Patterns in Algal Recruitment from Sediment to Water in a Dimictic, Eutrophic Lake

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Patterns in Algal Recruitment from Sediment to Water in a Dimictic, Eutrophic Lake

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In the large, dimictic, and highly productive Lake Mendota (Wisconsin, USA), the recruitment rates from sediment to water were determined for some characteristic and dominating algal species during a 1-yr cycle. Quantifying recruitment in relation to abundance in the water on a whole-lake basis revealed that recruitment usually accounted for less than 1% of the total standing stock of each species per day, indicating that recruitment may not be an important population variable in Lake Mendota, but may instead function as an inoculum for future growth in the water column. The recruitment of *Cryptomonas erosa* and *Ceratium hirundinella* showed a dephasing among sites, suggesting that algae on the sediment surface rise into the water column in response to some depth-related cue. With the exception of one recruitment period for *Aphanizomenon*, no recruitment was recorded below the thermocline during the stratification period, indicating that a variable associated with stratified conditions affected algal movements from the hypolimnion to the euphotic zone. We argue that the understanding of recruitment patterns from sediment to water is a key factor in managing algal blooms in highly productive lakes.

Dans le lac Mendota (WIsconsin, É.-U.), un grand lac dimictique très productif, on a déterminé les taux de recrutement dans la colonne d'eau de certaines espèces d'algues caractéristiques et dominantes en provenance des sédiments au cours d'un cycle annuel. La quantification du recrutement en rapport avec l'abondance des algues dans l'eau dans l'ensemble du lac a montré que le recrutement ne fournit habituellement que moins de 1 % de la quantité totale d'algues de chaque espèce par jour, ce qui indique que le recrutement ne serait pas une variable importante des populations d'algues dans le lac Mendota; il pourrait plutôt agir comme un processus d'inoculation assurant la croissance future des algues dans la colonne d'eau. On a observé un déphasage spatial entre les recrutements de *Cryptomonas erosa* et *Ceratium hirundinella*, ce qui laisse penser que les algues présentent à la surface des sédiments s'élèvent dans la colonne d'eau en fonction d'un signal lié à la profondeur. À l'exception d'une période de recrutement d'*Aphanizomenon*, le recrutement était nul sous la thermocline durant la période de stratification, ce qui indique qu'un facteur lié aux conditions de stratification a entravé le passage des algues de l'hypolimnion à la zone euphotique. La compréhension des processus de recrutement des algues dans la colonne d'eau à partir des sédiments est de toute première importance pour la gestion des proliférations d'algues dans les lacs très productifs.

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Algal migration within the water column is a phenomenon that has been discussed in the scientific literature for decades (Lund 1954) and has been described for various algal groups, including flagellated species (Cullen and Horrigan 1981), and cyanophytes (=cyanobacteria) (Reynolds 1972). Although the physiological structures responsible for migration, such as flagella and vacuoles, have been evaluated in detail (Reynolds 1972; Walsby and Klemer 1974; Kromkamp et al. 1988), surprisingly few studies have focused on the ecological consequences of the differences in migratory behaviour among different algal species. An obvious advantage of being motile is that such cells can remain in the euphotic zone, which is especially important in highly productive lakes where light attenuation is rapid (Konopka et al. 1978). Another advantage on a longer time scale is that cells or colonies may be recruited from the sediment surface when conditions become favourable in the water column and vice versa. One habitat may be used as an inoculum for rapid colonization of the other. The cyanophyte *Microcystis* is known to form dense vegetative mats on the sediment surface during fall and winter (Fallon and Brock 1981), and *Ceratium hirundinella*, for example, regularly forms cysts on the sediment surface (Heaney et al. 1983). The use of and the shift between different habitats, in this case the water column and the sediment surface, opens up intriguing aspects of algal ecology.

Frequent blooms of different cyanophytic species often cause severe problems in highly productive lakes. Blooms appear rapidly (within hours; Reynolds and Walsby 1975), implying that not only growth but also other factors such as migration to surface waters may be involved (Klemer 1976; Konopka et al. 1978; Klemer and Konopka 1989). Several recent studies have suggested that migration of blue-green algae may be a considerable factor behind internal nutrient loading in eutrophic lakes (Osgood 1988; Barbiero and Welch 1992; Pettersson et al. 1992; Barbiero 1993). Hence, knowledge of algal recruitment patterns and of the factors initiating recruitment from the sediment surface is necessary for understanding bloom formation in productive lakes and developing tools to manage such blooms. Moreover, migratory behaviour may have an impact on dynamics in the algal community and may partly explain rapid alterations in dominance and succession patterns (Hansson 1993).

Our aim in this study was to measure changes in environmental variables (nutrient and oxygen concentrations, temperature and light regimes, wind speed, and water column stability) simultaneously with recruitment and sinking patterns of selected algal species during a 1-yr cycle. Among the many species that performed regular migrations in the lake we investigated (Lake Mendota, Wisconsin, USA), four (*Aphanizomenon flos-aquae*, *Microcystis aeruginosa*, *Cryptomonas erosa*, and *Ceratium hirundinella*) were selected and studied in detail because (1) they showed migratory behaviour, (2) they were common in the lake, (3) they are commonly found in highly productive lakes, and (4) these four species represent different life strategies and morphologies (e.g., they differ in size, have gas vacuoles or flagella, and are vegetative or form cysts) that should lead to differences in migratory behaviour.

Material and Methods

Lake Mendota is a dimictic, hardwater lake situated in southcentral Wisconsin, USA, with a surface area of 39.1 km^2, a maximum depth of 25 m, and a mean depth of 12.4 m. The lake has a long history of limnological studies (Birge and Juday 1922; Fallon and Brock 1980; Brock 1985; Kitchell 1992).

In our study, recruitment and sinking patterns of four algal species were studied in detail, including *C. erosa*, *C. hirundinella*, *M. aeruginosa*, and *A. flos-aquae*. *Cryptomonas erosa* is small compared with the other three species (greatest axial linear dimension (GALD) 18 μm; biovolume 504 μm3) and probably highly vulnerable to grazing, suggesting that the abundance of grazers may affect recruitment patterns and abundance in the water column. *Ceratium hirundinella* is large (GALD 193 μm; biovolume 44 000 μm^3), with large spines protecting it from grazing, suggesting that grazer abundance may not affect this species. Furthermore, *Ceratium* has a complicated life cycle including cyst formation in the sediments (Heaney et al. 1983). The blue-green alga *M. aeruginosa* (GALD per colony 40 μm; biovolume 4074 μm^3) is a colonial form with a mucus cover, probably reducing its vulnerability to grazing. Finally, *A. flos-aquae* is a filamentous alga (GALD per filament 115 μm; biovolume 709 μm^3) able to form macroscopic bundles.

Traps to measure recruitment and sinking of algae were made of glass jars filled with filtered lake water (i.e., no algae present in the trap at the start) with a funnel through the lid. A 300-μm-mesh net covered the entrance of the funnel to reduce grazing by zooplankters on trapped algae. We sampled 16 times from January to December 1991, and each trapping period lasted 48 h. On each sampling occasion, two funnel traps (one with the funnel facing up, the other down, catching downward and upward migrations, respectively) were attached to an aluminium cube frame (Fig. 1), fixing the trap entrances at 0.75 m from the sediment surface. This depth was chosen to avoid disturbance of the soft sediment surface, including the algal community, which would have been the case if traps had been put direcly on the sediment surface. On each sampling occasion, three cube frames were set at 2, 7, and 23 m water depth, respectively. After 48 h, the traps were recovered and trapped algae were preserved in Lugol solution. Subsamples were filtered on 0.45-μm membrane filters (GN-6; Gelman) and permanently mounted on slides with HPMA (2-hydroxypropyl metacrylate; Crumpton 1987), prior to counting and identification.

A potential problem with this trapping method is the influence of horizontal, current-driven, transport of algal cells below the recruitment traps (0–0.75 m from the sediment surface). Since traps are covered with 300-μm-mesh net and the current velocity is lower inside the trap than outside, this artefact is unlikely to have affected the recorded recruitment rates. Moreover, when Hansson (1993) put traps inside plastic enclosures, where current velocities were at a minimum, recruitment rates were in the same order of magnitude as in the present study.

Samples for routine limnological analysis, including temperature profiles, dissolved oxygen, nutrients, transparency, and phytoplankton and zooplankton abundances, were collected at either weekly or biweekly intervals throughout the open-water season. During winter, samples were taken monthly through the ice at a deep hole in the middle of the lake. Samples were always collected during the same week as recruitment and sinking of algae were quantified. Temperature and oxygen measurements were done at 1-m intervals with a calibrated YSI thermistor and oxygen probe. Light profiles were measured with a Li-Cor quantum meter (micromoles quanta per square metre per second) and expressed as extinction coefficient (light attenuation per metre). For days when the extinction coefficients were not determined, Secchi depth measurements were transformed to extinction coefficients using the relationship

$$\text{Extinction coefficient} = 1.11/\text{Secchi depth} + 0.25 \quad (n = 30;\ r = 0.84).$$

Zooplankton were collected with vertical tows using a plankton net (diameter 0.70 m; mesh size 130 μm). The animals were counted and measured in the laboratory under a dissecting microscope. Phytoplankton were collected from an unfiltered integrated tube sample (inner diameter 21 mm) from 0 to 8 m (epilimnion) and preserved in glutaraldehyde. Phytoplankton were identified and counted from permanent slides (St. Amand; Phycotech Inc.) for all dates associated

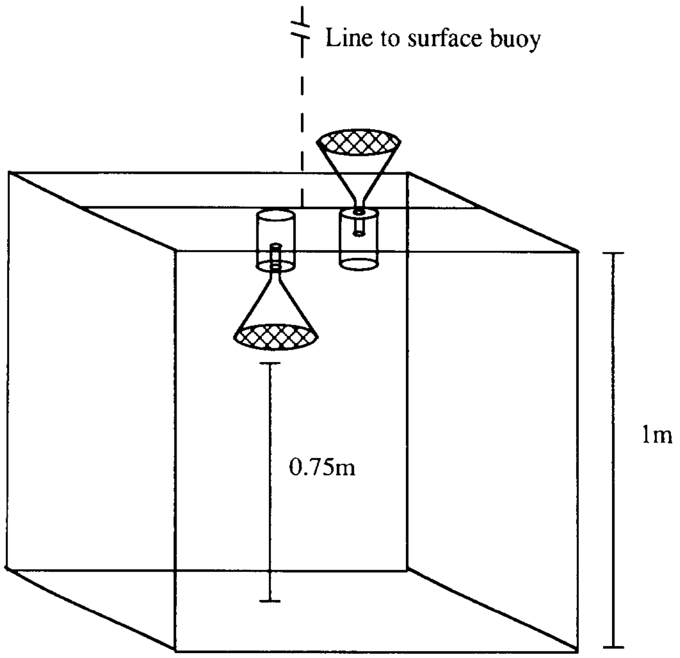

FIG. 1. Equipment used to trap algae migrating to and from the sediment surface, consisting of an aluminium cube frame (1 m^3), with one funnel-trap facing downwards trapping upward migration, and one facing upwards, trapping downward migration. The funnel gaps were covered with 300-μm-mesh nylon nets, excluding the major part of the zooplankton from the traps.

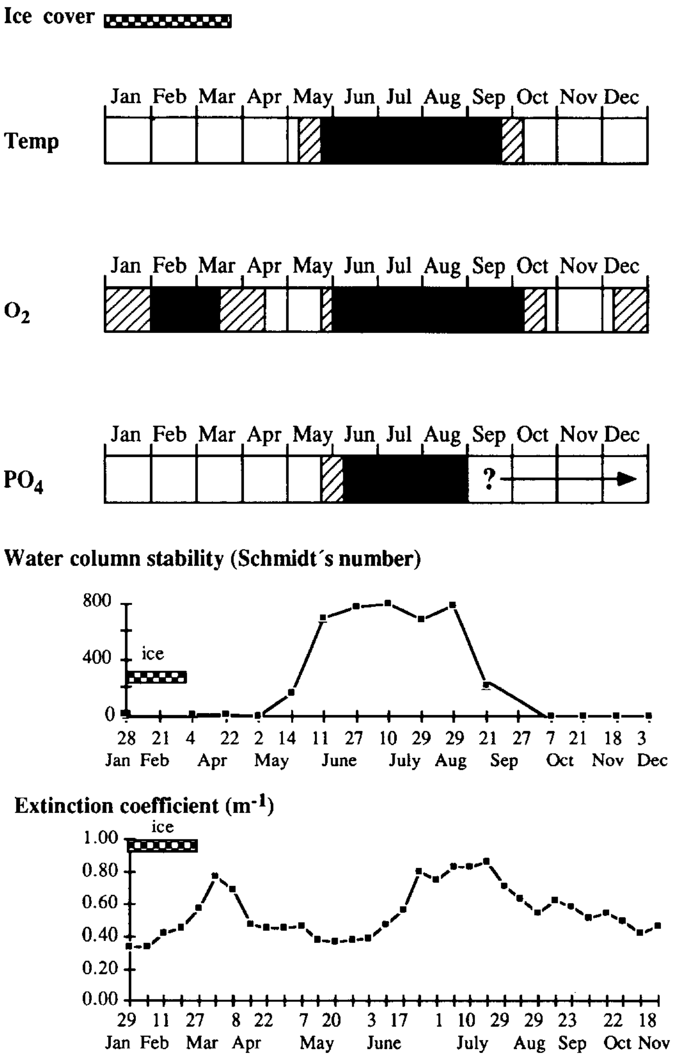

FIG. 2. Periods when Lake Mendota was stratified (black) with respect to temperature, dissolved oxygen, and dissolved phosphate phosphorus (PO_4-P) from 1 January to 31 December 1991. White areas indicate complete mixing of the variable (i.e., the concentration of the variable was equal throughout the water column). Hatched areas indicate transitional periods between mixing and stratification. Water column stability and light extinction coefficients as well as periods with ice cover are also given.

with trap data. Water for analysis of dissolved reactive and total phosphorus was taken from the integrated tube sample. Water column stability was calculated from the temperature profiles and expressed as Schmidt stability (Schmidt 1928). This number depends on density differences in the water column and is high when the temperature gradient between the epi- and hypolimnion is large and estimates the amount of work required to mix the lake to uniform density without adding or subtracting heat. Mixed conditions give a Schmidt stability number close to zero. Additional details on the routine sampling program are described in Kitchell (1992). Data on wind speed was collected daily at the Dane County regional airport, Madison, Wis., by the National Climatic Data Center.

Results

Lake Mendota was stratified with respect to temperature between 20 May and 23 September and completely mixed between 1 January and 7 May, and 7 October and 31 December (Fig. 2). The periods between 7 and 20 May, and 23 September and 7 October may be regarded as transitional periods between stratified and mixed conditions. The strength of the stratification is also expressed by the water column stability (Schmidt's number), which was close to zero (indicating mixed conditions) from the beginning of the year to 2 May (Fig. 2). Thereafter, values rapidly increased to a stable maximum that lasted until 21 September. In October, water column stability values again decreased to low values similar to those seen in the spring (Fig. 2). With respect to dissolved oxygen, Lake Mendota was stratified from the first sampling occasion (29 January) until ice-out (24 March). From ice-out until 20 May, the oxygen concentration was similar throughout the entire water column. Between 31 May and 7 October the oxygen concentration in bottom water (23 m) was usually zero, and always below 4 $mg \cdot L^{-1}$. A few weeks after the fall turnover in mid-October, oxygen-rich water had reached the sediment surface at 23 m (Fig. 2). A summer stratification in dissolved reactive phosphorus (PO_4-P) developed simultaneously with oxygen stratification (Fig. 2).

The light extinction coefficient varied between 0.34 and $0.88 \cdot m^{-1}$ during the year (Fig. 2), with one maximum (high light attenuation) in the beginning of April and one from late June to late July. Between these maxima, the extinction coefficient was usually below $0.5 \cdot m^{-1}$ (Fig. 2).

Zooplankton were divided into three groups: large (*Daphnia galeata* and *Daphnia pulicaria*; mean lengths 1.46 and 1.49 mm, respectively); small: calanoid and cyclopoid copepods (mean lengths 0.66 and 0.67 mm, respectively), and Rotifers (length <0.50 mm). The abundance of zooplankton

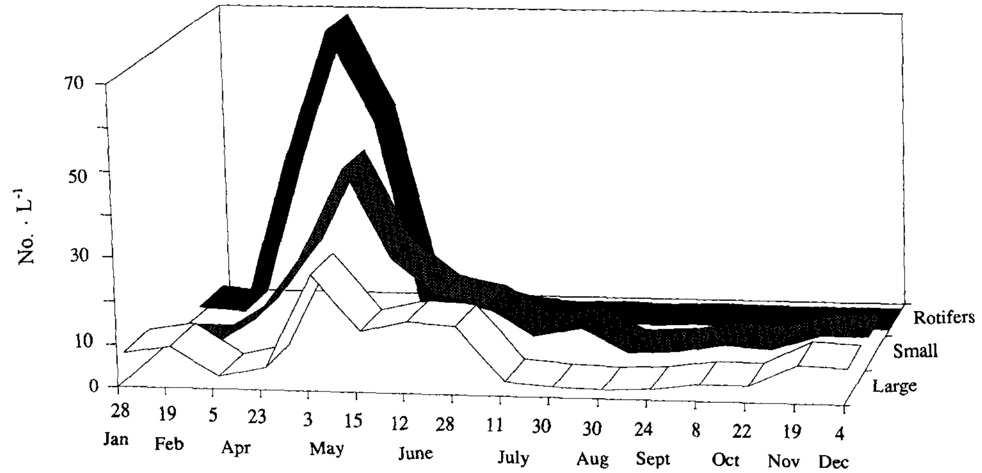

FIG. 3. Abundance of large (*D. galeata* and *D. pulicaria*) and small copepods and rotifers in Lake Mendota during 1991.

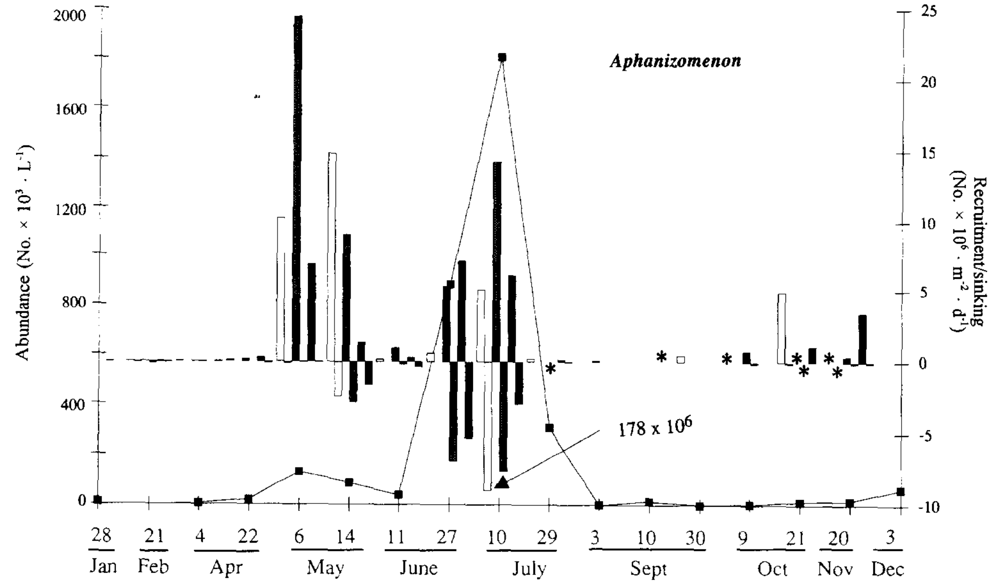

FIG. 4. Population dynamics of *A. flos-aquae* in Lake Mendota during 1991. Line shows abundance in the water column (integrated sample from 0 to 8 m). Positive bars show recruitment rate from the sediment surface and negative bars the sinking rate. White bars show recruitment and sinking at the shallow site (2 m), grey bars show recruitment and sinking at the intermediate site (7 m), and black bars show recruitment and sinking at the deep site (23 m). Note that the sinking rate on 10 July was extreme (-178×10^6 cells·m^{-2}·d^{-1}). Asterisks indicate missing values due to lost traps.

was generally low during January–March. In the beginning of April, the number of rotifers showed a peak (Fig. 3), followed by peaks in small zooplankton in mid-April and in large zooplankton in the beginning of May. The rotifer maximum declined within a month whereas the abundances of *Daphnia* and copepods slowly declined and reached minima in mid-July and September, respectively.

The abundance of *Aphanizomenon* showed one minor peak in abundance in May with about 180×10^3 cells·L^{-1} and a major bloom during June and July with abundances 10 times higher than in May (Fig. 4). In December, a slight increase in abundance occurred. These three humps in the abundance curve corresponded with the recorded maxima in recruitment (Fig. 4). Although the number of cells recruited differed among the stations at 2, 7, and 23 m, maxima and minima generally occurred simultaneously among stations. Sedimentation rate of *Aphanizomenon* filaments was low relative to the recruitment rate during the May and October–November recruitment maxima whereas sedimentation balanced recruitment during the June–July maximum, except for 10 July when the sedimentation rate was more than 30 times the recruitment rate (Fig. 4).

Cryptomonas erosa had its maximum abundance in the water column from early February to late April (Fig. 5). From May to mid-July, *C. erosa* was almost absent from the water column of Lake Mendota. From mid-July to mid-November the abundance was relatively stable at around 10×10^3 cells·L^{-1} (Fig. 5). Of the four selected species, only *C. erosa* showed any recruitment before the end of April (Fig. 5). Recruitment maxima generally corresponded

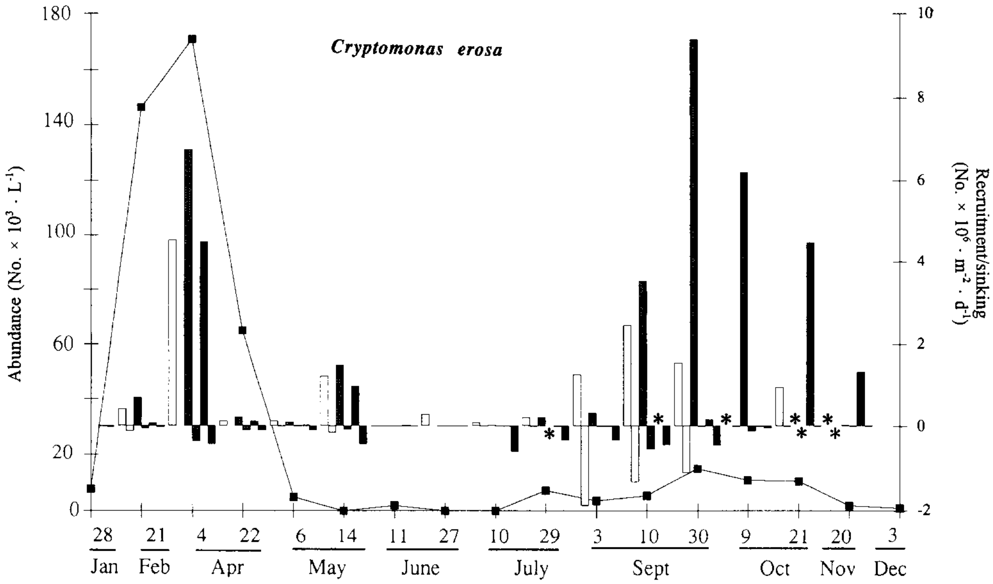

FIG. 5. Population dynamics of *C. erosa* in Lake Mendota during 1991. Line shows abundance in the water column (integrated sample from 0 to 8 m). Positive bars show recruitment rate from the sediment surface and negative bars the sinking rate. White bars show recruitment and sinking at the shallow site (2 m), grey bars show recruitment and sinking at the intermediate site (7 m), and black bars show recruitment and sinking at the deep site (23 m). Asterisks indicate missing values due to lost traps.

to maxima in abundance in the water. During summer and autumn, recruitment maxima did not occur simultaneously at the three stations. Between 3 September and 21 October (maximum 10 September; Fig. 5), *Cryptomonas* was mainly recruited from shallow areas, between 10 September and 7 October from intermediate depths (7 m), and from late October the importance of recruitment from the deep sediments increased (Fig. 5). This dephasing of recruitment patterns did not occur during spring, when patterns were similar and simultaneous among stations (Fig. 5). Sedimentation of *Cryptomonas* was usually moderate compared with recruitment, except at the shallow site during August and September (Fig. 5).

No *Microcystis* were recorded in the water before 27 June when a sudden outbreak occurred with 7 × 10^6 cells·L^{-1}, followed by a crash 10 d later (Fig. 6). A minor recovery was recorded in late July, whereafter the abundance of *Microcystis* oscillated between 0 and 0.2 × 10^6 cells·L^{-1} (Fig. 6). Recruitment began in the beginning of June, about 2 wk before the maximum abundance in the water. The major part of the recruitment occurred at the shallow station whereas only small amounts of *Microcystis* were recruited from the intermediate and deep stations (Fig. 6). Except for 27 June, the sinking rate was equal to or higher than the recruitment rate. The maxima in sinking rate in mid-July and end of August corresponded well to the major crashes of the pelagic *Microcystis* population (Fig. 6).

Ceratium hirundinella was either absent or occurred in very low numbers before July and showed maximum abundance in the water column in late August (Fig. 7). By mid-September, the abundance was down at normal and low values (less than 2000 cells·L^{-1}), and after late October, no *Ceratium* were recorded in the lake. Recruitment from the sediment was first recorded on 27 June, 2 wk before the species was recorded in the water column (Fig. 7). Similar to *Cryptomonas*, the recruitment patterns for the different stations were dephased, with recruitment mainly at the shallow station from 27 June to 21 September, followed by the intermediate station from 21 September to 7 October. Finally, one short maximum in recruitment was recorded at the deep station in late October. Maximum sinking rate was recorded during the decline of *Ceratium* in the water during September (Fig. 7).

There was no correlation at the 5% level between wind speed and recruitment if all sampling dates were included ($r <$ 0.39; $p >$ 0.27). This was also the case when excluding sampling occasions when no cells of the investigated species were present in the water column from the analysis, except for *Microcystis* at the intermediate site (r = 0.70; t = 2.57; $p <$ 0.04).

The recruitment of the four selected species was quantified for the shallow (0–4.5 m), intermediate (4.5–16 m), and deep (16–23 m) intervals, constituting 6, 23, and 71% of the total lake volume and 29, 26, and 45% of the lake area, respectively. On a whole-lake basis, recruitment rarely added more than 1% to the standing stock per day, but in the shallow interval (high area to volume ratio), recruitment occasionally accounted for 6% of the standing stock per day (Table 1).

Discussion

The increase in light extinction coefficient (higher light attenuation) in Lake Mendota during March and April 1991 corresponded to high abundances in *Cryptomonas* and diatoms whereas the high extinction coefficients during June and July corresponded to population maxima in *Microcystis* and *Aphanizomenon*.

The extremely high sedimentation rate of *Aphanizomenon* at the shallow site around 10 July corresponded with the crash of the population between 10 and 29 July. The reason for this rapid late summer decline is unknown, but constitutes

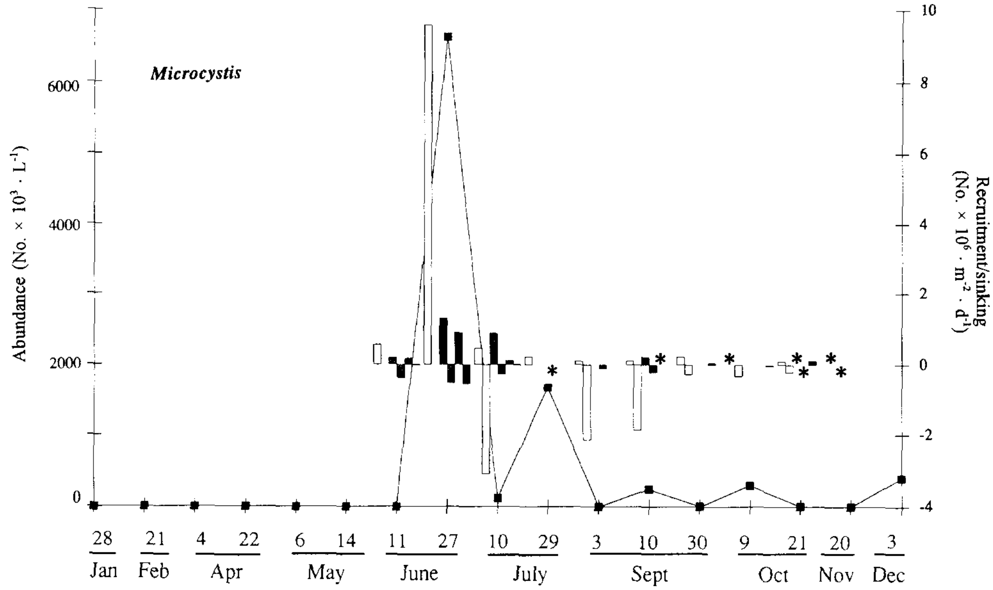

FIG. 6. Population dynamics of *M. aeruginosa* in Lake Mendota during 1991. Line shows abundance in the water column (integrated sample from 0 to 8 m). Positive bars show recruitment rate from the sediment surface and negative bars the sinking rate. White bars show recruitment and sinking at the shallow site (2 m), grey bars show recruitment and sinking at the intermediate site (7 m), and black bars show recruitment and sinking at the deep site (23 m). Asterisks indicate missing values due to lost traps.

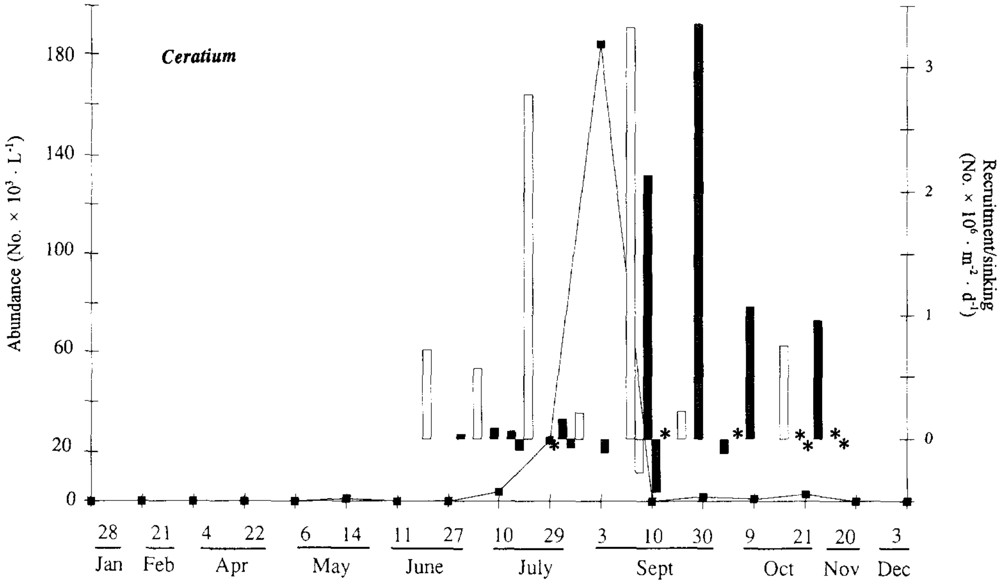

FIG. 7. Population dynamics of *C. hirundinella* in Lake Mendota during 1991. Line shows abundance in the water column (integrated sample from 0 to 8 m). Positive bars show recruitment rate from the sediment surface and negative bars the sinking rate. White bars show recruitment and sinking at the shallow site (2 m), grey bars show recruitment and sinking at the intermediate site (7 m), and black bars show recruitment and sinking at the deep site (23 m). Asterisks indicate missing values due to lost traps.

a regular phenomenon in Lake Mendota (Fallon and Brock 1980). Sinking rate was low during the first recruitment maximum of *Aphanizomenon* in May, but equal to the recruitment rate at the intermediate and deep sites during recruitment maxima in June and July (Fig. 4). One explanation is that this later recruitment was successful and that the high sinking rate was caused by a pelagic population that was beginning to decline. Another possibility is that the recruitment in June–July was unsuccessful (recruitment balanced sinking, i.e., no net recruitment; Fig. 4) because stratification (that was completely established 31 May) physically or chemically affected the migration to the euphotic zone. If so, recruitment to the euphotic zone may have been successful only during May, and the population maximum in the water during June and July originated mainly from the May recruitment period.

TABLE 1. Number of cells/colonies recruited (*R*) per day from the sediment surface of Lake Mendota during selected days with high recruitment rates of *A. flos-aquae*, *C. erosa*, *M. aeruginosa*, and *C. hirundinella*. Recruitment was recorded at 2, 7, and 23 m water depth, representing the depth intervals 0–4.5 m (29% of the total area), 4.5–16 m (26%), and 16–23 m (45%). Whole-lake recruitment constitutes the sum of the recruitment in each interval. Total number of cells/colonies in the water on the selected sampling days is also given for each interval, assuming that an integrated sample from 0 to 8 m water depth is an estimate of the cell number throughout the water column. Recruitment is also calculated as the portion ($\%\cdot 24\ h^{-1}$) of the total cell number in the water. Due to a lost trap the recruitment rate of *Ceratium*, 30 July is estimated as the mean of the recruitment rates at the shallow and deep sites.

		Interval (m):	0–4.5	4.5–16	16–23	0–23
		Area ($\times 10^6\ m^2$):	11.2	10.5	17.5	39.1
		Volume ($\times 10^6\ m^3$):	27	110	349	486
	Day		Shallow	Intermediate	Deep	Whole lake
Aphanizomenon	6 May	$R(\times 10^{14}\cdot d^{-1})$	1.2	2.5	1.2	4.8
		No. ($\times 10^{14}$)	35	143	454	632
		%	3.3	1.7	0.3	0.8
	12 July	$R(\times 10^{14}\cdot d^{-1})$	0.6	1.4	1.1	3.1
		No. ($\times 10^{14}$)	5	20	63	88
		%	0.1	<0.1	<0.1	<0.1
Cryptomonas	6 April	$R(\times 10^{14}\cdot d^{-1})$	0.5	0.6	0.8	2.0
		No. ($\times 10^{14}$)	45	187	593	826
		%	1.2	0.4	0.1	0.2
	27 Sept.	$R(\times 10^{14}\cdot d^{-1})$	0.2	1.0	0.03	1.2
		No. ($\times 10^{14}$)	3.9	16	52	68
		%	4.6	6.0	<0.1	1.8
Microcystis	27 June	$R(\times 10^{14}\cdot d^{-1})$	1.1	0.1	0.2	1.4
		No. ($\times 10^{14}$)	1780	7260	23030	32070
		%	<0.1	<0.1	<0.1	<0.1
	12 July	$R(\times 10^{14}\cdot d^{-1})$	0.05	0.09	0.02	0.16
		No. ($\times 10^{14}$)	30	121	384	535
		%	0.2	0.1	<0.1	<0.1
Ceratium	12 July	$R(\times 10^{14}\cdot d^{-1})$	0.06	0.01	0.01	0.08
		No. ($\times 10^{14}$)	1	4	13	18
		%	6.1	0.2	<0.1	0.4
	30 July	$R(\times 10^{14}\cdot d^{-1})$	0.3	0.2	0.03	0.50
		No. ($\times 10^{14}$)	7	27	85	119
		%	4.9	0.6	<0.1	0.4

Interpolation of the recruitment data from the three depths may give a rough estimate of the importance of algal recruitment for the pelagic populations of the investigated algae. Despite high recruitment rates in June and July, less than 0.1% of the standing stock was added through recruitment during this period (Table 1), further indicating that recruitment in May constituted the inoculum for the bloom in June and July (Fig. 4). A parallel case is the slight increase in *Aphanizomenon* filaments in the water column following a few weeks after the modest recruitment period in October and November when the lake was completely mixed, again suggesting that recruitment of *Aphanizomenon* in Lake Mendota operates mainly as inoculum for future growth.

The use of any trapping device for quantifying biomass or transport of organisms usually introduces artefacts. The major concern with respect to the funnel traps used in the present study is the possibility that algae caught in the traps are not recruits from the sediment, but simply planktonic cells passively transported by currents. There are, however, several observations suggesting that this is unlikely. (1) Water currents are higher at high wind speed, suggesting that recruitment generally should be higher at high wind speed. With one exception (*Microcystis* at the intermediate site, $r = 0.70$; $p < 0.04$; $n = 9$), there was never any relationship between wind speed and recruitment for any of the investigated species. (2) Funnel traps set inside plastic enclosures (i.e., no influence of currents) gave recruitment and sinking rates in the same order of magnitude as in the present study (see Hansson 1993). (3) Some algal groups, e.g., diatoms, were often common in the water column, but rarely found in the recruitment traps (although present in sinking traps during population crashes). These observations do not show that currents or resuspension are unimportant vectors for the vertical transport of algae, but indicate that they may not have been major artefacts in the quantification of algal recruitment in Lake Mendota. Instead, the temporal and spatial differences in recruitment among species, in combination with the fact that only some of the species present in the lake were found in the traps, suggest that recruitment is mainly an active process.

Ceratium hirundinella is able to form resting cysts on the sediment surface (Heaney et al. 1983). In a eutrophic pond, Heaney et al. (1983) recorded an 18-fold increase in vegetative *Ceratium* within a week simultaneously with the presence of empty cysts on the sediment surface, indicating that encystment directly affected cell numbers in the water. In their study pond, encystment, and the following increase in cell number, occurred when the temperature at 1 m depth increased from 3 to 5°C. In Lake Mendota, neither recruitment nor an increase in cell number in the water occurred before the surface water temperature had reached 24°C, suggesting that temperature is not the general triggering factor for the recruitment of *Ceratium*.

Microcystis is known to form dense overwintering mats on the sediment surface during fall and winter, which constitute the inoculum for the coming year's pelagic population in many lakes (Sirenko 1987), including Lake Mendota (Fallon and Brock 1981). The *Microcystis* colonies caught in our funnel traps likely originated from such vegetative mats. In late June, *Microcystis* showed the only recruitment period of significance during 1991 (Fig. 6). The sudden crash of the pelagic *Microcystis* population between 27 June and 10 July occurred simultaneously with an increase in the abundance of *Aphanizomenon*. In a Swedish eutrophic lake, recruitment of *Aphanizomenon* occurred before and after, but not during, the recruitment maximum of *Microcystis* (personal observations). Such temporal adjustments in abundance and recruitment patterns may be an indication of competitive interactions between different cyanophytes.

The increase of the anoxic zone during stratification has been suggested to initialize the recruitment of cyanophytes (Trimbee and Prepas 1988). In Lake Mendota, no recruitment of *Microcystis* occurred before the onset of stratification (Fig. 2 and 6), which supports this hypothesis. However, the main recruitment occurred at the shallow site, far from anoxic water. The recruitment of *Aphanizomenon* had already begun at the beginning of May, when the concentration of dissolved oxygen at the sediment surface (23 m) was above 10 $\mathrm{mg{\cdot}L^{-1}}$. Furthermore, in March the oxygen concentration was close to zero (0.4 $\mathrm{mg{\cdot}L^{-1}}$), but no recruitment of either *Aphanizomenon* or *Microcystis* occurred. Hence, the suggestion that anoxic conditions per se are the initializing factor for cyanophyte recruitment from sediment to water is not corroborated by our results.

The lake stratified between 7 and 20 May and was completely mixed again by 7 October. The thermocline fluctuated between 6 and 12 m water depth, indicating that our intermediate station at 7 m depth sometimes was above and sometimes below the thermocline. Only *Aphanizomenon* showed any significant recruitment at the deep or intermediate sites during stratification, which may have been an unsuccessful colonization because the sinking rates were as high as recruitment rates. *Ceratium* and *Microcystis* showed high recruitment rates at the shallow site (above the thermocline), but low rates at the intermediate and deep sites during stratification. After about 6 September, when the thermocline was below 10 m, the recruitment of *Ceratium* and *Cryptomonas* from the intermediate site increased. When the lake was again mixed after 7 October, recruitment of *Aphanizomenon*, *Cryptomonas*, as well as *Ceratium* was initiated at the deep site (Fig. 4, 5, and 7). Hence, it may be suggested that a variable associated with stratified conditions reduced the upward migration. This factor may either be a chemical substance associated with stratified conditions or the thermocline itself may function as a physical "lid" for recruitment to the euphotic zone. The latter notion is in contrast with the observed diurnal migrations of *Cryptomonas marssonii* through temperature gradients of 10°C in a small Finnish lake (Salonen et al. 1984), as well as with studies on *Oscillatoria* (Klemer 1976; Konopka et al. 1993). However, with the exception of *Aphanizomenon*, none of the species investigated in Lake Mendota even attempted to colonize the water column from below the thermocline during stratification, but instead seemed to stay on the sediment surface until stratification was broken. A possibility is that algae have receptors detecting, for example, oxygen concentrations, indicating a thermocline impossible to penetrate. The existence of such receptors may explain why most algae avoided migration to the planktonic habitat during stratification. The onset of recruitment when stratification was broken may be a passive phenomenon induced by mixing currents. However, maximum recruitment at the intermediate and deep sites should then occur as a short pulse during the breakup of stratification, which was not the case. Another possibility is that habitat shift from sediment to water is actively regulated by the algae, e.g., by means of chemoreceptors monitoring environmental variables. As stratified conditions seem to be associated with low rates of vertical migration, possible variables may be low oxygen and high phosphate concentrations. In line with this notion, the recruitment rate of *C. erosa* was positively correlated with the oxygen concentration at the sediment surface at the deep site ($r = 0.57$; $t = 2.302$; $p < 0.042$). Moreover, experimental field studies have shown that phosphorus additions reduce the buoyancy of *Oscillatoria* filaments (Konopka et al. 1978).

Although the thermocline may affect migration from hypolimnetic sediments, algae recruited from epilimnetic sediments are able to colonize the whole water column via horizontal currents. This is particularly illustrated by *Ceratium* that showed recruitment almost exclusively from shallow areas during summer followed by a peak in abundance during late July and early August.

The recorded sedimentation of *Cryptomonas* was usually low, indicating that other factors were important for the decline in cell numbers, such as grazing or decomposition before reaching the sediment surface. The increase in grazer abundance during April (Fig. 3) coincided with the rapid decline in *Cryptomonas* abundance, suggesting that grazing may have caused the decrease in cell numbers of *Cryptomonas* during this period. Including *Daphnia* abundance and the concentration of oxygen as independent variables in a multiple regression explained 48% of the variation in recruitment of *Cryptomonas* ($F = 4.56$; $p < 0.039$). An even higher explanatory value ($r^2 = 0.54$; $F = 5.95$; $p < 0.020$) is revealed if *Daphnia* is substituted with the abundance of small zooplankters (copepods). This negative relationship between grazer abundance and recruitment indicates that *Cryptomonas* avoided shifting habitat from sediment to water during high grazer abundances (Hansson 1993). However, we cannot rule out the alternative explanation that grazing between the sediment surface and the trap (a distance of 0.75 m) caused a reduction in the observed recruitment of *Cryptomonas*. There was a positive correlation between grazer (*Daphnia*) abundance and recruitment of *Aphanizomenon* ($r = 0.57$; $t = 2.470$; $p < 0.028$), an observation in line with the suggestion that *Daphnia* may positively affect bloom formation of *Aphanizomenon* (Shapiro 1980). There was no relationship between grazer abundance or oxygen concentration and recruitment rates of *Microcystis* or *Ceratium*.

The major part of the recruitment periods of the four investigated species was successful (i.e., mirrored in population increases), suggesting that algae are able to temporally adjust their recruitment toward favourable periods. The relationships between recruitment rates and such diverse factors as oxygen concentration, stratification, and grazer abundance indicate that habitat shift from sediment to water is not regulated by a single factor. It is also obvious that recruitment of different species is governed by different factors. The understanding of these processes is an important tool in predicting and managing algal blooms.

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