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Population dynamics of *Ceratium* spp. in three English lakes, 1945–1985

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Abstract

Changes in the annual population densities of *Ceratium* spp. in three adjacent English lakes, Windermere, Esthwaite Water and Blelham Tarn, are summarised over the 41 year period 1945–1985. In these lakes the genus is represented by two species, *C. hirundinella* (O.F. Müll) Bergh. and *C. furcoides* (Levander) Langhans. Although the species have not been distinguished over the entire study period, they have been shown by examination of preserved samples to undergo marked changes of relative abundance in Esthwaite Water. Both long-term (years) and short-term (within year) changes of populations densities of *Ceratium* spp. are considered in relation to possible controlling factors including recruitment of the inoculum, nutrient enrichment, physical stability and fungal epidemics. Given an early inoculum, the relative success of *Ceratium* populations in these lakes decreases along gradients of increasing mixed depths, increasing turbulence and decreasing retention times. The potential for good population growth is regulated by energy inputs, lake bathymetry and hydraulic characteristics. The realisation of such growth is governed by nutrient availability and microbial grazing. The significance of large between-year differences of populations of *Ceratium* spp. for general lake metabolism is illustrated for summers of contrasting production in Esthwaite Water.

Introduction

Our present knowledge of phytoplankton production and ecology is based on observations and experiments of autecological or synecological studies over different scales of time. These may be of relatively short (seconds, minutes, hours), moderate (days, weeks, years) or, more rarely, long-term duration (decades) (Harris, 1980). So far, much has been learned from studies of short and moderate duration but there is an increasing interest in processes controlling long-term changes. A small number of laboratories have been collecting uninterrupted observations of populations of phytoplankton and associated variables over tens of years and the importance of analysing long-term community changes and their species components is becoming increasingly recognised (e.g. Lund, 1972a, b; Bailey-Watts, 1978; Gibson, 1981; Gibson & Fitzsimons, 1982; Harris, 1986).

This work presents the results of 41 years of continuous observations of population changes of the large dinoflagellates *Ceratium* spp. in three adjacent lakes (four lake basins) of varying size and productivity. Planktonic populations are relatively slow-growing with maximum population doubling times of c. 5 days (Heaney, 1976) and there is usually only a single phase of annual increase (Heaney *et al.*, 1983). This genus with its simple annual cycle thus provides a useful model system to investigate factors which may influence both between-year and longer-term changes in population dynamics.

The biology of *Ceratium* has been intensively studied over the past 20 years in Esthwaite Water (Talling, 1971; Heaney, 1976; Heller, 1977; George & Heaney, 1978; Harris *et al.*, 1979; Heaney & Talling, 1980a, b; Lund, 1981; Chapman *et al.*, 1982, 1985; Heaney *et al.*, 1983; Canter & Heaney, 1984; Frempong, 1981a, b, 1982, 1984; Heaney & Butterwick, 1985; Heaney *et al.*, 1986). Major changes in summer populations of *Ceratium* in this lake are compared to those in nearby Blelham Tarn in relation to recruitment of the inoculum, physical stability and recent infections of parasitic fungi. The significance of the development of large populations of *Ceratium* for aspects of lake metabolism is assessed for years of contrasting population size.

Although cells of *Ceratium* are conspicuous and readily reconizable, the genus as a whole consists of a complex of taxa often difficult to differentiate at the species level (e.g. Entz, 1927; Canter & Heaney, 1984; Hickel, 1987b). In the lakes concerned only *C. hirundinella* and *C. furcoides* have at present been recognized. The importance of a sound understanding of the taxonomy of this genus is emphasized.

Description of sites studied

Esthwaite Water, Blelham Tarn and Windermere are situated in the English Lake District and details of their morphology and bathymetry are given in Ramsbottom (1976). Windermere is divided into a larger, deeper (8.05 km^2, 64 m, mean depth 25.1 m) north and a smaller, shallower (6.72 km^2, 42 m, mean depth 16.8 m) south basin by shoals and islands. Esthwaite Water and Blelham Tarn are small shallow lakes with areas, and maximum and mean depths of 1.0 km^2, 15.5 m, 6.4 m and 0.1 km^2, 15.1 m, 6.8 m respectively. The average retention time for Windermere is about 36 weeks (Sutcliffe & Carrick, 1983); for its south basin it is about 14 weeks and similar to Esthwaite Water (13 weeks, Heaney *et al.*, 1986). The average replacement time of water in Blelham Tarn is about 6 weeks but fluctuates widely falling to about 10 days or less in periods of floods.

Methods

From 1945 to present there has been a regular weekly (or biweekly in winters since 1983) sampling programme near the deepest positions in the lakes.

Vertical profiles of water temperature (±1 °C) were made using a thermistor at either regular depth intervals or by locating the depths of specific isotherms. Water temperatures for Esthwaite Water and Blelham Tarn at 0 and 6 m depths, either measured directly or determined by interpolation, have been converted to density using the equation given by Kell (1967). These density values were used to give a measure of the stability of the epilimnion or upper mixed layer of these two lakes during summer stratification by calculating weekly values of N^2 (Mortimer, 1974), i.e.,

$$N^2 = \frac{g}{\bar{\rho}} \times \frac{\partial \rho}{\partial z}$$

where N = the Brunt-Väisälä frequency, g = the acceleration due to gravity, ρ = density of water, $\bar{\rho}$ = average density of water over the relevant depth interval, z = depth.

Water samples for chemical analyses and algal counts were collected using a weighted plastic tube (Lund, 1949) from the 0–5 m layer (Esthwaite Water and Blelham Tarn) and for both basins of Windermere 0–5 m (1945–62), 0–10 m (1962–64), 0–7 m (1964 onwards). Further details of sampling are given by Sutcliffe *et al.* (1982). A sub-sample was immediately fixed in the field with Lugol's iodine for subsequent algal counts by the Utermöhl inverted-microscope technique (Lund *et al.*, 1958).

From 1945 analyses have been made for soluble reactive silicon expressed as SiO_2, soluble reactive phosphorus (SRP) and nitrate nitrogen (NO_3-N). During this period there have been changes in methods (details in Mackereth, 1963 and Mackereth *et al.*, 1978). The most important are:

a) Change of the Si method from a non-reductive 'yellow' colorimetric determination used up to May 1956 to the more sensitive spectrophotometric determination by reduction of silicomolybdate to molybdenum blue using metol. Before 1956 concentrations below c. 0.5 mg SiO_2 l^{-1} may have been overestimated.

b) Change of the SRP method from a colorimetric determination used up to December 1955 to two spectrophotometric methods for determining molybdenum blue after formation of phosphomolybdate and extraction into hexanol. The hexanol was omitted during 1981 and 1982 which resulted in unrealistically high values during the late spring-summer period for these two years.

c) A number of changes in the determination of NO_3-N using a phenol disulphonic acid (PDS) method to May 1956 (colorimetric) and then to June 1965 and April to December 1971 (spectrophotometric) and at other times using variations on the cadmium/copper hydrazine reduction techniques. The former (PDS) method gives values (x) which are appreciably less than those by the latter (y). This disparity has been corrected for in Fig. 3 by increasing the PDS values according to the relationship.

$$y = 1.2x + 30 \text{ (y and x in } \mu g \text{ N l}^{-1})$$

derived from a year long series of samples analysed by both methods (Talling, pers. comm.).

Alkalinity was determined during 1971 and 1984 by Gran titration and during 1972 using 'BDH 4.5 indicator'; further details of both methods are given by Mackereth *et al.* (1978). Particulate phosphorus was determined during 1971 and 1972 as the difference between total phosphorus and total dissolved phosphorus obtained from aliquots of the same sample according to Heaney *et al.* (1986), and during 1984 as a potassium persulphate digest (under pressure) of samples filtered onto pre-washed 47 mm Millipore HAWP filters (Eisenreich *et al.*, 1975). Particulate carbon and nitrogen were determined by high-temperature dry combustion, followed by gas chromatographic detection in a Hewlett-Packard CHN analyser (1971, 1972), or using a Erba Science 1106 Elemental analyser (1984) (Hilton *et al.*, 1986), of material collected by filtration in duplicate on pre-combusted glass-fibre filter discs (Whatman GF/C, 1971, 1972; GF/F, 1984).

Counts of fungal infection were made from vertical tows using a plankton net of c. 65 μm mesh in cross section. Percentage infection was obtained from examination of specimens on a slide at 500–1200× magnification. During the height of an epidemic not less than 200 *Ceratium* cells were examined. In some instances, cotton-blue stain in lactophenol was added to a slide in order to facilitate detection of any fungal thalli present.

Results

Taxonomy

Before 1981 all cells of *Ceratium* were identified as *C. hirundinella* (O.F. Müll.) Bergh. Cells resembling *C. furcoides* (Levander) Langhans were considered as form variation of *C. hirundinella*. There is now compelling evidence based on morphological distinctions of vegetative cells and cysts (Entz, 1927; Chapman *et al.*, 1982; Hickel, 1987a) and cyst germination experiments (Heaney & Jaworski, unpublished results) that *C. hirundinella* and *C. furcoides* are well defined species which co-exist in the English Lake District. So far, vegetative cells and cysts resembling those of *C. rhomvoides* Hickel (Hickel, 1988b) have not been recognized in these lakes although that does not mean they do not occur.

At the same time as the regular samples were collected for quantitative counts, sub-surface tows were also taken using plankton nets. Samples of these tows, preserved in Lugol's iodine or formaldehyde, have been stored since 1945. An attempt has been made to determine retrospectively for Esthwaite Water the relative proportions of cells of *C. hirundinella* and *C. furcoides* at the time of maximum density of *Ceratium* cells. The species were distinguished on the basis of morphology, in particular the diameter and angle and slope of the transverse furrow. Figure 1 shows marked differences in the relative abundance of the two species. From 1964 to 1973 *C. furcoides* was the dominant form, being replaced by *C. hirundinella* until 1982, the last year of large population densities of the genus in the lake.

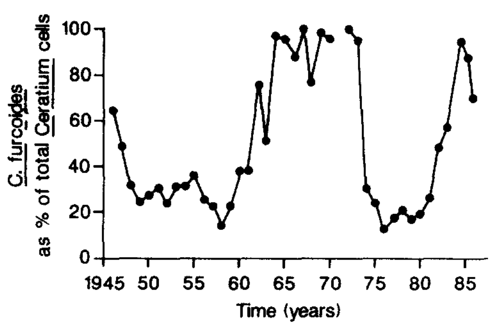


Fig. 1. *Ceratium furcoides* as a percentage of the maximum total population of *Ceratium* spp. in Esthwaite Water. Gap indicates time when samples were not collected or were unsuitable for examination.

Although there are clearly large annual differences in the relative abundance of these two species in these lakes, their life histories are nevertheless similar in respect to the timing of the major growth phase, both being essentially 'summer' forms. For the rest of this work the species will be combined as *Ceratium* spp.

Long-term population changes

The population changes of *Ceratium* spp. from 1945–1985 in Esthwaite Water, Blelham Tarn and both basins of Windermere are summarised in Fig. 2 as mean weekly cell concentrations during period of occurrence, and annual maximum cell concentrations. There is a strong correlation between these two indices of annual population density except for one very large cell count in Esthwaite Water in 1973 on an occasion of considerable algal patchiness (George & Heaney, 1978).

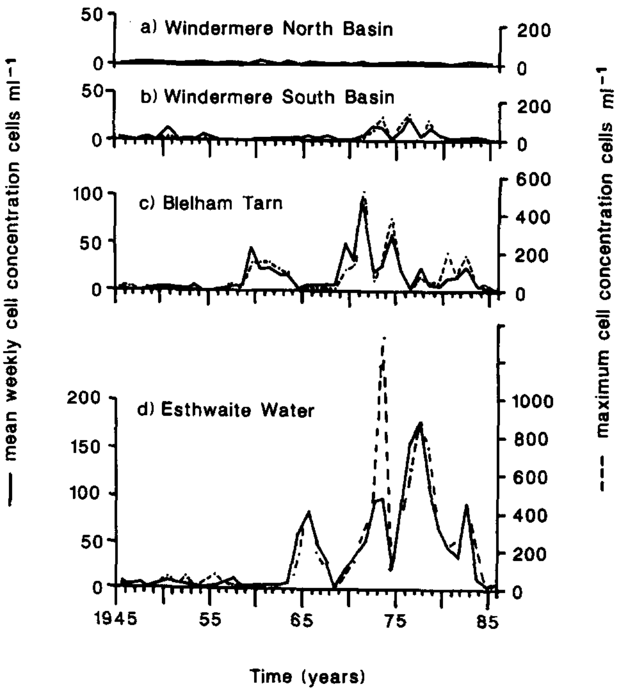


Fig. 2. Long-term changes (1945–1985) in the mean weekly concentration (occurrence dates only) (—) and maximum cell concentrations (– – –) of *Ceratium* spp. in the 0–7 m layer of a) Windermere North Basin b) Windermere South Basin and 0–5 m layer of c) Blelham Tarn and d) Esthwaite Water.

Over the 41 year period, *Ceratium* populations in the north basin of Windermere have remained small with very little change. In the south basin of the lake populations have also remained small although with a number of years of moderate biomass in the seventies. By contrast, Blelham Tarn and Esthwaite Water have produced moderate to large populations of *Ceratium* spp. from the late fifties and mid-sixties respectively. There is considerable between-year variation in these two lakes and since 1983 populations in both have declined to low numbers. Some of the factors influencing these long-term and between-year changes are considered below.

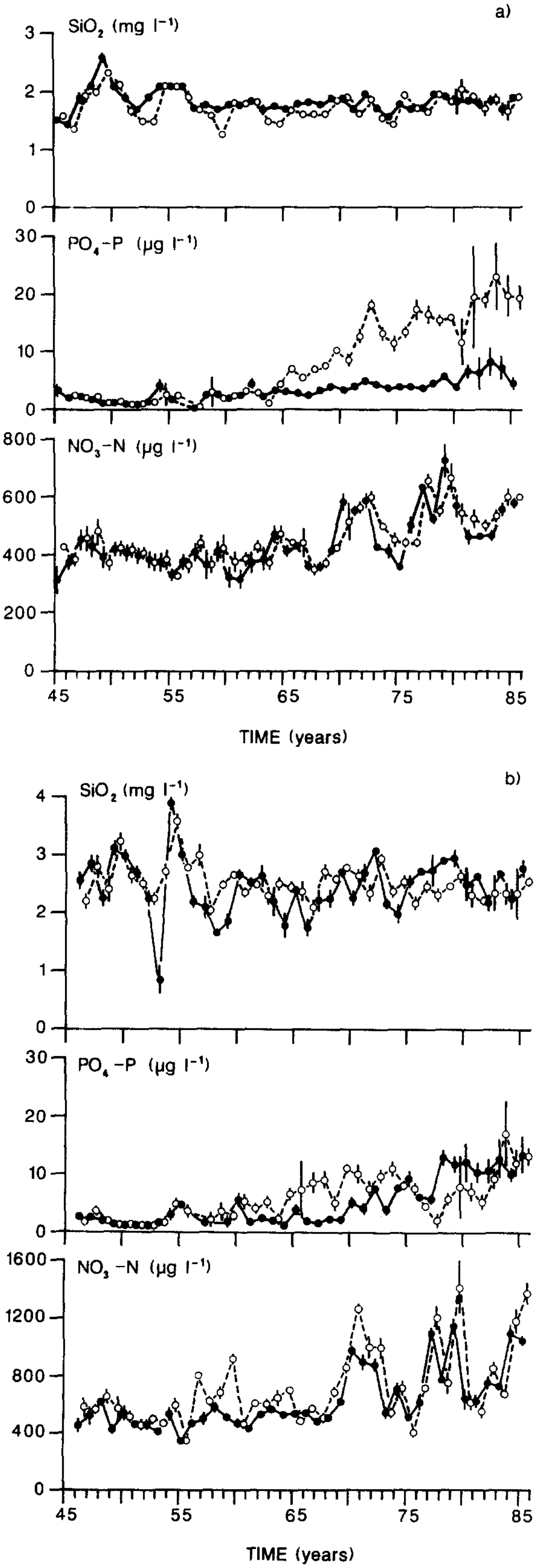
Nutrient enrichment

In order to sustain large algal biomass during summer lakes must receive a sufficient supply of plant nutrients. Concentrations of such nutrients increase to their annual maxima during winter when algal growth is least. Increases in mean winter nutrient concentrations are therefore a measure of nutrient enrichment.

Sutcliffe *et al.* (1982) calculated mean values ±95% confidence limits from 1945–1980 for SRP and NO_3-N (uncorrected) in all four lake basins in the autumn-winter-spring period when these variables reached their highest concentrations. Their values, extended to 1985 and with method correction for NO_3-N are shown in Fig. 3 together with similarly derived ones for SiO_2. In all basins there have been slight changes in mean winter concentration of SiO_2. The larger changes about the mid-fifties may be real or a result of the less sensitive analytical method used up to that time. More pronounced long-term increases are shown for SRP and NO_3-N.

Mean winter concentrations of NO_3-N showed little change in any lake basin before 1970. Thereafter there has been a gradual and oscillating increase which is in phase for all four lake basins.

SRP differs from NO_3-N in that marked increases in winter concentrations occurred in the south basin of Windermere and Blelham Tarn in the mid-sixties. A similar rise in Esthwaite Water was delayed until the early-seventies and the increase in winter SRP concentrations in the north basin of



Windermere have been smaller and more gradual. These increases in winter concentrations of SRP and NO$_3$-N are most likely to be caused by the installation of sewage works discharging into the basins, the introduction of polyphosphate builders in detergents, increased tourism, and the application of nitrate-rich agricultural fertilizers (Lund, 1972b, 1979, 1981).

It is clear that with increasing nutrient enrichment Blelham Tarn and Esthwaite Water have had the potential to support large populations of *Ceratium* since the early to mid-sixties respectively. Calculations to be presented elsewhere indicate annual loadings of SRP to the north and south basins of Windermere of 0.28 and 0.91 g P m^{-2} per year respectively. These loadings are sufficient to support appreciable growths of summer phytoplankton ($>$1.2 mg C m^{-3} within 0–7 m layer) which occur in some years. Nevertheless, moderate populations of *Ceratium* have not developed in Windermere except for a few years in the seventies in the south basin.

Between-year population changes

Although Esthwaite Water and Blelham Tarn are only about 2 km apart and share the same weather patterns, there appears to be little or no coincidence of annual *Ceratium* population attainment (Fig. 4). What is a good year for *Ceratium* growth in one lake is frequently the reverse in the other. Several factors may regulate successful population growth.

The inoculum

For these slow-growing dinoflagellates the production of large summer populations is dependent upon

Fig. 3. Long-term changes (1945–1985) in mean concentrations (±95% confidence limits) of Si as SiO$_2$, PO$_4$-P (SRP), and NO$_3$-N during periods of annual winter-spring maxima for a) ● Windermere North Basin, ○ South Basin, b) ● Esthwaite Water, ○ Blelham Tarn. To avoid overlap, the values of Windermere South Basin and Blelham Tarn are offset to the right of those of Windermere North Basin and Esthwaite Water respectively.

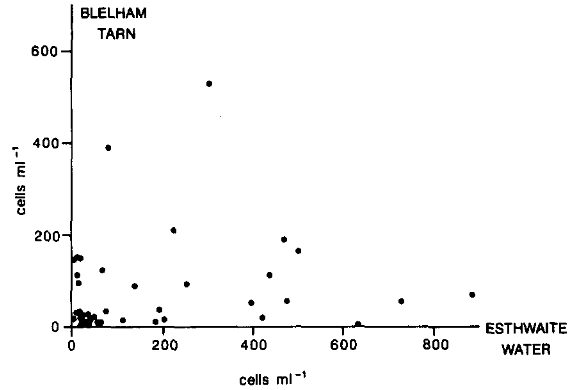


Fig. 4. The annual maximum population densities of *Ceratium* spp. in Blelham Tarn in relation to those of Esthwaite Water (1945–1985).

a sufficient inoculum. The earlier this is established the greater is the time available for nutrient uptake and growth once sufficient temperature has been reached. For present purposes the 'inoculum', mainly derived from excystment of perennating cysts in the benthos (Heaney *et al.*, 1983), is considered operationally as the concentration at which *Ceratium* cells are first recorded at a density of c. 0.1 cells ml^{-1}.

Figure 5 shows the relationship between mean weekly cell concentration and the number of days from 1 January before the first record of *Ceratium* in the plankton. This indicates that for mean weekly cell concentrations of greater than 50 cells ml^{-1} (c. 250 cells ml^{-1} maximum population density) within the 0–5 m layer, a cell density of c. 0.1 cells ml^{-1} must be present before June. For both lakes larger populations are generally associated with earlier appearance in the plankton and the effect is more clearly seen with the very large populations in Esthwaite Water. However, the converse does not necessarily apply and years with early appearance of *Ceratium* do not always result in large summer populations.

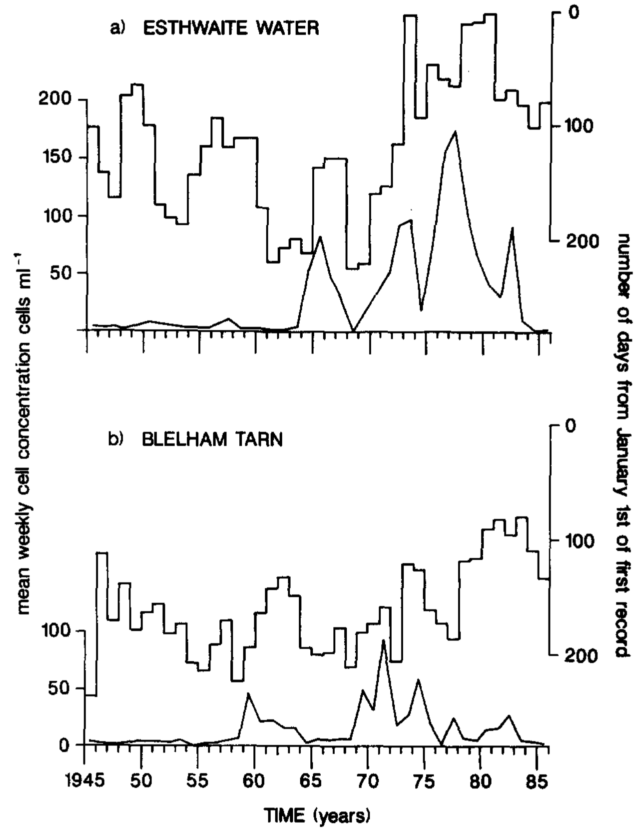


Fig. 5. The timing of the inoculum of *Ceratium* spp. shown by histograms as the number of days from 1 January before the first record of a cell density of c. 0.1 cells ml^{-1} in relation to the mean weekly cell concentration during period of occurrence for a) Esthwaite Water and b) Blelham Tarn.

Weather-induced changes

Periods of strong mixing have been shown to inhibit the growth of dinoflagellate populations (Pollingher & Zemel, 1981; Reynolds *et al.*, 1983; Heaney & Butterwick, 1985). The stability of the epilimnion of Esthwaite Water from 1971–1983, determined as the value of N^2 over the 0–6 m layer, was considered by Heaney & Butterwick (1985) as a factor regulating the size of *Ceratium* populations. With the exception of 1983, summers (mid-June until the end of August) with mean weekly N^2 values of $>5.0 \times 10^{-4}$ s^{-2} correlated with large populations of *Ceratium;* below this value growth was relatively poor and diatoms were more abundant. The values of mean weekly N^2 similarly calculated are shown for Esthwaite Water and Blelham Tarn from 1960–1985 (Fig. 6) in relation to mean weekly cell concentration of *Ceratium*.

Over the 25 year period there were nine summers in Esthwaite Water with mean weekly N^2 values of

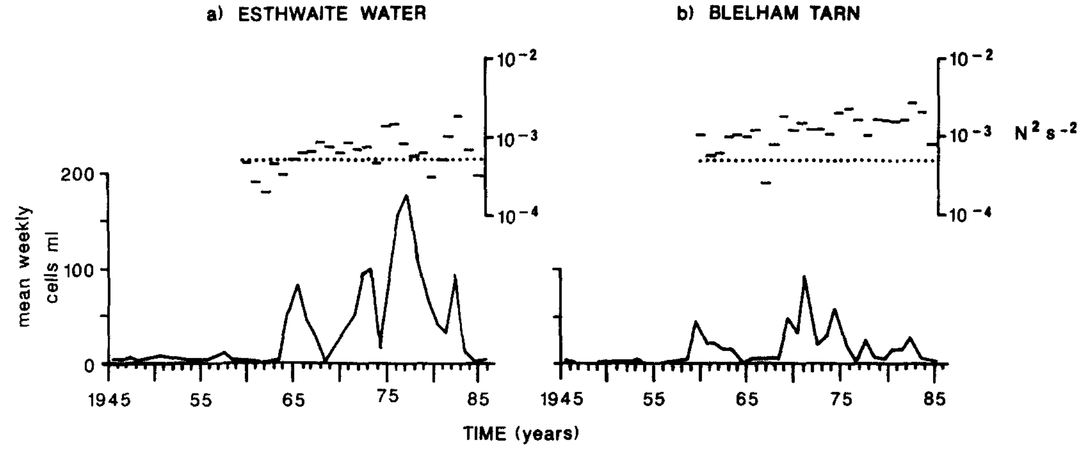


Fig. 6. Relationship between mean weekly physical stability, N^2 (0–6 m layer, mid-June until end of August), and mean weekly cell concentration (0–5 m layer) during period of occurrence of *Ceratium* spp. for a) Esthwaite Water and b) Blelham Tarn. Dotted line indicates value of 5×10^{-4} s^{-2} plotted on a log scale.

$<5 \times 10^{-4}$ s^{-2}. All of these were characterized by moderate or poor *Ceratium* populations. Applying the same criterion to Blelham Tarn, only in 1967 did the value of N^2 fall below the 'critical' value of 5.0×10^{-4} s^{-2} and this was the result of the lake being artificially mixed from the second half of June until late August. Thus on the grounds of stability alone, Blelham Tarn would always be able to support large *Ceratium* populations, although its propensity to do so has been less than for nearby Esthwaite Water.

As there are few years of appreciable growth of *Ceratium* populations in Windermere, values of mean weekly N^2 during summer have not been calculated for its basins which normally have upper mixed layers several metres deeper than the shallower lakes. It is significant, however, that notable populations only developed in the south basin of Windermere during the warm stable summers of the seventies.

Parasitism

Both the vegetative cells and cysts of *Ceratium* are subject to parasitism by fungi or predation by lowly forms of protozoa. An account of the organisms associated with the vegative cells of *Ceratium*, up to 1983 is given by Canter & Heaney (1984).

Before 1982 the biflagellate fungus *Aphanomycopsis cryptica* Canter (Fig. 8a) had only been recorded within cells of *Ceratium* from a sample collected from the south basin of Windermere in 1952. During 1982 a very high percentage (87%) of *Ceratium* cells in Esthwaite Water were determined as parasitized by *A. cryptica* just after encystment had commenced. By 1983 there were appreciable infections of *Ceratium* populations in all four basins by this fungus (Canter & Heaney, 1984). Figure 7 shows the occurrence of *A. cryptica* within *Ceratium* populations from 1982–1985 in Esthwaite Water and Blelham Tarn. It can be seen that infections of the fungus are normally associated with marked decreases in the density of *Ceratium* populations. Since 1982 *A. cryptica* has regularly parasitized *Ceratium* populations in Esthwaite Water (i.e. 4, 6 July 80% 1983; 3 July, 14 August 42%, 1984; 9–23 July 1985; 16–22 July 54%, 23 September 1986, 25 August 72%, 22 September 1987. For the last two years the annual maximum density of *Ceratium* only reached 15 and 35 cells ml^{-1} respectively in striking contrast to the large populations present in the seventies and early eighties (Fig. 2). These regular parasitic attacks are a major cause of the recent decline of *Ceratium* populations in this lake.

In Blelham Tarn infections of *Ceratium* popula-

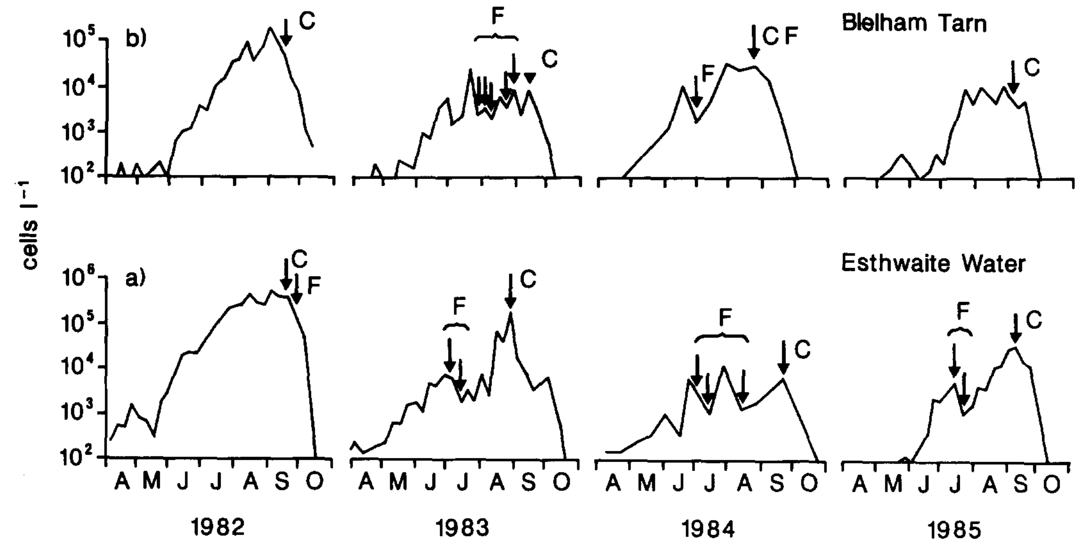


Fig. 7. Population numbers of *Ceratium* spp. and incidence of *Aphanomycopsis cryptica* (arrow F) and cyst formation (arrow C) for the years 1982–1985 for a) Esthwaite Water and b) Blelham Tarn.

tions by this fungus were only recorded during 1983 (19, 27 July 49%; 2, 16, 23 August) and in 1984 when numerous specimens were found (3–6 July and 28 August). *A. cryptica* was not observed during 1985 and 1986. For these later years in Blelham Tarn *Ceratium* growth was nevertheless secondary to earlier developing populations of the blue-green algae (1985) *Anabaena solitaria* Kleb. and (1986) *Oscillatoria aghardhii* Gom. var. *isothrix* Skuja.

During their time of formation and occurrence in the upper layers of the lakes (i.e. in plankton tows taken from the 0–5 or 0–7 m water column) cysts of *Ceratium* are known to be parasitized by the chytrid *Rhizophydium nobile* Canter (Canter, 1968). Observations, so far, suggest that this fungus (Fig. 8b) is confined to cysts of *C. furcoides* (Canter & Heaney, 1984).

Although plankton samples had been examined for parasites more or less on a weekly basis by HMC since 1947, it was not until September 1957 in Blelham Tarn, that *R. nobile* was first noticed. It was again seen in this lake in September 1963 and then in Esthwaite Water and Windermere south basin in October 1964. Between 1960–1963 very few samples were examined. From 1964–1973 (except 1971) 1976 and 1982–1986 lake samples were examined regularly. Overall *R. nobile* has been noted as follows:

Esthwaite Water 1964, 1965, 1966, 1967, 1969, 1972, 1973, 1983;

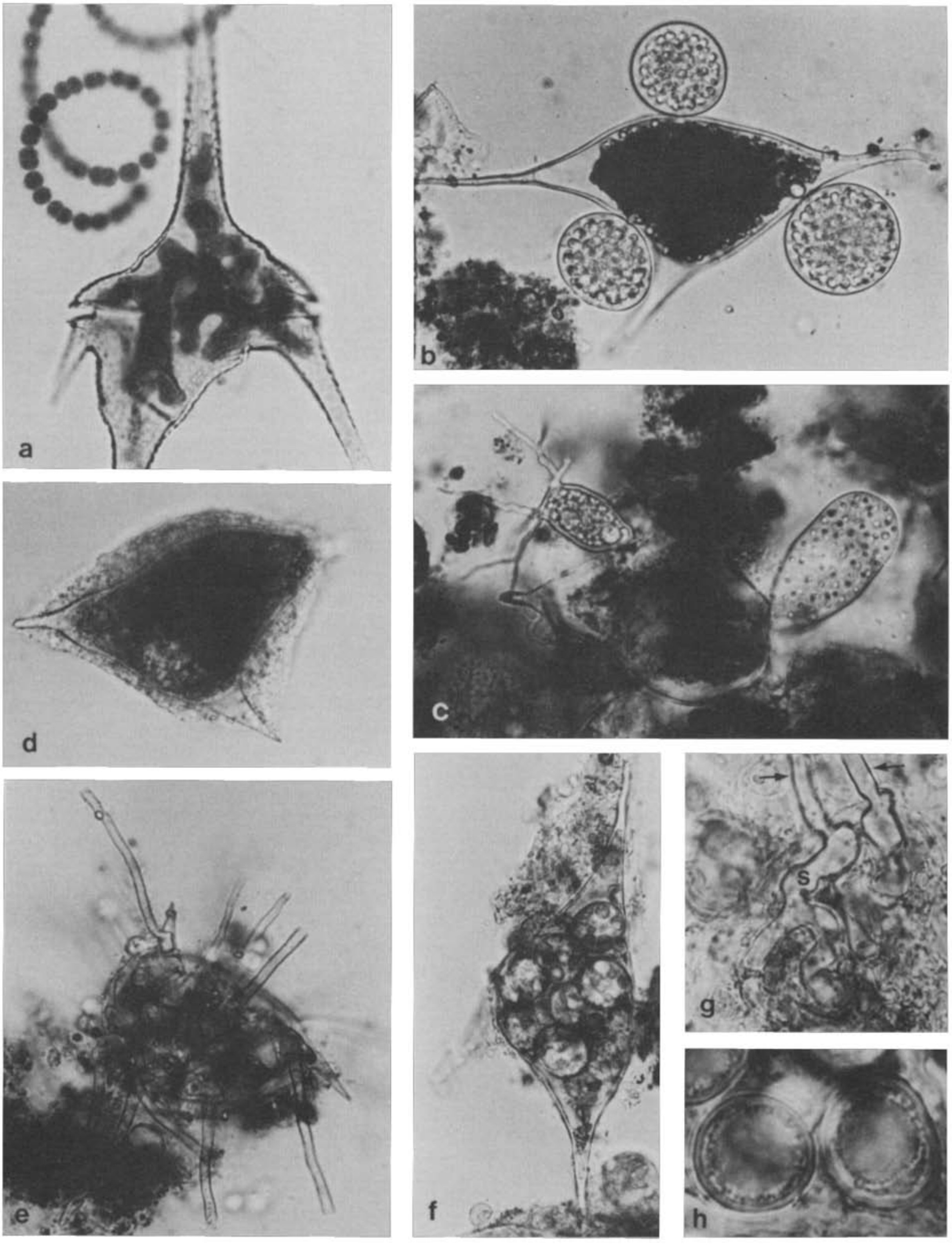
Windermere, south basin 1964, 1965, 1967, 1970, 1972, 1973;

Blelham Tarn, 1957, 1963, 1969, 1970, 1971, 1972, 1974, 1980 (SIH), 1982, 1985.

Dates when the fungus has been recorded are between the latter half of September and the end of October (Fig. 9). To date this species has not been found in Windermere north basin.

In rare instances cysts of *Ceratium* parasitized by

Fig. 8. a–h. Examples of the variety of organisms which kill vegetative cells and cysts of *Ceratium*. a, e–h biflagellate fungi, b, c chytridaceous fungi; d protozoan. a, *Aphanomycopsis cryptica*, tubular thallus ramifying within host cell ×640. b Three sporangia of *Rhizophydium nobile* ×640. c An undescribed chytrid. Mature sporangium (right), resting spore (left) ×640. d Vampyrellid-type organism with ingested cyst ×640. e–h An undescribed biflagellate fungus. e Cyst which contains a sporangial thallus, now dehisced. Several long exit tubes extend through the host wall ×640. f Several immature resting spores inside a cyst ×640. g Small portion of tubular sporangial thallus (s); two exit tubes visible (arrowed) ×1008. h Two mature resting spores ×1600. a, b from plankton; rest from mud sediment. a, c–e *C. hirundinella;* b, f *C. furcoides.*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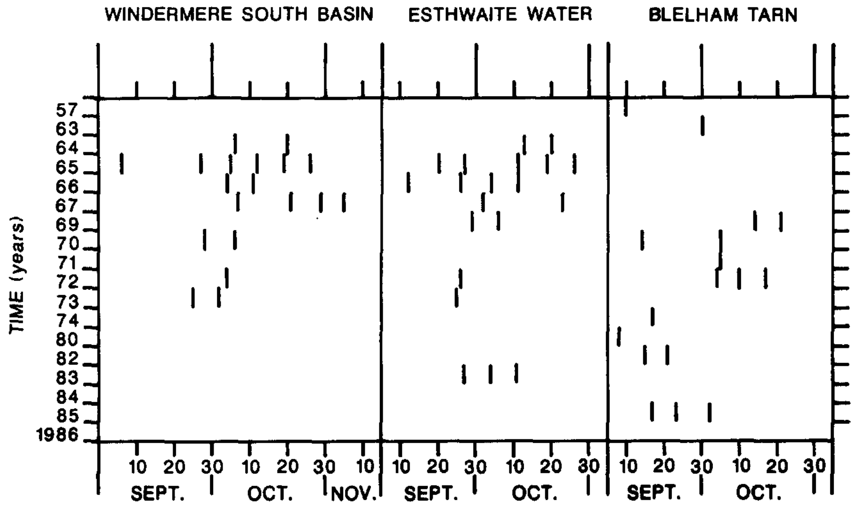

Fig. 9. Records of *Rhizophydium nobile* on cysts of *Ceratium* since the first observation in Blelham Tarn in 1957. For details of periods of examination of material see Canter & Heaney (1984).

a biflagellate fungus have been encountered in the plankton (Esthwaite Water, August 1949, September 1964; Blelham Tarn, October 1969; Windermere south basin, September, 1973). Biflagellate fungi have also been observed in cysts present in the sediment collected from traps laid in Esthwaite Water during September–December 1981 and September–October 1982. It is probable that two different fungi are involved. The most abundant species is shown in Fig. 8e–h. Within the cyst a tubular thallus is formed (Fig. 8g) which later in development is believed to segment into a number of separate portions. Each portion usually bears one exit tube (Fig. 8g arrowed) which projects beyond the algal cyst wall (Fig. 8e). The zoospores become delineated and mature in a vesicle at the apex of each tube. Many spherical or oval resting spores develop within the *Ceratium* cysts (Fig. 8f, h).

Very little is known concerning the life-history of the second biflagellate fungus. However, it differs from the one above in that the zoospores encyst and form a clump of primary zoospore cysts attached to the apex of the exit tube, thus resembling species of *Aphanomycopsis.* These two biflagellate fungi exhibit certain similarities with the fungus *A. peridiniella* (Boltovskoy, 1984) which parasitizes cysts of *Peridinum willei.*

Yet other organisms were found in the sediment which must also contribute to the depletion of viable cyst populations. Some cysts had clearly been ingested by a multinucleate vampyrellid-like protozoan (Fig. 8d) while many bore sporangia and resting spores of an as yet undescribed chytrid (Fig. 8c). The elongate sporangia of the latter stand out from the surface of the cyst and the highly destinctive resting spore is ornamated at its apex with extrusions which resemble deer antlers.

Ceratium populations and chemical transformations

The presence or absence of large *Ceratium* populations can result in marked differences in nutrient utilization, chemical transformations and overall lake metabolism. Figure 10 gives the major soluble and particulate nutrient changes in Esthwaite Water during 1971, 1972 and 1984, three years with warm stable summers but of contrasting *Ceratium* populations.

The summer phytoplankton maximum during 1971 and 1972 consisted mainly of cells of *Ceratium* spp. and, expressed as particulate carbon, was at least 3 times greater than for 1984 when *Ceratium* populations were reduced by repeated infections of fungal parasites. Changes in particulate phosphorus

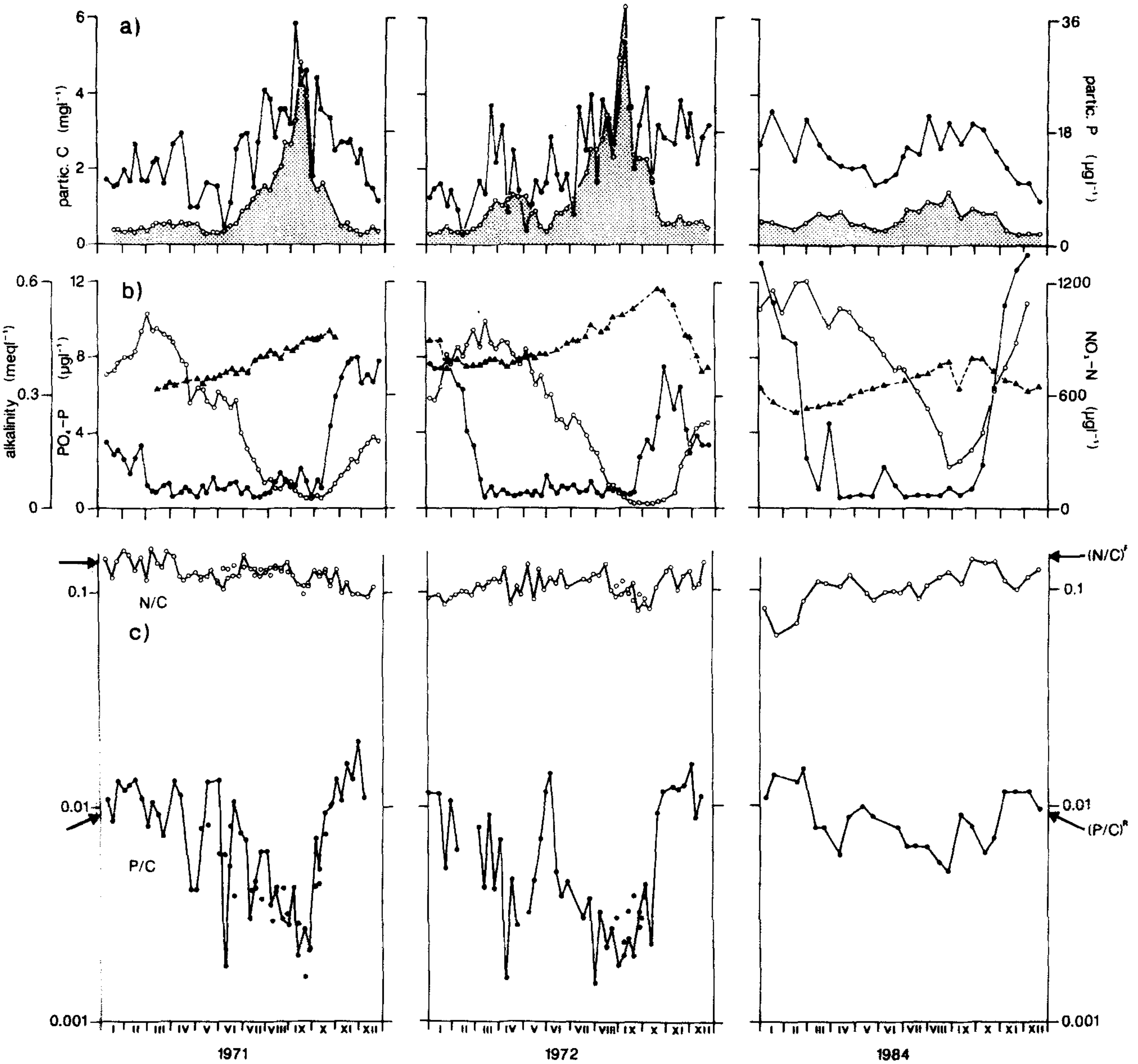

Fig. 10. The seasonal variation in 0–5 m layer of Esthwaite Water during 1971, 1972 and 1984 of a) particulate matter as carbon (o , shaded) and phosphorus (●), b) alkalinity (▲), SRP (●), NO_3-N (o), and c) the ratio by atoms of particulate P/C and particulate N/C. Unjoined points represent mean values from 0, 2, 4 m depth samples. Arrows indicate the generalised Redfield ratios.

were much smaller. The differences in the accumulation of these particulate fractions are also given as the ratio (by atoms) of particulate P/C. There are notable minima in this ratio for the denser *Ceratium* dominated phytoplankton in 1971 and 1972 compared with the same period of 1984. Although the summer phytoplankton had a much higher content of cellular phosphorus relative to carbon in the later year, the concentration of SRP remained close to the limit of detection (0.6 $\mu g\,l^{-1}$) from April to September in all three years.

Between-year changes of NO_3-N and alkalinity were greater than for SRP. The summer minimum concentration of NO_3-N was appreciably higher during 1984 and the rate of decrease less acute than in the two earlier years, although it could be argued that in the later year it was declining from a higher winter maximum. 1984 was an exceptionally dry summer however, with rainfall between May and August less than half that recorded for the same period in 1971 and 1972. This much lower rainfall with little inflow would reduce the external input of NO_3-N for summer production during 1984.

Corresponding to the much smaller summer biomass during 1984, the increase in alkalinity was also reduced between May and September (0.095 mequiv. l^{-1}) compared to 1971 and 1972 (0.115 and 0.155 mequiv. l^{-1} respectively). This occurred in spite of reduced dilution effect from low inflow in 1984.

Discussion

Many factors contribute to the production of particular species of algae in lakes. Considerable progress has been made in understanding the periodicity and succession of phytoplankton (e.g. Munawar & Talling, 1986 and papers therein), yet it is generally not possible to predict the production of individual species for a given lake and year. Although this may be an unrealistic objective, the important factors regulating the potential for successful production of major species can be determined. The present work shows that these factors may operate over long periods of years or be seasonal in effect giving rise to between-year variability.

Many algae which tend to become dominant during summer in productive lakes are relatively slow-growing (e.g. Sommer, 1981) with high temperature thresholds for growth (e.g. Nicklisch & Kohl, 1983; Heaney *et al.*, 1983; Heaney & Butterwick, 1985). Their production is therefore seasonally restricted and dependent, in part, upon the size of the inoculum when the temperature threshold for growth is reached. The presence of an early inoculum in the plankton results from an overwintering planktonic population, recruitment from overwintering perennating stages in the benthos or a combination of both. A delayed inoculum will be disadvantageous if this allows other 'summer' species to become established and take up available nutrients.

In small temperate lakes with short retention times the inoculum for *Ceratium* populations is mainly derived from the excystment of overwintering cysts in the sediment. For years of high cyst formation and deposition in Esthwaite Water, Heaney *et al.* (1983) calculated that, assuming no losses, only 0.03% would be required to excyst the following spring to give an inoculum of c. 0.1 cells ml^{-1}. Like seed production, cyst formation is often prolific providing a reservoir of viable cysts in the sediment (Huber & Nipkow, 1923). This may compensate for years of poor cyst production, assuming buried cysts may be returned to the sediment surface. Apart from years of poor cyst production, those formed suffer losses. Some will be removed through the outflow although this loss is almost certainly small as a result of rapid transport of cysts to the sediment (Heaney *et al.*, 1986; Heaney, unpublished results). Other potential losses are grazing in the sediment and infections by parasitic fungi. These include the fungus *Rhizophydium nobile* Canter (Canter, 1968) which occurs on *C. furcoides* (Canter & Heaney, 1984) and others observed by Canter & Heaney on cysts of both *C. furcoides* and *C. hirundinella* but as yet undescribed. If the reservoir of cysts in the sediment is greatly depleted it is probable that recruitment from excystment will decrease and the establishment of a subsequent 'inoculum' will take longer. Moreover, differential gains or losses of particular species of cysts in the sediment may be important for the observed changes in dominance of species of *Ceratium* in Esthwaite Water.

That parasitism may be a controlling factor for dinoflagellate populations has been expressed by Sommer *et al.* (1984) based on observations relating to *C. hirundinella* in Lake Constance, Federal Rep. Germany and by Boltovoskoy (1984) for *Peridinium willei* in a peat bog from Tierra del Fuego, Argentina. It now seems firmly established that the biflagellate fungus *Aphanomycopsis cryptica* can play an important role in the reduction of *Ceratium* populations in Esthwaite Water and Blelham Tarn. However, the capacity for losses due to *Lagenidium* sp. and a monad-type protozoan which ingests the chromatophore of *Ceratium* cells (Canter & Heaney, 1984), as well as the organisms responsible for the deaths of *Ceratium* cysts and thus affecting the potential inoculum, require further study.

Rhizophydium nobile appears to be one of a number of parasites which were not present or occurred in insufficient numbers to be detected in the lakes until some years after the 1947 survey had begun. When *R. nobile* was first described (Canter, 1968) *C. furcoides* had not been distinguished from *C. hirundinella* and hence the latter species was named the host. Although not yet fully substantiated, it is now believed that *R. nobile* parasitizes only the cysts of *C. furcoides* (Canter & Heaney, 1984). The first sighting of the fungus in Esthwaite Water was in 1964, with further records in 1965, 66, 67, 69, 72, 73, 83 and these records correspond to the period of dominance (1964–1973) of *C. furcoides* in that lake (as determined retrospectively from preserved samples by KG and quite oblivious to the records held by HMC). It would thus appear that the occurrence of *R. nobile* does not immediately hinder the subsequent recruitment of vegetative populations. As yet there has been no report of *R. nobile* from outside the English Lake District.

Temperature is important for the development of *Ceratium* populations. A high temperature threshold (10 °C) was found by Heaney *et al.* (1983) to be necessary for vegetative growth. Newly formed cysts require a resting period during which cellular reorganisation takes place (Chapman *et al.*, 1982), and Anderson (1980) have shown this period of dormancy to be temperature dependent for the marine dinoflagellate *Gonyaulax tamarensis* Lebour. It has also been shown experimentally (Huber & Nipkow, 1923; Jaworski, unpublished results) and with natural populations (Heaney *et al.*, 1983) that cysts of *C. hirundinella* and *C. furcoides* do not exist at temperatures below 4 °C.

The English Lakes share a temperate oceanic climate. Temperatures usually cool to below 4 °C during winter but during very prolonged winters temperatures may not regain this value until mid-April, as in Windermere north basin 1947 (Lund *et al.*, (1963), considerably delaying the development of the inoculum. During mild winters (e.g. 1964, Talling, 1966) annual temperatures may never fall below 4 °C. In such circumstances (and at low latitudes) temperature may determine the timing of excystment in relation to the period between formation of cysts and their temperature-dependent maturation.

The significance of stability and strength of mixing in stratified lakes has long been recognized as a major factor in regulating both quantitative and qualitative development of phytoplankton (e.g. Lund, 1971; Steel, 1972; Pollingher & Zemel, 1981; Reynolds *et al.*, 1983). The results of the present study provide additional evidence that large populations of *Ceratium* are restricted to summers where the time-averaged stability, as determined as an N^2 value, is above a 'critical' value. However, there may be marked differences in this characteristic in nearby lakes of different size and exposure.

Depression of *Ceratium* growth with greater mixing may result from reduced light availability, or lower temperatures due to entrainment of deeper colder water. Increased mixing will give rise to a greater mixed depth and an inability for depth-regulation by *Ceratium* cells to positions of preferred optical depths during day and vertical migrations into depths of potentially nutrient-rich layers at night (e.g. George & Heaney, 1978; Heaney & Talling, 1980b; Heaney *et al.*, 1986). Furthermore, Heaney & Butterwick (1985) have shown that cultures of *C. furcoides* (incorrectly named as *C. hirundinella* by Heaney & Butterwick) have higher light requirements for the onset and saturation of growth than the diatom *Asterionella formosa* Hass. and the blue-green alga *Oscillatoria bourrellyi* Lund and will thus respond less favourably to mixing to greater depths. Turbulence may also inhibit cell division in dinoflagellates, as shown by Pollingher & Zemel (1981) for *Peridinium cinctum* forma *Westii* (Lemm.) Lefèvre, but this effect has yet to be demonstrated for species of *Ceratium*.

Although there has been increased nutrient enrichment to Windermere, Esthwaite Water and Blelham Tarn during the study period, depletions of cellular phosphorus during large populations of *Ceratium* strongly suggest that this is the main element controlling summer production. Nevertheless, Heaney *et al.* (1986) demonstrated that in Esthwaite Water, carbon, nitrogen and light are also potential sources of growth limitation and Lund (1979) provided evidence from bioassay experiments that iron may be important in Blelham Tarn.

There are considerable between-year differences in summer production which are indicated in the greater variability in summer depletions of NO_3-N and increases of alkalinity. Such changes are likely to be the result of the generation of alkalinity from the assimilation of nitrate by phytoplankton as demonstrated for algal cultures by Brewer & Goldman (1976) and Goldman & Brewer (1980). As well as the results shown here for Esthwaite Water, even more striking between-year differences of epilimnetic concentrations of NO_3-N occur in the south basin of Windermere associated with qualitative changes in algal production and hypolimnetic oxygen depletion (Heaney, 1986). Thus although nutrient fluxes can determine the magnitude of algal biomass before light limitation, the relative success of component species can strongly influence the extent of nutrient utilization and regeneration.

The four lake basins have shown differences in the timing and size of *Ceratium* populations since 1945. A general hypothesis concerning these changes is now considered. There is little doubt that the major factor enabling the development of dense populations since the mid-fifties has been nutrient enrichment. The degree of enrichment and annual loading of phosphorus is least in the north basin of Windermere. However, this basin is now capable of producing growths of phytoplankton almost as dense (>1.2 mg C l^{-1}) as the south basin. That *Ceratium* populations have been negligible in the north basin and only achieve sizable populations in the south basin during warm stable summers indicates the importance of the greater mixed depths in these basins (c. 10 m) compared to c. 5 m for the shallower Esthwaite Water and Blelham Tarn. The sensitivity to mixing and relatively high light requirement for *Ceratium* growth (Heaney & Butterwick, 1985) makes this genus more suitable for the latter two smaller and more stable lakes where population development has been greatest. The basins of Windermere on the other hand provide an environment favourable for the production of algae such as non-gas vacuolate blue-green alga *Oscillatoria bourrellyi* capable of growing at lower irradiances (Heaney & Butterwick, 1985). This alga now frequently dominates the summer phytoplankton of Windermere (Heaney, 1986, unpublished data) where daily mixing as a result of the oceanic climate assists in maintaining it within the upper layers.

In Blelham Tarn *Ceratium* populations are generally smaller than in Esthwaite Water. This may reflect the lower retention time of the former (c. 10 days to 6 weeks) where, of all the lakes considered here, the probability of appreciable washout is greatest. Further analysis is required, but washout can be especially important for slow-growing species during the planktonic stages of their life cycles.

The relative success of *Ceratium* populations may thus be expected to decrease along gradients of increasing mixed depths, increasing turbulence and decreasing retention times, assuming nutrient sufficiency. The potential for good population growth is governed by energy inputs, lake bathymetry and hydraulic characteristics. The realisation of such growth is regulated by nutrient availability and biological considerations.

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