

Dinoflagellate bloom development and collapse in Lake Kinneret: a sediment trap study

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Warm monomictic Lake Kinneret, Israel, is characterized by a winter–spring water bloom of the large (~50 µm diameter) dinoflagellate *Peridinium gatunense* NYGAARD. Usually the *P. gatunense* bloom declines in May–June and a less prominent bloom of smaller dinoflagellates (mostly *Peridiniopsis* spp. of ~20–30 µm diameter) develops. Water column abundances and sedimentation losses to those dinoflagellates were followed throughout 1994 and 1995. The objective was to quantify the variables that describe population dynamics, that in turn will shed more light on the seasonal patterns of bloom dynamics. Sedimentation losses were measured by means of sediment traps with and without a preservative (formaldehyde) that were exposed for 24 h once every 2–3 weeks. Annual sedimentation losses of *Peridinium* (hypolimnetic trap catches) were 209 g wet wt m⁻² year⁻¹ in 1994 and 187 g wet wt m⁻² year⁻¹ in 1995, which constituted 16 and 23% of *Peridinium* production in those years, respectively. This study revealed that increased death rates preceded a mass sedimentation flux of *Peridinium* and caused the decline of the bloom in Lake Kinneret. Annual sedimentation losses of *Peridiniopsis* were 55 g wet wt m⁻² year⁻¹ in 1994 and 34 g wet wt m⁻² year⁻¹ in 1995. In contrast to live *Peridinium* cells, *Peridiniopsis* cells continued to swim to the lower trap after the onset of thermal stratification, possibly taking advantage of the higher nutrient concentrations below the thermocline, at a time when the lake is already stratified and the epilimnion is nutrient depleted. This could be an important factor allowing *Peridiniopsis* spp. to peak after the decline of *Peridinium*.

INTRODUCTION

Dinoflagellate blooms are common phenomena in marine and freshwater systems. Blooms eventually decline when loss rates, mostly by grazing, decomposition or sedimentation, exceed growth rates. The fate of algal blooms is crucial for the understanding of food web interactions, energy transformation and nutrient cycling. In stratified lakes losses of the bloom biomass in epilimnetic water through grazing and decomposition lead to regeneration of nutrients in a temporally short cycle. In contrast, sedimentation of algal biomass removes nutrients from the trophogenic layer, at least until holomixis.

Lake Kinneret, (170 km²) in northern Israel (32°45–53'N and 35°30–38'E) is a warm monomictic freshwater lake. The lake level fluctuates between 208.9 and 214 m below sea level, the mean and maximum depths when the lake is full are 24 m and 43 m, respec-

tively. The lake typically stratifies from May to December, during which the epilimnion becomes increasingly depleted of nutrients, while the hypolimnion turns anaerobic, with increasing concentrations of sulfide and ammonia (Berman *et al.*, 1992; Hadas and Pinkas, 1992). Lake Kinneret is characterized by a winter–spring bloom of the large (48–66 µm diameter) armored dinoflagellate *Peridinium gatunense* NYGAARD (Hickel and Pollinger, 1988). *Peridinium gatunense* (hereon: *Peridinium*) is accompanied by several smaller (~20–30 µm diameter) dinoflagellate species of the genus *Peridiniopsis* (*Peridiniopsis elpatiewskyi*, *Ps. cunningtonii*, *Ps. borgei*, *Ps. penardiforme* and *Ps. polonicum*), which usually reach their maximum abundance when the *Peridinium* bloom declines in early summer (Pollinger and Hickel, 1991).

Like many other dinoflagellates *Peridinium* and *Peridiniopsis* are motile and are able to perform diel vertical migration. In Lake Kinneret the dinoflagellates exhibit

characteristic diel depth dispersion (Berman and Rodhe, 1971; Pollinger and Hickel, 1991). Generally, the dinoflagellates are dispersed fairly uniformly throughout the water column at night. Towards the morning they tend to rise, and a population peak is often found close to the water surface (2–4 m) during the early morning hours. The cells migrate to deeper water by later afternoon and again disperse throughout the water column at night.

During the bloom period, *Peridinium* standing stock typically exceeds 180 g wet wt m⁻², but by early to mid summer it falls below 30 g wet wt m⁻² (Pollinger, 1986; Pollinger and Hickel, 1991). Causes for the bloom crash were proposed to be N and P limitation, high solar radiation (Häder *et al.*, 1990), elevated temperature (Berman and Dubinsky, 1985), high turbulence (Pollinger and Zemel, 1981) and CO₂ limitation (Berman-Frank *et al.*, 1994). A 5-year study of dinoflagellate bloom dynamics and sedimentation (Zohary *et al.*, 1998) suggested that sedimentation was not a major cause for the bloom decline but rather a secondary process that enhances the elimination from the water column of a population handicapped by a combination of other factors. The objective of this study was to carry the investigation one step further and measure the *in situ* variables of dinoflagellate dynamics in population parameters for Lake Kinneret. Here we present the results of a 2-year study that was based on analysis of short-term (24 h) sediment trap data. Short-term deployment of sediment traps minimized within-trap decomposition losses and enabled us to follow the temporal dynamics of growth and death rates of the dinoflagellate populations.

METHOD

Field work was conducted throughout 1994 and 1995 at a central station (A) that is situated at the deepest part of Lake Kinneret (~43 m). Sampling was conducted always between 08:00 and 11:00. Depth profiles of water temperature and dissolved oxygen concentration were recorded biweekly with a profiling thermistor (Model STD-12; Applied Microsystems Ltd, Sidney, Canada) and a YSI model 58 dissolved oxygen meter. Thermocline depth was defined as the depth >10 m at which the temperature over 1 m gradient exceeds 0.3°C (Hambright *et al.*, 1994). The water column abundance of *Peridinium* and of *Peridiniopsis* spp. (treated as one group) were recorded weekly from depth integrated (0–7 m) water samples collected with an integrating water sampler (type Hy 72; Zullig Ltd, Rheineck, Switzerland) and preserved with formaldehyde (2% final concentration). From depth distribution studies (Pollinger and Hickel, 1991) we know that during the daytime most dinoflagellate cells are contained within these upper 7 m. Live cells, dead cells,

cysts (resting forms), thecae and naked protoplasts (Figure 1) of all dinoflagellates in the sample were counted using the inverted microscope technique (Utermöhl, 1958). Dead cells are distinguished from live cells by the contracted protoplast (it does not fully occupy the theca) (Figure 1). Cell counts were converted to wet weight biomass by measuring the linear dimensions, applying appropriate geometric shapes and assuming a specific density of 1 g cm⁻³ (Hillebrand *et al.*, 1999). The water column biomass (in g wet wt m⁻²) for the upper 7 m was obtained by multiplying the volumetric concentration (in g wet wt m⁻³) values by 7 m.

Sedimentation rates were estimated from algal accumulation in sediment traps with and without formaldehyde, which were deployed for 24 ± 2 h at 2–3-week intervals throughout 1994 and 1995. Two sets of positively buoyant traps, each consisting of four opaque PVC cylinders (5.3 cm internal diameter; opening surface area 2206 mm²; 60 cm length; aspect ratio of 11.3) adapted with replaceable 300 ml screw-cap jars at their bottom end, were deployed one above the other on a tight cable at station A (Viner *et al.*, 1998). The lower trap was placed at 35 m (hypolimnion), the upper trap was placed near the base of the epilimnion at a depth varying from 15 to 25 m, depending on the depth of the thermocline. A dialysis bag containing 10 ml of concentrated formaldehyde and a glass-bead weight was placed in two of the four jars in each trap. The traps were retrieved after 24 h exposure, during the morning hours. At that time of the day dinoflagellates have already migrated up to the surface layers thus we reduced the probability of catching cells that reached the traps by active migration and not by passive sinking. The material collected in the replaceable jars was fixed with 2% formaldehyde (final concentration). Cell count and biomass estimates were made as detailed for the water column samples. Sedimentation rates (g wet wt m⁻² day⁻¹) were obtained by division of the accumulated biomass (g wet wt m⁻³) by the duration of trap deployment.

Preliminary experiments were conducted to assess whether there is an overestimation of *Peridinium* sedimentation into traps filled with ambient water at the time of trap deployment. Prior to deployment, half of the jars and cylinders in each trap were filled with ambient lake water, the rest with prefiltered (GF/C) Kinneret water. After 24 h incubation the traps were retrieved and the water in the jars was used to determine the chlorophyll content of the whole water and of water passing through a 20 µm mesh [after (Holm-Hansen *et al.*, 1965)]. The chlorophyll attributed to *Peridinium* was calculated by subtraction of the chlorophyll value of the <20 µm fraction from that of the whole sample chlorophyll. A paired *t*-test showed no significant differences between the

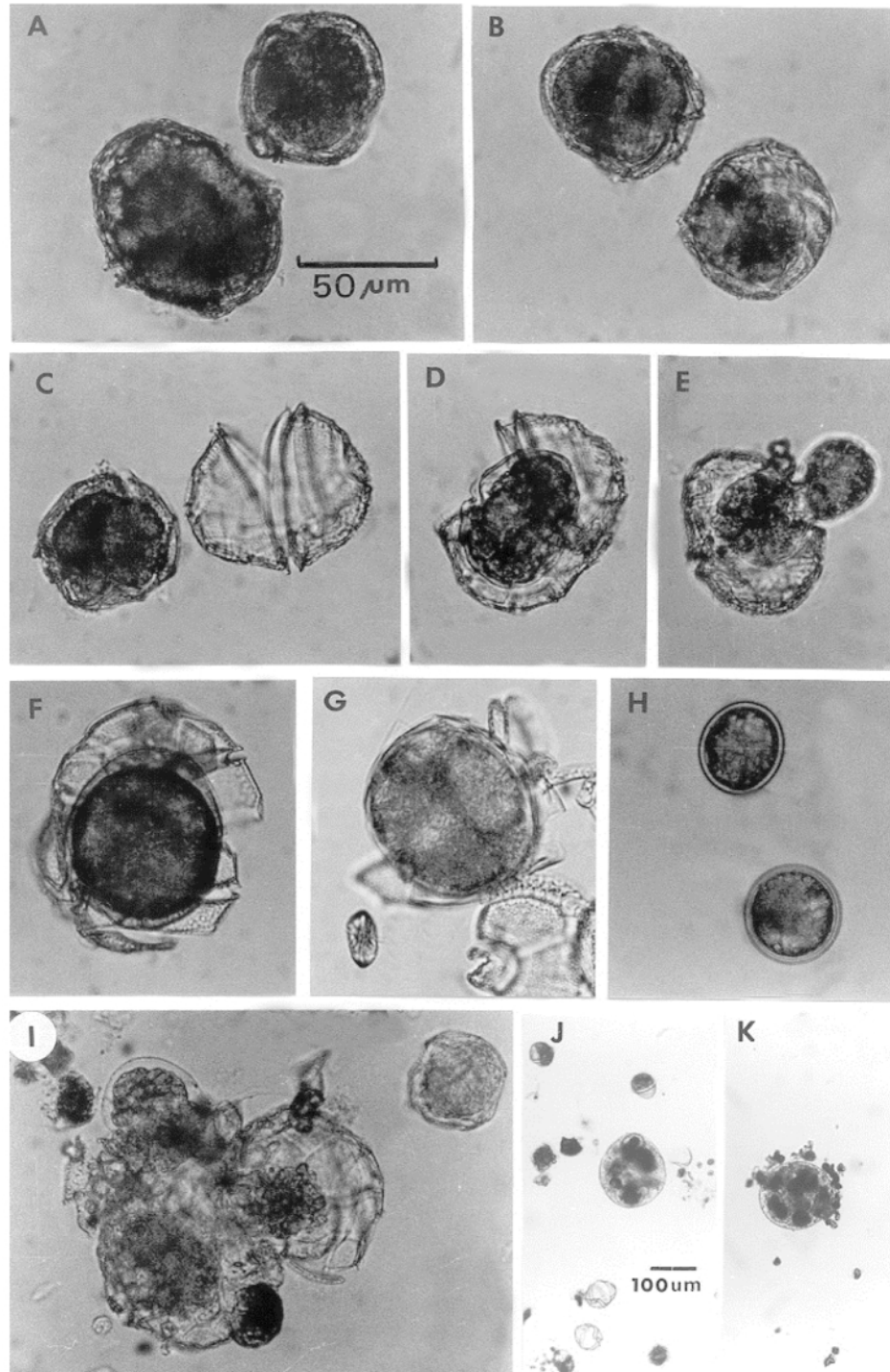


Fig. 1. Microscope photos of *P. gatunense* NYGAARD (A–G; I–K) and *Peridiniopsis* spp. (A) Live cells. (B) Live (upper) and dead (lower) cells. (C) A live cell (left) and an empty theca (right). (D) Cell division, showing how prior to the formation of two daughter cells the theca breaks open and constriction develops in the middle of the protoplast. (E) Dead cell, with protoplast bursting out of the theca. (F, G) Cell shedding its theca during cyst formation. (H) *Peridiniopsis* cysts (50 μm size bar applies to A–I). (I) Decomposed *P. gatunense* cells. (J, K) *P. gatunense* cells grazed by the ciliate *Bursaria truncatella* (100 μm size bar applies to J and K).

two treatments ($P > 0.05$, $n = 9$, $t = 0.4$). Our explanation is that during the 24-h exposure live dinoflagellates in the ambient water that were trapped during the trap filling procedure migrated upwards to a depth of optimal conditions. Therefore, the error introduced by filling of the traps with lake water is insignificant.

In an earlier study (Viner *et al.*, 1998) we showed that sedimentation rates of vertically migrating dinoflagellates measured by means of sediment traps containing a preservative were subject to severe overestimation of the vertical flux for live cells. The number of *Peridinium* and *Peridiniopsis* live cells trapped over a 24-h period in formaldehyde-containing (F+) traps was often 5–10-fold greater than in traps without formaldehyde (F–) traps. Such differences between catches in F+ and F– traps were not observed for dead matter (e.g. thecae) of both dinoflagellate genera (catch ratios of F+ to F– being close to 1) in both upper and lower traps. The high catches of live cells in F+ traps was explained by the daily vertical migration behaviour of these dinoflagellates (Zohary *et al.*, 1998). The similarity between F+ and F– traps in catches of dead material implies that during the 24 h exposure period within-trap decomposition and grazing of *Peridinium* and *Peridiniopsis* were minor. In view of these findings calculations of sedimentation rates of live cells of *Peridinium* and *Peridiniopsis* were made using the cell counts from the F– traps, while sedimentation rates of dead cells, thecae and protoplasts were computed using cell counts from the F+ traps. These values are reported in the Figures, with the exception of an unusual event in the summer when live cells were caught in large numbers in F+ traps, at a time when they appeared to be absent in the water column.

Sinking velocities (m day^{-1}) of *Peridinium* and *Peridiniopsis* were computed by dividing the sedimentation rates ($\text{g wet wt m}^{-2} \text{ day}^{-1}$) by the average water column biomass concentration (g wet wt m^{-3}) as described previously (Hargrave and Burns, 1979). Population dynamics variables, in day^{-1} units, were calculated from the water column and upper sediment trap cell counts, assuming that the potential growth rate, μ , is equal to the sum of the apparent growth rate, k , plus the losses, according to the equation:

$$\mu = k + \delta + \sigma + \gamma. \quad (1)$$

where δ is the death rate, σ is the sedimentation rate and γ is the grazing rate (Sommer, 1984a,b). The equation was further simplified assuming that grazing losses of *Peridinium* were negligible (Serruya *et al.*, 1980), i.e. $\gamma = 0$.

Apparent growth rates (k), were calculated as:

$$k = \frac{\ln N_2 - \ln N_1}{t_2 - t_1} \quad (2)$$

where N_1 and N_2 are the 5-week running averages of *Peridinium* cell numbers per m^2 of the upper 0–7 m water column at times t_1 and t_2 . Running averages were used to reduce the effect of horizontal patchiness (Berman and Rhode, 1971). Population dynamics variables were calculated separately for the growth and decline phases of the bloom.

$$\sigma = \frac{N_s \times k}{N_1 (e^{k(t_2 - t_1)} - 1)} \quad (3)$$

where N_s is the number of live *Peridinium* cells per m^2 accumulated in the sediment traps without formaldehyde between t_1 and t_2 .

The death rate was calculated as:

$$\delta = \frac{N_d \times k}{N_1 (e^{k(t_2 - t_1)} - 1)} \quad (4)$$

where N_d is the number of dead cells and protoplasts per m^2 , based on the numbers accumulated in the formaldehyde-containing traps. The maximum potential standing crop of *Peridinium*, which would have been developed in the water column during the bloom (January–July) if loss processes were not taking place, was calculated by replacing k with μ in equation (2) and solving for N_2 to give:

$$N_2 = N_1 e^{\mu(t_2 - t_1)} \quad (5)$$

Finally, we converted N_2 from cells ml^{-1} to biomass (g wet wt m^{-2}), and added the biomass of thecae that were shed during cell division [1 theca per division, thecal biomass $\sim 30\%$ of live cell biomass; (Zohary *et al.*, 1998)]. The sum was assumed to represent the annual *Peridinium* production.

The total biomass of *Peridinium* and *Peridiniopsis* lost by sedimentation was computed as the sum of empty thecae + dead cells + naked protoplasts. The flux of live cells into the traps was considered mostly as an artefact and not included in the calculation of the total biomass lost by sedimentation (see Discussion). Daily sedimentation fluxes were time-integrated to give annual sedimentation rates ($\text{g wet wt m}^{-2} \text{ year}^{-1}$). The fraction of *Peridinium* production lost annually via sedimentation was estimated as the ratio between the annual sedimentation and annual *Peridinium* production.

The parameters of population dynamics of *Peridiniopsis* could not be calculated because the group *Peridiniopsis* consisted of a number of species, each one with its own rate of increase and decline. Moreover, as mentioned earlier the basic assumption underlying the calculation of μ is that grazing losses are negligible, and this is not true for *Peridiniopsis* spp. in Lake Kinneret (Zohary *et al.*, 1994).

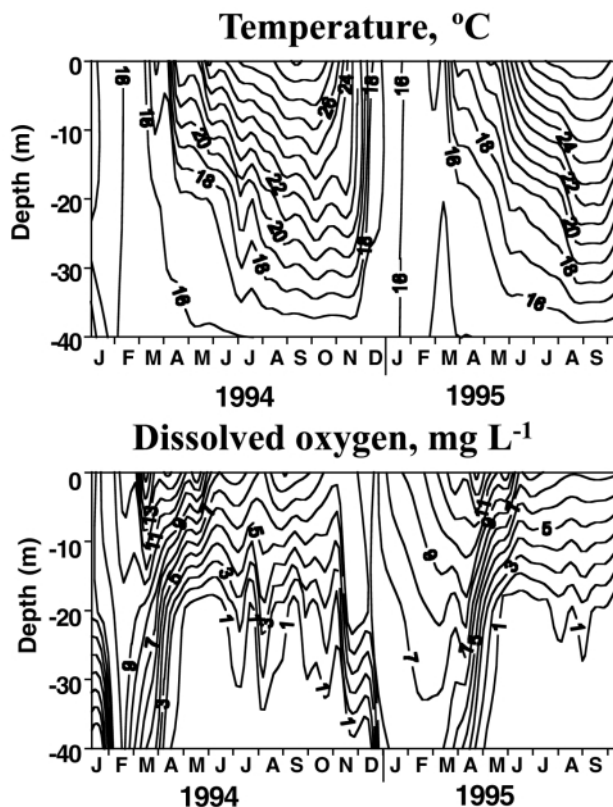


Fig. 2. Changes with time and depth in temperature ($^{\circ}\text{C}$; left) and dissolved oxygen (mg L^{-1} ; right) at station A, 1994–1995.

RESULTS

The physical chemical environment

In 1994, mixing was completed by the end of January and holomixis was maintained for ~ 2.5 months until mid-April. Water temperature ranged from 14°C during mixing to 29°C at the surface in September (Figure 2). In 1995 holomixis started a month earlier than in 1994, already in late-December, and was maintained for ~ 2.5 months, until mid-March. The temperature ranged from 16°C during mixing to 28°C at the water surface during August–September (Figure 2). Following the onset of the stratification oxygen was rapidly depleted in the hypolimnion and by May the entire hypolimnion became anoxic (Figure 2).

Water column biomass and sedimentation

Peridinium gatunense

In 1994, *Peridinium* appeared in the water column in relatively high biomass already in January ($24 \text{ g wet wt m}^{-2}$), peaked in late April after stratification had started ($333 \text{ g wet wt m}^{-2}$), and sharply declined in mid-May (Figure 3).

In 1995 the bloom started to develop relatively late in the year (March), peaked in late April at the onset of thermal stratification ($190 \text{ g wet wt m}^{-2}$) and then gradually declined (Figure 3). Empty thecae appeared in the water column throughout the bloom, while dead cells and protoplasts appeared in the water column in relatively high biomass only in March–May during the bloom peak and decline phases (Figure 3). The biomass of the non-living parts of *Peridinium* in the water column was lower than that of the live cells by about two orders of magnitude (Figure 3).

Catches of *Peridinium* live cells and dead matter in the sediment traps tracked the bloom development in the water column in both years (Figure 3). Trap catches in 1994 were generally higher than in 1995, in accordance with the higher water column biomass in 1994. The annual sedimentation losses of *Peridinium* (dead matter only) in the upper traps was $277 \text{ g wet wt m}^{-2}$ in 1994 and $224 \text{ g wet wt m}^{-2}$ in 1995. The values for the lower traps were $209 \text{ g wet wt m}^{-2}$ in 1994 and $187 \text{ g wet wt m}^{-2}$ in 1995 (Table I).

In the upper traps, sedimentation rates of *Peridinium* live cells (F– treatments) increased in March, peaked in April and declined in May, coinciding with the disappearance of *Peridinium* live cells from the water column. Thecae (in the F+ treatments) were trapped throughout the bloom and in 1994 reached a peak during the time of the bloom decline. Sedimentation rates of dead cells and protoplasts were low to negligible during the phase of increase of the bloom and then sharply peaked after the bloom ended in May–June of both years (Figure 3). In the lower (hypolimnetic) traps the sedimentation rate of *Peridinium* live cells was generally lower (approximately four times) than in the upper (epilimnetic) traps (Figure 3). Sedimentation rates of *Peridinium* thecae, dead cells and protoplasts were similar in pattern to those observed in the upper traps.

Peridinium biomass trapped within the epilimnion was composed mainly of live cells (53–65%). In contrast, the biomass trapped in the hypolimnion was mainly (58–80%) dead matter (thecae, protoplasts and dead cells).

Peridiniopsis spp.

In the water column, *Peridiniopsis* biomass was generally lower by an order of magnitude than *Peridinium* biomass because of smaller cell size and lower cell numbers. *Peridiniopsis* biomass in the water column peaked in May–June after the peak of the *Peridinium* bloom, and declined in June of both years (Figure 4).

Sedimentation rates of *Peridiniopsis* were also much lower than those of *Peridinium* (Figure 4). The highest sedimentation rate for live *Peridiniopsis* cells in the epilimnion ($\sim 35 \text{ g wet wt m}^{-2} \text{ day}^{-1}$) was observed in August 1994

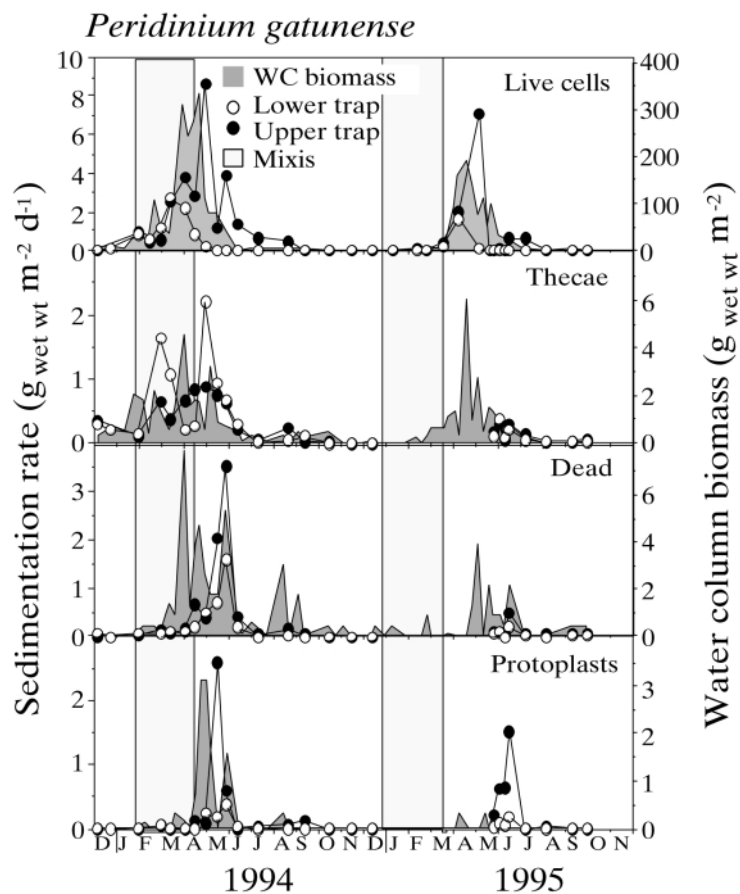


Fig. 3. Sedimentation rates ($\text{g wet wt m}^{-2} \text{ day}^{-1}$) of the different *Peridinium* components into 24-h sediment traps without formaldehyde, located at the base of the epilimnion (upper traps; full circles) and in the hypolimnion at 35 m (lower traps; empty circles) at station A. Gray areas show water column biomasses (g wet wt m^{-2}) of *Peridinium* live cells, thecae, dead cells and protoplasts. Dashed areas indicate the period of holomixis. WC, water column.

Table I: Mass balance for P. gatunense biomass in Lake Kinneret pelagic water, at station A for 1994 and 1995

Year	Water column Annual production g wet wt m^{-2}	Upper trap Σ Biomass g wet wt m^{-2}	% of annual production	Lower trap Σ Biomass g wet wt m^{-2}	% of annual production
<i>P. gatunense</i>					
1994	1337	277	21	209	16
1995	820	224	27	187	23
<i>Peridiniopsis</i> spp.					
1994	n.d.	81	n.d.	55	n.d.
1995	n.d.	52	n.d.	34	n.d.

Annual *Peridinium* production was calculated from μ (Table III) according to equation (5), plus the biomass of thecae that were shed during cell division. Σ biomass is the annual *Peridinium* biomass (thecae, dead cells and protoplasts but excluding live cells) that accumulated in the sediment traps. n.d., Not determined.

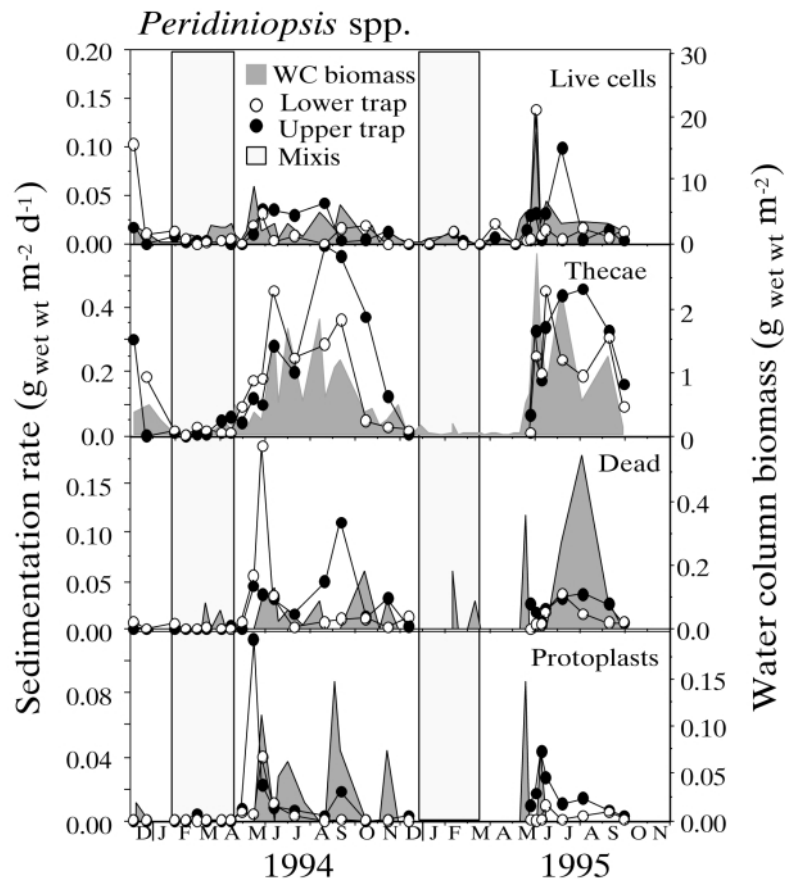


Fig. 4. Same as Figure 3 for *Peridiniopsis* spp.

and in July 1995. The sedimentation rates of *Peridiniopsis* thecae and dead cells peaked in August–September of both years, whereas the sedimentation rates of the protoplasts peaked in May (Figure 4). The sedimentation rates in the hypolimnion were comparable with or higher than those recorded in the epilimnion and peaked in May of both years (Figure 4).

The annual sedimentation losses of *Peridiniopsis* (dead matter only) in the upper traps was $81 \text{ g wet wt m}^{-2}$ in 1994 and $52 \text{ g wet wt m}^{-2}$ in 1995. The values for the lower traps were $55 \text{ g wet wt m}^{-2}$ in 1994 and $34 \text{ g wet wt m}^{-2}$ in 1995.

Sinking velocities

The annual mean sinking velocities (m day^{-1}) for the dinoflagellates at each depth and year are summarized in Table II. Relatively high sinking velocities were observed for *Peridinium* thecae ($1.2\text{--}8.3 \text{ m day}^{-1}$), protoplasts ($1.6\text{--}9.1 \text{ m day}^{-1}$, not shown) and dead cells ($0.5\text{--}4.4 \text{ m day}^{-1}$). The sinking velocities calculated for *Peridinium* live cells were consistently lower ($0.03\text{--}0.2 \text{ m day}^{-1}$) and

practically no different from zero, as expected for motile organisms that can regulate their position in the water column.

For *Peridiniopsis*, a similar picture emerged: high sinking velocities were calculated for the thecae ($1.7\text{--}4.8 \text{ m day}^{-1}$) and dead cells ($0.1\text{--}4.3 \text{ m day}^{-1}$), whereas the sinking velocities for live cells were close to zero ($0.04\text{--}0.1 \text{ m day}^{-1}$) (Table II).

Population dynamics of *Peridinium*

The calculated net growth rate (k) of *Peridinium* during the bloom development phase was 0.04 day^{-1} in 1994 and 0.08 day^{-1} in 1995. During the decline phase of both years this value was negative, -0.04 day^{-1} (Table III). The potential maximum growth rate (μ) of *Peridinium* was $0.06\text{--}0.1 \text{ day}^{-1}$ during the bloom development phase and declined to 0.02 day^{-1} during the decline phase. The death rate (δ) was negligible (0.001 day^{-1}) during the bloom development phase but was 20-fold higher (0.02 day^{-1}) during the decline phase.

Table II: Annual mean sinking velocities \pm SD and number of observations of *P. gatunense* and *Peridiniopsis* spp. components at station A in Lake Kinneret, 1994 and 1995

Year	Trap	Annual mean sinking velocities (m day ⁻¹)		
		Dead cells	Thecae	Live cells
<i>P. gatunense</i>				
1994	Upper	4.4 \pm 3.73 (9)	5.02 \pm 4.1 (13)	0.24 \pm 0.24 (9)
1994	Lower	2.74 \pm 3.37 (10)	8.3 \pm 8.57 (11)	0.1 \pm 0.15 (10)
1995	Upper	1.08 \pm 1.62 (5)	1.69 \pm 1.17 (7)	0.12 \pm 0.12 (13)
1995	Lower	0.45 \pm 0.6 (5)	1.16 \pm 0.71 (7)	0.03 \pm 0.06 (10)
<i>Peridiniopsis</i> spp.				
1994	Upper	4.25 \pm 3.64 (3)	3.63 \pm 1.9 (14)	0.054 \pm 0.062 (13)
1994	Lower	3.4 \pm 5.36 (7)	4.8 \pm 5.78 (14)	0.07 \pm 0.08 (11)
1995	Upper		3.3 \pm 3.26 (8)	0.07 \pm 0.08 (12)
1995	Lower	0.1 \pm 0.05 (3)	1.7 \pm 0.85 (8)	0.04 \pm 0.06 (9)

Calculations for live cells were based on cell counts in traps without preservative and for dead matter on cell counts in traps containing a preservative.

Table III: Population dynamics parameters (growth and loss rate coefficients; units: day⁻¹) for *P. gatunense*

Year	Bloom phase	<i>k</i>	σ	δ	μ
1994	Growth	0.04	0.02	0.0009	0.06
	Decline	-0.04	0.04	0.02	0.02
1995	Growth	0.08	0.02	0.001	0.1
	Decline	-0.04	0.04	0.02	0.02

Data from Lake Kinneret at station A, computed from the water column and upper sediment trap cell counts data, using equations used by Sommer (Sommer, 1984a) $k = \mu - \sigma - \delta$ and assuming that grazing losses are negligible.

Biomass balance for *Peridinium*

Only 20–30% of the total *Peridinium* biomass produced in the water column at the deepest part of the lake (station A) reached the epilimnic trap as recognizable *Peridinium* matter (Table I). The proportion reaching the hypolimnic traps was somewhat lower (15–25%).

DISCUSSION

Shortening the collection periods of sediment traps (to 24 h in our case) without preservative reduces the magnitude of some of the problems associated with use of sediment traps, like decomposition inside the traps or overestimation of sedimentation rates of motile plankton. The percentage of *Peridinium* production lost via sedimentation

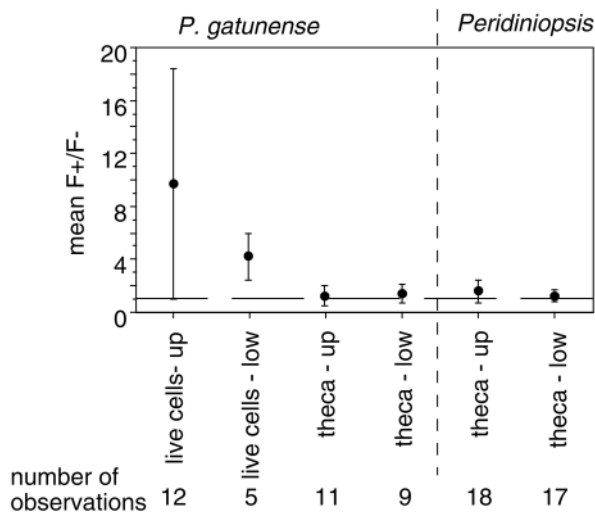


Fig. 5. The mean (\pm SD) F+/F- ratio for trap catches of *Peridinium* live cells and thecae and of *Peridiniopsis* thecae. Data shown are based on cases when at least 50 cells or thecae were counted in both F+ and F- traps. Upper traps (up) were placed at 15 m (epilimnion), lower traps (low) were placed at 35 m (hypolimnion) at the deep station. The horizontal dashed line at F+/F- = 1 indicates no difference between formaldehyde-containing and formaldehyde-free traps.

in 1994, calculated from 24 h trap data (this study) was twice as high as that calculated from 2-week trap data for the same year (Zohary *et al.*, 1998). This difference is attributed to the relatively high within-trap decomposition rates ($\sim 55\%$ per day) reported by Zohary *et al.* to occur inside their 2-week traps.

The sinking velocity of live *Peridinium* and *Peridiniopsis* cells was not more than a few cm per day (Table II), not surprising for motile organisms. In a 40 m water column, this is practically a negligible rate, which implies that passive sinking cannot explain the presence of live cells in traps located at 15 and 35 m depth after 24 h exposure. This led us to conclude that the sedimentation rates of live cells we observed (Figures 3 and 4) were overestimated. Healthy motile cells are able to compensate for gravitational sinking, moreover, dinoflagellates migrate up and down the water column and thus passive sedimentation may be masked by migration in and out of the traps without fixative. Furthermore the migration behaviour of the cells may be disturbed when caught in the traps and interfere with the estimation of the net downwards biomass flux. For that reason in our mass balance for *Peridinium* (Table I) we considered sedimentation rates of live dinoflagellate cells to be zero, although we know it is an underestimation that does not take into account sedimentation of senescent cells or cells that lost their flagella.

In contrast to reports by others (Sommer, 1984a; Heiskanen and Konnonen, 1994; Heiskanen, 1995a,b), our findings in Lake Kinneret show that the sedimen-

tation rates of *Peridinium* and its remains, except for theca, are generally higher in the epilimnion than in the hypolimnion (Figure 3). This might be related to the existence of a sharp thermocline and to the development of an oxycline towards the peak of the bloom. The highest sedimentation rate for live *Peridinium* cells in the deeper traps was observed before the lake stratified, in March 1994. After the onset of thermal stratification the biomass of live *Peridinium* cells that reached the hypolimnion was low ($0.9 \text{ g wet wt m}^{-2} \text{ day}^{-1}$) although the bloom in the water column was at its peak (Figure 3). On the other hand, in the epilimnion the highest sedimentation rate of live cells was recorded after the onset of thermal stratification, and coinciding with the peak of the bloom in the water column. Our conclusion is that after the onset of the thermal stratification live *Peridinium* cells are mostly contained in the epilimnion and do not swim below the thermocline, avoiding anoxic conditions. This behaviour is also typical of the dinoflagellate *Ceratium hirundinella* that usually does not penetrate the anoxic hypolimnion (Harris *et al.*, 1979).

We support the findings of Pollinger and Berman (Pollinger and Berman, 1975) that stratification of dinoflagellates starts before the onset of thermal and chemical stratification in the lake. Contrary to the statement by Serruya *et al.* (Serruya *et al.*, 1980) we suggest that the thermocline per se is not a physical barrier for actively swimming *Peridinium* cells, it is the lack of oxygen that constitutes a barrier. Other dinoflagellate species have been shown to cross temperature gradients of more than 7°C (Kamykowski, 1981), and the dinoflagellate *Gonyaulax tamarensis* can cross a pycnocline (Rasmussen and Richardson, 1989). The absence of a physical barrier is supported also by the penetration of *Peridinium* thecae, dead cells and protoplasts into the hypolimnion after the onset of thermal stratification (Figure 3). The somewhat lower sedimentation rates and sinking velocities of *Peridinium* dead cells and protoplasts in the hypolimnion compared with that in the epilimnion may be attributed to decomposition and grazing in the water column, which reduces the amount of material reaching the lower traps.

Grazing losses to *Peridinium* by mesozooplankton and fish are reported to be low (Serruya *et al.*, 1980; Zohary *et al.*, 1994). These studies did not quantify grazing pressure by micrograzers (protozoans). In the hundreds of microscope samples examined during our 2 year study we rarely witnessed grazing by micrograzers on *Peridinium*. An exception occurred during the bloom decline phase when the ciliate *Bursaria truncatella*, which prior to this period was absent, appeared in the water column. This ciliate is known to feed on *Peridinium* cells (Pollinger, 1987), and indeed was observed actively grazing on *Peridinium* (Figure 1). We do not know whether this ciliate

consumes live cells or dead cells or both, but our observations suggest that the effect of this grazing pressure is limited temporally and to the removal of cells already destined to die.

The potential growth rate for *Peridinium* during the decline phase is three to five times lower than during the phase of population increase. Nevertheless, μ is positive during the decline phase, indicating that cell division still occurs despite the intensive loss processes. We calculated μ using σ values that are higher than zero although we know they result in overestimation. This is justified considering that when σ is nullified the annual *Peridinium* production that is calculated from μ is underestimated and the proportion of *Peridinium* production sedimenting into the traps is more than 100%. The death rate (δ) during the decline phase is higher than during the growth phase by more than one order of magnitude. This increase in death rate shifts the balance from a net increase to a net decline of the population and leads us to conclude that increased death rate, possibly preprogrammed (Vardi *et al.*, 1999), is a major cause for the bloom crash. The cellular processes which lead to the rapid death of *Peridinium* at the end of the bloom in Lake Kinneret are still unknown, but they are apparently activated by the changes in environmental conditions in the lake, especially CO₂ depletion (Berman-Frank *et al.*, 1994; Vardi *et al.*, 1999).

Serruya *et al.* (Serruya *et al.*, 1980) suggested that an early onset of the *Peridinium* bloom and a long mixing period would increase the percentage of total *Peridinium* biomass that sinks to the hypolimnion. According to this hypothesis, we would have expected that a greater proportion of the bloom biomass would reach the hypolimnion in 1994 than in 1995, because in 1994 the bloom started to develop during holomixis, while in 1995 the bloom started to develop only after the lake stratified. Instead, we found the opposite: a greater proportion of the bloom biomass reached the lower traps in 1995 than in 1994 (Table I). We conclude that other factors must have had a greater influence on the amount of *Peridinium* biomass reaching the bottom traps.

Based on the C, N and P content of *Peridinium* remains (Zohary *et al.*, 1998), and wet weight to dry weight conversion factor of 2.5 (Berman, 1978), we roughly estimated the annual sedimentation rates of C, N and P (g m⁻² year⁻¹) to the upper and lower traps at station A (live cells were excluded). The sedimentation rates for C, N and P into the upper traps were 43–53, 3.2–4.4 and 0.17–0.24 g m⁻² year⁻¹ and to the lower traps 36–38, 2.6–4.9 and 0.14–0.25 g m⁻² year⁻¹, respectively. Based on overall yearly sedimentation rates for total particulate matter of ~1400 g m⁻² and for organic matter of ~300 g m⁻² (Klein and Koren, 1998; Koren and Klein, 2000), we

estimated that during the study period *Peridinium* contributed annually ~5–10% of the total sedimentation and 20–35% of the organic matter sedimentation to both epilimnion and hypolimnion. It should, however, be noted that Klein and Koren used traps without a preservative for 2–3-week exposure periods and their sedimentation rates are likely to be underestimated due to within-trap decomposition. The implication is that our estimates of the % of total sedimentation are overestimated.

Our results demonstrated that 15–25% of *Peridinium* production sedimented in 1994 and 1995 as microscopically recognizable matter of *Peridinium* origin. Those estimates are higher than those obtained for 1994 by Zohary *et al.* (Zohary *et al.*, 1998) using sediment traps with 2-week collection periods, but they still show that only a small percentage of the bloom biomass is lost from the water column via sedimentation. With grazing being only a minor loss process for *Peridinium*, it is likely that the main fate of the bloom is decomposition. Experimental work by Zohary *et al.* (Zohary *et al.*, 2000a,b) suggested that dead *Peridinium* cells decompose rapidly, such that within 1–3 days 50% of the biomass is lost. Decomposition rates were similar under aerobic and anaerobic conditions. In particular the thecae, which are C-rich and N and P depleted, disappeared first but their decomposition could not proceed under nutrient limitation. Our sediment trap results, based on microscope counts of recognizable *Peridinium* cells, do not rule out the possibility that much of the dinoflagellate biomass settles slowly as amorphous phytodetrital matter that can no longer be recognized as *Peridinium* or *Peridiniopsis*. A similar fate was proposed by Heiskanen (Heiskanen, 1995b) to be dominant for dinoflagellate blooms in the Baltic Sea.

While the knowledge base regarding *P. gatunense* in Lake Kinneret is intensive, much less is known to date about the four or five species of the genus *Peridiniopsis* that are also a prominent component of the Kinneret phytoplankton (Pollinger and Hickel, 1991). Since the completion of this study, the abundance and relative importance of *Peridiniopsis* spp. in Lake Kinneret has increased especially in the years 1996, 1997, 2000 and 2001, when *Peridinium* failed to bloom (T. Zohary, unpublished data).

In this study we learnt that, in contrast to live *Peridinium* cells, *Peridiniopsis* cells continued to swim to the lower trap after the onset of thermal stratification, possibly taking advantage of the higher nutrient concentrations below the thermocline, at a time when the lake is already stratified and the epilimnion is nutrient depleted (Berman *et al.*, 1992). This could be an important factor allowing *Peridiniopsis* spp. to peak after the decline of *Peridinium*.

However, *Peridiniopsis* spp. never reached cell concentrations as high as those obtained by *Peridinium* [Figures 3 and 4 (Pollinger and Hickel, 1991)], implying that either

the growth rates of *Peridiniopsis* are low, or that its loss processes are relatively high, or both. We also know from this study that sedimentation losses of *Peridiniopsis* normalized per unit biomass of the standing stock (or in fact, the sinking velocities) are low (Table II). Thus, sedimentation is not a major factor removing *Peridiniopsis* biomass from the epilimnion. We conclude that *Peridiniopsis* spp. are probably subjected to higher grazing pressure relative to *Peridinium*. Zohary *et al.* (Zohary *et al.*, 1994) also strongly suggested that during the *Peridinium* bloom decline phase in Lake Kinneret the smaller dinoflagellates are an important food source for zooplankton. Although *Peridiniopsis* spp. never reached cell concentrations as high as those obtained by *Peridinium* the number of *Peridiniopsis* resting cysts was higher than for *Peridinium* (data not shown). These observations highlight different ecological roles in the same lake of two taxonomically close genera.

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