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Diatom communities – their response to changes in acidity

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The non-planktonic habitats of some Welsh lakes were studied to determine the composition of the diatom component in each, the seasonality of the diatoms, discreteness or otherwise of each community, and the relation of each community to the mean pH of the water of the lakes. A discussion on the diatom plankton of acid waters is also presented in this symposium.

Introduction

Interpretation of diatom data obtained from lake cores depends entirely on information derived from the ecology of extant species. That individual diatom communities respond to changes in acidity is not in doubt. There is, however, little definitive data in the literature on diatom habitats, and extracting habitat information from core material (which is a mixture of at least five discrete communities) is hampered by confusion over the exact composition of the communities, apart from that of the plankton. This arises from the complexity of the micro-habitats present in the benthos and the inevitability of some natural contamination from one habitat to another, added to which is the likelihood of unnatural contamination during sampling.

In this study of lakes in Wales, only the epipelon, the epipsammon, the epilithon and the epiphyton were sampled. The plankton community was relatively unimportant so this is considered separately and more generally.

Methods

Epipelic samples were obtained without contaminants by using appropriate sampling techniques that remove only the live (raphid and hence motile) cells, that is, by harvesting live cells off cover glasses placed on sediment surfaces (see Round (1981) for further details on all community structure and sampling). The sand was freed of all other silt, plant detritus, etc., before the discrete epipsammon was removed by heating in sulphuric acid. The epilithon was the most difficult to remove as material from other communities settles on to stone surfaces and this has to be separated by washing the stone surface before scraping off the diatoms. The epiphyton was usually fairly clean and could be scraped off the plant surfaces. It is never possible to remove all contaminant cells during sampling and laboratory processing so at the counting stage these were discounted. A minimum number of 100 valves was counted for community analysis. Counting excessive numbers is counter productive when determining dominance in communities as contaminants can confuse the data.

The location of the lakes is given together with the mean pH values of the water in figure 1. A few lakes were sampled monthly for three years but the majority were visited only once or twice during that period.

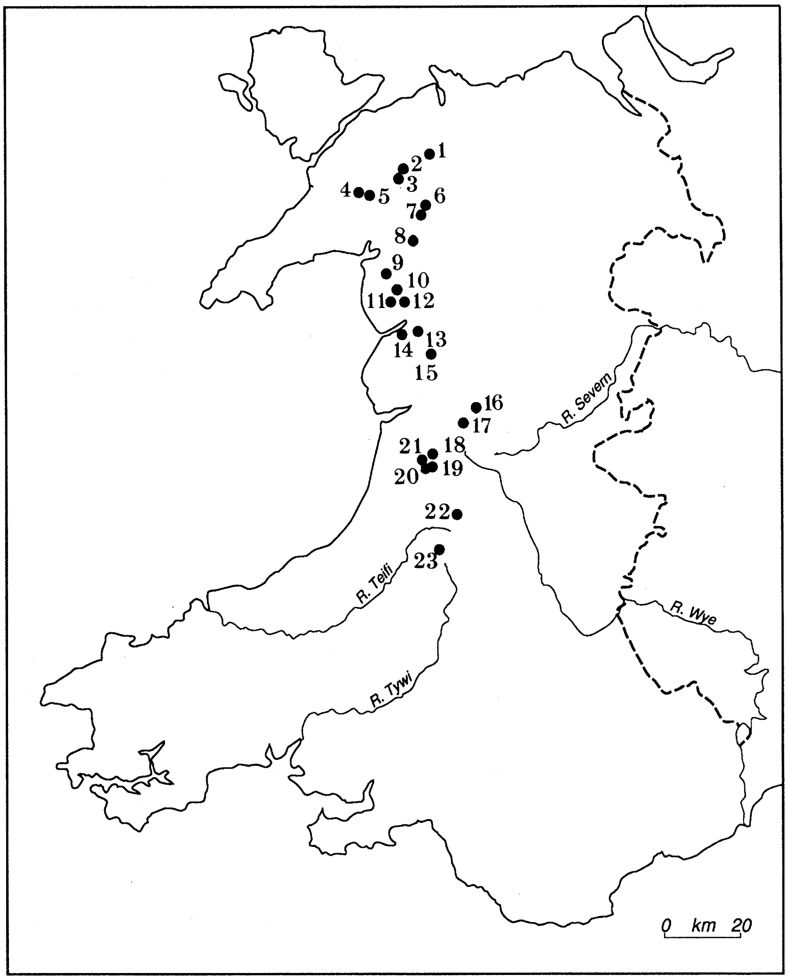

Figure 1. Map of Wales showing location of sites mentioned in the text (pH values are given in parenthese). 1, Llyn Geirionydd (6.6); 2, Llyn Ogwen (4.9); 3, Llyn Idwal (5.6); 4, Llyn Nantlle (6.6); 5, Llyn y Gadair (6.1); 6, Llyn Newydd (4.5); 7, Llyn y Manod (5.0); 8, Llyn Mair (5.4); 9, Llyn cwm Bychan (5.6); 10, Llyn Dulyn (4.9); 11, Llyn Bodlyn (5.4); 12, Llyn cwm Mynach (5.6); 13, Llyn Gwernan (6.2); 14, Llyn Cregennen (6.8); 15, Tal-y-Llyn (6.5); 16, Glaslyn (4.9); 17, Bugeilyn (4.4); 18, Llyn Syfydrin (4.7); 19, Llyn Blaenmelindwr (4.9); 20, Llyn Rhosgoch (5.4); 21, Llyn Pendam (5.1); 22, Llyn Hir (4.8); 23, Llyn Berwyn (4.4).

Results

To use diatom associations based on discrete communities, so as to extend the analysis of diatom data from cores, several aspects required investigation. First, is there a seasonal succession of diatoms in the benthic associations? As there is a very pronounced seasonal succession in the plankton in both acid and alkaline lakes, necessitating frequent sampling through the year, this feature was checked. For the epiphytic and epilithic communities, no or only slight seasonal variation occurred. For example, in Llyn Syfydrin, *Frustulia rhomboides* was dominant in over 90% of the sampling times over three years. This is a raphid diatom, but in this habitat is immobilized in mucilage. *Eunotia incisa* was subdominant and on one occasion the next most abundant species, *Tabellaria flocculosa*, was dominant. On all sampling dates these three species formed the only conspicuous elements. In the epipelon of this lake, *Pinnularia* *subcapitata* was dominant on all sampling dates. An epiphytic example of species on *Isoetes* from Llyn Rhosgoch shows dominance of *Eunotia incisa* and subdominance of *Tabellaria flocculosa* and *T. quadriseptata* through three years' sampling. Such data answer a second question: how many samples are needed for defining any benthic association? At least in the acid lakes this study suggests that one will suffice, though more are preferable. A third question is, how many species are needed to characterize an association and can the dominant one alone be used? In this study only a few species at each site were needed, as the associations were dominated by only between one and three species.

Epilithon

The lakes sampled fell into two discrete groups when the epilithic diatom populations were tabulated: the ones with *Eunotia incisa–Tabellaria flocculosa sensu lato* dominant and those with *Achnanthes minutissima* dominant. The distinction is clearly related to pH–Ca^{2+}–conductivity levels: low in the former and higher in the latter. This feature agrees well with the effect of liming on some of these lakes (for example, Hir and Pendam) where, after liming, *A. minutissima* became the dominant species. This is also in agreement with data from Galloway (Flower *et al.* 1986) where *A. minutissima* does not become an important component of the flora until the alkalinity (calcium carbonate) reaches around 2.0 mg l^{-1}. At > 3.4 mg l^{-1} it is usually the dominant in the surface sediment diatom assemblage. Also associated with the higher pH lakes are *Brachysira vitrea*, *Cymbella minuta*, *Fragilaria capucina* and *Peronia fibula*. In the low pH group there are scattered occurrences of *Eunotia praerupta*, *E. denticulata*, *Cymbella aequalis*, *Eunotia curvata* and *Pinnularia subcapitata*. *Oxyneis* (*Tabellaria*) *binalis* is also common in a few of the acid lakes, but more common in the epipsammon (see below). It is significant that *E. incisa* does not extend into the less acid lakes, though *Achnanthes austriaca* and *Tabellaria flocculosa* do. *Brachysira vitrea*, *Denticula tenuis*, *Cymbella minuta*, *Peronia fibula*, *Tabellaria flocculosa*, *Oxyneis binalis*, is a possible sequence in relation to increasing acidity.

Other distinctive sub-groupings can be picked out, for example, the very high percentage of *Achnanthes austriaca* in Llynnau Dulyn, Pendam and Mair, and of *Frustulia rhomboides* in Llynnau cwm Bychan, Berwyn and Syfydrin. The count of *Brachysira vitrea* in Llyn Rhosgoch may show high metal content, as it is correlated with this in Llyn Geirionydd. *Tabellaria flocculosa* is abundant in Glaslyn, Bodlyn and Llyn y Gadir, and *Oxyneis binalis* in Llyn cwm Mynach together with *Tabellaria quadriseptata* and *Eunotia faba*. These latter three species can be used to subdivide the low-pH group lakes.

The less acidic group has *Peronia fibula* in one subset and *Cymbella minuta* in another. The occurrence of *Stenopterobia delicatissima–Denticula tenuis–Cymbella microcephala* seems to distinguish Llynnau Gwernan and Cregennen and *Gomphonema gracile* divides Llynnau Nantle, Tal-y-Llyn, Ogwen and Idwal from the remainder.

The species from the most acidic group, which are also found in the less acidic sites are *Achnanthes austriaca*, *Tabellaria flocculosa* and *Frustulia rhomboides* but in none of these lakes do they achieve any degree of dominance.

A species that occurs as isolated valves in samples is *Fragilaria virescens* v. *exigua* and this is recorded in quantity in some lakes (R. J. Flower, personal communication) but I have never encountered it in quantity in any micro-habitat. Jones & Flower (1986) also found that this taxon was present in the deep-water sediment but not in the epipsammon or epilithon of Round Loch of Glenhead.

There do not appear to be any good minor species to characterize the epilithon. The dominants *Eunotia incisa*, *Tabellaria flocculosa* and *Achnanthes minutissima* are, as might be expected, attached non-motile diatoms. The less abundant *Frustulia rhomboides* and *Brachysira vitrea* are raphid, and to some extent motile, but they both tend to live in mucilage masses (tubes?) and are only motile when released from the mass.

Epiphyton

The host flora varies from lake to lake and the following have been sampled when present at the collecting site: *Isoetes lacustris* L., *Littorella uniflora* (L.) Aschers, *Lobelia dortmanna* L., *Equisetum fluviatile* L., *Juncus bulbosus* L., *Nuphar lutea* (L.) Sn, *Glyceria fluitans* (L.) R. Br. and *Sparganium* spp. The data show clearly the overwhelming abundance of *Eunotia incisa* with *Tabellaria flocculosa* subdominant and *T. quadriseptata* and *Peronia fibula* frequently present and occasionally becoming dominant.

Tabellaria flocculosa achieved high percentage cover on *Isoetes* in three lakes, in one lake on *Equisetum* and in one lake on *Glyceria*. In the case of its occurrence on *Glyceria* this was in Llyn Bodlyn and in this lake it is also the dominant on *Isoetes*. In the case of three different hosts (*Juncus*, *Equisetum* and *Nuphar* in Bugeilyn and *Isoetes*, *Juncus*, *Lobelia* in Dulyn), all were overwhelmingly colonized by *Eunotia incisa* (the same species dominated in the epilithon of these lakes), suggesting that when water chemistry is the major stress many species will be prevented from competing and a single species is often favoured; this then tends to colonize all the available substrata. The only exception seemed to be *Equisetum* in Dulyn, which had *Tabellaria* dominant rather than *Eunotia*. However, resampling of this *Equisetum* revealed an outer layer of *Tabellaria* and an adnate layer of *Eunotia incisa* that could be removed from the stem only by scraping with a razor blade. With the *Tabellaria* removed the flora would appear just as on the other hosts.

Disappointingly, there seems to be little or no specificity in the colonization of the different aquatic macrophytes. The epiphytic flora is, however, slightly less diverse than the epilithic. More sites have an epiphytic flora that is dominated by a single species (more than 75% in the counts). Contamination of the epiphyton by species from stones or sediments is surprisingly slight, for example, *Achnanthes austriaca*, *Brachysira vitrea* and *Frustulia rhomboides* are only rarely present. In the case of plants from Llyn Berwyn there is a *Gomphonema* species, which I can only place in *G. parvulum*, which is abundant in the epiphytic flora but absent from the epilithon. This species requires detailed study (see comments in Krammer & Lange-Bertalot (1986) as it is frequently recorded as a dominant species in polluted rivers and different ecotypes must be involved).

Epipelon

The sediment was not easily sampled in many of these upland lakes and hence the data for this habitat are sparse. The lake margins were stony and as sampling was by wading, the deeper, probably more productive sites, could not be reached. Hence the large species of *Pinnularia*, *Neidium*, *Surirella* are possibly under-recorded. However, these genera are well known as true epipelic inhabitants and their occurrence in quantity in cores would show a rich epipelic community. The near-shore sediments do differ somewhat in composition from the deeper sediments and this survey has extended knowledge only of the near-shore segment of the epipelon.

The dominant species vary greatly from lake to lake, for example, *Pinnularia subcapitata* in Llyn Syfydrin, *Cymbella aequalis* (usually accompanied by *C. hebridica*) in Llyn Blaenmelindwr

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and Llyn cwm Bychan, *Neidium hercynicum* in Llyn Manod and Llyn Newydd. *Stenopterobia delicatissima* and *Navicula leptostriata* are often present but never in quantity.

Plankton

This community was not sampled in the Welsh lakes visited and this section is a discussion based on previous experience and data from the literature.

The majority of species occurring in the plankton have never been recorded live for any period of time in the benthic associations. One must write 'for any period of time', since immediately after rapid declines in planktonic populations, live planktonic species can be quite common, especially in the epipelon and epilithon, but they rarely remain as live cells for more than a few days and are usually undetectable after a week or so. Diatoms are not common in the plankton of highly acidic lakes (Davis 1987) and in these Welsh lakes the only taxa that might commonly occur and contaminate the benthos are species of *Cyclotella* and *Aulacoseira* (particularly the *Aulacoseira* (*Melosira*) *distans* group, see Haworth (1988). However, *Cyclotella* has not been found in any of the benthic samples investigated and *Aulacoseira* (*distans* type) are rather rare and either form only a small component of the plankton, or perhaps occur in some unsampled microhabitats. In my samples from Llyn Hir it is hard to find a single cell of *Aulacoseira*, yet in the core, four different forms occur and the percentage occurrence of the genus is 15%, which is, in fact, the highest percentage figure for any genus (S. C. Fritz, personal communication). Similar results were obtained for *Melosira* (*Aulacoseira*) *perglabra* in a north American lake, where its centre of distribution was the epipelon (De Nicola 1986) though not ever recorded in any quantity. There are still many diatoms recorded in material from lake cores that cannot be attributed to any of the benthic communities; some may be contaminants from the watershed but years of intensive work will be required before the distribution of many species can be satisfactorily determined. Some planktonic diatoms, for example, *Rhizosolenia* and *Attheya* are so delicate that they may not survive to contaminate the benthos, they have to occur in considerable quantity to be detected in cores.

Most planktonic diatoms (for example, *Aulacoseira italica*, *A. granulata*, *Cyclotella* spp., *Stephanodiscus* spp., *Rhizosolenia longiseta*, *R. eriensis*, *Attheya zachariasi*, *Diatoma elongatum*, *Centronella reicheltii*, *Fragilaria crotonensis*, *Asterionella formosa* and *Synedra acus* are almost never found actively growing or even as contaminants in benthic communities and when found in core material can be regarded as certain indicators of planktonic phases. In a few Welsh lakes, *Asterionella ralfsii* valves have been found in the benthos; these are presumably contaminants from planktonic populations of this rare (in the U.K.) diatom. It is abundant in some low pH Finnish lakes (Ronkko & Simola 1986). Although not encountered in this study, the author has found small *Cyclotella* species live and constantly present in the mucilage secreted by some epiphytic communities. This is, however, very rare though reported elsewhere, for example, Jenkerson & Hickman (1986) who found *Cyclotella* but not *Stephanodiscus*, though both were present in quantity in the plankton. In another study, Moss (1981) found that *Synedra* and *Diatoma* species occurred in both the epiphytic and planktonic habitats; they multiplied in both so were not casual in either habitat. However, this was a study in eutrophic waters and these do seem to have somewhat different habitat characteristics compared with oligotrophic acid lakes. A problem genus is *Tabellaria*. First, it is a very confused genus (see Flower & Battarbee 1985; Lange-Bertalot 1988); secondly, some species are planktonic and others benthic; and thirdly, there are reports that populations multiply in the benthos and then migrate into the plankton, an aspect that needs a careful modern study. One species, *T. binalis* (now transferred to the new genus *Oxyneis*, Round *et al.* 1990) is quite clearly benthic–epipsammic. *T. flocculosa* in its commonest form (Type III of Koppen) and *T. quadriseptata* are attached, occurring in the epilithon and epiphyton. There are, however, planktonic forms of *T. flocculosa* (for example, it is in the plankton that this species achieves overall dominance in one of the ponds sampled by DeNicola (1986), while *T. fenestrata* is said to be totally planktonic. It is extremely difficult to identify some of the variants. The morphological colony variants in the plankton of the English Lake District (Knudsen 1955) are not easily distinguished in core material. There is evidence that variants are stable entities in lakes as similar forms were found in Irish loughs (Round & Brook 1959) and records from the turn of the century had the same forms in the same loughs (West & West 1906), a rare opportunity to study populations over a 60-year period.

In some waters there are substantial interactions between planktonic populations and macrophytes. Certain macrophytes have an adverse effect on planktonic diatoms, and conversely, excessive phytoplankton may reduce macrophytes (and hence diatom epiphytes), though in some instances excessive growth of epiphytes can reduce the host plants, which has repercussions on the diatom content of cores (Phillips *et al.* 1978). It has also been shown (Reynolds *et al.* 1982) that the flux of planktonic diatoms to the sediments is an important transport path of the trace metals zinc and lead, and hence perturbations of the phytoplankton populations may influence the contents of these in sediments.

Conclusions

Diatom-community changes associated with acidification, which are detectable from core studies are usually confined to demonstration of the loss of the planktonic community (Davis 1987), though a shift from an epipelic to an epiphytic flora has been shown in a Finnish lake (Simola *et al.* 1985). The low representation of attached or motile diatom species in counts of diatoms from most core material from acid lakes makes it most difficult to reconstruct community changes, although the sediments are sometimes dominated by species from these communities (for example, the 34 Galloway lochs investigated by Flower *et al.* (1986)).

There are distinct epipelic, epipsammic, epiphytic and epilithic communities in acid lakes, but there is considerable overlap between the latter two, and there are no real indicator species to separate them. In addition, the epiphyton developed on the aquatic angiosperms tends to be similar on each host genus.

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