

numbers we must give highest priority to maintaining the excellence and originality of the science we do. To this end we must have resources available to enable us to continue to appoint young creative scientists of high promise to the staff. We should also ensure that, within broad limits, they are allowed to pursue their own bent and are provided with the essential facilities to enable them to exercise their inspiration. I may tend to be optimistic, but in these ways I believe that the FBA can continue to thrive and follow the policy guidelines that I outlined in the *Annual Report* of two years ago. The reduction in financial support may mean that we cannot do as much research as we have done in recent years, but I am confident that we should be able to maintain the quality of the work we do; that should be our primary aim.

*E. D. Le Cren.*

## REVIEW ARTICLES

### *CERATIUM HIRUNDINELLA*—ECOLOGY OF A COMPLEX, MOBILE, AND SUCCESSFUL PLANT

S. I. HEANEY & J. F. TALLING

One of the largest and most conspicuous cells to be found in the fresh-water phytoplankton is that of the dinoflagellate, *Ceratium hirundinella*. Under even low magnifications of the microscope, the rich-brown cells with multiple horns and a central furrow (Plate 5, *l.*) attract notice—accentuated, in living material, by their revolving motion. The species is less well represented at low latitudes, but in temperate lakes it is widespread and may dominate the largest seasonal biomass of phytoplankton. This is seen, for example, in the well-studied, productive lakes of Erken in Sweden and Mikofajskie in Poland, in some of the English meres (e.g. Reynolds 1973a, b), and in some of the more productive lakes of the English Lake District. It is with the last that this contribution, surveying recent work at Windermere, is primarily concerned.

Two developments in the late 1950s and early 1960s served to direct attention to the quantitative influence of *Ceratium* on productive Cumbrian lakes, notably Esthwaite Water and Blelham Tarn. Firstly, there was a pronounced increase in the abundance of the organism, as judged from weekly samples over the 0-5 m water column (Lund 1972, 1978). Secondly, estimations of chlorophyll *a* for population census (e.g. Talling 1971) emphasized the large biomass associated with maxima of *Ceratium*, less evident from cell counts alone. Thus a few hundred cells of *Ceratium* per ml yielded concentrations of chlorophyll *a* that would have required tens of thousands per ml of another algal cell used locally as a yardstick—that of the diatom *Asterionella formosa*. Comparisons between the two algae could be extended to depth-distribution patterns and photosynthetic activity, after work on these aspects of some maxima of *Asterionella* (Lund, Mackereth & Mortimer 1963; Talling 1966) and of *Ceratium* (Talling 1971, 1976, and unpublished; Heaney & Talling 1980).

Later work showed that the distribution of *Ceratium* could not be understood without finer resolution in both space and time and further experimental studies. Finer resolution of cell activity in time was also taken up in studies of photosynthetic rates, fluorescence from photosynthetic pigments, and cell division. The last aspect has recently been extended in diel (day-night) studies by E. Frempong, who has also followed short-term changes in cellular composition. Most recently of all, D. B. Chapman is exploring the ecological implications of cellular fine structure, using electron microscopy and building on the foundation laid by Dodge & Crawford (1971).

Before looking at these features in more detail we might consider the

wider ecological context. The quantitative and physiological ecology of dinoflagellates in fresh waters lies parallel to a corresponding field within oceanography, which has claimed much more effort and has developed extensively in recent years. Yet the fundamental problems (e.g. of complex spatial distributions, diel rhythms) are similar, and a freshwater ecologist is not out of place in a major oceanographic institute. Complexities of dinoflagellate ecology arise partly from cell characteristics such as mobility, partly from success in warm and stratified waters. In the English Lakes, the earlier and basic studies of the population dynamics of phytoplankton concentrated upon diatoms (e.g. *Asterionella*) and their spring maxima. An extension of detailed autecological studies to major constituents of the more massive summer maxima is therefore timely and desirable. Such studies are almost inseparable from the work being done on the general dynamics of summer stratification in the productive lakes.

#### The seasonal growth cycle

Some gross quantitative features of the summer maxima of *Ceratium* are illustrated in Fig. 1, which is a semilogarithmic plot of cell densities in the upper layer of one productive lake, Esthwaite Water, during three successive years. During winter and spring fewer than 100 cells per litre ( $0.1 \text{ cell ml}^{-1}$ ) can be found in the plankton, but in June and July there is a

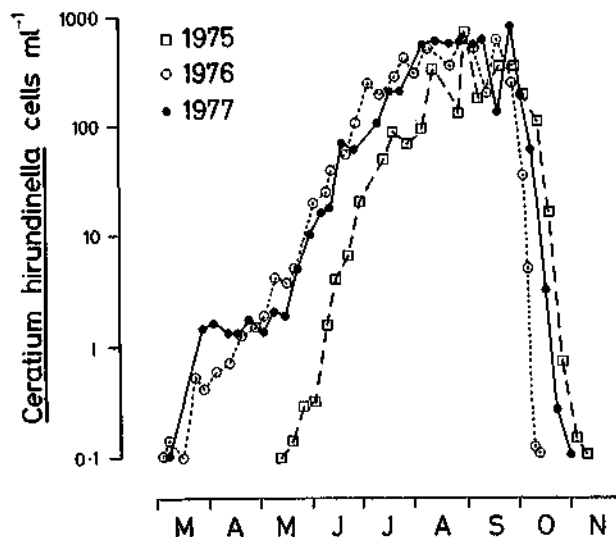


FIG. 1. Seasonal growth and decline of *Ceratium hirundinella* in Esthwaite Water during 1975-77, measured at a central station as the average concentration of cells in the 0.5 m layer. From Heaney & Talling (1980).

phase of exponential increase which yields the high densities of late summer. Fig. 1 shows that the onset of this phase varies somewhat from year to year, and it may suffer a temporary halt as in 1977. In August-September there is a phase of high and more constant population density, although some real or apparent fluctuations occur. It is ended by a rapid exponential decline, in which many vegetative cells turn into non-motile and thick-walled cysts (Plate 5, r.).

These bodies, of distinctive appearance, sink quickly and can be recognized in the surface sediments at this and other times of the year. After a period of maturation, their 'germination' or excystment can be observed in the laboratory under suitable conditions (Livingstone 1979). The process probably occurs in the lake during spring to early summer, and may be significant for recruitment of the population. The vegetative cells usually encyst during the final deepening of the epilimnion which accompanies autumnal destratification, although sometimes the vegetative cells persist longer, and mass death may occur without many cysts being formed. Little is known quantitatively about mortality of the cysts, but H. M. Canter has shown that they may be parasitized by a chytrid fungus (Canter 1968). Another chytrid occurs as a saprophyte on the vegetative cells of *Ceratium* (Ingold 1944; Canter 1979).

At times when populations are dense, a brown discoloration of the lake water can be obvious to anyone dipping his oars or merely contemplating the lake from the shore. With rather more effort, one can use a submersible lamp and photo-cell to trace the depth-distribution of the populations by their attenuation of a horizontal light beam (*beam attenuation*) (e.g. Fig. 6 and Heaney & Talling 1980). Rougher but still useful indications of this distribution can sometimes be obtained (Harris et al. 1979) from the vertical attenuation of solar radiation. The latter also has important implications for performance of the populations as photosynthetic systems, as the upper cells shade their sisters below and so limit activity. Quantitative aspects of such self-shading by *Ceratium* in Esthwaite Water have been taken up by Talling (1971), Heller (1977a), and Harris et al. (1979). The magnitude of self-shading per unit concentration of biomass (here assessed by chlorophyll *a* content) appears to be smaller than is found in many other algae, including *Asterionella formosa*. This feature may be connected with the relatively bulky cells, between which more light passes unintercepted ('sieve effect') than would occur with the same biomass distributed in small cells. With suitable equipment, having sufficient spectral resolution, the red absorption maximum of chlorophyll *a* can be demonstrated directly in the lake itself (Harris et al. 1979, Fig. 4).

The limitation of light to an average cell in dense populations is only one example of a resource depletion which might potentially control or halt further growth. The build-up of other nutrients, such as nitrogen and phosphorus, in the population is often accompanied by a depletion in the

water (e.g. Harris et al. 1979, Fig. 2), although other seasonal processes such as denitrification by microbes are also involved. Large depletions of inorganic carbon also occur (Talling 1976). A more comprehensive assessment of the long-term past records of *Ceratium* abundance in relation to nutrient concentrations (and other environmental factors) would be welcome. Also desirable is an experimental approach through cultures to ecological aspects of nutrition. An essential prerequisite for this was the cultivation of *Ceratium* in complex (biphasic or soil-extract-containing) media, achieved by G. Jaworski. Such cultures have had other uses; one example, involving cultures in large tubes, is mentioned later.

#### The diel (24-h) growth cycle

In recent years much attention has been given to diel, as opposed to seasonal, events in *Ceratium* populations. As regards population increase this approach might appear unrewarding, because the doubling time is rarely much less than one week (cf. Fig. 2) and so the daily increments would be technically difficult to detect. However, population increase depends upon cell division, which is an all-or-none event; in large dinoflagellates it is easily recognized and counted under the microscope, and is often confined or 'phased' to a brief period of the diel cycle. The percentage of dividing cells during that phase can then be used to calculate the specific growth rate of the population.

This approach has been applied to a number of dinoflagellate populations, marine and freshwater. Its first use in the English lakes was by

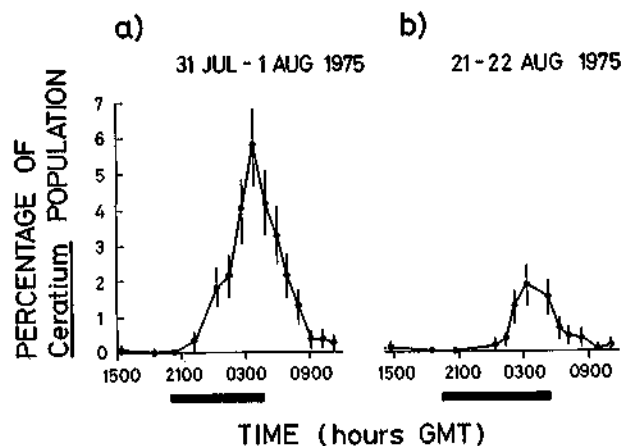


FIG. 2. Percentage of dividing cells of *Ceratium hirundinella* in Esthwaite Water, at various times of day and night. Vertical bars represent the random counting error (95% confidence limits), and horizontal bars darkness. Modified from Heller (1977b).

Heller (1977b), who studied *Ceratium* in Esthwaite Water during the summers of 1974 and 1975. He found the highest frequency of dividing cells at 03.00 hours G.M.T., with but a small carry-over into the daylight hours following (Fig. 2). However, the highest frequency on any night was only 5.8 (+ 1.0)% of the total cells, and on three of the four nights studied was 2% or slightly less. These figures are low when compared to those obtained on some other growing dinoflagellate populations; for example, U. Pollinger found division frequencies of up to 45% for populations of *Peridinium cinctum* f. *westii* in Lake Kinneret (Sea of Galilee). Nevertheless, the lower frequencies in Esthwaite Water demonstrate the existence of significant cellular growth in apparently 'stationary' or even declining populations. Later efforts were made by M. D. Heller, H. J. Robbins and E. Frempong to test for higher frequencies during the exponential phase of population growth, but rather low values were still obtained.

#### Photosynthesis

Up to 1961, photosynthetic activity measured during spring population maxima of the diatom *Asterionella formosa* (Talling 1957, 1966) was regarded as an indication of intense activity in the English lakes. In September 1961 a whole-lake experiment was performed in Blelham Tarn, involving an artificial mixing by injection of compressed air, during which a dense population of *Ceratium* developed. Its photosynthetic activity, measured *in situ* by D. B. Driver, obviously surpassed that of the *Asterionella* populations. However, further analysis showed that the photosynthetic capacity per unit biomass was rather low. This feature was repeatedly confirmed in later work on *Ceratium* populations, which also brought out an inverse relation between photosynthetic capacity and biomass concentration. An illustrative sequence from sampling and experimentation in 1971 is shown in Fig. 3. Here intense photosynthetic activity in Esthwaite Water is indicated by the pH of surface water rising, due to depletion of CO<sub>2</sub> (Talling 1976), to daytime values above 9 in July and around 10 in parts of August and September. Then dominated by *Ceratium*, biomass reached a maximum in September, albeit somewhat unequally in the two basins of the lake. At this time the photosynthetic capacity per unit biomass was lowest, although it could be enhanced by enriching samples with CO<sub>2</sub>. It appears, therefore, that some rate-limitation of photosynthesis is associated with conditions of strong CO<sub>2</sub>-depletion and high pH.

Under such conditions, the handicap for some other common phytoplankters (including *Asterionella formosa*) appears to be still greater (Talling 1976). This may partly account for the near-monospecific purity of many dense populations of *Ceratium*, which makes them attractive for much physiological and autecological work. One occasional associate in

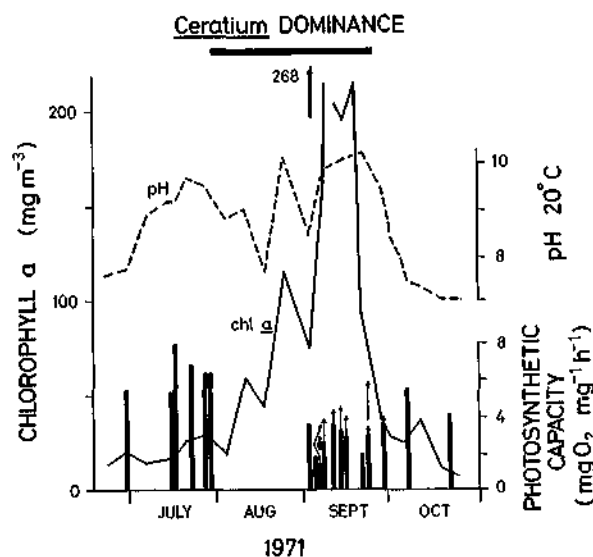


FIG. 3. Esthwaite Water 1971: seasonal changes of chlorophyll *a* concentration and pH (corrected to 20 °C) in surface samples, with periodic measurements (at lake surface temperature) of photosynthetic capacity of surface samples (histograms). Enhancements of capacity by CO<sub>2</sub> enrichment are indicated by triangles. Modified from Talling (1971).

Esthwaite Water, the blue-green *Microcystis aeruginosa*, shares the capability of *Ceratium* for photosynthesis in CO<sub>2</sub>-depleted media. Both these algae are probably dependent on uptake of bicarbonate ions for their performance.

Relatively low specific rates (per unit biomass) of photosynthesis by *Ceratium* may be connected with its relatively low specific rates of population growth. However, an exploration by Heller (1977a) of photosynthesis-growth relationships in natural populations indicated that 'loss factors' (e.g. respiration) were important. On the other hand, recent work by Harris (Harris et al. 1979) suggests that the overall photosynthetic performance of *Ceratium* populations in Esthwaite Water may be enhanced by short-lived responses of cells which circulate vertically and so experience fluctuating illumination.

#### *Vertical distribution and migration*

The possible complexity of vertical distribution, in which dense congregations of cells are often observed below the surface during calm periods, was first appreciated from the work in 1961 on Blelham Tarn. Later in the 1960s the diel mobility of distribution patterns was

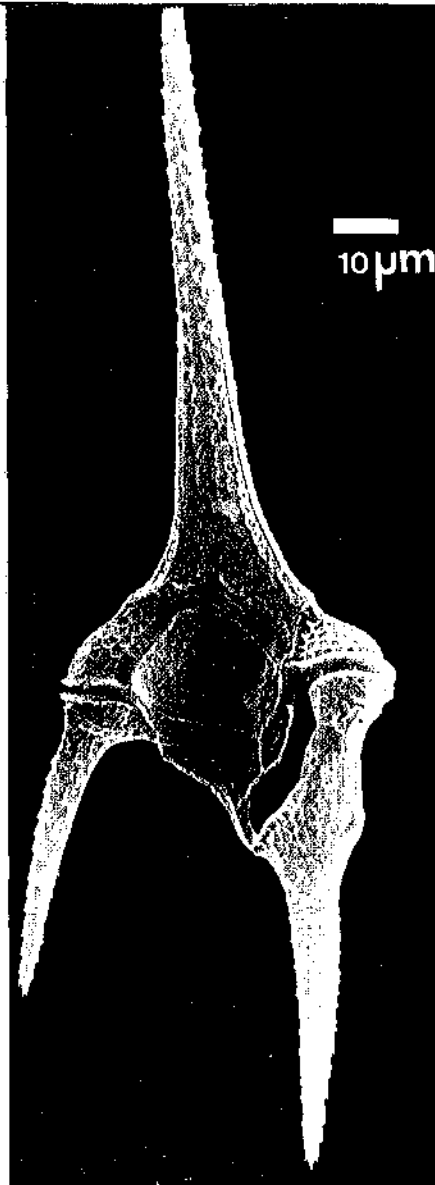
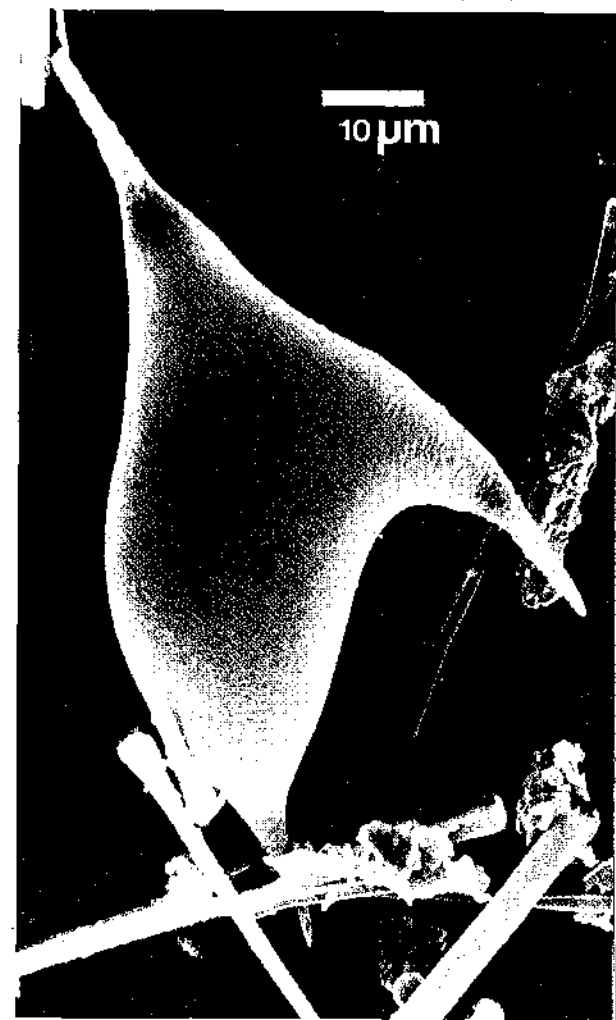


PLATE 5. *Ceratium hirundinella*: l. vegetative cell; r. cyst. (Photographs by D. C. Chapman).



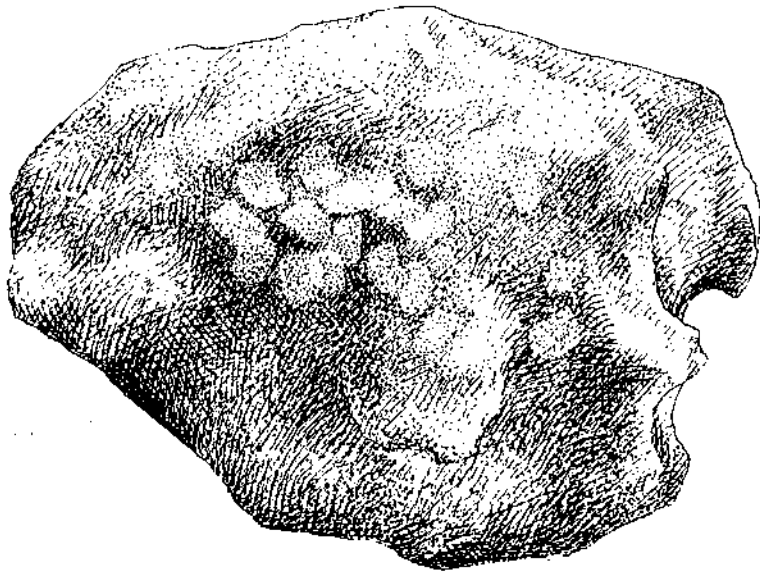
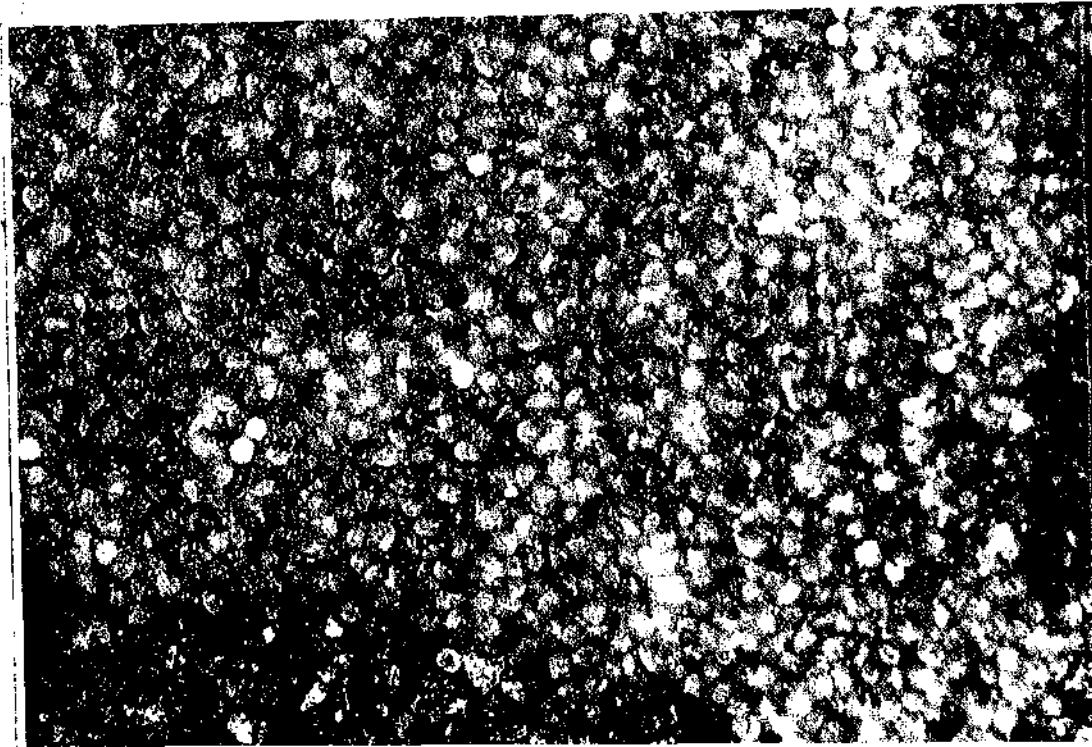


PLATE 6. Above: Eggs of *Baëtis rhodani* on a stone (drawn by M. Mizzaro-Wimmer).  
Below: Eggs of *Baëtis rhodani* (photograph by H. W. Bohle).



demonstrated (Talling 1971), with examples of apparent ascent by day and descent at night (Fig. 4a). Since then we have increased our sampling methods to include micro-samplers (Heaney 1974), measurements *in situ* of fluorescence by chlorophyll *a* (George & Heaney 1978, Heaney 1978), and rapid profiling of light attenuation (Heaney & Talling 1980, Talling unpublished); these provide much better resolution in time and space. As a result, it is now known that populations may also form deep aggregations which do not show daily migrations (Fig. 4b).

Studies in recent years have greatly extended earlier knowledge of the factors that influence vertical migrations (Heaney 1976; George & Heaney

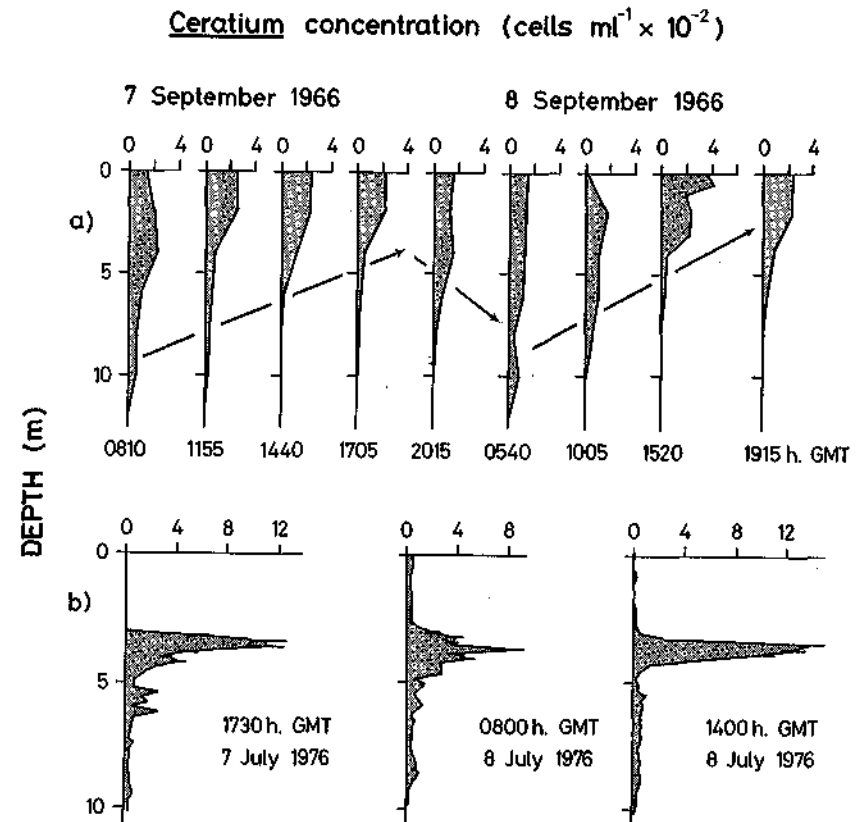


FIG. 4. Diel changes in the vertical distribution of *Ceratium hirundinella* in Esthwaite Water on two occasions during summer stratification. Modified from Talling (1971) and Heaney & Talling (1980).

1978; Harris et al. 1979; Heaney & Talling 1980). *Ceratium* is almost always absent from the anoxic hypolimnion, either by direct avoidance or because of rapid destruction in that layer. An avoidance of the uppermost (0-2 m) layer is also common, especially in calm sunny weather. As a further complexity, large thermal gradients appear to prevent downward movement at night, even when the lower layers are well oxygenated. It seems, therefore, that bright sunshine, temperature gradients and anoxic conditions interact in restricting vertical movements of natural populations. Laboratory experiments with cultures of *Ceratium* in a tall tube have confirmed that high surface irradiance and thermal gradients restrict vertical migrations to give large, sub-surface maxima similar to those found in Esthwaite Water under comparable natural conditions (Fig. 5, and Heaney & Furnass 1980). More work is needed to determine the possible effect of nutrient limitation, which has been shown to alter patterns of vertical migration in marine dinoflagellates (Heaney & Eppley unpublished).

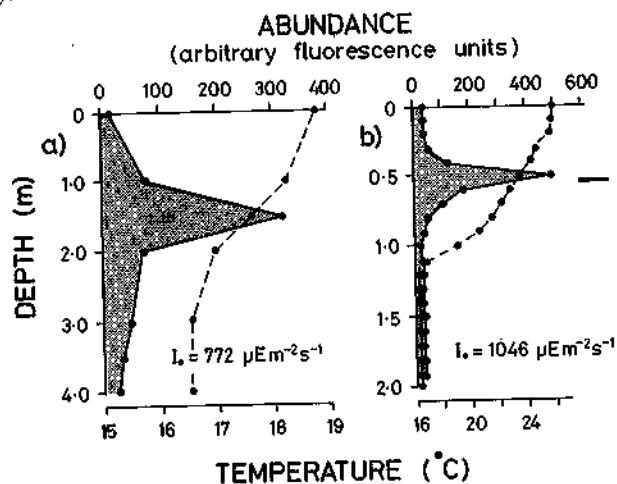


FIG. 5. Comparison of the vertical distributions of *Ceratium hirundinella*, expressed as chlorophyll *a* fluorescence (shaded): (a) Esthwaite Water on 24 August 1973, 14.30 hours GMT and (b) in an experimental tube 4 hours after the lights came on in a 12:12 h light/dark cycle. Note the difference of depth scales. The values of temperature ( $^{\circ}\text{C}$ ) and surface quantum-irradiance ( $I_0$ , visible spectrum) are given; the horizontal bar indicates the depth corresponding to 10% of the surface-penetrating irradiance. (a) Modified from George & Heaney (1978).

The disposition of *Ceratium* populations may be determined by internal as well as external factors, although it is often difficult to distinguish between their effects. Experiments with cultures (Heaney & Furnass

1980) suggest that the diel timing of migrations may alter with population age. There is some evidence that, after the main phase of growth is over, cells may have an increased tolerance for high irradiance. They may then more readily enter the surface layer (Fig. 6, and George & Heaney 1978), although there are also good examples of surface avoidance at this time (Fig. 4, and Talling unpublished). Moreover, during this phase George & Heaney (1978) found that only a portion of the population descended in the night, and this may lead to a temporary spatial separation of physiologically distinct cells within the lake. Vertical migration appears to be a complex matter, affected by interactions which depend on both the environmental factors and the physiological state of the cells.

#### Horizontal distribution

Several studies have shown that populations of *Ceratium* tend to be patchy over a lake (e.g. Heaney 1976; George & Heaney 1978; Harris et al. 1979, Heaney & Talling 1980). Such uneven distribution in Esthwaite Water was most obvious on days with light winds, below  $4 \text{ m s}^{-1}$ , blowing along the axis of the lake. These winds set up stable horizontal flow of the

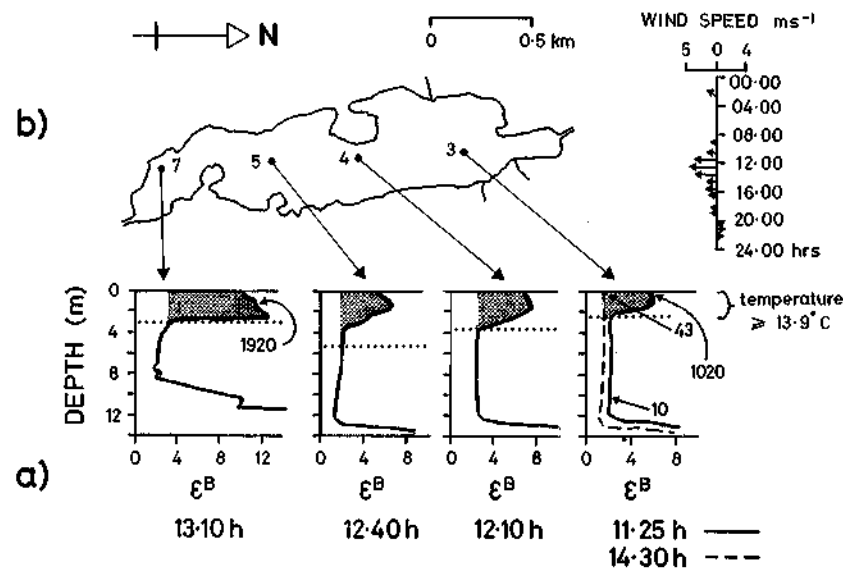


FIG. 6. Shifts in the superficial abundance of *Ceratium* (shaded) along Esthwaite Water during the afternoon of 15 September 1977 (a), influenced by a northerly wind (hourly wind vectors in (b)). Abundance is indicated by high coefficients of light beam attenuation ( $\epsilon^B$ , units  $\text{m}^{-1}$ ), recorded as shaded parts of vertical profiles at the times indicated, and (arrowed) by some concentrations as cells  $\text{ml}^{-1}$  at certain depths.

surface layers and a return flow at greater depths. The horizontal distribution of *Ceratium* in such small water-bodies largely depends upon the extent to which the alga maintains its position in the water column and the relative motion of water at different depths.

Advantage has been taken of several different sampling techniques to demonstrate the interaction of wind, water movements and vertical distribution in producing patterns of horizontal distribution. From a combination of discrete water samples and vertical profiles of beam attenuation, mentioned earlier, Fig. 6 shows the effect of light northerly wind in transporting large surface populations to the southern end of the lake within a few hours. On other occasions we have demonstrated high densities of cells at the surface resulting from combined action of horizontal transport and upwelling of deeper water rich in *Ceratium* (Heaney & Talling 1980). Care must be taken to distinguish the upwelling of cells by water movements from the active upward swimming of the flagellate.

More extensive surveys of horizontal distribution have been made using samples taken randomly throughout the lake over the 0-5 m layer with a

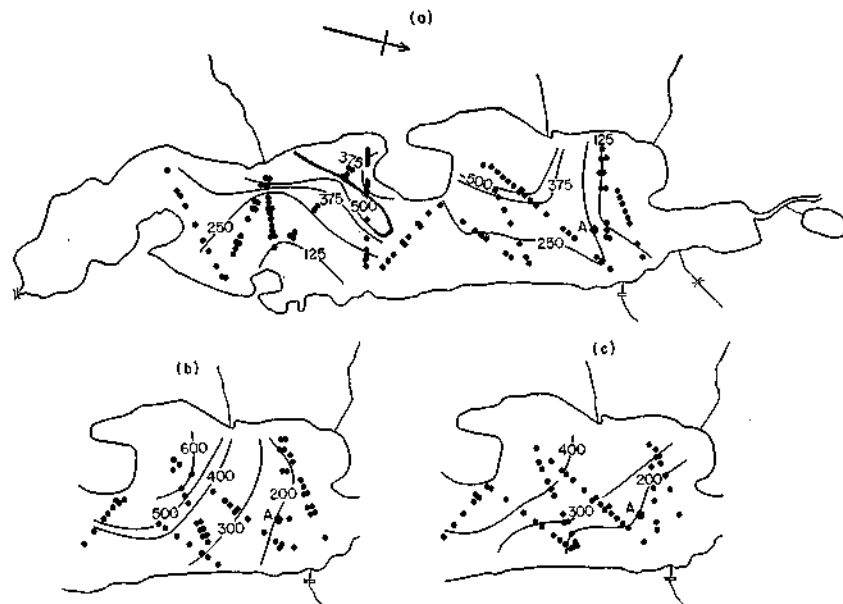


FIG. 7. The unequal horizontal distribution of *Ceratium hirundinella* in Esthwaite Water, on (a) 15 August (b) 28 August (c) 5 September, 1975. Lines of equal abundance are drawn from samples collected at random positions (dots) along transects; A indicates the regular sampling station. From Heaney (1976).

vertical plastic tube (Fig. 7). These also indicated difficulties in obtaining reliable estimates of population size. Extensive sampling from many stations sometimes gave population estimates which differed by over 100% from samples at the regular sampling station (Fig. 7b, and Heaney (1976)). Errors of this size have a large bearing on sampling procedures for assessing population changes over short periods of time, but have less importance if only gross seasonal changes are involved, as in Fig. 1.

#### Interaction of factors

The success of *Ceratium* may be attributed to a number of interacting factors. Once populations are established, the formation of cysts in autumn and their germination in spring probably reduces the necessity for the survival of overwintering vegetative cells in the plankton as the inoculum for later growth. Although the maximum rate of population increase is not high, losses are probably relatively small. The cell is so large that grazing by zooplankton is negligible, and no parasitic fungus is known for the vegetative cell. The alga's mobility enables it to remain in the euphotic zone and avoid sedimentation during periods of thermal stability, even though this must place an appreciable energy requirement upon the cell.

The ability of *Ceratium* to perform vertical migrations or actively regulate its depth in the water column under calm conditions may enable it to improve its position in vertical gradients of light, temperature, dissolved gases and nutrients. The growth of *Ceratium* itself can set up conflicting gradients of light and nutrients, as discussed by Talling (1979) for the situation in Esthwaite Water during the summer of 1972. Prolonged periods of fine weather and low turbulence can lead to sharply stratified situations which may be unfavourable. This was seen in Esthwaite Water during July 1976 (Fig. 8), when high surface irradiances gave rise to warm surface layers above a well-developed thermocline, restricting *Ceratium* to a narrow layer between depths of 3 and 5 m (Fig. 4b). Later, in August, deoxygenated water below about 4 m further restricted the downward movement of the cells, and inorganic nitrogen had become depleted in the upper layer. Thus there was a severe compression of the growing zone where unfavourable conditions were probably exacerbated by high irradiance, high pH and low nutrient availability. Although *Ceratium* can compete well with other phytoplankters under these conditions, occasional mixing of the epilimnion appears to be favourable in that it restricts deoxygenation and transfers nutrients from the lower layers. Such mixing, especially later in the season, may enable the alga to make use of its migratory abilities to find better conditions for photosynthesis, nutrient uptake and growth.

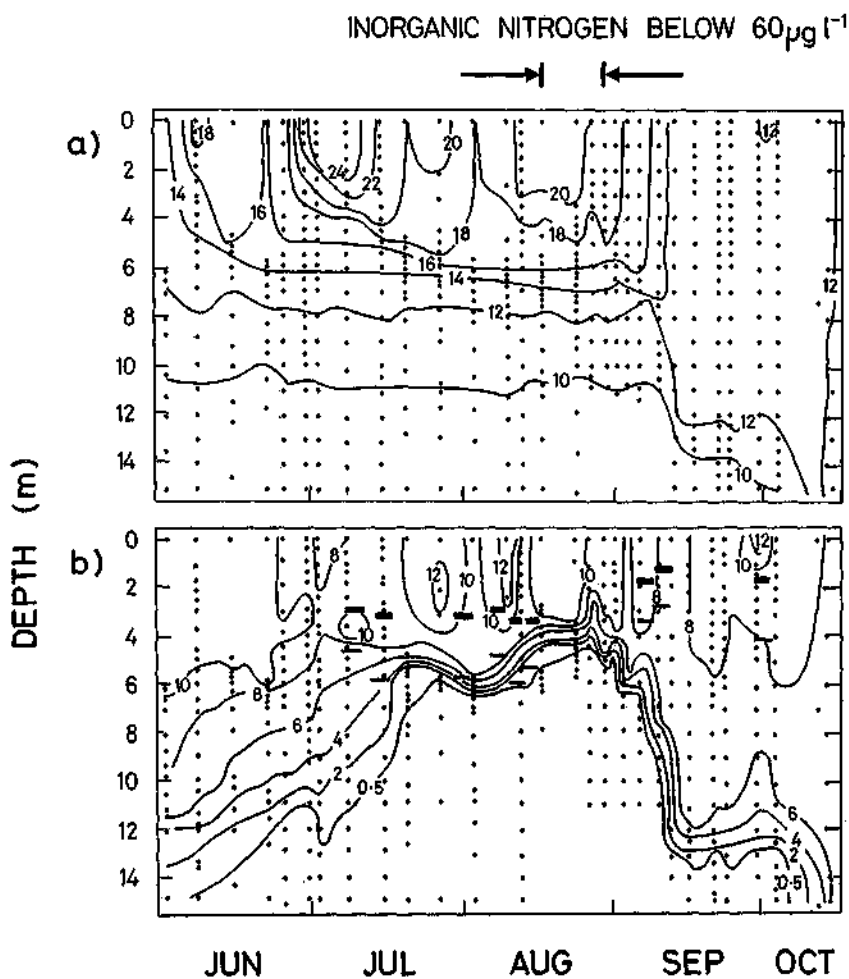


FIG. 8. The distribution with depth and time of some interacting environmental variables in Esthwaite Water during the summer of 1976. They include (a) temperature ( $^{\circ}\text{C}$ ), (b) dissolved oxygen ( $\text{mg l}^{-1}$ ), the period when the concentration of inorganic (nitrate + nitrite + ammonium) nitrogen was less than  $60 \mu\text{g l}^{-1}$ , and light penetration. The last is indicated by bars in (b), which mark the depths that correspond to 10% (■) and 1% (◄) of the surface-penetrating irradiance (as quantum flux, visible spectrum). Modified from Harris et al. (1979).

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## EGGS OF EPHEMEROPTERA

J. M. ELLIOTT &amp; U. H. HUMPECH\*

*Introduction*

The life cycles of Ephemeroptera vary considerably between species (see Macan 1979), and are often complicated by an overlap of cohorts (a cohort is a group of individuals that were born at the same time, or in practice born over a short period of time). These cohorts must be recognized and separated before estimates can be made for growth rates, mortality rates and production. Information on eggs, especially their rates of development, facilitates the identification and separation of cohorts, and is therefore an essential part of quantitative studies on the life cycles of Ephemeroptera.

Several workers have described the swarming and mating behaviour of European Ephemeroptera (see references in Savolainen (1978)). Degrange (1960) describes the morphology of the eggs of 51 species from Europe, whilst Koss (1968) describes the eggs of 60 species from North America. The eggs of most species have a length of between 150 and 200  $\mu\text{m}$  and a width of between 90 and 150  $\mu\text{m}$ , but the eggs of the larger species may be 250-300  $\mu\text{m}$  long by 150-200  $\mu\text{m}$  wide. Various attachment structures ensure that the eggs adhere to submerged objects or the substratum. The eggs of some species have an external adhesive layer that swells on contact with water, whilst eggs of other species have their surface covered with suckerlike discs or plates, adhesive projections or coiled or uncoiled threads that often have terminal knobs. Species in a third group have polar caps at one or both ends of their eggs. Each polar cap swells on contact with water and releases a large number of threads with terminal knobs.

This short review summarizes information on the fecundity, oviposition behaviour, egg hatching and parthenogenetic development of Ephemeroptera. The emphasis is on British species, but other European and North American species are mentioned where necessary. The nomenclature follows Macan (1979) for the British species, Illies (1978) for the other European species, and Edmunds, Jensen & Berner (1976) for the North American species. Fishermen's names for British species are listed by Kimmins (1972).

*Fecundity*

Fecundity is usually defined as the number of ripening eggs in the female prior to oviposition. Although information on fecundity is available for twenty-four of the forty-seven species in Britain (Table 1), most of this information is for only a few females of each species and usually the size of

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