REPRESENTATION OF DIATOM COMMUNITIES
BY FOSSIL ASSEMBLAGES IN LOCH FLEET,
GALLOWAY, SCOTLAND

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ABSTRACT

Fossil assemblages of diatom valves from lake sediments are used as a record of former diatom communities. Past water quality, for example pH, can be inferred from the composition of these assemblages. However, the relationship between mixtures of diatom valves in lake sediment and the diatom communities from which they are formed is not necessarily a direct one. In order to test the representative quality of fossil assemblages, valve assemblages in recent sediment have been compared with the contemporary diatom flora of a lake.

Loch Fleet, Galloway, Scotland was an acidified lake. Experimental liming of the lake catchment produced changes in water quality and a consistently higher pH has been maintained. The marked response of diatom species to changing water quality provided a means of tracing events from living communities to the fossil assemblage.

Diatom periphyton and plankton were sampled during a 20 month period and in addition archived material was available. These samples were compared with fossil diatom assemblages from sediment cores and from sediment traps taken during the same period.
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1. Rationale

The technique of diatom analysis has been given much attention recently as a means of reconstructing past lake-water pH (Battarbee 1984, Flower 1986). In the development of methods in this area efforts have generally focused on refinement of concepts of diatom taxonomy (eg. Camburn & Kingston 1986, Flower & Battarbee 1985) and the improvement of numerical procedures for the reconstruction of pH (eg. Stevenson et al. 1989, Birks et al. 1990). Few studies have been concerned with the taphonomy of the fossil diatom assemblage: the relationship between the assemblage and the living flora from which it was formed. In particular there have only been a few studies concerned with the representativity of fossil assemblages (DeNicola 1986, Jones & Flower 1986).

In palaeoecology the term "representativity" was first used by Faegri (1966). He identified three problems of representativity in pollen analysis. One of these was the question, "how well does the pollen flora of a sample represent the vegetation of the area around the site investigated?" Equivalent questions in diatom analysis are "how representative is the diatom flora of a fossil sample from lake sediment of the diatom flora of that lake?" and "how accurately are changes in lake flora reflected by changes in fossil assemblages?"

Loch Fleet is a convenient system in which to investigate these issues. Like many lakes in the UK that have recently acidified (Battarbee et al. 1988) Loch Fleet lies on granite at an exposed upland site. Diatom analysis has already shown that the loch has acidified (Anderson et al. 1986), and a project has been implemented at Loch Fleet to examine the effectiveness of catchment liming as a means of reversing acidification (Howells & Brown 1987). This short-term method of alleviating the symptoms of acidification has provided a means of observing the response of diatoms to changing pH on a feasible timescale. In addition the response and representativity of the sediment record can be tested on the same timescale by comparing marked changes in living communities with their reflection in the fossil record.
2. Taphonomy

The literature dealing with the imperfection or incompleteness of fossil records is large. At the evolutionary level it is recently exemplified by debates about the rate of evolutionary processes and effects of catastrophic environmental change on the stratigraphic record (Gould & Eldredge 1977). On a shorter timescale investigations of the mode of formation of the fossil record have dealt with more subtle differences between living communities of organisms and their representation in fossil assemblages. These studies have been of two general types: approaches using modern analogues where the characteristics of living communities are compared with the record of the corresponding death assemblage and investigations which use the evidence of the fossil assemblage itself, of the enclosing sediments and the history of formation. Taphonomy is a useful term to describe the study of the events that intervene between the death of organisms and the recovery of fossil remains, and the effects these events have on retrieval of information about the past (Shipman 1981).

The term "taphonomy," (Gr. taphos, burial; nomos, law), literally "the laws of burial", was introduced by Efremov (1940), who defined it as, "the study of the transition of animal remains from the biosphere to the lithosphere". Efremov recognised four potential problems in interpreting the fossil record of vertebrates; these problems resulted from the mode of formation of fossil assemblages. First, in older strata the state of preservation of fossils is often poorer and the numbers of individuals less, because the chances of destruction increase over time and in addition there may have been fluctuations in the sizes of the faunas sampled. Second, although a complex of terrestrial mammals found together in one place may be referred to as a "fauna", a term meant to imply that the animals were associated in life, such a complex may have come together accidentally. This mixing may have occurred at death or after death. Third, the sudden appearance in the fossil record of a new fauna without clearly identifiable ancestors in the preceding strata may or may not reflect a genuinely new group of species; its sudden appearance may be an artefact of preservation. Fourth, the likelihood of preservation of different body parts or species is so different in different sedimentary environments that complexes of species derived from a single community may be taken as different faunas because the original community has been sampled so differently. Though Efremov was concerned specifically with the vertebrate fossil record these general considerations are applicable to other groups of fossil organisms and on different timescales.
German palaeontologists working in the first three decades of the 20th century (see Behrensmeyer & Kidwell 1985, Gifford 1981) preceded Efremov in their studies of living and recently dead organisms as potential fossils, a subject given the name Aktuopalaontologie (Schäfer 1972). However, these early workers were concerned primarily with pre-burial processes and paid less attention to the effects of post-burial (diagenetic) change. It is significant that Efremov’s concept of taphonomy encompassed all the events that intervene between death and fossilisation of living organisms. The history and development of taphonomic studies has been reviewed by several authors and will not be discussed further here (see for example Behrensmeyer & Kidwell 1985, Gifford 1981, Olsen 1980).

At Loch Fleet the investigation of taphonomy uses the modern analogue approach (Shipman 1981). Living communities are seen as analogues of past communities and contemporary death assemblages as analogues for fossil assemblages.

3. The equivalence of death/fossil assemblages and living communities

Living communities of organisms can be considered to be made up of contemporaneous individuals that live within habitats having measurable physical limits (Staff et al. 1986). A critical problem in palaeoecological investigation is the extent to which a fossil assemblage represents and can be considered as a community.

In ecology communities of organisms may be described using characteristics such as taxonomic composition and diversity. The fossil assemblage derived from such a community or communities may be described in the same terms, but the limits of these similarities should be recognised (Macdonald 1976, Lawrence 1968).

Most of the organisms from the original community will not be preserved and therefore the fossil assemblage will consist of only a small fraction of the organisms from the living community. In addition the fossil assemblage may be composed of the preservable fractions from several distinct and different communities that may have existed in different environments. Consequently the meaning or usefulness of community characteristics is uncertain when applied to fossil assemblages.

The response of fossil assemblages to changes in the source communities is connected with this question of representation. When temporal variability occurs in living communities how well is this resolved by the fossil record? The ability to resolve the
changes is determined by the extent of "time-averaging", which is the mixing of individuals from non-contemporaneous communities (eg. Badgley 1982, Behrensmeyer 1983, Schindel 1980).

An example of the problem of equating ecological and palaeoecological communities is the use of measures of diversity. Ecological theory would suggest (Sanders 1968) that stability increases diversity. The effect of time-averaging, to produce the temporally mixed fossil assemblage, means that the opposite effect may be recorded by the fossil community. Changing, and probably less diverse living communities are mixed together in time to produce a fossil assemblage of increased diversity. As temporal variability in the living community increased or as the length of time averaged by the fossil assemblage increases the "palaeocommunity" and live community decrease in similarity. In using the modern analogue approach to test the representativity of death assemblages, assumptions about the equivalence of live community and potential fossil assemblage should not be carried too far. This consideration is particularly relevant in the Loch Fleet study, where the time span involved is short and rate of environmental change rapid.

4. Examples of the modern analogue approach to the study of taphonomy.

A common aim in many taphonomic investigations has been to derive accurate estimates of species relative abundances in palaeocommunities based on the composition of fossil assemblages. Vertebrate palaeontologists (eg. Shotwell 1955), environmental archaeologists (eg. Kenward 1982), marine palaeontologists (eg. Warme 1969), palaeobotanists (eg. Spicer & Wolfe 1987, Warner & Barnett 1986) and palynologists (eg. Davis 1963) have all attempted to develop methods for more rigorous numerical reconstructions of former communities. The approaches used in work on aquatic environments and on vegetational reconstruction through pollen analysis are probably of most relevance to diatoms in palaeolimnology.

Apart from the diatom work on taphonomy there has been little work on the taphonomy of aquatic organisms in recent lake sediments. However, a single detailed study of the representation of cladoceran communities in recent lake sediments has been published (Mueller 1964). Like diatoms, cladocerans live in both littoral and planktonic habitats. Mueller (1964) quantified the proportional contributions of these communities according to habitat area and volume respectively. He concluded that the relative contributions of
littoral and planktonic communities was in good agreement with the ratio of remains from these communities in the sediment assemblages.

The major assumption made in comparing living communities with death assemblages is that the death assemblage is equivalent to the fossil assemblage. For example in the case of diatoms preserved in lake sediments, the death assemblage would be the group of valves recovered from the surface sediment; these might be assumed to represent the contemporary, living flora. The fossil assemblage would be the equivalent assemblage after a period of "fossilization". Although the extent to which this occurs in recent lake sediment is questionable, the fossil assemblage will undergo additional alteration and loss of information. However, the initial processes involved in the formation of both the death assemblage and fossil assemblage should be similar.

Among aquatic organisms marine invertebrates have been best represented in comparisons of live communities with death assemblages. Communities of molluscs (e.g. Lawrence 1968, Warme 1969, Miller 1988), foraminiferans (Murray 1982, Smith 1987) and whole benthic communities (Stanton 1976, Staff et al. 1986) have been compared with corresponding death assemblages. The differences between whole benthic communities consisting of many taxonomic groups of varying degrees of preservability and the fossil assemblages dominated by organisms with hard shells or skeletons were particularly great both quantitatively and qualitatively (Stanton 1976). Studies of single taxonomic groups of persistent fossils, especially marine microfossils, have been less common (Kidwell & Behrensmeyer 1988). The analogies available from these fields of study are therefore limited.

Like palaeontologists, pollen analysts investigating Holocene sediments have used techniques for comparing live communities (vegetation) with death assemblages (surface pollen samples) as a means of interpreting fossil pollen spectra (see reviews in Birks & Birks 1980, Birks & Gordon 1985, Parsons & Prentice 1981). The reconstruction of past plant communities from the pollen record is particularly problematic due to factors such as differential production and differential transport of pollen amongst plant taxa, the possibility of significant long distance pollen inputs and the problem of defining the source area of pollen (see for example Oldfield 1970). However, palynologists have taken these techniques further in using the modern analogues directly to interpret fossil spectra rather than as estimators of the reliability of the pollen record.
Pollen analysts have developed two methods for reconstructing Late Quaternary vegetation from fossil pollen spectra by use of the modern pollen-vegetation relationship (Birks 1973). The first method involves the comparison of fossil pollen spectra with a range of modern, surface sediment pollen spectra from different vegetational regions in an attempt to find a modern analogue for the former vegetation. The actual comparison of pollen spectra may involve numerical methods, for example the use of dissimilarity coefficients (Overpeck et al. 1985), but the approach is essentially a qualitative one. The other method has involved applying pollen-vegetation conversion factors (eg. R-values), estimated from modern pollen spectra in conjunction with quantitative descriptions of the vegetation around the modern pollen sampling sites. The use of R-values in palynology has been comprehensively reviewed by Parsons & Prentice (1981). Most attempts at deriving R-values (eg. Anderson 1970, Davis 1963, Fagerlind 1952, Parsons et al. 1980, Tauber 1965) have relied upon the use of pollen accumulation rate data i.e. concentrations of pollen grains per unit time. More recently (Prentice & Parsons 1983, Webb et al. 1981) it has been realised that proportional pollen data may be more appropriate for the derivation of R-values.

In common these reconstructions of past vegetation have all assumed that a single dominant community, usually forest, produced the fossil pollen spectrum. Factors such as small local pollen inputs from patchy communities or long distance transport from different vegetation are reduced to error terms in the reconstructions (eg. Prentice & Parsons 1983). In contrast to this, the diatom community of a lake can be considered to be made up of discrete communities in several habitats, for example attached to rock surfaces (epilithon), macrophyte vegetation (epiphyton and epibryon), sand grains (epipsammon), and a planktonic community which completes its entire life cycle in the open water. In addition external inputs from catchment soils or from stream communities might be significant (Battarbee & Flower 1984). The fidelity of some taxa to particular communities allows them to be assigned, at least predominantly, to a single habitat, but most taxa may be components of more than one community. In the latter case any comparison of a taxon in the death assemblage with its proportions in more than one live community would require statistical procedures to separate the most likely proportional contributions from each. Though these procedures, based on the statistical theory of likelihood (Edwards 1972), have not previously been used in palaeoecology for this purpose the methods do exist (Campbell 1984, Day 1969, Everitt 1980, Ghose 1970, Holtzmann 1979, Marriot 1975). The existence of taxa with high fidelity for particular communities should provide a means of independently testing
community contributions derived for overlapping taxa if it is assumed that there is a constant proportionality between taxa from the same community.

5. Diatom taphonomy in lakes

i. Representativity studies

The fidelity with which sediment diatom assemblages represent the source communities from which they are derived involves a number of considerations (Battarbee 1986). These include:

1. the representation of diatom productivity by the concentration and accumulation rates of valves,

2. the representation of the composition of source communities in the composition of sediment assemblages,

3. spatial variability in the sediment record,

4. the temporal resolution of sediments.

The first question is one of numbers of valves; how many of the valves produced in the live community are preserved in the sediment, and therefore how well is past productivity reproduced in the fossil record? With the development of accurate techniques for estimating diatom concentrations in sediment (Battarbee & Kneen 1982) and as a result of radiometric time control (Appleby & Oldfield 1978) allowing more reliable estimation of diatom accumulation rate, it is possible to recognise trends in diatom productivity through time (Battarbee 1978).

However, the variability of the sediment record and losses due to breakage and dissolution make the absolute measurement of palaeo-productivity problematic. Anderson (1986) has shown that a single sediment core is not strictly representative of diatom accumulation rates for a whole basin. Diatom concentrations may be non-uniform in both space and time.

The second question is one of representation of community composition in the sediment record. The use of diatom compositional data in transfer functions to reconstruct past
environments eg. pH (Flower 1986) makes this aspect of representativity particularly important. It is usually assumed that the diatom flora of a lake is evenly represented in a death/fossil assemblage and that allochthonous inputs from the catchment or from reworked older sediment are negligible.

One method that has been used to test how faithfully fossil diatoms reproduce the composition of former lake communities is the comparison of old algal records with the stratigraphic record (Battarbee 1979, Battarbee 1981a, Flower 1986, Haworth 1979, Haworth 1980). Battarbee (1979) discussed the problems of this approach, stressing particularly the need for taxonomic consistency between fossil and archived material and the need to take into account the representative quality of the old algal samples themselves. Battarbee (1981a) found excellent agreement between old plankton samples and the sedimentary record over 60 years in Lake Växjösjön, Sweden, both in terms of species rank dominance and the temporal pattern of species composition. However, all these studies have dealt with lakes where the non-planktonic contribution to the sediment record of diatoms was considered to be low compared with the planktonic component. The descriptions of living communities were therefore based on the composition of a single community only, that of the plankton. Acidified lakes such as Loch Fleet provide the opportunity to investigate the representation of non-planktonic communities in the sediments since attached taxa are the dominant life-forms of these lakes.

A second approach to the question of diatom community representation has been to compare the composition of contemporary, live communities with the composition of surface sediment assemblages (DeNicola 1986, Jones & Flower 1986, Sweets 1983). Jones & Flower looked at seasonal and spatial variability in epipsammic and epilithic diatom communities, in an acidified lake in which planktonic diatoms were absent. A surface sediment sample was found to have very similar frequencies of some taxa to the mean frequencies of these taxa in epipsammon plus epilithon samples. However, some species were more common in these habitats than their representation in the sediment would suggest, and conversely other taxa were found almost exclusively in the surface sediment. It was suggested that the taxa poorly represented in the live communities compared with the surface sediment might be dominantly epipelic, a community that was not surveyed, or alternatively that the surface sediment contained diatoms no longer existing in the lake, implying reworking of older deposits. Overall the surface sediment was considered to provide a good record of the floristic
composition of non-planktonic diatom communities and this conclusion was reinforced quantitatively by ordination.

DeNicola (1986) used estimates of annual relative valve production for diatoms in planktonic, epipelic and epibryon communities to compare with the relative abundances in the surface sediment assemblages of two lakes. Using an iterative procedure numerical weightings were produced for each community to obtain best fit between the proportional contributions of the three communities and the resultant mixed fossil assemblage. The resulting community weights were presumed to indicate the degree to which the valve production of each community was represented in the surface sediment. It was concluded that in one lake, Loon Pond, the fossil assemblage was most similar to the planktonic community and that this community was over-represented. In the other lake, Crystal Pond, the fossil assemblage was found to be most similar to the epipelic diatom community. The reasons put forward for these between-lake differences were that Loon Pond had a higher plankton density, lower littoral area to lake volume ratio, shorter overturn periods (which would cause redeposition of benthic taxa), and a steeper sided basin that increased focusing of planktonic diatoms to deep water sediments.

The third question of diatom representativity is concerned with spatial variability in the fossil diatom record and the effect that the position of a sediment core has on the stratigraphy observed. For diatoms this problem has been investigated by Meriläinen (1969, 1971), Bradbury and Winter (1976), and most extensively by Anderson (1986). Meriläinen (1971) observed an uneven distribution of frustules in the sediments of four meromictic lakes. The sedimentation of diatoms was influenced mainly by the chemical and thermal stratification of the water and their preservation across the lake was also determined by a significant amount of silica dissolution. Bradbury and Winter (1976) examined variation in the diatom composition of surface sediments along a transect in Lake Sallie, Minnesota and showed that diatom valves were preferentially deposited in the area of their living habitats. Periphytic taxa characterised the sediments of the littoral whilst plankton dominated profundal sediments. Similarly Anderson (1986) found differences between littoral and profundal sediment profiles, mainly in planktonic representation. Again planktonic representation, measured by accumulation rates, was higher in deeper water sediments, but biostratigraphy across a lake basin was approximately similar. Where non-planktonic diatoms dominate the flora, as at Loch Fleet, it is unclear how their representation varies across the lake basin (Anderson, in press).
Fourth is the question of the temporal resolution of sediments; how well do sediment assemblages resolve the sequence of diatom assemblages deposited from live communities? Like the problem of representation of diatom community composition, it has been possible to compare dated algal records with the sediment sequence (Battarbee 1981a, Haworth 1980, Livingstone & Cambray 1978). In Rostherne Mere, Cheshire, (Livingstone & Cambray 1978) close agreement was found between the algal sequence in the sediment and algal records. This was used as means of testing the $^{137}$Cs dating method. Battarbee (1981a) also found a good agreement between the pattern of dominance of diatoms in old algal data and the biostratigraphic record of Växjösjön, thus reinforcing the results of $^{210}$Pb dating. Haworth (1980) confirmed that the sediment of Blelham Tarn retained the identity of successive phytoplankton populations despite potential disturbances. She suggested that the correlation was sufficient to produce an algal-based time scale.

Other investigators, utilising annually laminated lake sediments, have been able to resolve seasonal changes in diatom and chrysophyte populations (Battarbee 1981b, Simola 1977, 1979).

ii. Taphonomic processes

The processes leading to variability of the diatom record in sediments and the divergence between live communities and death assemblages include diatom dissolution and breakage, sediment bioturbation and mixing, and diatom/sediment transport.

a. Dissolution and breakage of diatom valves

Recognition of fossil diatom valves requires that at least part of their structure remains. If gross dissolution or breakage occur, differential preservation of individual taxa, or of whole assemblages may result.

In life the diatom frustule is prevented from dissolving. Maintenance of the silica is likely to be provided by some chemical process or processes whose nature is uncertain. The surface of the silica may be protected from dissolving by a coating of insoluble silicates formed by bonding with polyvalent cations eg. Mg, Fe, Al. Alternatively the coating may be organic; a membrane only a few molecules thick and attached by siloxane bonding (Cooper 1952, Lewin 1961). A system for active reabsorption of
silicic acid, able to compensate for the dissolution of silica is less likely, due to the relatively high energy demands this would create for a cell (Lewin 1961).

Lewin (1961) demonstrated that killing diatom cells leads to an increased rate of dissolution of their frustules and that the rate could be accelerated further by treatment with a chelating agent eg. EDTA. This suggests that maintenance of valve silica is an active process and that inorganic cations are involved.

On death the possibility of dissolution occurs both in water and in lake sediment. The likelihood of this is determined by several factors. These include the degree of silicification of the diatom valve, the physical and chemical conditions of lakewater, grazing by animals, and diagenetic processes in the sediment.

The degree of silicification of a valve will affect its chances of survival after death of the enclosed cell. Those individuals that are heavily silicified are less susceptible to dissolution than weakly silicified valves. This is due to the greater thickness of silica available for erosion and as a result of the lower surface to volume ratio available for reaction. Variation in robustness occurs within and between taxa (Jørgensen 1955, Kamatani & Riley 1979). There is variation in silica thickness within different parts of the same valve and some fine detail may be lost under dissolving conditions without completely destroying the valve. However, some types are invariably more robust than others and interspecific differences in thickness of silica can be as much as 2 orders of magnitude in marine diatoms (Jørgensen 1955).

If the physical and chemical conditions of lakewater promote dissolution then the period spent in the water will be related to the intensity of dissolution. Both in movement from the lifetime habitat to the sediment, and during possible phases of resuspension, valves are exposed to water conditions eg. extremes of pH, low concentrations of dissolved silica, and relatively high temperature, that are more likely to cause dissolution than conditions in the sediment. Hurd (1972) and Hurd & Birdwhistell (1983) describe equations for the quantitative relationships between these factors and the rate of silica dissolution. Therefore it may be important that those taxa of greatest density sink more quickly and may be removed from the open water more rapidly.

The transport of littoral or colonial taxa, which remain attached to a substrate or intact as a group of cells, will be determined by the mass of the whole rather than individual
cells or valves. Therefore sinking rates estimated for detached, isolated cells will not necessarily apply.

In both marine and freshwaters grazing by animals and subsequent egestion may determine sedimentation rates (Haberyan 1985, Schrader 1971). The faecal pellets of copepods have a membrane which can enclose several diatom valves. In saltwater Schrader (1971) found that these pellets sank considerably more rapidly than the individual valves contained within. In addition the membrane prevented exchange of water with the exterior. The selective grazing of animals, along with the faster rate of sedimentation and partition from the open water provided by the faecal membrane could all bias the preservation of those species grazed. In effect where significant dissolution in sedimentation occurs, the diatom record might reflect the feeding habits of invertebrates. It is likely that this would be important only in sedimentation in the deep ocean and in deep lakes where large depths are involved. Haberyan (1985) found no significant variation in the diatom composition of pelletised and non-pelletised fractions from Lake Tanganyika in Africa. Ferrante and Parker (1977) found that copepod grazing was unlikely to enhance fossilisation of species since faecal membranes were decomposed by bacteria in relatively shallow water.

Dissolution of silica in the sediment as well as losses in the water will cause a further reduction of diatom valves. Rapid burial will not necessarily lead to better preservation because the death assemblage remains in an aqueous environment, in contact with the interstitial water of the sediment. The most critical factor is likely to be the dissolved silica concentration of the pore water. Lower concentrations of dissolved silica in the pore water would lead to increased rates of valve dissolution in the sediment.

However, Hecky and Kilham (1973) found excellent preservation of fossil valves in lakes despite the low interstitial silica concentrations.

Diagenesis of diatom death assemblages may affect solubility of the valves. Crystallographic analyses of diatom deposits of varying geologic age revealed that valves from pre-Quaternary assemblages can have silica of crystalline form (Cooper 1952). Such fossilization of amorphous silica would affect its solubility. However, diagenetic changes were not found in diatoms of Holocene or Pleistocene age.

Johnson (1974) has suggested that hydraulic sorting of marine sediments may influence dissolution rates. He found that currents caused differential sorting of siliceous
microfossils from other particles. This resulted in an increased input of silica into deeper sediments (cf. sediment focusing). It is suggested that this additional input of silica might act as a buffer against solution so that deeper depositional sites would have better preserved fossil assemblages even where silica dissolution did not vary significantly with depth.

The importance of silica dissolution as a determinant of the diatom fossil record clearly varies from site to site. Certainly in undersaturated environments dissolution of biogenic silica in the water and in the sediment can approach the rate of accumulation, and therefore the sedimentary record is scant or absent (Parker & Edgington 1976). For example Nriago (1978) calculated silica budgets for Lakes Erie and Ontario and showed that the regeneration of biogenic silica from the sediment far exceeded the annual input from external sources or sedimentary silica of minerogenic origin. Only a small fraction of the diatom crop was 'fixed' in the sediment. In contrast, lakes of high alkalinity, with low concentrations of silicic acid in the sediment pore water, which would be predicted to be poor preservational environments (Bradbury 1973), may have little or no dissolution of valves (Hecky & Kilham 1973). It has been suggested that acid lakes might be expected to be poor preservational environments (Round 1964). However, the fossil records of such lakes shows that this rarely the case (Battarbee 1984).

Related to the problem of dissolution is that of breakage. The diatomist examining a fossil assemblage is able to deal with a certain level of frustule damage. Counting strategies are adopted which allow valve fragments to be enumerated and give estimates for minimum numbers of individuals (Battarbee 1986, Beyens & Denys 1982). Where breakage has resulted in many fine fragments, the fossil record of the most susceptible taxa may be partially lost or disappear completely.

Like dissolution, fragmentation of valves is more evident in lightly silicified species, especially those taxa that are of fine, narrow structure eg. *Fragilaria crotonensis* (Round 1964). The fracture of diatom valves also promotes dissolution, by making a larger surface available for reaction (Hurd 1972).

Causes of breakage are numerous (Beyens & Denys 1982). Damage is likely to be most intense in shallow water where turbulence is greatest. Abrasion or fragmentation will also occur in the sediment, especially when it is coarse-grained. Sediment compaction can also result in breakage. Should valves be exposed to air, corrosion can be enhanced
and may be related to the period of exposure (Beyens & Denys 1982). Selective grazing and subsequent breakage in the guts of herbivores could affect the survival of valves, though in many cases the organic part of the cell may be digested leaving the frustule intact (Cooper 1952, Schrader 1971). In acid waters dissolution is rare but breakage problems vary, probably due to mechanical damage in exposed shoreline environments. Finally, the treatment of diatom valves during sampling, storage, 'cleaning' and slide preparation will also determine the state of preservation.

b. Bioturbation

Bioturbation is the mixing of sediment due to the activities of benthic organisms. These processes will cause both vertical and lateral movement of sediment. In addition biological disturbance may affect dissolution rates of diatom valves through resuspension; mechanical damage eg. during ingestion; and indirectly, by increasing silica concentrations in pore water (Guinasso & Schink 1975).

The transport of sediment by bioturbation is due to a variety of processes. Organisms may ingest mud during feeding and egest it elsewhere, burrowing creatures will displace mud excavated from their tunnels, mud may slump into empty burrows, movement through the sediments will smear deposits and in general the locomotory and feeding activities of organisms will result in a loosening of sediment.

The organisms involved in causing bioturbation are diverse. Håkansson and Jansson (1983) have categorised 3 types of biological transport in sediments, based on the predominating direction of sediment movement. Firstly, processes which result in an overall upward movement of sediment which exceeds the downward component. This type of transport is exemplified by tubificid worms which feed at depth and defaecate on the sediment surface (Davis 1974, Fisher et al. 1980). Secondly processes of bioturbation at the sediment-water interface which cause upward and downward transport of approximately the same magnitude. The activities of the amphipod Pontoporeia are typical of this group (Robbins et al. 1979). The third category encompasses all processes not covered by the other two groups. For example chironomids, which presumably produce a net downward movement of sediment, bottom foraging fish causing sediment surface disturbance or bivalve molluscs displacing sediment along their paths of movement.
The magnitude of bioturbation has been estimated from the vertical migrations of radioisotopes in freshwater and marine sediments both experimentally and through consideration of the relative movements of isotopes in cores (Anderson et al. 1987, Benninger et al. 1979, Benninger & Krishnawami 1981, Fisher et al. 1980, Sickle et al. 1983). Guinasso and Schink (1979) showed that where biological mixing rates are slow compared with sediment accumulation rates bioturbation will cause little modification of stratigraphy. In contrast where mixing was intense and sedimentation slow the evidence of short term variations in radioisotope stratigraphy could be smoothed over the depth in which biological mixing occurred.

Fewer studies have examined the behaviour of microfossils under bioturbation. R.B. Davis (1967) recognised the problem of contamination of surface sediment by older pollen brought to the surface by burrowing metazoa. Davis (1974) demonstrated experimentally that a significant proportion of pollen in surface sediments could be transported from older deposits by the feeding of a tubificid worm, Limnodrilus. A small amount of sediment was transported from depths of up to 15cm. Differential sorting was also observed; the smallest grains were ingested and displaced at higher rates than larger grains. Under the same conditions diatom valves might be expected to behave in a similar way to pollen grains.

Berner (1980) has pointed out that the quantitative description of bioturbation is difficult because of the variety and complexity of the processes involved. Different benthic organisms have different mixing activities and are unevenly distributed within lakes in both space and time. It is important to recognise this when reconstructing environmental change using lake sediments, since the agents of bioturbation may change in parallel with the environment.

However, the results of palaeolimnological work using more than one group of fossils and with independent time control shows that in most cases bioturbation is not so severe as to completely obscure the stratigraphic record. At the other extreme, varved lakes may have algal records preserving seasonal changes (Simola 1981) or anaerobic mud can be more or less devoid of benthic fauna allowing fine resolution of events (Livingstone & Cambray 1978). Clearly the importance of bioturbation at any site will be determined by the suitability of the lake for benthic fauna and will include such factors as depth, trophic status and sediment type. In the sediments of acid lakes such as Loch Fleet evidence of organisms which cause bioturbation can be seen at the
Sediment surface, clearly visible in most lakes of this type are chironomid tubes, but as yet there is no quantitative evidence for their effects.

Sediment resuspension and focusing

The deposition of diatom valves over a lake bed is not necessarily uniform in composition or quantity (Anderson 1986). A hypothetical lake of even depth and with well mixed water should produce a fossil record of even composition and quantity across the bed. In reality these conditions are not satisfied, resulting in spatial variability in sediment deposits. Several processes are involved in determining the pattern of sediment deposition.

The shape of the lake basin will influence the position of sediment accumulation (Lehman 1975). The influence of lake morphometry is further complicated by evolution of the lake basin through time. This factor is particularly important in the interpretation of sediment sequences covering long periods. Accumulating sediment fills the lake basin and may result in a reduction in slope angles. Sediment may therefore accumulate in areas that were previously dominated by erosion. As a lake basin fills the area of sediment may also increase significantly; more recent sediment is spread over a larger area than older deposits. This effect could register a misleading decline in the accumulation rate measured at a single point, even though sediment inputs to the whole lake bed had remained constant (Davis & Ford 1982, Likens & Davis 1975), but this is not a significant factor for very recent studies such as this one.

In addition to the morphometry of the lake basin itself the surrounding topography and exposure of the site will be influential in controlling the distribution of sediment (eg. Pennington et al. 1972). Factors such as effective fetch and prevailing wind direction are particularly important at exposed upland sites such as Loch Fleet. These factors might also change through time, for example the removal of surrounding forest would increase exposure.

Resuspension of lake sediment is an important taphonomic process which is controlled by the pattern of water circulation (eg. Pennington 1974). Resuspension may be a seasonal phenomenon, being most intense at overturn when thermal stratification breaks down. However, in the littoral, which will be in the circulating epilimnion during stratification and where wave action is most intense, resuspension may continue throughout the year. Clearly, depth of water and exposure at any point in a lake can
determine the chances of resuspension occurring. There will be a reduction in turbulence with depth and therefore sediment will be most stable in the deepest water (Smith 1975). Tutin (1955) observed that following an autumn gale at Windermere there was a large increase in numbers of dead Asterionella cells in surface plankton and suggested that this was the result of currents resuspending sediment from shallower water. Davis (1968, 1973) showed that in a dimictic lake pollen grains were resuspended from lake mud during spring and autumn overturn. The overall effect of resuspension was found to be a reduction in the variability of pollen composition across the sediment, but that redeposition resulted in greater accumulation of sediment in deeper water.

Like processes of bioturbation resuspension will have a time-averaging effect by mixing the remains of non-contemporaneous communities. Depending on the depth of sediment that has been stirred up, this effect may be advantageous in smoothing out short term variations, or disadvantageous in decreasing the time resolution of the fossil record.

Basin morphometry and resuspension are both factors associated with the phenomenon known as "sediment focusing". This is the differential deposition that results in accumulation of greater amounts of sediment in the deeper parts of lake basins (Davis & Ford 1982, Lehman 1975, Likens & Davis 1975). Other factors that contribute to the focusing of sediment will include slumping of sediments on slopes which have exceeded a critical gradient to provide support and the composition (particle size, density and properties of friction) of the sediment itself. The centre of focusing will not necessarily remain stationary through time since the evolution of basin morphometry over time may result in a shift of the area of focusing (Davis & Ford 1982, Dearing 1983).

An important conclusion of the work on sediment focusing and resuspension is that the processes involved do not result in differential deposition of microfossil taxa (eg. Davis 1973). The mixing of sediment is assumed to result in an even mixing of the suspended fossils which may have been deposited initially in different areas of the sediment. Recently, however, Bennett (1986) has observed coherent slumping of post-glacial, laminated lake sediments. This form of sediment focusing resulted in overturning and replication of parts of the pollen sequence and, unlike previously described mechanisms, may be a source of error in the interpretation of fossil percentages as well as their accumulation rates. This distorting effect would be difficult to detect in non-laminated sediments.
Whatever the distorting effects of these processes; bioturbation, differential preservation, sediment resuspension and focusing, along with the direct transport of diatom valves from habitat to death assemblage are the means by which non-planktonic communities are "fossilised". It is the efficacy and relative importance of these processes that is the subject of this study.
CHAPTER 2: SITE DESCRIPTION

1. Location

Loch Fleet (National Grid Ref. NX560695) lies in the southern part of the Galloway Hills, in the region of Dumfries and Galloway, South West Scotland (Fig 2.1). The site lies at a height of 340m, remote from human settlement. New Galloway (National Grid Ref. NX 634776) is the nearest town, over 25km away by road, most of this forest track. The surrounding relief is upland, the summit of Cairnsmore of Fleet, 6km to the south-west, rising to 711m.

2. Bathymetry

A bathymetric survey was carried out by Murray and Pullar (1910) and more recently by Anderson and Battarbee (1985) (Fig 2.2). The Loch covers an area of 17 ha and has a catchment area of 128 ha. There is a single basin of maximum depth 16.8 m and the mean depth is 6.2 m. The lake bed is of steepest gradient to the north, elsewhere the slope is shallow. Lake volume is $1.051 \times 10^6$ m$^3$ and the turnover time is approximately half a year.

3. Streams

Loch Fleet has only two clearly defined inflow streams, one to the north, and the main inflow at the north east corner, the Altiwhat (Fig. 2.1). The latter is more clearly delineated, running through a distinct gulley resulting from a fault or shear zone in the granite bedrock (Edmunds et al. 1986). The outflow at the south end of the Loch is the source of the Little Water of Fleet.

4. Lake Chemistry

The lake was chosen by the CEGB as an acidified lake to be used for a catchment liming experiment (Howells 1986, Howells & Brown 1987, Howells 1989). A total of 445 tonnes of limestone was applied to the catchment, 362 tonnes in April 1986 and 83 tonnes in April 1987. The chemical data presented here is taken from Howells (1989).
Fig. 2.1: Loch Fleet; site location and map showing catchment sectors

- **Main inflow to Loch, Altiwhat**
- **Outflow from Loch**

Legend:
- Borehole
- Streams
- Watershed reasonably well defined
- Watershed less well defined
- Experimental embayment
- Coniferous plantation
Fig. 2.2: Loch Fleet; bathymetry and pre-liming core location
Table 2.1 shows annual mean chemistry (major ion concentrations), measured at the outflow, before and after liming. The response to liming for the key determinands pH, Ca and Al is shown in Fig. 2.3. Before liming the lake had a mean pH of 4.5 (April 1985-March 1986). Within 10 weeks the pH rose to 6.3, (reaching a mean value of 6.6 (April 1987-March 1988)) and in the same period the calcium concentration increased from 50-150 μeq l⁻¹. Total aluminium declined from almost 0.2 mg l⁻¹ to values typically between 0.1 to 0.15 mg l⁻¹, but the labile monomeric form of aluminium dropped from about 0.05-0.06 mg l⁻¹ to about 0.01 mg l⁻¹. The water quality resulting from liming was maintained throughout the period of diatom sampling, October 1986-April 1989.

5. Geology

Loch Fleet is on the Cairnsmore of Fleet intrusion, an oval-shaped pluton 17km long and 11km wide (Greig 1971). Outcrops are composed of two related granites both of Lower Old Red Sandstone Age. A central area of muscovite-biotite granite is encircled by an almost continuous margin of biotite granite (Gardiner and Reynolds 1932). The rocks surrounding the pluton are mainly greywackes of Silurian and Ordovician age. Loch Fleet is at the centre of the intrusion, lying on the muscovite-biotite granite.

The Cairnsmore of Fleet granites are coarse-grained and grey-coloured. The principal constituents of the central rocks being muscovite, biotite, quartz, and microcline, with oligoclase and orthoclase; hornblende is rare. Analyses of these rocks show 73% silica, a fairly high potassium content, with low calcium and magnesium.

Three boreholes were drilled in the Loch Fleet catchment to establish the ground water regime at the site (Edmunds et al. 1986). The second of these, BH2, located at the mouth of the Altiwhat gulley (Fig 2.1), indicated that there was a small contribution of relatively high pH, high alkalinity ground water to the Loch. Petrographic analysis revealed calcite and it was concluded that the high alkalinity results from reaction with this mineral. Although the ground water is not saturated with calcite and the volume of water contributed by this source, through baseflow and seepage, is small, (estimated in the range 2-4 l s⁻¹), the input is important in the elemental mass balance of the Loch, and may have been important in delaying the acidification of the loch (Anderson et al. 1986).
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<tr>
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<td>44.4</td>
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<td>Cl⁻ μeq l⁻¹</td>
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<tr>
<td>SO₄²⁻ μeq l⁻¹</td>
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<td>93.3</td>
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<tr>
<td>NO₃⁻ μeq l⁻¹</td>
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<tr>
<td>HCO₃⁻ μeq l⁻¹</td>
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<td>TOC mg l⁻¹</td>
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<td>8.7</td>
<td>4.8</td>
<td>4.8</td>
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</tbody>
</table>
Fig. 2.3: Response of key chemical determinands to liming (source Howells 1989)
6. Glacial Geology

Successive glaciations in the Galloway Hills probably followed a similar pattern of development. Snow and ice accumulating in the higher parts of the Southern Uplands formed valley glaciers which expanded to form local ice sheets. Flowing out from dispersal areas these coalesced to form a single large ice sheet (Greig 1971).

In Galloway the accumulation and dispersal areas for local ice sheets appear to have been the higher ground around the Merrick, Rhinns of Kells and Cairnsmore of Carsphairn (Jolly 1868). Ice radiated from this Loch Doon basin southwards to the Fleet Hills and the Solway Firth, northwards it was deflected by southward moving Highland ice.

The retreat of the most recent (Late-Devensian) ice sheet in Scotland was probably complete by 12500 BP. However, between about 11000-10000 BP a stadial period of colder climate occurred. During this stage, known as the Loch Lomond Readvance, glaciers built up on a much more restricted scale than during the full glacial stage (Cornish 1981, Gray & Lowe 1977). Moraines in the upper Fleet valley, of mainly unsorted and coarse-textured material, may be associated with this readvance and subsequent deglaciation (Bown & Heslop 1979). Horne (1870) observed moraine in the Loch Fleet catchment and southward trending glacial striae on the east shore of the Loch. More recently the occurrence of glacial till has been recorded and quantified in the catchment (Hudson et al. 1986). Over 13% of the area is classified as till; to the east it is common along the ridge and lodged between rock outcrops and to the south-west it forms a more continuous cover below widespread, thick peat.

7. Soils

Three soil types of the South-West Scotland regional classification (Bown & Heslop 1979) occur in the catchment of Loch Fleet. At the south end of the Loch, around the outflow, is an area of peat, but dominating the catchment are two soil types of a group known as the Dalbeattie Association. Most abundant are soils of the Loch Fleet complex, and on the higher ground, to the north and east of the Loch, are soils of the Garrary complex. Both of these soil complexes are characterised by shallow, peaty surface layers and have peaty gley, peaty ranker, or peaty podzol profiles. The Garrary complex, typical of higher ground, is distinguished from the Loch Fleet complex principally by the greater relative abundance of outcropping rock.
The soils of the Loch Fleet catchment have been described in detail by workers from the Macauley Institute Aberdeen (Hudson et al. 1986, Howells & Brown 1987). A summary of that work is given here. Soils originate from 3 parent materials: organic deposits, colluvium and weathered rock. The peaty ranker is the principal soil type, covering 39% of the catchment, whilst peaty gleys cover 24% of the area. Shallow peat covers 33% of the surface, the depth of accumulation only exceeds 0.5m in one third of these samples. Minerals are either absent or highly leached in surface horizons. The pH of the soil surface ranges from pH 2.5-4.6. Spatial variations in pH values are accounted for by the influences of land use, flushing and soil type. This effect is particularly marked in the afforested southern section of the catchment where all measured values were less than pH 2.9. The low percentage base saturation (mean <10%) and low content of exchangeable bases provide little neutralising capacity.

8. Climate

This description of the climate at the Loch is based on data from the Meteorological Office Climatological Memorandum for the region (Dight 1966) and Chapter 2 in Bown & Heslop (1979).

The general wind regime in the west of Scotland is dictated largely by the approach and passage of North Atlantic depressions. It is assumed that the distribution and strength of winds at Loch Fleet conform closely to recordings made at Lowther Hill (723m), 60km to the north east. Westerly winds predominate (57%), mostly in summer and autumn, whilst an easterly airstream is frequent in the winter. In spring winds from all directions are well represented. Wind speeds (measured in spring and autumn) are 6-11 m s\(^{-1}\) on 45% of occasions and winds in excess of 11 m s\(^{-1}\) occur for more than 25% of the time. In these seasons gales blow for 5.5-6% of the period, but in winter the gale frequency almost doubles reaching 9.5% and there is a corresponding increase in the duration of strong winds.

Precipitation (30 year mean) is 2135 mm a\(^{-1}\) with a mean pH of 4.8. Over 80% of this rainfall is likely to be of westerly origin (Smithson 1969). Snowfall may occur on over 60 days a\(^{-1}\) at the summit of Cairnsmore of Fleet.

Birse & Dry (1970) and Birse & Robertson (1970) in assessments of climatic conditions in Scotland have classified the highest ground in Galloway as 'cool' or 'cold' (550-
110 day °C accumulated temperature) with 'rather severe winters' (110-230 day °C accumulated frost). At Clatteringshaws (180m), 8km north of Loch Fleet, the range of mean daily temperatures (1966-79) was 0.2-17.5 °C (Boatman 1983). Loch Fleet lies 160m higher. Using an estimate for the reduction of daily mean temperature of -0.6 deg C per 100m (Dight 1966), the estimated temperature range at Loch Fleet is -0.8 °C -16.5 °C. The growing season, (defined as that period of the year during which the daily mean temperature is 5.6 °C or above), is likely to be about 200 days in the period mid-April to late October (estimate of Dight (1966) for an altitude of 366m).

9. Vegetation

A phytosociological classification of the semi-natural plant communities of Southern Scotland has been published (Birse 1980, Birse 1984, Birse & Robertson 1976). Complementary with the soil survey of the Loch Fleet catchment Macauley Institute have made a vegetation survey (Hudson et al. 1986) and have attempted to recognise the affinities of the Loch Fleet catchment communities with the vegetation associations described for Southern Scotland. This description of vegetation is summarised here along with the main characteristics of the communities. Nomenclature follows Clapham et al. (1981) for flowering plants and Watson (1968) for mosses and liverworts.

Loch Fleet catchment is dominated by Calluna vulgaris, occurring at 85% of sampling points, and Molinia caerulea, occupying 75% of sampling points respectively. However, 16 discrete but species-poor plant communities were recognised, comprised of 70 species in total. This low species richness and diversity reflects the acidic, impoverished nature of the habitats, together with former land-management practices such as burning and grazing.

Of the 16 plant communities 5 are abundant, comprising 90% of the vegetation. Most common, at 34% of sample sites is moist Atlantic heather moor. The dominant species of this sub-association is Calluna vulgaris and the differential species Scirpus caespitosum, Molinia caerulea and Erica tetralix. Dry Atlantic heather moor was recorded at 15% of the sites surveyed, confined to the steep slopes of mounds and gullies; clearly better drained habitats. Characteristic species are Carex binervis and Erica cinerea and the differential species is Nardus stricta. The community is most extensive on the steep upper slopes to the north of the Loch where it is grazed by deer.
Lowland blanket bog covers 15% of the catchment mainly on the lower slopes and especially under coniferous plantation to the south-west of the Loch. Upland blanket bog replaces this community on the high ground above the plantations and on the high peat plateau of subcatchment VII (see Fig. 2.1). *Empetrum nigrum* is characteristic of this community and differential species are *Vaccinium myrtillus*, and the mosses *Plagiothecium undulatum* and *Rhytidiadelphus loreus*.

Two flush communities occur, both dominated by dense tussocks of *Molinia caerulea*. These communities are flying bent grassland and flying bent bog. Flying bent grassland covers 18% of the area in the northern part of the catchment, but is absent from the southwest. Differential species are *Scirpus caespitosum* and the mosses *Sphagnum capillaceum* and *Aulacomium palustre*. Flying bent bog was recorded at 8% of sites spread throughout the catchment, but most common to the north and east. This community is differentiated by the presence of *Eriophorum vaginatum*.

In 1961 about 10% of the Loch Fleet catchment was planted with conifers. At present, plantations of *Picea sitchensis*, *Pinus contorta* and *Larix eurolepis* occupy areas to the south and west of the catchment (Fig 2.1). To the west mixed *Picea/Pinus* plantings are more mature so that the original ground vegetation is shaded out; a ground flora of mosses and a few higher plants remains. The peripheral plantings of *Larix* have an open canopy and the ground vegetation is little altered. This is also true in the younger *Picea/Pinus* stands, lying at the south, to the east of the outflow.

10. Pre-liming aquatic macrophytes

This description refers to the pre-liming aquatic macrophyte vegetation of Loch Fleet and is taken from the work of Raven (1985, 1986, 1988). Estimates of species area, and changes in the aquatic macrophyte flora associated with catchment liming, will be discussed elsewhere.

Raven (1986) surveyed the aquatic vegetation of Loch Fleet (1983-5) before the application of lime to the catchment. At the time of the surveys pH range was pH 4.5-4.6 and conductivity 47-60 μS cm⁻¹ at 18°C.

Loch Fleet has a species poor aquatic macrophyte flora typical of an upland, oligotrophic lake. Marsh plants found along the shoreline, such as *Juncus articulatus*, *J. acutiflorus* and *Ranunculus flammula*, were not considered to be truly aquatic.
Emergent vegetation was restricted to stands of *Carex rostrata* in two sheltered embayments on the west side of the Loch. Submergent macrophytes were more abundant in the littoral of the western shore where sand is more frequent than along the exposed eastern shore. No living macrophytes were sampled below 5m depth of water, but *Sphagnum* debris was found in deeper parts of the Loch.

A zonation of macrophyte species was found from shallow to deep water: *Littorella uniflora* - *Lobelia dortmanna* - *Isoetes lacustris/Sphagnum spp.* This zonation was best developed on the west side of the Loch, *Littorella* and *Lobelia* being almost exclusively confined to inshore, sandy substrates. A leafy liverwort (*Scapania undulata*) and filamentous algae (predominantly *Mougeotia spp.*) were also confined to shallow waters, the algae frequently coating the underwater portion of *Lobelia* stems. *Isoetes* was most abundant further offshore (1.5-2.0m water depth) particularly on the west side of the Loch. Although *Sphagnum* was often found growing with *Isoetes* it extended deeper than any other macrophyte and had the most widespread distribution.

Two species of *Sphagnum* were present in the Loch. *Sphagnum auriculatum* was dominant, occurring in all *Sphagnum* samples and prolific in the north-west embayment. *Sphagnum cuspidatum* was recorded in 25% of samples containing *Sphagnum*.

Other aquatic species found less frequently were *Juncus bulbosus* var. *fluitans*, *Utricularia vulgaris*, *Isoetes echinospora* and the moss *Fontinalis antipyretica*. The effect of liming on aquatic macrophytes in Loch Fleet has been investigated by Raven (1989). Changes in macrophyte species cover and dominance, in particular the reduction in *Sphagnum* area, are important as they provide a habitat for diatom epiphyton.

11. Palaeolimnology

The palaeolimnology of Loch Fleet has been described by Anderson *et al.* (1986). A summary of that work is given here.

i. Sediments and selection of coring site

Investigations of the stratigraphy and mapping of the sediment surface of Loch Fleet (Anderson & Battarbee 1985, Anderson *et al.* 1986, Battarbee *et al.* 1985) have shown that sediment distribution is complex in both space and time.
In order to locate a site containing a continuous post-glacial record of sediment accumulation, they mapped the areas and stratigraphy of sediment types. The distribution of sediment in the Loch Fleet basin was found to be highly asymmetric. The strategy of coring in the deepest water was found not to be appropriate at Loch Fleet because the deepest part of the lake was not the site of most rapid sediment accumulation. In addition, $^{210}\text{Pb}$ dating of a core LF L1 taken from the deepest part of the lake (Fig. 2.2) showed that a reliable chronology could not be established from this part of the lake (Battarbee et al. 1985). Radiocarbon dates are not available for this core, but pollen evidence suggests that one major hiatus occurred between about 9000-5000 BP, and another immediately before the onset of rapid catchment inwash associated with ploughing in 1961-3.

Dry weight and loss on ignition (LOI) data indicated that longer and possibly more continuous records of sediment accumulation could be found in relatively shallow areas in the north-east corner and in the sheltered north-west corner of the lake. Cores were taken from both these sites and a master core LF L3 (Fig. 2.2) was selected from the north-eastern area. The transition from organic post-glacial sediments to late-glacial clays occurred at 3.10m in the master core. The uppermost 1.3m of this core represents sediment that has rapidly accumulated since deep drainage of the catchment prior to afforestation in 1961. $^{210}\text{Pb}$ dating of the core (Anderson et al. 1986) showed that sediment accumulation rates reached over 10 cm a$^{-1}$ between 1968 and 1972 before declining to present (1985) levels, about 1.5 cm a$^{-1}$. More recently $^{14}\text{C}$ dates have also been obtained for this core, and show that there is a conformable Holocene sequence (Battarbee pers. comm.).

**ii. Vegetation and land-use history**

The Holocene pollen record from the core shows a typical sequence for South-West Scotland (cf. Birks 1972). Pre-Boreal and Boreal pine-birch forest were replaced by mixed deciduous woodland which was in turn replaced by moorland vegetation. Since about 5000 BP pollen spectra are dominated by *Calluna, Cyperaceae* and *Gramineae*. Most recently there has been an increase in coniferous pollen which is associated with the expansion of forestry in the locality and in the catchment (Anderson et al. 1986)
iii. Lithostratigraphy, diatom record and pH history

The stratigraphy of the uppermost 240cm of core LF L3 was analysed (Fig. 2.4, Fig. 2.5). It represents a time period of approximately 5000 years (Battarbee pers.comm.).

The base of LF L3 has low percentage LOI values (about 10%) representing the late-glacial period (Fig. 2.4). Values rise to about 20% at 312cm and between 310cm and 240cm values vary between 25-40%. LOI values decline to about 20% by 110cm. Above 110cm there is a rapid increase in LOI values to over 70% reflecting inwash of peat resulting from catchment ploughing, for forestry planting, in 1961-1963. LOI values in the uppermost section of the core vary between 60 and 90%, but there is a declining trend in percentages after a maximum at 60cm. This trend represents the stabilisation of catchment peat following tree canopy closure.

Three stratigraphic units were established from the LOI data. Unit A (above 110cm) with high (>40%) organic content, often preceded by mineral inwash indicated by low and fluctuating LOI values. Unit A corresponds to the post-ploughing phase. Unit B (110-312cm) is characterised by medium (15-40%) LOI values and corresponds to the pre-ploughing, post-glacial phase. Unit C (below 312cm) comprises grey clays of very low organic content (<10%) and corresponds to the late-glacial phase.

In order to provide a basis for the description of post-liming cores from Loch Fleet and for comparison of post-liming diatom assemblages with possible historical analogues, the established system of diatom biostratigraphic zones is copied here. Anderson’s original taxonomy has been modified to match recently agreed names, established during the Surface Water Acidification Project (SWAP) (Munro et al. 1990).

a. Diatom zones

6 diatom biostratigraphic zones were identified in the core LF L3 (Fig. 2.5).

LF L3-D1 (<208cm).

The main taxa in this zone are Cyclotella kuetzingiana, Fragilaria virescens var. exigua and Aulacoseira perglabra. Achnanthes minutissima declines initially, but recovers somewhat towards the end of the zone. Other important taxa are Brachysira vitrea, Brachysira brebissonii v.thermalis, Cymbella lunata and Frustulia rhomboides v.saxonica.
Fig. 2.4: Core LF L3; dry weight and loss on ignition
LF L3-D2 (208-196cm).
This zone is characterised by a very rapid expansion of the small planktonic diatom *Cyclotella comensis* and there is a small percentage increase in *Achnanthes minutissima*. *Cyclotella kuetzingiana* declines briefly but begins to recover by the end of the zone. The other main taxa are the same as for zone LF L3-D1.

LF L3-D3 (196-101cm).
In this zone *Cyclotella kuetzingiana* returns to maximum values, *Fragilaria virescens* var. *exigua* has high, but variable, percentages, while *Achnanthes minutissima* reaches a peak in mid-zone and thereafter remains relatively constant to the upper zone boundary. *Brachysira vitrea* has consistent values of around 8% throughout the zone, but *Aulacoseira perglabra* declines steadily. *Navicula cocconeiformis*, *Eunotia incisa*, and *Eunotia pectinalis* v.minor are present at significant, but low percentages. *Frustulia rhomboides* v.saxonica and *Cymbella lunata* remain constant.

LF L3-D4 (101-20.5cm).
*Cyclotella kuetzingiana* declines abruptly to less than 1% of the total and there are corresponding increases in *Brachysira vitrea* and *Tabellaria flocculosa*, while *Achnanthes minutissima* declines steadily. *Fragilaria virescens* var. *exigua* has lower values throughout and *Eunotia incisa* begins to increase towards the end of the zone. *Eunotia pectinalis* var. *minor* increases and *Navicula bryophila* reaches maximum values.

LF L3-D5 (20.5-4.5cm).
The increase of *Eunotia incisa* to maximum values corresponds to a rapid decline in *Brachysira vitrea* and *Achnanthes minutissima*. Other taxa which increase in this zone are *Cymbella perpusilla*, *Navicula subtilissima* and *Eunotia naegelii*. *Tabellaria quadriseptata* becomes important for the first time.

LF L3-D6 (4.5-0cm).
The uppermost zone is characterised by a small decrease in *Eunotia incisa*, an increase to a maximum of *Tabellaria quadriseptata* and a small but significant increase in *Tabellaria binalis*. 
b. Summary of diatom changes

The early sediments are typical of pre-acidification Galloway lakes with the planktonic species *Cyclotella kuetzingiana* well represented. The pH reconstruction gives a value of pH 6.0. Except for a peak of *Cyclotella comensis* (200-208cm), the causes of which are discussed by Anderson *et al.* (1986), the flora remains stable until afforestation in 1963 (100-110cm). At Loch Fleet there is no tendency towards acidification in the late 19th or early 20th century despite the increased acid loadings likely to have begun at this time. In this respect Loch Fleet is unusual amongst the Galloway lakes lying on granitic rocks. It is implied that there must be one or a number of sources of alkalinity in the Loch Fleet catchment which do not occur or are unimportant at other sites in the region. This is supported by the findings of Edmunds *et al.* (1986).

Following afforestation of the catchment there is an almost complete disappearance of the diatom plankton. This effect may be the result of a loss of habitat caused by inwashed sediment increasing the turbidity of the water and decreasing light penetration. Despite the change in the diatom flora the reconstructed pH drops only slightly; this pH change may be real or may be an artefact of the loss of the planktonic habitat for diatoms. Attached, circumneutral taxa such as *Brachysira vitrea* and *Achnanthes minutissima* are not significantly affected by the sediment inwash.

Sudden and acute acidification is recorded at 0-25cm in the main core, $^{210}$Pb dating places the base of this event at about 1975-6. During this time reconstructed pH falls from pH 5.6 to pH 4.6. The diatom sequence is typical of that seen in other Galloway lakes over much longer periods. *Brachysira vitrea* and *Achnanthes minutissima* decline and *Eunotia incisa* increases. Ultimately, as the lake loses its alkalinity, acidobiontic taxa, notably *Tabellaria quadriseptata* and *Tabellaria binalis*, become dominant (Fig. 2.5). The short cores taken in this study cover the upper (post-afforestation) part of this record.

During the period of this study site characteristics have remained largely unchanged except for the addition of lime to the catchment and the construction of embayments associated with the liming experiments. Embayment construction, invertebrate sampling and other scientific work associated with the Loch Fleet project have caused some localised disruption, but did not affect the sampling strategy of this project. It is therefore assumed that the major species changes that have occurred since 1986 are due entirely to the liming experiments.
CHAPTER 3: METHODS

1. Introduction

The study required following the response of live diatom communities in the lake to liming and assessing their representation in deep-water sediments. Living communities, sediment traps and lake sediment cores were therefore used. This project, however, began in October 1986 shortly after liming (April 1986). Evidence for pre-liming conditions therefore depends on: archived algal samples dating from 1981 onwards held on the DISCO diatom database at the Palaeoecology Research Unit, previous sediment core data (see Chapter 2), and the pre-liming characteristics monitored as part of the CEGB study (Howells 1986).

2. Field methods

i. Live communities

Diatom samples were collected from all the important habitats in the loch. The development of a sampling strategy and sample replication is described in Chapter 4, however the methods used for each habitat are outlined below. All samples were preserved with Lugols Iodine on the day of collection.

(a) Surfaces of rocks (epilithon) - initially (October 1986) epilithon samples were collected by removing stones, visibly uncontaminated by sediment, from c.40-50cm water depth in the littoral. Algal growth on the stone surface was removed from the whole of the upper surface using a toothbrush and by washing with distilled water. The sample was collected in a wide diameter plastic tray and poured into a perspex sample tube. During 1987 and 1988 a diatometer (Flower 1985) was used to remove in situ epilithon samples from submerged bedrock in the chosen sampling locations, sites F and J (see Fig. 4.2).

(b) Surface of sand (epipsammon) - sand cores of c. 1cm depth and area c. 5cm² were removed from c. 40-50cm water in the littoral. The core was retained in the tube by stopping the top with a bung and the sample then deposited in a sample bottle. The 'true' epipsammic flora (see Round 1965) was separated by addition of distilled water, the sample was then agitated and sand grains allowed to settle for a few seconds, the water was then decanted off (and initially retained). This procedure was repeated at
least 3 times or until the water became relatively clear. The washed sand grains remaining constituted the sample, and diatoms were removed from the surfaces using standard techniques (Battarbee 1986). Pooled replicates of this kind were used during 1987 and 1988. At the beginning of the project both fresh and cleaned material subsampled from the decanted water was examined. This revealed a low concentration of diatoms with a very high proportion of 'dead' cells. Epipellic species were not seen and it was concluded that the washings contained a very high proportion of species sedimenting from other communities. In succeeding samples only the 'true' epipsammon was retained.

(c) Surface of macrophytes (epiphyton, epibryon) - where possible whole plants were removed by hand from c.40-50 cm water depth in the littoral. The use of entire plants was adopted to avoid problems of within plant variability in diatom composition and density of growth. The roots of vascular plants were removed to prevent sediment contamination. Bryophyte samples consisted of several leafy stems. All plant samples were placed in perspex tubes or polythene bags, immersed in distilled water, and preserved with Lugols iodine.

The epiphytic habitat was initially subdivided into separate groups according to substrate species. However, following a study of the variability of species composition between macrophyte species (see Chapter 4) sampling was reduced to 2 groups of macrophyte habitat each having diatom communities of similar composition. These communities were the epiphyton, the diatom community attached to higher plants including the isoetids and the aquatic rush Juncus bulbosus var. fluitans, and the epibryon, the diatom community associated with bryophytes most commonly a leafy liverwort Scapania undulata.

(d) Mud surface (epipelon) - the epipelon was not routinely sampled. The epipellic habitat in Loch Fleet was estimated to be small, since only a limited area of exposed mud was present in the photic zone of the lake. Where mud accumulation in the littoral occurred, for example on the western shore of the Loch macrophyte growth was dense. Following liming a dense summer growth of the green alga Mougoetta occupied these areas.

Attempts were made to recover samples of the 'true', motile epipellic diatom flora from both fine grained sediments (mud, obtained from Kajak cores and Ekman grabs) and from coarse grained sediment (sand) using the lens tissue trapping technique of Eaton
& Moss (1966). These efforts were unsuccessful on all occasions. Examination of the diatom catch revealed mostly empty valves and frustules of species which had presumably settled out on these surfaces, and cells with chloroplasts present but not epipelic eg. *Tabellaria flocculosa*. Known epipelic taxa such as *Surirella* and surface sediment diatoms such as *Aulacoseira* were completely absent. It was therefore decided to eliminate the epipelic community from the sampling program.

(e) Open water (plankton) - plankton sampling followed standard techniques eg. Lund *et al.* (1958): 2 l of lake water was collected from the surface water above the deepest point of the lake and Lugols Iodine was added immediately.

Plankton sampling was not replicated since planktonic diatoms were initially absent from the lake. However, Loch Fleet is relatively small and constantly exposed to strong winds so it was assumed that the surface water would be well mixed.

**ii. Sediment traps.**

Simple cylindrical sediment traps were used suspended at various depths in the water and attached to a rope anchored on the lake bed and supported by a float. The design of traps followed the suggestions of Bloesh & Burns (1980) and Blomqvist & Håkanson (1981) but was modified to suit the lake conditions. A further discussion of trap array and location is made in Chapter six, construction details are given below.

Following unsuccessful attempts to establish a moveable array of sediment traps on a fixed anchor rope a simple design of trap line was used. This arrangement was of pairs of collecting cylinders held at each sampling depth and permanently attached to an anchored line. Retrieval of the collecting cylinders therefore required removal of the whole trap array.

Two types of sediment trap array were used.

1. Four lines each consisting 2 pairs of traps placed in 7.5m depth of water at the periphery of the profundal zone.

2. A single line of sediment traps, consisting 4 pairs of cylinders at 3m depth intervals along an anchored rope and placed near to the deepest point of the lake, (17m water depth).
The collecting cylinders were constructed from PVC grey drainpipe, internal diameter c. 5.0cm cut to 25cm lengths to give 5:1 aspect ratio. Cylinder bases were made from a PVC sheet cut into circular sections and bonded to the pipe with suitable PVC adhesive, 24 plain cylindrical sediment traps were constructed in this way.

Trap holders were constructed from c. 6.4cm internal diameter PVC black drainpipe cut to 10cm sections and bonded to circular PVC bases. The collecting cylinders were secured in these holders by increasing the external diameter of the basal 10cm of each using rubber cut from pneumatic tyre inner tubing and held in place by insulating tape. In this way the collecting cylinders were held firmly, but could be removed easily when sampling.

Pairs of sediment trap holders were attached to 16cm square, 5cm thickness wood blocks by drainpipe clips screwed to the wood. A hole drilled centrally in each block allowed the holder to be threaded onto the anchor rope. Each pair of traps in their holders were held at the required distance along the rope by ‘jubilee’ clips secured on the anchor rope above and below the wooden block.

### iii. Cores.

Short cores were taken from various locations, but the primary site was close to LFL3 the site of most rapid accumulation (Anderson *et al.* 1986). The corer used was a Kajak sampler (Kajak 1966, or see Håkanson and Jansen 1986) and cores were extruded at the site to avoid disturbing the sediment surface in transit. Longer cores were also taken during the study using a Mackereth mini-corer (Mackereth 1969), but these were not analysed. In addition attempts were made in April 1989 to recover surface sediments using a freezer corer (Meriläinen & Huttunen 1978). However, analysis of the uppermost levels, sliced at fine (mm) intervals revealed that the sequences of all 3 cores had been truncated.

### 3. Laboratory methods

#### i. Water chemistry, physical limnology

In addition to the physical and chemical data available from the Loch Fleet Project, analysis of further chemical parameters and physical conditions was carried out. This
was for the purpose of familiarising the author with lake characteristics and for possible comparison with biotic data at a later time. These data are not presented here since more detailed physical and chemical data has been published for the site (Howells 1989). However, the parameters measured and methods used are described briefly.

Soluble reactive phosphorus (SRP), dissolved silica, nitrate and total dissolved solids analyses were performed on samples taken from the lake outflow and Altiwhat inflow. These sites were sampled at 2-4 weekly intervals from April 1987 to December 1988. Nitrate analyses were performed using a colorimetric method, all measurements made using an 'autoanalyser' at Solway River Purification Board (SRPB), Dumfries. From April 1987 to April 1988 SRP and dissolved silica analyses were carried out by hand at SRPB on the day of sampling. Standard colorimetric techniques were used (Golterman & Clymo 1969). The dry weight of total dissolved solids was determined by filtration and drying to constant weight in an oven at 100°C. From April 1988 to December 1988 the three chemical parameters were analysed at monthly intervals by colorimetric measurements using an autoanalyser at SRPB. Measurement of total dissolved solids was also continued.

The variation of dissolved oxygen, temperature, conductivity and pH with water depth were monitored at the deepest point (17 m) of the lake at approximately fortnightly intervals during the period April 1987 to April 1988 and at approximately monthly intervals during the period April 1988 to December 1989.

Dissolved oxygen and temperature measurements were made using a combined oxygen/temperature probe suspended from a boat and attached to a 'YSI Model 57 Dissolved Oxygen Meter'. Water samples for pH and conductivity analyses were recovered by a narrow bore plastic tube connected to an electrically powered pump. Samples were collected in acid washed bottles and pH and conductivity determinations made on the day of collection. pH was measured using a twin electrode device, an 'Orion Research model 407A specific ion meter', the device was standardised using a 2 buffer calibration and conductivity was measured using a 'pHOX Series 52' portable conductivity meter.

ii. Wet density, dry weight and loss on ignition determinations

Wet densities were measured by filling a 2cm³ weighed brass vial with a subsample of homogenised sediment. This was done soon after core extrusion to avoid drying.
Dry weights were determined by placing 1-2g of wet sediment in a weighed crucible and drying overnight to constant weight at 105°C. Loss on ignition was measured after placing the crucible in a muffle furnace at 550°C for 2 hours. Crucibles were cooled in a desiccator before reweighing.

iii. Preparation of samples for diatom analysis

Cleaned diatom samples were prepared by oxidation in hydrogen peroxide (30% H₂O₂) and valves were mounted in Naphrax or Mikrops; methods follow Battarbee (1986). Diatom cell concentrations were estimated by adding a known number of microspheres to a known weight of dried sediment (Battarbee & Kneen 1982).

Uncleaned diatom samples were prepared by mounting wet samples in distilled water under a large coverslip. Where sediment samples were too concentrated cells were disaggregated by gentle agitation of the sample in a test tube and by dilution with distilled water.

iv. Diatom identification and counting

Cleaned diatoms were identified and counted under oil immersion at a magnification of x750, x1000 or x1250 under phase contrast using a Leitz (SM-Lux or Ortholux) or Wild (M20EB) microscope. Plankton samples were examined using a Leitz (‘Diavert’) inverted microscope.

Initially for periphyton samples 500 valves per sample were counted, but this was reduced to 200-250 valves per sample where diversity was low (see below). A total of 400 to 500 valves per sample was counted from slides prepared from sediment traps. In sediment core samples approximately 500 valves per sample were counted. However, in the lower levels of cores, where the species composition was required only for stratigraphic matching, a count of 250 valves was considered to be adequate.

In studies of sediments from acid lakes in Galloway it has been usual to count 500-600 diatom valves per slide in order to have a sufficient sample size to represent species composition for pH reconstruction. Initially this strategy was continued when examining periphyton samples. However, the species richness and diversity of the living communities is clearly not so great as that of the mixture of valves occurring in the sediment and counting to such a high sum of valves is unnecessarily time consuming.
In addition a much larger number of periphyton samples were involved than from sediment studies; it was considered better to replicate samples to gain a picture of overall lake variability than to attempt to record the composition of individual samples 'over accurately'.

A sample from the most diverse of the periphyton communities, the epilithon, was chosen from an area where contamination by valves from other habitats was least likely (sampling area L, see Fig. 4.2), an area where sediment was not accumulating in shallow water. In a count of 610 valves 27 diatom taxa were recorded. A plot of cumulative number of diatom taxa recorded against total number of diatom valves (Fig. 3.1) counted shows a distribution comparable with that in many ecological quadrat size vs. number of species observed type studies. Initially the number of new taxa rises steeply as more valves are counted (increasing area of coverslip traversed). The gradient of the graph then decreases and fewer new taxa are observed as the sum of valves counted increases. The return of new taxa for increased counting effort is diminished to a point where it becomes unproductive to continue increasing the number of diatom valves counted. Although it is possible to predict sample size for a required degree of accuracy (see for example Heck et al. 1975), in this study it was considered adequate to determine the cut off point by observation of the asymptote of the graph. At a sum of c.200-250 valves there is a decreasing gradient indicating a reasonable cut off point for counting.

The results of this epilithon counting exercise were extrapolated to other, less diverse periphyton communities, where counting to a sum of 200-250 valves was considered to be more than adequate.

In the case of the phytoplankton samples, the 2 l of water was settled in a large measuring cylinder, the supernatant removed, and the concentrated volume was quantitatively subsampled and placed in the settling/counting chamber of the inverted microscope. Cell counting followed standard techniques (Lund et al. 1958, Wetzel & Likens 1979).

Fig. 3.1: Cumulative number of diatom species vs. valves counted
4. Data analysis and presentation

The project involved the analysis of multivariate data from a large number of samples. Raw data were entered onto the University College London, Dept. of Geography mainframe computer (VAX VMS 11/750) using RB programmes and later in the project using DISCO database programmes. Data were manipulated using a combination of programmes and packages on both the VAX mainframe computer and on IBM PC compatible. These packages included PARADOX (Borland International, 1988) a relational database for PC, BRIEF (UnderWare Inc. 1984) a data editing package for PC, and a mainframe computer version of MINITAB (Ryan et al., 1976) a package for statistical analysis of data. Multivariate analysis of data (DCA) was carried out using the programmes CANOCO (Ter Braak, 1987) and TWINSPAN (Hill, 1979). Diagrams were produced using the MAPICS computer graphics package (MAPICS, 1987).
1. Introduction

The purpose of the study, to examine the representation of living diatom communities by fossil diatom assemblages, required that living diatom communities were described. It was necessary to characterise the live flora, its composition and species' relative abundances for comparison with the core record. However, problems such as habitat variability, variability of composition within habitats and the unknown relative productivity of species and communities were recognised in making these characterisations. It was also necessary to devise a sampling strategy, for each habitat based on this information, to follow diatom changes through time caused by liming. (see Chapter 5).

2. Diatom habitats and diatom productivity in Loch Fleet.

Before beginning a more intensive sampling programme for living diatoms at Loch Fleet it was necessary to determine the relative importance of the habitats available for diatom growth in the Loch. For this purpose the results of a survey of surface sediment types (Anderson and Battarbee 1985) and aquatic vegetation surveys (Raven 1985, 1986) were used. Because the structure of the aquatic macrophyte community has been affected by liming (Raven 1989) consideration was also given to the relative importance of these changes.

i. Photic depth

The attenuation by lakewater of light wavelengths active in photosynthesis restricts the maximum depth to which diatoms and macrophytes can grow. The depth at which 1% of the most penetrative waveband remains is conventionally used to approximate the compensation depth for algal photosynthesis (Moss 1980). This depth is estimated at Loch Fleet by using Secchi disc measurements before (2.7m) and after (2.0) liming in 1988 (Raven 1989). In general Secchi disc depth corresponds to the depth of approximately 10% of surface light and the relationship:

\[ n \, m^{-1} = 1.7/z_{ad}, \]
where \( n \) is the extinction coefficient and \( z_{sd} \) is the Secchi disc transparency in metres, has been shown to be a good approximation for a variety of inland waters (Idso and Gilbert 1974). The percentages (intensity) of surface light remaining at successive depths show an exponential distribution and can be described by the equation:

\[
I = I_0 e^{-nz}
\]

where \( I \) is the light intensity at a depth \( z \) and \( I_0 \) is the light intensity at the surface (Wetzel 1975). By substitution, the depth at which light intensity is reduced to 1% of that at the surface is:

\[
z_{ou} = \frac{4.6}{n}
\]

where \( z_{ou} \) is the depth of the euphotic zone. Substituting the Loch Fleet Secchi disc estimates for \( n \) in this equation gives approximate compensation depths of 7.3m before liming and 5.4m following liming. These estimates are very approximate since they are point estimates which take no account of short-term variability or of the relative conditions during Secchi disc measurements and their effects, for example, the surface scattering of light by waves and the effect of weather conditions on the observations. Further, only specific parts of the visible light spectrum are used by plants and this will vary with the (algal) photopigments involved. Strictly it is inappropriate to consider all visible light as photosynthetically active.

Despite the pitfalls of such estimates they are useful at the scale involved here. It is apparent that before acidification the water transparency was greater than in the period after liming. Increased transparency associated with acidification has been inferred elsewhere (eg. Davis et al 1985). The reduction in Secchi depth and inferred reduction in photic depth has been discussed by Raven (1989) and is in part associated with shading by filamentous green algae.

From these estimates of photic depth, by examination of fresh, epiphytic diatom material for live cells and from observations of the zonation of living macrophytes, which were restricted to water less than 5m deep (both pre and post-liming) (Raven 1989), it was clear that the euphotic zone did not extend below about 5-6m.
ii. Substrates

Anderson and Battarbee (1985) present a map of Loch Fleet surface sediments (Fig. 4.1), this has been used as a basis for a qualitative assessment of surface types. The photic zone is taken as the area of the lake above the 5m contour. The map shows the periphery of Loch Fleet dominated by sand, silts and gravels with localised rocks and patches of clay. A large area dominated by solid rock lies within the photic zone at the south-east corner of the lake and only a small area of mud lies within the photic zone. However, this large scale mapping of surface sediments was performed from a boat and was therefore restricted to water depths of greater than 1m. This necessarily led to under-estimation of the dominance of rock surfaces and to the amalgamation of discrete surface types into a single category.

From repeated sampling in the littoral zone distinct areas of particular surface types were recognised, at least in the shallower water (to 2m maximum depth). Firstly rock surfaces are most abundant, occurring in 2 forms. Exposed bedrock (slabs) cover approximately 3/4 of the eastern side of the lake, including the bay to the south-east, and extend across to the east in the relatively shallow water above the outflow. This surface type is also dominant along most of the shore running south-west to north-east. A second type of rock surface are isolated boulders and stones. These are very abundant around the entire littoral of the lake overlying other surfaces and are particularly dense in the two bays in the middle of the shore running south-east to north-west and in the northern-most quarter of the eastern shore. Other than a few very small accumulations sand is restricted to 2 sites within the lake, the bay at the south-west corner and another smaller area at the north end. Coarser gravels occur locally where streams enter the lake, notably in the north-east corner. Silts and gravels, common on the western and upper part of the eastern shore are densely colonised by macrophytes therefore restricting the mineral and sediment surfaces themselves as potential diatom habitats.

Aquatic macrophytes are most abundant along the western side of the lake and in the upper part of the eastern shore where silts and gravels provide suitable substrates. Aquatic liverworts, most commonly Scapania undulata, are attached to rock surfaces and are therefore most common on the large areas of rock. However, bryophyte growth is sparse on the rock surfaces and nowhere becomes dominant over the 'exposed' rock surface itself.
Fig. 4.1: Loch Fleet surface sediments
(source Anderson & Battarbee 1985)

Loch Fleet Surface Sediment

- Organic sediment
- 10-30% loss-on-ignition
- >30% loss-on-ignition
- Late-glacial silts/clays at surface; localised rocks
- Solid rock with localised patches of silts & gravels
- Sand/silts & gravels with localised rocks; patches of clays

100 metres
Raven (1989) has assessed the percentage occurrence of macrophyte species taken by random Ekman grab sampling above 5m before and after liming (Table 4.1).

*Sphagnum auriculatum* was the dominant macrophyte during the pre-liming period, occurring in over 50% of Ekman grab samples. This moss was particularly abundant in water 2-5m deep off the sheltered western shore. However, *Isoetes lacustris* was also abundant and was present in 35% of samples before liming (1985). *Lobelia dortmanna* was present in 19% of samples and *Littorella uniflora* in 8% of samples. Raven describes a distinct *Littorella - Lobelia - Isoetes - Sphagnum* depth zonation of these species.

Following liming *Lobelia* remained the most frequently recorded macrophyte in shallow water (<1m). This plant showed little change in percentage occurrence and was recorded in over 10% of samples during the post-liming period. The distribution of *Isoetes lacustris* in water 1 - 3m deep was similar before and after liming and percentage occurrence of the species remained similar following liming (38% in September 1988). However, Raven calculated an approximate relative abundance index, taking account of species abundance in grab samples as well as simple presence and absence attributes. According to this index the abundance of *Isoetes lacustris* had increased by about 50% by 1988. The most significant change in macrophyte abundance was that of *Sphagnum auriculatum*. The occurrence of this species declined from 54% before liming to 8% both 18 months and 30 months after liming.

A reduction in the maximum depth for plant growth was indicated by the presence and absence of macrophytes. Raven observes that the maximum depth of macrophyte growth was about 5m in 1985-1987 and was reduced to 4m in 1988. The proportion of lake-bed area available for plant growth was estimated to be reduced from 45% (7.7 ha) to 38% (6.5 ha).

Although no estimates of the absolute surface areas of diatom habitats was attempted, based on the semi-quantitative and qualitative assessments made between 1985 and 1988 the importance of benthic habitats can be ranked.

1. It is clear that the epilithic (rock surface) habitat is dominant in Loch Fleet. Approximately two-thirds of the photic zone is estimated to lie over 'exposed' rock surfaces, largely slabs of exposed bedrock and large, detached boulders. This habitat occurs principally on the eastern and northern shores of the lake. However, smaller
Table 4.1: The percentage occurrence of aquatic macrophytes in Loch Fleet before and after catchment liming

<table>
<thead>
<tr>
<th>Macrophyte</th>
<th>Before</th>
<th>After Liming</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sphagnum auriculatum</em></td>
<td>54.0</td>
<td>57.5</td>
</tr>
<tr>
<td><em>Isoetes lacustris</em></td>
<td>34.5</td>
<td>36.8</td>
</tr>
<tr>
<td><em>Lobelia dortmanna</em></td>
<td>18.7</td>
<td>10.3</td>
</tr>
<tr>
<td><em>Solenostoma triste</em></td>
<td>12.1</td>
<td>20.7</td>
</tr>
<tr>
<td><em>Sphagnum cuspidatum</em></td>
<td>9.3</td>
<td>5.7</td>
</tr>
<tr>
<td><em>Littorella uniflora</em></td>
<td>8.4</td>
<td>2.3</td>
</tr>
<tr>
<td><em>Filamentous green algae</em></td>
<td>5.6**</td>
<td>4.6</td>
</tr>
<tr>
<td><em>Juncus bulbosus v. fluitans</em></td>
<td>0.9</td>
<td>2.3</td>
</tr>
<tr>
<td><em>Utricularia sp.</em></td>
<td>0.9</td>
<td>4.6</td>
</tr>
<tr>
<td><em>Fontinalis antipyretica</em></td>
<td>***</td>
<td>-</td>
</tr>
<tr>
<td><em>Isoetes echinospora</em></td>
<td>***</td>
<td>-</td>
</tr>
<tr>
<td><em>Amlystegium serpens</em></td>
<td>-</td>
<td>2.3</td>
</tr>
<tr>
<td><em>Batrachospermum spp.</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Bryum pallens</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Calypogeia mulleriana</em></td>
<td>-</td>
<td>1.1</td>
</tr>
<tr>
<td><em>Cephalozia connivens</em></td>
<td>-</td>
<td>1.1</td>
</tr>
<tr>
<td><em>Drepanocladus fluitans</em></td>
<td>-</td>
<td>1.1</td>
</tr>
<tr>
<td><em>Lophozia sp.</em></td>
<td>-</td>
<td>1.1</td>
</tr>
<tr>
<td><em>Polytrichum commune</em></td>
<td>-</td>
<td>1.1</td>
</tr>
<tr>
<td><em>Scapania undulata</em></td>
<td>-</td>
<td>1.1</td>
</tr>
</tbody>
</table>

* includes *Sphagnum* showing signs of die-back
** mainly Mougetia sp.
*** recorded during littoral mapping survey

Figures represent occurrence in Ekman grab samples from water < 5m deep. Taxa arranged in order of initial relative frequency.

Source: Raven (1989)
stones overly sand, silt and gravel elsewhere and increase the potential area of this habitat.

2. Aquatic macrophytes form a dense canopy over a large proportion of the photic zone where fine sediment has accumulated. A sparser cover of bryophytes (Scapania undulata) occurs particularly on the sides of large boulders to the north and east. The main areas for the growth of vascular plants are the more sheltered western side of the lake and the northern end of the eastern shore. Clearly before liming Sphagnum was dominant in water 2-5m deep, but was reduced to very low abundances in the post-liming period. The isoetids Littorella uniflora, Lobelia dortmanna, and Isoetes lacustris are dominant in the post-liming period. The leaves of these plants increase the effective surface area of the lake bed and since they are perennial provide a relatively stable habitat. As a result of the complex surfaces of the macrophytes it is difficult to estimate their surface area. Though less than one-third (5 ha) of the area of the photic zone is covered by macrophytes the true surface area of this habitat available for diatom growth is likely to be significantly greater.

3. Sand is restricted to small areas of the photic zone of Loch Fleet and is estimated to cover less than 5% (<1ha) of this area, principally the bay in the south-west of the lake. However, like the epiphytic habitat the total area of sand for diatom growth is increased by the habitat’s complex shape. The most dense growth of epipsammic diatoms occurred in the uppermost 1cm of a core taken from the bay at the south-west (data not presented here). Diatom density decreased rapidly below the surface and in addition counts from lower levels probably included many dead cells.

4. Where small areas of fine grained organic sediments occur in the photic zone of the lake their surface was usually covered with dense macrophyte growth and during 1988 especially with heavy growth of filamentous green algae. Repeated attempts were made to recover motile epipelic diatoms from mud taken from various areas of the photic zone using the tissue paper technique of Eaton and Moss (1966) and the same method was applied to sand samples, both without success. The occasional presences of epipelic taxa in live diatom sample, for example Surirella spp., suggests that a limited epipelon is present. However, examination of living material, sediment trap catches and core material along with the observation that the area of mud in the photic zone is small lead to the conclusion that the epipelon is a small diatom community in Loch Fleet.
iii. Diatom production versus relative abundance

It would be preferable to estimate total diatom productivity of each diatom species and from each habitat. From these estimates the 'true' percentages, for each taxon, of the total amount of valves produced during a period could be calculated. By comparing diatom valve productivity with the surface sediment death assemblage the representativity of percentages of valves counted from sediment could then be assessed. In practice, however, it is difficult to make any useful estimates of diatom productivity. Firstly the true areas of each (diatom) habitat available for diatom growth are problematic to estimate, and diatom growth across any habitat will not necessarily be uniform. The qualitative ranking of habitat importance attempted above might be as close to a real value as a more sophisticated approach, given the large errors that are likely. Secondly attempts to estimate cell division rates for individual diatom species would be necessary to extrapolate from measures of standing crop density to absolute cell production. Though increasing relative cell production rates can be related to decreasing cell size no estimates of division rates for the species involved at Loch Fleet exist in the diatom literature. The instability of the Loch Fleet diatom communities following liming and transient fluctuations in species percentage abundance would also suggest that large variation occurred in cell productivity of individual species.

Instead an approach using percentage data only has been used analogous to the procedure for comparison of proportions of plant taxa in modern vegetation with their representation as percentages in pollen surface samples (eg. Prentice & Parsons 1983, Webb et al. 1981). It is assumed that the underlying productivity of a diatom species in a community is related in some way to its percentage abundance in the community. Though this relationship is not necessarily straightforward, percentage estimates of species importance may be subject to less bias than 'absolute' estimates. The alternative, to calculate the total productivity of each (common) species for all habitats would be subject to large errors. The total surface area of each habitat would need to be known accurately. Cell density would then need to be calculated and related to cell production, or cell production per unit habitat area calculated in some other way. Figures for the total number of cells produced per unit time for each species from all communities could then be compared with the percentage of the species in the sediments. At present the relationship between species percentage and species absolute productivity in terms of valves remains a 'black box'.
This study began approximately 1 year after liming. Consequently the *ad hoc* frequency (Table 4.2) and location of pre-liming and the initial post-liming samples was unavoidable. However, for the remainder of the post-liming study spatial variability within and between habitats was assessed in order to design a program for representative sampling of the living diatom communities. A study was carried out in May 1987 for this purpose. In particular it was important to test whether each substrate, rocks, sand, macrophytes, could be treated as a distinct habitat occupied by a characteristic diatom community, and could therefore be treated as a uniform sampling category.

52 diatom samples were taken on one day from a range of habitats and the position and substrate of each sample was recorded (Fig. 4.2). Cleaned diatom slides were prepared from each sample and percentage diatom counts (for a total of approximately 500 valves) made for each.

The survey of habitats taken from all 13 zones of the littoral (Fig. 4.2, Table 4.3) included 7 substrates: rock (13 samples), sand (7 samples), *Juncus bulbosus var. fluitans* (6 samples), *Isoetes lacustris* (11 samples), *Lobelia dortmanna* (4 samples), *Littorella uniflora* (3 samples), *Scapania undulata* (8 samples). The number of samples from a habitat reflected the relative importance of the substrate around the Loch.

A total of 92 taxa were recorded, 14 taxa occurred at percentages greater than 10%; these taxa are tabulated (Table 4.4). Of the 92 taxa 11 were cosmopolitan whilst 29 were unique to a particular substrate. 15 taxa were only epipsammic, 11 taxa were only epilithic, 3 taxa only associated with the leafy liverwort species *Scapania undulata* and a single taxon associated with *Isoetes lacustris* (no other taxa were only epiphytic). However, these results are not necessarily a good indication of distinct communities growing on particular substrates. For example 17 of the 29 'unique' taxa were single occurrences within a particular habitat as well as within the whole survey, so could not be considered good differential species. Also only 6 of the 29 'unique' taxa occurred at percentages greater than 1% so consistent presences or absences were not likely for most. The use of presence and absence of individual indicator species to differentiate diatom communities was only good in a few cases. For example *Achnanthes altaica* was present at significant percentages (minimum 2%, maximum 32%) in all 7 epipsammic samples. *Achnanthes austriaca var. helvetica* and *Eunotia vanheurkii var.*
<table>
<thead>
<tr>
<th>Date of Sample</th>
<th>Substrate</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>21.05.81</td>
<td>Scapania undulata</td>
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</tr>
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<td>21.05.81</td>
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</tr>
<tr>
<td>09.11.81</td>
<td>Scapania undulata</td>
<td>?, ?</td>
</tr>
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<td>Rock</td>
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<td>Sand</td>
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</tr>
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<td>22.02.82</td>
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<td>?</td>
</tr>
<tr>
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Fig. 4.2: Sampling sites

Loch Fleet
All contours in metres

0 metres 150
Table 4.3: Habitat and sampling sites for survey of live communities

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Table 4.4: Common taxa found in survey of live communities
were present in 4/7 epipsammic samples. *Fragilaria virescens* var. *exigua* was present in 5/13 epilithic samples and *Navicula subtilissima* 6/13 epilithic samples.

Since the purpose was to examine the whole diatom community including rare taxa which might have high fidelity to a particular substrate/community, it was decided that the most appropriate method of analysis was (detrended) correspondence analysis (DCA). The use of an ordination method meant that all the percentage data for each sample could be utilised in measuring the similarity of samples, rather than just the presences and absences of species or percentages of selected taxa (Fig. 4.3).

The grouping of sample scores along the first 2 ordination axes shows the similarity within each group of substrata when samples were taken from sites in the open water. However, samples from all substrata taken from the enclosed embayment sites IV, V, VIII and IX often appear as outlying points. This is an effect of the extreme local chemistry conditions resulting from heavy local liming, absence of liming, use of nitrate fertilizer, afforestation, or simply from enclosure from conditions in the open lake. In addition samples taken very close to the inflows of streams, sites VI and VII, were occasionally affected by local variation in water chemistry. Clearly at open water sites unaffected by local influences, the lake water is well enough mixed to support a similar diatom community on each substrate and this was reinforced by similar pH and conductivity values around the lake (not presented). There is clearly species overlap between communities, but each community is distinctive enough to provide an appropriate sampling unit.

4. Within habitat variability and sample replication

Since diatoms growing on the same substrate but in different areas of the loch were sufficiently similar to be considered as a single community, sampling was rationalised to specific areas for each community. A further study was then carried out, on the most diverse periphyton community (epilithon) and on the least diverse (epiphyton, *Lobelia*) to determine a reasonable number of replicate samples to take in each selected area for determination of species composition.

i. Epilithon

Thirty diatom samples were removed using a diatometer from c.40-50cm of water at 10 randomly picked stations along a 200m transect below the shoreline of subcatchment
Fig. 4.3: DCA, between habitat variability
Z2 (Fig. 4.4). These 30 samples were amalgamated in groups of 3, corresponding to the 10 sampling stations. The entire sample was then dried, weighed and cleaned with addition of microspheres to estimate density of cell growth.

A total of 53 diatom taxa were recorded in the 10 samples, the 2 richest samples contained 31 taxa (567 & 554 valves counted) and the least species rich 17 taxa (402 valves counted). In the group of samples 11 taxa occurred at frequencies greater than 1% and only 4 taxa were present at above 5%. Histograms of the species occurring at frequencies of more than 1% shows the overall similarity in species composition (Fig. 4.5). In all samples *Achnanthes minutissima* (maximum 66%, minimum 33%) and *Brachysira vitrea* (maximum 43%, minimum 17%) are dominant. Other common species are present at less than 10% in all samples. Despite the overall similarity in composition it is clear from the range of values that replication of samples can improve the accuracy of determination of species composition.

**ii. Epiphyton**

Thirty complete rosettes of *Lobelia dortmanna* were removed from c. 40-50cm of water at 10 randomly picked stations along a 100m transect below the shoreline of subcatchment I (Fig. 4.4). These 30 samples were amalgamated in groups of 3, corresponding to the 10 sampling stations. The 10 samples were then prepared for diatom counting with the addition of microspheres to estimate density of cell growth.

A total of 44 taxa were recorded in the 10 samples, the most species rich contained 31 taxa (593 valves counted) and the least species rich 14 taxa (3 samples containing 524, 558, and 415 valves respectively). 13 taxa occurred at frequencies greater than 1% and only 3 taxa were present at above 5%. Histograms of the commonest taxa (>1%) show the overall similarity in species composition (Fig. 4.6). In all samples *Achnanthes minutissima* (maximum 90.5%, minimum 63.8%) is the dominant species. Other common species are present at less than 10%. As for the epilithon the compositions of samples are similar but the range of compositions, especially for the dominant taxon, show that replication of samples can improve the accuracy of measurement of species composition.
Fig. 4.4: Transect locations for within habitat variability study
Fig. 4.5: Diatom percentages: epilithon variability study
Fig. 4.6: Diatom percentages; epiphyton (Lobelia) variability study
iii. Method for determining number of replicates

The purpose of mixing subsamples is an attempt to provide an "average" sample to represent a particular diatom community and to minimise the effects of unusual single samples.

There are 2 possible methods for mixing samples. Firstly to mix sampled material either as collected, uncleaned, or by combining cleaned diatom solutions to give a single sample. Secondly samples can be prepared individually, separate slides made and a diatom count made for each slide.

Here a combination of the 2 methods was used. Initially 3 rock scrapes were taken using a diatometer (Flower 1985) and then amalgamated to give a single sample. This procedure was used for 2 reasons. Firstly sampling a larger surface area (3 x 7.5 cm²) ensured that a great enough density of diatoms was removed for slide preparation and diatom counting. (In retrospect a single sampled area (7.5 cm²) would have provided an excess of diatoms). More importantly sampling a larger area from a particular stone or slab of rock would decrease the likelihood of small scale (topographic) variation in diatom composition (and density) biasing the sample.

Having aggregated samples from any sampling point to remove small scale variation aggregate samples were taken from several points and counted individually. After inspection of the separate percentage counts the results were then combined. In this way measures (average, minimum, maximum, range, standard deviation) of variation within any group of samples could be seen and any outlying values recognised. Again it should be noted that all samples in any group were artificially given equal weighting by combining percentages rather than raw counts.

a. Theory

In the study of variation 30 equal areas of diatom growth were removed from a defined sector of the littoral. These were combined to give 10 samples. The assumption, based on the earlier study of spatial variation and depth variation, was made that these 10 samples adequately represented the whole epilithic diatom community of Loch Fleet (statistical universe).
The method of Adam and Mehringer (1975), which they used on surface pollen samples was applied here to determine an adequate number of subsamples for combination. If a sample is composed of \( n \) subsamples of equal size, when an additional subsample of unknown size is added to the group the effect on the relative frequencies of the addition can be calculated. In the worst possible case if the original sample is composed exclusively of taxon A and the added subsample consists entirely of taxon B, the proportions of A and B in the new sample will be \( \frac{n}{n+1} \) and \( \frac{1}{n+1} \) respectively. If taxon A represents the "true" composition and taxon B some departure from this it follows that the maximum error that can be introduced by addition of a new subsample is \( \frac{1}{1+n} \). Clearly the more subsamples that are included in the sample, the more reliable the observed frequencies will be; as \( n \) increases the error term will decrease.

Continuing with the assumption that the 10 aggregate samples represent the "true" situation what is the smallest number of samples that can be used for adequate representation of a community?

The maximum possible range of percentages for each of the commonest taxa from \( n \) subsamples has been plotted (Figs. 4.7-4.20). The maximum possible frequency that could have been found for \( n \) taxa was found by averaging the \( n \) highest frequencies (upper, dotted line on graphs). Similarly the minimum possible frequency for \( n \) subsamples was calculated by averaging the \( n \) lowest frequencies (lower, solid line on graphs). The mean of all 10 aggregate samples is assumed to represent the "true" situation (middle, dashed line on graphs).

b. Epilithon (Figs. 4.6-4.11)

The 6 commonest species were plotted as described above (note the different y-axis scales). The 95% confidence limits for the mean counting error (Mossiman 1965) have not been shown here, in all cases they are within 1% of the mean because the total combined diatom count was very high (>2000 valves). The range of values observed in the sub-dominant taxa, for example Brachysira brebissonii (Fig. 4.7), Eunotia incisa (2%) (Fig. 4.8), Nitzschia angustata (6%) (Fig. 4.9), and Synedra acus (2%) (Fig. 4.10) is very small. Even in the worst possible case of choosing a single epilithon sample to represent the community the percentage of any of these taxa would fall close to the mean, within 3% at the worst. In the case of dominant species, Achnanthes minutissima (Fig. 4.11) and Brachysira vitrea (Fig. 4.12) the range is greater, 33% and
25% respectively. Replication of samples would improve estimation of the mean percentages. From the plot it can be seen that the 5 lowest or highest percentages of either species averaged together would fall within 10% of the sample mean, but even this figure is exaggerated since the random selection of such a set of samples is unlikely. It was concluded that 5-6 samples from the epilithon would adequately represent the composition of that community. In the case of *Achnanthes minutissima* the dominant and most variable species, even in the worst case of selecting the 5 'lowest' or 5 'highest' samples the mean would be within 1 standard deviation unit of the 10 sample mean (50.7% +/- 10.5%).

c. Epiphyton *(Lobelia)* (Fig. 4.13-4.20)

The same procedure used to test variation in epilithon composition was applied to the epiphyton. The 7 commonest taxa were plotted. Again the 95% counting error for the combined sample mean was small, within 1% of the mean. Percentages of the single dominant taxon, *Achnanthes minutissima* (Fig. 4.13), were less variable than for the epilithon; the range was 27%. Again the percentage ranges of sub-dominant taxa were small: *Eunotia incisa*, 5% (Fig. 4.14); *Brachysira vitrea*, 3% (Fig. 4.15); *Gomphonema angustatum*, 6% (Fig. 4.16); *Gomphonema angustatum* var. *producta*, 3% (Fig. 4.17); *Gomphonema gracile*, 2% (Fig. 4.18); *Peronia fibula*, 2% (Fig. 4.19); *Fragilaria vaucheriae* 2% (Fig. 4.20). For the sub-dominant taxa, at worst, a single sample chosen at random would fall within 3% of the estimated population mean. Again replication of samples would improve the estimation of the percentage of the dominant taxon, *Achnanthes minutissima*. The 5 lowest or highest percentages of this species averaged together would be within 10% of the sample mean. As for the epilithon, even in the unlikely, worst case of selecting the 5 'lowest' or 'highest' percentage samples for the dominant species the 5 sample mean would be within 10% of the 10 sample mean and inside 1 standard deviation from that mean (77.4% +/- 9.5%). It was therefore concluded that the amalgamation of 5 samples from a site would be adequate to represent the composition of the community.

5. Variation of species composition with water depth

Varley, unpub.) suggested that the variation of diatom composition with depth was not significant. However, following the liming treatment of the lake and its catchment it was necessary to establish whether or not diatom samples taken from c.30-50cm water depth remained representative of the species composition of diatoms growing at any depth in the photic zone.

In September 1987 a survey of macrophytes was made (Raven 1989) along 4 transects and using random samples throughout the lake (Fig. 4.21). Macrophytes were removed from the lake bed by Ekman grab and plant samples from 2 of the transects were chosen to examine for diatom composition. The 2 transects (B and D) were selected because their positions were in open water, outside locally treated embayments, and therefore comparable with the littoral habitat in most of the lake.

28 plant samples were recovered, 19 from transect B and 9 from transect D. There was no replication of samples within depths along either of the transects, all plant material brought to the surface in the grab was pooled to give a single sample for each depth where any living macrophytes were found. This strategy was used for 3 reasons: the density of diatom cells growing on macrophytes was generally low therefore pooled samples were required, accurate replication of grab sampling at equal depths was limited by time, and an earlier pilot survey (see previous section) had shown that at least trends could be established from few or even single samples.

i. Transect B

Transect B on the west shore of the loch ran from a water depth of 0.5m, 2m from the shore to 2.8m, 38m from the shore, macrophytes were present throughout the transect. 69 diatom taxa were identified growing on 4 macrophyte species. Diatom species diversity was low. Of the 69 diatom taxa only 6 species occurred at abundances greater than 5% in any sample. These were Achnanthes minutissima, Brachysira vitrea, Eunotia incisa, Peronia fibula, Gomphonema gracile and Gomphonema angustatum/gracile. Only 4 of these species occurred in all 19 samples, Achnanthes minutissima, Brachysira vitrea, Eunotia incisa and Peronia fibula. Achnanthes minutissima (mean abundance 36%, maximum abundance 65%) and Peronia fibula (mean abundance 24%, maximum abundance 60%) were dominant in most samples with Brachysira vitrea (mean abundance 17%, maximum abundance 41%) and Eunotia incisa (mean abundance 12%, maximum 27%) as sub-dominant species.
Scatter diagrams (Figs. 4.21-4.26) of species abundance against depth for each of the commonest species do not reveal any simple pattern in the distribution of dominant and sub-dominant taxa. The range of percentages for all of the species is high, and to some extent is influenced by substrate, for example *Achnanthes minutissima* (Fig. 4.22) consistently reaches high abundances on *Sphagnum* spp., but systematic variation in percentages with depth is not seen. However, in the two less common *Gomphomema* taxa (Figs. 4.23 and 4.24) there is some evidence that there is a negative correlation between depth and species abundance. Again the influence of substrate (*Lobelia/Juncus*) cannot be eliminated. However, random variation in the percentages of the most abundant taxa; *Achnanthes minutissima*, *Brachysira vitrea* (Fig. 4.25), *Eunotia incisa* (Fig. 4.26) and *Peronia fibula* (Fig. 4.27), leads to the conclusion that depth is not a strong influence on diatom species composition.

ii. Transect D

Transect D began near to the mouth of the Altiwhat inflow stream and ran across the steeply sloping bed of the lake at the north-east corner of the loch. The transect began in water depth 0.3m at the shore, running to a depth of 7.8m 30m from the shore. Living plants were recovered from a maximum depth of 3.2m, 16m from the shore. 65 diatom taxa were identified growing on 4 macrophyte species. As in transect B diatom species diversity was low and of the 65 diatom taxa present in counts, only 5 species occurred at abundances greater than 5% in any sample (Figs. 4.27-4.31). Plant surfaces were dominated by *Achnanthes minutissima* (Fig. 4.28) (average abundance 25%, maximum abundance 34%), *Brachysira vitrea* (Fig. 4.29) (average abundance 15%, maximum abundance 50%), *Eunotia incisa* (Fig. 4.30) (average abundance 21%, maximum abundance 38%), and *Peronia fibula* (Fig. 4.31) (average abundance 21%, maximum abundance 39%). These species were present in all 9 samples. *Eunotia pectinalis* var. *minor* (Fig. 4.32) (average abundance 3%, maximum abundance 8%) the other taxon occurring at above 5% was present in 7 of the 9 samples.

Scatter diagrams of common species abundances against water depth do not show any clear depth/composition pattern (Figs. 4.28-4.32). As for transect B the distributions of species abundances with water depth appear to be random.
iii. Test of pattern for pooled transect data

Since it had already been demonstrated that spatial variation in diatom samples from the open loch was not significant it was considered reasonable to pool data from the 2 transects to give a larger data set. Possible variation in the communities of different basiphyte species has already been shown to be unimportant (see section 3, this chapter). The pooled data for each species abundance was plotted against depth for the commonest taxa; *Achnanthes minutissima* (Fig. 4.33), *Brachysira vitrea* (Fig. 4.34), *Peronia fibula* (Fig. 4.35), *Eunotia incisa* (Fig. 4.36). The simplest hypothesis, that the abundance of a species is not linearly related to water depth, was then tested by linear regression (regression lines are not drawn).

Again it is clear from the distribution of each species abundance that there is no strong correlation of species percentage abundance and water depth. This conclusion is reinforced by regression analysis (*Achnanthes minutissima* $r^2=0.07$, *Brachysira vitrea* $r^2=0.13$, *Eunotia incisa* $r^2=<0.01$, *Peronia fibula* $r^2=<0.001$). The null hypothesis cannot be rejected.

The data show that there is no simple relationship between common diatom species composition and water depth in the littoral of Loch Fleet. Examination of scatter diagrams and testing of a simple linear depth/abundance model showed that no simple pattern exists. Therefore it was considered reasonable to assume that samples representative of non-planktonic diatom composition at any photic depth could be taken from any permanently submerged situation in the littoral of the lake.

6. General conclusions and sampling strategy

The conclusions of these surveys of diatom habitats, spatial variation, sample replication and depth variation can be summarised:

1. Four important benthic diatom habitats were recognised in Loch Fleet. These were, in order of importance: rock surfaces, 'higher' macrophyte surfaces, bryophyte surfaces and sand grain surfaces. The epipelic habitat, if present was small, and not thought to be significant. The fifth habitat sampled was the plankton.

2. Sufficiently distinct diatom compositions were associated with these habitats for each to be considered a separate diatom community. There was overlap in species between
communities, but generally between community variation was greater than within community variation.

3. The measured composition of any community was not greatly influenced by sample location around the lake. However, small scale local variability resulting from experimental embayments and stream inflows was recognised and could be avoided.

4. Despite general similarity in the composition of single samples from a particular community, local variability was evident. The estimation of 'mean' community composition could be improved by amalgamation of samples and by replication of such pooled samples.

5. Diatom composition was not influenced by water depth or substrate macrophyte.

Therefore the following sampling strategy was adopted for routine sampling of non-planktonic diatom communities. The shoreline below each subcatchment was marked with canes at 10 or 20m intervals. Sample site selection within a subcatchment was by random numbers taken from a table. Locations are shown in Fig. 4.2.

1. Epilithon.
Since this area covered by this community was largest 2 sampling sites were selected, sectors F and L, below subcatchments X and Z₂. These sites were where stone surfaces were not prone to contamination with settling mud and where areas of flat rock were common. Rock scrapes were taken using a diatometer on flat stone surfaces and 18 samples from 6 sites were pooled to give 6 replicates from each area.

2. Epiphyton.
Isoetid species, primarily *Lobelia dortmanna*, were sampled and pooled (3 rosettes per sample) from 4 sites, A, B, C and J, below subcatchments I, II, III and Z₂ respectively (Fig. 4.2). These were areas where large stands of these plants grew and could be randomly taken.

3. Epibryon.
Six pooled replicates, each replicate consisting of 3 groups of stems of *Scapania undulata* were taken from the littoral below subcatchment X, sampling area F, on each sampling occasion.
4. Epipsammon.
Six pooled replicates, each consisting of 3 c.5cm² x 1cm deep sand cores were taken from below subcatchment I, sampling area A, using a perspex tube. Each pooled sample was mixed and then subsampled before preparation.

5. Plankton.
Phytoplankton samples were taken from a boat, from the surface water above the deepest point of the lake, site P (Fig. 4.2). Cells were concentrated from 2l of lakewater. This strategy assumed that since the lake is relatively small and that lakewater was well mixed then a single point sample from the open water would approximately represent the composition and concentration of cells from the whole lake.
Fig. 4.7: Percentage range vs. number of samples mixed; *Brachysira brebissonii* (epilithon)
Fig. 4.8: Percentage range vs. number of samples mixed; *Eunotia incisa* (epilithon)
Fig. 4.9: Percentage range vs. number of samples mixed; *Nitzschia angustata* (epilithon)
Fig. 4.10: Percentage range vs. number of samples mixed; *Synedra acus* (epilithon)
Fig. 4.11: Percentage range vs. number of samples mixed; *Achnanthes minutissima* (epilithon)
Fig. 4.12: Percentage range vs. number of samples mixed; *Brachysira vitrea* (epilithon)
Fig. 4.13: Percentage range vs. number of samples mixed; *Achnanthes minutissima* (epiphyton)
Fig. 4.14: Percentage range vs. number of samples mixed; *Eunotia incisa* (epiphyton)
Fig. 4.15: Percentage range vs. number of samples mixed; *Brachysira vitrea* (epiphyton)
Fig. 4.16: Percentage range vs. number of samples mixed; *Gomphonema angustatum*
Fig. 4.17: Percentage range vs. number of samples mixed; *Gomphonema angustatum* var. *producta*
Fig. 4.18: Percentage range vs. number of samples mixed; *Gomphonema gracile* (epiphyton)
Fig. 4.19: Percentage range vs. number of samples mixed; *Peronia fibula* (epiphyton)
Fig. 4.20: Percentage range vs. number of samples mixed; *Fragilaria vaucheriae* (epiphyton)
Fig: 4.21: Location of transects B and D

Loch Fleet
All contours in metres
Fig. 4.22: Abundance of *Achnanthes minutissima* vs. water depth (transect B)
Fig. 4.23: Abundance of *Gomphonema gracile* vs. water depth (transect B)
Fig. 4.24: Abundance of *Gomphonema angustatum/gracile* vs. water depth (transect B)
Fig. 4.25: Abundance of *Brachysira vitrea* vs. water depth (transect B)
Fig. 4.26: Abundance of *Eunotia incisa* vs. water depth (transect B)
Fig. 4.27: Abundance of *Peronia fibula* vs. water depth (transect B)

**TRANSECT B, ABUNDANCE OF *PERONIA FIBULA* VS WATER DEPTH**

![Graph showing the abundance of *Peronia fibula* vs. water depth for transect B](image)
Fig. 4.28: Abundance of *Achnanthes minutissima* vs. water depth (transect D)
Fig. 4.29: Abundance of *Brachysira vitrea* vs. water depth (transect D)
Fig. 4.30: Abundance of *Eunotia incisa* vs. water depth (transect D)
Fig. 4.31: Abundance of *Peronia fibula* vs. water depth (transect D)
Fig. 4.32: Abundance of *Eunotia pectinalis* var. *minor* vs. water depth (transect D)

TRANSECT D, ABUNDANCE OF EUNOTIA
PECTINALIS VAR.MINOR VS WATER DEPTH
Fig. 4.33: Abundance of *Achnanthes minutissima* vs. water depth (combined data)
Fig. 4.34: Abundance of *Brachysira vitrea* vs. water depth (combined data)
Fig. 4.35: Abundance of *Peronia fibula* vs. water depth (combined data)
Fig. 4.36: Abundance of *Eunotia incisa* vs. water depth (combined data)
CHAPTER 5: CHANGES OF LIVE COMMUNITIES THROUGH TIME AND THEIR RESPONSE TO LIMING

1. Pre-liming communities 1981-1986

Information about pre-liming diatom communities is based on archived material collected during *ad hoc* visits to the site between 1980 and 1986 by members of the Palaeoecology Research Unit, UCL. These samples were taken for the purposes of assessing the likelihood of lake acidification, for taxonomic use and for undergraduate student projects. Flower (1985) also used Loch Fleet as a test site for a quantitative diatom epilithon sampler and material from this exercise was archived. Samples were preserved in 3 forms:

1. cleaned material mounted on a slide,
2. unmounted cleaned material in solution but in some cases dried to form a pellet,
3. "fresh", preserved (in either formalin, alcohol or Lugol's iodine) material.

Prior diatom percentage counts had been made by others for some archived slides. However, the experience of other investigators (eg. Battarbee 1979, 1981a) has shown that, where possible, material should be recounted to maintain at least internal taxonomic consistency. As a result of storage and cataloguing of the original diatom material in the DISCO diatom database re-examination of samples was possible for all the samples used.

The contexts of all archived material used was recorded to varying degrees. For all samples the site (lake), substrate (habitat) and sample date (day) was available. For most a location (bay/stream) within the lake was given. Other characteristics, for example, depth of water from which the sample was taken, cleaning treatment and the person who took the sample, was also given for many samples. This information was listed on DISCO index cards.

In total 59 pre-liming diatom samples were counted. These samples were taken on 15 separate dates, between May 1981 and September 1985, and represented the communities of 10 substrates (Table 4.2). A single archived epilithic sample was available from the immediate post-liming period before October 1986.

Diatom samples collected during the post-liming period were collected according to the sampling strategy outlined in Chapter 4.

3. Presentation of data

For the reasons discussed in Chapter 4 the diatom communities were considered in 4 groups defined by the substrate to which the valves were attached: epilithon (rock), epiphyton (higher/isoetid plants), epibryon (mosses/liverworts), and epipsammon (sand). A fifth group consisted of the planktonic community. Samples were counted separately, grouped by habitat, community and sampling date. Where within community replication of samples occurred on any date species percentage counts were amalgamated to give mean values. Though not strictly the correct statistical procedure for calculating the mean, because percentages are 'closed' data, where sample sizes (total valves counted) are not equal, the addition of percentages rather than raw counts means that all samples are given equal weighting in the calculation. This standardisation avoids the problem of outliers biasing the calculated average.

Boxplots have been used to summarise percentage data of the most common taxa in each community both before and after liming. A boxplot is a graphical display that shows a measure of the location (median), the dispersion (interquartile range), the presence of outliers and also gives an indication of the symmetry or skewness of a distribution. These data are represented on the boxplot as follows:

1. Horizontal lines are drawn at the median, the upper and the lower quartiles and are joined by vertical lines to produce the box.

2. A vertical line is drawn upwards from the upper quartile to the most extreme data point that is within a distance of 1.5 (the interquartile range) of the upper quartile. A similarly defined vertical line is drawn downwards from the lower quartile.

3. Each data point falling beyond the ends of the vertical lines is marked with a small cross (+).
4. Epilithon (Figs. 5.1-5.11)

Pre-liming data was not sufficiently frequent or well replicated to be used for box plots, results are presented in Table 5.1.

The diatom epilithon was sampled on 10 dates during the pre-liming period, the earliest time was May 1981 and the latest September 1985. Dominant species during this period were consistently *Tabellaria quadriseptata* (maximum 71%), *Eunotia incisa* (maximum 31%) and *Tabellaria flocculosa* (maximum 28%) along with *Brachysira brebissonii* (maximum 24%) and *Frustulia rhomboides* var. *saxonica* (maximum 30%).

Boxplots showing post-liming trends in epilithon species composition are presented in Figs. 5.1-5.11. The 11 taxa selected had mean abundances of greater than 2% on at least one sampling occasion.

Despite the lack of systematic sampling immediately following liming, the two post-liming sampling occasions of 1986, approximately 2 months and 6 months after treatment, show a rapid shift in species composition and are described along with other post-liming samples.

*Tabellaria quadriseptata* the dominant species of the epilithic community in pre-liming samples from 1981 to 1985 is rapidly reduced following liming. The species decreases from 69% in the immediate pre-liming samples from both 1984 and 1985 to 7% 2 months after liming and less than 2% 6 months after liming (Fig. 5.1). In all samples after this time *Tabellaria quadriseptata* occurs at abundances of less than 1%.

*Eunotia incisa*, a common sub-dominant species in the pre-liming epilithon, expands immediately following liming (Fig. 5.2). Samples taken 2 months and 6 months after liming show a rapid increase in the percentage of *Eunotia incisa* where the species occurs at 41% and 36% respectively. Following this maximum in *Eunotia incisa* abundance the species percentage declines to 10% by April 1987 one year after liming and is steadily reduced to minimum of less than 2% by April 1988. However, during July 1988 the species abundance recovers to a maximum of 18% and maintains percentages of 5-8%.

*Brachysira brebissonii* is present at fluctuating percentages in all pre-liming samples reaching a maximum of 24% in a single sample, but at other times it is present at less
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Table 5.1: Common diatom species; mean abundances in archived epilithon samples
than 10%. *Brachysira brebissonii* increases to 14% in the first post-liming sample (July 1986) and then to a maximum of 28% in the second post-liming sample (October 1986) (Fig. 5.3). The species then declines to a minimum of less than 1% by June 1988. There is a small peak of 5% in July 1988 followed by a decline to 1% by November and December of 1988.

The abundance of *Frustulia rhomboides* var. *saxonica* is variable in pre-liming samples. In 2 samples it is absent and it reaches a maximum abundance of 30%. This variability in the species percentage is probably a reflection of the inadequate replication in pre-liming samples. However, post-liming samples show a maximum of 8% 2 months after liming, declining to 5% 5 months after liming and less than 1% 14 months after liming (Fig. 5.4). The species abundance remains at 1% or less in succeeding samples.

*Peronia fibula* is absent or present at abundances of less than 1% in pre-liming epilithon samples. Following liming the species abundance increases reaching a maximum of 10% in October 1986 5 months after liming (Fig. 5.5). The percentage falls to 6% by April 1987 1 year after liming and reaches less than 1% by November 1987. In following samples the mean species abundance is 1% or less.

*Brachysira vitrea* reaches a maximum of 2% in a single pre-liming sample. The species is absent or present at less than 1% in other pre-liming samples. 2 months after liming the species is absent from the epilithon, but by 5 months the percentage has reached 12% and increases to a maximum of 65% by July 1987 approximately 15 months after liming (Fig. 5.6). The abundance of *Brachysira vitrea* then declines to a minimum of 7% in April 1988 almost 2 years after the initial liming. A second maximum, of 38%, occurs in July 1988 and declines to 19-20% in October to December 1988.

*Achnanthes minutissima* is absent from most pre-liming samples and where it does occur it is present at abundances of less than 2%. 2 months after liming the species is absent from the epilithon and by 5 months after liming (October 1986) *Achnanthes minutissima* has not increased above 1% (Fig. 5.7). From April 1987, approximately 1 year after liming, the species increases to 17% and then to a maximum of 33% by May 1987. This is followed by a minimum of 13% in July 1987 and then a maximum of 78% during April 1988. The species mean abundance then decreases to a minimum of 20% by October 1988 recovering to a maximum of 38% by November 1988. The species, though one of the post-liming dominants, clearly shows some significant fluctuations in abundance during this period.
Diatoma tenue var. elongatum is absent from all pre-liming epilithon samples and is not present at any time represented by the Loch Fleet master core LF L3 (Anderson et al. 1986). The first appearance of this species (<1%) in the epilithon occurs approximately 1 year after liming in April 1987 (Fig. 5.8). With the exception of samples taken during October and November 1988, Diatoma tenue var. elongatum maintains a continuous presence, at less than 1%, in succeeding samples.

Fragilaria vaucheriae is absent from the pre-liming epilithon and does not appear until almost one year after liming (Fig. 5.9). Low percentage abundances, of generally less than 1%, are maintained from April 1987 until November 1987. A minor peak of abundance occurs in samples from April 1988 until June 1988 and reaches a maximum value of 6% during April 1988. The species abundance then decreases and remains at about 1%.

Synedra acus in Loch Fleet is primarily a planktonic species. However, valves of this species were also recorded in the epilithon (and other non-planktonic communities). The possibility that this species was a contaminant having settled from the plankton occurs. However, examination of fresh material from the epiphyton revealed that the species was attached to the substrate. In addition most of the post-liming epilithon samples were taken using a diatometer (Flower 1985) which used a distilled water source for washing diatoms from the closed sampling chamber. Finally, except for one period during 1988 the concentration of Synedra acus valves in the plankton is low and a relatively large volume of water (2 l) was required for plankton samples. The lakewater contained in the small volume of the diatometer chamber (x cm³) is unlikely to have caused serious contamination. It is therefore unlikely that significant contamination of epilithon samples by planktonic species could have occurred. The percentages of Synedra acus occurring in the epilithon and in other attached communities may be considered as true non-planktonic diatoms though they could not routinely be separated from the planktonic form.

Synedra acus occurs at less than 2% in a single epilithic sample from May 1981, it is otherwise absent from the pre-liming epilithon. The species appears again in the epilithon approximately 5 months after liming, occurring at less than 1% (Fig. 5.10). Synedra acus then increases to a maximum of 6% by May 1987 and decreases again to about 1% by July 1987. A second and higher maximum occurs in June 1988 when
the species reaches 10%. The abundance of Synedra acus then declines to 1% and remains below 2% in the following samples.

*Tabellaria flocculosa* is common in the pre-liming epilithon reaching a maximum of 28% in the community before liming. However, the percentage of this species is variable and in 2 pre-liming samples it occurs at a minimum of less than 1%. Following liming the species increases from less than 1% 2 months after liming to 4% approximately 1 year after liming (Fig. 5.11). *Tabellaria flocculosa* then declines to less than 1% between July 1987 and June 1988. There is a rapid rise to a maximum abundance of 50% by October 1988. The maximum declines to 16% one month later and then rises to 35% in December 1988.

5. Epiphyton (Figs. 5.12-5.25)

Species percentages for the pre-liming epiphyton are shown in Table 5.2.

The epiphytic diatom community was sampled on 9 occasions during the pre-liming period, the earliest in February 1982 and the latest September 1985. The dominant species during this period were *Tabellaria quadriseptata* (maximum 80%), *Eunotia incisa* (maximum 39%) and *Tabellaria flocculosa* (maximum 59%). Though the 3 most common taxa were the same as those of the epilithon the species diversity of the epiphyton was lower.

Boxplots showing trends in common epiphyton species composition after liming are presented in Figs 5.12-5.25. The 14 taxa selected had mean abundances of greater than 2% on at least one sampling occasion

*Tabellaria quadriseptata* is the dominant species of the pre-liming epiphyton between 1982 and 1985; the species reaches a maximum abundance of 80% during this period. By 5 months after liming the species abundance is reduced to less than 1% (Fig. 5.12) and continues at this low abundance or is completely absent from the epiphyton during the whole of the post-liming period.

*Eunotia incisa*, which is common in the pre-liming epiphyton, reaching a peak abundance of 39%, increases to a maximum in the earliest post-liming epiphyton samples (Fig. 5.13). 5 months after liming *Eunotia incisa* has a mean abundance of 75% and then declines to a minimum of 3% by December 1987. A second maximum
## Mean Abundances in Archived Epiphyton Samples

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<thead>
<tr>
<th>Common diatom species</th>
<th>8202</th>
<th>8205</th>
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<th>8210</th>
<th>8211</th>
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</thead>
<tbody>
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Table 5.2: Common diatom species; mean abundances in archived epiphyton samples
of 30% occurs in February 1988 but declines to 1% within 1 month. A third post-liming maximum of 13% occurs in June 1988 declining to less than 2% by December 1988.

*Peronia fibula* is absent or present at abundances of less than 1% in pre-liming epiphyton samples. 5 months after liming the percentage of *Peronia fibula* has increased to 12% (Fig. 5.14) and reaches a maximum of 43% by May 1987, approximately 1 year after the initial liming. The species abundance then falls to 1% by December 1987 and after January 1988 remains at abundances of less than 2% in the epiphyton.

*Brachysira vitrea* is absent from pre-liming epiphyton samples during 1982 and is present at abundances of less than 1% during 1984 and 1985. 5 months after liming the species abundance remains at less than 1% (Fig. 5.15), but then increases and reaches a maximum of 17% by September 1987. The percentage of *Brachysira vitrea* then falls and the species is absent from epiphyton samples taken in March 1988. During 1988 the percentage of *Brachysira vitrea* increases again, reaching a second maximum of 16% in October 1988 and then decreasing to less than 3% by December 1988.

*Achnanthes minutissima* is absent, or present at abundances of less than 2% in pre-liming epiphyton samples. 5 months after liming the species abundance is less than 1% (Fig. 5.16), but then increases rapidly and reaches a maximum of 83% by January 1988. After a brief minimum of 19% in February 1988 a second maximum of 86% occurs in July 1988. This peak abundance declines to 34% by October 1988 and recovers to 57% during November and December 1988. During the 2nd and 3rd years after the initial liming *Achnanthes minutissima* becomes the dominant diatom species of the epiphyton, though there are some fluctuations in the species abundance during this time.

*Fragilaria vaucheriae* is absent from the pre-liming epiphyton and following liming the species continues to be either absent or present at abundances of less than 1% until July 1987 (Fig. 5.17). 2 small peaks in the species percentage occur during August (3%) and November 1987 (7%). However, there is a significant increase in species abundance early in 1988 with a maximum of 30% in March 1988. *Fragilaria vaucheriae* decreases to 1% by July 1988 increasing to 3% by December 1988.
Synedra acus is absent from pre-liming epiphyton samples. Approximately 5 months after liming the species appears (Fig. 5.18), but at a mean abundance of less than 1%. Almost 1 year after liming the species reaches a maximum abundance of 4%. The species percentage falls to 1% by June 1987 and then increases to a second maximum (3%) by August 1987. Further peaks of Synedra acus occur in June 1988 (6%) and December 1988 (4%), however the species is generally present at mean abundances of less than 2%. It is possible that the traces of this species in the epiphyton (especially in July 1988) are a contaminant from the plankton, but at such low abundances planktonic and non-planktonic forms could not be separated in routine counting.

Tabellaria flocculosa is common in the pre-liming epiphyton reaching a maximum abundance of 59% and a minimum abundance of 3%. At about 5 months and 12 months after liming the species has a mean abundance of about 9% (Fig. 5.19). Tabellaria flocculosa then declines and is absent from samples taken during January 1988. In August 1988 the species reaches its highest post-liming abundance (47%) declining to a minimum of 12% by November 1988.

Gomphonema gracile is absent from the pre-liming epiphyton, but is commonly present in post-liming samples, but at abundances of less than 3% (Fig. 5.20).

Gomphonema angustatum, Gomphonema angustatum var. producta and Gomphonema angustatum/gracile are absent, or present at less than 1% in single samples, from the pre-liming epiphyton. 1 year after liming all 3 species are present at abundances of 1% or more (Figs. 5.21-5.23). A maximum of Gomphonema angustatum abundance (7%) occurs during November 1987, followed by a maximum of Gomphonema angustatum var. producta (9%) in March 1988. Both species decline towards the end of 1988. Gomphonema angustatum/gracile has a maximum abundance of 11% during November 1987 and declines to about 1% during 1988.

Eunotia rhomboidea reaches a maximum abundance of 4% in the pre-liming epiphyton. The species is present at less than 2% in post-liming samples until February 1988 when the mean abundance increases to 24% (Fig. 5.24). Eunotia rhomboidea then falls to less than 1% in August 1988 and reaches a second maximum of 12% in October 1988.

Eunotia vanheurkii var.1 is absent from pre-liming epiphyton samples and is generally present at low abundances following liming (<1%) (Fig. 5.25). However, during the
later part of 1988 a peak in the species abundance occurs, with a maximum of 8% during September 1988, and decreasing to 2% by December 1988.

6. Epibryon (Figs. 5.26-5.35)

The percentage abundances of common taxa during the pre-liming period are shown in Table 5.3. to indicate the distribution of the data.

Epibryon was sampled on 10 occasions before liming, the earliest was May 1981 and the latest September 1985. Like the epiphyton and the epilithon the dominant species during this period were *Tabellaria quadriseptata* (maximum 89%), *Eunotia incisa* (maximum 70%) and *Tabellaria flocculosa* (maximum 56%). As in the epiphyton, species diversity was low.

Boxplots showing the mean percentage abundances of epibryon species after liming are presented in Figs. 5.26-5.35. The 10 species selected had mean abundances of greater than 2% on at least one sampling occasion.

*Tabellaria quadriseptata* is common in the pre-liming epibryon dominant or co-dominant with *Eunotia incisa* on the surfaces of liverworts. The species reaches a maximum abundance of 89% during this period. Following liming *Tabellaria quadriseptata* is absent or present at low abundances (<1%) in the epibryon community (Fig. 5.26).

*Eunotia incisa* is abundant in the pre-liming epibryon dominant or co-dominant with *Tabellaria quadriseptata*. Approximately 5 months after liming the species remains at a high percentage abundance (54%), decreasing to 10% 1 year after liming and then increasing to 38% within one month of this minimum (Fig. 5.27). A third maximum occurs during January 1988 and then *Eunotia incisa* declines to a minimum of 2% by December 1988.

*Peronia fibula* is absent or present at abundances of less than 2% in epibryon samples taken before liming. 5 months after liming the species abundance has increased to 35% and mean abundances of greater than 20% are maintained until August 1987 (Fig. 5.28). The species abundance then decreases, declining to 2% or less by September 1988 and remaining at this level.
Table 5.3: Common diatom species; mean abundances in archived epibryon samples

<table>
<thead>
<tr>
<th>Common diatom species</th>
<th>8105</th>
<th>8111</th>
<th>8204</th>
<th>8205</th>
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<th>8208</th>
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<th>8211</th>
<th>8407</th>
<th>8509</th>
</tr>
</thead>
<tbody>
<tr>
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<td>52.2</td>
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<td>10.9</td>
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<tr>
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*Brachysira vitrea* is either absent from pre-liming epibryon samples or present at abundances of less than 1%. From 5 months after liming the species is seen to increase in abundance and by about 18 months after the initial liming the species reaches a maximum abundance of 25% (Fig. 5.29). *Brachysira vitrea* then declines and falls to a minimum abundance of 4% during May 1988. A second maximum occurs during July 1988 when the species recovers to 16%. By December 1988 the species has declined to 6%.

*Achnanthes minutissima* is either absent from the pre-liming epibryon or occurs at low abundances (<2%). 5 months after liming the species remains at less than 1% (Fig. 5.30). However, approximately 1 year after liming the species increases to 10% and reaches a maximum of 46% by November 1987. High mean abundances of *Achnanthes minutissima* continue, but the species shows some fluctuations during the remainder of the sampling period. Maxima occur during February 1988 (49%), June 1988 (77%) and November 1988 (69%).

*Diatoma tenue* var. *elongatum* is absent from the pre-liming epibryon. After liming this species is sporadically present in the community and reaches a mean abundance of 13% approximately 1 year after liming (Fig. 5.31).

*Fragilaria vaucheriae* is absent from the pre-liming epibryon. The species is still absent approximately 5 months after liming and then increases to a mean abundance of 7% by about 1 year after liming (Fig. 5.32). *Fragilaria vaucheriae* then falls to 1% or less until August 1987, but then increases to a maximum of 7% by June 1988. The species again decreases and is absent within 1 month. A third maximum (3%) occurs during December 1988.

*Syedrea acus* is absent from pre-liming epibryon samples. About 5 months after liming the species is present at less than 1%, it then increases to a maximum of 29% by May 1987, but is absent again within one month (Fig. 5.33). 3 sporadic maxima of 3 to 4% occur during the remainder of 1987 and 1988, but otherwise the species remains at abundances of 2% or less.

*Gomphonema angustatum* is absent from the pre-liming epibryon except for a single occurrence at less than 1%. There is no change in its abundance until approximately 18 months after the initial liming when the species increases to a maximum of 3%
The species continues to be intermittently present at variable percentage, reaching a maximum of 8% during November 1988.

*Tabellaria flocculosa* is common during the pre-liming period reaching a maximum abundance of 58%. The species declines after liming and by approximately 5 months after the first treatment it is reduced to 1% (Fig. 5.35). *Tabellaria flocculosa* continues to be present in the epibryon and reaches a maximum of over 5% about 1 year after the initial liming, but its abundances are generally low decreasing to less than 1%. However, there is a maximum during September 1988 when the species increases to 37%, this peak of species abundance is followed by a decline to 18% by December 1988.

### 7. Epipsammon

Pre-liming percentages of common taxa are shown in Table 5.4.

Epipsammon was sampled on 9 dates during the pre-liming period, the earliest was November 1981 and the latest September 1985. The epipsammic community was dominated by *Tabellaria binalis* fo. *elliptica* (maximum 42%) with *Tabellaria quadriseptata* (maximum 32%), *Eunotia rhomboidea* (maximum 26%), *Tabellaria flocculosa* (maximum 23%), *Eunotia incisa* (maximum 14%), *Eunotia vanheurkii* var. *intermedia* (maximum 56%), *Eunotia tenella* (maximum 30%)

Boxplots showing the mean abundances of common epipsammic species after liming are presented in Figs. 5.36-5.48. The 14 species presented had mean abundances of more than 2% on at least one sampling occasion.

*Tabellaria binalis* fo. *elliptica* is a dominant epipsammic taxon during the pre-liming period and reaches a maximum abundance of 38%. Approximately 5 months after liming the species remains dominant (24%), but in the following samples its importance rapidly decreases (Fig. 5.36). In April 1987 almost 1 year after the first liming *Tabellaria binalis* fo. *elliptica* is reduced to 4% and by August 1987 the species is reduced to 1%. A single maximum occurs during February 1988 when the species mean abundance increases to 8%. However, during the following months its abundance does not increase above 1%.
### Table 5.4: Common diatom species; mean abundances in archived epipsammon samples

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*Tabellaria quadriseptata* is common in some pre-liming epipsammon samples reaching a maximum abundance of 32%. Approximately 5 months after liming the species mean abundance is 7%, but it decreases to less than 1% by April 1987 almost 1 year after liming (Fig. 5.37). In succeeding samples the species does not increase above 2% and in most it is absent.

*Eunotia incisa* is common in pre-liming epipsammon samples and reaches a maximum of 12% during this period. Following liming the species abundance is maintained and then increases to a maximum of 23% by October 1987 approximately 18 months after the first liming treatment (Fig. 5.38). *Eunotia incisa* then declines and does not exceed 2% after March 1988.

*Achnanthes minutissima* is absent or present at less than 1% in most pre-liming samples. In a single sample (May 1982) the species increases to a maximum of 5%. 5 months after liming the species reaches a maximum of 13%, but decreases to 6% approximately 1 year after liming (Fig. 5.39). The species reaches a maximum of 17% in August 1987 and then decreases to abundances of 1 to 4% during 1988.

*Achnanthes altaica* is absent from most pre-liming epipsammon samples and only occurs at abundances of about 1%. 5 months after liming the species is absent from epipsammic samples, but by about 1 year after liming it increases to 23% and then reaches a maximum of 28% by July 1987 (Fig. 5.40). A minimum of 5% occurs in February 1988 and is followed by a second maximum (19%) in May 1988. *Achnanthes altaica* maintains abundances greater than 10% during the remainder of 1988.

*Brachysira vitrea* is uncommon in the pre-liming epipsammon community, not increasing to more than 1%. In the first post-liming epipsammic sample, taken about 5 months after liming, the species has increased to 4% and reaches a maximum abundance of 8% by August 1987 (Fig. 5.41). By the beginning of 1988 the species has declined to a mean abundance of less than 1% and remains at low abundances during the rest of 1988.

*Eunotia vanheurkii* var. *intermedia* is common in some pre-liming epipsamnic samples and reaches a maximum abundance of 56%. However, the species is absent from 2 pre-liming samples and its abundance is very variable. For most of the post-liming period *Eunotia vanheurkii* var. *intermedia* is absent, or occurs at abundances of less than 1% (Fig. 5.42). There is a single peak of abundance (5%) during June 1987.
Eunotia vanheurkii var.1 is absent from pre-liming epipsammon samples. 5 months after liming the species is still absent from this community, but by April 1987 about 1 year after the first liming treatment the species has increased to 27% (Fig. 5.43). The species percentage is variable immediately following this maximum but from July 1987 the species increases to consistently high percentages and reaches a maximum of 53%. Between November 1987 and December 1988 the species is present at abundances greater than 20% and is generally present at abundances of more than 30%.

The percentage abundance of Achnanthes marginulata is variable in pre-liming epipsammon samples and in most samples is less than 1%. A single peak of 6% occurs in September 1985. During the post-liming period the mean abundance of Achnanthes marginulata is also variable and it is difficult to recognise any clear pattern (Fig. 5.44). A peak percentage (18%) occurs during May 1987, declining to less than 1% and a second maximum (8%) occurs in February 1988. Further maxima in Achnanthes marginulata abundance are seen July 1988 (7%) and during the last 3 months of 1988 when the species percentage remains at 8%. During the intervening periods species abundances decline to less than 1%.

Eunotia rhomboidea is common in the pre-liming epipsammon, reaching a maximum abundance of 20%, but on 3 sampling occasions the species does not exceed 2%. Following liming the species is consistently among the dominant epipsammic taxa. 5 months after liming the species is present at less than 2% and during 1987 the species mean abundance is usually less than 20% (Fig. 5.45). However, during 1988 Eunotia rhomboidea rises to abundances of over 20% reaching a maximum of 47% in June 1988.

Achnanthes austriaca var. helvetica does not exceed 2% in pre-liming samples and is absent on most sampling occasions. Immediately following liming the species abundance stays low, but approximately 1 year after liming there is a peak of 5% (Fig. 5.46). The species mean abundance then returns to 1% followed by an increase to a second maximum (5%) in December 1988.

Tabellaria flocculosa is present at variable abundances in pre-liming epipsammon samples and has a maximum abundance of 23%, but is commonly present at abundances of 1% or less. After liming the species declines and does not exceed a mean abundance of 1% (Fig. 5.47).
Eunotia pectinalis var. minor does not exceed abundances of 1% in pre-liming samples. Following liming the species initially remains at low abundance, but then rises to a maximum abundance of 13% during August 1987 (Fig. 5.48). The species then declines and is absent, or present at abundances of less than 1% during 1988.

Eunotia tenella is dominant in the 2 earliest epipsammon samples taken in November 1981 (28%) and February 1982 (30%). During the remainder of the pre-liming period the species does not exceed 3% and is absent from some samples. After liming Eunotia tenella is absent from many samples and where it does occur is usually present at less than 1% (Fig. 5.49). A single maximum (4%) occurs during May 1987.

8. Plankton

Following the decline of Cyclotella kuetzingiana at a depth of about 1m in the sediment core LF L3 (Fig. 2.x), a horizon dated to the mid-1960s, there are no fossil records of planktonic diatom populations in Loch Fleet. This assertion was supported by 9 archived, non-quantitative plankton samples taken between 1981 and 1986 (settled from lakewater or taken by plankton net) which did not contain any live planktonic diatom cells.

Between March 1987 and December 1988, 22 plankton samples were taken at approximately monthly intervals. These samples were treated quantitatively according to the procedure outlined in Chapter 3. During this part of the post-liming period non-diatom phytoplankton were most common and included consistent presences of a μ-flagellate cf. Rhodomonas minuta (10-600 cells l⁻¹) and cells of Mallomonas spp. (maximum 20 cells l⁻¹), Dinobryon spp. (maximum 260 cells l⁻¹), Cryptomonas spp. (maximum 280 cells l⁻¹), the desmid genera Closterium (maximum 40 cells l⁻¹), Staurastrum (present) and Xanthidium (present), and the dinoflagellate genus Peridinium (present) were seen periodically.

There was a continuous presence, at low concentrations (maximum total of all non-planktonic diatom taxa, 40 cells l⁻¹), of diatoms derived from attached littoral communities. In particular Achnanthes minutissima reached a maximum concentration of almost 30 cells l⁻¹ during April 1988. However, most diatom cells recorded in plankton samples were clearly transported non-planktonic taxa.
Exceptionally 2 planktonic diatom taxa were recorded during the post-liming period, these were *Synedra acus* and *Asterionella formosa*.

*Synedra acus* was present in all post-liming plankton samples (Fig. 5.50) at various concentrations. A single bloom of this species occurred during April 1988 when cell concentrations reached 5530 cells l$^{-1}$, and then returned to concentrations of less than 10 cells l$^{-1}$ for the remainder of 1988.

*Asterionella formosa* was absent from the phytoplankton until October 1988 when it appeared at a concentration of 3 cells l$^{-1}$, but this did not increase above 10 cells l$^{-1}$ during November and December 1988 (Fig. 5.51). Routine sampling of living communities ended in December 1988, but a non-quantitative water sample taken from the lake at the beginning of April 1989 had an exceptionally high concentration of *Asterionella formosa* colonies. The concentration of cells was estimated to be at least as great as the concentration of *Syndra acus* cells during April 1988. Clearly a bloom of *Asterionella formosa* occurred during January, February or March 1989. In view of the high concentration of cells observed in the April 1989 water sample it is probable that the bloom began at the end of March 1989.

9. Summary of species changes

Summary diagrams showing the relationship between the changes in common species in each community and pH are presented in Figs. 5.52-5.55. The trends occurring in each community are summarised below.

i. Epilithon (Fig. 5.52)

It is clear from the earliest post-liming samples that the diatom species composition of the epilithon changes rapidly and the established community dominated by *Tabellaria quadriseptata* (seen in samples from 1981 to 1985) disappears. The community becomes less stable and by October 1986 there are sharp increases in the abundances of species associated with higher pH, notably *Eunotia incisa*, *Brachysira brebissonii* and *Peronia fibula*. By April 1987 one year after liming the mean percentages of *Eunotia incisa*, *Peronia fibula* and *Brachysira brebissonii* are reduced. The dominant epilithic species become *Brachysira vitrea* and *Achnanthes minutissima*. The epilithon community continues to be dominated by these species from April 1987 until March 1988 with a
trend of increasing Achnanthes minutissima percentages and decreasing percentages of Brachysira vitrea in late 1987 and early 1988.

From April 1987 onwards 2 taxa, absent from all earlier epilithon samples, Diatomata tenue var. elongatum and Fragilaria vaucheriae, appear and have (almost) continuous presences in succeeding samples.

A peak of Fragilaria vaucheriae occurs between March and June 1988 and following this there is a single peak of Synedra acus in June 1988. The percentage of Brachysira vitrea is reduced to a minimum during April 1988 whilst Achnanthes minutissima increases to a maximum at the same time. For the remainder of 1988 Achnanthes minutissima and Brachysira brebissonii are abundant and Eunotia incisa is common. However, from July 1988 the percentage of Tabellaria flocculosa increases and it becomes co-dominant with Achnanthes minutissima and Brachysira brebissonii, reaching a maximum in October 1988. These taxa remain dominant until December 1988.

ii. Epiphyton (Fig. 5.53)

The earliest post-liming epiphyton samples show a rapid change in species composition. As in the epilithon, Tabellaria quadriseptata shifts from dominance to almost complete absence by October 1986. At the same time Eunotia incisa rises to a maximum and Peronia fibula, which was absent or present at very low abundances, becomes important. Approximately 1 year after liming the percentage of Achnanthes minutissima begins to increase and the species is dominant by August 1987. Eunotia incisa and Peronia fibula percentages decrease. Achnanthes minutissima remains dominant during the remainder of 1987 and during most of 1988. However, peaks of other species are seen within this period. Eunotia incisa and Eunotia rhomboidea have maxima in February 1988. Brachysira vitrea has maxima during September 1987 and October 1988 and as in the epilithon the percentage of Tabellaria flocculosa increases to high abundances from August 1988.

iii. Epibryon (Fig. 5.54)

As in the epilithon and epiphyton, Tabellaria quadriseptata shifts from dominance in the epibryon to absence from most post-liming samples. The pre-liming abundance of Tabellaria flocculosa is also reduced in the post-liming period, but 6 months after
liming high percentages of *Eunotia incisa* are maintained. At the same time *Peronia fibula* becomes co-dominant. Peaks of *Synedra acus* and *Diatoma tenue* var. *elongatum* occur in May 1987 and *Achnanthes minutissima* and *Brachysira vitrea* begin to increase at this time. By May 1988 *Eunotia incisa* and *Peronia fibula* have declined to relatively low percentages and *Achnanthes minutissima* and *Brachysira vitrea* become dominant. A peak of *Tabellaria flocculosa* occurs in August 1988 and high percentages of this species continue until December 1988 whilst *Brachysira vitrea* declines and *Achnanthes minutissima* remains dominant.

iv. Epipsammon (Fig. 5.55)

Though *Tabellaria quadriseptata* is important in the pre-liming epipsammon, *Tabellaria binalis* fo. *elliptica* is the dominant taxon in this community. In addition *Eunotia rhomboidea* is important. By 1 year after liming *Tabellaria binalis* fo. *elliptica* is no longer dominant and in succeeding samples the species is generally present at low percentages. When higher percentages of this taxon do occur post-liming, it may reflect the problem of sampling the true live component of cells from the epipsammon. The remnant cells from the pre-liming community may remain attached, especially to deeper buried sand grains inadvertently taken in samples. From 1 year after liming *Achnanthes altaica*, *Eunotia vanheurkii* var. 1 and *Eunotia rhomboidea* become the dominant epipsammic taxa. *Eunotia incisa* is also common until approximately 18 months after liming and then declines. *Achnanthes minutissima* shows sporadic peaks in the post-liming period, but is not consistently dominant as in the other attached communities. *Achnanthes marginulata* also has infrequent maxima and *Achnanthes austriaca* var. *helvetica* shows a steady increase in abundance towards the end of 1988.

v. Plankton

Two marked blooms are recorded in the post-liming diatom plankton. High concentrations of *Synedra acus* occur in April 1988 (Fig. 5.50) and a high density of *Asterionella formosa* colonies occurs in early 1989 (Fig. 5.51).

The diatom communities of Loch Fleet all show distinct changes in composition, for example the general post-liming loss of *Tabellaria quadriseptata* and increase of *Achnanthes minutissima*. Not only are there shifts in species composition, but some new species also appear or previously rare taxa become common, for example *Diatoma tenue* var. *elongatum* or *Fragilaria vaucheriae*. The majority of species, and percentage
trends, are cosmopolitan, but a few taxa are predominantly or exclusively associated with a particular community, notably epipsammic taxa such as *Tabellaria binalis* fo. *elliptica*, and *Achnanthes altaica*. A combination of these induced/marked patterns: of species presence and absence, new species appearances, trends in species composition and the affinity of species for particular habitats, allow comparisons to be made with the fossil record.
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Fig. 5.1: Boxplot of *Tabellaria quadrisepata* in the post-liming epilithon
liming high percentages of *Eunotia incisa* are maintained. At the same time *Peronia fibula* becomes co-dominant. Peaks of *Synedra acus* and *Diatoma tenue* var. *elongatum* occur in May 1987 and *Achnanthes minutissima* and *Brachysira vitrea* begin to increase at this time. By May 1988 *Eunotia incisa* and *Peronia fibula* have declined to relatively low percentages and *Achnanthes minutissima* and *Brachysira vitrea* become dominant. A peak of *Tabellaria flocculosa* occurs in August 1988 and high percentages of this species continue until December 1988 while *Brachysira vitrea* declines and *Achnanthes minutissima* remains dominant.

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The diatom communities of Loch Fleet all show distinct changes in composition, for example the general post-liming loss of *Tabellaria quadriseptata* and increase of *Achnanthes minutissima*. Not only are there shifts in species composition, but some new species also appear or previously rare taxa become common, for example *Diatoma tenue* var. *elongatum* or *Fragilaria vaucheriae*. The majority of species, and percentage
Fig. 5.2: Boxplot of *Eunotia incisa* in the post-liming epilithon

PERCENTAGE OF EUNOTIA INCISA IN THE POST-LIMING EPILITHON
Fig. 5.3: Boxplot of *Brachysira brebissonii* in the post-liming epilithon

**PERCENTAGE OF BRACHYSIRA BREBISONII IN THE POST-LIMING EPILITHON**
Fig. 5.4: Boxplot of *Frustulia rhomboides* var. *saxonica* in the post-liming epilithon

PERCENTAGE OF *FRUSTULIA RHOMBOIDES VAR. SAXONICA* IN THE POST-LIMING EPILITHON

DATE

8612 8702 8704 8706 8708 8710 8712 8802 8804 8806 8808 8810 8812
8610 8701 8703 8705 8707 8709 8711 8801 8803 8805 8807 8809 8811
Fig. 5.5: Boxplot of *Peronia fibula* in the post-liming epilithon
Fig. 5.6: Boxplot of *Brachysira vitrea* in the post-liming epilithon
Fig. 5.7: Boxplot of *Achnanthes minutissima* in the post-liming epilithon
Fig. 5.8: Boxplot of *Diatoma tenue* var. *elongatum* in the post-liming epilithon

PERCENTAGE OF *DIATOMA TENUE* VAR. *ELONGATUM* IN THE POST-LIMING EPILITHON

DATE

8812 8702 8704 8706 8710 8712 8802 8804 8806 8808 8810 8812
8810 8701 8703 8705 8707 8709 8711 8801 8803 8805 8807 8809 8811
Fig. 5.9: Boxplot of *Fragilaria vaucheriae* in the post-liming epilithon
Fig. 5.10: Boxplot of *Synedra acus* in the post-liming epilithon
Fig. 5.11: Boxplot of *Tabellaria flocculosa* in the post-liming epilithon
Fig. 5.12: Boxplot of *Tabellaria quadriseptata* in the post-liming epiphyton
Fig. 5.13: Boxplot of *Eunotia incisa* in the post-liming epiphyton
Fig. 5.14: Boxplot of *Peronia fibula* in the post-liming epiphyton.

PERCENTAGE OF PERONIA FIBULA
IN THE POST-LIMING EPIPHYTON

DATE
Fig. 5.15: Boxplot of *Brachysira vitrea* in the post-liming epiphyton

PERCENTAGE OF *BRACHYSIRA VITREA*

IN THE POST-LIMING EPYPHTON
Fig. 5.16: Boxplot of *Achnanthes minutissima* in the post-liming epiphyton
Fig. 5.17: Boxplot of *Fragilaria vaucheriae* in the post-liming epiphyton

PERCENTAGE OF *FRAGILARIA VAUCHERIAE*
IN THE POST-LIMING EPiphyton
Fig. 5.18: Boxplot of *Synedra acus* in the post-liming epiphyton

PERCENTAGE OF *SYNEDRA ACUS* IN THE POST-LIMING EPIPHYTON
Fig. 5.19: Boxplot of *Tabellaria flocculosa* in the post-liming epiphyton
Fig. 5.20: Boxplot of *Gomphonema gracile* in the post-liming epiphyton
Fig. 5.21: Boxplot of *Gomphonema angustatum* in the post-liming epiphyton
Fig. 5.22: Boxplot of *Gomphonema angustatum* var. *producta* in the post-liming epiphyton
Fig. 5.23: Boxplot of *Gomphonema angustatum*/gracile in the post-liming epiphyton
Fig. 5.24: Boxplot of *Eunotia rhomboidea* in the post-liming epiphyton
Fig. 5.25: Boxplot of *Eunotia vanheurkii* var. 1 in the post-liming epiphyton

PERCENTAGE OF *EUNOTIA VANHEURKII* VAR. 1
IN THE POST-LIMING EPiphyTON

DATE
Fig. 5.26: Boxplot of Tabellaria quadriseptata in the post-liming epibryon

PERCENTAGE OF TABELLARIA QUADRISSEPTATA
IN THE POST-LIMING EPIBRYON

DATE
Fig. 5.27: Boxplot of *Eunotia incisa* in the post-liming epibryon
Fig. 5.28: Boxplot of *Peronia fibula* in the post-liming epibryon
Fig. 5.29: Boxplot of *Brachysira vitrea* in the post-liming epibryon
Fig. 5.30: Boxplot of *Achnanthes minutissima* in the post-liming epibryon
Fig. 5.31: Boxplot of *Diatoma tenue* var. *elongatum* in the post-liming epibryon
Fig. 5.32: Boxplot of *Fragilaria vaucheriae* in the post-liming epibryon
Fig. 5.33: Boxplot of *Synedra acus* in the post-liming epibryon

PERCENTAGE OF *SYNEDRA ACUS*
IN THE POST-LIMING EPIBRYON

DATE
Fig. 5.34: Boxplot of *Gomphonema angustatum* in the post-liming epibryon

**PERCENTAGE OF GOMPHONEMA ANGUSTATUM**

**IN THE POST-LIMING EPIBRYON**
Fig. 5.35: Boxplot of *Tabellaria flocculosa* in the post-liming epibryon

PERCENTAGE OF *TABELLARIA FLOCCULOSA*
IN THE POST-LIMING EPIBRYON

DATE
Fig. 5.36: Boxplot of *Tabellaria binalis* fo. *elliptica* in the post-liming epipsammon
Fig. 5.37: Boxplot of *Tabellaria quadrisepata* in the post-liming epipsammon
Fig. 5.38: Boxplot of *Eunotia incisa* in the post-liming epipsammon
Fig. 5.39: Boxplot of *Achnanthes minutissima* in the post-liming epipsammon
Fig. 5.40: Boxplot of *Achnanthes altaica* in the post-liming epipsammon
Fig. 5.41: Boxplot of *Brachysira vitrea* in the post-liming epipsammon
Fig. 5.42: Boxplot of *Eunotia vanheurkii* var. *intermedia* in the post-liming epipsammon.

PERCENTAGE OF *EUNOTIA VANHEURKII VAR. INTERMEDIA* IN THE POST-LIMING EPIPSAMMON
Fig. 5.43: Boxplot of *Eunotia vanheurkii* var. 1 in the post-liming epipsammon
Fig. 5.44: Boxplot of *Achnanthes marginulata* in the post-liming epipsammon
Fig. 5.45: Boxplot of *Eunotia rhomboidea* in the post-liming epipsammon
Fig. 5.46: Boxplot of *Achnanthes austriaca* var. *helvetica* in the post-liming epipsammon

PERCENTAGE OF ACHNANTHES AUSTRIACA VAR. HELVITICA IN THE POST-LIMING EPIPSAMMON
Fig. 5.47: Boxplot of *Tabellaria flocculosa* in the post-liming epipsammon
Fig. 5.48: Boxplot of *Eunotia pectinalis* var. *minor* in the post-liming epipsammon
Fig. 5.49: Boxplot of *Eunotia tenella* in the post-liming epipsammon

PERCENTAGE OF EUNOTIA TENELLA
IN THE POST-LIMING EPIPSAMMON
Fig. 5.50: *Synedra acus*; planktonic concentrations
Fig. 5.51: Asterionella formosa; planktonic concentrations
Fig. 5.52: Changes in pH and common epilithic diatoms in Loch Fleet

COMMON EPILITHIC TAXA IN LOCH FLEET 1981–1988

- Tabellaria quadriseptata
- Frustulia rhomboides var. saxonica
- Eunotia Incisa
- Brachysira brebissonii
- Peronella fibula
- Brachysira vitrea
- Fragilaria vaucheriae
- Achnanthes minutissima
- Tabellaria flocculosa
Fig. 5.53: Changes in pH and common epiphytic diatoms in Loch Fleet

COMMON EPiphytic TAXA IN LOCH FLeET 1982-1988

Tabellaria quadriseptata

Eunotia incisa

Peronia fibula

Achnanthes minutissima

Brachysira vitrea

Fragilaria vaucheriae

Tabellaria flocculosa

DATE

Fig. 5.54: Changes in pH and common epibyron diatoms in Loch Fleet

COMMON EPIBRYON TAXA IN LOCH FLEET 1981–1988

- Tabellaria quadriseptata
- Eunotia incisa
- Peronia fibula
- Brachysira vitrea
- Achnanthes minutissima
- Tabellaria flocculosa

DATE
Fig. 5.55: Changes in pH and common epipsammic diatoms in Loch Fleet

Common Epipsammic Taxa in Loch Fleet 1981-1988

- Tabellaria binalis fo. elliptica
- Tabellaria quadrisepatata
- Eunotia vanheurkii var. intermedia
- Eunotia incisa
- Eunotia rhomboidea
- Achnanthes altaica
- Eunotia vanheurkii var. 1

DATE

CHAPTER 6: SEDIMENT TRAPS

1. Introduction

The underlying aim of the project was to examine the relationship between living diatom communities and the record of these communities in recent sediment. Sediment traps provide a useful means of investigating this relationship for several reasons.

1. Sediment traps provide a link, in space, between non-planktonic and planktonic diatoms, and diatom assemblages accumulating in the lake sediments.

2. Sediment traps enable short term events to be resolved. Where these events give a weak signal being either of too short a duration or of too low an intensity, for example too few valves arriving to register in the stratigraphic record, traps may provide the only clear record.

3. Sediment traps provide a continuous, relative measure of the composition of the diatom mixture arriving at the sediment during any exposure period. They are a simple means of estimating relative diatom productivity as opposed to the measures of standing crop given by sampling of non-planktonic or planktonic standing crops.

4. Resuspension of sediment can be monitored by sediment traps. Comparison in space (depth) between traps of species composition, live to dead cell ratios, and dry weight sedimenting material (SM) collected may allow estimation of the intensity of resuspension.

2. Trap Design

The use of sediment traps in aquatic environments has been extensively reviewed (Bloesch and Burns 1980, Blomqvist and Håkanson 1981). The design of the traps themselves and the array from which they were suspended was based on the recommendations of these authors, but adapted for use in Loch Fleet (Fig. 6.1).

Simple cylindrical traps have been found to yield the best results, in terms of amount of sediment trapped (undertrapping vs. overtrapping) when compared with traps of different geometries. Though the primary purpose of the traps in this project was not
Fig. 6.1: Design of sediment traps and sediment trap array

SEDIMENT TRAP

SEDIMENT TRAP ARRAY-Centre

Marker Buoy
Rope
Subsurface Float
Pair of Traps
Trap Holder

Lake Bed
Anchor
to measure absolute flux rates the cylindrical configuration is in any case the simplest to construct. A related detail of design was that the internal diameter of traps be great enough to avoid aberrant effects due to unusual current flow, such as sorting of different fractions of SM. Experimental studies of these effects have been contradictory, but where the circular mouth of a trap is small (less than 4.5 cm) discriminate fractioning of SM has been observed (Blomqvist and Kofoed 1981). The 5.1 cm internal diameter of the trap cylinders used here was considered suitable to avoid this problem.

Retention of sediment already trapped and the avoidance of winnowing or resuspension of SM during turbulent periods is related to the protection of the SM by the trap walls. By using cylinders with a high enough aspect ratio, that is the ratio of the height of the cylinder to its internal diameter, this effect can be avoided. The aspect ratio used was greater than 5:1 which according to experimental studies should be adequate to retain the sediment collected.

The mooring system for the traps was of the type most commonly employed in lakes. An anchor weight on the lake bottom was attached to a rope, the rope at its top end was tied to a supporting subsurface buoy and marked by another buoy tied by a second rope (Fig. 6.1). The trap holders and traps were located at 3 m intervals (to avoid interference between trap pairs at each depth) along the rope stretched between anchor and subsurface buoy. The reason for supporting the traps with a subsurface float is that waves on the surface of the lake would cause oscillation of a surface float; the movement can be transferred down the line and cause resuspension of material in the trap. In Loch Fleet the amplitude of waves would be unlikely to exceed 2 m and, in any case, the maximum effective fetch of the lake was not at the points where trap arrays were placed (Fig. 6.2). Placement of the supporting buoy approximately 4 m (central trap array) and 3 m (peripheral trap arrays) beneath the surface was therefore ample. The lowest pairs of traps on any array were placed 1.5 m above the lake bed, in accordance with a general recommendation of Bloesch and Burns (1981). Bottom traps should not be too close to the mud surface (1-3 m above is suggested) because of the possibility of trapping (artificially) resuspended lake bottom sediments, especially those disturbed during sampling and replacement of the trap arrays.

Replicate pairs of traps were located at different depths in the water column and at different sites. The use of replicate traps enabled trends in the amount and composition of SM to be considered in relation to differences between replicate samples before considering between space and depth sample variation. The use of arrays of traps at
Fig. 6.2: Location of sediment traps

Loch Fleet
All contours in metres
different depths enabled the possibility of resuspension of lake bed sediments to be monitored, and testing of whether trap height above the lake bed influenced SM catches. In the event that trap catches were similar the use of multiple traps would enable further replication, and confidence in results.

The periods of exposure between emptying of SM from the traps was variable (Table 6.1). Several factors determined the length of sampling period. The initial test immersion of the central traps for a period of only 13 days was to gain some idea of the amount of sediment that might be expected to accumulate, its composition and variability. Following the results of this pilot study (see later) it was decided to lengthen the exposure period, to increase the amount of sediment collected and to reduce the number of samples for retrieval and analysis. Exposure times of 1-2 months were therefore used. During the winter period of 1987, after overturn, it was unnecessary to empty the traps for a longer period.

3. Spatial variability: peripheral vs. central traps

To determine the extent of spatial variability in the amount and composition of SM 4 arrays of peripheral sediment traps were exposed during sampling periods 2 & 3 (Table 6.1). The characteristics of SM collected from these peripheral traps are compared with those of the SM from the central trap arrays during the 2 equivalent periods of exposure (see below).

Peripheral trap exposure "Period 2P" (30.4.87 - 10.6.87, 41 days) is compared with central trap exposure "Period 2" (16.4.87 - 10.6.87, 55 days) and peripheral trap exposure "Period 3P" (10.6.87 - 21.7.87, 41 days) with central trap exposure "Period 3" (10.6.87 -28.7.87, 48 days).

Examination of uncleaned SM from the peripheral traps during Period 3P revealed that the top traps in the arrays (4.5m above lake bed in approximately 7.5m water depth) had a consistently higher percentage of diatom frustules containing intact chloroplasts (maximum 80.4%, minimum 66.7%) when compared with the traps suspended at 1.5m above the lake bed (maximum 41.1%, minimum 32.9%) (Fig. 6.3). In diatom counts of this wet material the species composition was also consistently different between top and bottom traps with 'live' cells of *Synedra acus* at higher percentages in the top traps.
Table 6.1: Exposure dates for sediment traps

<table>
<thead>
<tr>
<th>Exposure</th>
<th>Dates</th>
<th>Days</th>
<th>Position</th>
</tr>
</thead>
<tbody>
<tr>
<td>Period 1</td>
<td>3.4.87-16.4.87</td>
<td>13</td>
<td>Central</td>
</tr>
<tr>
<td>Period 2</td>
<td>16.4.87-10.6.87</td>
<td>55</td>
<td>Central</td>
</tr>
<tr>
<td>Period 2P</td>
<td>30.4.87-10.6.87</td>
<td>41</td>
<td>Peripheral (NW,NE,E,S)</td>
</tr>
<tr>
<td>Period 3</td>
<td>10.6.87-28.7.87</td>
<td>48</td>
<td>Central</td>
</tr>
<tr>
<td>Period 3P</td>
<td>10.6.87-21.7.87</td>
<td>41</td>
<td>Peripheral (NW,NE,E,S)</td>
</tr>
<tr>
<td>Period 4</td>
<td>6.8.87-18.2.88</td>
<td>196</td>
<td>Central</td>
</tr>
<tr>
<td>Period 5</td>
<td>18.2.88-29.4.88</td>
<td>71</td>
<td>Central</td>
</tr>
<tr>
<td>Period 6</td>
<td>29.4.88-17.6.88</td>
<td>49</td>
<td>Central</td>
</tr>
<tr>
<td>Period 7</td>
<td>17.6.88-20.8.88</td>
<td>64</td>
<td>Central</td>
</tr>
<tr>
<td>Period 8</td>
<td>20.8.88-24.10.88</td>
<td>65</td>
<td>Central</td>
</tr>
<tr>
<td>Period 9</td>
<td>24.10.88-30.12.88</td>
<td>67</td>
<td>Central</td>
</tr>
<tr>
<td>Period 10</td>
<td>30.12.88-7.4.89</td>
<td>98</td>
<td>Central</td>
</tr>
</tbody>
</table>
Fig. 6.3: Live:dead ratios from peripheral traps during period 3

LIVE:DEAD CELL RATIOS FROM PERIPHERAL TRAPS

(Period 3P)

<table>
<thead>
<tr>
<th>Position of Traps</th>
<th>Live (%)</th>
<th>Dead (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NW4.5m</td>
<td>80</td>
<td>20</td>
</tr>
<tr>
<td>NW1.5m</td>
<td>36</td>
<td>64</td>
</tr>
<tr>
<td>NE4.5m</td>
<td>67</td>
<td>33</td>
</tr>
<tr>
<td>NE1.5m</td>
<td>33</td>
<td>67</td>
</tr>
<tr>
<td>E4.5m</td>
<td>74</td>
<td>26</td>
</tr>
<tr>
<td>E1.5m</td>
<td>41</td>
<td>59</td>
</tr>
<tr>
<td>S4.5m</td>
<td>73</td>
<td>27</td>
</tr>
<tr>
<td>S1.5m</td>
<td>35</td>
<td>65</td>
</tr>
</tbody>
</table>

percentage of total cells

Legend:
- □ dead
- □ live
These observations, along with the knowledge that the top traps were only 3m below the water surface, lead to the conclusion that the upper traps of the arrays were in the photic zone (at least for some diatoms) and cells growing in situ were being added to the catch of SM. The discussion of spatial variability within the group of peripheral traps and between these and the central array of traps is therefore based on the catches of the lower traps, 1.5m above the lake bed and at least 6m below-the water surface, below the compensation depth for diatoms (see chapter 4, section 2i).

i. Dry weight of sediment collected (peripheral)

During Period 2P the maximum amount of SM collected was 83 mg dry weight (dw) (both traps in the NE) and the minimum 7 mg dw (one trap in the S) (Fig. 6.4a). A distinct pattern was seen with NW, S and E traps collecting similar amounts of SM (7-15 mg dw) whilst the pair of traps at the NE collected more than 5 times the maximum amount SM recorded elsewhere. During Period 3P (Fig. 6.4b) the maximum amount of SM collected was 64 mg dw (S replicate B) and the minimum 27 mg dw (NW replicate B). During this exposure period dry weight catches of the E, NE and NW traps were similar (maximum 36 mg dw, minimum 27 mg dw), but the S traps recorded about twice the dry weights measured at the other locations.

ii. Dry weight fluxes (peripheral vs central)

Converting dry weights to dry weight fluxes enables comparison between the amounts collected by the peripheral traps and the amount of SM collected by traps in the central array (at various depths) during Period 2 (55 days) and Period 3 (48 days) respectively (Fig. 6.5a,b).

In Period 2P (Fig. 6.5a) NW, E, and S traps recorded similar fluxes (maximum 0.018 mg cm\(^2\) day\(^{-1}\), minimum 0.08 mg cm\(^2\) day\(^{-1}\)) to traps in the central array in Period 2 (maximum 0.027 mg cm\(^2\) day\(^{-1}\), minimum 0.014 mg cm\(^2\) day\(^{-1}\)), even without allowing for the possibility that the rate of flux was different during the additional period of central trap exposure. The dw flux to the NE trap pair, however, was clearly greater (both traps 0.100 mg cm\(^2\) day\(^{-1}\)) than any of the other peripheral traps or the central traps. The high flux was probably related to the proximity of the site to the main inflow stream (Fig. 6.2) resulting in a considerable input of stream-transported sediment.
Fig. 6.4 (a) Dry weight of SM; collected period 2P (b) Dry weight of SM; collected period 3P

a Dry weight (peripheral traps, Period 2P)

b Dry weights (peripheral traps, Period 3P)
Fig. 6.5  

(a) Dry weight flux of SM; period 2P (peripheral traps) vs. period 2 (central traps)  
(b) Dry weight flux of SM; period 3P (peripheral traps) vs. period 3 (central traps)
In Period 3P (Fig. 6.5b) the higher rates of SM dw flux ( >0.07 mg cm\(^{-2}\) day\(^{-1}\)) recorded in the S traps were approached by the flux rates recorded by the central trap array (maximum 0.071 mg cm\(^{-2}\) day\(^{-1}\), minimum 0.049 mg cm\(^{-2}\) day\(^{-1}\)). Fluxes to both central and S traps exceeded rates measured in E, NE and NW traps (maximum 0.043 mg cm\(^{-2}\) day\(^{-1}\), minimum 0.032 mg cm\(^{-2}\) day\(^{-1}\)).

iii. Valve concentrations and fluxes (peripheral)

During Period 2P (Fig. 6.6a) valve concentrations in the peripheral traps were more variable than the dry weights measured for the same exposure (Fig. 6.4a). However, corresponding to the higher dry weights recorded in the NE traps compared with the NW, S and E traps, the diatom valve concentrations were greater than in the other peripheral traps (NE maximum 8.0 \(x\) 10\(^6\) valves, minimum 7.4 \(x\) 10\(^6\) valves cf. other peripheral traps maximum 5.4 \(x\) 10\(^6\), minimum 2.9 \(x\) 10\(^6\) valves). During Period 3P (Fig. 6.6b) valve concentrations range from 0.5 \(x\) 10\(^6\) valves to 5.0 \(x\) 10\(^6\) valves. Despite the peaks in dry weight occurring in the S traps during Period 3P (cf. Fig. 6.4b) peaks in diatom valve concentration are (like period 2P) in the NE traps.

Comparison of valve fluxes for central and peripheral traps during Periods 2 and 2P respectively (Fig. 6.7a) show that generally higher rates were recorded in the central array traps, particularly those in the deepest water, (maximum 15.5 \(x\) 10\(^3\) valves cm\(^{-2}\) day\(^{-1}\)) than in the peripheral traps. The peaks recorded by the NE peripheral traps (maximum 9.7 valves cm\(^{-2}\) day\(^{-1}\)) compared with the other peripheral traps were similar to the top central traps.

During Period 3P (Fig. 6.7b) there is again a peak in the valve fluxes measured in the NE traps (maximum 6.0 \(x\) 10\(^3\) valves cm\(^{-2}\) day\(^{-1}\)). Elsewhere the fluxes measured by the peripheral traps were smaller (maximum 1.5 \(x\) 10\(^3\) valves cm\(^{-2}\) day\(^{-1}\), NW replicate A). For Period 3 (Fig. 6.7b) the central traps recorded smaller fluxes than the peaks recorded at the NE in the equivalent period 3P, reaching a maximum (3.0 \(x\) 10\(^3\) valves cm\(^{-2}\) day\(^{-1}\)) of less than half the flux at the NE. In general the fluxes at the centre were more similar to the other peripheral traps (NW, E, S).
Fig. 6.6 (a) Diatom valve concentrations in peripheral traps; period 2P (b) Diatom valve concentrations in peripheral traps, period 3P

(a) Valve concentrations (peripheral traps, Period 2P)

(b) Valve concentrations (peripheral traps, Period 3P)
Fig. 6.7 (a) Diatom valve flux to sediment traps; period 2P (peripheral) and period 2 (central) (b) Diatom valve flux to sediment traps period 3P (peripheral) and period 3 (central)

Valve flux
(peripheral traps, Period 2P vs. central traps Period 2)

Valve flux
(peripheral traps, Period 3P vs. central traps Period 3)
iv. Diatom composition of trap assemblages (peripheral vs central)

Percentage frequency histograms of diatom taxa common (occurring at percentages greater than >5% in any sample) in the trap assemblages are presented in Fig. 6.8 & in Fig. 6.9.

During Period 2 and Period 2P central and peripheral traps (1.5m above the lake bed) recorded the same dominant species (Fig. 6.8). These were *Achnanthes minutissima*, *Eunotia incisa*, *Peronia fibula* and *Synedra acus*, but in the NE peripheral traps there were also high frequencies of *Diatoma tenue* var. *elongatum*, and *Achnanthes minutissima* was present at its maximum frequency. These local percentage peaks were possibly related to the proximity of the NE trap arrays to the main inflow stream, the Altiwhat, which was at higher pH than the lake. The higher part of the catchment of this stream (Sector IV Fig. 2.1) received a heavy application of limestone dust (10 tonnes ha⁻¹) during the first treatment of the catchment in 1986. With the exception of *Diatoma tenue* var. *elongatum* the range of species percentages was also similar between central and peripheral traps though wider for the peripheral traps. Making this comparison between trap assemblages using only the most common taxa results in a loss of information since most species are present at low percentages. An ordination method, DCA, has therefore been used to examine the similarity of the total species composition of each sample for Periods 2 & 2P (Fig. 6.10). A plot of the sample scores on the first two ordination axes, using all the species percentages from each sample, shows that the species composition within the group of central traps is more similar than within the group of peripheral traps. Individual pairs of peripheral traps, however, may have closer similarity to one another, for example the NE and S traps respectively. Secondly the ordination shows that though common species composition is generally consistent in space (cf.Fig. 6.8) the compositions of whole assemblages may not be so alike.

During Period 3 and Period 3P (Fig. 6.9) the relationship between central and peripheral trap assemblages is consistent with that in Period 2 and 2P. The common taxa are the same in all traps. *Achnanthes minutissima*, *Brachysira vitrea*, *Eunotia incisa*, *Peronia fibula* and *Synedra acus* are dominant, but again, exceptionally, in the NE traps *Diatoma tenue* var. *elongatum* is important. Dominant species percentages are similar with a slightly wider range in the peripheral traps. DCA of these data for Periods 3 and 3P (Fig. 6.11) show that both central and peripheral traps are grouped, and there is less
Fig. 6.8: Common diatom taxa in trap assemblages; period 2P (peripheral) and period 2 (central)
Fig. 6.9: Common diatom taxa in trap assemblages; period 3P (peripheral) and period 3 (central)

Common Taxa in Peripheral (Period 3P) and Central (Period 3) Sediment Traps

- Diatoma tenue var. elongatum
- Peronia fibula
- Brachysira vitrea
- Eunotia incisa
- Achnanthes minutissima
- Synedra acus

trap sample

percentage of total diatom valves

trap sample
Fig. 6.10: DCA of trap diatom assemblages, period 2 and period 2P
Fig. 6.11: DCA of trap diatom assemblages; period 3 and period 3P
variability in the diatom composition of traps from the periphery. Replicate traps from the NE can again be separated.

4. Temporal trends (central traps)

Having examined the performance of sediment traps located in different areas of the lake the sediment trapping strategy was rationalised on the basis of the information collected.

Despite variability between traps in terms of SM and valve flux the different spatial arrays of traps were shown to record similar percentages of dominant taxa. Where this was not the case, as in the NE group of traps, the cause was almost certainly a definable (inshore) local input, the Altiwhat inflow stream (see Chapter 4). Consequently it was decided to use only the central sediment trap array to monitor SM through time. The central array was also the one most suitably located for making eventual comparisons with sediment cores.

i. Dry weight of sediment collected

Exposure periods for the central traps are shown in Table 6.1. The mean dry weight of sediment collected in the central array of 8 traps during each of the 10 sampling periods is plotted in Fig. 6.12. The maximum mean amount collected is 0.2514 g per trap in period 10 (98 days) and the minimum amount 0.0071 g per trap in the initial test study, period 1 (13 days). The relatively wide range of 95% confidence intervals on some sampling occasions show that within-sampling period variation in dry weight of sedimenting material (SM) recovered is often high (e.g. periods 4, 6, 7 and 8) possibly due to systematic variation between the amount of SM collected at different water depths.

In order to provide large enough samples for a test of significance the 8 traps in the array were divided into 2 groups of 4 samples for each sampling occasion; a shallow water group of traps from 10.5m and 7.5m above the lake bed and a deep water group of traps from 4.5m and 1.5m above the lake bed. A t-test for small samples, which assumes that sample variances are equal, was used. The null hypothesis: that there was no significant difference in mean dry weight SM between traps in shallower water and those in deeper water was tested against the alternative: that there was a significant difference.
Fig. 6.12: Mean dry weight and sediment collected per trap (central trap array)
The critical value of "t" at the 0.05 significance level with 6 degrees of freedom is +/-2.447. It is found that the null hypothesis cannot be rejected for periods 1,3,4,5,7,8,10; but must be rejected for periods 2,6,9 when the calculated value of t falls outside of the set range. During periods 2,6 and 9 there were significantly greater amounts of dry weight SM collected 10.5m and 7.5m above the lake bed compared with the amounts at 4.5m and 1.5m above the lake bed. These differences in sediment trap catches at different heights may result from resuspension of sediment from the lake bed. Deeper traps, situated closest to the lake bed, are likely to catch more of this resuspended material.

In addition to the variability of SM within the arrays there is considerable variability between exposure periods (Fig. 6.12). This is related to the irregularity of the exposures with a maximum of 196 days in period 4 and a minimum of 13 days (test exposure) in period 1. However, a linear regression (Fig. 6.13) of mean dry weight SM on time period (days) of trap exposure shows that increasing or decreasing the period of trap exposure does not have a simple positive linear effect on the amount of SM trapped ($r^2=0.41$). This at least partly reflects the seasonal or sporadic nature of some events which affect the catches of the traps eg. planktonic algal blooms (especially diatoms).

The dry weight flux of SM to the traps was calculated (Fig. 6.14). The maximum flux recorded was $12.33 \times 10^{-2}$ mg cm$^{-2}$ day$^{-1}$ in period 10 and a minimum flux of $1.87 \times 10^{-2}$ mg cm$^{-2}$ day$^{-1}$ in period 2. Three peaks in sediment flux were recorded; period 3, period 7, and period 10. The tailing peaks at periods 6 and 8 appear to be associated with the peak at period 7. A fairly consistent background SM flux of approximately $2.5 \times 10^{-2}$ mg cm$^{-2}$ day$^{-1}$ dw was registered during periods 1,2,4,5 and 9.

**ii. Diatom valve concentrations and fluxes**

Mean number of diatom valves collected was calculated for each sampling period. The minimum number of diatom valves collected was $0.83 \times 10^{6}$ valves during period 1 and the maximum number of valves was $239.18 \times 10^{6}$ valves during period 10. A scatterplot of mean valve concentration against mean dry weight SM for each period (Fig. 6.15) suggests that these are correlated and is confirmed by linear regression ($r^2=0.81$). It is therefore concluded that diatom valves contribute a fairly consistent proportion to the dry weight of SM during the total sampling period. Moreover in view of the large fluctuations in SM amount, unless other types of SM can co-vary with inputs of diatom
Fig. 6.13: Linear regression of DW SM vs. sampling period

Linear regression of DW SM vs. sampling period
(all data included)

$r^2 = 0.41$
Fig. 6.14: Dry weight accumulation rate of sediment (central traps)
Fig. 6.15: Linear regression of number of diatom valves vs. dry weight SM trapped

Linear regression of diatom valves vs. dry weight SM trapped

\[ r^2 = 0.81 \]
valves, diatom valves and their cell contents are the major component of the dry weight of SM.

The mean flux of diatom valves to the traps is plotted in Fig. 6.16. Two peaks in the mean flux of diatom valves to the traps were recorded at period 6 and period 10; 6.9 x 10^4 and 12.0 x 10^4 valves cm^-2 day^-1 respectively. At periods 1,2,3,4,5,7,8,9 the mean flux of diatom valves did not rise above 1.7 x 10^4 valves cm^-2 day^-1 (period 5) and had a minimum value of 0.2 x 10^4 valves cm^-2 day^-1 (period 3). The 2 maxima are associated with spring blooms of planktonic diatoms: in 1988 (period 6) Synedra acus and in 1989 (period 10) Asterionella formosa. During the rest of the periods of trap exposure non-planktonic taxa were the dominant forms.

iii. Composition of trap diatom assemblages

In the 80 sediment trap samples 173 diatom taxa were recorded. Of these only 2 extant taxa, Synedra acus and Asterionella formosa, were regarded as planktonic. However, 4 planktonic Cyclotella species, absent from the present flora of the lake and probably derived from the resuspension of older sediment, were recorded at low abundances in the trap assemblages. The remaining diatom taxa are considered to be non-planktonic.

An initial comparison was made between all 80 diatom assemblages using a DCA ordination. A plot of the axis 1 and axis 2 scores from this ordination revealed that groups of 8 samples from the same sampling period were closely similar by comparison of species composition (Fig. 6.17). The mean percentages of the dominant taxa for each time period were therefore used to indicate trends in species composition (Fig. 6.18).

iv. Species composition of traps through time

Histograms showing the trends in species composition of the central trap array are presented in Fig. 6.18. The species percentages for each sampling period are means of the compositions of all 8 central array traps. The 16 species selected had mean abundances of greater than 2% during at least one sampling period.

The dominant species of the acidification period, Tabellaria quadriseptata is present during all sampling periods, having maximum abundance (5%) during period 1, but significant percentages (c.2-4%) occur in all sampling periods except 5 and 6 where the percentages of all non-planktonic taxa are suppressed by plankton. The initiation of
Fig. 6.16: Mean accumulation rate of diatom valves (central traps)

Diatom valve accumulation rate (central traps)
(error bars are drawn above and below means)

Exposure period
Fig. 6.17: DCA of central trap diatom assemblages; trapping periods 1 to 10
Fig. 6.18: Mean composition of common species; central array
trapping was too late to record the pre-liming levels of suspended *Tabellaria quadriseptata* and its immediate response to liming. However, the relatively low levels of the species throughout the trapping project is in accordance with the reduced abundances of *Tabellaria quadriseptata* in the post-liming non-plankton communities and subsequent evidence for its decline in sediment cores. That the species occurs at all in sediment traps, considering its very low percentages or complete absence in most post-liming non-plankton samples, can be accounted for by one or a combination of three factors: high cell division rates in the species leading to a poor (an unequal) correlation between species percentage abundance and cell production rates; resuspension of cells/valves from the surface sediment, including valves from the pre-liming period of maximum abundance and those lost from the non-plankton communities in the post-liming period; and slow lateral transport or sedimentation rates from life-time habitat to death assemblage resulting in constant suspension of recently removed valves.

*Tabellaria binalis* fo. *elliptica*, a predominantly epipsammic diatom, is present at above 1% during only the first three trapping periods. Its pattern of abundance in the sediment traps conforms with both its post-liming decline in the epipsammic community and declining trends in the surface sediments of the latest cores. Unlike *Tabellaria quadriseptata*, the abundance of *Tabellaria binalis* fo. *elliptica* is not modified significantly by taphonomic processes in the transition from live community to death assemblage. Its limited habitat, the restricted areas of sand in the littoral, is probably the cause of its low percentage representation in surface sediment even at its maximum abundance. The ratio between these two species in post-liming sediments is not obviously higher than in the surface sediment of LF L3 so the apparent difference in their representation in sediment traps may just be a function of relatively high (*Tabellaria quadriseptata*) and low (*Tabellaria binalis* fo. *elliptica*) maximum (absolute) abundances.

*Achnanthes marginulata*, another predominantly epipsammic diatom sporadically common before liming shows a similar pattern of abundance to *Tabellaria binalis* fo. *elliptica*, present at 1-2% during the first 4 trapping periods and then appearing at less than 1% or absent in the remaining 6 periods. The abundance of this species in the epipsammon is variable both pre- and post-liming and the relationship between its percentage in the non-plankton communities and traps is therefore unclear.

*Peronia fibula* is a mainly epiphytic diatom dominating or important on the surfaces of higher plants and bryophytes during the post-liming period. This species was present
in the core LF L3 at a maximum of almost 10% before acute acidification of the lake (Fig. 2.5b). Its mean abundance on the higher plants sampled was greater than 12% at all sampling times between October 1986 and October 1987, reaching a maximum of 43% (May 1987). On the surfaces of the bryophyte, Scapania undulata, its average abundance was not less than 13% during the period October 1986 to March 1988 and reached a maximum of 39% (July 1987). In both habitats Peronia fibula declines during the later part of 1987 or early part of 1988. This pattern of abundance is reflected in the composition of sediment trap catches. A peak of abundance occurring in Period 2 (8%) and a decline thereafter. The 2 trap sampling periods of maximum Peronia fibula abundance, Periods 2 and 3 (May to July 1987), correspond to the period of sustained maximum abundance in the epiphyton (May to July 1987 when minimum abundance was 25%) and epibryon (May to July 1987 when minimum abundance was 24%). Though mainly epiphytic it should be noted that Peronia fibula occurred at significant percentages in the epilithon and again May to July 1988 was a period of sustained high abundances (3-6%) followed by a decline.

Five taxa, Frustulia rhomboides, Frustulia rhomboides var. saxonica, Eunotia pectinalis, Eunotia pectinalis var. ventralis and Brachysira brebissonii are all present in core LF L3 and are consistently present at significant percentages in sediment traps. All 5 taxa decline overall during the trapping period and their percentages are suppressed when percentages of the planktonic diatom Synedra acus are highest (Periods 5-7). Neither of the Eunotia taxa are present at high percentages in any live community. However, the acidophilous diatoms Frustulia rhomboides var. saxonica and Brachysira brebissonii occur at maximum percentages in pre-liming and the earliest post-liming epilithon samples which does match the general pattern of abundance in the traps.

Eunotia incisa is present at high percentages in all live non-planktonic communities, co-dominant with Tabellaria quadriseptata in the pre-liming period, but rising to a maximum in the earliest post-liming samples from epilithon, epiphyton, epibryon and epipsammon communities. This post-liming trend in the species abundance is clearly reflected by the trend in mean percentage from the sediment traps, declining from 15% at Period 1 to less than 1% at Period 6. Though the reduction in Eunotia incisa percentages during Periods 5 and 6 is to some extent artificial resulting from the dominance of Synedra acus the declining trend in Eunotia incisa is clear before the planktonic diatom becomes dominant.
Brachysira vitrea rises to its maximum percentage in trap samples during Period 3 (12%), declines, again as Synedra acus blooms, and then rises to 6% in Period 9. This pattern of abundance is consistent with the species percentage in all non-planktonic habitats where it shows 2 post-liming peaks of abundance in 1987 and 1988 separated by a minimum in the spring of 1988.

Achnanthes minutissima is common in the core before acidification, reaching a maximum of 10%, but, during the post-liming period Achnanthes minutissima becomes the most important non-planktonic diatom and this is reflected in its abundance in trap samples. In period 1 Achnanthes minutissima has already reached a mean abundance of 16% in trap catches, consistent with its increase from sporadic pre-liming presences to consistent dominance of epilithon, epiphyton, and epibryon communities. The initial post-liming samples from all periphytic communities have low mean percentages of Achnanthes minutissima, for example it is absent from epilithic samples from July 1986 and by October 1986 it is present at only 1%. However, by April 1987 the species has increased to 17% of the epilithon composition and by May 1987 it is at 33%. This increase is followed in other non-planktonic communities and in the traps where there is a maximum of 37% at period 4. The percentage of Achnanthes minutissima is suppressed both by the dominance of Synedra acus in Period 6 (6%) but also reflects reduced percentages of the species in the periphyton. Achnanthes minutissima recovers to a maximum of 25% at period 9 again following the trend seen in epilithon, epiphyton and epibryon communities.

Fragilaria vaucheriae is rare or absent in pre-liming periphyton samples and occurs rarely in core LF L3. In the post-liming period it does not rise above 2% except in the epiphyton where it has sporadic, but relatively low maxima (eg. 7% November 1987). During this period the species occurs at less than 2% in the sediment trap catches, therefore its low relative abundance in the traps correlates well with that in the live communities. Fragilaria vaucheriae does not occur at any time at abundances of greater than 2% in the epipsammon. A clear, single maximum in Fragilaria vaucheriae occurs in sediment traps during period 5 (February to April 1988) and during the remainder of trapping its percentage declines (3-2%). This pattern of abundance matches that found in the non-plankton. Most significantly Fragilaria vaucheriae reaches a maximum abundance of 30% in the epiphyton during March 1988. In the epilithon the maximum (6%) of Fragilaria vaucheriae occurs in March 1988, and in the epibryon the maximum (7%) also occurs in March 1988.
Synedra acus, is primarily a planktonic diatom and the species was rare in the master-core LF L3. Valves of this species were also recorded in all non-planktonic communities, and examination of fresh material revealed that the species was attached to the respective substrates (see Chapter 5). The very high abundance of Synedra acus recorded in traps during period 6 (89%) is clearly caused by a bloom of a planktonic form of this diatom. Peaks occur in the non-planktonic communities (epilithon 10%, epiphyton 6% and epibryon 29%) at the same time May/June 1988 but part of this species component is probably contaminant from the plankton.

Pre-liming non-plankton samples show high percentages of Tabellaria flocculosa and the species is common at abundances of greater than 5% before acute acidification. During the immediate post-liming period it occurs at consistently low percentages. However, periphyton samples from August to October 1988 have high percentage maxima of the species (epilithon maximum 50%, epiphyton maximum 47%, epibryon 37%). This period of peak Tabellaria flocculosa percentages is followed by sediment trap catches where a maximum of 17% occurs in November/December 1988.

The planktonic diatom taxon Asterionella formosa is absent in samples from this community until late 1988 and the beginning of 1989 and rare in sediment trap catches during periods 1 to 9. The species occurs sporadically throughout the core LF L3. A significant increase of the species, to 1%, occurs in traps during November/December 1988 and during the period January to March 1989 there is a clear peak (16%) in Asterionella formosa. This maximum is clearly associated with a bloom of the species.

v. Source of diatom assemblages

The interpretation of the diatom assemblages collected by sediment traps is dependent on the provenance of the diatoms collected. It is clear that the composition of diatoms in the traps through time strongly reflects the changes in live plankton and non-plankton communities (Chapter 5). However, there are other possible sources including stream inputs, the atmosphere (assumed to be negligible) and resuspension. Aerial transport and deposition of significant numbers of diatoms is unlikely, although this may be a route for the migration of new species to the site. The lake catchment including inflowing streams is implied as a significant source of diatoms and at least localised inputs have been recognised (eg. Diatoma tenue var. elongatum associated with the Altiwhat stream). Resuspension from the lake bed includes both older sediment and contemporary material. To some extent older diatoms can be detected in this study because of the
floristic changes that have occurred. For example *Cyclotella* spp. occurring in traps are clearly resuspended and some *Tabellaria quadrisepata* has also been resuspended (see earlier discussion of this species).

vi. "Live":dead:broken diatom valve ratios

Detecting resuspended recent diatoms is more difficult although estimation of the "live":dead cell ratio can give some indication of the process’ relative importance. Counts of "live":dead:broken cell ratios were made for this purpose. The rationale of this technique was that "live" cells, i.e. those with stained chloroplasts visible, were recently living and represent a new input to the sediment: cells recently recruited from the non-plankton or plankton. Dead valves were empty valves and frustules and more importantly broken cells which were more likely to be older in origin having arrived through resuspension from sediments or resulting from turbulent or abrasive transport processes.

This approach to separating diatom sources is obviously optimistic because there is overlap in the condition of diatom valves from discrete sources. For example intact frustules with cell contents may be deposited in surface sediment remain there for sometime and then be resuspended and recorded in traps as apparently new inputs. Conversely recently living cells newly deposited in the traps may have been damaged in transport losing their contents or being broken.

A summary diagram showing the mean percentages of "live":dead:broken valves (Fig. 6.19) is shown. Three maxima in live cells are recorded at periods 3, 6, & 10. The peaks recorded at period 6 (62%) and period 10 (73%) are clearly associated with planktonic diatom blooms, *Synedra acus* and *Asterionella formosa* respectively. (The origin of the live cell peak at period 3 (52.5%) is enigmatic particularly in view of low valve concentration recorded at this time).

Since the possibility of *in situ* diatom growth in traps was eliminated previously the live component of cells is known to represent recent diatom growth in natural habitats. Secondly the input of broken cells is never greater than 20%. Given the turbulent conditions of the lake, and comparing this to the level of breakage in cores where most valves might be at least partly damaged it would suggest that resuspension of lake bed material into traps, though occurring, is not severe and that the proportion of older (i.e.
Fig. 6.19: Mean percentages of "live":dead:broken valves in central traps
pre-liming) frustules in the traps is very small eg. more than 80% of the diatoms collected by traps are diatoms that did not occur in surface sediment.

It is therefore reasonable to make comparisons between living diatom communities and trap assemblages. Further, the traps may provide an integrated record of diatom percentages from all communities, reinforcing and improving the quantification of species abundances estimated through spot percentage counts made on the live material. Finally, if the resuspended component of sediment trap catches is small the use of sediment traps to compare with the records of sediment cores is justified. Where the sampling periods are short (months) sediment traps provide a means of assessing the potential to resolve events of short duration in sediment cores (see Chapter 7).
1. Introduction

Diatom analysis of sediment cores has been used to investigate changes in the diatom flora of lakes and for environmental reconstruction (eg. Battarbee 1978, 1986, Evans & Walker 1977, Haworth 1969, Round 1957, 1961). The use of a stratigraphic record of diatoms to investigate environmental history has a number of advantages compared to other methods of reconstruction, such as the use of historical ecological data, or physical and chemical measurements. Even in studies of the very recent past the palaeoecological record may provide the only reliable quantitative data available. Historical biological, physical or chemical measurements may be absent, sporadic, or have used non-comparable techniques of measurement through time while diatom analysis of lake sediment cores can potentially provide continuous and compatible data for reconstructing the diatom flora and lake environment (Battarbee 1984).

The central aim of this project is to assess how accurately sediment cores taken from the main sampling area of Loch Fleet adjacent to the position of LF L3 (see Chapter 2) record actual changes in live communities. The strategy adopted was to take short Kajak cores at intervals of several months (see Table 7.1). An advantage of the selection of Loch Fleet as the study site was that cores could be sampled with fine time resolution. \(^{210}\)Pb dating (Anderson et al. 1986) showed that the present rate (core taken in 1985) of sediment accumulation was just less than 1.5 cm a\(^{-1}\) so the 0.5 cm slicing interval used in routine sampling of Kajak cores was both appropriate and convenient to use in assessing the resolution of these cores.

In addition freezer coring was carried out (April 1989) to check whether greater resolution was possible. However, despite recovering frozen sediment with an apparently undisturbed sediment/water interface the initial analyses of the surface sediments from 3 cores showed that the sequences had been truncated. This artefact of the stratigraphies was attributed to severe disturbance of the flocculant sediment surface as the corer entered. Therefore all results are based on sequences taken by Kajak corer. These cores were located close to LF L3 and the main trap array (Fig. 7.1- on standard lake map). Coring dates are shown in Table 7.1.

Each core was analysed down to a depth sufficient to place the core record in the context of the previous phase of acidification (cf. Anderson et al. 1986) and to allow
Table 7.1: Dates of coring, Kajak cores

<table>
<thead>
<tr>
<th>Core</th>
<th>Date</th>
<th>Length (cm)</th>
<th>Water depth(m)</th>
<th>Months after 1st liming</th>
<th>Months after 2nd liming</th>
</tr>
</thead>
<tbody>
<tr>
<td>K1086</td>
<td>01.10.86</td>
<td>14</td>
<td>c. 10.5</td>
<td>5</td>
<td>-</td>
</tr>
<tr>
<td>K0687</td>
<td>18.06.87</td>
<td>18</td>
<td>c. 10.5</td>
<td>14</td>
<td>2</td>
</tr>
<tr>
<td>K0987</td>
<td>16.09.87</td>
<td>20</td>
<td>c. 10.5</td>
<td>17</td>
<td>5</td>
</tr>
<tr>
<td>K0288</td>
<td>20.02.88</td>
<td>18</td>
<td>c. 10.5</td>
<td>22</td>
<td>10</td>
</tr>
<tr>
<td>K0788</td>
<td>12.07.88</td>
<td>27</td>
<td>c. 10.5</td>
<td>27</td>
<td>15</td>
</tr>
<tr>
<td>K1088</td>
<td>25.10.88</td>
<td>23</td>
<td>c. 10.5</td>
<td>30</td>
<td>18</td>
</tr>
<tr>
<td>K1288</td>
<td>30.12.88</td>
<td>21</td>
<td>c. 10.5</td>
<td>32</td>
<td>20</td>
</tr>
<tr>
<td>K0489</td>
<td>07.04.89</td>
<td>24</td>
<td>c. 10.5</td>
<td>35</td>
<td>23</td>
</tr>
</tbody>
</table>
Fig. 7.1: Location of post-liming cores

Loch Fleet
All contours in metres

Location of post-liming cores.
approximate dates and accumulation rates to be calculated by biostratigraphic correlation with LF L3. Dating of individual cores was not necessary given the high degree of resolution required compared with the relatively large standard errors attached to $^{210}$Pb dates. An attempt was made to $^{210}$Pb date a single Kajak core, K0987, but a reliable chronology was not obtained (S. Hutchinson pers. comm.). However, post-liming cores could be correlated and approximately dated by reference to the *Tabellaria quadriseptata* peak representing the surface sediment at the time of liming in 1986 (see below).

Recently Anderson (in press) considered the variability of the post-acidification, pre-liming sediment diatom assemblages in Loch Fleet, comparing 28 surface samples and 11 short cores (0-40 cm) taken from different sites around the lake. In most of the surface samples there was a 'reasonable uniformity of taxa.' Seven atypical samples were clearly influenced by the presence of reworked diatom taxa or *in situ* growth of diatoms. All of these atypical samples were from sites in shallower water, less than 10m deep, most less than 5m, where it might be anticipated that modifying processes such as reworking of older sediments and *in situ* growth of diatoms would occur.

Species trends in the cores were found to be less variable than in the surface sediment samples. Anderson argues that this is probably the result of post-depositional time averaging processes where sediment mixing smooths the short term variability (noise) in the record. His study indicates that it is valid to use a time sequence of cores taken from a small area to follow temporal trends in diatom assemblages, especially since sediment accumulation rates are unlikely to vary greatly over such a limited distance (see above).

In order to provide a basis for the description of post-liming cores from Loch Fleet and for comparison of post-liming diatom assemblages with possible historical analogues the established system of diatom biostratigraphic zones (Anderson *et al*. 1986) is copied here. Anderson's original taxonomy has been modified to match recently agreed SWAP names (Munro *et al*. 1990). Six diatom biostratigraphic zones were identified in the core LF L3, and these together with a summary diagram are presented in Chapter 2.

On the basis of this earlier work at Loch Fleet it was decided that the area of sediment accumulation in the north-east of the lake should be used as a primary coring site. This site was chosen for 3 reasons. Firstly there was known to be a continuous sediment record in that area, secondly it was shown to be the zone of most rapid sediment
accumulation, thirdly the site was close to the location used for the earlier Loch Fleet master core, LF L3, facilitating comparison between this core and the new cores.

2. Wet density, dry weight and loss on ignition (LOI) of Kajak cores (Fig. 7.2)

All cores were composed of visibly homogeneous, dark brown mud unless described otherwise. Wet density measurements were only carried out on K1086 and K0687, since this parameter is used principally for calculating sediment accumulation rates by radiometric dating. The core codes are based on the date (month and year) of sampling.

i. K1086 14cm (Fig. 7.2a)

K1086 was taken approximately 6 months after liming. Wet density fluctuates from 1.08 to 1.11 g cm$^{-3}$ and percentage dry weight is consistent, 9 to 11%. LOI decreases overall by about 10% from a peak value of 57% (8-9cm) to a surface minimum of 46%.

ii. K0687 18cm (Fig. 7.2b)

K0687 was taken approximately 13 months after liming. Wet density increases from the base of the core from a minimum of 1.06 g cm$^{-3}$ (16-17cm) to a maximum of 1.12 g cm$^{-3}$ at the surface. Percentage dry weight also follows an increasing trend upwards with a minimum at 13-14cm (12%) and maximum 0-0.5cm (18%). LOI decreases from 80% (14-15cm) to 41% (0-0.5cm). The sharp decline in LOI at 1-0cm (15%) is matched by distinct increases in wet density and dry weight.

iii. K0987 20cm

K0987 was taken 16 months after liming, and $^{210}$Pb dated. However this was unreliable (see above). Consequently no LOI measurements were made on the core. Four of the uppermost levels were subsequently analysed for diatoms.

iv. K0288 18cm (Fig. 7.2c)

The core was taken 21 months after liming. Percentage dry weight declines from a maximum of 11% (17-18cm) to a minimum at the surface of 8%. LOI decreases from
68% (13-14cm) to 39% (1.0-1.5cm). A distinct increase in organic sediment (to 45%) at the surface (0-2cm) follows the decreasing trend in dry weight in this section. The abrupt change in both percentage dry weight and LOI at 2.0-2.5cm is taken to be the result of sediment loss during measurement and is therefore an artefact.

v. K0788 27cm (Fig. 7.2d)

Percentage dry weight shows a decreasing trend from a maximum of 13% at 24-25cm to a minimum of 9% at 2-2.5cm. A small peak in percentage dry weight (11%) occurs just below the surface at 1.5-2.0 cm. Overall LOI measurements show a decreasing trend with a maximum at 26-27cm (64%) and maxima at 20-23cm (69%) and 4.5-5.0cm (61%). The lowest organic content is at 1.5-2.0cm (43%).

vi. K1088 23cm (Fig. 7.2e)

The core was taken 29 months after liming. Percentage dry weight has a declining trend from the bottom of the core (12%) to 4.5-5.0cm (9%). A maximum occurs at 2.5-3.0cm, declining to 7% at the surface. LOI has 2 peaks with maxima at 21-22cm (63%) and 12-13cm (62%). The trend is to a reduced organic content; 56% at the core base to 36% at 2.5-3.0cm. There is a rise in LOI at the surface, reaching 48% at 0.0-0.5cm.

vii. K1288 21cm (Fig. 7.2f)

This core was taken 31 months after liming. Percentage dry weight declines from a maximum of 11% at the bottom of the core to a minimum of 7% at the surface. There is an overall decline in organic content from the base of the core (63%) to 1.5-2.0cm (38%) (there is a maximum value of 67% at 13-14cm). The declining trend of organic content is followed by a rise in LOI, to 42% at the surface.

viii. K0489 24cm (Fig. 7.2g)

This core was taken 35 months after liming. Percentage dry weight is approximately 10% to 1.5-2.0cm, declines to 5% at 0.5-1.0cm and increases to 7% at the surface. LOI is maximum (68%) at 22-23cm declining to a minimum at 1.5-2.0cm (40%) followed by a peak (51%, 0.5-1.0cm) and decline, to 41%, at the surface.
Fig. 7.2a: (a-d) Post-liming cores, lithostratigraphy

a K1086

b K0687

c K0288

d K0788
Fig. 7.2b: (e-g) Post-liming cores, lithostratigraphy

\[ \text{e K1088} \]

\[ \text{g K0489} \]

\[ \text{f K1288} \]
3. Diatom concentrations of Kajak cores (Fig. 7.3)

Fig. 7.3 shows profiles of diatom concentrations for the cores on which diatom percentage counts were made. The units are cells per gramme dry weight of sediment (cells g\(^{-1}\) dw).

i. **K1086** (Fig. 7.3a)

Diatom concentration is highest at the bottom of the core (1.7 \( \times \) 10\(^8\) cells g\(^{-1}\) dw) decreasing to 0.6 \( \times \) 10\(^8\) cells g\(^{-1}\) dw by 7-8cm. A small peak in concentration occurs at 4-5cm (1.1 \( \times \) 10\(^8\) cells g\(^{-1}\) dw) falling to 0.7 \( \times \) 10\(^8\) cells g\(^{-1}\) dw at 2.5-3.0cm. Cell concentrations then rise towards the surface where they reach 1.6 \( \times \) 10\(^8\) cells g\(^{-1}\) dw.

ii. **K0687** (Fig. 7.3b)

Concentrations rise from the base of the core to a maximum of 1.0 \( \times \) 10\(^8\) cells g\(^{-1}\) dw at 12-13cm. Between 10-2cm cell concentrations are stable at about 0.5 \( \times \) 10\(^8\) cells g\(^{-1}\) dw and then increase to 0.7 cells g\(^{-1}\) dw at the surface.

iii. **K0987** (Fig. 7.3c)

Cell concentrations are maximum at the base of the core (1.8 \( \times \) 10\(^8\) cells g\(^{-1}\) dw), decreasing to about 1.1 \( \times \) 10\(^8\) cells g\(^{-1}\) dw between 14-8cm, and then rising again to 1.5 \( \times \) 10\(^8\) cells g\(^{-1}\) dw at 4.0-4.5 cm. There is a sharp decrease to 0.3 \( \times \) 10\(^8\) cells g\(^{-1}\) dw at 1.5-2.0cm and then a rise to 0.8 \( \times \) 10\(^8\) cells g\(^{-1}\) dw at the surface.

iv. **K0288** (Fig. 7.3d)

As a result of loss of sediment samples, cell concentrations were only available for 3 levels of this fragmentary core. At 3.0-3.5cm the diatom concentration is 1.9 \( \times \) 10\(^8\) cells g\(^{-1}\) dw, and the surface concentration is 1.3 \( \times \) 10\(^8\) cells g\(^{-1}\) dw.

v. **K0788** (Fig. 7.3e)

Diatom cell concentration is minimum at the base of the core (0.5 \( \times \) 10\(^8\) cells g\(^{-1}\) dw) then increases to about 1.6 \( \times \) 10\(^8\) cells g\(^{-1}\) dw, remaining at this level between 15-8cm. The concentration declines to 0.9 \( \times \) 10\(^8\) cells g\(^{-1}\) dw at 4.0-4.5cm and then rises to a
maximum of $2.2 \times 10^8$ cells g$^{-1}$ dw at 3.3.5cm. There is a sharp decline in cell concentration towards the surface (0-0.5cm, $1.1 \times 10^8$ cells g$^{-1}$ dw).

vi. K1088 (Fig. 7.3f)

Cell concentrations decline from the base of the core and then rise to a maximum of $2.4 \times 10^8$ cells g$^{-1}$ dw at 14-15cm. After decreasing to a minimum ($0.9 \times 10^7$ cells g$^{-1}$ dw) at 6.0-7.0cm there are peaks of $2.0 \times 10^8$ cells g$^{-1}$ dw at 4-4.5cm and 1.5-2.0cm. Following a fall in cell concentration at 1.0-1.5cm ($1.1 \times 10^8$ cells g$^{-1}$ dw) there is an increase towards the surface (0-0.5cm, $1.6 \times 10^8$ cells g$^{-1}$ dw).

vii. K1288 (Fig. 7.3g)

Cell concentration is minimum at the base of the core (19-20cm, $0.7 \times 10^8$ cells g$^{-1}$ dw). A maximum occurs at 8-9cm ($1.9 \times 10^8$ cells g$^{-1}$ dw) followed by a sharp decline 3.0-3.5cm ($1.7 \times 10^8$ cells g$^{-1}$ dw) to 0.5-1.0cm ($0.7 \times 10^8$ cells g$^{-1}$ dw). The concentration then rises at the surface ($1.3 \times 10^8$ cells g$^{-1}$ dw).

viii. K0489 (Fig. 7.3h)

Cell concentration is minimum at the base of the core (19-20cm, $1.2 \times 10^8$ cells g$^{-1}$ dw), increases to $1.8 \times 10^8$ cells g$^{-1}$ dw at 13-14cm, but is approximately level from the bottom up to 4.0-4.5cm ($1.3 \times 10^8$ cells g$^{-1}$ dw). The concentration rises to a maximum at 3.0-3.5cm ($3.2 \times 10^8$ cells g$^{-1}$ dw), declines to $1.3 \times 10^8$ cells g$^{-1}$ dw at 1.0-1.5cm and then increases to the surface (0-0.5cm $2.8 \times 10^8$ cells g$^{-1}$ dw).

4. Diatom percentages of Kajak cores

The percentages of selected common taxa are shown in Figs. 7.4 to 7.11. These stratigraphic diagrams have not been divided into diatom assemblage zones since it was not considered appropriate to constrain the description of the uppermost sediments, post-liming, to fixed units. It is clear, especially in the later cores that due to time-averaging processes the composition of the upper centimetres is dynamic. However, the lower levels of the post-liming cores have been compared with the zones established by Anderson et al. (1986) for the core LF L3 (Fig. 2.5) in order to locate the positions of these cores in relation to the full sediment profile. All cores show the final acidification stages of the lake, most clearly seen in the transition from *Eunotia incisa*
Fig. 7.3: (a-h) Post-liming cores, diatom concentration
dominated assemblages to assemblages dominated by *Tabellaria quadriseptata*. This feature has been most convenient for biostratigraphic correlation and dating transfer.

A single boundary has been fixed as a point of reference. This is the upper level of the *Tabellaria quadriseptata* maximum in any core. It is argued that this level must correspond either to the time immediately before liming, when *Tabellaria quadriseptata* was most common, or else a time immediately after liming when there was catastrophic loss of this acidobiontic species from the live communities to the sediments. The mean date of this feature is therefore 1985/86.

**i. K1086 (Fig. 7.4)**

This core was taken approximately 5 months after liming. At 13-14 cm *Brachysira vitrea*, *Fragilaria virescens* var. *exigua*, *Tabellaria flocculosa*, *Cymbella lunata*, *Eunotia pectinalis* var. *minor* and *Achnanthes minutissima* are important taxa. This section of the core represents the post-afforestation, but pre-acidification zone (LF L3-D4) of Anderson et al. (1986). Above this level *Eunotia incisa* increases to become dominant (6-7 cm, 30%) whilst the taxa important at the base of the core all decline. The rise of *Eunotia incisa* is accompanied by increasing percentages of *Eunotia naegelii*, *Brachysira brebissonii*, *Cymbella perpusilla* and *Frustulia rhomboides*. From 4-5 cm the curve of *Tabellaria quadriseptata* begins to rise, and there is also a slight increase in *Frustulia rhomboides* var. *saxonica*. At the surface *Tabellaria quadriseptata* is dominant (24%) and the presence of *Tabellaria binalis* fo. *elliptica* (0-0.5 cm, 1.7%) is established. *Eunotia incisa*, *Eunotia naegelii*, *Eunotia pectinalis* var. *minor*, *Cymbella perpusilla* and *Brachysira vitrea* percentages decrease at the surface. Although this core was taken over 5 months after liming, and the non-planktonic community had already changed, the diatom composition in the sediment shows no evidence of liming.

**ii. K0687 (Fig. 7.5)**

This core was taken approximately 14 months after liming. At 13-18 cm *Brachysira vitrea*, *Eunotia incisa*, *Eunotia pectinalis* var. *minor*, *Achnanthes minutissima*, *Fragilaria virescens* var. *exigua* and *Cymbella lunata* are the dominant taxa. This basal section of the core again corresponds to zone LF L3-D4 of the long core. At 14-15 cm the percentage of *Eunotia incisa* begins to rise, reaching 33% by 7-8 cm. The *Eunotia incisa* increase is closely followed by increases in the percentages of *Cymbella perpusilla*, *Frustulia rhomboides* var. *saxonica*, *Brachysira brebissonii* and *Eunotia naegelii*, whilst
Fig. 7.4: Diatom percentages, core K1086

[Graph showing diatom percentages for various species, e.g., Asterionella formosa, Fragilaria vaucheriae, Gomphonema minutissimum, Tabellaria fenestrata, Tabellaria flocculosa, etc.]
Fig. 7.5: Diatom percentages, core K0687
the importance of other taxa dominating the bottom of the core is reduced, the percentages of *Achnanthes minutissima*, *Brachysira vitrea*, *Eunotia pectinalis* var. *minor*, *Fragilaria virescens* var. *exigua* and *Cymbella lunata* all decrease. From 5cm depth the percentage of *Tabellaria quadriseptata* rises, increasing to 8% at the surface, and *Navicula subtilissima* establishes a continuous curve. In the top 2cm *Tabellaria binalis* fo. *elliptica* is present. Following (slight) reductions in the curves of *Eunotia incisa* (4-5cm, 18%) and *Brachysira brebissonii* (3.0-3.5cm, 2.1%) there is some evidence of their recovery after liming in the upper 2.5cm of the core; *Eunotia incisa* reaches 24% at 0-0.5cm and *Brachysira brebissonii* 4.2% at 0-0.5cm. This core has a very similar record to K1086. Species changes take place at almost the same depths suggesting almost identical accumulation rates, but the slight increase in *Eunotia incisa* and *Brachysira brebissonii* may indicate the first record of a response to liming.

iii. K0987 (Fig. 7.6)

This core was taken in September 1987 approximately 18 months after liming. At 19-20cm the core has maximum percentages of *Achnanthes minutissima*, *Brachysira vitrea*, *Fragilaria virescens* var. *exigua*, *Eunotia pectinalis* var. *minor* and *Cymbella lunata*. At 8-9cm these taxa have declined in importance. *Eunotia incisa* becomes dominant (8-9cm, 34%) along with *Eunotia naegelii*, *Frustulia rhomboides*, *Frustulia rhomboides* var. *saxonica*, *Brachysira brebissonii* and *Cymbella perpusilla*. Again the base of the core corresponds to zone LF L3-D4 of core LF L3 with the establishment of *Eunotia incisa* dominance corresponding to zone LF L3-D5. At or below 4.0-4.5cm the curve of *Tabellaria quadriseptata* begins to rise reaching a maximum percentage of 27% at 1-1.5cm. The increase in *Tabellaria quadriseptata* is accompanied by the appearance of *Tabellaria binalis* fo. *elliptica* and generally higher percentages of *Navicula subtilissima*. In the same section of the core *Eunotia incisa*, and some of those taxa dominant with it eg. *Eunotia naegelii* and *Cymbella perpusilla* decline. Between 1 and 0cm a reduction in the dominance of *Tabellaria quadriseptata* occurs (0-0.5cm, 14%) and there is a significantly greater percentage of *Achnanthes minutissima* (0-0.5cm, 8%), *Frustulia rhomboides* decreases to 2%, *Brachysira vitrea* increases to 3% at the surface and *Fragilaria vaucheriae* appears in the top 1cm of sediment. The significance of fluctuations in the percentages of *Eunotia incisa* (increase then decrease) and small increase in *Tabellaria flocculosa* is uncertain. The accumulation rate of this core is very similar to K1086 and K0687. However, in contrast to those cores there is a clear signal in the uppermost 1cm of the effect of liming, shown by the reduced percentage of *Tabellaria quadriseptata* and marked increase of *Achnanthes minutissima*. At the same
Fig. 7.6: Diatom percentages, core K0987

[Diagram showing diatom percentages for various species across different core depths.]
levels there is also a clear indication of sediment mixing since during the post-liming period *Tabellaria quadriseptata* is no longer of any importance in the live communities (see Chapter 5) and yet maintains high percentages in the top 1cm.

iv. K0288 (Fig. 7.7)

*Eunotia incisa*, *Cymbella perpusilla*, *Brachysira vitrea* are maximum at 3.0-3.5cm. All decline to surface along with declining *Eunotia naegelii*, *Eunotia pectinalis* var. *minor* and *Cymbella lunata* and later *Frustulia rhomboides* var. *saxonica*. *Tabellaria quadriseptata* rises to 16% and *Tabellaria binalis* fo. *elliptica* 3% at the surface. There is also a rise in *Brachysira brebissonii* to the surface. At 0-0.5cm *Achnanthes minutissima* reaches 6% abundance, a clear response to liming.

v. K0788 (Fig. 7.8)

This core was taken over 2 years after the initial liming of the lake catchment. Below 8cm the dominant taxa are *Brachysira vitrea*, *Achnanthes minutissima*, and *Eunotia incisa*. *Eunotia incisa* rises to a maximum of 27% at 3.0-3.5cm along with an increase in the percentages of *Cymbella perpusilla*, *Frustulia rhomboides* var. *saxonica* and later *Eunotia naegelii* and *Navicula subtilissima*. The basal levels therefore correspond to the zone LF L3-D4 of the long core and the section of increasing *Eunotia incisa* dominance to the zone LF L3-D5. *Tabellaria quadriseptata* increases to a maximum (22%) at 1.0-1.5cm and *Tabellaria binalis* fo. *elliptica* reaches a maximum at the same level. Where these acidobiontic taxa reach their maxima the level is equated with liming in April 1986. From 2.0cm the curve of *Synedra acus*, which appears in abundance for the first time, begins to increase and reaches 17% at the surface. In the surface 1cm *Achnanthes minutissima* and *Fragilaria vaucheriae* appear at significant percentages whilst *Tabellaria quadriseptata*, *Navicula subtilissima*, *Eunotia naegelii*, *Frustulia spp.*, and *Cymbella perpusilla* have all declined. This core appears to have a slow accumulation rate, reflecting changes in both the non-plankton and plankton, but in the top 1 cm pre-liming taxa continue to be among the dominant species.

vi. K1088 (Fig. 7.9)

The core was taken approximately two and a half years after the first liming of the lake catchment. The base of the core has maximum percentages of *Brachysira vitrea* and *Tabellaria flocculosa*, along with relatively high percentages of *Fragilaria virescens*
Fig. 7.7: Diatom percentages, core K0288
Fig. 7.8: Diatom percentages, core K0788
Fig. 7.9: Diatom percentages, core K1088
var. exigua, Cymbella lunata and Eunotia incisa. This level of the core corresponds to the zone LF L3-D4 of the Loch Fleet master core. However, an anomalous peak of Tabellaria quadriseptata (7%) occurs at this level and is possibly the result of contamination of basal sediment by core extruding rather than being a real feature of the core stratigraphy. The assemblage dominated by Brachysira vitrea then declines and Eunotia incisa becomes the most common species. The rise in Eunotia incisa is accompanied by increases in the percentages of Eunotia naegelii, Frustulia spp., Brachysira brebissonii, and Cymbella perpusilla. This section of the core corresponds to the zone LF L3-D5. Above 6cm depth Eunotia incisa declines along with Eunotia naegelii and Frustulia rhomboides. The base of the core therefore begins at a time equivalent to the LF L3-D4 zone and shows the transition to LF L3-D5 as Brachysira vitrea declines and Eunotia incisa rises to dominance.

Tabellaria quadriseptata increases to dominance, reaching a maximum of 21% at 2.0-2.5cm, this level represents the time of maximum acidity and immediately above the sequence is equated with liming of the lake. Tabellaria binalis fo. elliptica and Navicula subtilissima reach maxima at 1.5-2.0cm. From 2.5cm the percentages of Synedra acus and Achnanthes minutissima begin to increase, rising sharply in the surface centimetre where these species dominate (0.0-0.5cm Synedra acus 30%, and Achnanthes minutissima 14%). Fragilaria vaucheriae, Brachysira vitrea and Tabellaria flocculosa increase significantly in the top 1cm. Eunotia incisa, Eunotia naegelii and Brachysira brebissonii decline further in the surface sediment whilst the percentages of Tabellaria quadriseptata, Tabellaria binalis fo. elliptica, Frustulia rhomboides var. saxonica and Navicula subtilissima are abruptly reduced. The increasing curves of Synedra acus and Achnanthes minutissima penetrating to 2.5 cm clearly reflect mixing processes. This is apparent for 2 reasons. Firstly the peak percentage of Tabellaria quadriseptata is suppressed compared with that of its pre-liming maximum in surface sediment. Secondly the establishment of a continuous presence of Synedra acus is attributable to the post-liming period. However, the accumulation rate of sediment cannot have been so rapid as to allow over 2cm of sediment to have accumulated within the post-liming period, the time period during which Synedra acus appeared at significant abundance.

vii. K1288 (Fig. 7.10)

The core was taken approximately 2 years and 8 months after the first liming. The base of the core begins during a period equivalent to LF L3-D4. At 19-20cm the assemblage
Fig. 7.10: Diatom percentages, core K1288
is dominated by *Achnanthes minutissima*, *Brachysira vitrea*, *Cymbella lunata*, *Fruzulia rhomboides* var. *saxonica*, *Asterionella formosa* and *Eunotia incisa*. At 8-9cm the percentage of *Achnanthes minutissima* is reduced and *Fragilaria virescens* var. *exigua* increases to 10%. By 4.0-4.5cm the assemblage is dominated by *Eunotia incisa* (28%), *Eunotia naegelii*, *Cymbella perpusilla*, and *Fruzulia spp.* *Brachysira vitrea* and *Fragilaria virescens* var. *exigua* decline. This part of the core is like zone LF L3-D5 and the replacement of circumneutral taxa such as *Achnanthes minutissima* and *Brachysira vitrea* by acidophilous diatoms, such as *Eunotia incisa* and *Eunotia naegelii*, indicates the onset of acidification. Above 3.5cm the curve of *Tabellaria quadriseptata* rises, reaching a maximum of 20% at 1.0-1.5cm. At the same depths the curves of *Tabellaria binalis* fo. *elliptica*, *Navicula subtilissima* and *Brachysira brebissonii* rise whilst *Eunotia incisa* and *Cymbella perpusilla* decline. This depth of the core represents the time of maximum acidity. From 1.5cm depth *Synedra acus* and *Achnanthes minutissima* increase. The importance of these species in planktonic and non-planktonic communities and the associated increases in abundance in the sediment are clearly post-liming events. These 2 taxa are dominant at the surface (*Synedra acus* 20%; *Achnanthes minutissima* 13%) along with *Fragilaria vaucheriae* which increases in the top 1cm of the core. However, again the depth (1.5cm) to which the dominant post-liming taxa penetrate is suggestive of downward mixing of sediment. In the surface sediment 0.0-0.5cm there are also small increases in the percentages of *Brachysira vitrea* and *Fragilaria virescens* var. *exigua*. Percentages of *Tabellaria quadriseptata*, *Tabellaria binalis* fo. *elliptica*, *Navicula subtilissima* and *Brachysira brebissonii* decrease sharply in the surface centimetre. *Eunotia incisa*, *Eunotia naegelii*, *Fruzulia rhomboides* and *Cymbella perpusilla* decline further as *Synedra acus* and *Achnanthes minutissima* increase. Although a small increase *Eunotia incisa* 0.5-1.0cm may be significant and related to its immediate post-liming maximum. In addition to the downward mixing of sediment inferred from the behaviour of post-liming taxa, the continuing high percentages of species associated with acidification, show that upward mixing of sediment has occurred. In particular *Tabellaria quadriseptata*, a species shown to be virtually absent from the post-liming non-planktonic community, remains at high percentages in the top 1cm of the core (15% at 0.5-1cm, 10% at 0-0.5 cm).

viii. K0489 (Fig. 7.11)

This core was taken almost 3 years after the first liming of the lake. The base of the core is dominated by *Achnanthes minutissima*, *Brachysira vitrea*, *Fragilaria virescens* var. *exigua* and *Eunotia incisa*. There are also relatively high percentages of *Eunotia*
Fig. 7.11: Diatom percentages, core K0489
pectinalis var. minor and Cymbella lunata. The base of the core therefore corresponds to the LF L3-D4 zone, of post-afforestation, but pre-acidification times. *Eunotia incisa* becomes the most common species and its increase is accompanied by increases in the percentages of *Frustulia* spp., *Brachysira brebissonii*, *Cymbella perpusilla* and *Eunotia naegelii*. Other species dominant at the base of the core, such as *Achnanthes minutissima* and *Brachysira vitrea*, decline. This part of the core, dominated by *Eunotia incisa*, is equivalent to the LF L3-D5 zone and represents the onset of acidification. At or below 3.5cm depth the curve of *Tabellaria quadriseptata* begins to rise, reaching a maximum of 11% at 1.0-1.5cm. *Tabellaria binalis* fo. *elliptica* and *Navicula subtilissima* increase in the same section of the core. *Eunotia incisa* and co-dominant species decrease. The maximum percentage of *Tabellaria quadriseptata* at 1-1.5 cm represents a time immediately before or immediately following liming. From about 2cm depth the curves of *Achnanthes minutissima* and *Synedra acus* increase to their maxima (*Achnanthes minutissima* 21% at 0.5-1.0cm and *Synedra acus* 29% at 0.0-0.5cm). The increases of these species corresponds to their post-liming expansion in the non-planktonic and planktonic communities respectively. The curve of *Tabellaria quadriseptata* is sharply reduced and the percentages of *Eunotia incisa*, *Eunotia naegelii*, *Frustulia* spp. and *Cymbella perpusilla* decrease further. In the surface 1.5cm *Fragilaria vaucheriae* appears at significant percentages; the curve of *Brachysira vitrea* rises gradually from about 2.5cm. At the surface *Asterionella formosa* appears (0.0-0.5cm, 8%). This sudden appearance of *Asterionella formosa*, a planktonic taxon not present in the lake at high percentages since before the post-afforestation period, is the result of a bloom of the species during the early part of 1989.

5. Discussion

i. Lithostratigraphy and relative accumulation rate

Comparing the results of lithostratigraphic analysis of the post-liming cores with the pre-liming master core, LF L3, and with other cores from the pre-liming period provides a preliminary method of relating stratigraphies, before the detailed biostratigraphies are compared.

Anderson *et al.* (1986) divided the core LF L3 into 3 lithostratigraphic units. Clearly all the post-liming cores can be matched to the upper part of the core (Fig. 2.4), the zone of high organic values (>40% LOI). These cores which have consistently high organic content therefore represent post-ploughing (post 1961-1963) sediments.
A general declining trend is seen in LOI values of the post-ploughing sediment in all cores to the surface or just below the surface. This trend was observed by Anderson et al. (1986) in pre-liming cores and is probably related to the stabilisation of catchment soils after tree canopy closure. However, the surface sediment organic content of 40% is still considerably higher than pre-afforestation levels (Fig. 2.4) suggesting that accelerated erosion is still occurring.

In the 3 latest cores, K1088, K1288 and K0489 a rise in LOI values is seen at the surface. In K1088 this rise begins at a 2.5-3.0cm, in K1288 the rise in LOI begins at 1.5-2.0cm, and in K0489 LOI increases from 1.5-2.0cm and then decreases from 0.5-1.0cm to the surface. These surface peaks in LOI relate to the post-liming period (above *Tabellaria quadriseptata* maximum, see later). Their origin is uncertain, but the increased organic content is probably the result of increased productivity within the lake, rather than organic inputs from the catchment where there is no evidence for significant peat disturbance at this time. Whether the autochthonous organic source was the result of increased algal productivity and in particular the blooms of planktonic taxa such as the chlorophytes or diatoms like *Synedra acus* (this might also result in increased silica fluxes to the sediment), or whether it is the result of the post-liming die-back of higher plants or bryophytes (in particular *Sphagnum*) is not clear.

### ii. Diatom concentrations between cores

Diatom cell concentrations in all cores were of the same order of magnitude and were comparable with the range of cell concentrations measured in the master core LF L3 during the post ploughing period (c. 10-20 x 10^7 cell g^-1 dw). Maximum cell concentrations were approximately 30 x 10^7 cells g^-1 dw of sediment and minimum values were slightly less than 5 x 10^7 cells g^-1 dw and cell concentrations were commonly in the range 10-20 x 10^7 cells g^-1 dw.

Without calibrating the data to compensate for cell size, especially since the taxonomic composition of diatom assemblages changed significantly, or variations in sediment accumulation rate, it is not possible to equate trends in cell concentration to productivity or silica inputs. Moreover, since only cores at a single location in the lake have been considered there is no basis for calculating basin-wide diatom storage in the sediments. The data, however, indicate that between core variations in concentration are
relatively small and that the pre- and post-liming cores are broadly comparable in this respect.

iii. Diatom composition

Though backup replicate cores were taken on most sampling occasions, these were not usually prepared or counted. Replication was unnecessary for two reasons. Firstly, previous work at Loch Fleet (Anderson, in press) has shown that temporal trends in core diatom assemblages can be replicated in space and a primary coring site, of rapid and continuous sediment accumulation had already been located. Secondly, along with the other sources of data used there was no time to replicate core data in space for each sampling period. It was decided to concentrate on time series and assume, on the basis of other studies of spatial variability, that temporal variation in diatom assemblages would be greater than spatial variation.

The results of the diatom analyses described indicate that the variability of pre-liming sequences of cores in time, though present, is not great. However, considerable variation in sediment accumulation rates occurs even though cores were closely spaced. This observation is in agreement with work at Loch Fleet (Anderson in press) and at other sites (eg. Anderson 1986, Battarbee 1978) where replicate cores, though located close together and exhibiting similar diatom changes, recorded different accumulation rates. This is important for the resolution of recent events. For example the accumulation rate of core K1088 is relatively fast whilst that of K0788 is slow. Mean accumulation rates can be inferred from the post-afforestation *Eunotia incisa* rise, in K1088 this transition from *Brachysira vitrea* to *Eunotia incisa* occurs at about 22 cm whilst in K0788 the equivalent transition is seen at a maximum depth of about 7cm. In the master-core LF L3 the zone boundary LF L3-D4 to LF L3-D5 at 21cm is placed at this point and $^{210}$Pb dating (Anderson *et al.* 1986) dates the boundary at 1976. Using the date of this boundary the mean annual accumulation rate can be estimated at about 1.8 cm a$^{-1}$ for K1088 and about 0.6 cm a$^{-1}$ for K0788. Both cores have slower mean accumulation rates than LF L3 (c.2.3 cm a$^{-1}$ from the equivalent depth).

The composition of surface sediment from core K1086, taken 5 months after liming, shows no evidence for the effects of liming. K0687, taken 14 months after the first liming and 2 months after the second liming does show compositional changes. However, these changes are slight compared to those seen in the live communities (Chapter 5). The maximum percentage of *Tabellaria quadrisepata* is reduced to less
than 10% and there is a slight rise in *Eunotia incisa* at the surface. At this time there are no increases in the percentages of circumneutral taxa, such as *Brachysira vitrea* and *Achnanthes minutissima*, which dominate the contemporary living communities. By September 1987 the core K0987 does show clear increases in these species and a decrease in *Tabellaria quadriseptata* at the surface.

The first post-liming non-plankton samples show a transitional *Eunotia incisa* or *Peronia fibula* assemblage, followed by a delayed shift to an *Achnanthes minutissima* dominated community. However, there is clearly an even longer time-lag in these post-liming changes being registered by sediment cores. Whilst the living communities of the lake are dominated by a post-liming flora in June 1987 there is only a slight indication of this change in sediments at the same time. The first clear response occurs in core K0987, taken in September 1987, approximately 17 months after liming.

It is clear that this slow sediment response is only partly, if at all attributable, to the rate of transport of diatoms from the littoral to the sediment (see Chapter 6). Mixing of sediment has resulted in the integration of diatom assemblages from different times. Upward mixing of sediment is demonstrated by the abundance of *Tabellaria quadriseptata*, still important in the surface sediment 2-3 years after liming whereas it has been rare or absent from living communities for most of the post-liming period.
1. Comparability of data

Information about diatom assemblages was derived from 3 sources: living diatom communities; sedimenting material trapped in the water; and sediment cores. The comparison of data from these sources is not straightforward.

Samples from living communities represent the instantaneous composition/and standing crop of diatoms. Different division rates of diatom taxa are not compensated for in the percentage counts used to estimate the relative importance of species. The contribution of each community to the pool of new valves is inferred by interpolation between sampling times and by assuming that percentage cover is positively related to the rate of valve production.

In sediment traps diatoms were collected during a known period, a flux rate of cells can therefore be calculated and the relative productivity of species estimated. Though sediment traps introduce a time dimension because they sample continuously, interpretation of the diatoms trapped is complicated by their provenance. Since most (abundant) diatom taxa are common to different diatom communities eg. *Tabellaria quadriseptata*, *Eunotia incisa*, *Achnanthes minutissima*, *Brachysira vitrea*, and *Tabellaria flocculosa*, the source of valves cannot usually be identified, except where it is obviously discrete as in the cases of some epipsammic, eg. *Tabellaria binalis* fo. *elliptica* and *Achnanthes altaica*, and planktonic taxa, eg. *Asterionella formosa*. In addition resuspension of mud adds a fossil component to the assemblages collected by traps eg. *Cyclotella kuetzingiana* or the continued presence of *Tabellaria quadriseptata* in traps after its disappearance from living communities (see Fig. 8.1). Lastly although the flux rates measured by sediment traps do allow comparison of cell fluxes between traps, the flux rate of cells to the traps is not necessarily equivalent to that on the lake bed.

In cores a continuous record of diatom assemblages was available, but the resolution of changes on a timescale of months was seen to be modified by mixing processes and resuspension of older material.

Attempts were made to eliminate the technical component of mixing resulting from Kajak core extrusion and its minimum possible slice thickness of 0.5 mm. A freezer
corer was used to test whether the potential resolution of the sediment was greater, but this was not successful. The type of freezer corer used caused severe disturbance of the sediment-water interface and truncation of the surface sediment sequence.

Mixing of valves within the sediment resulted in identifiable time averaging of assemblages.

The need to use archived diatom samples from the pre-liming period meant that sampling sites were not always known or were not consistent and that sampling intervals were variable. Usually only a single archived sample from any habitat on any date was available and, despite a general conformity of species composition outlying samples occur, eg. the first pre-liming epilithon sample (May 1981) which is dominated by *Eunotia incisa* and has a relatively low abundance of *Tabellaria quadriseptata* compared with other pre-liming epilithon samples. The importance of short term and local variation in species composition that may be represented by such samples is difficult to assess. However, the reasonable consistency of the group of archived samples taken during 1982 suggests that the annual variability of living communities during the pre-liming period is small.

More intensive sampling of diatom communities, sediments and trapping of suspended material did not begin until almost 1 year after liming (April 1987) whilst the project was designed. Therefore the deficiencies of the data (sampling period, sample site, sample replication problems) described for the pre-liming period also apply to the immediate post-liming period. However, even during a preliminary visit to the site in October 1986 sample site was recorded and there was replication of live samples. Nevertheless, despite these deficiencies of sampling in time and space, extremely clear responses to liming were recorded by the live communities, the traps and the cores.

2. Live communities

i. Sampling

Surveys of the most variable and least variable periphytic communities, the epilithon and epiphyton showed that within site replication of samples could improve the estimation of mean percentages of taxa. Though the use of single, archived samples from live communities showed that in most cases diatom communities are homogeneous
enough for the approximate composition to be recognised from single samples. A priori pooling of multiple (3) epilithon samples, surface sand samples and whole plants for each replicate reduced the influence of local, small scale variation over each habitat surface. Secondly it was determined that 5 such replicates were adequate to represent both the most variable epilithon and least variable epiphyton. Replicate samples were counted individually and mean abundances calculated for the group rather than physically pooling samples to arrive at a mean composition. In this way the range and standard deviation between subsamples could be inspected and the reliability of trends determined. The within community variation of diatom composition in space around the littoral and with depth was shown to be small (except where local influences were dominant, for example the outlet of the heavily limed Altiwhat stream).

ii. Changes in live communities

The pre-liming diatom communities, epilithon, epiphyton and epibryon are all dominated by the acidobiontic taxon *Tabellaria quadriseptata* (Fig. 8.1), usually with *Eunotia incisa* (Fig. 8.2) as the second most common species. In the epipsammon at the same time *Tabellaria binalis* fo. *elliptica* is important. Live communities at this time were represented by single samples on any sampling occasion and therefore detailed comparison with the surface samples of the pre-liming master core LF L3 is not warranted. However, despite the irregular times and positioning of the samples the dominant taxa in the uppermost levels of the core reflect the abundance of different species in living communities. The absence of diatom plankton, seen in archived plankton material, is also shown by the core with only sporadic records of *Cyclotella kuetzingiana*. These occurrences are clearly older fossils derived either from disturbance of exposed fossil surfaces elsewhere in the lake or result from the unlikely process of low intensity upward mixing extending from considerable depths in the core.

Following liming of Loch Fleet catchment in April 1986 the first samples taken from live communities (July 1986 and October 1986) reflect the changing composition of living communities with a shift to *Eunotia incisa* dominance in the epilithon, epiphyton and epibryon (Fig. 8.2). However, *Tabellaria binalis* fo. *elliptica* remains the dominant taxon in the epipsammon. The rate of response of the live communities, marked by a shift to communities dominated by new taxa, is not accurately measurable from these samples but is clearly of the order of weeks, if not days. The rapid response of live communities to liming is consistent with the relatively high division rates of diatoms (cf.larger organisms) and may partly reflect species pre-liming population sizes as well
Fig. 8.1: *Tabellaria quadrisepata*; percentage of non-planktonic diatoms in live communities, traps, and surface sediments.
Fig. 8.2: *Eunotia incisa*; percentage of non-planktonic diatoms in live communities, traps, and surface sediments.
as species physiology. The populations of diatoms which increased during the immediate post-liming period (e.g. *Eunotia incisa* and *Brachysira brebissonii*) were present in the lake before liming. These taxa were already abundant and therefore a significant lag time, of species migration and establishment, was not apparent. However, taxa (e.g. *Achnanthes minutissima* and *Brachysira vitrea*) common in lakes having similar pHs to that of Loch Fleet following liming (see Battarbee *et al.* 1988), only begin to be established approximately 1 year after liming (Figs. 8.3 & 8.4). It may be significant that these taxa are absent or present only at very low abundances in live communities during the pre-liming period. The assertion that these taxa were rare before liming is supported by the diatom sequence of core LF L3 which shows only sporadic presences of *Achnanthes minutissima* and low percentages of *Brachysira vitrea* in the uppermost 20 cm, a depth of accumulation dated to cover a period of approximately 10 years before liming. It is therefore possible that, although water conditions were apparently favourable for their growth, the pre-liming absence or very low abundances of these species in living communities was influential in delaying expansion of their populations. Alternatively other aspects of the Loch’s chemistry may have initially been unsuitable for the species growth.

*Peronia fibula* is absent or only present at very low abundances in live samples from the pre-liming period. However, in levels just below the surface of the core LF L3 it occurs at relatively high abundances suggesting that its decline was recent (within the decade before liming). The species is most abundant in the post-liming epiphyton and epibryon communities (Fig. 8.5), it is also recorded at significant percentages in the epilithon, but the species is predominantly associated with plant surfaces. The species reaches its maximum abundances in mid-1987 over 1 year after liming.

The decline of *Eunotia incisa* and *Peronia fibula* in epilithon, epiphyton and epibryon communities is followed first by an increase in *Brachysira vitrea* and then by an increase in *Achnanthes minutissima*. These compositional changes are consistent with the pH of the lake being maintained at approximately pH 6.5.

The response of the epipsammic community to liming is seen as *Eunotia incisa*, *Eunotia rhomboidea*, *Eunotia vanheurkii* var. 1 and *Achnanthes altaica* become dominant and *Tabellaria binalis* fo. *elliptica* declines. After November 1987 *Eunotia incisa* declines and *Eunotia rhomboidea*, *Eunotia vanheurkii* var. 1 and *Achnanthes altaica* are consistently dominant, in varying proportions, from this time. In contrast to the other non-planktonic communities, with the exception of a single peak to *Eunotia*
Fig. 8.3: Achnanthes minutissima; percentage of non-planktonic diatoms in live communities, traps, and surface sediments
Fig. 8.4: *Brachysira vitrea*; percentage of non-planktonic diatoms in live communities, traps, and surface sediments.
Fig. 8.5: *Peronia fibula*; percentage of non-planktonic diatoms in live communities, traps and sediment traps.
rhomboidea in June 1988, the species composition of the epipsammon remains relatively stable during 1988.

Fluctuating patterns of species abundances are seen in the epilithon, epiphyton and epibryon communities during the later part of 1987 and in 1988. During late 1987 *Brachysira vitrea* declines and *Achnanthes minutissima* increases to its maximum abundance in the epilithon, along with a minor peak in *Fragilaria vaucheriae*. *Achnanthes minutissima* then declines and *Brachysira vitrea* and *Eunotia incisa* reach maxima, these species then decline and the abundance of *Tabellaria flocculosa* increases from July 1988 (Fig. 8.6). In the epiphyton *Achnanthes minutissima* is abundant from the end of 1987 onwards, except during February 1988 when *Fragilaria vaucheriae* reaches a maximum (at the same time as it does in the epilithon). *Brachysira vitrea* is less abundant in the epiphyton than in the epilithon, but shows 2 maxima, related to those in the epilithon. The peak of *Tabellaria flocculosa* seen in the epilithon during the later half of 1988 is also seen in the epiphyton. In the epibryon *Achnanthes minutissima* increases to a maximum in June 1988 whilst *Brachysira vitrea* declines along with *Peronia fibula* and *Eunotia incisa*. As in the epilithon and the epibryon *Tabellaria flocculosa* has a maximum at the end of 1988. The reasons for these later post-liming fluctuations in the abundances of non-planktonic species is unclear, but they are not, as the initial post-liming shift in species composition was, primarily driven by a large shift in pH. Although a second, lighter liming of the catchment in April 1987 may have been influential. The post-liming pH of the lake has remained relatively stable at around pH 6.5, but the small fluctuations in pH that occurred may have produced large shifts in alkalinity and other ions.

Whatever the causes of the changing abundances of dominant diatom taxa summarised above these large scale variations can be compared with their record in traps and sediments.

3. Sediment Traps

i. Sampling

The performance of sediment traps in different areas of the lake was evaluated. Despite variability between traps in terms of SM and valve flux the different spatial arrays of traps were shown to record similar percentages of common diatom taxa. Exceptionally
Fig. 8.6: *Tabellaria flocculosa*; percentage of non-planktonic diatoms in live communities, traps, and surface sediments.
a local input of SM was seen but could be defined (Altwha stream). Therefore the central sediment trap array, of pairs of traps suspended at 4 depths was selected as a suitable location to routinely sample SM and was also at the most appropriate location to make comparisons with sediment cores.

ii. Changes in the diatom composition of trapped sediment

Sediment trapping did not begin until April 1987, approximately 1 year after liming. Therefore direct, trapped analogues of diatoms assemblages from the pre-liming communities are not available for comparison with the post-liming assemblages. However, a clear relationship was seen between the composition of the dominant living communities and trapped diatom assemblages during the period of sediment trapping.

Corresponding to the shifts in species composition seen in the epilithon, epiphyton and epibryon during late 1986 and 1987, the first 4 trapping periods, (April 1987-February 1988), record declining abundances of *Eunotia incisa* and *Peronia fibula*. The dominant pre-liming species of these communities, *Tabellaria quadriseptata* is also present at significant, but decreasing percentages along with the epipsammic species *Tabellaria binalis* fo. *elliptica*. At the same time increasing percentages of *Brachysira vitrea* and *Achnanthes minutissima* are seen. This pattern of compositional change conforms with that of the epilithon, epiphyton and epibryon communities at this time.

The peak of *Fragilaria vaucheriae* recorded in epiphytic and epilithic communities during March and April 1988 is registered by sediment traps during period 5 (February to May 1988). At this time the increase in the trap percentages of *Synedra acus* corresponds to the maximum concentration of this species in the plankton (April 1988). However, the maximum concentration of *Synedra acus* in the traps (period 6, 29.4.88-17.6.88) follows its maximum in the plankton. Percentages of non-planktonic species are reduced when *Synedra acus* percentages are high, but cell concentrations in the traps suggest that this effect results from a suppression of percentages rather than a true reduction in non-planktonic cell numbers.

As the maximum abundance of *Synedra acus* declines in the traps (periods 6 and 7) the percentages of non-planktonic species such as *Achnanthes minutissima* and *Brachysira vitrea* recover. In addition the abundance of *Tabellaria flocculosa* rises and reaches a maximum during period 9. This pattern matches the rise and maxima in the species seen in epilithon, epiphyton and epibryon during the latter half of 1988.
During trapping period 10 high percentages of *Achnanthes minutissima* and *Synedra acus* are maintained. The planktonic species *Asterionella formosa* which appeared at a low abundance during period 9 increases so that the species becomes a dominant component of the trapped assemblages. The increase in *Asterionella formosa* abundance corresponds to high concentrations of this species observed in the plankton during April 1989. Clearly a bloom occurred during the first 4 months of the year.

In addition to recording the dominant species of living communities the traps continued to register low, but significant percentages of species that had disappeared from the living communities. Notably *Tabellaria quadriseptata* (Fig. 8.1) which is present at above 1% in all trapping periods, except for periods 5 and 6 when it is probably suppressed by high abundances of *Synedra acus*. The disappearance of *Tabellaria quadriseptata* from living communities following liming was abrupt and therefore its prolonged occurrence in traps is probably a reflection of sediment resuspension from the lake bed where concentrations of the species were high. (This property of a presently 'extinct', but formerly common diatom, might allow a quantitative estimate of the magnitude of resuspension to be made, by comparison of the percentages of *Tabellaria quadriseptata* in the surface sediment with the fraction of the species collected by sediment traps).

The fundamental signal in the sediment traps is, however, one from the live communities. The time lag between species change in these communities, in particular changes in the composition of epilithon and the epiphyton, is very short. At the sampling scale used (months) no significant time lag is seen. There is for example no evidence that periodic extreme (catastrophic) events, such as lake overturn or storms, are necessary to remove enough attached diatom cells to register in the SM. The implication is that there is a constant input of cells from living communities and that at this site an almost continuous, high resolution, record of species composition is available from sediment traps. The input from smaller and probably less easily transportable communities, for example the epipsammon, is less clearly discernible. This is suggested by the virtual absence or low percentages of post-liming epipsammic taxa such as *Eunotia vanheurkii* var. 1, *Eunotia rhomboidea* and *Achnanthes altaica*. 
4. Cores

i. Sampling

A primary coring site was selected on the basis of the findings of earlier surveys at Loch Fleet (Anderson and Battarbee 1985, Anderson et al. 1986). An area of sediment in the north-east of the lake in about 10.5m water depth was chosen for 3 reasons. Firstly, continuous sediment accumulation occurred at this site, secondly it was shown to be the area of most rapid sediment accumulation and thirdly the site was close to the site of LF L3 the pre-liming master core thus facilitating comparison of later cores with this core. Although spatial replication of core sites was attempted the results are not presented. Anderson (in press) has confirmed that compositional trends in diatom species can be replicated across this lake basin. Cores were taken at intervals of 2-9 months.

ii. Changes in core diatom assemblages through time

The dominant taxa associated with acidification such as *Tabellaria quadriplecta* and relatively high percentage of the epipsammic taxon *Tabellaria binalis fo. elliptica* in the surface sediment of LF L3 is matched by the maximum abundances of these species in pre-liming live communities. The abrupt shift in live community composition following liming and registered by sediment trap samples is not at once visible in post-liming sediment cores. This inertia in core response can be seen by examining the diatom sequence of surface sediments and the species stratigraphy immediately underlying.

Core LF1086, taken about 5 months after liming, shows no significant change in the composition of the surface sediment assemblage and *Tabellaria quadriplecta* remains dominant. K0687 taken about 14 months after liming does show compositional changes, but these changes are slight compared to those seen in the live communities. Most clearly the maximum percentage of *Tabellaria quadriplecta* is reduced and there is a slight increase in the abundance of *Eunotia incisa* at the surface, but no increases in those taxa which dominate the contemporary living communities are seen eg. *Achnanthes minutissima* and *Brachysira vitrea*. It is not until approximately 17 months after liming (core K0987) that clear increases in these important post-liming taxa, along with a reduction in *Tabellaria quadriplecta*, occur. The surface sediment sample of K0288 taken 5 months later than K0987 also reflects similar changes. Though taken
almost 2 years after liming the post liming diatom assemblages are clearly not discrete from earlier assemblages. *Tabellaria quadriseptata* is still present at high percentages although it was absent from all living communities within about 6 months of liming and present only at low percentages in sediment traps. Clearly no living source of this species survived, but resuspended valves of *Tabellaria quadriseptata* from surface sediments are the probable source of its component in sediment traps.

Core K0788 shows the first occurrences at abundances of greater than 1% of *Synedra acus*. This diatom was only sporadically present in the previous core K0288, taken 5 months earlier, and the abrupt appearance of the species must be associated with the bloom of planktonic *Synedra acus* during the intervening period. The penetration of the sediment to a depth of 2cm by significant percentages of this diatom must be an artefact of one or more processes since the accumulation of this depth of sediment in a period of less than 5 months is unlikely given the declining sediment accumulation rates estimated by $^{210}$Pb dating. A combination or one of three processes might be involved: physical mixing eg. caused by currents, bioturbation caused by benthic organisms, or mixing caused by the technical processes of retrieving sediment samples eg. smearing by the sides of the corer and time averaging of samples by core slicing thickness.

*Fragilaria vaucheriae* has a peak in the surface 1 cm of K0788 and can be associated with the maxima recorded in the attached live communities and also in the sediment traps at this time. *Achnanthes minutissima* shows a clear peak in the surface 1 cm of the core. By October 1988 the core K1088 shows high percentages of *Achnanthes minutissima* in the surface sediment and a significant increase in *Brachysira vitrea* in the top 0.5cm along with reduced percentages of *Tabellaria quadriseptata* in the top 1 cm. A continuous record of *Synedra acus* at abundances of greater than 1% penetrates to 2.5 cm again suggesting that down-mixing had occurred and the peak of *Fragilaria vaucheriae* remains in the top 1 cm.

K1088 was taken about 30 months after liming, and by this time valve accumulation from the post-liming flora has clearly superceded the influence of sediment mixing. However, upward mixing is clear, for example from the continued presence of *Tabellaria quadriseptata* in the surface sediment and downward mixing can be inferred from the penetration of the *Synedra acus* curve to 2.5 cm. The magnitude of mixing in each direction can be approximated by using the biostratigraphy to date the core. If the *Tabellaria quadriseptata* peak at 2-2.5 cm (assuming a greater maximum did not occur in the level below it) is taken as representing a time immediately before or
immediately after liming in 1986, and knowing the species disappeared from the flora soon after this time, then in the c.2-2.5 years to October 1988 2cm of upward mixing had occurred. Conversely the downward penetration of a continuous Synedra acus curve allows estimation of the magnitude of down-mixing. Synedra acus which has become important during the post-liming period, firstly at relatively low percentages as an attached species (1987), and then as a dominant species resulting from a planktonic bloom (1988), is mixed downwards. This is shown in core K1088 by the rising abundance of Synedra acus coinciding with the peak of Tabellaria quadriseptata at 2-2.5 cm. The origin this curve is associated with the species bloom at the end of April 1988. If the Tabellaria quadriseptata maximum at 2-2.5cm is again taken as marking a time immediately before or just after April 1986 then within the c.6 months from the time of the Synedra acus bloom until the time of coring (October 1988) the species has reached to a depth of 2.5 cm. Only a fraction of this depth can be accounted for by new sediment accumulation since the appearance of the bloom. $^{210}$Pb dating of LF L3 (Anderson et al. 1986) shows decreasing accumulation rates in accordance with the stabilisation of catchment soils. By 1985 the sediment accumulation rate was 1.47 cm a$^{-1}$. Given the decreasing trend in accumulation rates post-ploughing (Anderson et al. 1986), it is unlikely that more than about 0.7 cm of sediment would have accumulated in the 6 month period since the increase in planktonic Synedra acus concentration. Subtracting this estimate (0.7cm) from the depth to which the Synedra acus curve penetrates (2.5cm) gives an estimate of the magnitude of down-mixing. Therefore in the 6 month period over 2 cm of down-mixing may have occurred. Whether further (more efficient) or deeper mixing is still taking place is not known.

The only alternative to the above explanation of the species stratigraphy is that 2.5 cm of sediment has accumulated since the Synedra acus bloom in 1988 and that upward mixing, but not downward mixing occurs.

K1288 shows a similar pattern of species change to K1088. However, the Synedra acus curve does not penetrate below 1.5 cm. Distinct maxima are seen for Achnanthes minutissima, Brachysira vitrea and Fragilaria vaucheriae whilst pre-liming and early post-liming taxa such as Tabellaria quadriseptata and Eunotia incisa persist at relatively high percentages at the surface.

The final core K0489 shows an immediate response to the bloom of Asterionella formosa that occurred during early 1989 with a single peak in the surface sediment. The patterns seen in other common post-liming taxa are similar to the previous 2 cores,
but they are amplified and the percentages of *Tabellaria quadrisepata* and *Eunotia incisa* are reduced. No clear rise of *Tabellaria flocculosa*, comparable with the maxima in the live communities and sediment traps, is discernable in either K0489 or K1288.

5. Comparison of whole species assemblages

i. Attached live communities vs. sediment traps

The composition of diatom assemblages in sediment traps has been compared with the composition of each of the 4 non-planktonic communities using correspondence analysis to produce time tracks for each group of percentages. Only the sample scores on the first 2 axes are shown. Successive samples are linked together to produce a time track for the individual community and the sediment trap assemblages. This technique has the advantage that all species percentages in a sample can be used in the comparison of similarity between samples.

In common each of the 4 plots show the greater variability of live communities compared with trap assemblages. The time tracks of trap samples are attenuated because they are mixed assemblages, both temporally and in terms of source diatom communities.

a. Epilithon

In the first DCA plot the non-planktonic components of sediment traps are compared with the epilithon (Fig. 8.7). The initial section to the left hand side of the plot shows the trajectory of pre-liming samples (these have been omitted from the plots for other communities). The similarity of most pre-liming samples can be seen and clearly their composition is dissimilar to the later epilithon and trap samples. However, at the left hand side of the diagram where assemblages and traps are contemporaneous the trajectories of both tracks can be matched. At the beginning of 1987 the tracks go from left to right, followed by a track to the upper right, downward to the left and to the right and then left again. In sequence the 5 patterns of the epilithon trajectory are seen in the sediment trap trajectory. The initial shift in both time tracks from left to right reflects the shift from *Eunotia incisa* (low axis 1 score) dominated epilithon to *Achnanthes minutissima* (high axis 1 score) dominated communities. DCA has the advantage that the influence of less common species is also significant in the analysis.
Fig. 8.7: DCA time tracks; sediment trap assemblages vs epilithon (non-planktonic)
Despite the sediment traps being time integrated mixed assemblages and the epilithon being point samples at an instant, the sequence of post-liming change in the epilithon is summarised remarkably well by the sediment traps.

b. Epiphyton

Sediment traps are compared with the epiphyton (Fig. 8.8). From October 1986 until the beginning of 1988, the trajectory of the epiphyton time track is from top left to bottom right along axis 1. The sediment trap trajectory is seen to follow this general direction of change, top left to bottom right. The diatom assemblages represented by both time tracks then become relatively stable and show smaller distance changes, both plotting at points to the bottom right relative to their starting positions. It is possible to distinguish a shift upward and to the right in the epilithon, followed by a general downward track to the left ending at December 1988. This pattern is to some extent followed by the sediment trap trajectory. Because the sediment traps are time integrated assemblages and cover longer periods, it is difficult to match patterns more accurately on this short time-scale. However, the comparison of time tracks illustrates the similarity between a component of the trap catches and the composition of the epiphytic community. Again, it can be seen that when whole species assemblages are used rather than common species alone, there is a good correspondence between species trajectories.

c. Epibryon

Sediment traps are compared with the epibryon (Fig. 8.9). The predominant direction of change for the whole time track is top left to bottom right (October 1986 to December 1988), although some clear excursions from this route are seen. Again, the trajectory is shadowed by the plot of the trap assemblages (April 1987 to April 1989) and finally both plots track upward.

d. Epipsammon

Sediment traps are compared with the epipsammon (Fig. 8.10). Although the shape of the time trajectories is superficially similar, examination of the dated sequences of change reinforces the idea that the epipsammic component of trap catches (and therefore diatom assemblages in the lake sediment) is relatively small. The large changes in composition seen in the epipsammon during 1987 are not reflected in the sediment
Fig. 8.8: DCA time tracks; sediment trap assemblages vs epiphyton (non-planktonic)
Fig. 8.9: DCA time tracks; sediment trap assemblages vs epibryon (non-planktonic)
Fig. 8.10: DCA time tracks; sediment trap assemblages vs epipsammon (non-planktonic)
traps. Conversely the stability of the epipsammic community during 1988 is not reflected by the relatively large scale changes seen in the traps at this time.

ii. Sediment traps vs. surface sediment

A joint plot of some important diatom taxa and the relative trajectories of sediment traps and surface sediments is presented (Fig. 8.11).

The largest boxes indicate relative positions of species influential in the ordination (the joint plot). The solid line is the trajectory of sediment traps and the dotted line indicates the trajectory of the trap assemblages. Both planktonic and non-planktonic taxa have been included in the ordination. Where points are crowded labels have been omitted from samples to avoid confusion, however the sequence of surface sediment samples follows the sequence of post-liming cores (Table 7.1). The time track of the sediment traps begins in April 1987 and the time track of the surface sediments begins in October 1986, both end in April 1989.

The trajectories of both traps and surface sediments show parallel changes, but the trajectory of the traps is both amplified and pre-dates changes in the sediment. Despite different starting dates both tracks remain to the left of the plot with relatively low axis 1 scores (cf. *Eunotia incisa* and *Peronia fibula*) until 1988. The trap trajectory then tracks to the right and is followed by the core trajectory in mid-1988. This strong signal in both is driven to a great extent by *Synedra acus* but other taxa such as *Fragilaria vaucheriae* are probably influential. The trap assemblages reach their maximum distance to the right in June 1988 whereas the surface sediments reach this point in October 1988. Both trajectories then track to the left and finally upwards when the primary species driving the plot is clearly *Asterionella formosa* which has a very high axis 2 score.
Fig. 8.11: DCA time tracks; sediment traps and surface sediments, with a joint plot of common species.
6. Conclusions

Despite sampling being non-uniform before and immediately after liming, as well as the problems of comparing the different classes of data that have been discussed, a number of clear conclusions arise from the project.

A relatively homogenous diatom flora exists in each habitat irrespective of other factors such as location or water depth. In general there is greater between habitat variation than within habitat variation.

The overlap between the species communities of the habitats is considerable. Epipsammic and planktonic communities are distinct, but epilithon, and particularly the epiphyton and epibryon are more similar.

The diatom communities in all habitats respond rapidly to liming on a time-scale of weeks. Initially a shift is seen to new dominant species recruited from the indigenous flora, but later species that were rare or absent become important. The most abundant diatom of the immediate pre-liming flora, *Tabellaria quadriseptata* disappears.

Post-liming species succession occurs despite relatively stable pH. This is at least in part due to other chemical effects and may be generated by other factors, for example the sudden emergence of phytoplankton, more efficient nutrient recycling or delay in immigration and colonisation.

Sediment diatom assemblages have been shown to be strongly related to the live communities in the lake. Sediment trapping shows that an external (stream) input can be detected, although in this case it was not usually important.

Although sediment traps were not set before or immediately after liming it is clear from various comparisons that sediment traps can track changes in live communities almost instantly. Therefore there is no time lag in diatoms being removed and transported to the area of the lake where cores were located. The exception to this is the epipsammon. This may be the result of one or a combination of factors, for example, small habitat area, sheltered location or slow division rates. However, the responses of trap assemblages to changes in other communities indicate that continuous turbulence and mixing in this wind-stressed system result in the rapid transport of diatoms.
Traps contain only small proportions of pre-liming material arriving through resuspension. *Tabellaria quadrisepata* which could be derived from contemporary surface sediment across the whole lake bed and *Cyclotella kuettzngiana* from more distant, marginal sources (the species is buried under 1m of mud in the primary coring area).

Because of source integration and time-averaging the composition of traps is less variable in time than in live communities. In addition the trap assemblages are so little affected by older sediment contamination that they provide an excellent monitoring tool. Perhaps this indicates that in this lake resuspension is not the dominant process of sediment mixing.

In contrast surface sediments appear to be less responsive to the changes since clear biostratigraphic evidence of liming does not appear until over 12 months after treatment. This is clearly not due to the delayed arrival of post-liming diatom species (cf. the evidence of sediment traps above) but probably due to dilution and mixing with existing surface sediment assemblages.

The surface sediment composition gradually approaches that of the traps. However, two and a half years after the disappearance of acidobiontic diatoms from the lake they are still important in surface sediment. The processes responsible for this appear to be both upward and downward mixing probably through bioturbation since physical mixing and resuspension would cause more contamination in traps.

In Loch Fleet fossil diatom assemblages have been found to represent the composition of living diatom communities accurately. In this system preservation is excellent, transfer from lifetime habitat to the area of sediment accumulation is very good and common species are well represented, the resolution of cores is limited only by mixing and some resuspension of sediment.
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