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Algal recruitment from lake sediments in relation to grazing, sinking, and dominance patterns in the phytoplankton community

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Abstract

I assessed the importance of algal recruitment from the sediment surface to the water relative to other population variables such as grazing, growth, and sinking. In four low-productivity lake basins, which were stratified throughout the study, 32% of the identified algal taxonomic groups exhibited recruitment, whereas the other 68% spent their entire lives in the pelagic habitat. For most species, recruitment from sediment to water occurred primarily at shallow depths (<8 m) and often increased total phytoplankton abundance by 10–50% per day. Grazing was the main loss process, reducing algal abundance by usually between 10 and 50% per day; sinking rates were usually one order of magnitude lower. Recruitment was highest in shallow water (<10 m deep); when maximum recruitment occurred below the thermocline, no relation was found between recruitment and abundance in the euphotic zone, suggesting that the thermocline functioned as a physical barrier for algal vertical migration. In three of the lakebasins, recruiting algae dominated more often than expected by chance ($P < 0.05$), suggesting a competitive advantage with the adaptation to perform recruitment. Successful recruitment may have a considerable impact on dominance patterns in the phytoplankton community.

Algae with morphological adaptations for migration (flagella, gas vacuoles, or ballast molecules) are known to perform short-term migrations in the water column (e.g. Walsby and Klemer 1974; Ilmarvita 1975; Konopka 1982). In many lakes, flagellated algae frequently exhibit a population maximum during spring and are later replaced by *K*-strategists (e.g. cyanobacteria with gas vacuoles) during summer (Harris 1986; Sommer 1989). This temporal succession among phytoplankton has been attributed to variations in growth, grazing, and sinking. However, another variable that may affect succession patterns in phytoplankton communities is the recruitment of algae from the sediment surface to the water column. The sediment surface and the water column offer completely different environmental conditions with respect to grazing pressure and light, oxygen, and nutrient availabilities. Thus, in a temporally changing environment, there may be adaptive gains in migrating between these two habitats. Recruitment from the sediment has been observed among various algal groups, including cyanobacteria (Barbiero and Welch 1992; Pettersson et al. 1993; Hansson et al. 1994), *Gymnodinium* sp., *Synura* sp., *Cryptomonas* sp. (Hansson 1993), and *Ceratium* (Heaney

et al. 1983), although the ecological causes and consequences are not well understood.

Algae adapted to undertake directional migrations may be recruited from the sediment surface to the water column, where they grow and are subject to grazing by zooplankters and in this way affect both phytoplankton community composition and species succession patterns. Eventually, the recruited algae return to the sediment surface as dead cells, as cells initiating another cycle, or as resting stages such as cysts or spores (Fryxell 1983). Furthermore, there may be adaptive gains in having the ability to migrate from suboptimal conditions, thereby increasing the reproductive period. Finally, the benthic population may function as a "seed bank" that provides insurance against catastrophic events in the planktonic part of the population (Barbiero and Welch 1992).

Complex life cycles, in which the organism spends different stages of its life in spatially separated habitats, are well-studied phenomena in animal ecology, especially in insects and marine invertebrates, where the theoretical basis is well developed (Roughgarden et al. 1988). However, effects of complex life cycles among algae, such as recruitment from benthic to pelagic habitats, are rarely studied, although they are frequently referred to as possible phenomena (Lund 1954; Reynolds and Rogers 1976).

In this paper, I argue that studies of the links between benthic and pelagic habitats may improve the understanding of unexplained variation in population dynamics and succession patterns in algal communities. My specific aims have been to determine those algal species for which recruitment from lake sediments may be important relative to other population variables, such as grazing, sinking, and growth. In particular, I have tried to assess whether species with significant recruitment from the sediment are more successful than other species.

Acknowledgments

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Materials and methods

Site description—Peter, Paul and, Long Lakes are unproductive, dimictic forest lakes with maximum depths of 17, 11, and 14 m, respectively. Surface areas range between 10,000 and 35,000 m², and total volumes between 60,000 and 246,000 m³ (Table 1). The lakes lie within 1 km of each other on University of Notre Dame properties (northern Michigan; 46°13'N; 89°32'W). Peter and Paul lakes have been involved in whole-lake experiments for ~40 yr (Hasler 1964; Carpenter et al. 1987). Long Lake was not included in any experimental program before 1991, at which time the lake was divided into two basins as a first step in a fish-nutrient manipulation program (Carpenter et al. in prep.). The western basin was left as a control; the eastern basin, as well as Peter Lake, were treated with rotenone in early spring 1991. Hence, at the beginning of this study (15 June 1991) there were two lakebasins lacking fish predation on zooplankters [Peter and east Long Lake (ELL)] and two control lakes [Paul and west Long Lake (WLL)]. In most other aspects, including lake morphometry and nutrient status, the basins are similar. The study was performed in June–August 1991, when all the lakes were stratified.

Organism abundances—To assess the abundance of different algal species in the water column, I used a Plexiglas pipe (75-mm diam; 2 m long) to take a water sample (4 liters) in the middle of the lake on each sampling occasion. All algal samples were concentrated through a 10- μ m net and poured into 20 ml scintillation vials. Samples were stored at +8°C and later filtered through membrane filters (Gelman) and mounted on glass slides with HPMA (2-hydroxypropyl methacrylate; Crumpton 1987). Algal cells/colonies were counted at 200 \times magnification.

Zooplankton were sampled by means of two net hauls (mesh size, 80 μ m) from bottom to surface. The two samples were pooled and preserved in formaldehyde (2% final concn). I measured the length of as many animals as required to ensure that the standard error was <10% of the mean length of each species. Abundance was determined from length-weight regressions (Downing and Rigler 1984).

Grazing experiment—The grazing rate of herbivorous zooplankters on algae was determined in WLL and Paul Lake in August 1991. Zooplankton were sampled with a 150- μ m net because smaller mesh sizes also concentrated algae. Zooplankton were left overnight at constant temperature and then rinsed to reduce nutrient addition to the experiment. Lake water was filtered through a 80- μ m net and poured into six plastic containers (20 liters). Zooplankters were then added to each container in concentrations 0.5–10 \times the ambient concentration. The plastic containers were attached to a floating frame at 1-m depth in WLL and Paul Lake to eliminate the risks of photo-inhibition and too high fluctuations in temperature. After 74 h, 4 liters of water from each container were filtered through a 10- μ m net and thereafter treated in the same

Table 1. Ranges in the position of the lower part of the thermocline and depth of the euphotic zone (1% of surface light values) for Peter, east Long (ELL), Paul, and west Long (WLL) Lakes from June to August 1991. Volume and surface area of each lake are also given.

	Peter	ELL	Paul	WLL
Thermocline (m)	5.5–6.5	4.5–5.0	4.5–5.0	4.5–5.0
Euphotic zone (m)	7.0–7.6	2.5–3.1	5.4–5.8	3.0–3.5
Area ($\times 10^3$ m ²)	28	24	10	35
Volume ($\times 10^3$ m ³)	230	168	60	246

way as the other phytoplankton samples. The net growth rate (r) of each species along the grazer gradient was calculated as

$$r = \ln(N_t/N_0)/\Delta t.$$

N_0 and N_t are initial and final cell abundances, and Δt is the duration of the experiment (Lehman and Sandgren 1985). r was then plotted against zooplankton abundance in each container (compensated for deaths during the incubation period), and the slope of this regression provided an estimate of the filtering rate on each algal species (volume filtered per mg zooplankton per day; Lehman and Sandgren 1985).

The species-specific grazing rate on each species in each lake (number of algal cells grazed per day and unit volume) was calculated by multiplying zooplankton abundance, filtering rate, and algal cell number on each sampling occasion. The water temperature varied little during the investigation period (range, 5.6°C), and the zooplankton community composition showed only moderate changes. Therefore, grazing rates were corrected only for fluctuations in zooplankton abundance during the study period. No experiments were performed in ELL and Peter Lake because of extremely low zooplankton abundances, which probably resulted from the rotenone addition. Grazing rates per zooplankter obtained from the experiments in WLL and Paul lake were used to calculate grazing pressures in ELL and Peter Lake, respectively.

Traps to catch migrating algae were made of 120-ml glass jars filled with GF/C- (Whatman) filtered lake water (i.e. no algae present in the trap at the start) with a funnel through the lids (funnel diam, 0.14 m). At each location, two traps were attached 0.5 m above the sediment surface for 48 h. One of the traps collected sinking algae (funnel facing up); the other, algae recruited from the sediment (funnel facing down). Because the sampling periods always included two day and two night periods and algae migrating up as well as down were sampled, the effect of short-term (diel) migration was regarded as having a negligible impact on the recorded net recruitment.

Each trap funnel was covered with a 300- μ m nylon net. Although the net kept large, efficient grazers out of the trap, small copepods and rotifers could enter, suggesting that zooplankton grazing on the trapped algae was reduced but not absent. Moreover, the net reduced the effective surface area of the traps, another factor suggesting that the results are conservative estimates of the actual

Table 2. Ranges (No. $\times 10^6 \text{ m}^{-2} \text{ d}^{-1}$) and coefficients of variation (C.V.%) in recorded recruitment and sinking rates for *Gymnodinium* and *Cryptomonas* cells at similar depth and along a depth gradient from 2 to 14 m in WLL. The table shows that ranges, as well as coefficients of variation, are higher along a depth gradient than within the same depth.

	Same depth		Depth gradient	
	Range	C.V.	Range	C.V.
<i>Gymnodinium</i>				
Up	1.03–1.22	10	0.13–2.70	118
Down	0–0.04	87	0–0.15	167
<i>Cryptomonas</i>				
Up	8.97–13.4	20	0.26–13.4	147
Down	6.46–8.56	14	0.06–6.46	149

vertical migration. A major part of the dead, sinking cells is decomposed through the water column and becomes unidentifiable in microscopic counts (Fallon and Brock 1980). Based on this, I corrected all sinking rates with a factor of 50% of recorded values. Moreover, funnel traps that catch sinking particles have been shown to underestimate the actual sinking rate by $\sim 10\%$ (Blomqvist and Håkansson 1981), which I have also corrected for.

A rope with floats, constituting a transect from shore to shore (across the maximum depth), was stretched across each lake. Lines with traps were attached to the transect at fixed positions. Because the water level fluctuated < 0.1 m between samplings, no correction for water level variation was necessary. In WLL, traps were attached at water depths of 2.3, 5, 8, 11, and 14 m, and in ELL at 1.7, 4, 8, 11, and 14 m. In Peter Lake the sampling depths were 2, 3.7, 7, 10, 13, and 17 m, and in Paul Lake, 1.2, 3, 6, 8, and 10 m.

Quantification of recruitment—A bathymetric map was divided into depth intervals of 3 m. The surface area of each interval was determined by weighing the cutouts of depth strata. Recruitment of algal cells was assumed constant within each interval. Recruitment rate per square meter of each algal taxon was multiplied by the surface area of each interval, producing an estimate of recruitment within each depth interval. Recruitment of each algal taxon from all intervals was then summarized. The procedure was repeated for all six sampling occasions. In this way, total recruitment was weighed for different surface areas of each depth interval. Similarly, the abundance of each species was multiplied by lake volume and used as a rough estimate of the total cell number of each algal species in the water column.

Methodological tests of the traps—Different types of funnel traps have been used to trap migrating algae (Reynolds 1975; Trimbee and Harris 1984), but no thorough methodological tests have been performed. Any kind of trapping provides only estimates of real fluxes and adds errors and artifacts. Therefore, possible sources of error must be identified and methodological tests must be per-

formed. With respect to recruitment traps, the following sources of error can be identified: algae are forced into the trap during its setting, the net covering the funnel entrance may prevent large algae from entering the trap; patchiness in recruitment may result in variance within the same depth as high as the variance along a depth gradient, reducing the relevance of depth-related studies; algal cells may be passively transported horizontally by currents near the sediment surface (i.e. the cells caught in the traps may not have originated from the sediment surface). Such transport may be an important artifact when recruitment is quantified. I performed tests for the first three possible errors in WLL in 1991; the test for the fourth possible error was conducted in Finjasjön, south Sweden.

Effect of trap setting: Lowering a trap to the desired depth may force algal cells into the trap, thereby overestimating algal migration. To quantify this error, I lowered a trap containing filtered water to 5-m depth, let it hang there for 15 s and then retrieved it. The sample was then treated in the same way as the other samples (see above). Compared to the simultaneous routine trapping at 5-m depth, the setting procedure added 0.1% of *Synura*, 1.2% of *Cryptomonas*, and 0.1% of *Gymnodinium*. Hence, trap setting can be viewed as a negligible source of error, and no corrections of routine trap samples were made.

Effect of nets covering the funnel entrance: Parallel to some of the netted recruitment traps, I ran traps without nets to ensure that all size classes of algae were able to enter the trap. No algal species occurred in higher numbers in traps without than with nets, indicating that nets did not exclude any algae in this study. Instead, in traps without nets, the mean total cell number was only 34% of what was found in traps with nets (paired *t*-test; $t = 5.09$; $P < 0.002$). The ratios between cell numbers in traps without and with nets were well correlated with zooplankton abundance ($r = -0.91$), suggesting that grazing within the trap was the process behind lower cell number in traps without nets. Traps without nets were excluded from further analysis.

Effect of patchiness at similar depth: The test was performed simultaneously with a routine depth-gradient sampling (17 August 1991), which was expanded with a total of three replicate traps (2 m apart) at 5-m depth. Ranges in the amount of cells collected were narrower in traps attached at the same depth than in traps along the depth gradient (2–14-m water depth; Table 2). Except for *Gymnodinium* in traps catching downward migration, where the cell number was extremely low, coefficients of variation (C.V.) were $< 20\%$ at similar depth and always $> 100\%$ along the depth gradient (Table 2). The test indicates that variance with depth is higher than at similar depth, suggesting a likely effect of depth on recruitment rates.

Passive, horizontal transport into the traps: Because water movements in a lake can be substantial, the possible impact of algae transported by currents into the traps may be a severe objection against this method. To test for possible passive transport, I attached two recruitment traps to metal frames 0.50 m above the sediment surface.

The sides of one of the frames were covered with Plexiglas to cut the trap off from any horizontal addition of algal cells (frame dimensions, 0.75 × 0.75 × 0.75 m; Hansson et al. 1994). Both frames were set at 5-m depth and left for 48 h. The study was repeated five times from 4 May to 4 July 1994. I performed this test in the large and wind-exposed Finjasjön, where wind- and current-induced transport of algae was assumed to be more pronounced than in the small kettle lakes of the northern U.S. Samples were treated in the same way as the routine samples, and a pairwise *t*-test was used to test for differences in recruitment between traps with and without Plexiglas walls. There was no difference between traps for any algal species ($P > 0.06$; $n = 5$), suggesting that current-driven algal transport was not an important artifact for recruitment traps. Additional tests on this possible artifact have been performed, including comparison of traps put inside and outside enclosures (Hansson 1995) and correlations between recruitment rate and wind speed (Hansson et al. 1994). The tests strengthen the suggestion that algae caught in the traps originate from the sediment surface.

In summary, the tests indicate that the trap setting is a negligible source of error and that the net preventing grazing zooplankters from entering the trap is crucial for proper estimation of algal migration, suggesting that earlier studies performed without nets have considerably underestimated algal vertical migration. Furthermore, the algae caught in the traps was not planktonic algae passively transported by currents. Hence, these methodological tests suggest that funnel traps are acceptable for estimating recruitment rate of algae from the sediment to the water.

Results

Six genera, *Gymnodinium*, *Synura*, *Cryptomonas*, *Dinobryon*, *Merismopedia*, and *Peridinium (pusillum)*, were selected and studied in detail. The selected genera usually dominated the phytoplankton community in all four lake-basins, although a few other species occasionally showed high abundances. In WLL and Peter Lake, *Dictyosphaerium* sp. occurred in high numbers in mid-June, and in ELL, *Peridinium wisconsinense* became one of the dominating species in late July. *Sphaerocystis* sp. occasionally showed high numbers in WLL and Paul Lake. Similarly, an unidentified colonial species was among the dominating species in Paul Lake throughout the season.

In Peter Lake, the euphotic zone (>1% of the surface light) reached 7.5-m depth (seasonal mean; $n = 10$; SD = 0.3 m). In Paul Lake, the euphotic zone reached 5.6 m ($n = 7$; SD = 0.2 m), in WLL, 3.2 m ($n = 10$; SD = 0.2 m), and in ELL only 2.9 m ($n = 7$; SD = 0.3 m; Table 1). The temporal variations within lakes were small (SD < 0.3 m in all lakes), whereas there were significant differences in light attenuation between lakes ($H = 29.9$; $P < 0.001$; Kruskal-Wallis one-way ANOVA). The range in water temperature at 0.5-m depth (all lakes included) was 20.1–25.7°C during the study period. There were no differences in temperature among lakes ($H = 0.43$; $P < 0.90$; Kruskal-Wallis one-way ANOVA).

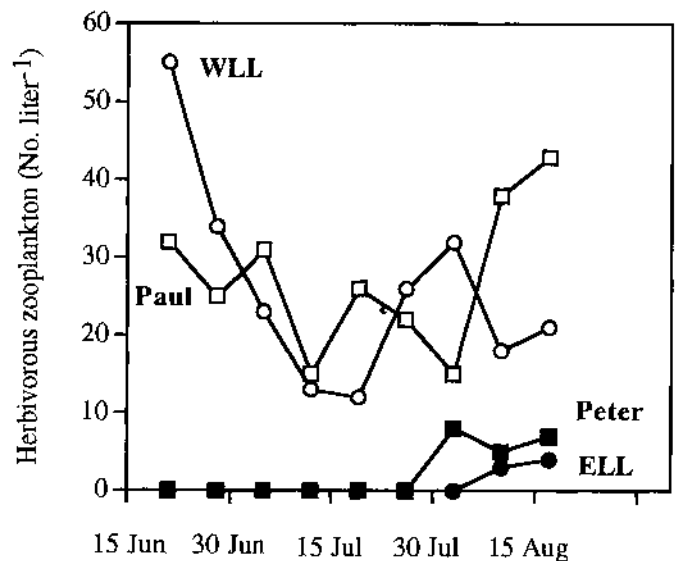


Fig. 1. The abundance of herbivorous zooplankton (mean No. liter⁻¹ through the water column) from June to August 1991. Due to experimental manipulations, no or very few macrozooplankters were present in June and July in Peter Lake and ELL.

Grazing—The abundances of herbivorous macrozooplankters (cladocerans and omnivorous copepods) were close to zero in Peter Lake and ELL from June to the end of July when the abundances increased somewhat, although they never exceeded 10 ind. liter⁻¹ (Fig. 1). In Paul Lake, the herbivorous zooplankton numbers fluctuated around 20 ind. liter⁻¹ during June and July but increased above 40 ind. liter⁻¹ in August. In WLL, the pattern was the opposite: high abundances (>50 ind. liter⁻¹) in June and ~20 ind. liter⁻¹ in July and August (Fig. 1). The mean weight per herbivorous zooplankter was 2.62 μg in Paul Lake during the investigation period, whereas the mean weight was almost two times higher in WLL (4.35 μg). The ranges in clearance rate (slope of the regression of algal net growth rate (r) and zooplankton abundance) of the six algal species investigated in WLL and in Paul Lake are given in Table 3. The herbivorous zooplankters in WLL showed the highest filtering rate on *Synura* sp. and *P. pusillum* and the lowest on *Cryptomonas* and *Gymnodinium* (Table 3). In Paul Lake, *Dinobryon*, *Cryptomonas*, and *Gymnodinium* suffered from the lowest grazing rates, whereas the grazing rates on *Merismopedia* and *P. pusillum* were high (Table 3).

Recruitment in relation to loss processes—Recruitment, sinking, and grazing were normalized as the percentage of total cell-colony density in the water. This means that during periods when low densities were recorded at the sampling site, which may be influenced by wind and other processes not related to recruitment, grazing, or sinking, population variables may sometimes show extremely high values. However, the aim with normalizing the population variables was to relate recruitment to sinking and grazing, variables that are traditionally quantified in ecological studies, and not to quantify recruitment in relation

Table 3. Clearance rate (liters filtered \times mg zooplankton⁻¹ \times d⁻¹) by the zooplankton community on six algal genera in Paul Lake and WLL in August 1991. The clearance rate is the slope of a regression between net growth rate vs. zooplankton biomass ($n = 6$). Algal species are arranged from lowest to highest grazing pressure. Please note that the coefficients of determination for *Cryptomonas* are low, indicating that the grazing rate for this genus may have been underestimated.

WLL			Paul Lake		
Genus	Clearance rate	r^2	Genus	Clearance rate	r^2
<i>Cryptomonas</i>	0.16	0.24	<i>Dinobryon</i>	0.86	0.86
<i>Gymnodinium</i>	1.39	0.86	<i>Cryptomonas</i>	1.09	0.24
<i>Dinobryon</i>	1.44	0.92	<i>Gymnodinium</i>	1.32	0.91
<i>Merismopedia</i>	1.49	0.94	<i>Synura</i>	1.59	0.49
<i>Peridinium pusillum</i>	1.95	0.54	<i>P. pusillum</i>	2.22	0.73
<i>Synura</i>	2.89	0.92	<i>Merismopedia</i>	2.81	0.68

to cell density. For a proper budget calculation, more rigorous determination of algal abundances in the water must be performed, including sampling at several depths and sites in the lake.

Recruitment of *Cryptomonas* was usually high compared to sinking and grazing, whereas the grazing and sinking loss processes together ranged from 1 to 236% of total abundance per day (Fig. 2). In Peter Lake and ELL, daily recruitment of *Gymnodinium* never or seldom exceeded 10% of the abundance. In the lakes with high abundances of macrozooplankters (Paul and WLL), daily recruitment was, with one exception, always >10% of the abundance (Fig. 2). In these lakes, grazing reduced the abundance of *Gymnodinium* by 6–50% per day, whereas grazing was negligible in Peter Lake and ELL throughout the investigation period. The recorded sinking rate rarely exceeded 5% of the abundance per day in any of the lakes (Fig. 2). The recruitment rate of *P. pusillum* was higher than the rates of the loss processes in Peter, Paul, and ELL (Fig. 2). In WLL, however, loss processes for most species usually exceeded the portion added through recruitment. With only two exceptions (WLL: 16–18 July; Peter Lake: 31 July–2 August), the recruitment rate of *Synura* was lower than or similar to the rate of abundance loss via sinking and, especially, grazing (Fig. 2). *Merismopedia* was, with one exception, never recorded in the lakes with low abundances of macrozooplankton and was excluded from further analysis in these lakes. Recruitment of *Merismopedia* was negligible, and sinking rarely exceeded 2%, whereas grazing reduced the abundances of *Merismopedia* by 6–54% per day (Fig. 2). The recruitment of *Dinobryon* was low, rarely above 1% of the total abundance (therefore not shown in Fig. 2), whereas grazing reduced the abundance by up to 52% per day and sinking by between 0 and 8% per day. Loss rates were always higher than recruitment rates for *Dinobryon* and *Merismopedia*. Recruitment rates of *Cryptomonas*, *Gymnodinium*, and *P. pusillum*, however, usually exceeded loss rates (Fig. 2).

The major part of the recruitment of *Cryptomonas* occurred below the thermocline in Peter, ELL, and Paul Lakes and during the first four sampling occasions in

WLL (Fig. 3). In Paul Lake, most of the recruitment of *Gymnodinium* was always below the thermocline, as was the case for *Synura* in Peter Lake (Fig. 2).

Temporal and spatial variations in recruitment—Of the 51 taxa identified, 68% did not show any migratory behavior (definition: present in the water but not caught in the traps), whereas 32% showed recruitment from the sediment (definition: seasonal mean recruitment rates >1% of total abundance in the water per day or >5% per day at least one sampling occasion). If the adaptation to shift habitat has no influence on the competitive ability of an organism, representatives from each group would be expected to dominate in proportion to their group size (i.e. recruiters in 32% of the cases and nonrecruiters in 68% of the cases). Dominance was estimated as the number of times representatives from the group of recruiting and nonrecruiting species occurred among the five most abundant species. In Peter Lake, WLL, and ELL the frequency of dominance for recruiters was 67, 67, and 93%, respectively ($P < 0.05$, 0.05, and 0.001; χ^2 -test; $df = 5$). In Paul Lake, recruiters showed the expected frequency in dominance (37%; NS; χ^2 -test; $df = 5$).

The total number of cells or colonies recruited showed maximum values at water depths <4 m, and then a decreasing trend toward deeper water in all lakes except Paul Lake (Fig. 3). Besides a high littoral recruitment, Paul Lake showed a recruitment maximum at 6–8-m depth, mainly because of high recruitment of *Gymnodinium*. Total recruitment was <10⁷ cells m⁻² d⁻¹ beyond 10-m water depth in all lakes (Fig. 3). The high littoral recruitment in ELL was almost exclusively caused by *P. pusillum* and *Gymnodinium* (together always constituting >70% of the total numbers recruited).

P. pusillum was exclusively recruited from sediments shallower than 4 m in all four basins (see Fig. 5). No dramatic fluctuations in the total abundance of *P. pusillum* was recorded in Paul Lake (Fig. 4). Except on the first sampling occasion (year-day 166), the recruitment rate of *P. pusillum* in WLL was <5 \times 10⁶ cells m⁻² d⁻¹ (Fig. 5), which was negligible compared to the other lakes.

The recruitment of *Synura* was very low in Peter Lake,

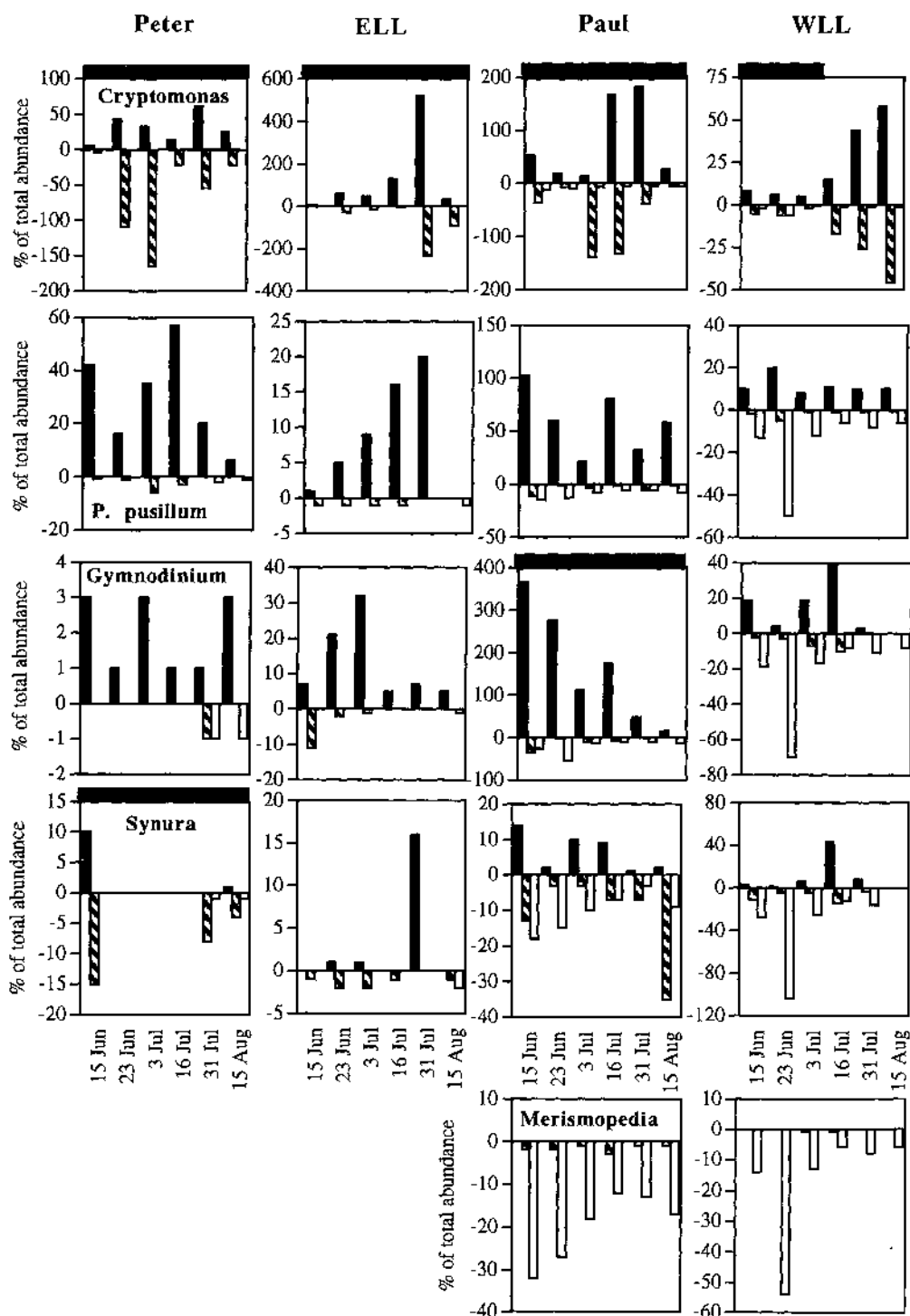


Fig. 2. Normalized values [% per day of the abundance recorded in surface waters (0–2 m)] for recruitment (black bars), sinking (striped bars), and grazing (white bars), mid-June to mid-August 1991. All values are calculated on a whole-lake basis. Recruitment and sinking estimates are integrated trap samples from five (Paul, WLL, and ELL) or six (Peter) depths. Sinking is corrected for underestimation due to decomposition (50% underestimated; Fallon and Brock 1980) and funnel trap construction (10% underestimated; Blomqvist and Håkansson 1981). *Merismopedia* was not recorded in Peter Lake and ELL. The horizontal black bars at the top of the figures of *Cryptomonas* (all lakes), *Gymnodinium* (Paul Lake), and *Synura* (Peter Lake) indicate that recruitment was mainly below the thermocline, suggesting that recruitment is not mirrored in increased biomass in the euphotic zone (see text and Table 4). Note different scales on the figures.

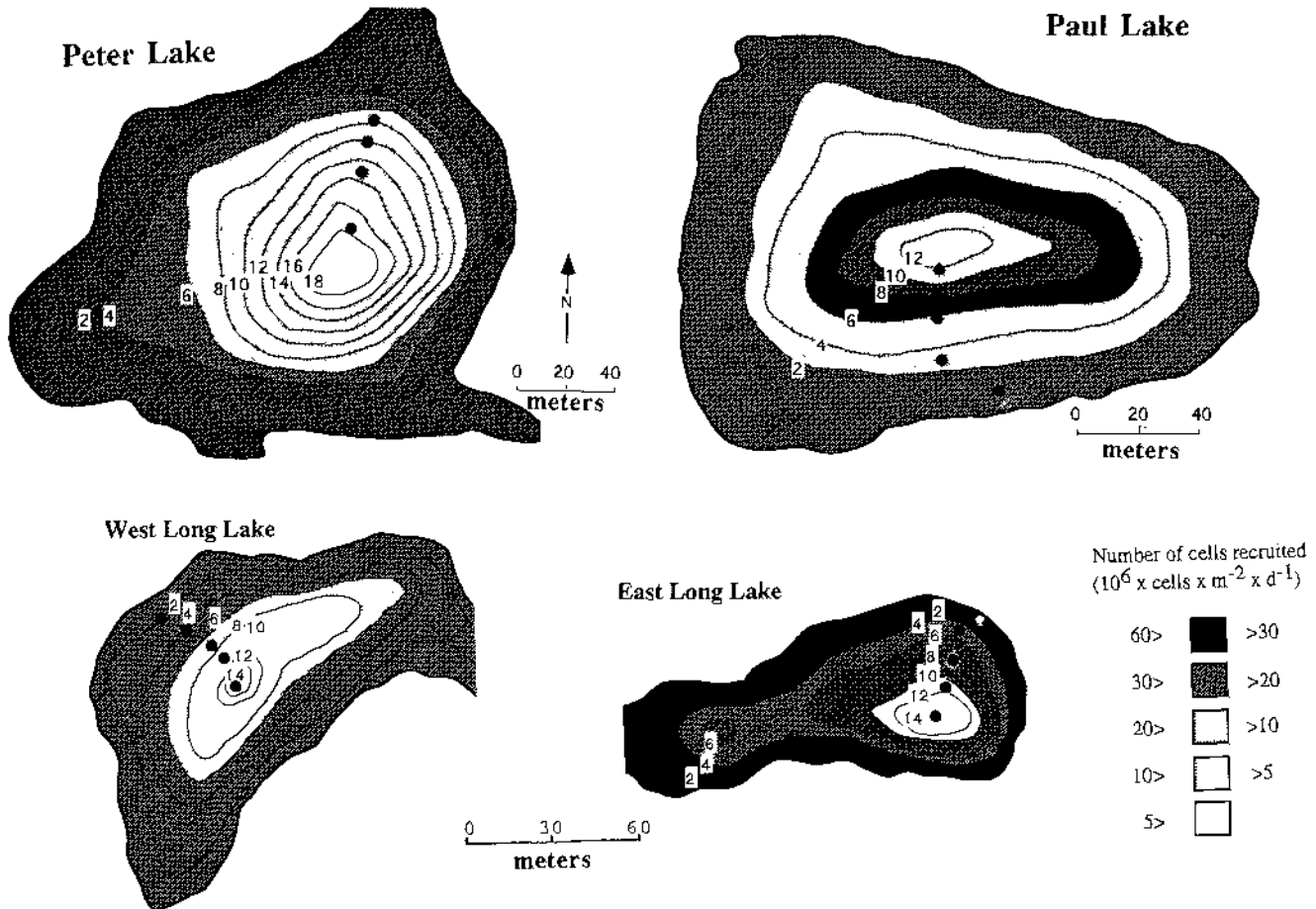


Fig. 3. Total number of algae recruited (seasonal mean; $n = 6$) at different depths. Darker color indicates higher recruitment rates. The figure shows that recruitment was highest at shallow depths except in Paul Lake, where a maximum occurred at 6–8 m. Distance between depth contours is 2 m. Sampling stations are indicated with dots (note the white dot at 1.2 m in ELL).

reaching maximum in relatively deep water (7–10 m; Fig. 5). The abundance of *Synura* was always very low in Peter Lake (Fig. 4) and showed no correlation with recruitment ($r = 0.07$ NS; Table 4). Recruitment of *Synura* in ELL usually reached a maximum at 4-m depth, and no recruitment was recorded from sediments deeper than 8 m (Fig. 5). The pattern of high recruitment rates in June and July corresponded well with the abundance fluctuations (Fig. 4). Recruitment of *Synura* in Paul Lake usually showed a maximum at 3 m and was negligible beyond 6 m (Fig. 5). The recruitment rate showed a sudden increase on the last sampling occasion (Fig. 5), which was mirrored in an fivefold increase in total abundance (Fig. 4). In WLL, the recruitment of *Synura* was higher than in the other lakes (Fig. 5), with maximum recruitment always from shallow water (2 m). As in ELL, the recruitment of *Synura* in WLL increased in June and early July and then dropped.

In Peter Lake, maximum recruitment of *Gymnodinium* was usually between 3- and 7-m depth, and, as in WLL and ELL, a maximum was reached in early July (Fig. 5). This pattern was well mirrored in the total abundance in all three basins (Fig. 4). Recruitment of *Gymnodinium* in ELL showed a maximum at 2 m during the end of June

and early July, and no recruitment was recorded from deeper than 8 m (Fig. 5). *Gymnodinium* was the genus that recruited most cells in Paul Lake (Fig. 5). Recruitment always showed a maximum between 6- and 8-m depth, whereas a negligible number of cells were recruited from shallow (<3 m) and deep sediments (10.5 m). Just as the recruitment rates, the total number of *Gymnodinium* in Paul Lake was relatively constant throughout the season (Fig. 4). However, the high recruitment rates were not mirrored in high abundances, and, in contrast to the other lakes, no correlation was found between abundance and recruitment ($r = 0.21$ NS; Table 4). In WLL, recruitment of *Gymnodinium* was highest at 4 m except on days 184 and 229, when the maximum was at 2 m (Fig. 5). A negligible number of cells was recruited beyond 8 m.

In Peter Lake, recruitment of *Cryptomonas* was low compared to the other lakes (Fig. 5). Maximum recruitment was usually at 7–10-m depth. In ELL, *Cryptomonas* always showed maximum recruitment at 8 m (Fig. 5). Recruitment of *Cryptomonas* in Paul Lake was skewed toward depths >6 m on the first three sampling occasions (Fig. 5). The following 2 weeks (18–31 July), recruitment increased drastically and showed two maxima, one at 6 m and one in the deep hole (10.5 m). On the last sampling

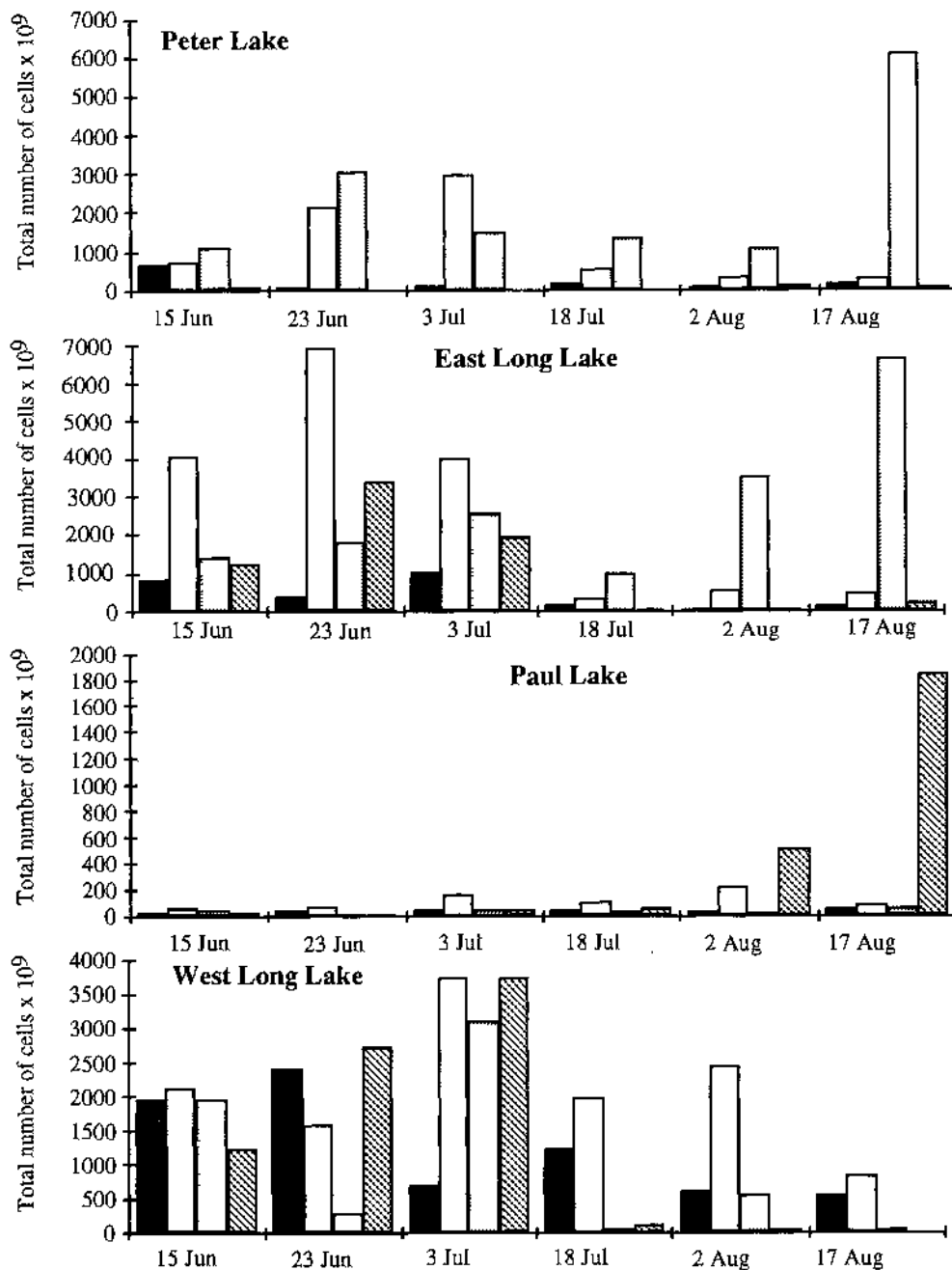


Fig. 4. Total number of cells-colonies in the water of *Cryptomonas* (black), *Gymnodinium* (white), *Peridinium pusillum* (gray), and *Synura* (hatched), 15 June–17 August 1991.

occasion, recruitment returned to a level similar to that during early summer (Fig. 5). As in Paul Lake, recruitment of *Cryptomonas* in WLL was low until early July (day 184), when it increased considerably at 4-m depth (Fig. 5).

Discussion

My results indicate that algal recruitment from the sediment is a highly dynamic and fluctuating phenomenon,

varying both spatially and temporally among lakes and along depth gradients within lakes. However, clear and repeatable patterns can be distinguished. Different taxa have their main recruitment at different depths (i.e. species composition differed among traps along the depth gradients), which makes it unlikely that catches were planktonic algae passively entering the traps by currents. This conclusion is strengthened by the methodological test in which no difference in recruitment was recorded between traps with and without Plexiglas walls. Some species, such as *P. pusillum*, were exclusively recruited

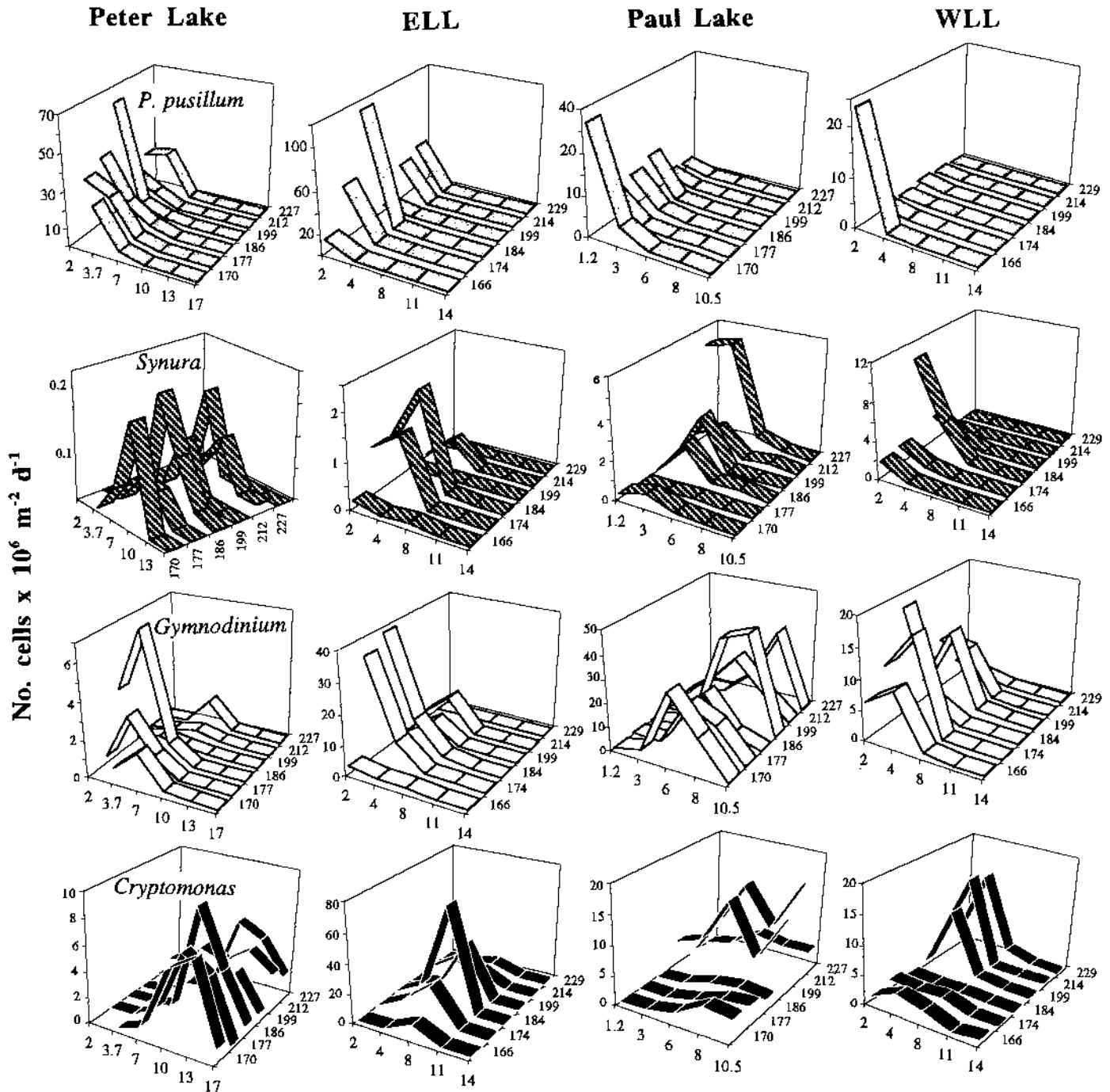


Fig. 5. Recruitment rates of *Peridinium pusillum*, *Synura* sp., *Gymnodinium* sp., and *Cryptomonas* sp. along temporal (15 June–17 August 1991, corresponding to year-day 166–229) and spatial (depth gradient) scales. Note different scales on the y-axes.

from very shallow sediments; others, such as *Synura* and *Gymnodinium*, had high recruitment at depths down to 7 m, whereas *Cryptomonas* was mainly recruited from depths of 4–9 m. None of the species showed recruitment maxima at water deeper than 9 m, indicating that recruitment is primarily a littoral phenomenon.

The selected species in these lakes can be divided into three groups with respect to recruitment patterns: species not exhibiting recruitment, which were never or rarely

found in the recruitment traps but were common in the water (e.g. *Merismopedia* sp. and *Sphaerocystis* sp., (pers. obs.); species that shift habitat but for which recruitment is quantitatively of minor importance (e.g. *Dinobryon* sp.); and finally, species regularly exhibiting recruitment and for which recruitment is quantitatively important for the planktonic part of the population (e.g. *Gymnodinium* sp., *Cryptomonas* sp., *P. pusillum*, and *Synura* sp.).

Several abiotic factors may initiate or prevent recruit-

Table 4. Correlation coefficients for total recruitment per day vs. total biomass (both on a whole-lake basis). Probability values based on t -tests are given ($n = 6$). According to the hypothesis that the biomass is unaffected by recruitment below the thermocline, no correlation is expected for *Cryptomonas* in any lake, *Gymnodinium* in Paul Lake, and *Synura* in Peter Lake (boldface), whereas high correlation coefficients are expected for *Gymnodinium* and *Synura* in all lakes except Paul and Peter. t -values for the regression between recruitment and abundance in the water are higher when the recruitment maximum is above rather than below the thermocline ($U = 0$; $P < 0.004$; $n_1 = n_2 = 6$; Mann-Whitney U -test), suggesting that the thermocline affects the success of a recruitment attempt.

	Peter Lake	ELL	Paul Lake	WLL
<i>Cryptomonas</i>	-0.19 ($t=0.38$; $P>0.70$)	0.53 ($t=1.23$; $P>0.29$)	-0.20 ($t=0.41$; $P>0.70$)	-0.30 ($t=0.64$; $P>0.55$)
<i>Gymnodinium</i>	0.89 ($t=3.96$; $P<0.02$)	0.71 ($t=2.01$; $P<0.11$)	0.21 ($t=0.43$; $P>0.68$)	0.67 ($t=1.79$; $P<0.15$)
<i>Synura</i>	0.07 ($t=0.13$; $P>0.90$)	0.80 ($t=2.67$; $P<0.06$)	0.98 ($t=9.48$; $P<0.001$)	0.79 ($t=2.57$; $P<0.06$)

ment in algae. Variables of potential importance for initiating recruitment are fluctuations in light (Reynolds 1975; Hansson 1993) and in oxygen concentration (or a factor related to oxygen concentration) at the sediment surface (Trimbee and Harris 1984; Hansson 1993). Upward migration may not always be successful because there are factors that prevent the algae from reaching water with suitable light conditions. Such a factor is the thermocline, which may function as a "lid" for algal migration to the euphotic zone (Hansson et al. 1994). This hypothesis is in contrast to studies on *Cryptomonas marssonii* (Salonen et al. 1984) and *Oscillatoria* (Klemer 1976; Konopka et al. 1993), in which the algae were able to penetrate the thermocline. In the present study, the total abundance of algae in the water was determined from an integrated sample from 0- to 2-m depth taken in the middle of the lake. If algae are unable to penetrate the thermocline, it may be hypothesized that recruitment from sediments below the thermocline will not contribute to epilimnetic abundance. The lower part of the thermocline was relatively constant at 5 m in Paul Lake, ELL, and WLL and at ~6 m in Peter Lake throughout the season. *Synura* was mainly recruited from sediments above 4-m water depth in Paul Lake, ELL, and WLL but not in Peter Lake, where recruitment mainly occurred between 7- and 10-m depth (i.e. below the thermocline). The high correlation coefficients between the abundance and recruitment rate of *Synura* in Paul Lake, ELL, and WLL ($r > 0.79$; $P < 0.06$) and the low correlation between abundance and recruitment rate in Peter Lake ($r = 0.07$; $P > 0.90$) support this hypothesis. Similarly, recruitment of *Gymnodinium* was correlated with abundance fluctuations in the surface water of all lakes except Paul (Table 4), where the major part of recruitment was at 6–8 m (i.e. below the thermocline). Hence, despite recruitment of *Gymnodinium* being usually 10 times higher in Paul than in Peter Lake, the effect of recruitment on abundance in the euphotic zone was negligible. *Cryptomonas* was recruited mainly from below the thermocline in Peter, Paul, and ELL, whereas recruitment above the thermocline was high during the last three sampling occasions in WLL (Fig. 5). Paul Lake showed consistent imbalance between recruitment and loss processes for *Cryptomonas* and *Gymnodinium* (Fig. 2). This may have been because both *Cryptomonas* and *Gymnodinium* were recruited mainly below the thermocline, as indicated by the recruitment

maximum at 6–8-m depth in Paul Lake (Fig. 3). Hence, the fact that maximum recruitment of both *Cryptomonas* and *Gymnodinium* occurred below the thermocline may have contributed to the consistently lower abundances in the surface water of Paul Lake (Fig. 4). This notion is strengthened by the successful recruitment of *Synura* from above the thermocline in Paul Lake (Fig. 5), which was well mirrored in abundance oscillations in the planktonic population ($r = 0.98$; $P < 0.001$; Table 4). Separating the t -values for the regression lines of recruitment vs. abundance into situations in which recruitment maxima occurred above and below the thermocline (the latter indicated with boldface in Table 4) reveals higher t -values for situations in which R -maxima occurred above the thermocline. Hence, for the species investigated, the thermocline has a crucial impact on whether a recruitment period will be successful (i.e. whether the algae will reach the euphotic zone). If a major part of the recruitment of a species occurs below the thermocline, a large meta- or hypolimnetic population of cells would be expected—a notion that seems to hold true for these lakes, which often show 10 times higher metalimnetic chlorophyll values than they do above the thermocline (Carpenter et al. unpubl.).

The grazing rates on the algal species investigated differed between Paul Lake and WLL, probably due to differences in zooplankton size. For example, the mean abundance per zooplankton was almost two times higher in WLL than in Paul Lake. Differences in zooplankton community composition may also have caused different grazing pressures on different algal sizes and morphologies. In both lakes, grazing pressure on the small *P. pusillum* was high relative to most of the other recruited species (Table 3). In WLL, the abundance of *P. pusillum* was high when the abundance of herbivorous zooplankton was low and vice versa (Figs. 2 and 4). In lakes with low grazer abundances (ELL and Peter Lake), *P. pusillum* showed high abundances, suggesting that grazing was a key factor in the population dynamics of *P. pusillum*. Hence, high abundances of grazers may also prevent recruitment from having a large effect on pelagic abundance of algae susceptible to grazing, although indirect effects such as responses in recruitment rates to zooplankton exudates cannot be excluded (Hessen and van Donk 1993; Hansson 1993).

The adaptation to migrate, either by means of flagella

or vacuoles, is energetically costly (Kromkamp et al. 1988), which may, under certain environmental conditions, be compensated for by gains in the form of improved nutrient and light availabilities (Raven and Richardson 1984). Based on this notion, I hypothesized that species that perform recruitment should have a competitive advantage and should therefore occur more often among the dominating species than nonmigratory species do. In Peter Lake, WLL, and ELL, where the recruitment maximum was above the thermocline, the frequencies in dominance of migrating algae were higher (67, 67, and 93%; $P < 0.050$; χ^2 -test) than would be expected from the portion of the algae in the taxonomic spectrum (32%); this result supports the hypothesis that adaptation to shift habitat is related to a higher frequency of dominance. However, the euphotic zone of Paul Lake was often dominated by nonmigratory, small blue-green colonies, and the frequency in dominance of the species that perform recruitment (37%) did not diverge from the expected based on their portion in the taxonomic spectrum (32%). This is in accordance with the hypothesis because recruitment in Paul Lake was mainly at depths below the thermocline (Fig 3), which allowed nonmigratory species to dominate in the euphotic zone.

Records of fluctuations in phytoplankton populations usually show tremendous temporal variation in abundance and species composition (Harris 1986; Sommer 1989). Such successional patterns are traditionally explained by variations in growth rates of different species at different times and by fluctuating grazing and sinking rates. This study suggests that migration from the sediment surface via recruitment as well as growth may be important factors contributing to increased abundances of different species during succession in phytoplankton communities. Hence, although the traditional model for fluctuations in population size (ΔB) that includes terms for growth (μ), grazing (G), and sinking (S) holds true for many algal species, addition of the variable recruitment rate (R) may improve the predictability of the model for other common algal species:

$$\Delta B = \mu - G - S + R.$$

The design of my study does not allow for calculations of a budget because ΔB was determined at only one site and may have been affected by other processes, such as wind and current. Moreover, R , G , and S were probably not determined often enough to allow for a balanced whole-lake budget. Finally, algal abundances in the water were sampled from 0- to 2-m depth (i.e. the entire depth of the euphotic zone was not sampled). Because algae were concentrated in the metalimnion (S. R. Carpenter pers. comm.), I may have underestimated actual algal abundance. Hence, the estimate of recruitment as a percentage of the recorded abundance in the water may have been too high. Due to these methodological shortcomings, it is not possible to calculate a balanced biomass budget based on the present data. Instead, my study should be viewed as a comparison of the order of magnitudes in recruitment and loss processes in these lakebasins during a summer season.

In a review, Kalff and Knoechel (1978) concluded that progress in understanding and predicting the relation between algal abundance and environmental variables has been slow—a notion supported several years later by Reynolds (1984). A conclusion from my study is that a better understanding of recruitment in algal communities may improve the predictability of fluctuations in the phytoplankton community. Quantification of recruitment can thus help predict population maxima in the water column, which is of special interest for management and prevention of outbreaks of bloom-forming algae. The results also point to important relations between the sediment surface and the water column as well as between littoral and pelagic zones, connections that may seem obvious but are seldom discussed in the literature. Migration is energetically costly and may lead to lower growth rate (Kromkamp et al. 1988). However, in situations in which resources (e.g. nutrients) limit growth, it may be advantageous to build up a population or to form resting stages at the sediment, where nutrient availability is high. Then the benthic population can rapidly shift habitat and become planktonic, thereby having access to both nutrients and light. The advantage of this strategy was manifested in dominance in the phytoplankton community of the lakes investigated.

A parallel case is the recruitment of many cyanobacteria, which regulate their vertical position by means of gas vacuoles and ballast molecules. In highly productive lakes, recruitment of cyanobacterial colonies from the sediment is often followed by complete dominance in the phytoplankton community (Reynolds and Rogers 1976; Fallon and Brock 1981; Trimbee and Harris 1984; Hansson et al. 1994). Previous studies have pointed out the importance of algal recruitment for transport of phosphorus from sediment to water (Barbiero and Welch 1992; Pettersson et al. 1993). My study suggests that recruitment may also be important in explaining observed dominance and succession patterns in phytoplankton communities.

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Notice

The mailing of this issue marks the end of my 32-yr association with *L&O*; the editorial office will remain at the School of Oceanography, University of Washington, and all mailing addresses are unchanged. The new managing editor is Kevin C. Oliver (kco@u.washington.edu), who comes to *L&O* from Allen Press.

Of further interest, authors are advised that *L&O*, although still supported by ASLO, will no longer operate as a journal completely independent of the Society and equally accessible to all authors. Editor-in-chief David Kirchman has requested and the Board has agreed that henceforth free publication will be limited to ASLO members. Non-members will be charged a \$100 publication fee, in addition to any page or other charges associated with publication for both members and non-members. Waivers may be granted on a case-by-case basis.—Raelyn Cole