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Vertical distribution and diel migration of flagellated phytoplankton in a small humic lake

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Abstract

The vertical distributions and migrations are described of the most abundant flagellated phytoplankton species from the summer community of a small forest lake in southern Finland. The lake showed a steep and stable thermal stratification with a shallow oxygenated epilimnion. Horizontal variation of phytoplankton distribution within the lake was tested on two scales and found to be statistically significant only in the case of *Mallomonas reginae*. The vertical distribution of flagellated phytoplankton was assessed by reference to the distribution of a non-motile, neutrally buoyant species *Ankyra judayi*. Statistically significant, active vertical positioning was demonstrated for all the flagellates examined with the exception of *Spiniferomonas bourrellyi*. Diel vertical migrations were apparent for all species showing active positioning and the pattern of an evening descent and a morning ascent was ubiquitous. The extent and timing of diel migrations varied between species. The most extensive migrations were by *Cryptomonas marssonii* which crossed a temperature gradient of 14 °C and penetrated far into the anoxic hypolimnion. Several categories of competitive advantage can be gained by species undertaking such diel vertical migrations.

Introduction

Individuals within a phytoplankton community are free to move in both the horizontal and vertical planes. Such movement may be passive, the result of being suspended in a turbulent, fluid medium. However, some organisms also possess the capacity to influence their spatial location, in which case their active movements are superimposed upon the underlying passive distribution. As understanding of the functional ecology of phytoplankton has developed, it has become increasingly necessary to take account of the spatial distribution of different species as well as of the whole community (e.g. Platt & Denman, 1980; Reynolds, 1984).

Considerable attention has rightly been directed towards phytoplankton spatial heterogeneity in the horizontal plane. Knowledge about horizontal spatial variability is necessary for the design of effective whole-lake sampling programmes which aim to estimate the average phytoplankton density (Irish & Clarke, 1984). Horizontal 'patchiness' is known to occur on several scales and a variety of statistical techniques have been used to detect it (Reynolds, 1984). Except in small water bodies, where edge effects may become pronouced, this variability is probably more a function of passive, than of active, movement of phytoplankton.

Studies on the vertical distribution of phytoplankton include those concerned with populations occupying fixed, but restricted, depth intervals (e.g. Klemer, 1976; Fee, 1976). However, of equal or greater interest are the observations that certain species periodically change their vertical distribution, fre-

quently with a diel periodicity. Such diel vertical migrations have been reported for decades (see Reynolds, 1984) and may involve changes in cell buoyancy (e.g. Ganf & Oliver, 1982) but more usually concern actively motile, flagellated phytoplankton (e.g. Nauwerck, 1963; Soeder, 1976; Happey-Wood, 1976; Heaney, 1976; Frempong, 1981.

Vertical migrations may be a direct response to a changing environment (e.g. Heaney & Talling, 1980) or be affected by endogenous rhythms (Sournia, 1974). In either case, the ability to select favourable conditions can clearly confer a considerable competitive advantage on motile algae, especially in markedly heterogeneous environments. Possible advantages to be gained include selection of optimal irradiance conditions (e.g. Tilzer, 1973; Ilmavirta, 1974), retrieval of nutrients from below the depth of water circulation (Salonen *et al.*, 1984b) and reduction of loses due to grazing and hydraulic washout. Better understanding of these behavioural responses will be necessary for the improvement of current models to explain phytoplankton community composition (Reynolds, 1980).

The study of vertical migrations within mixed populations of phytoplankton invariably involves sampling several depths down a water column repeatedly over selected time intervals, followed by microscopic enumeration of individual species. A variety of graphical plots have been used to represent the temporal sequence of the resulting cell density-depth profiles. Interpretation of such plots is confounded by the possibility that changes in vertical distribution may result from horizontal patchiness and water movements as well as from any behavioural response of the phytoplankton. Unfortunately, decisions as to whether a particular set of observations indicates active migration or not have mainly been subjective, with little attempt to assess the statistical significance of any changes; a notable exception is the more careful analysis by Happey-Wood (1976). While subjective analysis may lead to correct interpretation of the more dramatic examples of migrations, some form of objective distinction between active migrations and other mechanisms of vertical redistribution is clearly needed. This paper explores some possible approaches to this problem using data for phytoplankton distribution in Lake Nimetön, a small, steeply stratified, humic, forest lake in southern Finland.

The study site

Samples were collected during summer 1982 from Lake Nimetön (Fig. 1), a small dystrophic lake in the Evo district of southern Finland. The sheltered position of the lake together with its overdeepened morphometry (surface area 0.4 ha, max. depth 11 m) minimizes turbulent mixing and at the time of the study, shortly after clear-cutting of the catchment, the lake was apparently still meromictic (Salonen *et al.*, 1984a). The high humic content of the water is indicated by the water colour (c. 300 mg Pt l^{-1} in the surface layers) and restricts the euphotic zone to little more than 1 m (Jones & Arvola, 1984). The lake is mesotrophic with summer phytoplankton dominated by chrysophytes and cryptophytes. Further de-

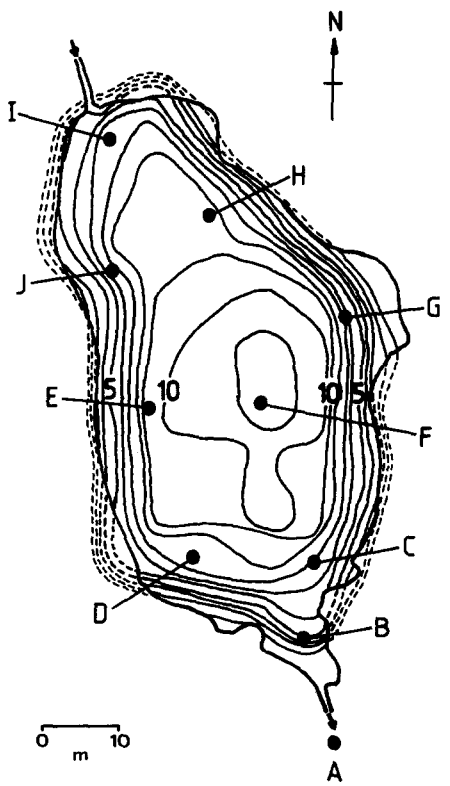


Fig. 1. Bathymetric map of Lake Nimetön showing the location of the sampling sites.

tails of the seasonal characteristics of the lake and its plankton are given by Arvola (1983) and Salonen *et al.* (1983).

Methods

On 16 July 1982, between 10.00 and 11.00, a series of samples was collected from around the lake in order to assess the horizontal variability of the phytoplankton. The position of the 10 sampling sites is shown in Fig. 1. Samples of the outflowing water (site A) were taken from the overflow of a V-notch weir directly into a polythene bucket. At the lake sites integrated samples of the upper 2 m were collected with a perspex tube of 5 cm diameter. From each site, 5 such primary samples were collected, and at sites F and J subsamples of 100 ml were reserved from each primary sample. At all sites 500 ml portions from each primary sample were mixed together to give a bulked sample of 2.5 l, and a 100 ml subsample was then reserved from each bulked sample. Particular care was taken to thoroughly mix samples prior to any subsampling. All the 100 ml subsamples were preserved with Lugol's iodine.

The vertical distribution of the phytoplankton was investigated by sampling at site F (Fig. 1) in early August. Previous information indicated that the main changes in vertical distribution patterns in this and similar small forest lakes could be expected around sunset and sunrise (Arvola, 1984; Salonen *et al.*, 1984b). On 2 August samples were collected at 17.00, 19.00, 21.00 and 23.00 and on 4 August at 03.00, 05.00, 07.00 and 09.00. On each occasion detailed depth profiles were obtained using a close-interval syringe sampler (Blakar, 1979) operated pneumatically from a boat at 2–3 m distance from the point of sampling. The sampler was fitted with 50 ml syringes located at 10 cm intervals along a total depth interval of 1 m. Two sets of samples thus covered the upper 2 m of the water column. Additional samples from 2.5 and 3 m were obtained with a 1 l Patalas-type sampler. All samples were preserved immediately with Lugol's iodine.

For enumeration of phytoplankton, between 10 and 50 ml of thoroughly mixed sample was sedimented for at least 24 hours in a 2.6 cm diameter, compound chamber (Leitz Instruments). Cells of selected, more abundant species were then counted in 100 randomly selected fields of view at a magnification of ×400 using a Zeiss IM35 inverted microscope with phase contrast illumination. Counting of random fields rather than patterned transects is strongly recommended when using sedimentation chambers with an inverted microscope (Sandgren & Robinson, 1984). Although some of the species in this study tended towards a contagious distribution on the bottom of the sedimentation chamber, an adequate estimate of the mean cell density within the chamber was still obtained by the use of a large number ($n > 30$) of replicate fields of view. In this case the central-limit theorem is applicable (Elliott, 1977) permitting use of the normal approximation; counts of any species from a single sample generally showed a standard error of 10–15% of the mean. Since the variance of counts was found to be strongly dependent of their means, a square root transformation was applied prior to any parametric statistical tests; the adequacy of this transformation was confirmed graphically and by Bartlett's test for homogeneity of variances (Sokal & Rohlf, 1981).

Temperature and oxygen profiles for the water column were obtained with a combined temperature and oxygen probe (Yellow Springs Instruments). The time course of irradiance increase at sunrise was monitored above and below the water surface on 4 August using an underwater sensor (Lamda Instruments, Model Li2190) responsive to photosynthetically active radiation (PAR) between 400 and 700 nm.

Results

During the period of study the lake was strongly stratified (Fig. 2) and the vertical stratification showed very little variation through July and August. The main source of turbulence in the upper water layers appears to be from convectional mixing induced by night-time cooling at the surface. The maximum and minimum temperatures obtained from continuous monitoring equipment show that the effect of such mixing was negligible by 1 m

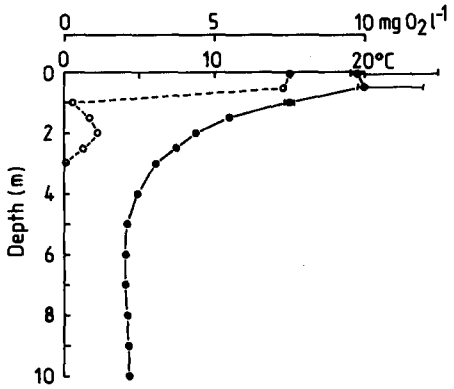


Fig. 2. Depth profiles of temperature (● – ●) and dissolved oxygen (o -- o) in Lake Nimetön on 4 August 1982 at 06.00. Horizontal bars show maximum and minimum temperatures on that date.

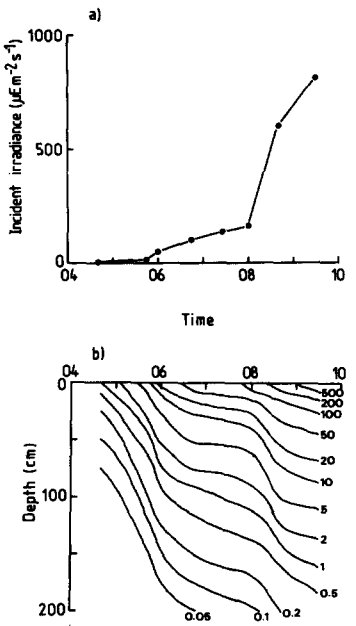


Fig. 3. Surface incident irradiance (a) and isopleths of underwater irradiance (b) as $\mu E\ m^{-2}\ s^{-1}$ in Lake Nimetön during early morning on 4 August 1982.

(Fig. 2). Oxygen concentration decreased rapidly below 0.5 m to complete anoxia below 3 m (Fig. 2).

The increase in incident irradiance after 05.00 (Fig. 3a) occurred at sunrise, while the more substantial increase seen from 08.00 occurred when the sun rose above the surrounding forest so that direct sunlight was then incident on the lake surface. Irradiance changes at different depths (Fig. 3b) reflect the increase in incident irradiance and the rapid attenuation of light by the highly coloured water. Less than 0.1% of subsurface irradiance penetrated to 2 m.

Counts of phytoplankton in the integrated 0–2 m samples from 16 July (Table 1) showed the community to be dominated by flagellated species. The only relatively abundant non-flagellate was the chlorophyte, *Ankyra judayi* (G. M. Smith) Fott. The community was composed mainly of chrysophytes (*Mallomonas akrokomos* Ruttner, *Mallomonas reginae* Teiling and *Spiniferomonas bourrellyi* Takahashi) and cryptophytes (*Chryptomonas marssonii* Skuja and *C. ovata* Ehrenberg). One flagellated chlorophyte (*Chlamydomonas* sp.) was also counted and in August also the colonial, flagellated chrysophyte, *Dinobryon divergens* Imhof. *Uroglena americana* Calkins was also a substantial part of the phytoplankton biomass, but the large colonies were not sampled effectively and disintegrated during preservation, so were not counted for this study. Other species were present in only very low numbers.

Table 1. Densities (cells ml^{-1}) in the upper 2 m water column of the seven most abundant phytoplankton species at the ten sites sampled on 16 July. Values are means of three replicate counts from five bulked samples.

Site	A	B	C	D	E	F	G	H	I	J
Ankyra judayi	24	12	13	29	11	19	19	13	16	13
Chlamydomonas sp.	11	13	20	4	11	8	24	16	17	15
Cryptomonas marssonii	733	227	213	231	139	117	231	195	305	175
Cryptomonas ovata	4	197	121	201	193	138	144	172	195	199
Mallomonas akrokomos	262	1003	1061	629	707	903	829	648	553	845
Mallomonas reginae	88	73	151	19	47	145	213	199	217	141
Spiniferomonas bourrellyi	37	32	56	41	28	49	55	53	23	17

Horizontal variability in phytoplankton density

For sites F and J, two replicate counts were made on each of the preserved five primary samples. ANOVAR revealed no significant ($p > 0.05$) variation between the primary samples for any of the species. Partitioning the variance into its components (Sokal & Rohlf, 1981) showed the 'counting' variation to be generally equal to or greater than the 'sampling' variation. Hence the procedure adopted of bulking the primary samples had little effect in this particular case.

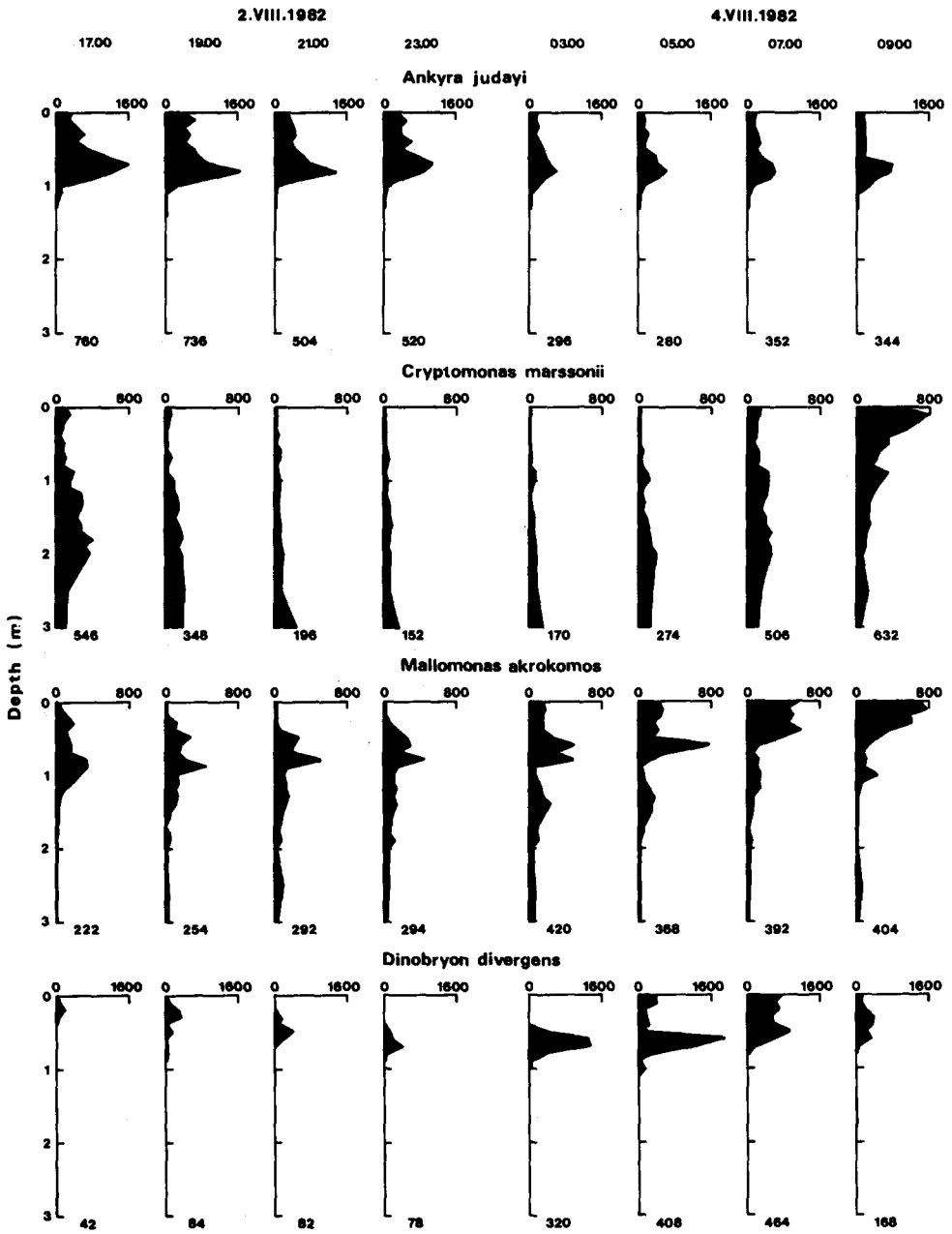
Variation between the 10 sites (Table 1) was also tested by ANOVAR for each species using the replicate counts of the bulked samples. No significant between site variation was found for *Ankyra judayi, Chlamydomonas* sp., *Mallomonas akrokomos* or *Spiniferomonas bourrellyi.* For the three species which did show significant ($p < 0.05$) between site variation, the differences were further investigated by calculating the minimum significant difference (MSD) for $p < 0.05$ (Sokal & Rohlf, 1981). *Cryptomonas ovata* showed significantly lower density at the outflow (site A) but no difference between the other sites; this is explained by this species avoiding the surface water (see later) and therefore being under-represented in the outflow samples. Conversely, *Cryptomonas marssonii* showed significantly higher density at site A, being concentrated in the surface waters of the lake at the time of sampling and therefore becoming over-represented in the outflow samples. *Mallomonas reginae* was the only species which showed significant variation in density between the nine lake sites. This species showed a distinct gradient of increasing abundance from SW to NE across the lake.

Vertical distribution of phytoplankton

The vertical distribution of the seven most abundant phytoplankton species at each interval during the two sampling periods in August is shown in Fig. 4. Of these seven species, only *Ankyra judayi* is not flagellated. This species can be considered approximately neutrally buoyant (Reynolds, 1984) and during this study was effectively restricted to the upper 1 m of the water column (Fig. 4) which corresponds to the maximum depth of mixing (Fig. 2). The distribution of this species is evidently the product of the interaction between any tendency of the cells to sink and the limited water circulation. Therefore it can be used as a reference distribution against which to evaluate the distributions of the other species which, being flagellated, all possess the potential for some degree of self determination in their vertical distributions.

If possible changes in vertical distributions through time are to be detected, it is essential that account is taken of any variation in the total population of cells in the water column. The vertical profiles of cell density for each species (Fig. 4) were planimetrically integrated to yield values for the total population (cells m^{-2}) within the 0–3 m water column at each sampling interval. For each sampling period the coefficient of variation (CV) was then calculated (Table 2). Variation is produced by: counting 'error'; real population changes (cell division, grazing etc.); passive horizontal movement; active horizontal movement; and loss to, or recruitment from, the unsampled water column below 3 m. Since losses from sedimentation below 3 m were clearly negligible, only the first three factors will be applicable to non-motile species (*Ankyra judayi*) or weak swimmers restricted to the epilimnion (e.g. *Spiniferomonas bourrellyi*). Moreover, it has already been shown that horizontal variability within the lake was small during the period of study. Therefore the much higher CV associated with certain species, particularly *C. marssonii* (Table 2), confirm the impression gained from inspection of the vertical profiles (Fig. 4) that some species were not restricted to the 0–3 M water column. In view of this it was not considered appropriate to express the density of cells at any depth as a percentage of the total population in the water column in order to standardize the depth profiles from each sampling interval (cf. Happey-Wood, 1976).

In order to compare the shapes of the profiles, the counts for each depth were ranked within each sampling interval. The four sets of ranks from each sampling period were then subjected to Friedman's method for randomised blocks (Sokal & Rohlf, 1981) to test for the effect of depth on cell density for each



species. The resulting χ^2 values and their level of significance are shown in Table 3. Also shown are values of W, Kendall's coefficient of concordance (Sokal & Rohlf, 1981) which indicates the degree of similarity between the four profiles from each sampling period on a scale from 0 (no similarity) to 1 (exact similarity). It can be seen that, as expected from examination of the profiles, the effect of depth on the distribution of *Ankyra judayi* was highly significant ($p < 0.001$) and the distributions showed a remarkably high degree of similarity over the sampling intervals within each sampling period. Since the distribution of *Ankyra* is assumed to be passive, it follows that any species whose distribution showed no significant effect of depth was not passively distributed and must therefore have been influencing its

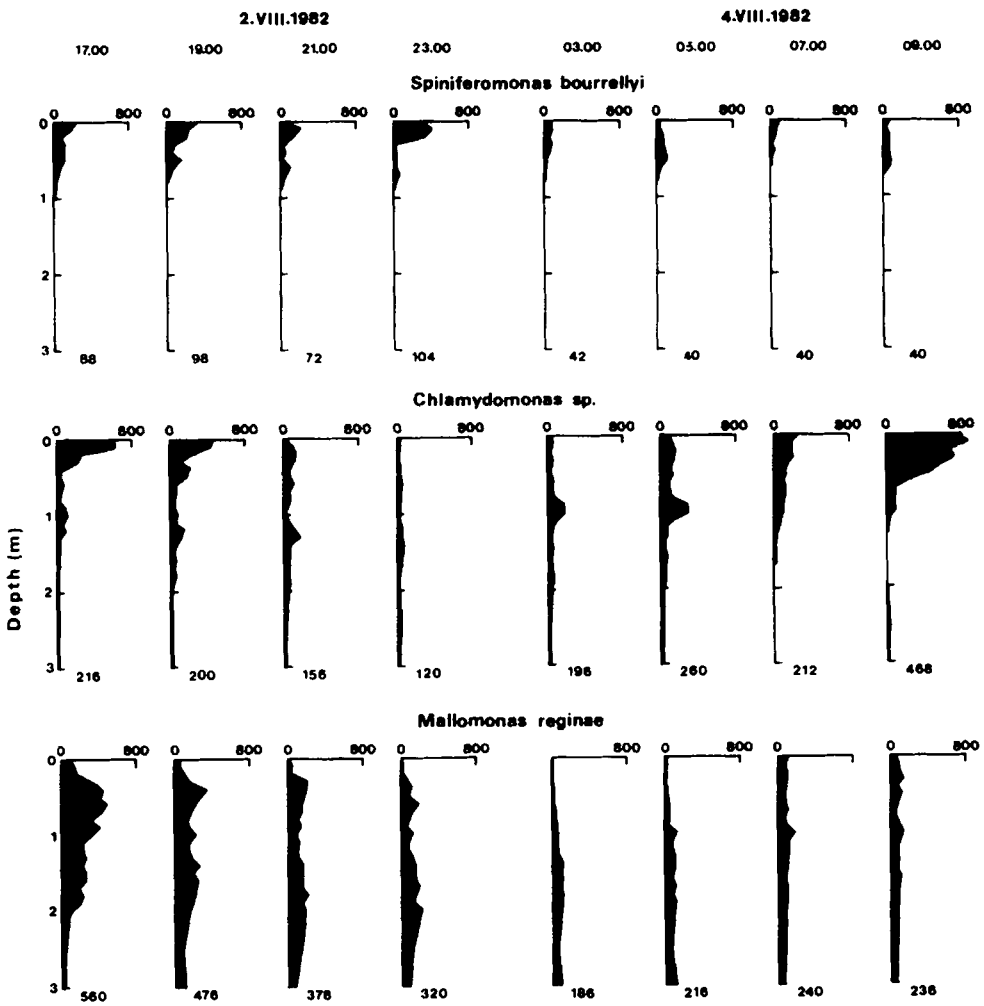


Fig. 4. Depth profiles of densities (cells ml^{-1}) of seven selected phytoplankton species at the four sampling intervals during each sample period. The integrated cell content of the 0–3 m water column (10^6 cells m^{-2}) is shown for each profile.

Table 2. Coefficient of variation, determined from the four sampling intervals on each of the two sample periods, for the integrated number of cells within the 0–3 m water column of the seven most abundant phytoplankton species.

	CV %	
	2 August	4 August
Ankyra judayi	22	11
Chlamydomonas sp.	25	44
Cryptomonas marssonii	57	53
Dinobryon divergens	28	38
Mallomonas akrokomos	13	6
Mallomonas reginae	25	11
Spiniferomonas bourrellyi	16	3

own distribution pattern. Several species showed a departure from a passive distribution in this manner on one sampling period (Table 3) and hence also a low similarity between profiles over the sampling intervals.

Of course, it does not follow that those species which did demonstrate a significant effect of depth on vertical distribution were necessarily also passively distributed; they could be showing a significant depth effect produced in a different manner to that for *Ankyra*. This possibility was tested for each species which had shown a significant depth effect, by summing the ranks at each depth over the four sampling intervals. These summed ranks were then cor-

Table 3. Results from each sampling period for the most abundant phytoplankton species of tests for the effect of depth on vertical distribution (Friedmans method, χ^2), the similarity between repeated vertical profiles (Kendall's coefficient of concordance, W) and the similarity between profiles for each species and those of the 'reference' species *Ankyra judayi* (correlation coefficient, r). Significance levels are shown as * ($p<0.05$), ** ($p<0.01$) and *** ($p<0.001$).

	2 August			4 August		
	χ^2	W	r	χ^2	W	r
Ankyra judayi	82.9***	0.942		82.2***	0.934	
Chlamydomonas sp.	39.6*	0.450	0.048	60.5***	0.688	0.800***
Cryptomonas marssonii	51.4***	0.584	−0.811***	24.4	0.277	
Dinobryon divergens	14.3	0.162		40.0**	0.454	0.704***
Mallomonas akrokomos	69.1***	0.785	0.547*	26.0	0.295	
Mallomonas reginae	51.8***	0.588	−0.171	34.7*	0.394	−0.710***
Spiniferomonas bourrellyi	67.8***	0.771	0.741***	60.4***	0.686	0.539**

related with those for *Ankyra* from the appropriate sampling period. For those species which showed a significant positive correlation with *Ankyra* it is not possible to reject the null hypothesis that their vertical distribution may most easily be described as a passive one.

Distribution of individual species

Ankyra judayi

The distribution of this small, non-motile species was used as a reference for assessing the distributions of the other, flagellated species. Although the distribution of *Ankyra* may be assumed passive, it was certainly not random. No significant horizontal variability was detectable on either of the scales tested (replicate samples at single sites and between sites). The vertical distribution showed a highly significant effect of depth (Table 3) with the cells concentrated in the upper 1 m. The maximum density of cells was consistently found between 0.6 and 0.8 m, where the temperature-associated metalimnetic density gradient was maximal (Fig. 2). Few cells were ever detected below a depth of 1 m. These results suggest that the sinking rate of this small alga was very low; slow sinking through the upper water layers was largely arrested at the metalimnion and the resulting concentration of cells at that depth was not effectively redispersed by the limited (mainly convective) mixing generated in the shallow epilimnion. Hence the two series of successive depth profiles both gave values for the coefficient of concordance which were only slightly below exact similarity. This distribution pattern for *Ankyra* in Lake Nimetön is a more extreme form of the pattern reported for this species from large enclosures in Blelham Tarn by Reynolds & Wiseman (1982).

Spiniferomonas bourrellyi

This small flagellate consistently exhibited a vertical distribution which differed little from that of *Ankyra* (Fig. 4, Table 3). With a volume of only around 80 μm^3 and several long, slender spines, the spherical cells probably have a rate of sinking little different from that of *Ankyra*. Certainly *Spiniferomonas* did not show the same tendency to accumulate in the metalimnion (Fig. 4). On 2 August the highest density of cells was found at, or 0.1 m below, the surface while on 4 August the cells were evenly distributed within the shallow epilimnion. It appears that this species has limited swimming capacity, but sufficient to counter any tendency to sink and perhaps also to achieve small scale orientation in water columns with only weak turbulence.

Chlamydomonas *sp.*

Vertical profiles of *Chlamydomonas* showed a significant depth effect (Table 3). However, on 2 Au-

gust the profiles showed no correlation to those of *Ankyra* and also gave a low coefficient of concordance. At the start of the sequence the cells were concentrated near the surface and thereafter became progressively more evenly distributed to 3 m or below (Fig. 4). No downward moving peak of cell density was evident, suggesting that the movement of cells was only loosely synchronised. On 4 August the sequence of profiles showed a high correlation to that of *Ankyra* with a similar tendency towards a metalimnetic maximum. In view of the greatly increased total number of cells in the final profile (Fig. 4) the apparent upward redistribution must be treated with caution. Nevertheless, this species appears to have been undertaking active, but weakly synchronised, vertical migrations with downward movement in the evening and upward movement through the morning.

Cryptomonas marssonii

On 2 August the depth distribution of this species showed a significant depth effect (Table 3) but the strong negative correlation with the distribution of *Ankyra* and the rather low coefficient of concordance show the observed pattern to be the result of active orientation. At 17.00 the bulk of the cells were already between 1 and 2 m and continued downward movement is shown in the depth profiles (Fig. 4) and from the decline in total cell numbers in the 0–3 m water column. A large proportion of the population evidently moved below 3 m during the night. A reverse sequence was evident in the series of profiles from the morning of 4 August, with the ascent having apparently just started at 03.00 and being almost complete by 09.00. The migrations of this species showed a greater degree of synchrony than was apparent for *Chlamydomonas*.

The magnitude of the migrations undertaken by *C. marssonii* was surprising. The movement of cells from near the surface to below 3 m took them across a temperature gradient of 14 °C (Fig. 2). This is far in excess of most previous reports (see Kamykowski & Zentara, 1977), although migrations across equivalent temperature gradients have recently been reported from another lake in the Evo district (Arvola, 1984). Moreover, the cells clearly descended to depths at which no oxygen was present and presumably remained there for several hours. This contrasts with the consistent avoidance of the anoxic hypolimnion by *Ceratium hirundinella* observed by Heaney & Talling (1980).

There was some indication that *Cryptomonas ovata* was following a similar migration pattern to *C. marssonii*, but cell counts were too low at this time to permit further analysis. The pattern of migration of *Cryptomonas* at this time in Lake Nimetön, descending around sunset and ascending around sunrise, is the same as that reported previously for several species of *Cryptomonas* from a variety of lakes (Soeder, 1967; Happey-Wood, 1976; Burns & Rosa, 1980; Frempong, 1981; Arvola, 1984) and may be a widespread behavioural trait of this genus.

Dinobryon divergens

Like *Ankyra*, this species was effectively confined to the upper 1 m water layer (Fig. 4). Despite this, no significant effect of depth was demonstrated on 2 August (Table 3) due to the constantly changing shape of the profiles. The very low coefficient of concordance for this sequence of profiles reflects the discrete peak of cells moving progressively down through the water column (Fig. 4). On 4 August a significant depth effect was indicated as well as significant correlation with the distribution of *Ankyra* (Table 3), although the rather low coefficient of concordance is indicative of some changes in the depth distribution. The observed sequences can be interpreted as sinking during the evening and some active movement in the morning to locate more favourable conditions for photosynthesis.

Mallomonas akrokomos

On 2 August the vertical distribution of this species showed a significant effect of depth, significant positive correlation with that of *Ankyra* and a moderately high coefficient of concordance (Table 3) and consequently may be considered primarily passive. However, on 4 August no significant

depth effect was detected and the very low coefficient of concordance indicates a shifting vertical distribution. During this early morning period, upward movement of cells was taking place (Fig. 4).

Mallomonas reginae

As noted earlier, this species was the only one to show significant horizontal variation between the lake sites. The vertical profiles showed a significant effect of depth on both occasions, but no, or negative, correlation with the distribution of *Ankyra* (Table 3). On both occasions the coefficient of concordance was moderately low, indicating directional but loosely synchronised shifts in distribution. An evening descent was apparent (Fig. 4) but commencing later than for the cryptomonads, and even by 09.00 on 4 August only a partial ascent had occurred. Since the cells evidently descend well below 2 m and may not return until late in the morning, the observed horizontal variability between lake sites (Table 1) could be caused by failure of the 2 m tube sampler to capture the entire water column population at some of the sites. This would occur if the vertical migrations were out of phase at different sites, for example in response to varying irradiance conditions around the lake.

Discussion

This work has investigated the vertical distributions of some flagellated phytoplankton species by referring them to that of a non-motile and close to neutrally buoyant species. Use of a non-motile alga as a marker of possible effects of water turbulence on vertical distributions has been made previously by Soeder (1967) and Happey-Wood (1976). However, use of a reference species in this way does assume that passive influences on distribution have an equal effect on the reference species and those to be compared with it. This assumption may be violated in a number of ways, for example by differences in sinking rates or susceptibility to grazing, as well as by variations in horizontal heterogeneity between species. In this study horizontal heterogeneity was insignificant except in the case of *Mallomonas reginae,* while differential loss rates would hardly have been apparent over the short sampling intervals employed. Therefore the use of a reference species was valid in this case.

All the flagellated species examined, with the exception of *Spiniferomonas bourrellyi,* showed vertical distributions which both deviated significantly from the reference distribution and shifted significantly during 6 hour periods around sunset or sunrise. Since these shifts in vertical distribution appeared to involve most of the population of each species and also produced no net directional movement over a 24 hour period, they may be considered examples of true vertical migration, as the term has been traditionally used in limnology. This is equivalent to the 'homeostatic migration' category defined by Taylor (1986).

Although the migrations undertaken by different species varied in their vertical extent and degree of synchrony, they all clearly conformed to a single temporal pattern. This involved downward movement in the evening and a return, upward journey in the early morning. This pattern is the one most frequently observed in migrating phytoplankton, both freshwater and marine (Taylor, 1980). Only rarely has the opposite pattern been reported (e.g. Tilzer, 1973). The data presented here do not allow any judgement of the regularity of these diel migrations, but other studies in Lake Nimetön and nearby lakes strongly support the view that diel vertical migrations are a constant feature of healthy populations of these species of flagellates (Arvola, 1984; Salonen *et al.*, 1984b; Arvola *et al.*, 1987).

The extent of vertical movements differed between species (Fig. 4). *Dinobryon divergens* was restricted to the upper 1 m of the water column and may therefore have been avoiding oxygen depleted water. The phased downward movement of this species on 2 August (Fig. 4) indicates a rate of travel of 2 m d^{-1}, which is far greater than reported typical sinking rates even for large diatoms (Burns & Rosa, 1980; Reynolds, 1984) and suggests the colonies were actively swimming downwards rather than settling passively. The more extensive distance (several metres) covered by other species, particularly the cryptomonads, involved crossing a temperature gradient

>14 °C and penetrating far into the anoxic hypolimnion. This must have entailed strong swimming in both directions; cryptomonads typically have only very low sinking rates (Burns & Rosa, 1980; Reynolds & Wiseman, 1982).

Some species (*Dinobryon divergens, Cryptomonas marssonii*) showed strongly synchronised movements which must reflect a uniform and sensitive response of individuals within the population to an appropriate stimulus. This might be internal (circadian) or it could be external, provided the stimulus affected all individuals in a similar fashion (e.g. changing irradiance). Both types of stimulus have been reported. The evening descent noted for most species in this study could certainly have been a direct response to decreased irradiance, and the post-sunrise ascent of species such as *Mallomonas akrokomos* could equally have been a response to increasing irradiance. However, such a response seems unlikely to explain the timing of ascent by species such as *Cryptomonas marssonii* which commenced before any detectable increase in incident irradiance and was from depths at which light penetration was infinitesimal (Figs. 3, 4). These species may have been responding to endogenous rhythms. Apparent circadian rhythms have been demonstrated with dinoflagellates in experimental tanks (Eppley *et al.*, 1968; Heaney & Furnass, 1980; Cullen & Horrigan, 1981). Phototactic responses have been reported from laboratory and field studies, although the latter will rarely allow firm identification of the mechanisms underlying observed movements. Other possible stimuli for vertical migrations such as nutrient depletion are unlikely to act on all individuals in the same way and would not produce the synchronous migrations observed here. However, nutrient depletion may modify underlying rhythms of migration in at least some species of phytoplankton (Heaney & Eppley, 1981).

The adaptive significance of flagellate migrations remains uncertain. In the weakly turbulent water columns of forest lakes such as Lake Nimetön, phytoplankton must be able to effectively counter their natural tendency to sink. Small cell size with a low sinking rate may be an adequate strategy (e.g. *Ankyra*) but diatoms are notably absent from these environments in which the overwhelming bulk of the phytoplankton is flagellates (Jones & Arvola, 1984). Motility allows these algae to remain in suspension, but that does not account for the high frequency of species which undertake diel migrations.

Cost benefit analysis of diel migrations of dinoflagellates (Raven & Richardson, 1984) revealed the costs (primarily the energy and nutrients required to produce and operate the flagella apparatus) to be substantially outweighed by the benefits (increased acquisition of photons and nutrients relative to non-migratory cells). In that analysis the assumed swimming speeds (up to 40 m d^{-1}) were an order of magnitude greater than the highest values which can be deduced from the vertical profiles in Lake Nimetön (Fig. 4). The costs of the shorter migrations in Lake Nimetön may therefore be assumed to be less. Since some flagellate species in the lake do not undertake migrations but can sustain an advantageous position in the euphotic zone (e.g. *Spiniferomonas*), the chief metabolic benefit to migratory species is probably the access they gain to the substantial reserves of nutrients present in the hypolimnion. Retrieval of phosphorus from the hypolimnion in Lake Nimetön by diel vertical migrations of phytoplankton was experimentally verified by Salonen *et al.* (1984b). Comparison with areal loading of phosphorus to the lake via inflows suggests that migratory retrieval of phosphorus from the hypolimnion can be the largest source of fresh phosphorus input to the epilimnion during drier periods in the summer.

However, vertical migrations may confer other advantages besides metabolic ones. It was already noted that *Cryptomonas ovata* was under-represented in the outflow when, at the time of sampling, the population was still mainly well below the surface. All those species which move below the water layer which is feeding the outflow from the lake will similarly reduce population losses through washout. The mean flushing rate for the epilimnion of Lake Nimeton during the ice-free period is around 0.5 d^{-1} (L. Arvola, unpublished data). Spending 8 hours of darkness below the epilimnion would not therefore be of great selective advantage to migratory species with respect to this population loss process, except during storm events when flushing rates are much higher. However, small flagellates, and particularly

naked species, are favoured food for herbivorous zooplankton and may face severe grazing pressure. Reynolds *et al.* (1982) showed that >96% of the losses from a population of *Cryptomonas ovata* in large enclosures was due to grazing. In Lake Nimetön most zooplankton are migratory, coming to the upper waters to feed at night and spending the day in deeper strata (Arvola *et al.*, 1986). Phytoplankton migrations on the reverse pattern, as were all those found in this study, would therefore substantially reduce grazing pressure without imposing any loss of growth potential.

Separating the relative importance of these advantages gained from vertical migrations is difficult. The evolution of phytoplankton migratory behaviour, whether endogenous or exogenous, may have responded to a number of separate selective advantages. The situation is further confused by the spectrum of behaviour displayed by even the small number of flagellate species in this study. What is clear is that more rigorous investigation of vertical distributions is needed. Laboratory experiments in which possible stimuli can be controlled must be coupled with field studies designed to permit objective interpretation of distributions. This paper has presented some approaches to the latter, but more sensitive statistical tests may be needed to evaluate vertical migration patterns in water columns with greater physical mixing.

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