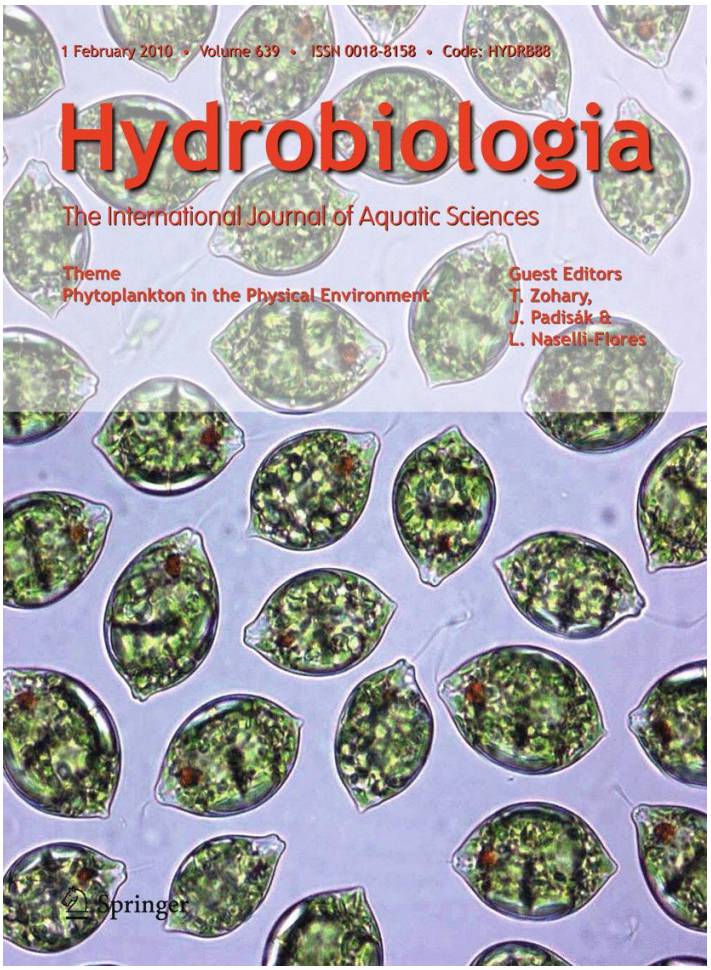
ISSN 0018-8158, Volume 639, Number 1



Hydrobiologia (2010) 639:185–196
DOI 10.1007/s10750-009-0023-3

PHYTOPLANKTON

Carbon:chlorophyll *a* ratio, assimilation numbers and turnover times of Lake Kinneret phytoplankton

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Published online: 13 December 2009

Abstract Carbon to chlorophyll *a* (C:Chl) ratios, assimilation numbers (A.N.) and turnover times of natural populations of individual species and taxonomic groups were extracted from a long-term database of phytoplankton wet-weight biomass, chlorophyll *a* concentrations, and primary production in Lake Kinneret, Israel. From a database spanning more than a decade, we selected data for samples dominated by a single species or taxonomic group. The overall average of C:Chl was highest for cyanophytes and lowest for diatoms, while chlorophytes and dinoflagellates showed intermediate values. When converting chlorophyll *a* to algal cellular carbon this variability should be taken into account. The variability in C:Chl within each phylum and species (when data were available) was high and the variability at any particular sampling date tended to be greater than the temporal variability. The average chlorophyll *a*-normalized rate of photosynthetic activity of cyanophytes was higher and that of the dinoflagellates lower than that of other phyla. Turnover time of phytoplankton, calculated using primary productivity data at the depth of maximal photosynthetic rate, was longest in dinoflagellates and shortest in cyanophytes, with diatoms and chlorophytes showing intermediate values. The more extreme C:Chl and turnover times of dinoflagellates and cyanobacteria in comparison with chlorophytes and diatoms should be taken into consideration when employed in ecological modeling.

Keywords C:Chl ratio · Monitoring database · Optimal depth

Guest editors: T. Zohary, J. Padisák & L. Naselli-Flores / Phytoplankton in the Physical Environment: Papers from the 15th Workshop of the International Association for Phytoplankton Taxonomy and Ecology (IAP), held at the Ramot Holiday Resort on the Golan Heights, Israel, 23–30 November 2008

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Introduction

Chlorophyll *a* (Chl) is probably the most frequently measured compound of biological origin in aquatic sciences. The ease of its extraction and the relatively widespread occurrence of instruments for its measurement make it an attractive surrogate for estimation of algal biomass. As algal biomass cannot be physically separated from other particulate components suspended in the water in natural aquatic environments (Banse, 1977), determination of algal biomass is usually based on cell count and measurement of linear dimensions, followed by calculation of approximate cell volume based on geometrical shapes (Hillebrand et al., 1999). Thus, a common quantity is established, which subsequently is often

expressed in terms of carbon (C), a universal cellular component. Cellular C content was strongly correlated with cell volume in protists of diverse taxonomic groups; diatoms, which were found to be significantly less carbon dense than other taxa fit a different correlation equation for the conversion from cell volume to C (Menden-Deuer & Lessard, 2000).

In contrast to the narrow limits of cellular volume:C, C:Chl varies widely as chlorophyll content changes in response to changes in environmental factors such as light and nutrients (e.g., Riemann et al., 1989; Baumert & Petzoldt, 2008). As a result, Chl is considered an imprecise measure of algal biomass (Llewellyn et al., 2005). However, C:Chl ratios are closely related to phytoplankton growth rate and to its photosynthetic efficiency. These ratios are utilized in aquatic food-web and ecosystem models (e.g., Håkanson & Boulion, 2002; Bruce et al., 2006; Gal et al., 2009), therefore they are valuable for the assessment of aquatic environments (Langdon, 1988; Cloern et al., 1995; Zonneveld, 1998; Lefèvre et al., 2003).

Measurement of the C:Chl ratios of individual species in natural populations is usually impossible, due to the high species diversity in most natural phytoplankton assemblages, and C:Chl ratios are typically determined on algal cultures. Exceptions occur during algal blooms, when a single species dominates the phytoplankton. On such occasions, measurement of Chl and phytoplankton biovolume may be attributed with high confidence to the dominant species, and allow the estimation of C:Chl under natural conditions. Bloom events also provide an opportunity to investigate physiological rates (e.g., photosynthesis, respiration, and nitrogen fixation) of individual algal species or taxa in their natural environment.

Microscopic examination of phytoplankton and measurement of Chl concentration and primary productivity are part of a long-term ongoing lake monitoring program in Lake Kinneret, Israel. The objective of this study was to explore the variation in structural and functional variables occurring in natural phytoplankton populations. In order to accomplish that assignment, we extracted from the Kinneret Monitoring database relevant measurements for computing C:Chl ratios, assimilation numbers (A.N.), and turnover times of individual species and taxonomic groups dominating the phytoplankton of Lake Kinneret and examined the natural variability of those parameters. This analysis provides essential parameter values for ecosystem models, designed and applied for the knowledgeable and efficient management of natural and man-modified aquatic ecosystems.

Materials and methods

Lake Kinneret and its phytoplankton

Lake Kinneret is a subtropical, warm monomictic lake situated in northern Israel. It is a freshwater lake of medium size (surface area: 170 km^2, mean depth: 24 m, and max depth: 43 m), the only one in the region and therefore a major source of drinking water and a site for intensive research and monitoring. Until the mid-1990s phytoplankton succession in Lake Kinneret followed a predictable annual pattern, with the bloom forming dinoflagellate *Peridinium gatunense* dominating from February to June; after the early summer bloom collapse the phytoplankton maintained a low-biomass, high-diversity assemblage of chlorophytes, diatoms, and small dinoflagellates (Pollingher, 1986). In summer 1994, the filamentous cyanophyte, *Aphanizomenon ovalisporum* appeared and bloomed comprising the first-ever bloom of a nitrogen fixer (Pollingher et al., 1998). Since that year, the previously predictable annual pattern became less predictable, *Peridinium gatunense* showed extremely high concentrations in some years, but was altogether missing in other years, and algal species not recorded before appeared in massive concentrations (e.g., *Carteria* sp., *Mougeotia gracillima*, and *Cylindrospermopsis raciborskii*; Zohary, 2004a).

The Lake Kinneret database

Data collected as part of the routine monitoring program of Lake Kinneret, initiated in 1969 and ongoing, is deposited in the Lake Kinneret database which was made available for this study. The methods used to collect water samples and conduct analyses of the variables used for this study (chlorophyll, phytoplankton wet weight, and primary production) are specified below for reference only. The current study begins with the data selection process section.

Water samples were taken at 2-week intervals, between 08:00 and 09:00 h local time (GMT + 2 h), with a 5 l Aberg–Rodhe sampler from 9 to 11 depths at a pelagic mid-lake station (Station A, situated at the deepest part of the lake at the node of most intense seiche activities), and transferred immediately to polyethylene carboys kept in the dark. Subsamples were collected from each depth and preserved immediately with Lugol solution for microscopic cell count. Additional subsamples from the same samples were taken for Chl and C-uptake determinations. Taxonomic composition and species abundance were determined on samples treated by the sedimentation method (Utermöhl, 1958). Wet-weight biomass of each taxonomic unit (mostly at the species level) was derived from average cell dimensions and approximate geometry and assuming a specific density of 1.0 (Hillebrand et al., 1999). The overall biomass of each phytoplankton phylum was calculated by summing the wet-weight contributions of all species of the group. Sub-samples for determination of chlorophyll *a* (Chl) were processed in the laboratory approximately 1 h after collection. Particulate matter was collected by filtration of 5–50 ml (depending on phytoplankton density) water samples onto glass-fiber filters (Whatman GF/C), ground in 90% acetone and left overnight at 4°C in the dark. Chl concentration was determined fluorometrically (Holm-Hansen et al., 1965), following clearing of the extract by 3 min centrifugation at 1,100*g*. Following sample withdrawal, duplicate 50 ml subsamples were transferred to polycarbonate 60 ml bottles for carbon uptake measurement with a modified ^{14}C technique (Steemann-Neilsen, 1952; Yacobi, 2006). A spike of approximately 3×10^5 Bq of [^{14}C] bicarbonate was added to each bottle. The bottles were incubated in situ for determination of carbon assimilation, at the respective depths of the samples origin. After incubation, of approximately 3 h, the samples were filtered onto poly-acetate 25 mm 0.45 μm membrane filters under light vacuum (about 100 mg Hg), rinsed with filtered lake water and left over-night in the presence of HCl vapor to eliminate any remaining traces of inorganic ^{14}C. Control samples poisoned by Lugol's solution at time zero were run in each experimental series to compensate for non-biological absorption to filters. The total added ^{14}C was checked for each sampling series by counting 0.1 ml portions withdrawn directly from each of the incubated bottles. Total radioactivity in the particulate fraction retained on the filters was determined by liquid scintillation with quench correction. The average difference between duplicates was ~12%.

Data selection process

Data from the Lake Kinneret database for the period October 1994 until December 2007 were used in this study. The analysis began by selecting relevant data from this period, i.e. Chl, phytoplankton wet-weight biomass and primary production data for samples, in which a single species or taxonomic group constituted >60% of the total phytoplankton biomass. During that period, altogether 349 sampling trips were undertaken in the lake generating >3,500 samples. Four phyla surpassed the 60% criterion (Table 1). Further sample elimination was in cases where: (1) total biomass of the dominant phylum was <1 g wet weight m^{-3}, and (2) during stratification, from April to December, samples were withdrawn from the hypolimnion (depth ≥15 m). Both constrains were applied to exclude samples where a significant proportion of Chl was possibly contributed by debris.

Wet weight to C-biomass conversion factors

Wet biomass estimations were transformed to C-biomass, using the conversion factors given in Table 1. The conversion factors for cyanophytes, dinoflagellates, and diatoms were derived from measurements made on phytoplankton species collected from Lake Kinneret during monospecific blooms or in cultures (Zohary, 2004b). During monospecific blooms, cells were collected, concentrated on a GF/F filter, weighed, oven-dried at 60°C overnight, and weighed once again, and subsequently the carbon concentration was determined by loss on ignition at 550°C (APHA, 2005). Wet-weight biomass was determined microscopically as described above. The conversion factor for chlorophytes was taken from published data (Wetzel & Likens, 2000).

Calculation of C:Chl ratio

The wet-weight-derived C-biomass per unit volume of water for the species or phylum dominating any given sample was divided by the Chl concentration attributed to that taxon. The later was calculated by

Table 1 C:Chl ratio in Lake Kinneret phytoplankton

Taxon	# of cases	Wet biomass to C conversion factor	C:Chl *a* ratio				
			Average	Confidence interval 95% (±)	Std	Minimum	Maximum
All cyanophytes	123	0.22*	83	5.8	31	38	182
Aphanizomenon ovalisporum	35		77		30	43	144
Cylindrospermopsis sp.	44		83		33	38	142
Microcystis aeuroginosa	11		92		52	39	182
Chroococcus sp.	6		113		21	91	145
All chlorophytes	153	0.16**	44	2.5	15	15	96
Closterium aciculare	25		53		14	24	87
Mougeotia gracillima	37		45		6	34	59
Pediastrum spp.	26		57		19	24	96
All diatoms	97	0.11*	29	2.7	13	10	63
Aulacoseira granulata	87		26		11	10	57
Synedra sp.	10		49		10	37	63
All dinoflagellates	476	0.16*	55	1.9	21	11	167
Peridinium gatunense	429		55		19	13	135

Included are all records in which a phylum contributed >60% to the overall algal biomass. In most cases, in cyanophytes, diatoms, and dinoflagellates, a single species was the major, or the sole contributor, to the phylum biomass. In chlorophytes, it was mostly a combination of species. Wet-weight:C conversion factors were measured directly on Kinneret phytoplankton or literature-derived

*Zohary (2004b), **Wetzel & Likens (2000)

multiplication of the wet-weight biomass share of the taxon in total biomass, by Chl concentration of the relevant sample. Thus, it was assumed that a taxon comprising X% of total phytoplankton biomass, also comprised X% of total Chl. While this assumption is not necessarily accurate, it was considered the best objective estimate possible.

Determination of assimilation number

Assimilation number is the chlorophyll-normalized value of the photosynthetic rate, derived by division of the hourly photosynthetic carbon uptake rate by the respective concentration of Chl. In this communication, we present the A.N. recorded at the "optimal depth", i.e., for any given sampling date, the depth where the chlorophyll-normalized primary productivity showed that the maximum value.

Turnover time calculation

This parameter was also calculated at the optimal depth, as C-biomass divided by the respective primary production. Wet-weight biomass was transformed to carbon as described above. Primary productivity (mg cm^{-3} day^{-1}) values attributed to the dominant phylum were calculated by multiplication of the wet-weight biomass share of the phylum, by the rate of carbon assimilated. Thus, it was assumed that a taxon comprising X% of total phytoplankton biomass was responsible for X% of total primary production.

Results

Carbon to chlorophyll *a* ratio

There was a conspicuous difference between the four phytoplankton phyla with respect to the C:Chl ratio, with cyanophytes displaying the highest (83:1) and diatoms the lowest value (28:1; Table 1). The variation of the C:Chl ratio was highest in diatoms, with coefficient of variance of 47%, while in the other groups it ranged from 35 to 38%.

Selecting for analysis a sub-set of the samples in which chlorophytes contributed at least 70% of total biomass, rather than our standard of 60%, did not change the C:Chl ratio. A further increase of the limit to 80% increased the C:Chl ratio from 44:1 to 48:1. In cyanophytes, the C:Chl ratio was 77:1 and 73:1, with

the increase of the contribution to total phytoplankton biomass to 70 and 80%. In diatoms, the C:Chl ratio changed to 29:1 and 27:1 with the increase of the contribution to total phytoplankton biomass to 70 and 80%, respectively, and in dinoflagellates it increased from 55 to 57, 58 and 59 in populations dominated by 60, 70, 80 and 90% by that phylum. Thus, there was a consistent trend in C:Chl within each phylum when one moves from 60 to 70, 80, and 90% indicating the importance of the remaining up to 40% of algal biomass in biasing the ratio. However, those differences in C:Chl within each phylum were not statistically different.

The entire dataset of C:Chl ratios of the different phyla and dominant species and how the ratios are distributed over time is shown in Fig. 1. Each data point in Fig. 1 represents one sampling depth, on each date there could be up to 11 sampling depths. The C:Chl ratio of all four taxonomic groups showed that substantial variability at any particular sampling date, which tended to be greater than the temporal variability. This variability could be due to the sampling depth (Fig. 2), species comprising (and thus C and Chl content) of the remaining ≤40% biomass, or due to possible measurement error, and/or assumptions made and factors used in the determinations of C and Chl (see "Discussion").

The overall depth-distribution of C:Chl was examined by plotting mean C:Chl of all samples analyzed from each depth. The ratio was fairly uniform in samples withdrawn from the uppermost 7 m water column, but declined in deeper layers

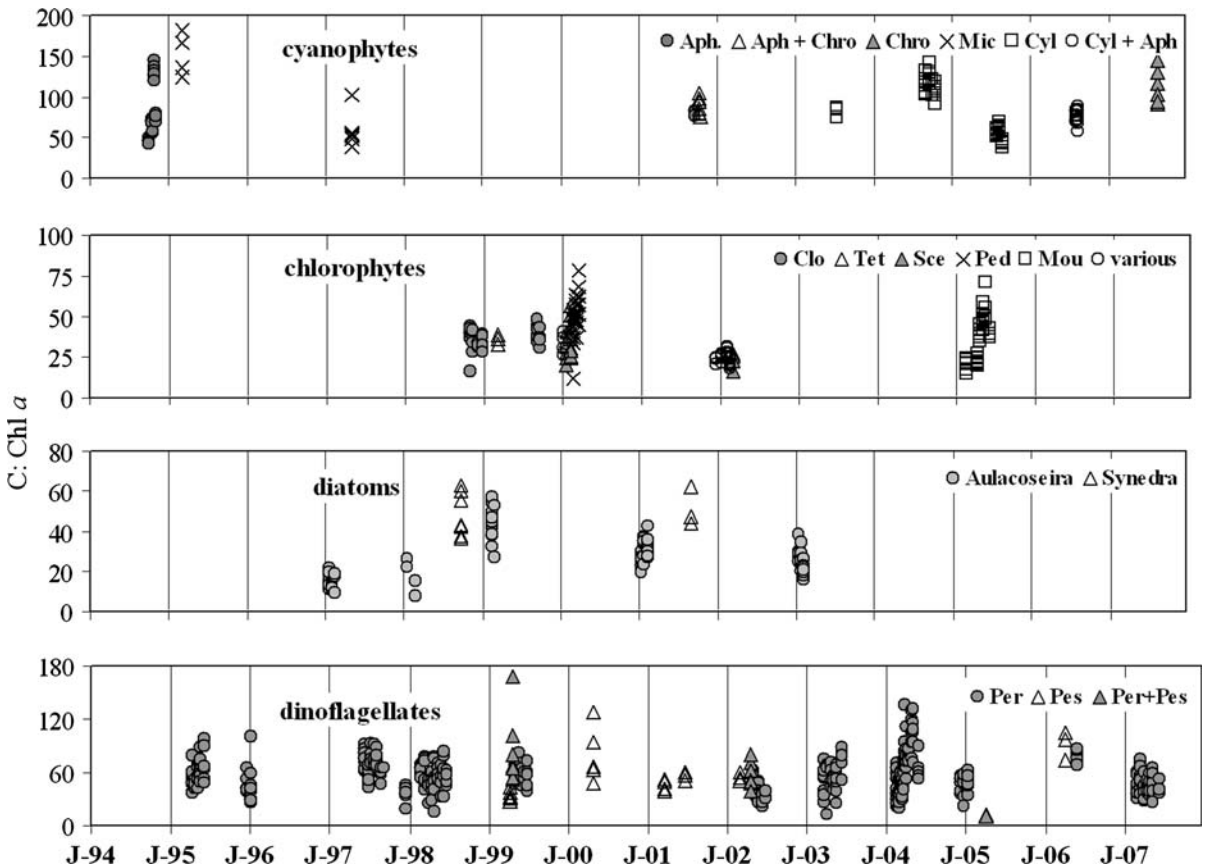

Fig. 1 Temporal variations in C:Chl ratio of the four dominant phyla in Lake Kinneret, 1994–2007. Each data point represents a single sample; on any single date, there could be up to 11 samples from different depths. Aph = *Aphanizomenon ovalisporum*; *Chroococcus* sp. = Chro; *Microcystis aureginosa* = Mic; *Cylindrospermopsis raciborskii* = Cyl; *Closterium aciculare* = Clo; *Tetraedron* + various desmids = Tet; *Scenedesmus* + various desmids = Sce; *Pediastrum* sp. = Ped; *Mougeotia gracillima* = Mou; *Peridinium gatunense* = Per; *Peridiniopsis* sp. = Pes

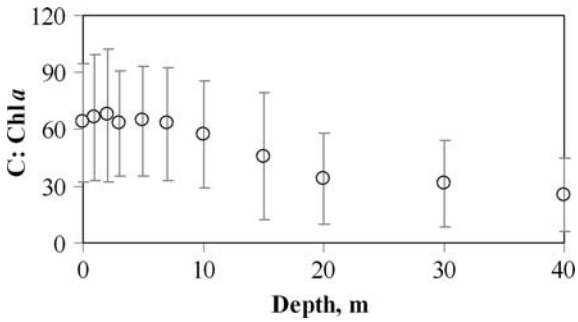

Fig. 2 Depth distribution of average (±standard deviation) C:Chl ratio in all samples from Lake Kinneret, 1994–2007. Samples were included in the analysis if: (a) >60% of phytoplankton biomass was formed by species belonging to any given phylum; (b) biomass surpassed 1 mg m^{-3} wet weight, and (c) sampling depth was <15 m during stratification

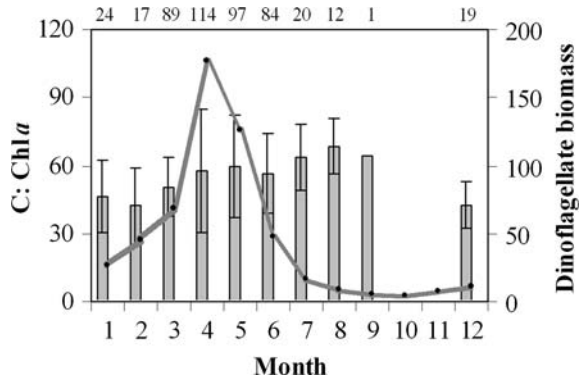

Fig. 3 Multi-annual (1994–2007) monthly average dinoflagellate biomass, in g wet weight m^{-2} (*line*) and C:Chl (*columns*) in Lake Kinneret. *Vertical bars*—standard deviation. The *numbers above the columns*—number of samples in analysis

(Fig. 2). This general pattern of vertical distribution of the C:Chl was observed also when each of the four phyla was plotted alone (not shown).

Figure 1 also indicates the times of year when each taxon dominated the phytoplankton assemblage. Cyanophytes dominated the phytoplankton either in the early spring (February–April, e.g., in 1995 and 1997) or in late summer-fall (e.g., 1994, 2001, 2003, 2005, 2006, and 2007). The dominance of chlorophytes was limited to five bloom events over the 14 years studied, some of them during no-*Peridinium* springs, e.g., in 2000, when *Pediastrum duplex*, *Pediastrum tetras*, and *Scenedesmus quadricauda* (accompanied by desmids) dominated and in 2005 when the filamentous *Mougeotia gracillima* dominated. Diatoms domination usually occurred during January–February (*Aulacoseira granulata*, e.g., in 1997, 1998, 1999, 2001, and 2003) but occasionally in the summer (*Synedra* sp. in 1998 and 2001). Dinoflagellate domination occurred mostly in the winter–spring, and was usually formed by *Peridinium gatunense*.

The large number of available samples with *Peridinium* domination enabled an examination of the annual cycle of its C:Chl ratios (Fig. 3). When *Peridinium* concentrations peaked, between March and May, the multiannual mean C:Chl ratio of 50–60, was higher than the ratio from December to February, when the population was just starting to increase. On the rare occasions, when *Peridinium* was dominant from July to September, C:Chl was higher than at peak density (Fig. 3). The annual C:Chl averages of dinoflagellates varied mostly around the overall average of 55:1, but there were upward exceptions in 2000 and 2006 and a downward exception in 2005, in cases when *Peridiniopsis* species were dominant or co-dominant.

A similar analysis of the seasonal changes in C:Chl for the other three phyla could not be made due to insufficient temporally spaced data. Differences in monthly average C:Chl within each taxonomic group could have been large, e.g., in February, the ratio for chlorophytes, composed of several desmid species, was 37 (average of 43 observations), and in March 56, represented by similar composition of desmids (average of 24 observations), but we lacked sufficient data for correlating those differences with environmental factors. The three chlorophyte species that ever exceeded the 60% dominance criterion (*Closterium aciculare*, *Mougeotia gracillima*, and *Pediastrum* spp.) did not differ significantly in their mean C:Chl ratio (Table 1). We had diatom data only for the months January, February, March, and September. In the first 3 months, when *Aulacoseira granulata* dominated, the monthly C:Chl average changed slightly between 24.7 and 26.4. However, annual averages for *A. granulata* were fairly variable and spanned from 14 ± 3.2 in 1997 to 43 ± 8.5 in 1999. In September, when the small pennatae diatom *Synedra* sp. dominated, the C:Chl was approximately 49. Only two species of cyanophytes, *Aphanizomenon ovalisporum* and *Cylindrospermopsis raciborskii*, dominated the phytoplankton over periods of several weeks, and their average C:Chl was fairly similar,

Table 2 Chlorophyll-normalized photosynthetic rate (A.N. = assimilation number) at optimal depth by natural populations of Lake Kinneret main phytoplankton taxonomic groups, 1994–2007

Group	Number of cases	A.N. (mg C mg Chl a^{-1} h^{-1})			
		Average	Std	Min	Max
Cyanophytes	13	4.2	1.6	2.3	7.8
Chlorophytes	16	2.3	1.1	0.4	3.6
Diatoms	8	2.1	0.4	1.3	2.6
Dinoflagellates	57	1.6	0.8	0.2	3.5

77:1 and 83:1, respectively. For *C. raciborskii*, distinct inter-annual variability of the C:Chl ratio was observed, with the average being 79 ± 6.5 in 2004, 116 ± 13.9 in 2005, and 52 ± 8.7 in 2006. *Microcystis aeruginosa* and *Chroococcus* sp. showed higher ratios, but those averages are based on a low number of samples (Table 1).

Photosynthetic rate at optimal depth

In the data base included in the current study, we found 94 cases, where a single phylum exceeded the >60% threshold of contribution to the overall algal population at the optimal depth. The average A.N. of cyanophytes was conspicuously higher than that of the other groups and that of the dinoflagellates prominently lower than that of other phyla (Table 2). The monthly average A.N. number for periods when *Peridinium gatunense* formed extremely dense populations, from March to May, was apparently lower, than in the summer (Fig. 4).

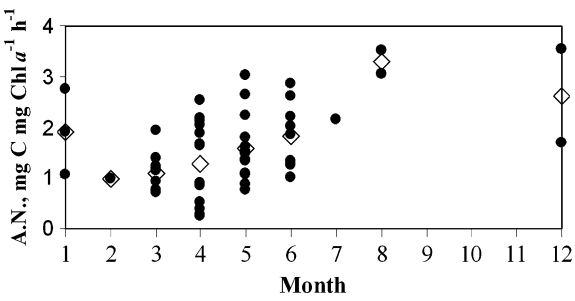

Fig. 4 Assimilation number at the optimal depth when dinoflagellates dominated the phytoplankton in Lake Kinneret, 1994–2007. *Circle*—actual measurement; *Diamond*—multi-annual monthly average

Table 3 C:Turnover time in natural populations of Lake Kinneret main phytoplankton taxonomic groups, 1994–2007

Group	Number of cases	Turnover time (*d*)			
		Average	Std	Min	Max
Cyanophytes	13	1.56	0.65	0.55	2.83
Chlorophytes	16	2.73	2.02	0.48	7.19
Diatoms	8	1.58	0.63	0.65	2.56
Dinoflagellates	57	5.91	4.53	1.76	24.89

Turnover time at optimal depth

Turnover time of phytoplankton was calculated using primary productivity and C-biomass data at the depth of maximal photosynthetic rate, from the same 94 cases used for computing A.N. Turnover time varied widely between groups and also within each group (Table 3). Dinoflagellates (mostly *P. gatunense*) displayed conspicuously longer turnover times with greater variability than the other groups. Making use of the 56 comparisons available of our *Peridinum* data, we found that the turnover time was independent of the C:Chl ratio. The longest turnover time values were recorded in April, when *P. gatunense* formed the densest populations, but the variation at this month was also the greatest (Fig. 5 upper). The turnover time of *P. gatunense* was moderately correlated with Chl (Fig. 5 lower); implying that at high cell densities competition for resources (light, nutrients) slows down *P. gatunense* reproduction. The temporal distribution of turnover times for cyanophytes, chlorophytes, and diatoms showed that a fairly limited range of values usually ranging 0.5–3 days, with few exceptions in April–May 2005 when the large filamentous chlorophyte *Mougeotia gracillima* (Zygnematales) dominated (Fig. 6). The average turnover time of that species, 5.9 days, was more than twice of the average of other chlorophytes, and within the range of generation times seen only in *Peridinium gatunense*.

Discussion

Our estimations of the C:Chl ratio have intrinsic shortcomings due to uncertainties deriving from (a) 10–20% measurement error in the determination of phytoplankton cell abundance using microscope

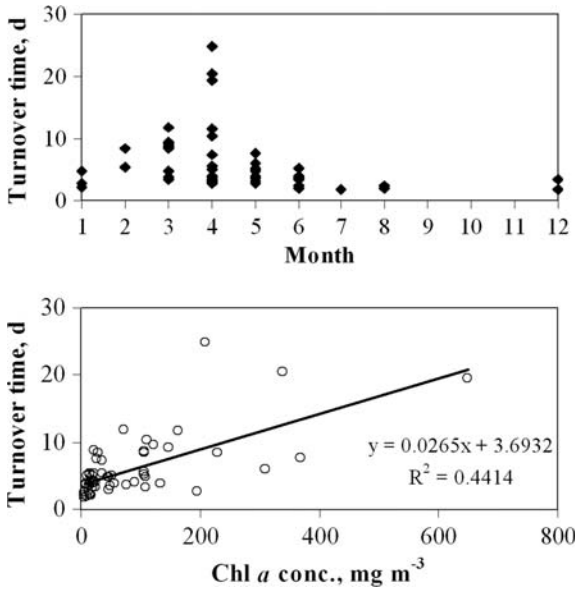

Fig. 5 Turnover time in dinoflagellates. Results of measurements in the years 1994–2007 are distributed to monthly bins (*upper panel*); Dinoflagellate turnover time versus chlorophyll *a* concentration at the optimal depth (*lower panel*)

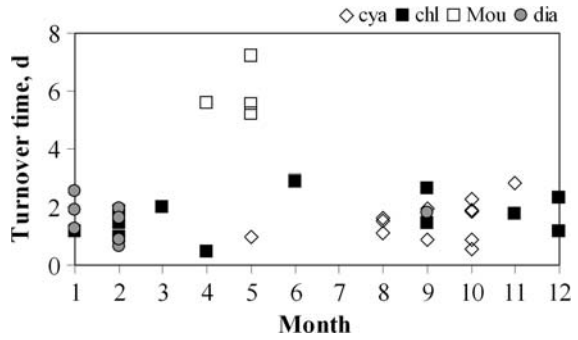

Fig. 6 Turnover time in cyanophytes (cya), chlorophytes (chl + Mou), and diatoms (dia). Results of measurements in the years 1994–2007 are distributed to monthly bins. Values >4 were recorded when the dominant chlorophyte was the large filamentous *Mougeotia gracillima* (Mou)

counts, then reflected also in the calculation of wet-weight biomass, (b) the computation of cell volume from measured linear dimensions to a volumetric value, (c) the assumption that a single factor is sufficient for conversion of volume to cellular weight, (d) the assumption that % contribution of a certain taxon to total phytoplankton wet-weight biomass also reflects its % contribution to total chlorophyll, and (e) the coefficients used for the conversion of cellular wet weight to carbon.

A 10–20% error in microscope counts is inherent with the method and cannot be avoided. Complex-shaped cells are naturally prone to distorted conversion from linear measurements to volume; however, a big bias is not expected for most of the dominant species in our study, as their volume may be quite well-described by a defined geometrical form, e.g., *Peridinium* (prolate sphaeroid), *Aulacoseira* (cylinder), *Mougeotia* (cylinder), *Closterium* (double cone), and *Aphanizomenon* (cylinder). Despite the well-recognized variability in cellular composition, and consequent cellular density, we converted the calculated volume to weight by considering a factor of 1. Cyanophytes may be lighter than 1 and diatoms heavier (Reynolds, 2006), but the average deviation from 1 does not exceed 10%. It is to say, that if we apply the reduced and increased density factors in our calculations, C:Chl ratios will not change dramatically and still show a conspicuous difference between the examined taxonomic units.

Our assumption that the share of a given taxon in the Chl pool is the same as its proportion in the bulk of microscopically estimated biomass is not necessarily accurate, as the species composition of the community making up the remaining (up to 40%) phytoplankton biomass varied from sample to sample and chlorophyll content of the different taxa differs considerably (Montagnes et al., 1994). In order to test our assumption, the concentration of total Chl was back-calculated using the C:Chl ratio for each one of the phytoplankton groups included in the study. The calculated value for the entire database ($n = 851$) was only 5% higher than the measured value, and r^2, the coefficient of linear correlation between the calculated versus measured concentration of Chl was 0.91. Consequently, we may assume that the bias introduced by allocation of Chl to a given phylum by multiplying total Chl by the proportion of that phylum in the microscopically determined biomass—does not introduce large error.

Yet another bias may be introduced by the use of a fixed conversion factor from cellular weight to carbon content for each taxonomic group and by the value chosen for this conversion. We took precaution by applying locally measured conversion factors where possible, based on locally occurring phytoplankton and under ambient condition of its development. As an alternative, we used the nonlinear algorithms for calculation of cellular carbon from cell volume,

devised by Menden-Deuer & Lessard (2000). The use of those algorithms with our data yielded C content of 0.17, 0.14, 0.08, and 0.12, for cyanophytes, chlorophytes, diatoms, and dinoflagellates, respectively; i.e., our experimental estimation of cellular carbon content was higher than the calculated value (Table 1). The use of the modeled factors would decrease C:Chl, and therefore impose further difficulty to accept the C:Chl ratio for diatoms in our study, which in any case scratches the limit of acceptable range of cellular content in that phylum (see below). Nevertheless, whether we use our own experimentally based conversion factor for carbon content, or published algorithms, C:Chl varies widely between the four phyla of microalgae dominant in Lake Kinneret. When converting chlorophyll *a* to algal cellular (C) carbon this variability should be taken into account.

Reynolds (2006), using measurements based on monoalgal cultures, put the average C:Chl ratio on 50:1, and located the limits from 30:1 to 70:1. Other sources are less restrictive; thus, for instance, C:Chl was found within the range from 17:1 to 1,000:1 in a large compilation of data on cultures of oceanic phytoplankton (Behrenfeld et al., 2002), and there is no reason to assume that in freshwater the variability is lower. Modeling efforts showed that C:Chl may range widely in nature, depending on latitude and season, with figures running from approximately 10:1 to 180:1 (Taylor et al., 1997; Flynn, 2003; Behrenfeld et al., 2005). Considering the latter limit range, our C:Chl ratios (Table 1) fall within the indicated range, with the lowest ratio calculated for diatoms, and particularly the large centric species, *Aulacoseira granulata*, and the highest ratio recorded for cyanophytes, probably as a result of their high wet-weight:C ratio. It should be noted that the low ratio of *A. granulata* was fairly consistent and the variation showed that (coefficient of variation = 42%) was not much different from *Peridinium gatunense*, the other single species in this study with a relatively large data base (Table 1). Diatoms are mostly characterized by a lower C:Chl ratio than species of other phyla (e.g., Montagnes et al., 1994), but the ratio seen in our study is biased toward the lower limit documented for diatoms. Extremely low C:Chl ratios were found in a controlled experiment, when vigorously growing diatoms were not limited by nutrient provision (Antia et al., 1963). *Aulacoseira granulata* in Lake Kinneret typically appears during thermal destratification when nutrients become abundant, and blooms for a brief period of 3–4 weeks. The low C:Chl ratios recorded for this species in Lake Kinneret are in agreement with the results of Antia et al. (1963). On the other hand, some individual measurements must be considered cautiously. A C:Chl ratio of 10:1 (the lowest found in our study) implies that photosynthetic pigments (chlorophyll *a* + chlorophyll *c* + fucoxanthin + diadinoxanthin + other pigments) make up approximately 20% of all cellular carbon as opposed to an average of 4–10%, a situation that hardly can be accepted, considering other C-containing constituents of algal cells (Kirk, 1994).

The dinoflagellate *Peridinium gatunense* was the only species that at times constituted almost a pure stand (>95% of total phytoplankton biomass), and in addition formed the largest dataset for calculation of C:Chl. The relative uniformity of C:Chl from March to May (Fig. 3) indicates that few changes occur in this species when it reaches a bloom state. *Peridinium* assimilation number showed that a trend of increase with time during bloom development which continued past the bloom peak (Fig. 4), i.e., more efficient chlorophyll-normalized photosynthetic activity. This trend could be explained by the concurrent increasing input of solar energy, and does not pertain to changes in cellular composition of phytoplankton. These findings agree with observations made during the 1970s when phytoplankton periodicity in the lake was fairly stable (Wynne et al., 1982). That relative stability also applies to the content of accessory pigments—the cellular concentration of chlorophyll *c*, peridinin, dinoxanthin, diadinoxantin, and *β*-carotene is almost uniform along the 0–7 m of the water column throughout the entire season when *Peridinium* dominates the lake phytoplankton (Yacobi, 2003).

Vertical uniformity of the C:Chl ratio of all algal taxa examined was typical within the illuminated part of the water column (Fig. 2). The uppermost part of the epilimnion in Lake Kinneret is well-mixed (Eckert et al., 2002), and thus specialized algal populations, in terms of light adaptation, usually do not evolve at any specific depth from the surface down to approximately 10 m depth. During the *Peridinium* bloom, the vertical distribution of algal cells is mostly heterogenous, as *Peridinium* is capable of vertical movement, and if not forced downwards by strong winds, cells ascend in the morning hours to the more illuminated upper layers (Pollingher, 1988;

Usvyatsov & Zohary, 2006). In the lower epilimnion, cells may be captured for a period of days under conditions of sub-optimal light, and subsequently synthesize chlorophyll *a* (Falkowski & Owens, 1980), to compensate for the reduced availability of light. The result of the latter is a decrease in C:Chl with depth between 10 and 20 m (Fig. 2), a phenomenon well-recognized from phytoplankton that resides in deep layers (Falkowski, 1983).

The parameters of photosynthetic rate (assimilation number) and the length of the period required to substitute a given carbon biomass (turnover time) for the different phyla were negatively correlated (Fig. 7). The relatively low-biomass-normalized photosynthetic rates of *P. gatunense*, and the relatively long turnover time of that species were recorded in the past, and are readily explained on the background of the large cell size (ca. 50 μm diameter) with low surface area to volume ratio and the high density of cells in their natural environment (Pollingher & Berman, 1982; Yacobi & Pollingher, 1993). At the other extreme of the relationship between the two parameters stand the cyanophytes with an assimilation number of more than double that of chlorophytes and diatoms. A possible explanation for the extremely high chlorophyll *a*-normalized photosynthetic rate of cyanophytes is their relatively low cellular content of Chl, as indicated by the high C:Chl in our study. In addition to Chl (and other thylakoid-bound pigments), cyanophytes harbor phycobilins, water soluble pigments that fulfill a major role in light harvesting (de Marsac, 2003), and thus may "afford" maintaining lower cellular Chl content than other phytoplankton. It should be noted that all the cyanophyte values of A.N. and turnover times were recorded when the lake was thermally stratified, and thus represented phytoplankton thriving in nutrient-deplete conditions. On the other hand, most values for chlorophytes, diatoms, and dinoflagellates were recorded, when the lake was homogenously mixed or when stratification just commenced, i.e., at times when the water column exposed to photosynthetically effective light was relatively nutrient-enriched. This contrast in cyanophytes versus other phytoplankton groups underlines the potential of cyanophytes to reproduce efficiently under nutrient-limiting conditions.

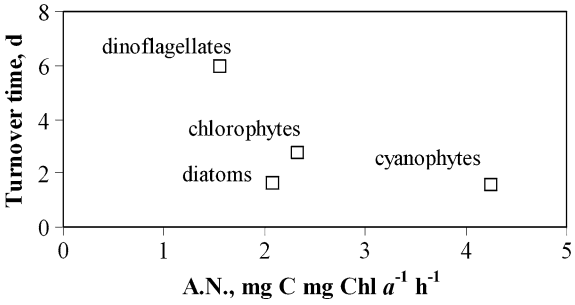

Fig. 7 Comparison of the average assimilation number and turnover time in algal populations, where a single phylum contributed >60% to the phytoplankton biomass. The results were compiled from a record taken in Lake Kinneret from 1994 to 2007

Our study portrays the potential for derivation of structural and functional parameters of phytoplankton using data collected for the purpose of routine monitoring. Although the type of long-term and consistent monitoring program as the one that runs in Lake Kinneret is apparently not widespread, it is worthwhile to delve into that type of information to satisfy needs required by the sophisticated tool of ecosystem modeling.

Structural and functional characteristics of phytoplankton are fundamental input parameters for aquatic ecosystem models. With the prospects of climate change and the need to be able to predict future changes to plan ahead, such models are becoming increasingly essential.

Acknowledgments This composition was presented as a contributed paper at the Bat Sheva de Rothschild seminar on Phytoplankton in the Physical Environment—the 15th workshop of the International Association of Phytoplankton Taxonomy and Ecology (IAP). The data used in this study are part of the Lake Kinneret Monitoring Program funded by the Israeli Water and Sewage Authority. We would like to thank two anonymous reviewers for providing a constructive criticism that helped improving the clarity and quality of the presentation.

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