

**THE OCCURRENCE OF TWO NEW PLANKTONIC DIATOM
POPULATIONS IN THE ENGLISH LAKE DISTRICT:
AULACOSEIRA ISLANDICA SUBSPECIES *HELVETICA* AND
*A. AMBIGUA***

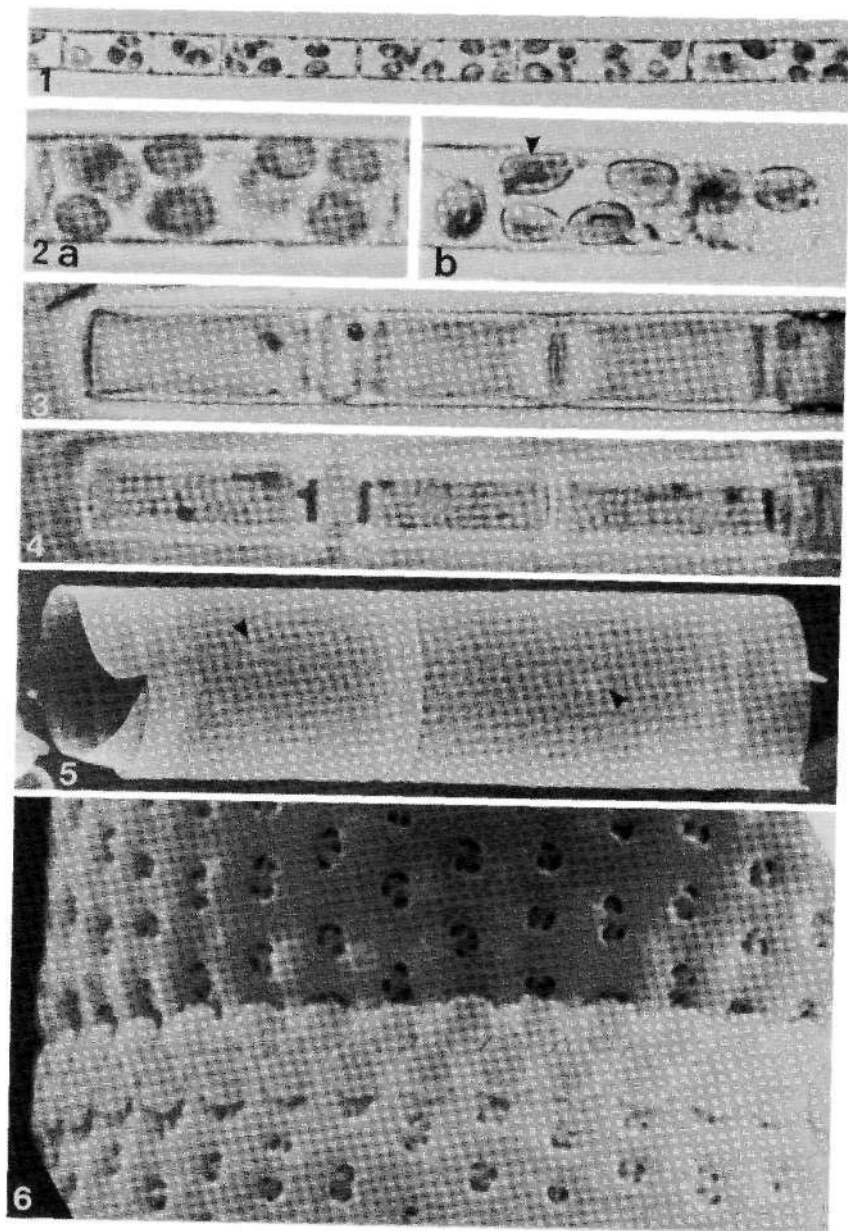
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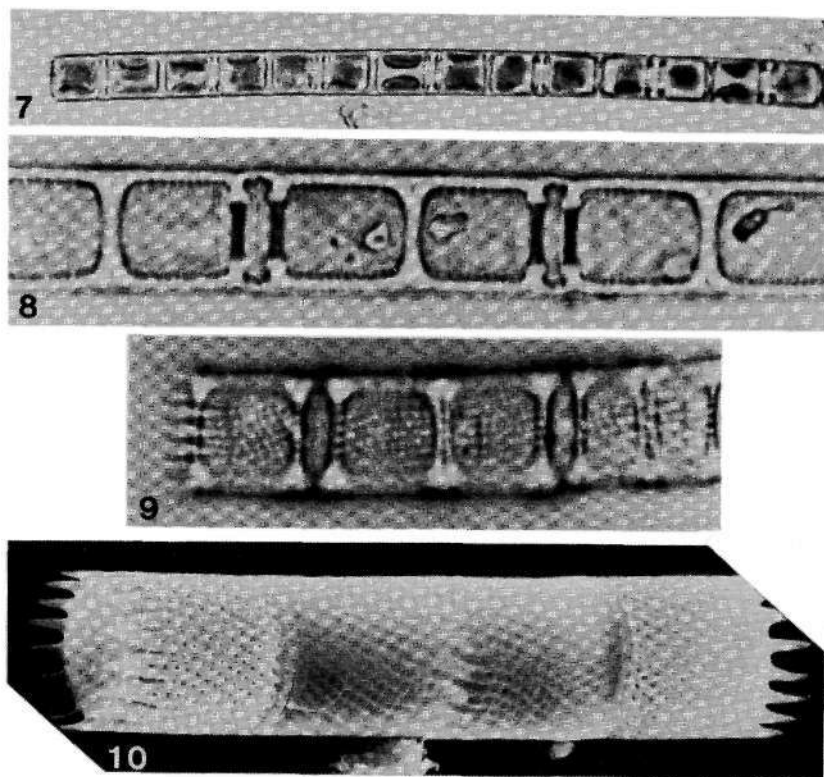
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Introduction

Samples of planktonic algae from major lakes in the English Lake District have been investigated over many years as part of a long-term monitoring programme set up by the FBA and continued by the IFE. Some lakes have been sampled regularly for long periods, others less frequently or only occasionally. Windermere north and south basins, and the neighbouring lakes Blelham Tarn and Esthwaite Water, have been under observation, mostly on a weekly basis, since the programme began in 1945. During this time diatoms have played a significant role in the population dynamics of these lakes (Lund 1954 and unpublished data; Tailing et al. 1986).

There have been very few published surveys of algal distribution in all the other large and small lakes or tarns in the English Lake District; Knudson (1954) collected material for a detailed study of the diatom genus *Tabellaria* and Lind (1980) studied desmids. In 1983 and 1984, samples of diatoms were collected from surface sediments of almost all the standing waters in the county of Cumbria, including the Lake District lakes (Haworth et al. 1988). One result was a review of all the *Melosira* taxa (now mainly transferred to the genus *Aulacoseira*) present in these waters at that time (Haworth 1988). Whilst several taxa are prominent in acidic lakes and tarns, *A. subarctica* (O. Miiller) Haworth is the most abundant species in the larger and more productive waters. This taxon, present throughout the post-glacial sediment profile of Windermere (Pennington 1943), was first noted in the plankton there in 1907 (West & West 1909) but it was misidentified as *M. granulata* Ehrenberg. The recent increases in abundance of this taxon led to an extensive study to explain its success (Lund 1954). However, in a footnote added in proof, Haworth (1988) revealed that a new taxon, *A. islandica* subspecies *helvetica* (O. Muller) Simonsen, had just been seen in the phytoplankton of Windermere. Recently a new study of Bassenthwaite Lake has shown that another *Aulacoseira* taxon, *A. ambigua* (Grunow) Simonsen, has now appeared there.





FIGS 7-10. (Above). *Aulacoseira subarctica* (O. Müller) Haworth. **7**, live filament with plastid arrangement (x800). **8**, shape and thickness of cell-walls and pseudoseptum (x2000). **9** and **10**, valves, showing spiral arrangement of areolae and spines as seen under the light microscope (x2000) and by SEM (x2700) with copulae visible overlying newly-formed valves.

FIGS 1-6. (Opposite). *Aulacoseira islandica* subspecies *helvetica* (O. Müller) Simonsen. **1**, live filament showing arrangement of plastids (x800). **2a**, unstained plastids; **2b**, plastids stained with iodine to show pyrenoids (→) (x2000). **3**, median view of cells to show wall thickness and pseudoseptum (x2000). **4**, surface view of the same filament with the straight areolar rows on the mantle (x2000). **5** and **6**, SEM micrographs of sibling valves showing the linkage and the valvocopula attached to the mantle-edge, as well as the frequent rimpertulae (→) on the mantle (x3000 and x15000).

***Aulacoseira islandica* subspecies *helvetica* in Windermere**

Occasional filaments of *Aulacoseira islandica* subspecies *helvetica* (syn. *Melosira islandica* subspecies *helvetica* O. Muller and hereafter referred to as *helvetica*) were first noted in the plankton of the south basin on 27 October 1987. Specimens were then seen during April and May 1988, from October 1988 to May 1989, and September 1989 to May 1990. In June 1988 a few valves of *helvetica* were also found in the top centimetre of a lake sediment core (Haworth, unpublished). By the spring of 1989, it was already clear that *helvetica* had begun to thrive in Windermere and by April 1990 it had increased so much that it was more abundant than *A. subarctica* (syn. *Melosira italica* subspecies *subarctica* O. Muller). It was first noted in the north basin of Windermere in the spring of 1988 and, although less numerous than in the south basin, numbers have steadily increased. Unpublished data (C. Butterwick, pers. comm.) shows that both species of *Aulacoseira* had reached their peak by 3 April 1990. The respective numbers of cells present in the south basin at that time were 643 ml⁻¹ for *A. subarctica* and 1273 ml⁻¹ for *helvetica*.

Filaments of *helvetica* are composed of cells containing up to 10 discoid plastids (Figs 1, 2) and the pyrenoids, as noted by Skuja (1948), show up well in cells stained with iodine (Fig. 2b arrowed). The silica cell-walls are thinner than those of *A. subarctica* (Figs 3, 8) and lack an especially thickened pseudoseptum. The areolae are arranged in straight longitudinal rows on the mantle (Figs 4, 5). Scanning electron microscope (SEM) micrographs show that the areolar pattern in *helvetica* consists of fine pores (Fig. 5) and the frustules are linked together by many small spatulate spines (Fig. 6) which are not able to slide apart in the same manner as the pointed spines of *A. subarctica*. As no separation valves have been noted in *helvetica*, filaments usually break by the disruption of a cell so that one frequently finds empty valves at the ends, often terminated by the first girdle-band (the valvocopula; Fig. 5). Several rimoportulae are visible on the valve mantle (Fig. 5 arrowed).

In comparison, live filaments of *A. subarctica* are readily identified by the thickness of the silica walls, especially the thickened area of the pseudoseptum (sulcus) (Fig. 8), the spiral lines of areolae on the mantle (Figs 9, 10), the shape and number of the plastids (up to 4, Fig. 7) and, above all, the ring of large equal-sized spines visible not only at the end of the filaments but often overlying the adjacent cells (Figs 9, 10). Under the SEM, the spines are seen to be straight, tapering from the base, and they fit into grooves in the sibling valve in a manner that allows cells to slide apart freely. Lines of areolae end both at the base of the spine and in the spine groove (Fig. 10 and Haworth 1988).

***Aulacoseira ambigua* in Bassenthwaite Lake**

In the autumn of 1990, phytoplankton samples were collected from Bassenthwaite Lake, near Keswick. These included a high proportion of *Aulacoseira* filaments which differed from those of *A. subarctica*, which is normally found there together with *Fragilaria crotonensis*, *Asterionella formosa* and *Cyclotella pseudostelligera*. The taxon (Figs 11-16), which now seems to have replaced *A. subarctica*, has been identified as *Aulacoseira ambigua* (syn. *Melosira ambigua* Grunow). Although the phytoplankton in Bassenthwaite Lake has only been examined infrequently, this species has not been observed here before, in either plankton or surface sediments analysis. Phytoplankton collected by R. Mubamba in 1987 and identified only to genus (Tailing et al. 1989) has now been re-examined and while spring samples include *A. subarctica*, the autumn samples contain several filaments of *A. ambigua* as well. As inclusion of *Melosira ambigua* in the species list for Grasmere (Reynolds & Lund 1988) refers to just a few dead cells, Bassenthwaite Lake represents another new record for the English Lake District and the rest of Cumbria.

Again, live filaments look different from those of *A. subarctica*; the cell walls are not as thick and the plastids are more numerous (Fig. 11). At high magnification one can often observe the hollow sulcus that is typical for this taxon (Fig. 12 arrowed). The areolae are spirally arranged on the mantle but are larger and more quadrate than those on *A. subarctica* (Figs 13, 14, 16) and there is usually one rimoportule visible close to the sulcus. *A. ambigua* is one of the species of *Aulacoseira* where terminal and middle cells differ greatly in their modes of linkage; most cells are held together by very tiny interlocking spines which are triangular with crescentic edges (Fig. 15), and are only separated by breakage; only rarely were end-valves observed with small, regularly-pointed spines.

Where have these diatoms come from?

Two *Aulacoseira* taxa appear to have invaded two different lakes in the English Lake District within the last few years. They have probably come from outside Cumbria, for neither taxon was observed in the surface sediment assemblages from any of the local lakes and tarns during the surveys made in 1983 and 1984 (Haworth 1988). Neither taxon is at all frequent in northern Britain, although *helvetica* has been recorded in North Wales (Woodhead & Tweed 1954-55) and the Shetland Isles (Carter & Bailey-Watts 1980), and is known from some Irish loughs (Gibson et al. 1980). It is frequently observed in eutrophic lakes in Scandinavia (Nygaard 1956; Molder & Tynni 1967) but was first found in Ziirichsee in 1905 (Muller 1906). Hustedt (1945) considered it to be indicative of meso- to eutrophic lakes which are less productive than those

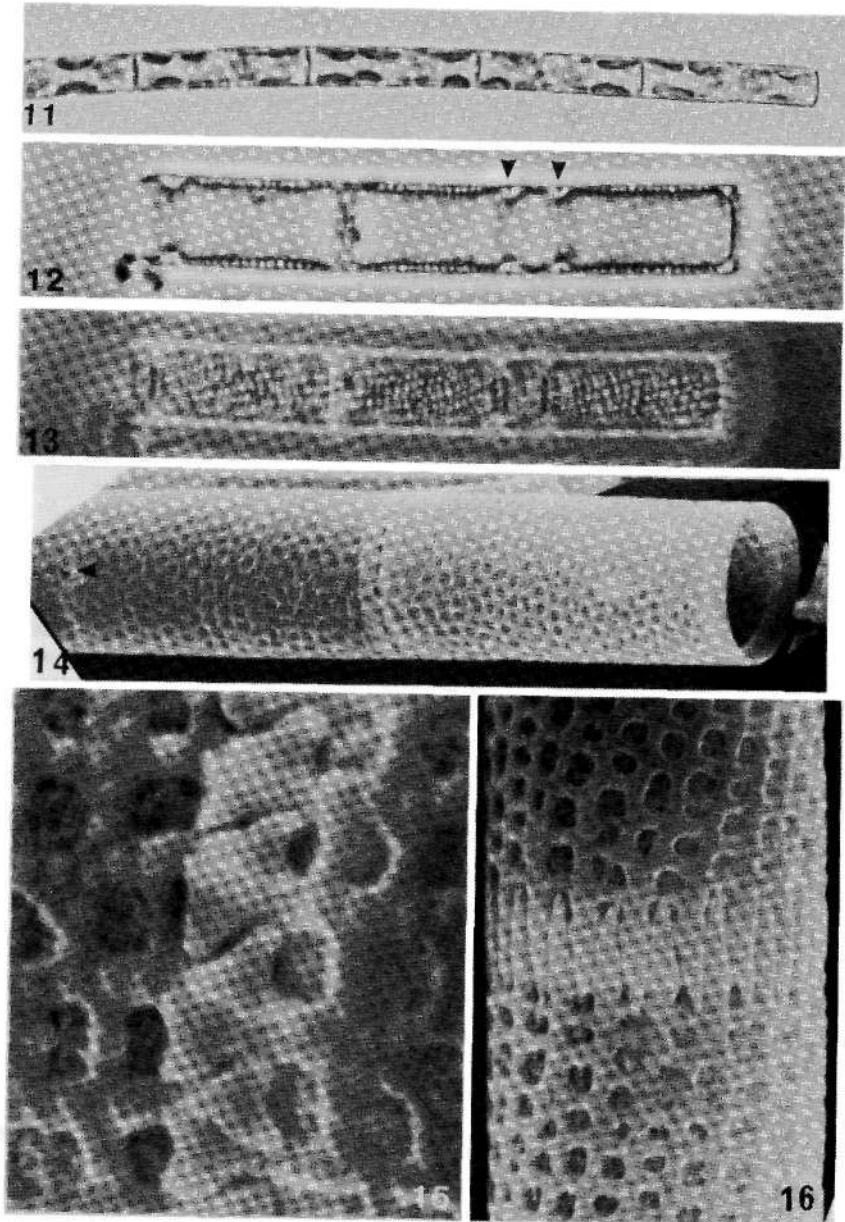
containing *A. granulata* (Ehrenberg) Simonsen; the latter has not yet been recorded from Cumbrian lakes. Occasional specimens of the species itself, *A. islandica* (O. Miiller) Simonsen, have been found in the earliest post-glacial sediments (age c. 9000 BP) of Windermere (Haworth, unpublished records). It is possible, but unlikely, that tiny populations continued to exist throughout the post-glacial despite unsuitable oligotrophic conditions. It is however a fact that neither *A. islandica* nor its subspecies *helvetica* had been seen in the several thousand algal samples which have been closely inspected over the last c. 50 years.

A. ambigua occurs in many water-bodies in England, in the Shropshire-Cheshire meres and in East Anglia; in the latter area it was widespread and abundant in the 1950s (Lund, unpublished data) and has been found in a recent survey (K. B. Clarke, pers. comm.). The only record from northern Britain is from a reservoir in Northumberland (J. R. Carter, pers. comm.). This diatom is also a recognized indicator of eutrophic lakes.

In both instances there are no known local sources of these two new taxa; the nearest recorded site of *helvetica* is over 160 km (c. 100 miles) distant, while that for *A. ambigua* is either 95 km (c. 60 miles) away in Northumberland or 145 km (c. 90 miles) away in the Cheshire-Shropshire meres.

Any new water-body is rapidly colonized by algae and a plankton readily develops in new reservoirs, e.g. Cow Green (Atkinson 1988), even though there are no suitable sources in the catchment. New taxa also arrive in established lakes, albeit at a slower rate since they must compete with resident populations. Although algae are obviously transported passively (Tailing 1951), there are no detailed studies showing how far viable cells or spores can travel. Algae are found in air samples but are they viable? Birds and animals are known to carry material on their bodies and in their guts, and diatoms have been found and cultured from faecal material from ducks (Holmes & Croll 1984; Atkinson 1972). Nowadays humans also provide a likely means for their dispersal; increasingly, lakes are used for recreational, educational and other purposes. Such pursuits may readily lead to the transfer of diatoms and other biota from lake to lake. This has serious implications for the spread of algal blooms and other nuisance organisms in amenity waters and for the safety of some endangered or rare species, especially as these movements are unpredictable.

FIGS 11-1.6. (*Opposite*). *Aulacoseira ambigua* (Grunow) Simonsen. 11, arrangement of plastids in the cells (x800). 12, median view of cells and valve showing the hollow sulcus (-*) (x2000). 13 and 14, spiral arrangement of quadrate-shaped areolae, with rimportula (-») adjoining the sulcus (x2000 and x4000). 15 and 16, SEM micrographs (x22000 and x9000 of linking (15) and terminal (16) spines.



Are these taxa indicative of rising nutrient levels?

Ecological information suggests that they are. Certain lakes in the English Lake District have been markedly enriched in the last 30 years due to increasing sewage input, use of detergents and, to a lesser extent, agricultural fertilizers (Lund & Moss 1990). Windermere has certainly been altered (Tailing et al. 1986) and Bassenthwaite Lake is changing too (Tailing et al. 1989).

It has already been noted that organisms continually arrive in new areas but they can only invade successfully when nutrient levels are suitable and a niche is available. New algae have been seen before in Windermere as well as in other lakes. It is possible that these two diatoms have been able to compete with the established populations because they grow better in eutrophic waters; their presence may indicate a plant succession due to increased nutrient availability. Clearly it takes several years for visible diatom populations to arise from the original inoculum, and the last few mild winters and warm summers have therefore merely enhanced very small and unseen populations that were already present.

It is too soon to say if these *Aulacoseira* taxa will thrive and if they will totally replace the more usual *A. subarctica* or coexist. Much will depend on the nutrient levels sustained in the lakes. In Windermere the main cause of enrichment has been the phosphate in sewage effluent. This input is now being reduced by North West Water with alterations already made to the Ambleside sewage works and soon to be working at the Tower Wood works. Reduced nutrients may reverse the current trend from *A. subarctica* to *A. islandica* subspecies *helvetica* or *A. ambigua*, or may lead to other changes. Changes may also be taking place elsewhere; there is therefore a general need for a continued programme of long-term monitoring. Where records are insufficient it is always possible to interpret past changes, using the diatom remains accumulated in the sediments of the lakes.

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References

- Atkinson, K. M. (1972). Birds as transporters of algae. *British Phycological Journal* 7, 319-321.
- Atkinson, K. M. (1988). The initial development of net phytoplankton in Cow Green Reservoir (Upper Teesdale), a new impoundment in northern England. In: *Algae and the Aquatic Environment* (ed. F. E. Round). Biopress, Bristol, 30-43.
- Carter, J. R. & Bailey-Watts, A. E. (1980). A taxonomic study of diatoms of standing waters in Shetland. *Nova Hedwigia* 33, 513-630.
- Gibson, C. E., Foy, R. H. & Fitzsimons, A. G. (1980). A limnological reconnaissance of the Lough Erne system, Ireland. *Internationale Revue der Gesamten Hydrobiologie* 65, 49-84.
- Haworth, E. Y. (1988). Distribution of taxa of the old genus *Melosira* (now mainly *Aulacoseira*) in Cumbrian waters. In: *Algae and the Aquatic Environment* (ed. F. E. Round). Biopress, Bristol, 135-164.
- Haworth, E. Y., Atkinson, K. M. & Newell, P. (1988). Distribution of certain diatom taxa in the waterbodies of Cumbria, UK. *Proceedings of the 9th International Diatom Symposium (Bristol 1986)*. Biopress & Koenigstein, 18-28.
- Holmes, R. W. & Croll, D. A. (1984). Initial observations on the composition of dense diatom growths on the body feathers of three species of diving birds. *Proceedings of the 7th International Diatom Symposium (Philadelphia 1982)*. Koeltz, 265-277.
- Husted VF. (1945). Die Diatomeenflora norddeutscher Seen. *Archiv fur Hydrobiologie* 41, 392-414.
- Knudson, B. M. (1954). The ecology of the diatom genus *Tabellaria* in the English Lake District. *Journal of Ecology* 42, 345-358.
- Lind, E. M. (1980). The distribution of desmids in some tarns in the English Lake District. *Naturalist, London* 105, 145-149.
- Lund, J. W. G. (1954). The seasonal cycle of the planktonic diatom *Melosira italica* ssp. *subarctica* O. Miiller. *Journal of Ecology* 42, 151-179.
- Lund, J. W. G. & Moss, B. (1990). Eutrophication in the United Kingdom - trends in the 1980's. Report to the Soap and Detergent Industry, 1-80.
- Molder, K. & Tynni, R. (1967). Uber Finnlands rezente und subfossil Diatomeen; 1. *Comptes rendus societie geologique Finlande* 39, 199-217.
- Miiller, O. (1906). Pleomorphismus, Auxosporen und Dauersporen bei *Melosira* -Arten. *Jahrbuch fur wissenschaftliche Botanik* 43, 49-88.
- Nygaard, G. (1956). Ancient and recent flora of diatoms and chrysophyceae in Lake Gribso. *Folia limnologica scandinavica* 8, 32-262.
- Pennington, W. (1943). Lake sediments: the bottom deposits of the north basin of Windermere, with special reference to the diatom succession. *New Phytologist* 42, 1 -27.

- Reynolds, C. S. & Lund, J. W. G. (1988). The phytoplankton of an enriched soft-water lake subject to intermittent hydraulic flushing (Grasmere, English Lake District). *Freshwater Biology* 19, 379-404.
- Skuja, H. (1948). Taxonomie des Phytoplanktons einiger Seen in Uppland Schweden. *Symbolae Botanicae Upsaliensis* 9, 1-399.
- Tailing, J. F. (1951). The element of chance in pond populations. *Naturalist, London* 839, 157-169.
- Tailing, J. F. (ed.), Atkinson, K. M., Elliott, J. M., George, D. G., Jones, J. G., Haworth, E. Y., Heaney, S. I., Mills, C. A. & Reynolds, C. S. (1986). A general assessment of environmental and biological features of Windermere and their susceptibility to change. Institute of Freshwater Ecology Report to North West Water Authority, Nov. 1986, 1-80 + 53 figs and 19 tables.
- Tailing, J. F. (ed.), Atkinson, K. M., Heaney, S. I., Elliott, J. M. & Mills, C. A. (1989). Bassenthwaite Lake: a general assessment of environmental and biological features and their susceptibility to change. Institute of Freshwater Ecology Report to North West Water, 1-44 + 22 figs and 23 tables.
- West, W. & West, G. S. (1909). The phytoplankton of the English Lake District. *Naturalist, London* 630, 260-267.
- Woodhead, N. & Tweed, R. D. (1954-55). Freshwater algae of Anglesey and Caernarvonshire. *North Western Naturalist*, 85-122.