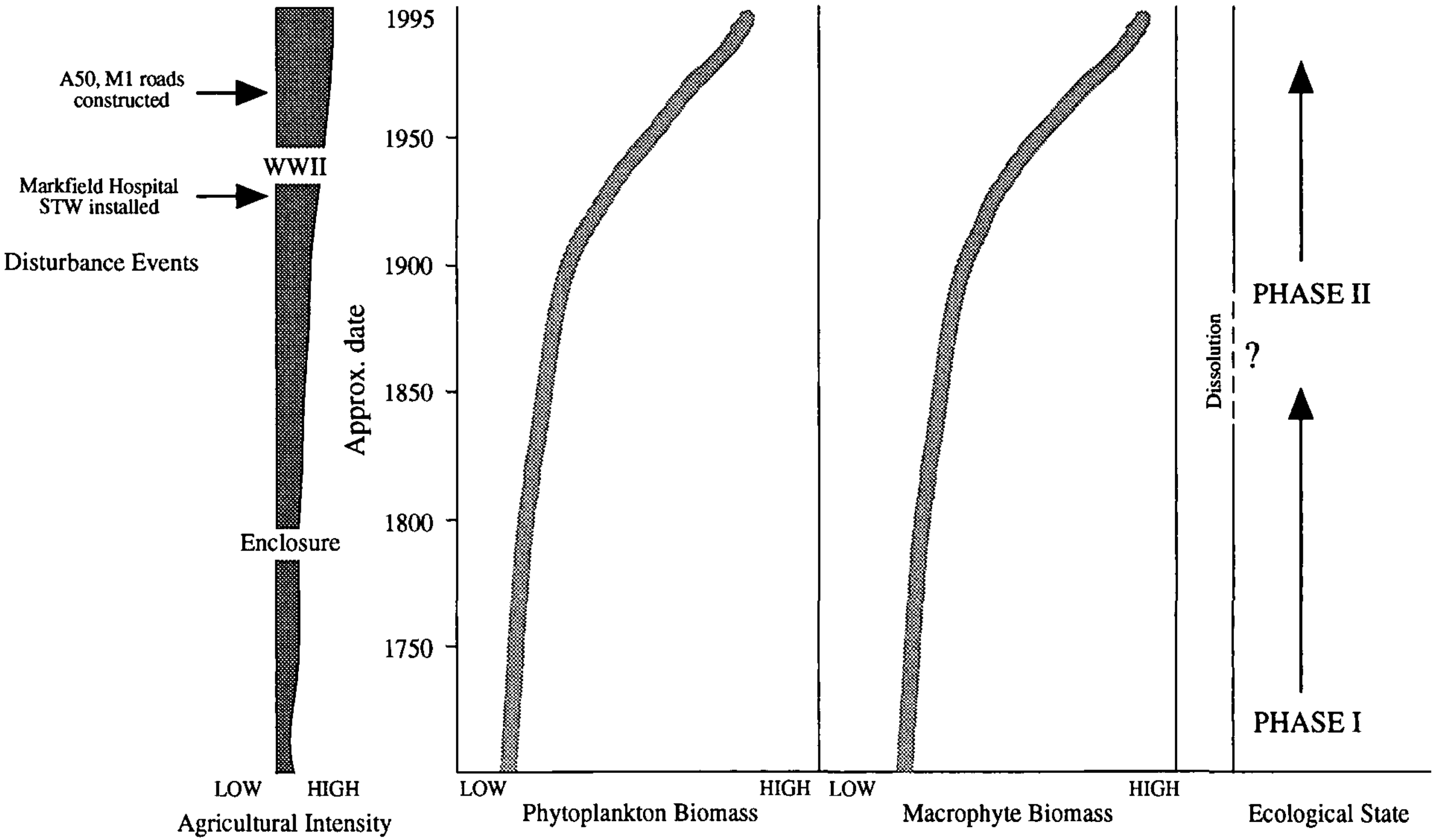


Fig. 6.9. Summary diagram showing reconstructed changes in phytoplankton and submerged plant biomass in Groby Pool over the last 250 years.

CHAPTER SEVEN

DISCUSSION

Introduction

Lowland England and indeed Europe abound with many shallow, often artificial lakes of varying size dotted around the countryside in fields, farm yards and in country estates. These lakes include medieval fish ponds and 'broads', estate lakes dug in the eighteenth and nineteenth centuries to enhance the estates of rich landowners, natural meres, castle moats, marl pits, 'horse' pits, irrigation reservoirs, duck decoy ponds, gravel-pit lakes and modern commercial fishing lakes. In many areas there are few natural standing water sites and artificial lakes afford vital local habitats for water plants, invertebrates, amphibians, fish and birds. However eutrophication has severely affected many of these lakes, resulting in a declining habitat for associated biological communities.

Unfortunately past water chemistry data are rare for the majority of shallow lakes and usually the only means of inferring shifts in trophic status is to use palaeolimnological approaches, export coefficient models, or to access old macrophyte records. Palaeolimnological approaches are potentially the most useful and diatoms are undoubtedly the best indicators of past nutrient conditions, but until relatively recently the majority of diatom-based status studies focused on deep, stratifying natural lakes such as, the ribbon lakes of the English Lake District (Pennington, 1943) and the Great Lakes of North America (Stockner & Benson, 1967). However research in the Norfolk Broads (Moss, 1988a), southwest England (O'Sullivan *et al.*, 1991; O'Sullivan, 1992), southeast England (Bennion, 1993), southwest Wales (Rees *et al.*, 1991) and even in the high Arctic (Douglas *et al.*, 1994) has shown that shallow lakes are also appropriate for applying diatom-based palaeo-trophic status techniques. The initial reluctance to study shallow lakes, was largely due to fears about the integrity of the sediment record in these sites. In shallow, isothermal environments, wind-induced sediment resuspension-redeposition cycles (Kristensen *et al.*, 1992) and bioturbation by benthivorous fish and invertebrates (Havens, 1991), may disturb the sediment record, much more than is possible in deep stratifying lakes (Anderson & Odgaard, 1994). However, extremely rapid sediment accumulation rates in shallow lakes (i.e. typically around 1 cm yr^{-1}), may offset this problem to a large extent. That high levels of temporal and perhaps more importantly ecological resolution are possible was demonstrated by the sediment core from Tween Pond. The influx of the R. Erewash into the lake in 1972 was accurately predicted by ^{137}Cs dating and the resulting sudden change in the lake environment was represented by an equally dramatic shift in the diatom assemblage. Thus the ecological sensitivity of the sediment record would appear to be excellent in this case and the potential for using shallow lakes in palaeolimnological studies is emphasised.

The effectiveness of diatom-based palaeoecological techniques for reconstructing lake trophic status has been extensively tested in deep, stratifying lakes. However the same can not be said of shallow lakes and their remains considerable scope for further improvement. The refinement of diatom-based palaeoecological techniques is dependent on modern 'system-level' level studies focusing on; (i) the taxonomy, present-day environmental preferences, and favoured habitat of the species found in the fossil record; and (ii) the degree to which the sediment record can be used to infer changes in the contemporary diatom flora of a lake and hence changes in its ecological status.

These types of studies have been undertaken in three typical shallow lakes of contrasting chemical and macrophyte status in the English Midlands and the data that were derived have been used to assist in the interpretation of the fossil diatom record from these sites. The discussion which follows summarises the findings of these studies and highlights some of the possibilities and problems associated with using fossil diatom remains to reconstruct the eutrophication histories of shallow lakes. It is divided into two parts, the first of which follows focuses on the potential for using diatom remains to reconstruct eutrophication-related shifts in phytoplankton-macrophyte interactions and the second on the potential limitations and problems associated with numerical, diatom-total phosphorus transfer functions which use fossil assemblages to quantify past P concentrations.

Phytoplankton-macrophyte interactions and the fossil diatom record

The symptoms of eutrophication in shallow lakes are expressed most dramatically by changes in the relative competitiveness of submerged macrophytes and phytoplankton. These types of changes have been studied in the Norfolk Broads, a series of shallow, medieval, marl lakes, where three distinct eutrophication phases have been recognised (Moss, 1987); Moss (1989) and Phillips (1992). Prior to the turn of the century it is thought that these lakes supported a 'unique', highly diverse set of submerged (particularly *Chara* and *Najas* spp.) and floating plants, growing in extremely clear water (phase I). However as P-rich sewage effluent and N-rich agricultural inputs towards the end of the nineteenth century, these communities were replaced by massive growths of tall, highly competitive submerged plants such as *Potamogeton pectinatus* L., *Ceratophyllum demersum* L. and *Myriophyllum spicatum* L. (phase II). In turn by the mid-twentieth century these plants were eliminated from most of the lakes which became turbid, barren environments dominated by dense populations of phytoplankton (phase III). Lakes in these three phases can be observed today (Phillips, 1992) and the transition between the phases can be detected in the lake sediments using diatoms, plant macrofossils, Cladoceran and mollusc remnants (Moss, 1987; Phillips, 1992).

The identification of changes in phytoplankton-submerged plant interactions using palaeoecolological techniques is relatively well established in the Broads. Those lakes which have been studied include Barton, Hickling, Strumpshaw, Alderfen, Upton, Martham and Hoveton Broads and it is apparent that there is a relatively consistent pattern of change between lakes (Osbourne & Moss, 1977; Moss, 1978; Moss, 1979; Moss *et al.*, 1979; Moss, 1988a). In the earliest, phase I sediments there are usually abundant snail and plant macrofossil remains and diatom assemblages tend to be dominated by plant-associated epiphytic forms such as *Epithemia, Cocconeis, Cymbella* and *Achnanthes* spp. and often small, bottom-dwelling *Fragilaria* spp. Planktonic diatoms are typically sparse in these sediments (i.e. <10%), but often include the nutrient intolerant forms *Cyclotella ocellata* and *Cyclotella radiosa*. The phase II sediments also contain abundant shell and macrophyte remnants, but there is usually a substantial increase in diatom accumulation rates and in the relative contribution of *Fragilaria* spp. and small centric, planktonic forms. In contrast the sediments laid down in the phase III stage have no shell or macrophyte remains and tend to be dominated by planktonic diatom species. The mechanisms which select for different diatom assemblages in the three trophic phases are unclear and possibly for this reason attempts at reconstructing phytoplankton-macrophyte relationships from fossil diatom assemblages have rarely been made outside of the Broads.

The seasonal monitoring in the three study sites, Tween and Clifton Ponds and Groby Pool has demonstrated how trophic phases II and III select for different fossil diatom assemblages. There were some consistent features evident in the behaviour of diatom communities in the two phase II lakes, Clifton Pond and Groby Pool. Both lakes were turbid with phytoplankton (largely diatoms) and suspended solids in late winter-spring. Periphytic forms were sparse and as a result diatom inputs to the sediment were dominated by planktonic forms. However with the development of a dense macrophyte canopy by late May, the water became very clear, planktonic diatom growth was minimal and periphytic diatom production was prolific. Thus diatom inputs to the sediment were dominated by epiphytic and benthic forms. These two distinct phases of diatom production resulted in the co-dominance of planktonic and periphytic forms in the sediments of these lakes (table 7.1). The phase II state in the Broads has been associated with an expansion of small *Fragilaria* spp. However in the two study lakes species in this group were rare and other epiphytic and benthic forms were dominant. The epiphytes *Cocconeis placentula*, *Rhoicosphenia abbreviata* and large benthic *Gyrosigma* spp. were prevalent in Clifton

Pond, while in Groby Pool *C. placentula* was important with the epiphytic species *Nitzschia paleacea* and the tychoplanktonic form *Fragilaria capucina* var. *mesolepta*.

	Phase III		Phase II	
	Tween Pond	Church Pond	Clifton Pond	Groby Pool
% Plankton	83	81	61	60
% Periphyton	17	19	39	40†
Mean annual PO_4 ($\mu g\ l^{-1}$)	1591	140	63	240* TP

Table 7.1. Percentages of planktonic and periphytic diatom species in the surface sediments of the phase III lakes Tween and Church Ponds and the phase II lakes Groby Pool and Clifton Pond. The samples from Tween and Clifton Ponds were collected in July 1993, the sample from Church Pond in Feb 1995 and the sample from Groby Pool in Oct 1995. † = includes the tychoplanktonic form *F. capucina* var. *mesolepta*. * = Mean annual PO_4 was not available for Groby Pool so values for total phosphorus (TP) are given.

The phytoplankton-dominated (i.e. phase III) situation was studied in Tween Pond. In this lake there was a large pulse of planktonic diatoms (mostly small cyclostephanoid forms) in the spring, but in the absence of macrophyte growth and the onset of clear water conditions in summer, periphyton growth was sparse. There was a return of substantial planktonic diatom populations in late summer-autumn and as a result planktonic forms were dominant in the sediments (table 7.1). The same plankton dominated life-form balance was evident in the sediments of all the 'plantless', phase III lakes in the Attenborough Ponds complex (fig. 5.7), with the exception of Coneries Pond which receives substantial inputs of diatoms from the R. Erewash. That the presence, or absence of submerged macrophytes (i.e. habitat) is of greater significance than water chemistry to the balance between periphytic and planktonic diatoms in the sediments is supported by the plankton-dominated assemblages in Church Pond (>80%) which maintains lower nutrient concentrations than Groby Pool (table 7.1).

Thus it would appear that the alternative stable states of macrophyte dominance and phytoplankton dominance can be clearly identified in the sediments of the study lakes. There is agreement with the Broads studies that in eutrophic lakes, where macrophyte growth is prolific, there is a co-dominance in the sediment of planktonic and periphytic forms and that in lakes where phytoplankton are dominant, planktonic forms are prevalent. Thus it seems probable that the shift between states (i.e. macrophyte loss, or reappearance) may be confidently identified in the sediments of many lakes by changes in the relative competitiveness of planktonic and periphytic species. However it is unlikely that particular diatom species can be uniquely associated with the two states as it is now well known that both can exist in a similar nutrient range (Timms & Moss, 1984). Thus the same diatom species may be found in either plant or phytoplankton dominated lakes, as related to nutrient concentrations, underwater weather and other physio-chemical controls.

The potential for using diatoms to distinguish between the different shallow lake eutrophication phases was demonstrated in the palaeoecolgical studies in Groby Pool (chapter six) and Tween Pond (chapter five). Prior to 1800 available historical evidence indicates that Groby Pool was probably a naturally fertile, mesotrophic lake comparable to the phase I Norfolk Broads and available macrophyte records indicate the presence of a diverse mixture of tall and short growing plant species. The corresponding sediments from the Pool are dominated by small *Fragilaria* spp. (particularly *Fragilaria construens* var. *venter*, *Fragilaria. brevistriata* and *Fragilaria. pinnata*), almost to the exclusion of other forms. This same situation has also been observed in Upton Broad, one of the few remaining phase I lakes in Broadland (Moss *et al.*, 1979). The prevalence of small *Fragilaria* spp. in the early sediments from the Pool indicates the dominance of the benthic life-form and the presence of several open areas of bare, macrophyte-free sediment amongst the diverse, plant stands.

The transition between phases I and II is thought to involve the crossing of a critical system threshold and is held to be a gradual process, reflecting linear increases in nutrient loading (Irvine *et al.*, 1989). However due to dissolution problems it is difficult to be certain of the timescale over which this change was propagated in Groby Pool. In the sediments which correspond to around the late nineteenth century, small *Fragilaria* spp. are of much reduced importance, having been replaced to a large extent by the planktonic form *Cyclostephanos dubius*, such that assemblages are co-dominated by planktonic and periphytic species. This suggests a substantial increase in the intensity of the spring bloom and possibly increased shading of the benthic habitat. That there had been important eutrophication-related changes in the submerged plant communities is indicated by the historical aquatic plant data (i.e. tables 6.2, 6.2). This reveals that nine plants which are recorded in the lake in the pre-1850 period are not found between 1850-1900. The plants which are absent from records in this period have relatively low mean trophic ranking score (TRS) of 7.9 using the classification scheme of Palmer *et al.*, (1992). Alternatively those species which are added to the list in this period have a high mean TRS of 9.3. The significant losses are the mesotrophic, nutrient intolerant species *Utricularia. vulgaris* L., *Littorella uniflora* L. and *Potamogeton gramineus* L. which are relatively rare species in lowland England. Thus by at least 1900, the Pool no longer supported a 'unique' diverse macrophyte community as characteristic of phase I and had probably become a disturbed phase II lake.

The switch from phase II to phase III conditions was studied in the sediment core from Tween Pond. The polluted River Erewash was diverted into the lake in 1972 and this resulted in the loss of macrophytes in the following summer. This state change is clearly represented in the sediments by dramatic reductions in percentages of the centric form *C. radiosa* and benthic *Gyrosigma* spp. and their replacement by small centric forms. The pre-diversion assemblages are co-dominated by planktonic and periphytic species, but in the post-diversion sediments planktonic species are dominant. Thus the diatom assemblages in the Tween Pond core seem to accurately record the elimination of submerged plants from the lake.

Model for predicting phytoplankton-macrophyte interactions

Using both the seasonal monitoring data from the three study lakes, the palaeolimnological reconstructions from Tween Pond and Groby Pool and the Norfolk Broads literature, it is possible to construct a simple habitat-based model for predicting shifts in phytoplankton-macrophyte interactions from the sediment record. The three shallow lake ecosystem states and idealised changes in the fossil diatom record are given in fig. 7.1.

Those lakes which might be classified as phase I sites with diverse, 'unique' plant communities such as Groby Pool pre-1800 and some Norfolk Broads (e.g. Upton and Martham Broads) are typically found in relatively undisturbed catchments and are usually largely unaffected by eutrophication (Moss, 1983; Phillips, 1992). Thus nutrient levels are typically low ($<50\ \mu g\ l^{-1}$), phytoplankton growth is sparse and light probably penetrates to the bottom throughout the year. This means that the sediments are usually dominated by periphytic forms (perhaps 80-90%) associated with the epiphytic and benthic life-form (particularly *Epithemia* spp., small *Fragilaria* spp., *Cymbella* spp., *Cocconeis* spp. and *Achnanthes* spp.).

In nutrient enriched, phase II lakes (e.g. present day Clifton Pond and Groby Pool), increased nutrient availability means that planktonic diatoms are often much more abundant in late winter-spring and high turbidity during this period may mean that periphytic diatoms have minimal available habitat. However the colonisation of macrophytes in late May-June and the onset of clear water conditions affords a massive potential habitat for periphytic species. Thus assemblages may be co-dominated (i.e. perhaps 50/50 or 60/40) by planktonic and periphytic forms reflecting these two growing phases and the shift from phase I to phase II is probably best marked by an expansion of the plankton. Phillips *et al.*, (1978) suggest that one of the initial effects of nutrient enrichment in shallow lakes is the stimulation of epiphyte production. This is known to reduce the amount of light available for plant photosynthesis and has been implicated in causing the shift from phase I to phase II conditions (Irvine *et al.,* 1989). Thus it is possible that the phase II state may also be recognised by increased epiphytic diatom accumulation rates in sediment cores (Phillips *et al.,* 1978) and by higher percentages of epiphytic as opposed to benthic forms. Unfortunately it was not possible to test this hypothesis from the Groby Pool sediment core, but the expansion of epiphytic forms toward the top of the core may indicate the possibility of tracking changes in macrophyte productivity.

In turbid, 'plantless', phase III lakes there are typically few opportunities for periphytic diatom growth and the prolific development of planktonic diatom populations in spring and often summer and autumn means that planktonic forms are usually dominant. Thus the loss of macrophytes from a lake can probably be identified by what will be a quite sudden (probably propagated over less than 10 years) increase in planktonic diatom percentages in the sediments (i.e. perhaps >75%) and a reduction in the importance of periphytic forms. An additional 'tool' for recognising the shift from clear to turbid water conditions may also be provided by increases in percentages of late season-adapted planktonic forms (as in Tween Pond) which may indicate a decline in the buffering capacity of the plant dominated state and the removal of 'top-down' control over the phytoplankton (chapter five).

The eutrophication-related lake successional sequence described above and shown in fig. 7.1. is idealised and it must be remembered that many recently created shallow lakes may never have existed in the phase I state. Moreover, depending on the nature of changes in nutrient loading some lakes may 'skip' a phase and move from a phase I to a phase III state, while others may even cycle between phases II and III with a return period of some 7-8 years (Moss *et al.,* 1990; Perrow *et al.,* 1994). There is still a requirement for the continued refinement and testing of this life-form based approach, but it has considerable potential for reconstructing past changes in phytoplankton-macrophyte relationships in lakes subject to eutrophication.

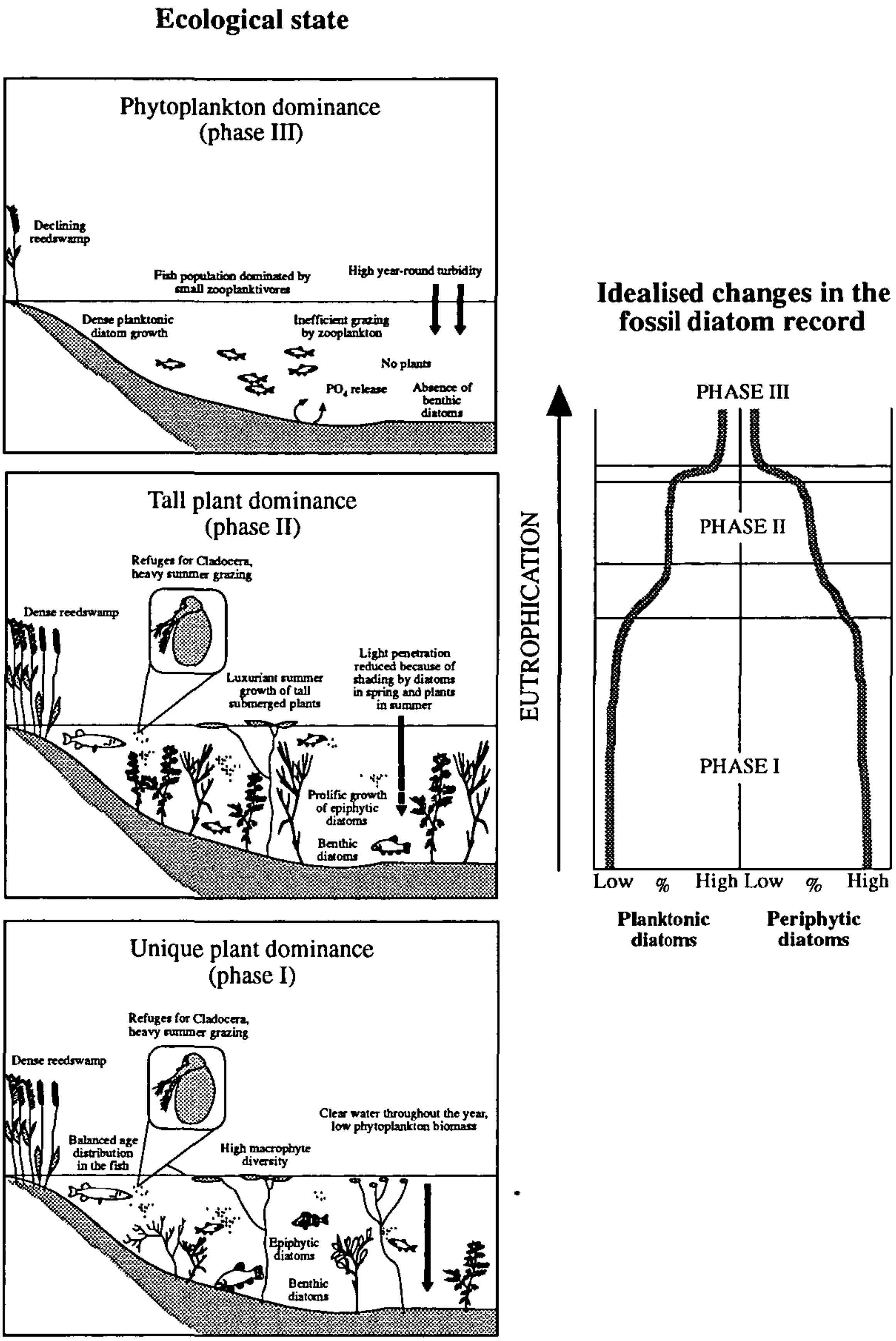


Fig. 7.1. Idealised changes in the fossil diatom record with changes in ecological state in a shallow lake subject to eutrophication.

* Ecological states after Phillips (1992)

Problems associated with diatom-total phosphorus transfer functions

The major recent advance in shallow lake palaeolimnology has been the development of diatom-TP transfer functions, which permit quantitative hindcasts of mean annual TP concentrations from fossil diatom assemblages. These models have been developed from and applied to shallow lakes in N. Ireland (Anderson *et al.*, 1993), southeast England (Bennion, 1994) and Denmark (Anderson & Odgaard, 1994) with some considerable success. However the errors associated with TP reconstructions are usually relatively large which limits the sensitivity and significance of the results which are generated (Fritz *et al.*, 1993). Also these models always 'force' out a TP result regardless of whether TP is the major factor controlling diatom abundance in a fossil assemblage. Thus it is impossible to be certain that TP reconstructions are reliable. The major source of error associated with the TP models is that TP is only one factor out of a range of interacting chemical, physical and biological controls which affect diatom growth and the representation of specific diatom populations in the sediments of a lake (Anderson *et al.*, 1993).

Using the modern and palaeoecological diatom data collected from the three shallow study lakes some of the problems associated with the TP transfer function approach are explored in the next part of this chapter. This is divided into two parts, the first of which focuses on the degree to which the modern diatom communities of the three lakes are accurately characterised by surface sediment samples and the second part on how other physio-chemical and biological factors detract from the diatom-TP relationship as modelled in surface sediment calibration data sets and predicted from sediment core profiles. Possible suggestions for the improvement of diatom-TP models are made in chapter eight.

The representativity of surface sediment diatom assemblages

The majority of studies attempting to model modern diatom-environment relationships have used surface sediment assemblages for calibration purposes. This is because; (i) these samples are directly analogous to the core samples which form the ultimate basis of reconstructions and; (ii) it is usually assumed that a strong relationship exists between modern diatom communities found in a lake and surface sediment assemblages. The second assumption is rarely tested, but studies relating long-term phytoplankton data to the fossil diatom have usually found an extremely accurate correlation (Haworth, 1980). Moreover sediment trap studies have demonstated order of magnitude similarities between planktonic diatom standing crops and specific fluxes to the sediment (Reynolds *et al.*, 1982; Trimbee & Harris, 1984). However these calibration studies have rarely been conducted in shallow lake environments where periphytic diatoms often make a substantial contribution to sedimentary assemblages.

The representation of contemporary diatom communities in the sediments of the three shallow study lakes was studied by comparing overlapping diatom samples collected from the plankton and periphyton with sediment trap and surface sediment assemblages (chapter four). Even accounting for the effects of sediment resuspension inputs and possible diatom losses due to grazing and outflow, the traps were found to accurately track seasonal changes in the dominant diatom species found in the lake. Those species which were abundant in the plankton and in major periphytic habitats were also prevalent in the sediment trap samples at the same time and seasonal changes in the relative scale of planktonic diatom production appeared to be accurately reflected. There were also strong similarities between the assemblages found in the sediment traps and at the sediment surface and the majority of the major and indeed minor species appeared to be relatively accurately represented.

However there were some species which were clearly misrepresented in the sediments, most important of which was the centric form *T. pseudonana*. This species was extremely abundant in the late winter plankton of Clifton Pond and given its abundance in the trap it was estimated that it should contribute to 53% of total diatom influx to the sediment during the study period. Theoretically this should have meant that it was at least as abundant in the surface sediments. However in both the trap II (sampled at the end of the study period) and surface sediment samples from Clifton Pond it contributed to below 9% of the assemblage. This species is extremely small (mean cell volume = 26 μm^3), with a high SA:V ratio, easily fractured and very delicately silicified, which means that it is extremely vulnerable to dissolution (cf. Barker *et al.*, 1994). Internal Si-recycling from the sediment store is often an important process in shallow lakes during the summer months as the temperature of the sediments increases (Battarbee, 1978; Rippey, 1983; Bailey-Watts *et al.*, 1989) and it is probable that this was responsible for the selective loss of *T. pseudonana* from the trap II and surface sediments shortly after the population settled out of the plankton in the spring. Thus it would appear that selective dissolution precluded the accurate representation of this form in the sediments. The same problem is probably important in many shallow lakes, particularly where small, fragile forms are prevalent alongside larger, or more heavily silicified species and the bias that this causes may be one of the important factors which weakens the relationship between diatom inferred and observed TP concentrations.

The important influence of dissolution and decomposition processes on the surface sediment assemblages was also evident in Tween Pond and Groby Pool, where the timing of surface sampling was found to be a crucial factor affecting the sedimentary

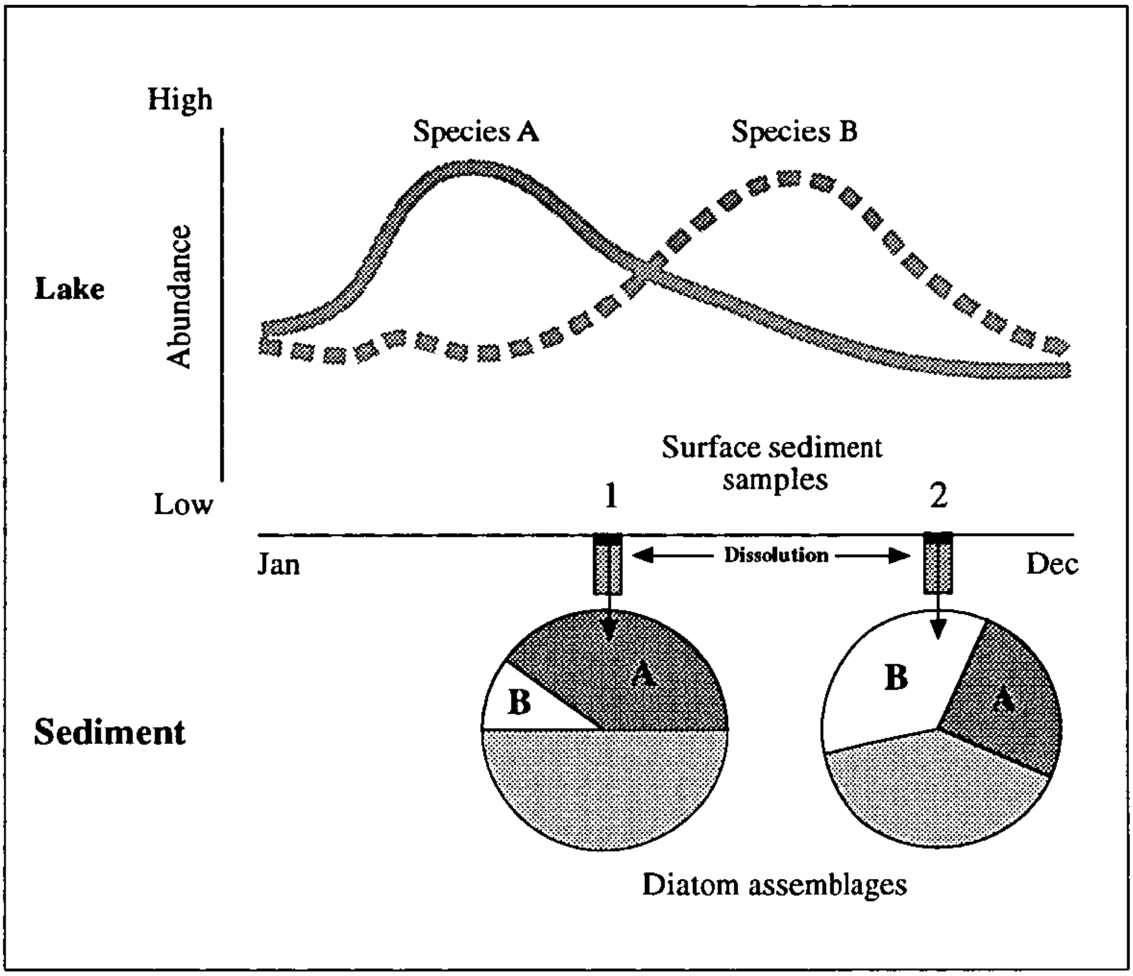


Fig. 7.2. The theoretical effects of the timing of surface sediment sampling on the representation in the sediments of species with different seasonal requirements.

biasing of particular samples towards different species with specific seasonal requirements. Moreover the high levels of heterogeneity observed in the transect of surface sediment samples from Groby Pool also indicates that sample location is also an important factor affecting the characterisation of modern diatom communities and this aspect of variability may also be important in this respect.

The diatom-TP relationship

Prior to the construction of a diatom-TP transfer function it is a prerequisite that TP is a major factor controlling the distribution of the species in the modern surface sediment assemblages. Moreover when these models are applied to sediment core eutrophication sequences it is also essential that major trends in species relative abundance are driven by changes in TP. TP has usually been found to have an important independent influence on modern diatom distributions alongside other trophic status surrogates such as PO_4, NO_3 and chlorophyll *a*. However there are a range of additional physical, chemical and biological factors which affect diatom abundance (Reynolds, 1984). These include nutrients, pH, salinity, trace elements, toxic substances, light, turbulence, habitat availability, phytoplankton competition, grazing and parasitism etc. Thus it is not surprising that considerable scatter is evident in the observed and diatom-inferred TP relationship. Using both the literature and the modern monitoring and palaeoecological data for the three shallow study lakes the importance of some of these additional factors are discussed in the next part of this chapter. This is divided into three parts which consider the influence of; (i) light and habitat availability; (ii) water chemistry; and (iii) turbulence and flushing rates.

(i) light and habitat availability

Physio-chemical factors may be important in determining which planktonic and to some extent periphytic diatom species are abundant in a shallow lake. However the major control over the seasonal balance between planktonic and periphytic diatom production is undoubtedly the light environment which is in turn dependent on ecological state, water depth and suspended solids concentrations. This affects the degree to which macrophytes are able to colonise and the available habitat for epiphytic and benthic diatoms. The importance of light and habitat availability has been demonstrated in a shallow southeast England diatom training set where strong correlations were found between diatom assemblages and water depth (Bennion, 1994). This was related to the dominance of small benthic *Fragilaria* spp. in the extremely shallow sites where light could penetrate to the bottom and indicates that the mere existence of habitats for attachment was the critical control over the relative abundance of these forms. The same is probably true of many diatom epiphytes for which the density and extent of submerged, floating and emergent macrophyte stands may be crucial and while *Fragilaria* spp. seem to be able to survive across a wide range of nutrient concentrations, many epiphytes such as *C. placentula* and *R. abbreviata* also appear to be extremely insensitive to changes in the nutrient environment. This was evident in the similar epiphytic diatom assemblages associated with submerged plant surfaces in Clifton Pond and Groby Pool (chapter four) and has often been attributed to 'substrate' effects and the possibility that many epiphytic species obtain nutrients from their hosts (Jørgensen, 1957; Eminson, 1978; Eminson & Moss, 1980). Thus the same periphytic diatom species may be present in signficant percentages across a broad water chemistry range as long as their is available habitat. This was demonstrated in the study lakes where irrespective of nutrient concentrations, the vital factor affecting the balance between planktonic and periphytic diatoms in the sediments was ecosystem state and the presence or absence of submerged plants (table 7.1). Thus there are clear difficulties in relating periphytic diatom species to nutrient concentrations in diatom-TP models and much of the scatter associated with the diatom inferred and observed TP relationship is likely to be related to the factors described above.

In Tween Pond the loss of macrophytes from the lake resulted in a dramatic shift from assemblages co-dominated by planktonic and periphytic diatoms to planktonic diatom dominated assemblages. As this sudden change was only partly related to changes in nutrient concentrations, potential problems in accurately predicting quantitative changes in TP can be visualised. Eutrophication-related changes in lake state pose particular problems for diatom-TP models. Experiments in the Norfolk Broads have shown that nutrients alone are in most cases insufficient to induce a shift from phytoplankton to submerged plant dominance, because the plant-associated buffers (see chapter one) resist externally-applied change (Irvine *et al.*, 1989; Balls *et al.*, 1989; Moss, 1994). Thus additional biological and physical switch mechanisms are thought to be necessary such as; (i) reductions in the abundance of large-bodied Cladocera due to pesticide ingress (Stansfield *et al.*, 1989) or increases in salinity (Bales *et al.*, 1993); (ii) mechanical damage by boat propellors and weed cutters (Moss, 1996) and; (iii) winter kills of piscivorous fish (Bronmark & Weisner, 1992). The latter mechanism may be of particular importance in the recent past due to outbreaks of diseases affecting perch. Thus the dramatic changes in light climate, habitat availability and zooplankton grazing associated with the shift from submerged plant to phytoplankton dominance may often be unrelated to a changes in the nutrient environment. Unfortunately the diatom-TP models are largely inequipped to deal with the dramatic shifts in diatom assemblages which occur as to result of these types of changes and may be expected to suggest a sudden change in nutrient concentrations when the nutrient environment may often have remained relatively stable.

(ii) water chemistry

TP is not always the major nutrient controlling the relative competitiveness of different diatom species in lakes and in many sites N, or NO_3, are more important, particularly when TP is not a major limiting factor, or is at background levels. Si-availability may also be important in lakes where it becomes a limiting resource and shortages in the supply of usable SiO_2 may selectively promote the growth of small, delicately silicified species with low Si-requirements relative to larger forms with higher Si-demands (Kilham, 1975). Moreover laboratory and field experiments have shown that planktonic diatoms may be arrayed along resource ratio (i.e. Si:P, N:P) gradients (Kilham & Kilham, 1984; Sommer, 1989). Thus nutrient interactions may also complicate and detract from the diatom-TP relationship.

If a diatom-TP transfer function is applied to a lake sediment eutrophication records it is assumed that TP is the major nutrient control, influencing assemblage changes in the core. However in the early eutrophication of many lowland lakes N is often critical. This is because initial eutrophication-related disturbances usually take the form of land-use changes and in particular agricultural intensification so that diffuse run-off is often the dominant nutrient source. Agricultural run-off typically contains abundant soluble N, but only small quantities of P which is usually in particulate form (Moss, 1988b). Thus in lakes without a major sewage effluent input, N is often the major nutrient in the eutrophication process. The early eutrophication history of Groby Pool demonstrates the problems associated with applying diatom-TP models to pre-twentieth century lake sediment sequences. Historical land-use records for the Pool indicate that agricultural run-off was probably the dominant nutrient source until the early-mid twentieth century and major changes in the fossil diatom record during this period were probably driven by changes in N. Thus while a TP model might pick out eutrophication trends confidence in the accuracy of actual reconstructed TP values would have to be low.

There are several other non-nutrient water chemistry parameters which are important for diatom species selection, most important of which are thought to be pH and salinity. Efforts are usually made to constrain pH in trophic status training sets, however the same is not usually so for salinity and this may indeed exert an important influence over diatom assemblages. The importance of dissolved salt concentrations was evident in both Tween and Clifton Ponds where high EC levels (i.e. typically $>1000\ \mu S\ cm^{-1}$) probably favoured the halophilous species *C. atomus*, *T. pseudonana*, *T. guillardii* and *S. potamos*, whereas these species were largely absent from Groby Pool. Thus in lakes where sewage or industrial effluent inputs favour high dissolved salt inputs diatom communities may be made up of those species which can withstand both high nutrient concentrations and high salinities and this again may detract from the diatom-TP relationship.

(iii) turbulence and flushing rates

The hydraulic characteristics of lakes are paramount to the organisation of the phytoplankton (Reynolds, 1987). Perhaps the most important factor in this respect is turbulence which selects for species with different buoyancy characteristics (Lund, 1959; Reynolds, 1987; Reynolds, 1994). The shallow mixed depth in shallow lakes often means that the vertical extent of turbulence is insufficient to maintain large, heavy diatom species (e.g. large *Stephanodiscus* spp. colonial *Aulacoseira* spp.) with rapid settling rates in a pelagic existence (Uhlmann, 1971; Reynolds, 1994). This may explain why shallow, eutrophic-hypertrophic sites such as the study lakes tend to be dominated by small, highly buoyant centric forms, whereas in deep, eutrophic reservoirs in the same region large *Stephanodiscus* species (i.e. >25 µm diameter) are frequently co-dominant with *Aulacoseira* spp. and *Asterionella formosa* (Sayer & Roberts, unpublished data). The critical factors affecting turbulence characteristics in uniformly shallow, non-stratifying environments are probably lake size, shape, exposure and orientation, which determine the intensity of wind-induced physical mixing processes and it is possible that some of the scatter in the diatom-TP relationship may be related to these factors. Evidence for this hypothesis is provided by Clarke (1989) who found that the heavily silicified centric species *C. dubius* was restricted to lakes with a maximum dimension exceeding 200 m in Norfolk. Thus it may be that larger, heavier forms such as *C. dubius* and *S.* cf. *medius* are unable to attain sizeable populations in small, sheltered lakes.

Undoubtedly turbulence characteristics select for particular morphological and physiological adaptive strategies amongst diatom species in shallow lakes. However flushing rates may also act as an important axis for competition (Bailey-Watts *et al.*, 1990; Reynolds, 1994). In rapidly flushed, highly riverine environments a species must be able to grow rapidly so that growth rates exceed outflow losses. In culture experiments the rates at which phytoplankton species grow has been found to be directly dependent on SA:V ratios and small forms with high SA:V ratios have been found to have the highest growth rates (Reynolds, 1989). Thus frequent flushing tends to favour tiny centric forms over larger, slower growing species and again some of the scatter in the diatom TP models may be related to this restriction. The importance of changing flushing rates on diatom communities was evident in the sediment core from Tween Pond (chapter five). The diversion of the R. Erewash outflow to the Barton lane outlet in 1980 resulted in an increase in lake retention time and is clearly marked by a significant increase in the mean volume of the centric species found in the corresponding sediments and the increased prevalence of the relatively large form *S.* cf. *medius*. This type of change would again pose problems for a diatom-TP transfer function as it seems likely that this event was largely unrelated to nutrient concentrations.

TP reconstruction for the core GR95B

The major problems that are inherent to diatom-TP models as discussed in the second part of this chapter are evident from the application of the south east England shallow lake transfer function of Bennion (1994) to the core from Groby Pool (fig. 7.3). Present day mean TP concentrations for Groby Pool (i.e. 240 $\mu g\ l^{-1}$) falls within the middle of the TP gradient for this model (i.e. 28-410 $\mu g\ l^{-1}$) and throughout the core over 75% (typically >80%) of the species in each fossil sample have listed TP optima. Thus Groby Pool would appear to be a reasonably suitable site for reconstructing past TP levels using this transfer function. There is a relatively large discrepancy between the diatom-inferred annual mean TP for the surface sediment sample (170 $\mu g\ l^{-1}$) and the measured annual mean TP concentration for Groby Pool (240 $\mu g\ l^{-1}$) and this indicates that the model is probably underestimating TP levels in the upper part of the core.

Reconstructed TP levels for the lower half (approx. mid eighteenth century-late nineteenth century) of the core are relatively stable, ranging between 88-110 $\mu g\ l^{-1}$. However it is doubtful whether TP levels were this high during this period and it seems likely that the early eutrophication of the Pool would have resulted largely from increased inputs of N derived from agricultural run-off. There is a sudden increase in diatom-inferred TP at 42-43 cm to 141 $\mu g\ l^{-1}$. This dramatic change which dates to around the turn of the century might suggest a sudden increase in nutrient levels at this time. It is associated with a quite rapid decline in percentages of small, benthic *Fragilaria* spp. and a marked increase in percentages of the centric forms *C. dubius* and to a lesser extent *S. parvus* (fig. 6.4). However again land-use reconstructions suggest that N was probably the most important nutrient input and the rapidity of this change may be more closely related to a sudden decline in rates of diatom dissolution in the sediment (chapter six). Thus it is unlikely that there was a sudden increase in mean TP concentrations. Diatom-inferred TP oscillates between from 130-165 $\mu g\ l^{-1}$ from 43-2 cm. A sewage works which was installed on the Slate Brook in the mid-1930s must have significantly increased TP concentrations in the Pool and this event is marked by an important shift from *C. dubius* to *S. parvus* dominance above 24-25 cm. However diatom-inferred TP is stable over this period and even makes a quite significant decline above 14-15 cm. Thus again it would appear that the diatom-TP model is producing inaccurate TP reconstructions. The decline in reconstructed TP values above 14-15 cm is closely related to increases in percentages of the epiphytic diatom *C. placentula*. This particular change has been associated with eutrophication-related increases in submerged plant biomass as the lake was colonised by tall growing, nutrient intolerant species (chapter six). Thus the inverse trend is suggested from the qualitative interpretation of the fossil diatom record. Again this illustrates the problems of inferring TP concentrations from habitat mediated assemblage shifts.

The sudden peak in reconstructed TP (i.e. 170 μg^{-1}) at the surface of the core is related to a dramatic peak in *S. parvus*. However as already stated *S. parvus* appears to be overrepresented in this sample, because the core was collected in the spring, just after the major input of this species to the sediment. Thus it seems unlikely that there has been a rapid recent increase in TP concentrations. Reconstructed TP for the October surface sediment sample (G3) is 136 $\mu g\ l^{-1}$ which would suggest relatively stable TP concentrations. Thus it is apparent that the timing of surface sediment sampling can have a significant effect on diatom-inferred TP values.

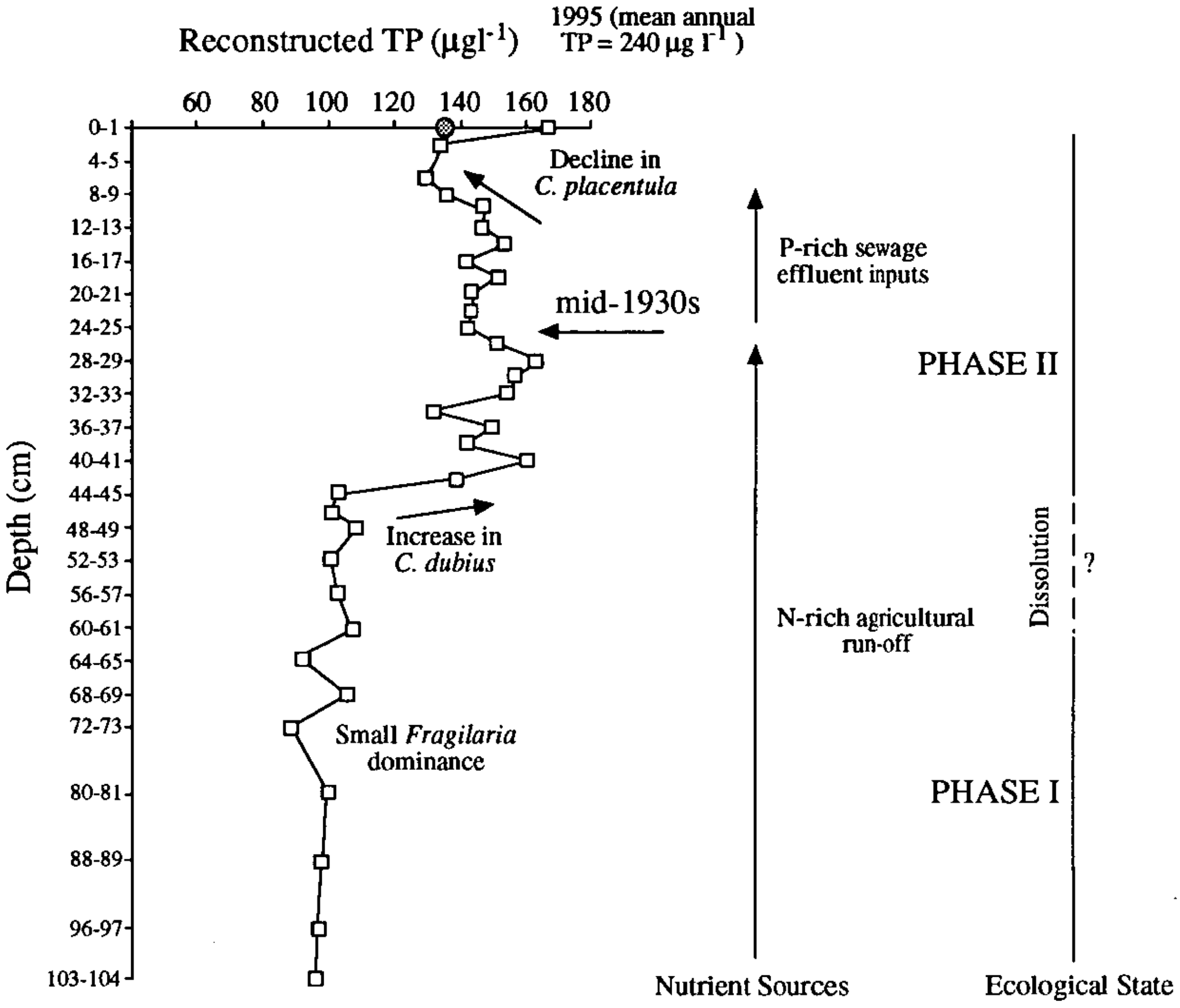


Fig. 7.3. Diatom-inferred past mean TP concentrations for core GR95B from Groby Pool.

* (◍) diatom-inferred TP for the October surface sediment sample

CHAPTER EIGHT

CONCLUSIONS

This thesis has explored the diatom taxonomy, ecology and palaeoecology of three small, shallow, artificial lakes in the English Midlands. In this concluding chapter the success of these modern and palaeolecological studies are assessed and implications for current 'state of the art' approaches to trophic status reconstruction are discussed. In the final part of this chapter a more holistic approach is advocated.

Modern studies

The taxonomic study has shown that a remarkably large number of different centric diatom species are found in the modern-day and palaeoecological samples from the three study lakes. However with careful LM and SEM microscopy it has been possible to make confident and consistent species separations. LM and SEM photographs are given of all the potentially 'problematic' species and these should assist future ecological and palaeoecological studies attempting to incorporate the 'up-to-date' SEM taxonomy at the LM level. There remains some confusion over the correct identity of some of the forms identified in this study and further research is necessary. In particular the status of the new genus *Pelagodictyon* needs to be re-assessed in the light of an extremely close relationship between *Pelagodictyon tenue* and *Stephanodiscus hantzschii.* Initial investigations suggest that these entities may be life-cycle variants of the same genetic entity. There are also close similarities between *Pelagodictyon fritzii* and *Cyclostephanos invisitatus* and again future studies are necessary to delineate the relationship between these forms.

The monthly monitoring studies indicate that diatom seasonality is very different in phytoplankton and macrophyte dominated lakes. In hypertrophic Tween Pond, extremely high nutrient concentrations and 'year-round' turbid, phytoplankton dominated conditions select for two phases of prolific planktonic diatom growth in spring and late summer-autumn. The absence of macrophytes and the shading of the sediment surface in this lake means that periphytic diatoms are sparse and as a result surface sediment diatom assemblages are plankton dominated. That this is a consistent phenomenon in phytoplankton dominated lakes is indicated by high plankton percentages in the sediments of all the 'plantless' sites in the Attenborough Ponds SSSI with the exception of Coneries Pond which receives substantial inputs of allochthonous, riverine diatoms. In macrophyte dominated Clifton Pond and Groby Pool planktonic diatom (again mostly of centric species) growth is mostly restricted to the late winter-spring period. The onset of clear water conditions and the development of substantial beds of submerged plants in summer and autumn results in the mass development of benthic and epiphytic diatoms and during this period planktonic forms are rare. These two distinct phases of diatom growth seem to result in surface sediment assemblages which are co-dominated by planktonic and periphytic forms.

The taphonomic studies indicate that surface sediment assemblages in the study lakes afford a reasonable approximation of the diatoms growing during different periods of the year in different lake habitats. However there are some potential problems related to selective dissolution. This is particularly evident for the centric species *Thalassiosira pseudonana* which appears to be significantly underrepresented in the surface sediment sample from Clifton Pond. Interestingly, perhaps the crucial factor affecting diatom representation is sample timing and it is apparent that surface samples tend to overrepresent recently sedimented species. This problem appears to be particularly acute for spring collected samples which may often be heavily biased towards planktonic forms.

Palaeoecological studies

The palaeoecological studies indicate considerable potential in the use of diatoms to reconstruct the eutrophication and disturbance histories of shallow lakes. However some potential problems are evident. Perhaps the most important of these is sediment dissolution which seems to have been the cause of poor diatom preservation in much of the core from Clifton Pond, in the basal part of the core from Tween Pond and in a short, mid-part of the core from Groby Pool. Indeed dissolution has largely precluded the use of Clifton Pond in the palaeoecological study and has much hindered the interpretation of the diatom stratigraphy from Groby Pool. The second major problem in this study concerns the interpretation of the diatom stratigraphy in the upper part of the Tween Pond core (Zones III) where in the absense of detailed data on the relative environmental requirements of many of the small centric forms, it has been impossible to make any environmental hindcasts.

The fossil diatom records from Tween Pond and Groby Pool clearly document important trends in nutrient loading and in both sites it has probably been possible to establish 'background' ecological conditions that may potentially form the ultimate basis of restoration targets. It has also been possible to differentiate between different rates of change and hence different types of eutrophication-related disturbance. Rapid shifts in the diatom assemblages subsequent to known disturbance events such as; (i) the diversion of the highly polluted R. Erewash into Tween Pond (1972); (ii) the altered position of the R. Erewash outflow in Tween Pond (1980); and (iii) the commencement of P-rich sewage effluent inputs into Groby Pool (mid-1930s) indicate that diatoms respond extremely rapidly to changes in the lake environmental conditions and that these changes are immediately recorded in accumulating lake sediments. Thus the potential for using diatoms in pollution monitoring and lake recovery studies is emphasised here.

Using a simple life-form based method based it has also been possible to reconstruct the effects of eutrophication on aquatic plant communities. In Tween Pond the sudden loss of submerged macrophytes after 1972 and the switch from a clear water (i.e. phase II) to a turbid water stage (i.e. phase III) is clearly documented in the sediment record by; (i) the sudden loss of *Cyclotella radiosa* and benthic *Gyrosigma* spp. and their replacement by small, eutrophic centric forms; (ii) the abrupt shift from assemblages co-dominated by planktonic and periphytic species to plankton dominated assemblages; and (iii) the appearance of much higher percentages of summer-autumn adapted centric diatom species. The fossil diatom record from Groby Pool has been compared with old macrophyte records and available historical catchment land-use data. These sources suggest that prior to 1800 the Pool was probably a mesotrophic site supporting a unique, diverse, 'unique' macrophyte community (i.e. phase I). The dominance of small benthic *Fragilaria* spp. in the lower part of the core suggest light penetration to the bottom throughout most of the year and minimal planktonic diatom development. However the rise in percentages of the centric *Cyclostephanos dubius* and the decline in benthic *Fragilaria* spp. indicate that by at least 1900, the Pool had probably become a highly enriched, tall plant dominated environment (i.e. phase II). This hypothesis is supported by the available macrophyte records which indicate the loss of nutrient intolerant species, a decline in diversity and the arrival of several, highly competitive plants.

Improvements in diatom-TP models

The development of diatom-TP transfer functions which permit quantitative hindcasts of TP concentrations from fossil diatom stratigraphies represents a major step forward in palaeoecology. However these models are hampered by large errors of prediction. The potential reasons for the scatter between observed and diatom-inferred TP have been explored in this study. Among many other physio-chemical and biological parameters which detract from the diatom-TP relationship such as salinity, N, Si-availability, nutrient interactions, nutrient seasonality, turbulence characteristics, flushing rates, phytoplankton competition and biotic interactions, perhaps the most crucial in shallow lakes is the relationship between phytoplankton and submerged macrophytes. This affects light levels, habitat availability and is crucial to the competitive balance between different diatom life-forms. The strength of the diatom-TP relationship could possibly be improved by more rigorous site screening and by increased efforts to constrain other significant environmental controls (particularly pH and salinity), or possibly by constructing separate training sets for phytoplankton and macrophyte dominated lakes. However such manipulations may lead to the loss of important ecological data. Moreover given the inherent natural complexity of shallow lakes and the different interactions between factors in different sites it is difficult to see how it might be possible to significantly reduce the errors of prediction in this way.

Perhaps the greatest opportunities for error reduction is through improved sampling. Presently diatom training-sets are constructed from single, quarterly, or at best monthly water chemistry samples collected either before, during or subsequent to the sediment sampling, while surface sediment diatom assemblages are collected randomly at different times of the year. Possible improvements in the diatom-TP models might be achieved by standardising the water chemistry and surface sediment sampling methods such that; (i) as many water chemistry samples are collected as frequently as is logistically possible to account for seasonal variability; (ii) sediment samples are taken at the end of the water chemistry sampling; (iii) sediment samples are collected at the same time of the year, preferably in early winter so that they are not differentially biased towards species with different seasonal preferences and are affected by spring dissolution processes in the same way as core samples; and (iv) more than one sediment sample is collected and analysed from each lake (possibly a transect of samples) to account for the effects of habitat patchiness on surface sample heterogeneity.

The Role of diatom-TP models?

The diatom-TP models offer a number of apparent advantages over 'indicator species' and simple index approaches. This is because; (i) actual quantitative TP estimates provide information which is easily communicable to the lake manager, or legislator and are readily converted into lake management targets; (ii) TP-models do not ignore subtle, random changes in species assemblages (i.e. as at the top of the sediment core from Tween Pond); and (iii) TP models may potentially provide more accurate estimates of the pathway and trajectory of trophic change. However this and other studies highlight a number of important weaknesses and potential problems which must also be recognised when these models are applied to sediment core records in that; (i) the rather large errors of prediction may limit the ability of diatom-TP models to identify fine-scale changes in trophic variables (e.g. Fritz *et al.*, 1993); (ii) the models may often provide unreliable TP estimates, particularly when the diatom-TP relationship is indirect, or weak due to other eutrophication related changes (i.e. changes in macrophyte abundance), or indeed the effects of non-nutrient related factors; and (iii) estimated TP restoration targets may be extremely inaccurate, particularly when pre-disturbance diatom assemblages are dominated by periphytic forms with extremely broad tolerances (e.g. small *Fragilaria* spp.) and the early eutrophication of a lake is largely a response to agricultural changes and increased N inputs.

The future of shallow lake palaeolimnology?

The advent of quantitative diatom-TP models represents an exciting breakthrough in palaeolimnology. However there are potential dangers associated with this approach to reconstruction. This is because purely focusing on TP, which is in itself just one isolated parameter in a massively complex ecological system, discourages the search for alternative environmental trends, many of which significantly weaken the diatom-TP relationship. The quantitative approach to trophic status reconstruction also encourages a narrow view of the eutrophication process, focusing purely on the perceived cause (i.e. increased nutrient levels) and not the consequences of eutrophication such as increases in macrophyte abundance and switches between the alternative equilibria of macrophyte and phytoplankton dominance. Thus, while an apparent exactness of TP prediction might appear desirable, a more holistic, less mechanistic approach to reconstruction is recommended here and it is suggested that TP models should not be used on a 'stand-alone' basis.

This study has shown that qualitative methods such as simple life-form and 'altered seasonality' approaches offer considerable potential for inferring eutrophication-related trends in shallow lake nutrient status, phytoplankton-macrophyte relationships and possibly changes in phytoplankton competition. Ideally these approaches should be used in conjunction with the diatom-TP models so that potential problems with TP reconstructions are identified and as much information is teased out of the diatom record as is presently possible. Moreover, wherever it is feasible, a 'multi-indicator' approach to reconstruction is advocated (e.g. Engstrom *et al.*, 1985; Fritz *et al.*, 1993), so that diatom-inferred changes in the lake environment can be independently tested. Plant macro-fossil and fossil Chironomid and Cladoceran data afford considerable potential for hindcasting changes in water chemistry and alterations in lake state. Also old plant records when they are available in sufficient quantity, can provide an unrivalled view of changes in macrophyte status, that is invaluable in assessing the effects of eutrophication at a site.

The results generated by diatom-TP models must be interpreted with some considerable caution and future research should continue to assess the reliability and validity of these models. However, while the TP models continue to be reviewed, efforts must also concentrate on more fully developing and testing other complimentary diatom-based techniques for reconstructing shallow lake trophic status. The life-form based methods described in this thesis provides a means of assessing 'total-ecosystem' responses to the nutrient enrichment process. However there remains considerable scope for the refinement of this approach, through multi-lake studies relating diatom assemblages to the presence, or absence of submerged and floating plants. Also to provide a more rigorous test of the effectiveness of this method it might be interesting to apply it to lakes which naturally cycle between phytoplankton and macrophyte dominance over relatively short periods of time. Possibly it is developments along these lines which may more closely link palaeolimnology into shallow lake restoration studies, providing a means of establishing biological as opposed to chemical restoration targets and an alternative perspective on the 'top-down', 'bottom-up' debates which are currently central themes in limnology.

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APPENDIX ONE

List of taxa mentioned in this thesis with authorities.

Achnanthes clevei Grun. in Cleve & Grun.
Achnanthes conspicua A. Mayer
Achnanthes delicatula (Kütz.) Grun.
Achnanthes lanceolata (Breb. ex Kütz.) Grun. in Cleve & Grun.
Achnanthes minutissima Kütz.
Amphora libyca Ehrenb.
Amphora pediculus (Kütz.) Grun.
Amphora veneta Kütz.
Asterionella formosa Hass.
Aulacoseira aff. *alpigena* (Grun.) Krammer
Aulacoseira granulata var. *angustissima* (O. Müll.) Simonsen
Caloneis silicula (Ehrenb.) Cleve
Cocconeis neothumensis Krammer
Cocconeis pediculus Ehrenb.
Cocconeis placentula Ehrenb.
Ctenophora pulchella (Ralfs & Kütz.) Williams & Round
Cyclostephanos delicatus (Genkal) Kling & Håkansson
Cyclostephanos dubius (Fricke) Round
Cyclostephanos invisitatus (Hohn & Hellerman) Theriot, Stoermer & Håkansson
Cyclostephanos tholiformis (Stoermer, Håkansson & Theriot) Håkansson & Kling
Cyclotella atomus Hust.
Cyclotella atomus var. *gracilis* Genkal & Kiss
Cyclotella cryptica Reimann, Lewis & Guillard
Cyclotella distinguenda Hust.
Cyclotella meneghiniana Kütz.
Cyclotella pseudostelligera Hust.
Cyclotella pseudostelligera type 2
Cyclotella radiosa (Grun.) Lemm.
Cyclotella sp. 1
Cyclotella ocellata Pant.
Cymbella caespitosa (Kütz.) Grun.
Cymbella microcephala Grun.
Cymbella minuta Hilse ex Rabenh.
Cymbella silesiaca Bleisch

Diatoma moniliformis Kütz.
Diatoma tenuis Ag.
Epithemia sorex Kütz.
Fragilaria brevistriata Grun.
Fragilaria capucina Desm.
Fragilaria capucina sp. 1
Fragilaria capucina sp. 2
Fragilaria capucina var. *mesolepta* (Rabenh.) Rabenh.
Fragilaria capucina var. *perminuta* (Grun.) Lange-B.
Fragilaria capucina var. *vaucheriae* (Kütz.) Lange-B.
Fragilaria construens var. *binodis* (Ehrenb.) Grun.
Fragilaria construens var. *construens* (Ehrenb.) Grun.
Fragilaria construens var. *subsalina* (Hust.) Hust.
Fragilaria construens var. *venter* (Ehrenb.) Hust.
Fragilaria elliptica Schum.
Fragilaria fasciculata (Ag.) Lange-B.
Fragilaria parasitica (W. Sm.) Grun.
Fragilaria pinnata Ehrenb.
Fragilaria ulna (Nitsch) Lange-B.
Fragilaria ulna var. *acus* (Kütz.) Lange-B.
Gomphonema aff. *clavatum* Ehrenb.
Gomphonema clavatum Ehrenb.
Gomphonema minutum (Ag.) Ag.
Gomphonema olivaceum (Hornemann) Bréb.
Gomphonema parvulum (Kütz.) Kütz.
Gyrosigma acuminatum (Kütz.) Rabenh.
Gyrosigma attenuatum (Kütz.) Rabenh.
Gyrosigma macrum (W. Smith) Griffith & Henfrey
Gyrosigma parkeri (Harrison) Elmore
Gyrosigma spenceri (W. Smith) Cleve
Melosira sp. 1
Melosira varians Ag.
Navicula aff. *lanceolata* (Ag.) Ehrenb.
Navicula capitata Ehrenb.
Navicula capitoradiata Germain
Navicula cryptotonella Lange-B.
Navicula exilis Kütz.
Navicula gregaria Donk.
Navicula lanceolata (Ag.) Ehrenb.

Navicula margalithii Lange-B.
Navicula menisculus Schum.
Navicula minima Grun. in van Heurck
Navicula pseudolanceolata Lange-B.
Navicula pupula Kütz.
Navicula submeniscula Manguin
Navicula tripunctata (O. Müll.) Bory
Navicula veneta Kütz.
Navicula viridula (Kütz.) Ehrenb.
Nitzschia acicularis (Kütz.) W. Smith
Nitzschia acula Hantzsch
Nitzschia aff. *agnita* Hantzsch
Nitzschia aff. *perminuta* (Grun.) M. Perag
Nitzschia aff. *sociabilis* Hust.
Nitzschia amphibia Grun.
Nitzschia capitellata Hust.
Nitzschia dissipata (Kütz.) Grun.
Nitzschia fonticola Grun.
Nitzschia frustulum (Kütz.) Grun. in Cleve & Grun.
Nitzschia gracilis Hantzsch
Nitzschia inconspicua Grun.
Nitzschia intermedia Hantzsch ex Cleve & Grun.
Nitzschia lacuum Lange- B.
Nitzschia liebetruthii Rabenh.
Nitzschia palea (Kütz.) W. Sm.
Nitzschia palea var. *tenuirostris* (Kütz.) W. Sm.
Nitzschia paleacea (Grun.) Grun.
Nitzschia recta Hantzsch ex Rabenh.
Nitzschia subacicularis Hust.
Nitzschia supralittorea Lange-B.
Nitzschia vermicularis (Kütz.) Hantzsch
Opephora olsenii Möller
Pelagodictyon fritzii Clarke
Pelagodictyon tenue Clarke
Pleurosigma salinarum (Grun.) Grun.
Rhoicosphenia abbreviata (Ag.) Lange-B.
Skeletonema potamos (Weber) Hasle
Stephanodiscus alpinus Hust.
Stephanodiscus binatus Håkansson & Kling

Stephanodiscus cf. *medius* Håkansson
Stephanodiscus hantzschii Grun.
Stephanodiscus parvus Stoermer & Håkansson
Stephanodiscus niagarae Ehrenb.
Stephanodiscus sp. 1
Surirella aff. *crumena* Bréb.
Surirella brebisonii Krammer & Lange-B.
Thalassiosira guillardii Hasle
Thalassiosira pseudonana (Hust.) Hasle & Heimdal
Thalassiosira weissflogii (Grun.) Fryxell & Hasle
Tryblionella hungarica (Grun.) D. G. Mann

APPENDIX TWO

The number of diatom valves counted in each sample from the the three study sites.

Site	Sample collection dates	Sample type	No. of diatoms counted
Tween Pond	24/2/93	plankton	325
	25/3/93		337
	28/4/93		383
	26/5/93		476
	22/6/93		479
	27/7/93		377
	25/8/93		805
	22/9/93		472
	20/10/93		358
Clifton Pond	24/2/93	plankton	698
	25/3/93		697
	28/4/93		442
	26/5/93		336
	22/6/93		318
	27/7/93		313
	25/8/93		318
	22/9/93		319
	20/10/93		314
	27/7/93	plankton tow	349
Groby Pool	31/1/95	plankton	276
	2/3/95		336
	29/3/95		311
	27/4/95		317
	31/5/95		315
	4/7/95		355
	2/8/95		305
	6/9/95		307
	20/10/95		405
Slate Brook	8/9/95	plankton	331

Site	Sample collection interval	Sample type	No. of diatoms counted
Tween Pond	3/2-24/2	trap I	662
	24/2-25/3	trap I	587
	25/3-28/4	trap I	641
	28/4-26/5	trap I	652
	26/5-22/6	trap I	549
	22/6-27/7	trap I	679
	27/7-25/8	trap I	623
	25/8-22/9	trap I	705
	22/9-20/10	trap I	559
	3/2-20/10	trap II	780
Clifton Pond	3/2-24/2	trap I	1947
	24/2-25/3	trap I	1151
	25/3-28/4	trap I	1452
	28/4-26/5	trap I	594
	26/5-22/6	trap I	557
	22/6-27/7	trap I	628
	27/7-25/8	trap I	627
	25/8-22/9	trap I	570
	22/9-20/10	trap I	500
	3/2-20/10	trap II	602
Groby Pool	31/1-2/3	trap I	602
	2/3-29/3	trap I	497
	29/3-27/4	trap I	494
	27/4-31/5	trap I	556
	31/5-4/7	trap I	625
	4/7-2/8	trap I	702
	2/8-6/9	trap I	576
	6/9-20/10	trap I	522
	31/1-20/10	trap II	601

Site	Core depth (cm)	No. of diatoms counted
Tween Pond TP193	2-4	571
	4-6	580
	6-8	625
	16-18	556
	20-22	620
	24-26	592
	28-30	577
	36-38	592
	42-44	782
	46-48	828
	50-52	760
	54-56	797
	58-60	598
	62-64	499
	64-66	698
	66-68	731
	68-70	523
	70-72	523
Clifton Pond CP193	0-2	530
	2-4	442
	4-6	506
	6-8	128

Site	Core depth (cm)	No. of diatoms counted
Groby Pool GR95B	0-1	517
	2-3	545
	4-5	536
	6-7	512
	8-9	514
	10-11	521
	12-13	502
	14-15	483
	16-17	503
	18-19	511
	20-21	481
	22-23	564
	24-25	594
	26-27	505
	28-29	500
	30-31	497
	32-33	554
	34-35	576
	36-37	533
	38-39	505
	40-41	515
	42-43	503
	44-45	277
	46-47	265
	48-49	426
	52-53	418
	56-57	483
	60-61	501
	64-65	533
	68-69	609
	72-73	542
	80-81	622
	88-89	617
	96-97	537
	103-104	522

Site	Sample / collection date	Sample code	No. of diatoms counted
Attenborough Ponds SSSI	Surface sediment (0-2 cm) 10/2/95	CL CH BE WO DU1 DU2 TW CO2	528 500 509 522 548 612 558 553
Groby Pool	Surface sediment (0-1 cm) 20/10/95	1 2 3 4	536 529 550 525

Site	Sample collection date	Sample type	No. of diatoms counted
Tween Pond	28/4/93 27/7/93	epilithic	252 251
Clifton Pond	28/4/93 27/7/93	epilithic	350 442
Groby Pool	29/3/95 6/9/95	epilithic	391 272

Site	Sample / collection date	Sample type	No. of diatoms counted
Clifton Pond	Epiphytic		
	28/6/93	*P. pectinatus*	251
	25/8/93	*P. pectinatus*	278
Groby Pool	Epiphytic		
	4/7/95	*P. pusillus*	283
	6/9/95	*C. demersum*	364
Groby Pool	Epiphytic		
	1867	*B. umbellatus*	155
	7/1883	*E. palustris*	284
	15/7/1897	*M. spicatum*	336
	6/1916	*R. truncata*	322
	14/7/1876	*M. spicatum*	390