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Bloom dynamics and sedimentation of *Peridinium gatunense* in Lake Kinneret

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Abstract

Temporal changes in the abundance of *Peridinium gatunense* Nygaard in the water column of warm monomictic Lake Kinneret were followed during 1990–1994. Sedimentation rates of this dinoflagellate were followed concurrently by means of sediment traps with and without a preservative (Formalin), positioned at the base of the epilimnion and within the hypolimnion, for exposure periods of 2–3 weeks. Upper trap catches of total *P. gatunense* (live cells + dead cells + thecae + protoplasts + cysts) were nearly always higher than lower trap catches, partly due to decomposition of the cells as they sank through the water column. Over the 5-year period, total *P. gatunense* sedimentation rates ranged over 4 orders of magnitude, from values <0.001 to 8.5 g (WW) m^{-2} d^{-1}. A typical seasonal pattern was observed in which sedimentation rates were relatively low during the bloom increase phase, with thecae (from cell division) being the main component, and increased substantially after the peak of the bloom, when the relative contribution of senescent cells, dead cells and protoplasts increased substantially. Cysts were trapped in low numbers, usually 1–2 orders of magnitude fewer than live cells. Interannual variations in total *P. gatunense* sedimentation were large and independent of the size of bloom—the proportion of annual *P. gatunense* production reaching the hypolimnetic traps ranged from 6% in 1994, the year with the largest bloom, to 68% in 1991, a year with an average-size bloom. The high value was exceptional and we speculated that it resulted from higher resuspension and more severe nutrient limitation of microbial decomposition during that low water level, drought year. On average, thecae accounted for 75% of total *P. gatunense* sedimentation despite being only 55% of the *P. gatunense*-produced biomass, suggesting that thecae were more refractory or less grazed than protoplasts. Thecal C:N:P ratio of >3,000:19:1 (vs. 276:51:1 for protoplasts) indicated that microbial decomposition of thecae is likely to require N and P inputs from other sources. Ultimately, our study highlights for the first time that annual dinoflagellate sedimentation rates may vary dramatically as a result of other processes such as decomposition, resuspension, and grazing, leading to dramatic variations in the amount of organic matter reaching the bottom sediments.

The fate of organic matter produced during seasonal phytoplankton blooms is crucial to the understanding of carbon flow, nutrient cycling, and ecosystem functioning. The main losses for bloom biomasses are grazing, decomposition, or sedimentation. In stratified lakes, grazing and decomposition lead mostly to recycling within the epilimnion, whereas sedimentation removes organic matter and nutrients to the hypolimnion and sediments.

The dinoflagellate *Peridinium gatunense* Nygaard, formerly identified as *Peridinium cincum* fa. *westii* (Hickel and Pollingher 1988), forms an annual spring bloom in mesoeutrophic Lake Kinneret, Israel (Fig. 1). From January–February to April–May it constitutes >90% of the phytoplankton biomass (Pollingher 1981; Pollingher and Hickel 1991) and is responsible for seasonally elevated rates of primary production, up to 4.5 g C m^{-2} d^{-1} (Berman et al. 1995). The bloom declines sharply in May–June, usually shortly after the establishment of stable thermal stratification in this warm monomictic, subtropical lake.

The fate of organic matter produced during blooms of armored dinoflagellates is compounded by the fact that these organisms are composed of two biologically and biochemically different constituents: protoplast and theca. The protoplast is the viable part of the organism, containing most of the proteins, nucleic acids and storage compounds, while the theca is a rigid carbohydrate shell (Loeblich 1969). Many

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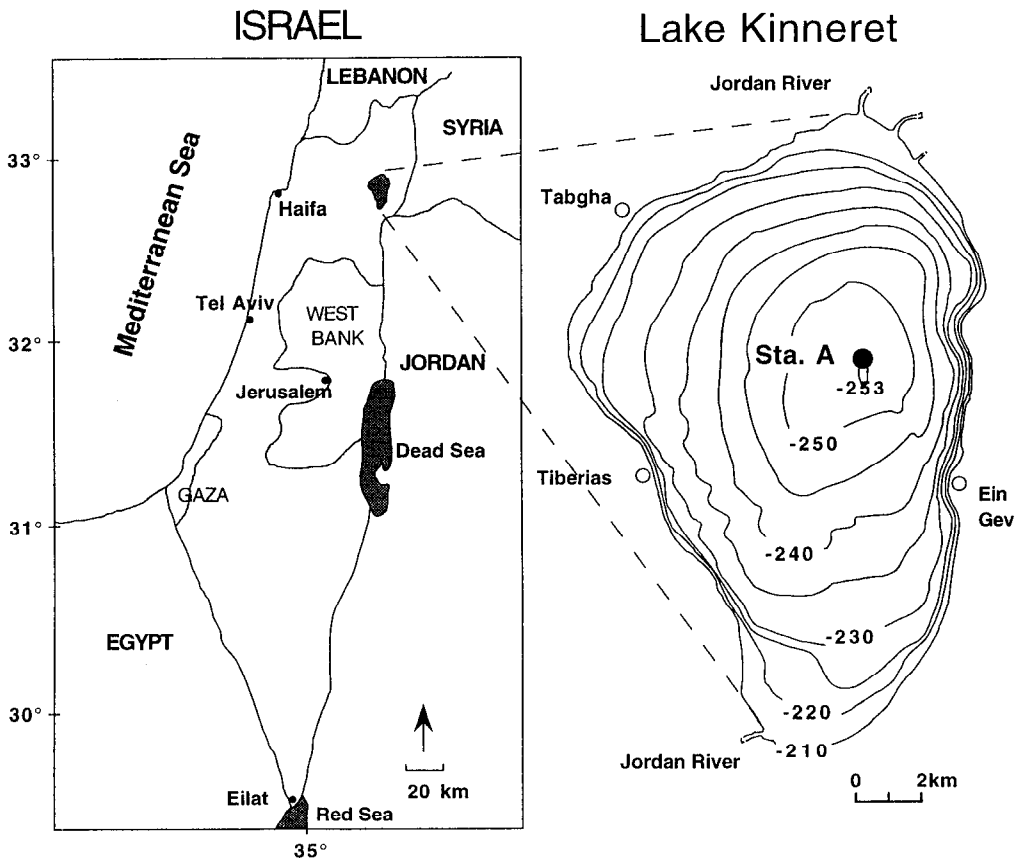

Fig. 1. Location and bathymetric map for Lake Kinneret, also showing location of Sta. A (modified from Parparov and Hambright 1996).

armored dinoflagellates, including the large (40–70-μm-diam) *P. gatunense,* shed their thecae when dividing (Pollingher 1988), thus producing a continuous "rain" of carbohydrates during bloom development. The two protoplasts resulting from cell division typically produce new thecae within hours. Naked protoplasts commonly appear in the water column only during the bloom decline phase. It seems reasonable that grazing, decomposition, and sedimentation are different for protoplasts and thecae, with different implications to carbon flow and nutrient cycling.

We report results of a sediment trap study conducted in Lake Kinneret over 5 years (1990–1994). Our objectives were to follow interannual variations in the dynamics of the *P. gatunense* bloom in the lake, to quantify sedimentation rates and highlight key factors controlling it, and to assess the proportion of *P. gatunense* production lost annually via sedimentation. Emphasis was given to the differential fate of thecae vs. protoplasts.

Methods

The study site, 1990–1994—The 5 years of our study spanned periods of hydrological and meteorological extremes for Lake Kinneret (Table 1). The first 2 years of the

Table 1. Interannual variations in some hydrological, physical, and chemical features in Lake Kinneret. Inflow and loading data are taken from Geifman and Rom (1995) and are given for hydrological years (October–September); other data are taken from the Lake Kinneret database and are for calendar years. Water level, temperature, and H_2S data are monthly means.

	Inflow vol. (10^6 m^3)	Annual N load (t)	Annual P load (t)	Water level (m alt.) Max. (spring)	Water level (m alt.) Min. (fall)	Period of holomixis	Min. winter water temp. (°C)	Max. hypolimnion H_2S concn (mg liter^{-1})
1990	387	481	30.7	−211.8	−213.0	14 Jan–17 Apr	15.3	10.9
1991	414	508	38.5	−212.0	−212.9	30 Dec–7 Apr	15.3	13.2
1992	1,526	4,668	186	−208.9	−209.7	6 Jan–12 Apr	12.3	5.3
1993	922	1,811	124	−208.9	−210.0	3 Jan–22 Mar	13.8	9.1
1994	530	861	56.3	−208.9	−211.1	17 Jan–17 Apr	15.9	9.0

study (1990 and 1991) were the second and third years of a 3-year drought, and were therefore characterized by low inflow volumes (~400 × 10^6 m^3), low nutrient loading, and, owing to continued pumping of water for domestic uses and irrigation, also exceptionally low water levels. The lake reached its lowest level on record (213 m below mean sea level) in December 1990, and remained at low levels throughout 1991. In both years, water-column temperature after overturn exceeded 15°C, thermal stratification started in April, and by May the hypolimnion was anaerobic. As a result of anaerobic decomposition of organic matter via sulfate reduction (Hadas and Pinkas 1995), H_2S accumulated in the hypolimnion, with concentrations at 30-m depth exceeding 11 mg $liter^{-1}$ in November 1990 and 13 mg $liter^{-1}$ in October 1991.

In contrast, 1992 was the coldest of the century and one of the wettest years on record, with total inflow volume of >1,500 × 10^6 m^3. Within 3 months water levels rose by 4.1 m, and after overturn (6 January 1992) mean monthly water-column temperature was 12.3°C, the lowest ever recorded in Lake Kinneret (Hambright et al. 1994). Thermal stratification stabilized in mid-April, but the hypolimnion remained oxygenated until July, much later than usual (Parparov 1994). Hypolimnetic H_2S appeared late in 1992, and reached considerably lower concentrations (5.3 mg $liter^{-1}$) than in other years.

In 1993 it was also cold and wet with high water levels, but was less extreme than in 1992. There was a distinctly shorter period of holomixis than for the 4 other years. In 1994 there were average inflows but water levels were still high. Winter water-column temperature in 1994 was higher than in all other years and the stratification pattern was normal, with anoxia developing in the hypolimnion by May and H_2S concentrations reaching ~9 mg $liter^{-1}$.

Field measurements and sampling—All fieldwork was conducted at Sta. A (Fig. 1), situated at the deepest part of the lake (43 m) at the node of most seiche activities (S. Serruya 1978). Depth profiles of water temperature were recorded weekly or biweekly with a profiling thermistor (Applied Microsystem, model STD-12). Water samples for *P. gatunense* cell counts were taken with a 5-liter vertical sampler from 0, 1, 2, 3, 5, 7, 10, 15, 20, 30 and 40 m, concurrently with the routine weekly chemical monitoring of the lake. Phytoplankton samples were preserved in 1% acid Lugol's solution. Thermocline depth was defined as the depth >10 m at which the temperature gradient exceeded 0.3°C over 1 m (Hambright et al. 1994).

Two sets of sediment traps, each comprised of four replicate cylindrical traps, were deployed one above the other at Sta. A. The lower set was placed within the hypolimnion at 26–30 m and the upper set near the base of the epilimnion at 14–18 m, depending on water level. In 1990, only the lower set was deployed. The cylinders were made of opaque PVC tubes (52-mm i.d., 60-cm length; aspect ratio of 11.5) with replaceable 300 ml plastic collection bottles at their lower end. The traps were secured in an upright position to a positively buoyant cross-shaped frame that was connected by a tight rope to a weight at the bottom of the lake. A second rope, connecting the weight to a permanent float, was used to retrieve the traps by lifting the weight and allowing the traps to float. Glass bead-weighted dialysis bags containing 10 ml of concentrated (40%) Formalin were placed in two of the four collection bottles in each set of trap. We assumed that material sinking into formalin-containing bottles (F+ traps) would be preserved in the state at which it entered the collection bottle, whereas decomposition and possibly grazing would take place in the bottles without preservative (F− traps). Sedimenting matter was collected at 2–3-week intervals by replacing the collection bottles in situ, providing a continuous 5-year record (January 1990–December 1994). The material in replicate bottles was combined and preserved in Formalin (2% final concn) for subsequent analyses.

Laboratory analyses—*P. gatunense* in water column and sediment trap samples were counted in 1 mL sedimentation chambers with an inverted microscope (Utermöhl 1958). The entire milliliter was counted, except during the peak bloom times, when *P. gatunense* abundances exceeded 1,000 cells ml^{-1}, during which samples of 0.2–0.5 ml were analyzed. In the sediment trap samples we distinguished between the different *P. gatunense* constituents, i.e. live and dead cells, protoplasts, thecae, and cysts (Fig. 2). Live cells could be distinguished from dead ones by the shape of the protoplast. In live cells, the protoplast occupied the entire thecal space, whereas in dead cells the protoplast was shrunken such that space could be seen between the protoplast and theca. Protoplasts were free of thecae and were usually shrunken in size (i.e. dead), while thecae were empty shells. Only whole or half thecae were counted; individual thecal plates were occasionally encountered in the samples but they were excluded from the counts. The counts were converted to wet weight biomass by multiplication by respective biovolumes previously computed by U. Pollingher (unpubl. data) from linear dimensions of at least 20 individuals and the closest geometrical shape (Table 2), assuming specific density of 1 for all cell parts except for cysts, where a specific density of 1.08 (Anderson et al. 1985) was used.

Calculations—The discrete-depth *P. gatunense* biomasses were depth integrated to give a water-column value in g (WW) m^{-2}. A 5-week running average was computed to reduce the effect of horizontal patchiness (Berman and Rhode 1971). The net rate of change (k), based on observed changes in the running average standing crop, was calculated from the equation

$$k = \ln(N_2/N_1)/(t_2 - t_1),$$

where N_1 and N_2 are the running average *P. gatunense* biomass at times t_1 and t_2.

Sedimentation fluxes were expressed as g (WW) m^{-2} d^{-1} and then time integrated to give annual sedimentation rates. Initially, F+ and F− traps were used to examine within-trap decomposition rates. However, we found that the differences between F+ and F− trap catches of live cells were up to 10-fold greater than for dead cells. Because there was no reason for live cells to decompose faster than dead ones, we attributed this to the diel vertical migration behavior of *P. gatunense* (Berman and Rhode 1971; Pollingher and Berman

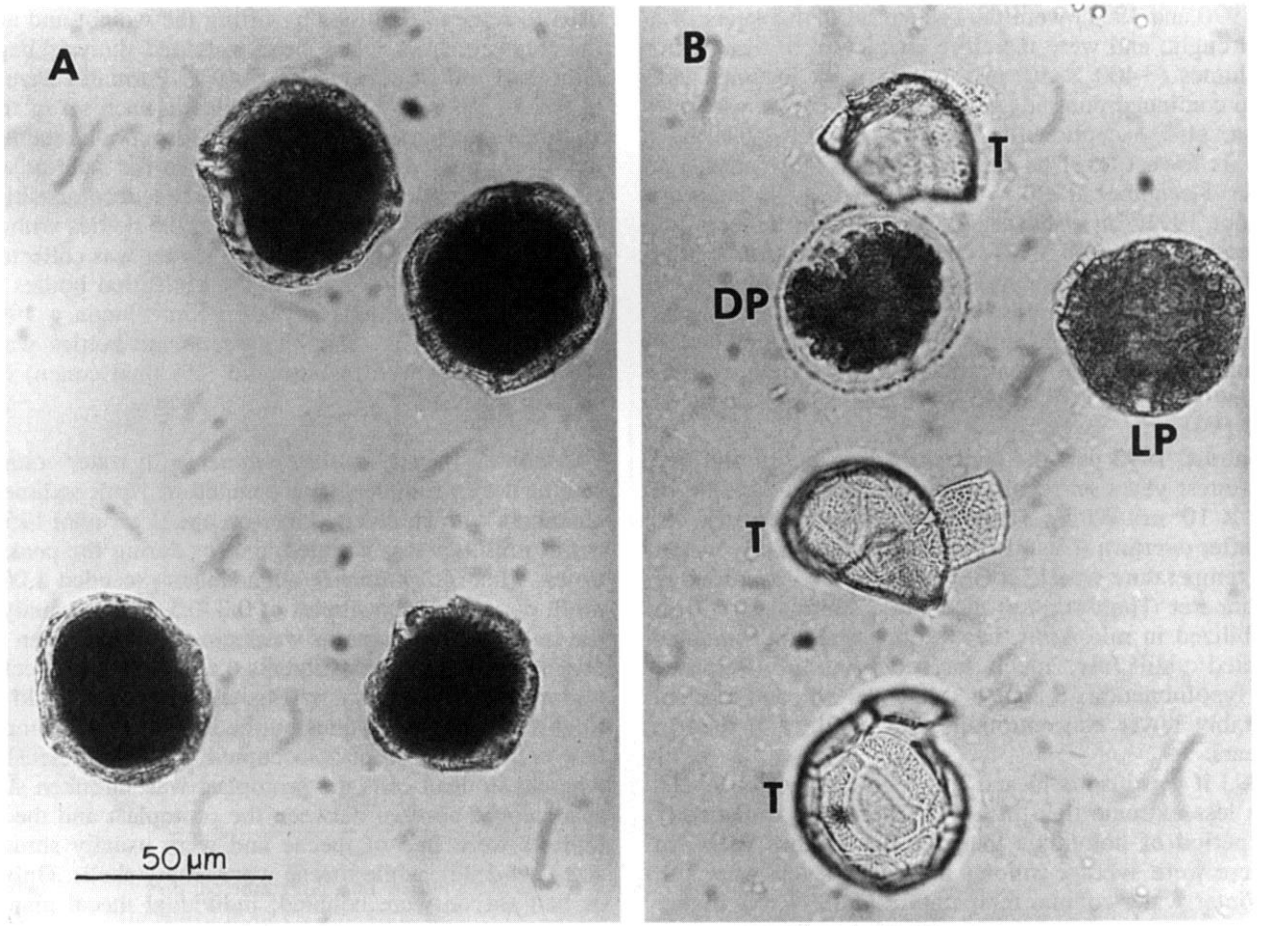

Fig. 2. Photomicrographs of *P. gatunense* from Lake Kinneret. A. Live cells. B. Other *Peridinium* constituents. T, empty theca; DP, dead protoplast (shrunken, membrane-bound); LP, live protoplast, filling the entire membrane-bound space.

1975). This assumption was based on three lines of evidence. First, comparison of catches of sediment traps with and without Formalin exposed for only 24 h revealed an order of magnitude difference in the number of live cells in F+ vs. F− traps, while the numbers of thecae, dead cells and protoplasts were similar (Winer 1998). Concurrent laboratory incubations at 22°C revealed that a 24-h period was shorter than the time needed for *P. gatunense* cells to decompose to a stage where they are microscopically unrecognizable (unpubl. data). Second, the differences between F+ and F− catches in the lower traps disappeared after the onset of chemical stratification, i.e. after *P. gatunense* ceased migrating into the hypolimnion (*see below*). Third, similar diel migration effects on dinoflagellate sedimentation catches in traps containing a preservative were reported from the northern Baltic (Lignell et al. 1993; Heiskanen 1995*a*).

Table 2. Calculated biovolumes (means for 20 ind.) for *Peridinium gatunense* used to convert cell counts into biomass. A specific density of 1 was used to convert the biovolumes into biomass, except for cysts, for which a specific density of 1.08 was used.

Cell part	Biovolume (μm^3)
Live cell	70,000
Dead cell	55,000
Protoplast	45,000
Theca	21,000
Cyst	4,500

Based on the above, the F− trap data were used for estimates of sedimentation rates of live *P. gatunense* cells, although owing to within-trap decomposition these data may underestimate the actual sedimentation rate of live cells by >50% (*see below*). The F+ trap data were used for the dead cells, protoplasts, thecae, and cysts, and we assumed no decomposition losses. Total *P. gatunense* sedimentation rates were then estimated as the sum of live cells in F− traps and dead cells, protoplasts, thecae, and cysts in F+ traps.

The sum of all thecae (empty thecae + thecae on live and dead cells) and the sum of all protoplasts (naked protoplasts + those in live and dead cells) were used to estimate relative budgets for thecae vs. protoplasts. The fraction of *P. gatunense* production lost annually via sedimentation was estimated as the ratio between the annual sedimentation and annual production. Primary production due to *P. gatunense* was computed from biweekly measurements of phytoplankton and *P. gatunense* biomasses (in g (WW) m^{-2} d^{-1}) and primary production (in g C m^{-2} d^{-1}; ^{14}C method), which are monitored as part of the Lake Kinneret routine monitoring

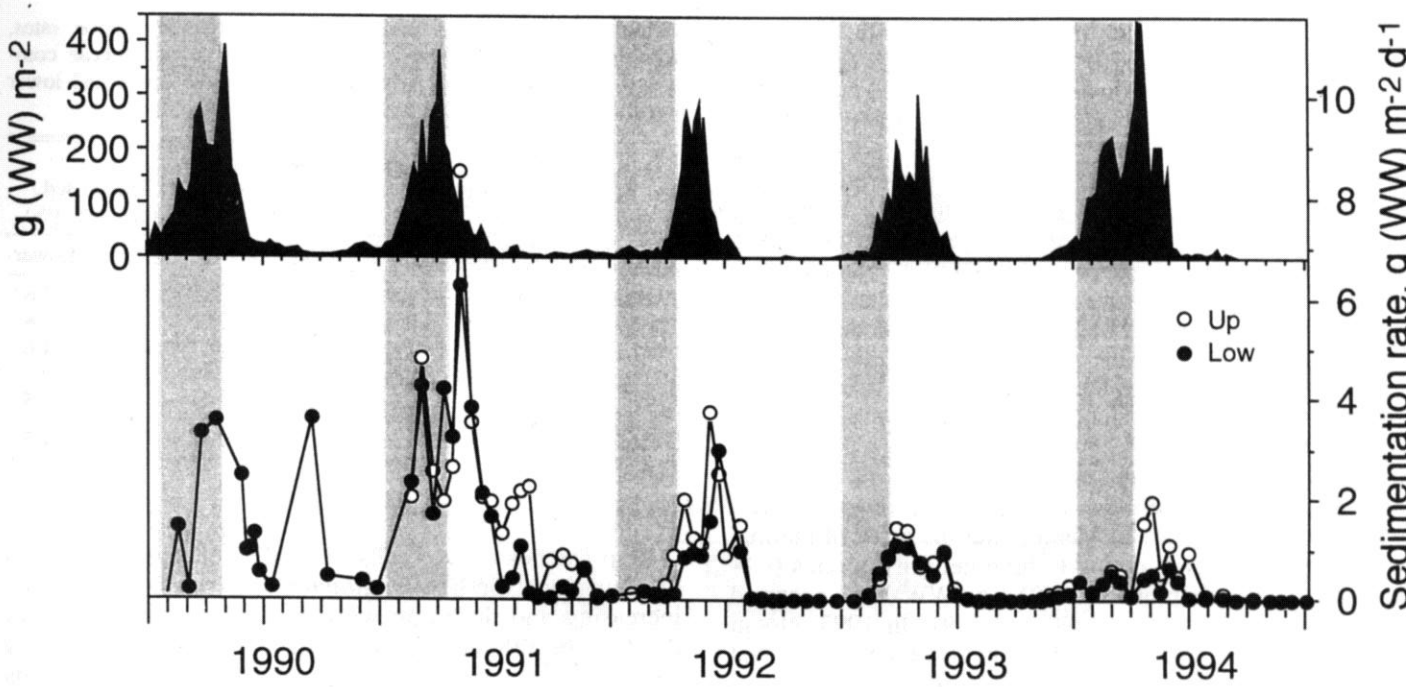

Fig. 3. Upper panel: The dynamics of five annual *P. gatunense* blooms in Lake Kinneret at Sta. A, 1990–1994. Data shown are depth-integrated (15–43 m, depending on stratification) wet weight biomasses (g (WW) m^{-2}). Lower panel: Total *Peridinium* sedimentation rates (g (WW) m^{-2} d^{-1}) for the upper traps (○, depth of 15–18 m) and lower traps (●, depth of 26–30 m). Shading indicates periods of holomixis.

program. The portion of total phytoplankton production attributed to *P. gatunense* was estimated by using a linear regression that related *P. gatunense* relative abundance and its relative production based on measurements by Pollingher and Berman (1982). *P. gatunense* production was time integrated over the entire bloom season and converted from C to wet weight biomass assuming C is 20% of wet weight (Berman 1978).

Within-trap decomposition rates for all constituents except live cells were computed from the differences between F+ and F− traps and expressed as the proportion of the amount in the F+ traps.

Cellular C, N, and P contents—Carbon, nitrogen, and phosphorus contents were measured on freeze-dried samples of whole cells and empty thecae suspended in GF/C-filtered lake water. Whole-cell samples were collected with a 20-μm mesh net during the growth and peak stages of the 1995 bloom, when ambient total dissolved P concentrations were low (5–8 μg $liter^{-1}$). Microscopic examination confirmed that >95% of the material was healthy *P. gatunense* (no separation of protoplasts from thecae). The thecae were collected from the bottom of a culture flask containing axenic *P. gatunense* isolated from Lake Kinneret and grown on Lindstrom 16 medium (Lindstrom 1985). To remove externally adsorbed phosphate originating from the P-enriched growth medium without affecting structural P, the dried thecae were washed in dilute (0.1 N) HCl and then three times in distilled water prior to resuspension in filtered lake water. The suspensions and their filtrates (Millipore, 0.45 μm) were analyzed for dry weight, total N, and total P by using standard methods (Am. Publ. Health Assoc. 1992) and for their C content with a CHN analyzer. C, N, and P contents of cells and of thecae were computed from the differences between suspensions and their filtrates. C, N, and P contents of protoplasts were calculated from the relative biomass-weighted differences between whole cells and thecae.

Table 3. Interannual variations in the timing, net growth, and decline rates (k; negative values indicate net mortality) and peak biomass (5-week running average; RA) for *P. gatunense* in Lake Kinneret, 1990–1994.

	Growth phase	k (d^{-1})	Peak RA biomass g (WW) m^{-2}	Decline phase	k (d^{-1})
1990	1 Jan–25 Mar	0.025	262	23 Apr–3 Jun	−0.030
1991	1 Jan–25 Mar	0.039	271	14 Apr–30 Jun	−0.036
1992	24 Mar–3 May	0.060	254	24 May–26 Jun	−0.049
1993	25 Jan–31 Mar	0.043	189	23 May–18 Jul	−0.080
1994	23 Nov 93–10 Apr	0.025	326	17 Apr–19 Jun	−0.053

Results

The Peridinium *blooms, 1990–1994*—The timing of the *P. gatunense* bloom development, peak and decline as well as the growth and decline rates and the peak biomass attained varied from year to year (Fig. 3, Table 3). Typical blooms (relative to long-term record; Pollingher 1981) were observed in 1990 and 1991, when bloom development was

initiated in January and its peak coincided with the establishment of thermal stratification, after which the decline phase began. The peak (5-week running average) biomasses in 1990 and 1991 were 262 and 271 g (WW) m^{-2}. The 1994 bloom was similar in its timing to those of 1990 and 1991, but was exceptional in the high peak biomass attained, 326 g (WW) m^{-2}, a record value in 25 years of monitoring in Lake Kinneret. Net growth rates during bloom development (range of 0.025–0.039 d^{-1}) and net loss rates during the declines were generally similar in those 3 years, with the exception of a somewhat faster decline rate in 1994. Also, following the bloom decline in those 3 years, *P. gatunense* remained in the water column throughout the summer, albeit at low abundances (5–10 g (WW) m^{-2}).

The 1992 and 1993 blooms were shorter and their initiation was delayed compared with 1990, 1991 and 1994. The more extreme case was in 1992, when *P. gatunense* development started only late in March, after the onset of thermal stratification; however, owing to high net growth rates (k = 0.06 d^{-1}), the peak biomass of 253 g (WW) m^{-2} occurred in May, similar to that of 1990 and 1991. In 1993, bloom initiation was postponed by 3–4 weeks relative to the typical case. This bloom had the lowest peak biomass in the 5-year record, 189 g (WW) m^{-2}. In both 1992 and 1993, the summer abundances of *P. gatunense* (consistently <2 g (WW) m^{-2}) were much lower than in the other years.

Bulk Peridinium *sedimentation rates*—Upper trap catches of total *P. gatunense* were nearly always higher than lower trap catches (Fig. 3). Over the 5 year period, total *P. gatunense* sedimentation rates ranged over 4 orders of magnitude, from values <0.001 to 6.2 g (WW) m^{-2} d^{-1} (lower traps) or 8.5 (WW) m^{-2} d^{-1} (upper traps). The seasonal pattern of the bloom was reflected in the trap catches, but the absolute amounts were not. Peak sedimentation rates coincided with the initiation of the bloom decline each year, but the magnitude of this peak varied considerably from year to year.

In general, 1990 and 1991 were high sedimentation years whereas 1992, 1993 and 1994 were years of lower *P. gatunense* sedimentation rates. The large interannual variability is evident from a six- to seven-fold difference between years in mean daily sedimentation rate averaged over the bloom period plus 1 month (Table 4), which ranged for the upper traps from 0.5 g (WW) m^{-2} d^{-1} in 1993 to 3.0 g (WW) m^{-2} d^{-1} in 1991, and for the lower traps from 0.36 g (WW) m^{-2} d^{-1} in 1994 to 2.6 g (WW) m^{-2} d^{-1} in 1991. This meant that 0.24% of the average *P. gatunense* biomass during the bloom season was lost daily via sedimentation and reached the lower traps in 1994 as opposed to 2.3% in 1991.

Sedimentation of different Peridinium *constituents*—Owing to the large interannual variability in bulk *P. gatunense* sedimentation rates and in order to magnify the details for the low sedimentation years of 1992–1994, the data for the individual *P. gatunense* constituents were plotted on a logarithmic scale (Fig. 4). As expected, different sedimentation rates and patterns were observed for the constituents.

Table 4. Interannual variations in daily sedimentation rates, within-trap decomposition rates, and the proportion thecae comprised of total *Peridinium* sedimentation for the upper and lower traps, averaged over the bloom season plus 1 month.

	Daily sed. rate (g m^{-2} d^{-1})		Within-trap daily decomp. (%)		Thecae sed./ total sed. (%)	
	Upper	Lower	Upper	Lower	Upper	Lower
1990	1.39	1.98	—	32.5	—	53.6
1991	2.62	2.97	47.0	59.1	67.8	72.8
1992	0.93	1.42	37.4	37.4	69.8	74.6
1993	0.43	0.51	80.1	59.6	76	69
1994	0.36	0.73	76.3	65.9	69.4	76.5
Overall mean	1.15	1.44	55.5	54.0	70.75	69.3

Trap catches of live cells generally reflected the pattern of abundance for live *P. gatunense* in the water column, increasing and declining with the waxing and waning of the bloom, although the absolute amounts varied greatly from year to year. Dead *P. gatunense* cells and protoplasts were absent or rare during the growth phase. Both forms increased in abundance after the peak. Whereas the sedimentation of live cells, dead cells, and protoplasts ended shortly after the end of the bloom, thecae were continuously trapped throughout the annual cycles of 1990 and 1991, but not in 1992–1994. Theca constituted 70% of the total sedimented *P. gatunense* matter (Table 4, Fig. 5). Cysts occurred in low numbers, usually 1–2 orders of magnitude less frequently than live cells in the F− traps. Cysts were considerably more abundant in the traps in 1993 and in 1994 than in the previous 3 years, and occurred mostly during the decline phase.

Peridinium *death and decomposition: microscopic observations*—Early signs of cell death, commonly observed during the decline phase, were microscopically visible oil droplets within the cells, which later leaked outside the enveloping membrane, followed by shrinkage of the protoplast. The thecae of dead cells were often infested with bacteria and their microflagellate grazers. Protoplast decomposition was initiated by the rupture of its outer membrane; without this rupturing, protoplasts remained intact. During the decline phase, protoplasts and dead cells often formed aggregates inside the F− traps, and a microbial grazer community developed, comprised of rotifers (*Asplanchna* and *Ascomporpha*) and ciliates (*Bursaria, Coenomorpha,* and *Colleps*). First stages of *P. gatunense* encystation were observed after the peak of the bloom (e.g. late in March 1991 and early in May 1992).

Within-trap decomposition rates—Within-trap decomposition rates, computed as the percentage difference between the F+ and F− trap catches of thecae + protoplasts + dead cells and averaged for the bloom season + 1 month each year, ranged from 30 to 80% (with a multiannual mean of 55%; Table 4), thereby justifying the use of Formalin-con-

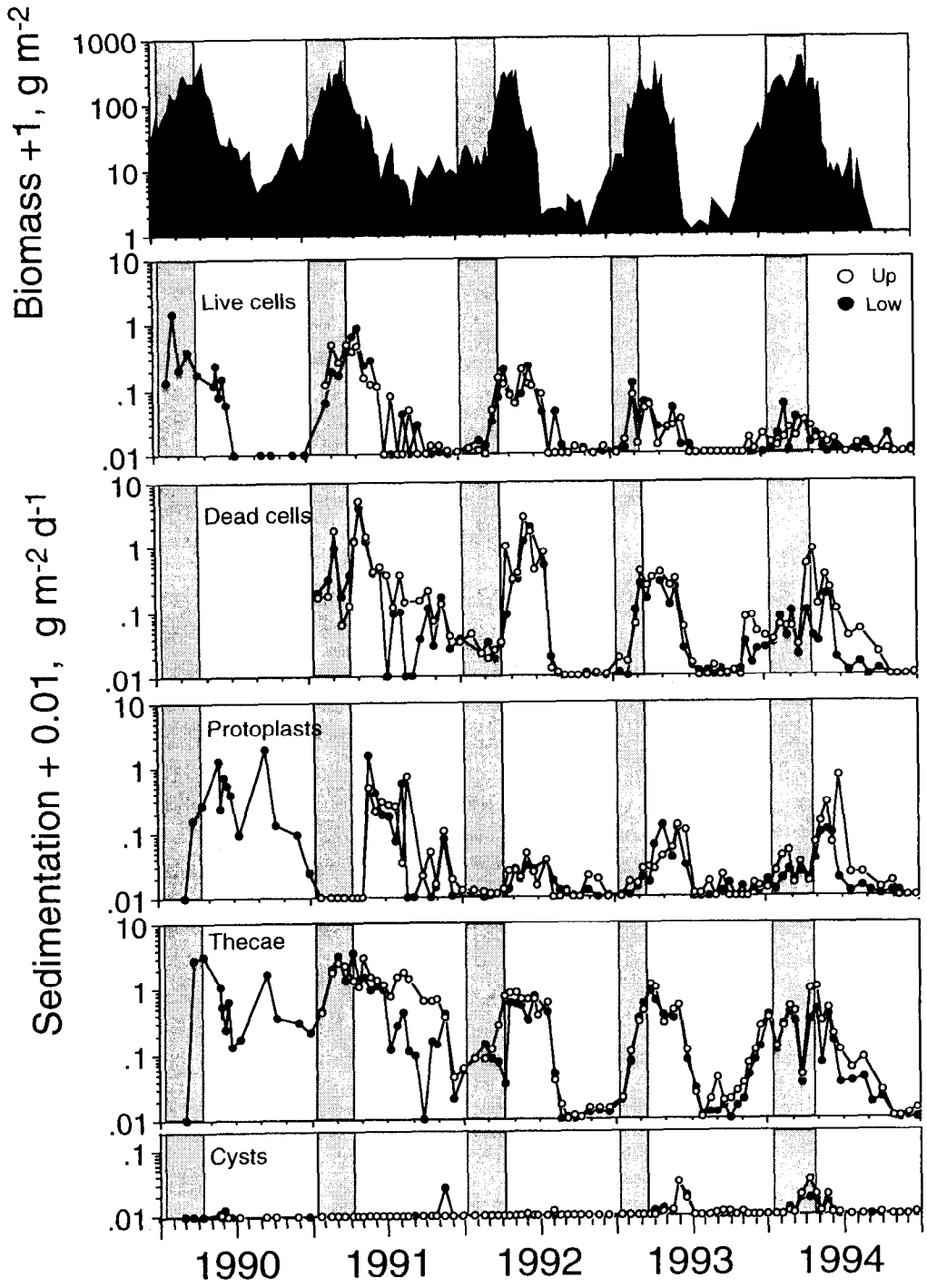

Fig. 4. The data from Fig. 3 redrawn on a log scale, with sedimentation rates split into the different *P. gatunense* constituents (live cells, dead cells, naked protoplasts, empty thecae). F−, traps without formalin; F+, traps containing formalin; U, upper traps; L, lower traps. In 1990, protoplasts and dead cells were counted as one category and are shown under protoplasts.

taining traps for estimating sedimentation rates of the non-motile *P. gatunense* components.

Loss of Peridinium *production*—Estimated annual production due to *P. gatunense* ranged from 679 g (WW) m^{-2} $year^{-1}$ in 1992 to 1,172 g (WW) m^{-2} $year^{-1}$ in 1994, with a 5-year mean of 924 g (WW) m^{-2} $year^{-1}$ (Table 5). Annual total *P. gatunense* sedimentation into the upper traps ranged from 143 g (WW) m^{-2} $year^{-1}$ in 1994 to 673 g (WW) m^{-2} $year^{-1}$ in 1992. Annual sedimentation into the lower traps was always lower than that into the upper traps, with 5-year means of 233 and 290 g (WW) m^{-2} $year^{-1}$, respectively. The

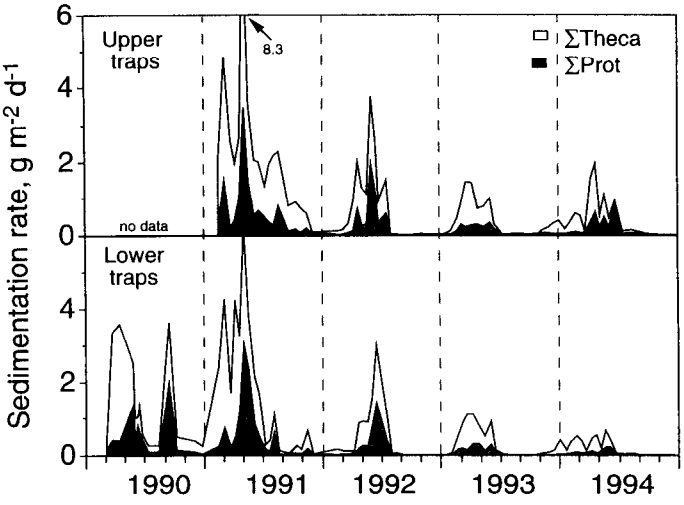

Fig. 5. The proportion of total *P. gatunense* sedimentation rates due to thecae and protoplasts, 1990–1994.

proportion of *P. gatunense* production lost annually via sedimentation varied considerably, from 12 to 88% in the upper traps and from 6 to 68% in the lower traps, with the lower values being more common (Table 5).

C, N, and P contents of Peridinium *cells and thecae*—C content of *P. gatunense* whole cells was 461.5 mg g $(DW)^{-1}$ and was somewhat higher for empty theca, 520 mg g $(DW)^{-1}$ (Table 6). P content of whole *P. gatunense* cells was 2.9 ± 1.2 mg g $(DW)^{-1}$ versus only 0.4 ± 0.26 mg g $(DW)^{-1}$ in thecae. Whole-cell N content was 55.4 ± 8.6 as compared with only 3.0 mg g $(DW)^{-1}$ for thecae. Assuming that whole cells represented the sum of theca + protoplast, the computed nutrient content of protoplasts was 434, 80, and 4 mg of C, N and P per gram dry weight of protoplast.

Discussion

The dynamics of five annual blooms of the dinoflagellate *P. gatunense* were followed in Lake Kinneret. Year-to-year variability was observed in various static and dynamic aspects of the bloom such as the net rates of increase and decline, the maximum biomass attained and the timing of the bloom initiation, peak and decline in relation to the thermal structure of the water column (Fig. 3, Table 3).

Table 5. Interannual variations in estimated *P. gatunense* primary production (PPP; converted from C to wet weight units assuming C = 0.2 wet weight), annual total sedimentation rates, and the percentage of PPP lost owing to sedimentation calculated for the upper and lower sediment traps.

		Upper traps		Lower traps	
	PPP (g (WW) m^{-2} $year^{-1}$)	Total sed. (g (WW) m^{-2} $year^{-1}$)	% PPP sedimented	Total sed. (g (WW) m^{-2} $year^{-1}$)	% PPP sedimented
1990	1,032	—	—	314	30
1991	764	673	88	523	68
1992	679	198	29	133	20
1993	974	145	15	128	13
1994	1,172	143	12	66	6
5-year mean	924	290	36	233	27

Typically, bloom development started at overturn and ended with the onset of thermal stratification, suggesting that *P. gatunense* development was closely linked to the period of holomixis. The 1992 bloom stood out as being different, with an ~6-week delay in its initiation so that the bloom increase phase took place mostly after the onset of thermal stratification. However, the increase was faster than in the other years, eventually reaching a peak biomass that was only slightly lower than those attained in 1990 and 1991. The delayed initiation of the 1992 bloom may be explained by suppressed initial division rates caused by lower than usual water temperatures (Table 1) and higher turbulence due to frequent storms. A delay in the development of chemical stratification and hypolimnetic oxygen depletion in that unusually cold and wet year enabled the development of the bloom even after the establishment of thermal stratification. We speculate that via diurnal vertical migrations *P. gatunense* was able to utilize nutrients from the metalimnion in 1992, as this layer remained oxygenated and free of H_2S until July, whereas in other years the metalimnion became anaerobic and therefore inaccessible to *P. gatunense,* by May.

Phytoplankton sedimentation rates usually depend on standing stocks, species composition, and the physiological state of individual cells (Sommer 1984; Reynolds 1984). In Lake Kinneret, annual *P. gatunense* sedimentation rates were conspicuous in not being directly related to the peak water column biomass. For example, in 1994 the highest water column standing stock was recorded, but the amount of *P. gatunense* matter collected in the sediment traps was the lowest of the 5-year series (Fig. 3, Table 5), whereas an average bloom in 1991 had the highest measured annual sedimentation. However, within each year the seasonal pattern of *P. gatunense* sedimentation tracked the seasonal pattern of bloom increase and decline, with a short time lag (Fig. 3), as could be expected (*see* Smetacek 1985; Horn and Horn 1993). Sedimentation rates remained low during the bloom increase phase but increased substantially after the peak of the bloom, when growth conditions worsened and most of the sedimenting cells were senescent or dead.

For some diatoms, mass sedimentation during periods of calm weather is a primary cause for bloom decline (Knoechel and Kalff 1975). In Lake Kinneret, sedimentation was not a cause for the bloom decline, but only a secondary process, enhancing the elimination of a population handicapped by a combination of other factors, such as CO_2 limitation, N + P limitation, elevated water temperature, turbulence and solar radiation (especially UVB) (Berman-Frank et al. 1994, Berman and Dubinsky 1985, Hader et al. 1990). Increased sedimentation losses of moribund populations were also reported for diatoms (Sommer 1984) and for *Microcystis* (Takamura and Yasuno 1988, Zohary and Robarts 1989).

Sedimentation rates have been estimated using sediment traps in many lakes. However, the rates vary considerably

Table 6. Carbon, phosphorus, and nitrogen content of *P. gatunense* whole cells, empty thecae, and protoplasts and their molar ratios. Data shown are means (±SD) with number of cases in brackets, except for protoplasts for which the values are calculated.

	C (mg g (DW)$^{-1}$)	N	P	C:N:P molar ratio
Whole cells	462±32 (11)	55.4±8.6 (13)	2.9±1.2 (13)	412:49:1
Thecae	520 (1)	3.0±0.03 (2)	0.4±0.26 (3)	3,336:19:1
Protoplasts	434	80	4	276:51:1

with the method of measurement, and the values must be compared with caution. In shallow eutrophic Lake Kasumigaura (Japan), *Microcystis* sedimentation was estimated to constitute 59% of gross primary production (Takamura and Yasuno 1988). Other values are 30–40% for cyanobacterial sedimentation in Lake Mendota (Fallon and Brock 1980), 14% in Lake Lucern, 30% in Lake Rotsee (Bloesch et al. 1977), and 25% in Lake Lugano (Premazi and Marengo 1982). For marine environments, Laws et al. (1988) reported that 40% of primary production sedimented out in Auke Bay, Alaska, and a higher estimate of 72% (mostly dinoflagellates) was reported by Lignell et al. (1993) for the northern Baltic. These studies do not show interannual variations. Our study, with annual values ranging from 6 to 88%, depending on the year and depth of the trap, demonstrates clearly that interannual variations cannot be disregarded.

The high proportion of *P. gatunense* production sedimented in 1991 was an exception, and in 4 out of 5 years in Lake Kinneret, annual sedimentation accounted for no more than 30% of *P. gatunense* primary production (Table 5). A similar estimate of <20% was obtained by C. Serruya (1978). Note that our values are somewhat underestimated since the contribution of the live cell component to total sedimentation is based on F− traps where within-trap decomposition may have led to substantial losses. Nevertheless, the question arises of why sedimentation losses in 1991 (and to a lesser extent also in 1990) were so much greater than in the other years. Although our data do not provide an answer to this question, some speculation is warranted.

It is evident that the high 1991 values (and to a lesser extent, also 1990) resulted from two main differences in *P. gatunense* sedimentation patterns: (1) during the bloom, sedimentation rates in 1990 and 1991 were much higher than in the following years; (2) in 1990 and 1991, *P. gatunense* sedimentation, most of which was empty thecae, continued throughout the entire summer, long after the bloom ended, whereas in the later years *P. gatunense* sedimentation ceased abruptly after the end of the bloom. Another critical difference was in water levels, which in 1990 and 1991 were at record lows, as much as 4 m lower than in subsequent years (Table 1). We therefore speculate that two factors that led to the high 1991 values were increased resuspension and reduced decomposition rates, both having resulted from the drought and low water levels.

Evidence exists that resuspension of sedimented material in Lake Kinneret may be enhanced at low water levels (Nishri et al. 1996). The resuspension is to a large extent due to boundary-mixing processes that result from internal waves at the thermocline breaking against the lake bottom and forming strong jets within the metalimnion (Imberger 1994). These jets carry particles from the lake periphery into its center, focusing sedimenting matter at the deeper parts of the lake.

Although some live *P. gatunense* remained in the water column throughout the summers of 1990 and 1991, these rare cells were not enough to explain the continued flux of *P. gatunense* matter into our traps throughout the summer. Moreover, and unlike all other years, during the stratified period of 1991 the upper traps collected substantially more dead cells and thecae than did the lower traps. We propose that these differences are indicative of increased resuspension, possibly via a focusing mechanism, as *P. gatunense* is typically more abundant in the littoral than in the pelagic zone (Pollingher and Berman 1975).

A complementary explanation to increased resuspension is that during the low water level years decomposition of *P. gatunense* in the water column, and particularly that of thecae, was slower than during the high water level years. Likely reasons for reduced decomposition rates are unsually low temperatures or lack of nutrients necessary for the microbial decomposer community. In our study, temperature was clearly not a factor contributing to lower decomposition rates in the low water level years, since those years were relatively warm (Table 1). The coldest year in the 5-year series (i.e. 1992) did not have the lowest annual total *P. gatunense* catches, nor did the warmest year (i.e. 1994) have the highest sedimentation flux.

On the other hand, the fact that *P. gatunense* sedimentation continued in 1990 and 1991 after the bloom ended and that nutrient-poor thecae were the main component of this flux hints to a crucial role for nutrient limitation of microbial decomposition processes. The seasonal mean C:P molar ratio in *P. gatunense* was 461:1 (*see* also Wynne et al. 1982), which was significantly higher than the 106:1 Redfield ratio typical of other algae, and obviously higher than the ~50:1 ratio in heterotrophic bacteria (Jürgens and Güde 1990). The ratio for thecae was >3,000:1 vs. 276:1 for protoplasts (Table 6). The important implication is that bacterial decomposition of the thecae is prone to be a P-limited process.

It is possible that more severe nutrient limitation in 1990 and 1991 resulted with undecomposed *P. gatunense* remaining in the water column or in the sediments. In laboratory decomposition experiments, we found that *P. gatunense* decomposition rates, especially those of the nutrient-deficient thecae in the absence of protoplasts, were greatly enhanced when inorganic P or N + P were added (unpubl. data).

Close examination of the depth and time variations in ambient nutrient concentrations in Lake Kinneret during those

5 years provided no direct evidence to justify the above hypothesis. However, ambient concentrations do not give information on the dynamics of nutrient-cycling processes, and without such information it is impossible to assess whether nutrients were indeed limiting to bacterial activity. Unfortunately, comparative information was unavailable on the dynamics of P cycling during those 5 years. Nevertheless, the nutrient-loading data (Table 1) supported our hypothesis. As is typical of dry years, total P loads entering Lake Kinneret via the Jordan River during the 1989–1990 and 1990–1991 hydrological years were low (30.7 and 38.5 t $year^{-1}$, respectively) compared with 186 t in the flood year of 1991–1992, 124 t in 1993–1994, and 56.3 t in 1994–1995. Total N loads were similarly lower in the drought years. Furthermore, it has been shown that nutrient deprivation of *P. gatunense* cultures can lead to theca shedding without cell division (Criscuolo et al. 1981). It is possible that during the low nutrient-loading years relatively more thecae were shed than in high nutrient-loading years.

The present study demonstrates that thecae and protoplasts disappear from the water column at different rates and via different processes. Protoplast decomposition involves rupture of its outer membrane or "pellicle" (Loeblich 1969) to allow leakage of cell contents or entry of microorganisms. The typical chemical resistance of the pellicular layer appears to be due to the presence of a material similar to sporopollenin (Taylor 1987). It is likely that the rupturing process is instantaneous and that within hours the damaged protoplast becomes microscopically unrecognizable. Theca decomposition, on the other hand is a more gradual process that can be followed microscopically. The thecae, infested by bacteria and heterotrophic nanoflagellates, become thinner with time and gradually disappear.

A last question arising from this study addresses the fate of the *P. gatunense* biomass that does not sediment out of the water column. With the exception of 1991, when 68% of the bloom biomass reached the lower sediment traps, processes other than sedimentation must have played an important role in removing the bulk of the bloom biomass from the water column—possible processes are encystment, grazing, or death and decomposition.

Encystment followed by mass sedimentation of cysts was shown to be the main fate of dinoflagellate blooms in the Baltic Sea (Heiskanen 1993). Dinoflagellate cysts are more resistant to decomposition and have greater specific density than do vegetative cells and they therefore sink faster (Anderson et al. 1985). In contrast, encystment in Lake Kinneret could explain only a fraction of the disappearance of bloom biomass. Cysts were trapped in low numbers. This is in accordance with Pollingher's (1988) observation that only ~1% of the *P. gatunense* population is transformed into cysts.

Cyst formation frequency is a species-specific phenomenon: some dinoflagellates, such as *P. cinctum* and *P. willei* are known to produce relatively few cysts (Chapman and Pfiester 1995), whereas others, such as *Scrippsiella hangoei* from the Baltic, and *Ceratium hirudinella* produce many cysts as a survival strategy. In fact, we did find *Ceratium* cysts in the traps at greater numbers than *P. gatunense* cysts, although *Ceratium* cells are much more rare in the water column. In Lake Sempach (Switzerland), *Ceratium* formed more cysts than did *P. willei* and *P. aciculeferum,* but the rate of survival of *Ceratium* cysts seemed to be lower than that of the *Peridinium* spp. cysts (Pollingher et al. 1993).

Owing to the large size of *P. gatunense,* zooplankton grazing pressure has been regarded as minor (Serruya et al. 1980). Some relatively low grazing pressure by herbivorous fish (mostly *Sarotherodon galilaeus*) and by specialized protozoans (*Bursaria, Lacimaria, Euplotes*) and rotifers (*Asplanchna, Ascomorpha*) does exist (U.P. unpubl.). Pollingher and Serruya (1976) calculated that the entire *S. galilaeus* population consumes ~1,000 t of *P. gatunense* per month, which was equivalent to daily consumption of 0.1% of the average *P. gatunense* biomass. A recent stable carbon isotope study (Zohary et al. 1994) supported the assumption that most zooplankton probably do not feed on live *P. gatunense* cells, but also suggested that zooplankton grazing on organic matter of *P. gatunense* origin during the bloom decline phase accounted for seasonally elevated zooplankton $\delta^{13}C$. The proportion of dead *P. gatunense* matter removed from the water column owing to zooplankton grazing remains unquantified.

Our finding that upper trap catches were consistently higher than lower trap catches may be interpreted as being due to decomposition while sinking, although thermal stratification will also contribute to this difference. Additional information on the decomposition of *P. gatunense* in Lake Kinneret is meager. Sherr et al. (1982) have shown that bacterivorous microflagellates enhanced thecal decomposition in *P. gatunense* but had no effect on the breakdown of the protoplast. They suggested that protozoan grazing increased the availability of inorganic nutrients to bacteria degrading the thecae. Hertzig et al. (1981) noted that the theca of lyophilized *P. gatunense* incubated in situ in experimental chambers was the first part of the cell to decompose, and that the fastest rates of breakdown were observed in the epilimnion toward the end of the bloom. Like Hertzig et al. (1981), we witnessed experimental situations in which thecal decomposition was completed within a few days whereas protoplasts remained undecomposed for months on end (T.Z. et al. unpubl.). However, our present study clearly demonstrates that this is not the typical situation in Lake Kinneret.

Thecae contributed to the *P. gatunense* settling flux a proportion greater than their relative contribution to total *P. gatunense* biomass in the water. Integrated over time, thecae constituted 70% of total *P. gatunense* sedimentation as opposed to only 55% of *P. gatunense* biomass in the water column (taking into account that for each cell produced an additional theca was shed). This implies that protoplasts disappear via decomposition and grazing more rapidly than do thecae, despite their faster sinking velocities (i.e. thecae are more refractory). As conditions in Lake Kinneret vary from year to year, different decomposer communities will develop, influencing the pattern of thecae vs. protoplasts degradation.

An important consequence is that the nutrients (N and P) contained in the protoplasts are being effectively recycled within the epilimnion, whereas the C-rich and N- and P-poor thecae are more likely to reach the bottom sediments. A similar phenomenon of selective C sedimentation is the mass sedimentation of *Phaeocystis*-derived organic matter, mostly

C-rich and N-deficient mucilage, in the Barents and Northern Seas (Wassman et al. 1990; Riebesell et al. 1995).

We conclude that thecal decomposition rates may be heavily dependent on N and P availability to the decomposer bacterial population and can therefore vary significantly. P is considered to be the main limiting nutrient in Lake Kinneret (Pollingher et al. 1988) and should therefore show the major impact on the decomposition dynamics. Furthermore, N depletion of the theca was even more severe than its P depletion—protoplasts contained 10 times more P, but also 27 times more N, than thecae. In the marine environment, where N is usually the limiting nutrient, the extreme N depletion of dinoflagellate thecae could be more crucial for nutrient cycling.

In a study of dinoflagellate sedimentation in the Baltic Sea, Heiskanen (1995b) concluded that only a small fraction of the populations (*Peridiniella catenata* and *Scrippsiella hangoei*) settled as intact vegetative cells, while the major part of the biomass remained in the water column and settled later as amorphous detrital material, or marine snow. It is possible that this process is the most prominent in Lake Kinneret as well, because we have no quantitative evidence that grazing and decomposition within the epilimnion can account for the remaining unexplained fraction of the bloom biomass disappearance.

Ultimately, our study highlights for the first time that annual dinoflagellate sedimentation rates may vary dramatically as a result of other processes such as decomposition, resuspension, and grazing, leading to dramatic variations in the amount of organic matter reaching the bottom sediments.

References

ANDERSON, D. M., J. J. LIVELY, E. M. REARDON, AND C. A. PRICE. 1985. Sinking characteristics of dinoflagellate cysts. Limnol. Oceanogr. **30:** 1000–1009.

AMERICAN PUBLIC HEALTH ASSOCIATION. 1992. Standard methods for the examination of water and wastewater. 17th ed. APHA.

BERMAN, T. 1978. General biochemical features, p. 269–270 *In* C. Serruya [ed.], Lake Kinneret. Monogr. Biol. 32. Junk.

———, AND Z. DUBINSKY. 1985. The autecology of *Peridinium cinctum* fa. *westii* from Lake Kinneret. Verh. Internat. Verein. Limnol. **22:** 2850–2854.

———, AND W. RODHE. 1971. Distribution and migration of *Peridinium* in Lake Kinneret. Mitt. Int. Ver. Limnol. **19:** 266–276.

———, AND OTHERS. 1995. Primary production and phytoplankton in lake Kinneret: A long-term record (1972–1993). Limnol. Oceanogr. **40:** 1064–1076.

BERMAN-FRANK, I., T. ZOHARY, J. EREZ, AND Z. DUBINSKY. 1994. CO_2 availability, carbonic anhydrase, and the annual dinoflagellate bloom in Lake Kinneret. Limnol. Oceanogr. **39:** 1822–1834.

BLOESCH, J., P. STADELMANN, AND H. BUHRER. 1977. Primary production, mineralization, and sedimentation in the euphotic zone of two Swiss lakes. Limnol. Oceanogr. **22:** 511–526.

CHAPMAN, A. D., AND L. A. PFIESTER. 1995. The effects of temperature, irradiance, and nitrogen on the encystment and growth of the freshwater dinoflagellates *Peridinium cinctum* and *P. willei* in culture (Dinophyceae). J. Phycol. **31:** 355–359.

CRISCUOLO, C. M., Z. DUBINSKY, AND S. AARONSON. 1981. Skeleton shedding in *Peridinium cinctum* from Lake Kinneret—a unique phytoplankton response to nutrient imbalance, p. 169–176. *In* H. Shuval [ed.], Developments in arid zone ecology and environmental quality. Balban ISS.

FALLON, R. D., AND T. D. BROCK. 1980. Planktonic blue-green algae: Production, sedimentation, and decomposition in Lake Mendota, Wisconsin. Limnol. Oceanogr. **25**: 72–88.

GEIFMAN, Y., AND M. ROM. 1995. Contribution of substances from the Jordan Basin to the Kinneret: Analysis of events and changes. Mekorot Water Company Report, 49 pp. (in Hebrew).

HADAS, O., AND R. PINKAS. 1995. Sulphafe reduction in the hypolimnion and sediments of Lake Kinneret, Israel. Freshwat. Biol. **33**: 63–72.

HADER, D.-P., S.-M. LIU, M. HADER, AND W. ULLRICH. 1990. Photoorientation, motility and pigmentation in a freshwater *Peridinium* affected by ultraviolet radiation. Gen. Physiol. Biophys. **9:** 361–371.

HAMBRIGHT, K. D., M. GOPHEN, AND S. SERRUYA. 1994. Influence of long-term climatic changes on the thermal dynamics of a subtropical, warm monomictic lake. Limnol. Oceanogr. **39**: 1234–1243.

HEISKANEN, A.-S. 1993. Mass encystment and sinking of dinoflagellates during a spring bloom. Mar. Biol. **116:** 161–167.

———. 1995*a*. Contamination of sediment trap fluxes by vertically migrating phototrophic micro-organisms in the coastal Baltic Sea. Mar. Ecol. Prog. Ser. **122:**45–58.

———. 1995*b*. Impact of dinoflagellates on the flux of organic matter collected by sediment traps in the gulf of Finland (Baltic Sea), p. 153–167. *In* S. Floderus, A.-S. Heiskanen, M. Olesen, and P. Wassmann [eds.], Sediment trap studies in the Nordic countries 3. NurmiPrint.

HERTZIG. R., Z. DUBINSKY, AND T. BERMAN. 1981. Breakdown of *Peridinium* biomass in Lake Kinneret, p. 179–185. *In* H. Shuval [ed.], Developments in arid zone ecology and environmental quality. Balban ISS.

HICKEL, B., AND U. POLLINGHER. 1988. Identification of the bloom forming *Peridinium* from Lake Kinneret (Israel) as *P. gatunense* (Dinophyceae). Br. Phycol. J. **23:** 115–119.

HORN, H., AND W. HORN. 1993. Sedimentary losses in the Reservoir Saidenbach: Flux and sinking velocities of dominant phytoplankton species. Int. Revue Ges. Hydrobiol. **78:** 39–57.

IMBERGER, J. 1994. Small transport processes in Lake Biwa, p. 65–71. *In* Proc. BITEX Symp., Otsu, Japan, 5–9 November.

JÜRGENS, K., AND H. GÜDE. 1990. Incorporation and release of phosphorus by planktonic bacteria and phagotrophic flagellates. Mar. Ecol. Prog. Ser. **59:** 271–284.

KNOECHEL, R., AND J. KALFF. 1975. Algal sedimentation: The cause of a diatom—blue-green succession. Verh. Internat. Verein. Limnol. **19:** 745–754.

LAWS, E. A., P. K. BIENFANG, D. A. ZIEMANN, AND L. D. CONQUEST. 1988. Phytoplankton population dynamics and the fate of production during the spring bloom in Aike Bay, Alaska. Limnol. Oceanogr. **33:** 57–65.

LIGNELL, R., AND OTHERS. 1993. Fate of a phytoplankton spring bloom: Sedimentation and carbon flow in the planktonic food web in the northern Baltic. Mar. Ecol. Prog. Ser. **94:** 239–252.

LINDSTROM, K. 1985. Selenium requirement of the dinoflagellate *Peridiniopsis borgei* (Lemm). Int. Revue Ges. Hydrobiol. **70:** 77–85.

LOEBLICH, A. R., III. 1969. The amphiesma or dinoflagellate cell covering. Proc. N. Am. Paleontol. Conv. **G:** 867–929.

NISHRI, A., G. HERMAN, AND M. SHLICHTER. 1996. The response of the sedimentological regime in Lake Kinneret to lower lake levels. Hydrobiologia **339**: 149–160.

PARPAROV, A. 1994. Oxygen depletion in Lake Kinneret: Recent events and long-term trends. Limnologica **24**: 137–145.

———, AND K. D. HAMBRIGHT. 1996. A proposed framework for

the management of water quality in ard regions. Int. Revue Ges. Hydrobiol. **81**: 435–454.

POLLINGHER, U. 1981. The structure and dynamics of the phytoplankton assemblages in Lake Kinneret. J. Plankton Res. **3**: 93–105.

———. 1988. Freshwater armored dinoflagellates: Growth, reproduction strategies, and population dynamics, p. 134–174. *In* C. D. Sandgren [ed.], Growth and reproduction strategies of freshwater phytoplankton. Cambridge.

———, AND T. BERMAN. 1975. Temporal and spatial patterns of dinoflagellate blooms in Lake Kinneret, Israel (1969–1974). Verh. Internal. Verein Limnol. **19:** 1370–1382.

———, AND ———. 1982. Relative contribution of net and nanoplankton to primary production in Lake Kinneret. Arch. Hydrobiol. **96:** 33–46.

———,———, B. KAPLAN, AND D. SCHARF. 1988. Lake Kinneret phytoplankton: Response to N and P enrichments in experiments and in nature. Hydrobiologia **166**: 65–75.

———, H. R. BÜRGI, AND H. AMBÜL. 1993. The cysts of *Certium hirudinella*: Their dynamics and role within a eutrophic lake (Lake Sempach, Switzerland). Aquat. Sci. **55:** 10–18.

———, AND B. HICKEL. 1991. Dinoflagellate associations in a subtropical lake (Lake Kinneret, Israel). Arch. Hydrobiol. **120**: 267–285.

———, AND C. SERRUYA. 1976. Phased division of *Peridinium cinctum* f. *westii* (Dinophyceae) and development of the Lake Kinneret (Israel) bloom. J. Phycol. **12:** 162–170.

PREMAZI, G., AND G. MARENGO. 1982. Sedimentation rates in a Swiss-Italian lake measured with sediment traps. Hydrobiologia **92:** 603–610.

REYNOLDS, C. S. 1984. The ecology of freshwater phytoplankton. Cambridge.

RIEBESELL, U., M. REIGSTA, P. WASSMANN, T. NOJI, AND U. PASSOW. 1995. On the trophic fate of *Phaeocystis pouchetii* (Hariot): VI. Significance of *Phaeocystis*-derived mucus for vertical flux. Neth. J. Sea Res. **33**: 193–203.

SERRUYA, C. 1978. Water Chemistry, p. 185–204. *In* C. Serruya [ed.], Lake Kinneret. Monogr. Biol. 32. Junk.

———, M. GOPHEN, AND U. POLLINGHER. 1980. Lake Kinneret: Carbon flow patterns and ecosystem management. Arch. Hydrobiol. **88:** 265–302.

SERRUYA, S. 1978. Water motions, p. 167–171. *In* C. Serruya [ed.], Lake Kinneret. Monogr. Biol. 32. Junk.

SHERR, B. F., E. B. SHERR, AND T. BERMAN. 1982. Decomposition of organic detritus: A selective role for microflagellate Protozoa. Limnol. Oceanogr. **27:** 765–769.

SMETACEK, V. S. 1985. Role of sinking in diatom life-cycles: Ecological, evolutionary and geological significance. Mar. Biol. **84**: 239–251.

SOMMER, U. 1984. Sedimentation of principal phytoplankton species in Lake Constance. J. Plankton Res. **6:** 1–14.

TAKAMURA, N., AND M. YASUNO. 1988. Sedimentation of phytoplankton populations dominated by *Microcystis* in a shallow lake. J. Plankton Res. **10:** 283–299.

TAYLOR, F. J. R. 1987. Dinoflagellate morphology, p. 24–92. *In* F. J. R. Taylor [ed.], The biology of dinoflagellates. Blackwell.

UTERMÖHL, H. 1958. Zur Vervolkommnung der Quantitativen Phytoplankton-Methodik. Mit. Int. Ver. Theor. Angew. Limnol. **9:** 1–38.

WYNNE, D., N. J. PATNI, S. AARONSON, AND T. BERMAN. 1982. The relationship between nutrient status and chemical composition of *Peridinium cinctum* during the bloom in Lake Kinneret. J. Plankton Res. **4**: 125–136.

WASSMANN, P., M. VERNET, B. G. MITCHELL, AND F. REY . 1990. Mass sedimentation of *Phaeocystis pouchetii* in the Barents Sea. Mar. Ecol. Prog. Ser. **66**: 183–195.

WINER, Y. 1998. The role of sedimentation processes in the *Peridinium* bloom dynamics in Lake Kinneret, Israel. M.Sc. thesis, Tel Aviv Univ. 170 p. (in Hebrew).

ZOHARY, T., J. EREZ, M. GOPHEN, I. BERMAN-FRANK, AND M. STILLER. 1994. Seasonality of stable carbon isotopes within the pelagic food web of Lake Kinneret. Limnol. Oceanogr. **39:** 1030–1043.

———, AND R. D. ROBARTS. 1989. The diurnal mixed layer and the long-term dominance of *Microcystis aeruginosa*. J. Plankton Res. **11**: 25–48.

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