

# An assessment of the influence of recruitment from the sediment on the development of planktonic populations of cyanobacteria in a temperate mesotrophic lake

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## SUMMARY

1. A number of planktonic cyanobacteria species form resting stages that survive in the sediments of lakes. The significance of this life history strategy to the ecology of new planktonic populations was investigated in Esthwaite Water, a mesotrophic lake in the English Lake District.
2. A simple trapping technique was used to quantify vertical movements of five species of buoyant gas-vacuolate cyanobacteria from close to the sediments, along a depth transect.
3. 'Recruitment' from the sediments was found to be widespread amongst the cyanobacteria species associated with the summer phytoplankton community.
4. Estimates of the vertical upward fluxes of cyanobacteria based upon trap catches could not account for observed increases in the planktonic populations suggesting that 'recruitment' was not a significant source of biomass.
5. Vertical upward movements of *Anabaena solitaria* were recorded prior to this species becoming established in the plankton suggesting that benthic populations might be a source of cells for initial pelagic growth of populations of this species.
6. Low numbers of vegetative filaments of *Anabaena flos-aquae*, *Aphanizomenon flos-aquae* and *Oscillatoria agardhii* were observed in the plankton through the winter. These small overwintering populations appeared to be the primary source of inocula for the large summer populations of these species.

**Keywords:** akinetes, blue-green algae, cyanobacteria, migration, recruitment, resting stages, vertical movement, trapping

## Introduction

The populations of cyanobacteria that form part of the phytoplankton communities in temperate lakes undergo periodic fluctuations in abundance. During unfavourable environmental conditions a number of species persist as resting stages in the surface sediments of lakes (Reynolds, 1984; Reynolds, 1987). Many filamentous planktonic cyanobacteria of the Nostocales and Rivulariaceae produce specialised

vegetative cells called akinetes (Paerl, 1988). Colonial Chroococcales genera such as *Microcystis* and *Gomphosphaeria* do not produce morphologically distinct resting stages, but can survive unfavourable conditions as 'dormant' colonies in the surface sediments. The sediments of lakes with periodically large populations of planktonic cyanobacteria will usually contain large numbers of these resting stages which represent potentially significant inocula for subsequent development of pelagic populations (Reynolds *et al.*, 1981; Takamura *et al.*, 1984; Barbiero & Welch, 1992).

There is continuing debate as to the quantitative importance of these benthic stages, particularly akinetes, in the annual life-history of planktonic

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cyanobacteria. Rother & Fay (1977) proposed that akinetes develop during adverse surface bloom conditions and sink from the surface to germinate deeper in the water column and ensure the survival of vegetative filaments in the plankton. Reynolds (1972) recorded the germination of *Anabaena circinalis* akinetes in circulation prior to the development of the spring population, and he suggested that circulation of the akinetes in the water column may be a precondition to germination. More recently, it has been reported that planktonic populations can originate from 'recruitment' following an initial period of development on the sediments (Barbiero & Welch, 1992; Takamura *et al.*, 1984; Trimbee & Harris, 1984; Hansson *et al.*, 1994). This meroplanktonic behaviour of some cyanobacteria has attracted attention in respect of the population dynamics of several species, including *Microcystis aeruginosa* (Reynolds, 1973; Takamura *et al.*, 1984), *Gloeotrichia echinulata* (Barbiero & Welch, 1992; Barbiero, 1993; Istvánovics *et al.*, 1993; Pettersson *et al.*, 1993; Forsell & Pettersson, 1995) and *Aphanizomenon flos-aquae* (Barbiero & Kann, 1994; Osgood, 1988).

Several studies have now demonstrated active recruitment of cyanobacteria from the sediments into the water column (Trimbee & Harris, 1984; Barbiero & Welch, 1992; Hansson, 1993; Barbiero & Kann, 1994; Hansson *et al.*, 1994; Hansson, 1996). The role that such movement may play in nutrient cycling has been the main stimulus for recent research; less attention has been paid to the possible impact of large recruitment events on the composition of the overlying phytoplankton community (Barbiero & Kann, 1994; Trimbee & Harris, 1984; Barbiero & Welch, 1992; Forsell & Pettersson, 1995). Besides quantitative evidence about the extent of recruitment of cyanobacteria from the sediments, a number of environmental parameters, including irradiance and oxygen levels, have been linked to recruitment events (Hansson, 1996; Trimbee & Prepas, 1988; Hansson *et al.*, 1994). However, the underlying processes that may initiate the development and upward movement of sediment cyanobacteria are still poorly understood.

Here we report the results from a study made to investigate the possible importance of cyanobacterial movements from the sediments of a dimictic, mesotrophic lake, and of the response of 'recruitment' to variable environmental conditions.

### Study site

The work was undertaken at Esthwaite Water (54°21' N, 3°0' W) which is one of the most productive lakes in the English Lake District, an area which has a cool oceanic climate. The lake has been extensively studied and is described in some detail elsewhere (Heaney *et al.*, 1992; Lund, 1961; Lund, 1972; Talling & Heaney, 1983; Heaney *et al.*, 1986). Esthwaite Water now regularly produces substantial summer phytoplankton crops of cyanobacteria in place of the population of *Ceratium hirundinella* which used to dominate the late summer phytoplankton (Heaney *et al.*, 1983). Previous work (Heaney *et al.*, 1983) had established that the *Ceratium* growth originated entirely from germination of cysts overwintering in the sediments. Esthwaite Water was therefore an appropriate site to examine the extent to which sediment derived inocula might also be important in the development of the cyanobacterial summer phytoplankton populations.

### Materials and methods

The lake was sampled from December 1992 until December 1993, initially at fortnightly intervals and from April 1993 at weekly intervals. Samples were taken at a permanent buoy anchored in 12.5 m of water in the northern basin of the lake. Dissolved oxygen and temperature were measured using a YSI Model 57 meter and 5739 probe. Photosynthetically available radiation (PAR) was measured with a LI Cor LI 189 meter fitted with a LI Cor LI 1925 A underwater quantum sensor. Euphotic depth (*Z<sub>eu</sub>*) was defined as the depth to which 1% of surface irradiance penetrates and was calculated from values of the vertical attenuation coefficient obtained from the PAR depth profiles (Kirk, 1994).

Samples of lake water were taken from the surface and at depths of 4 m, 8 m, and 12 m, using a 1 litre Ruttner sampler. Two replicate samples for phytoplankton counting were taken and fixed with acidified Lugol's iodine. Counts were made on a Zeiss IM35 inverted microscope using the standard Utermöhl inverted microscope technique (Lund *et al.*, 1958) and random fields of view were enumerated. Either 30 fields of view or a minimum of 100 individuals (95% confidence limits  $\pm 20\%$ ) of the most abundant species were counted. Counts were converted to biovolumes for the dominant species within the phytoplankton

community. Common phytoplankton cells and filaments were assumed to be made up of solid geometric shapes that most closely resembled the cell morphology (Rott, 1981; Wetzel & Likens, 1991). To allow the volumes of the shapes to be calculated, the dimensions of the cells were measured using an eyepiece graticule. Mean filament biovolumes were then calculated from an estimated cell number per filament. Cells of the colonial cyanobacterium, *Gomphosphaeria naegeliana* Unger, were very tightly packed in round colonies which were treated as spheres to estimate the biovolume. Phytoplankton biomass as chlorophyll *a* concentration was also estimated for two replicate surface water samples by standard methanol extraction (Talling & Driver, 1963).

The possible recruitment of benthic cyanobacteria to the pelagic populations was estimated using specially designed traps. These consisted of inverted glass funnels (diameter 15 cm) with the stems inserted through the lids of polystyrene collecting jars (115 mL volume). The collecting jars were painted black to exclude light and minimise growth of trapped photosynthetic cyanobacteria. Preliminary trials with the traps in early April yielded high densities of zooplankton and water mites but almost no phytoplankton. To prevent large zooplankters and mites from entering the traps and thus reduce the grazing pressure in subsequent work the ends of the funnels were covered in a 80- $\mu\text{m}$  mesh net. This mesh size was smaller than the length of some filaments which could exceed 100  $\mu\text{m}$  in length. Laboratory trials with sieves made from a selection of mesh sizes were undertaken to assess whether filaments would be excluded by the netting. Indications were that netting with a mesh size of 64  $\mu\text{m}$  and above allowed the longer filaments to pass through. Microscope examination of the netting revealed little evidence of tangling or exclusion. The netting was successful in excluding the larger grazers, but would also have excluded any large clumps or mats of cyanobacteria. In fact no such aggregations were recorded, on either the outside of the netting or in the water overlying sediment cores taken from close to the trap sites (Head, 1996).

The traps were suspended within 7 cm of the sediment surface in pairs from either end of a T bar that was attached to a central stand resting on the surface of the sediment. This arrangement assumes that buoyant cells move from the sediment directly up

into the trap from an area of sediment equal in surface area to the open end of the funnel, and directly below it. A trap catch can thus be used to calculate a migration rate per unit sediment surface (Barbiero & Welch, 1992). The frames with pairs of replicate traps were deployed by carefully lowering them on a rope from a boat at four depths (2.5, 5.0, 7.5 and 12.0 m) along a transect that extended out perpendicular to the north-east shore of Esthwaite Water into deeper water. Trapping began on 12 May 1995 and the collecting bottles were changed each week. Prior to deploying the traps they were filled with GF/C-filtered lake water or with Milli-Q water on occasions when filtered lake water was not available. From microscope observations the darkened trap environment appears to have had no adverse effects on the trapped buoyant cyanobacteria during the deployment time. Obvious lysis was not observed.

When traps were lowered through the water column there was a possibility that cyanobacteria in the phytoplankton could enter the traps in which case 'recruitment' from the sediment would be overestimated. To determine if such 'contamination' of the traps occurred, a second, identical trap was lowered at each site once a month when the experimental traps were being deployed, and was retrieved after 10 min. Cyanobacteria that had entered the trap during this short period were assumed to have come from the water column during the lowering process. In practice the numbers of filaments recovered by this 'control' trapping exercise were usually negligible (< 1%). Hansson (1996) reported similar low levels of contamination and concluded that no correction was necessary. Occasionally in the present study larger amounts entered the traps (5%), in these instances the contamination was taken into account during the calculation of trap accumulation rates. After recovering the traps, 2–3 drops of Lugol's iodine were added to the samples in the collecting bottles. Enumeration of the cyanobacteria samples in the bottles was done following the standard Lund chamber method (Lund, 1959) using a Vickers Photoplan microscope or a Leitz Dialux microscope fitted with a Whipple grid.

In order to assess the importance of recruitment events from the sediments to the development of pelagic populations of cyanobacteria in Esthwaite Water, estimates of the rates of pelagic population change were compared to the 'recruitment' occurring

in the lake. Using bathymetric data for Esthwaite Water (Ramsbottom, 1976) the lake volume was divided by depth into vertical layers (0–5 m, 5–8 m, 8–12 m and > 12 m). Estimates of the standing crop of each of the most abundant cyanobacteria species (filaments/colony per unit volume) in each layer ( $P_l$ ), and the total standing crop (as filament/colony number) of each species for the whole lake ( $P_{Lake}$ ), were made. Where  $V_l$  is the volume of the lake layer in litres and  $n_l$  is the mean number of filaments per litre in the water column of the layer ( $l$ ):

$$P_l = V_l \times n_l \text{ and } P_{Lake} = \sum P_l$$

Estimated biovolume data were pooled from the different depths sampled and rates of net population change ( $k_n$ ) for *Anabaena solitaria* Klebahn, *A. flos-aquae* Brébisson, *G. naegelianae* and *O. agardhii* Skuja were then calculated from the following (Trimbee & Harris, 1984):

$$k_{Lake} = (P_{Lake} \cdot t_2 - P_{Lake} \cdot t_1) / (t_2 - t_1)$$

where  $N t_2$  is the standing crop (biovolume per unit water volume) at time  $t_2$  and  $N t_1$  is the standing crop at time  $t_1$ . The time interval ( $t_2 - t_1$ ) represents the time between sequential samplings, and was typically around 7 days. Similarly, the difference in standing crop values from consecutive sampling occasions ( $t$ ) was determined and a daily rate of net change ( $k_{Lake}$ ) calculated for the whole lake population:

$$k_{Lake} = (P_{Lake} \cdot t_2 - P_{Lake} \cdot t_1) / (t_2 - t_1)$$

Recruitment of cyanobacteria to the plankton for the whole lake ( $R_{Lake}$ ) was estimated by dividing the lake-bed into sections of known surface area using contours from the bathymetric map (Ramsbottom, 1976). Daily trap catches ( $R_T$ ) were assumed to be representative of 'recruitment' from the lake bed within the contour sections. The daily recruitment ( $R_s$ ) from the total surface area of sediment within each section ( $A_s$ ) was then estimated:

$$R_s = R_T \times A$$

and

$$R_{Lake} = \sum R_s$$

Comparison of  $R_{Lake}$  with  $k_{Lake}$  then yielded estimates of the total recruitment occurring from the sediments relative to the observed population change in the whole-lake pelagic populations to determine if

'recruitment' was an important factor accounting for observed population increases in a particular species.

## Results

Esthwaite Water is a monomictic, temperate lake that was cold and well mixed at the beginning of the sampling period in 1992. Stratification developed during April and was well established by the beginning of May. A thermocline persisted throughout the period of the trapping experiments, the depth of the mixed layer extending to about 9–10 m (Fig. 1a) resulting in the 12 m traps always being in the hypolimnion. During periods of calm warm weather, weak secondary thermoclines developed but these were quickly broken down by wind-induced turbulence. The lake remained stratified until the end of September when the autumn overturn occurred and full mixing of the water column resumed. Dissolved

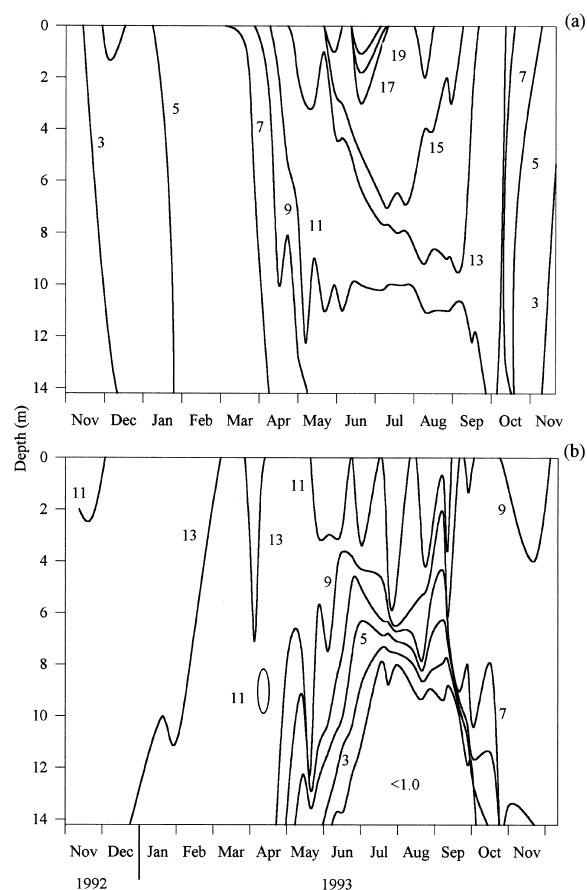


Fig. 1 Depth-time diagrams showing isopleths of (a) temperature (°C) and (b) dissolved oxygen concentration ( $\text{mg L}^{-1}$ ) in Esthwaite Water.

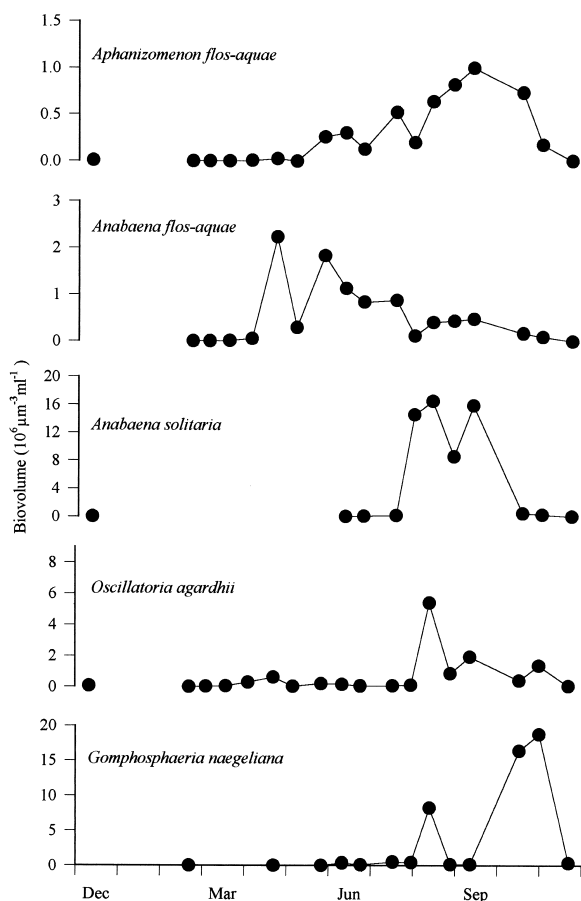


Fig. 2 Seasonal changes in biovolume of the five most abundant species of cyanobacteria in the epilimnetic phytoplankton of Esthwaite Water (note different vertical scales).

oxygen levels in the hypolimnion progressively decreased (Fig. 1b). From late June until the overturn of the water column, deeper parts of the hypolimnion (below 9 m), contained less than  $1 \text{ mg O}_2 \text{ L}^{-1}$  and were considered to be anoxic.

During the winter and early spring, the phytoplankton community was dominated by diatoms. A small and declining cyanobacteria community, dominated by *Anabaena spiroides* and *A. flos-aquae*, accounted for less than 10% of the total phytoplankton biovolume (Fig. 2). Two other species of cyanobacteria, *Oscillatoria agardhii* and *Aphanizomenon flos-aquae*, were also recorded, in very low amounts (<0.5% of total biovolume). Following a spring diatom maximum in late February/early March, total phytoplankton biomass (chlorophyll *a* concentration) decreased, increasing the clarity of the water and thus the depth of the euphotic zone (Fig. 3). The

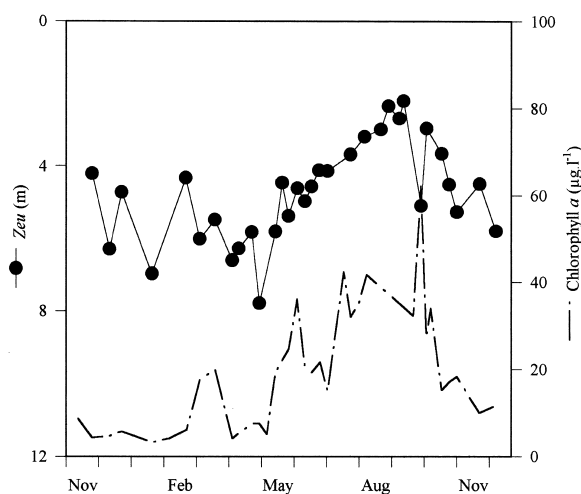


Fig. 3 Temporal variation in the euphotic depth ( $Z_{eu}$ ) and the biomass of phytoplankton (0–1 m) as chlorophyll *a* ( $\mu\text{g L}^{-1}$ ) in Esthwaite Water.

biovolume of the cyanobacteria, *Anabaena flos-aquae* and *O. agardhii*, began to increase as the diatom populations declined. Increased vertical stability was reflected by changes in the species composition of the phytoplankton.

Following the onset of stratification in April/May, the major part of the phytoplankton biomass was restricted to the epilimnion. Chlorophyll *a* concentration increased and as a consequence the euphotic depth steadily declined (Fig. 3). The phytoplankton community composition shifted to dominance by cyanobacteria (Fig. 2). Initially, a population of *Anabaena flos-aquae* developed, followed by a rapid rise in abundance of *A. solitaria* which represented over 70% of the summer biovolume maximum in August. Other, less prominent cyanobacteria (i.e. representing <1% of phytoplankton biovolume) included *Aphanizomenon flos-aquae*, *A. spiroides*, *O. agardhii* and an *Oscillatoria* species similar to that described in Tikkanen (1986) as *Oscillatoria limnetica*. *G. naegeliana* was found almost exclusively below the thermocline.

*In situ* rates of net population change ( $k_n$ ) that occurred between sampling dates of the four most abundant species of cyanobacteria, are presented in Fig. 4. These values do not represent the true growth rate which is difficult to measure directly due to the cumulative effects of growth, recruitment and loss processes, including sedimentation of cells, grazing, wash-out and parasitism. Initially the value of  $k_n$  for the *A. solitaria* population was very high reflecting a

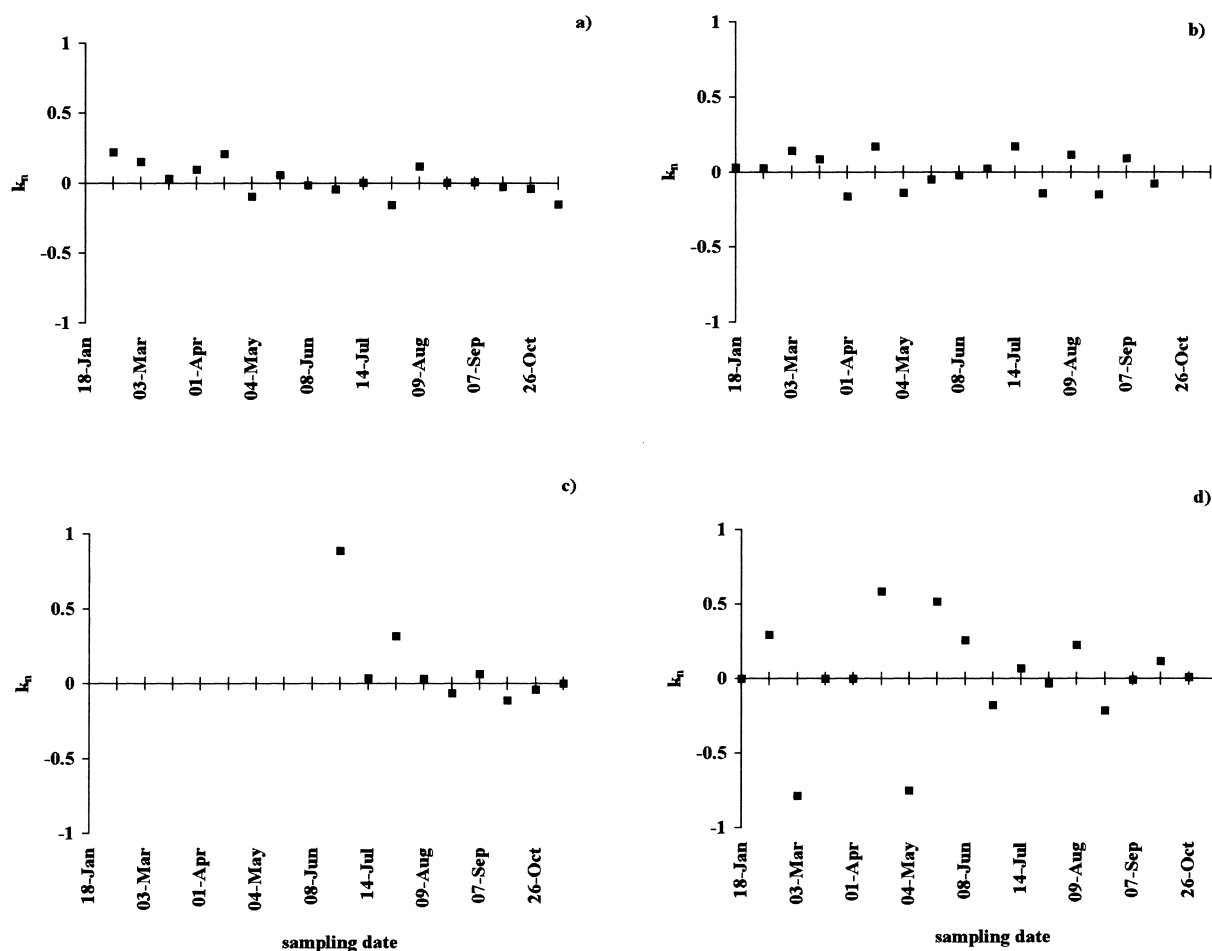


Fig. 4 Estimated values of exponential rates of population change ( $k_n$ ) for the dominant four species of cyanobacteria. (a) *Anabaena flos-aquae* (b) *Oscillatoria agardhii* (c) *Anabaena solitaria* (d) *Gomphosphaeria naegeliana*.

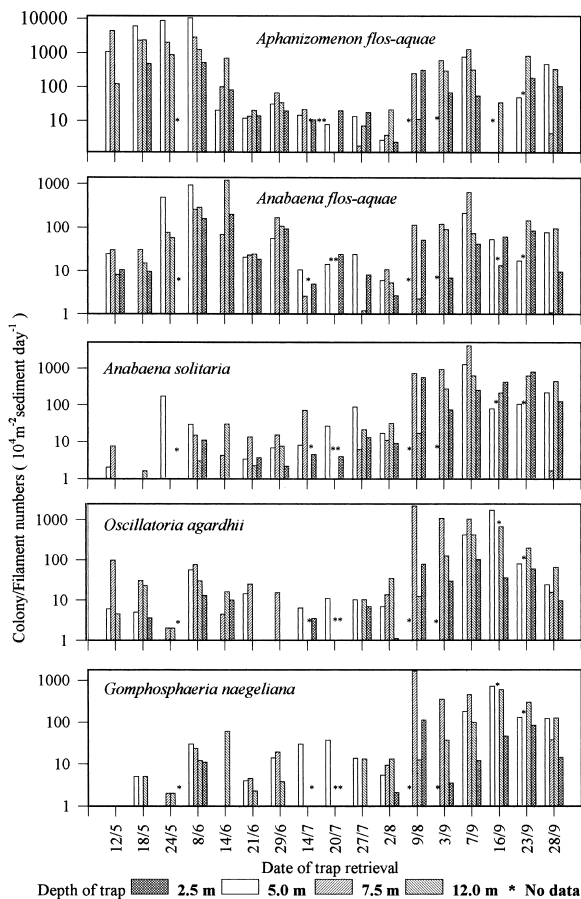
rapid initial period of population development in June. High rates of population change were also recorded for *G. naegeliana* in the top 10 m of the water column, these large fluctuations in the rate of population change in April and May seemed to reflect vertical movements of the population within the water column.

#### Trap catches

During the early stages of trapping to determine the recruitment patterns of the dominant cyanobacteria species, the most prominent species were *Aphanizomenon flos-aquae* and *Anabaena flos-aquae*, which showed similar movement away from the sediments (Fig. 5). The species were caught by the traps in late May and early June, and in greatest numbers at the

shallower sites. To determine if there were significant differences between the catches from traps deployed at different depths, pooled data from each month, and for the whole sampling period, were tested using the Kruskal–Wallis test. The analysis of variance showed no significant difference ( $P > 0.05$ ) between the trap catches from the different depths. This suggests that the changing environmental conditions, of those quantified along the depth transect, were not significantly affecting the movement of the buoyant cells.

The early catches coincided with the development of planktonic populations (Fig. 2) which could suggest that large-scale movements of cyanobacteria from the sediment were important in the initial development of these populations. Following low catches in July, a small rise was recorded during August and early September, this being mirrored by a slight



**Fig. 5** The daily movement away from the sediments of buoyant filaments/colonies of the main species of cyanobacteria estimated from catches in traps at four depths in Esthwaite Water. On occasions when traps were not recovered, due to technical problems or traps being lost, no data are available.

increase in the planktonic population of *Anabaena flos-aquae* and a more apparent increase in *Aphanizomenon flos-aquae*. The latter was redistributed throughout the water column during this period. Towards the end of September populations of both species declined, although buoyant filaments continued to accumulate in the traps.

A population of *A. solitaria* developed in the water column during June (Fig. 2), following several small trap catches during May and early June and two larger 'recruitment' events in late May and early June. Similarly, the planktonic population continued to increase rapidly, and there was a continual input of buoyant filaments from the sediments during July. Much larger trap accumulations were recorded dur-

ing August and September which may reflect a redistribution of filaments as mixing increased, in addition to movement from the sediments. Similar trapping patterns were recorded for *G. naegeliana* and *O. agardhii*. Trap catches of these two species began to decline towards the end of September when the *O. agardhii* population was in decline, although the biovolume of *G. naegeliana* increased until mid October. A number of other cyanobacteria were trapped on occasions. These included *Microcystis aeruginosa* Kützinger, *A. spiroides* and an *Oscillatoria* species similar to *Oscillatoria limnetica* Lemmerman.

Trap catches of all the main species were low during late June and July when the water column was at its most stable under stratification. During September, trap accumulations increased as the thermal stratification of the water column began to weaken and turbulence increased, even though overturn and full mixing did not occur until October (Fig. 1a). Throughout this period the deep water traps remained below the thermocline.

## Discussion

The present study has shown that vertical movements of cyanobacteria into the water column do occur from the sediments at a variety of depths in Esthwaite Water. This provides evidence in support of the supposition that benthic populations of cyanobacteria are able to act as inocula to planktonic populations (Roelofs & Oglesby, 1970; Kappers, 1976; Preston *et al.*, 1980; Fallon & Brock, 1981). The results are also consistent with those of recent studies of the migratory behaviour and recruitment potential of cyanobacteria in this respect (Barbiero & Kann, 1994; Barbiero & Welch, 1992; Pettersson *et al.*, 1993; Hansson *et al.*, 1994; Forsell & Pettersson, 1995).

A number of studies of the recruitment or 'life-form shift' (Hansson, 1993) of meroplankton have attempted to identify environmental conditions that may initiate migrations. The greatest accumulations of buoyant filaments in traps have usually been recorded at the shallower sites where insolation, temperature and dissolved oxygen levels were highest. In particular, the recruitment of *Aphanizomenon flos-aquae* appears to occur from shallow oxygenated sediments with high insolation (Trimbee & Harris, 1984; Barbiero & Kann, 1994) and recruitment of *G. echinulata* also seems to be favoured by high water temperatures and

**Table 1** The percentage of estimated daily standing crop in Esthwaite Water (as total filament/colony numbers) of the five main species of planktonic cyanobacteria, that could be accounted for by daily 'recruitment' from the sediments

Date	An. fa	An. so	Ap. fa	Os. ag	G. na
04/05/93	< 0.0001	$1.5 \times 10^{10}$	0.0099	0.0004	n.r.
24/05/93	0.0002	$4.5 \times 10^{11}$	0.0028	< 0.0001	$6.0 \times 10^9$
08/06/93	0.0002	$1.3 \times 10^{11}$	0.0009	0.0005	0.0093
21/06/93	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.0002
14/07/93	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.0002
27/07/93	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
09/08/93	< 0.0001	0.0002	0.0001	0.0025	n.r.
24/08/93	0.0001	0.0002	0.0001	0.0013	n.r.
07/09/93	0.0004	0.0003	0.0003	0.0006	0.0061
19/10/93	0.0003	n.r.	n.r.	n.r.	n.r.

An. fa, *Anabaena flos-aquae*; An. so, *Anabaena solitaria*; Ap. fa, *Aphanizomenon flos-aquae*; Os. ag, *Oscillatoria agardhii*; G. na, *Gomphosphaeria naegelianae*; n.r., no recruitment recorded.

The numbers in italics represent the estimated total daily recruitment occurring in the lake on sampling occasions when the species was not recorded in the phytoplankton samples.

light (Barbiero, 1993; Forsell & Pettersson, 1995). The requirements of these species for high insolation would suggest that an initial period of growth and development may occur on the sediment surface following the germination of akinetes. A consequence of this is that large areas of the benthos in steeply sided lakes which receive rapidly diminishing levels of irradiance and where temperatures are low will represent poor environments for the development of resting stages. Conversely, a lake with a large surface area of sediments in shallow, warm water and receiving high levels of insolation will represent a much more favourable environment for such benthic stages to develop and migrate into the overlying water column (Head *et al.*, 1998). Esthwaite Water fits into this latter category of lake. The current study did not find significant differences in numbers of cyanobacteria undergoing vertical movements along the depth transect, which encompassed a range of temperatures, oxygen conditions and levels of irradiance. This suggests that the variations in environmental conditions observed with depth in Esthwaite Water were not important factors. No evidence was found that stability of the water column or anoxic conditions influenced such movements; indeed the recruitment rates of all species were low when the thermal stratification was at its strongest during July. This was also a period of low insolation, when the euphotic depth was reduced due to shading by phytoplankton cells in the epilimnion. It would appear that no single over-riding environmental

factor of those investigated initiated the recruitment of cyanobacteria from the sediments in Esthwaite Water.

Few previous attempts have been made to estimate the importance of recruitment to the dynamics of the planktonic populations. Recruitment from the benthos has been estimated to account for over 40% of the number of colonies in the planktonic populations of Green Lake (Barbiero & Welch, 1992; Barbiero, 1993) and contributions from the benthic stock were similar in Lake Erken, accounting for  $\approx 50\%$  of the epilimnetic population prior to the maximum standing crop (Forsell & Pettersson, 1995). This recent work has confirmed earlier hypotheses that pelagic populations in Lake Erken were largely derived from benthic stocks (Istvánovics *et al.*, 1990; Pettersson *et al.*, 1990). Benthic recruitment of *Aphanizomenon flos-aquae* was found to account for up to 8.2% of the summer planktonic population in Agency Lake (Barbiero & Kann, 1994) but in other studies recruitment has not significantly affected the populations (Barbiero & Welch, 1992; Hansson *et al.*, 1994). Here we report that the upward vertical movements of the main planktonic species of cyanobacteria from the sediment-water interface in Esthwaite Water did not affect the magnitude of established planktonic populations (Table 1).

Four of the species found to be undertaking vertical movements (*Anabaena flos-aquae*, *Aphanizomenon flos-aquae*, *G. naegelianae* and *O. agardhii*) were present as planktonic populations throughout the sampling



period. *Anabaena flos-aquae*, *Aphanizomenon flos-aquae* and *O. agardhii* were already well established by the time the first quantitative trapping experiments were carried out; populations were estimated to be  $3.3 \times 10^{17}$ ,  $6.7 \times 10^{16}$  and  $2.8 \times 10^{16}$  filaments per whole lake volume, respectively. These pelagic populations were several orders of magnitude larger than the estimates attributed to vertical movements, and the level of recruitment occurring from the sediments was insignificant compared to the size of the planktonic population. The presence of the small, long-term planktonic populations, suggests that low numbers of filaments persisting in the water column, are likely to be more important inocula than recruitment from benthic stocks at the onset population increase. Such pelagic populations are already positioned in the water column to take immediate advantage of improved conditions. This overwintering strategy of maintaining a small population in the phytoplankton until the return of conditions conducive to population growth is common amongst phytoplankton (Reynolds, 1984), including cyanobacteria with known benthic resting stages (Rother & Fay, 1977; Jones, 1979).

Vertical upward movements were also recorded for *A. solitaria* and *G. naegelianiana*, but prior to either of these species being well established in the epilimnion. In the case of *A. solitaria*, as the planktonic population became established, a very high rate of net population change was recorded ( $K_n = 0.87$ ). Experimental work carried out with *A. solitaria* grown under laboratory conditions (20 °C under continuous PAR) showed a maximum rate of increase of only  $K_n = 0.5$  (Foy, 1980). The very high observed rate of net population increase in Esthwaite Water was therefore unlikely to be attributable solely to growth, but was probably accounted for by filaments moving into the pelagic from the benthos supplementing the growth occurring in the phytoplankton. Other studies have also concluded that growth rates can sometimes be insufficient to account for observed population changes (Lynch, 1980; Ganf, 1983). This evidence suggests that for the *A. solitaria* population at least, recruitment from benthic stocks played an important role in the initial development of this planktonic population. Recruitment from the benthos in Esthwaite Water was not sufficient to sustain populations of cyanobacteria once 'established' in the water column.

## Acknowledgements

This study was supported by a Natural Environment Research Council CASE studentship in partnership with the IFE held by R.M. Head. Thanks are due to the scientists of the Aquatic Sciences laboratory at Lancaster University for field assistance and to the staff of the IFE Windermere and Edinburgh for their help during the sampling programme.

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(Manuscript accepted 17 November 1998)