Article

Species-specific imprint of the phytoplankton assemblage on carbon isotopes and the carbon cycle in Lake Kinneret, Israel

Aram Goodwin,[1,2†] Jonathan Erez,[1] K. David Hambright,[3] Nir Koren,[2] Eugeni Barkan,[1] and Tamar Zohary[2*]

[1]*Institute of Earth Sciences, The Hebrew University of Jerusalem, Israel*
[2]*Kinneret Limnological Laboratory, Israel Oceanographic and Limnological Research, Migdal, Israel*
[3]*Plankton Ecology and Limnology Laboratory, Program in Ecology and Evolutionary Biology, Department of Biology, University of Oklahoma, USA*
[†]*Current address: Department of Earth, Ocean and Atmospheric Sciences, University of British Columbia, British Columbia, Canada*
** Corresponding author: tamarz@ocean.org.il*

Received 30 September 2015; accepted 15 March 2016; published 7 April 2016

Abstract

Lakes undergoing major changes in phytoplankton species composition are likely to undergo changes in carbon (C) cycling. In this study we used stable C isotopes to understand how the C cycle of Lake Kinneret, Israel, responded to documented changes in phytoplankton species composition. We compared the annual $\delta^{13}C$ cycle of particulate organic matter from surface water (POM_{surf}) between (1) years in which a massive spring bloom of the dinoflagellate *Peridinium gatunense* occurred (*Peridinium* years) and (2) years in which it did not (non-*Peridinium* years). In non-*Peridinium* years, the spring $\delta^{13}C$–POM_{surf} maxima were lower by 3.3‰. These spring $\delta^{13}C$ maxima were even lower in POM sinking into sediment traps and in zooplankton (lower by 6.8 and 6.9‰, respectively). These differences in the isotopic composition of the major organic C components in the lake represent ecosystem-level responses to the presence or absence of the key blooming species *P. gatunense*. When present, the intensive, almost monospecific bloom lowers the concentrations of $CO_{2(aq)}$, causing a reduction in the isotopic fractionation of the algae (higher $\delta^{13}C$ of POM_{surf}) and massive precipitation of calcium carbonate ($CaCO_3$). In non-*Peridinium* years, the phytoplankton cannot deplete $CO_{2(aq)}$ to similar levels; the algae maintain higher isotopic fractionation, leading to lower $\delta^{13}C$ maxima. These changes are reflected higher up in the food web (zooplankton) and in sedimenting organic matter. The consequences for the ecosystem in non-*Peridinium* years are lower export of both organic and inorganic C.

Key words: $\delta^{13}C$, carbon stable isotopes, isotopic fractionation, *Peridinium gatunense*, POM, sediment traps, zooplankton

Introduction

Over the past few decades, the number of reports on lakes undergoing major changes in phytoplankton species composition has been growing. A few examples include Lakes Arancio in Sicily (Italy), Balaton in Hungary, and Võrtsjärv in Estonia (Naselli-Flores and Barone 2005, Hajnal and Padisák 2008, Nõges et al. 2010). The impacts of such changes are obvious in extreme cases, as for example when toxin-producing cyanobacteria invaded the African soda lakes, resulting in massive flamingo kills (Ballot et al. 2004). But less obvious impacts could also occur, such as on the ecosystem's carbon cycle. Consumers may exhibit different affinities to the new algae after a major change in phytoplankton species composition occurs, and the new interactions between the prevailing species could therefore lead to alterations in ecosystem components such as recycled versus exported carbon. These potential impacts could be of major ecological importance and thus warrant close examination.

Stable carbon isotopes ($\delta^{13}C$; equation 1) can be used to follow the carbon cycle within an ecosystem (Fry and

DOI: 10.5268/IW-6.2.936

Sherr 1984, Fry 2007). Carbon isotopes are fractionated during photosynthesis, which preferentially fixes $^{12}CO_2$ over $^{13}CO_2$ (Raven 1996), leading to organic matter having lower $\delta^{13}C$ relative to its dissolved inorganic carbon (DIC) source (Rundel et al. 1989). If all the CO_2 that diffuses into the photosynthetic cell is fixed, however, then no fractionation can occur; therefore, the magnitude of fractionation depends on how much CO_2 is available relative to how much is being fixed. As a result, the $\delta^{13}C$ of phytoplankton and, consequently, particulate organic matter (POM) vary positively with increasing specific algal growth rates (Gervais and Riebesell 2001) and negatively with CO_2 availability (Erez et al. 1998). Furthermore, $\delta^{13}C$ can be a tracer of carbon flow into and within the food web, for example to distinguish between autochthonous and allochthonous material with distinct $\delta^{13}C$ (Rundel et al. 1989). Because there is little to no fractionation in consumption, $\delta^{13}C$ can also delineate consumer–diet relations between organisms (DeNiro and Epstein 1978, Martinez del Rio et al. 2009).

Lake Kinneret, a well-studied and intensively monitored meso-eutrophic lake in Northern Israel (Zohary et al. 2014b), is a suitable site to study the impacts of changes in phytoplankton species composition on carbon cycling using stable carbon isotopes. The lake has experienced dramatic changes in its phytoplankton species composition since around the mid-1990s. Before then, the dinoflagellate *Peridinium gatunense* (hereafter *Peridinium*) bloomed every year in spring, but from 1996 onward it bloomed only in a few high-rainfall years (Fig. 1). In the years it did not bloom (hereafter non-*Peridinium* years), no other single species took its place in terms of the maximum algal biomass reached, and a different species succession was observed from one year to another (details in Study Site). The objective of this study was to determine whether carbon dynamics, as recorded by carbon isotopic composition, have changed in Lake Kinneret in response to the changes in phytoplankton species composition.

Previous $\delta^{13}C$ studies of POM from surface water (POM_{surf}) and of plankton from Lake Kinneret during *Peridinium* years have revealed a recurring annual pattern strongly dominated by the seasonal *Peridinium* bloom (Stiller 1977, Zohary et al. 1994, Hadas et al. 2009). The massive bloom would exhaust the $CO_{2(aq)}$ to <2 μM (Berman-Frank et al. 1998), resulting in *Peridinium* exhibiting $\delta^{13}C$ as high as −16‰ (Zohary et al. 1994, Berman-Frank et al. 1998). In the fall, the isotopic composition of the Kinneret POM_{surf} declined gradually, reaching winter minima as low as about −30‰ as excess $CO_{2(aq)}$ with low $\delta^{13}C$ values in water from the deep layers mixed into the euphotic zone. Chemosynthetically derived POM with exceptionally low $\delta^{13}C$ (−35 to −40‰; Hadas et al. 2001) further contributed to the low isotopic composition of POM_{surf} during winter holomixis. Our current study differed from previous studies of stable carbon isotopes in Lake Kinneret by collecting new data from 2 non-*Peridinium* years (2008 and 2009), whereas previous studies were conducted during *Peridinium* years.

We hypothesized that the less intense phytoplankton blooms during non-*Peridinium* years (Fig. 1), coupled with the rise in atmospheric CO_2 over time, would both act to maintain higher levels of $CO_{2(aq)}$ in the more recent non-*Peridinium* years, resulting in lower $\delta^{13}C$ of $POM_{surf.}$ Because POM consumed by zooplankton or sinking to the

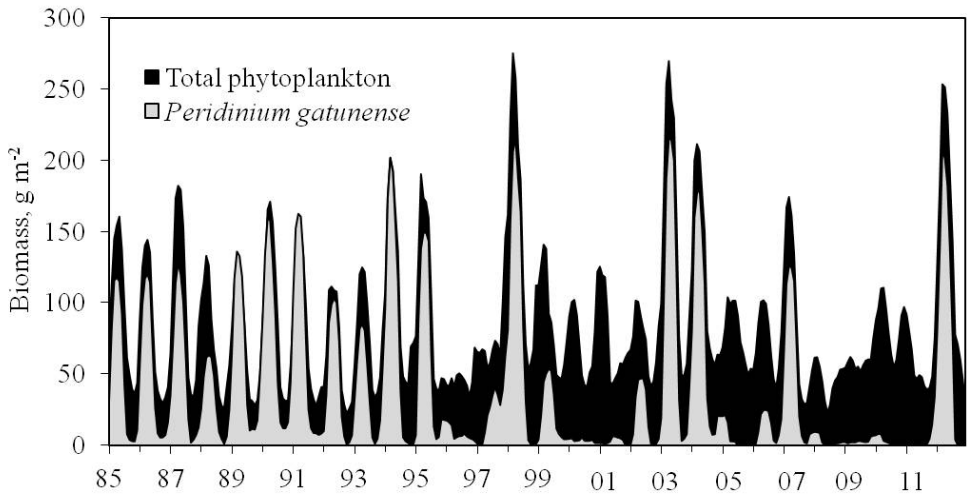

Fig. 1. Time series (1985–2012) of depth-integrated wet weight biomass of the dinoflagellate *Peridinium gatunense* and of total phytoplankton biomass in Lake Kinneret. Values shown are running means of 5 consecutive monthly means. Tick marks denote 1 January of the indicated year. Until 1995, *Peridinium* bloomed every spring, but since 1996 it bloomed only in springs 1998, 2003, 2004, 2007, and 2012. Original data of T. Zohary generated as part of the Kinneret monitoring program using methods described by Zohary (2004).

 DOI: 10.5268/IW-6.2.936

sediments is derived from surface water POM, we further hypothesized that zooplankton and POM collected in sediment traps would also exhibit lower $\delta^{13}C$ in non-*Peridinium* years.

To address our hypotheses, samples of POM_{surf} and of zooplankton were collected monthly and analyzed for their carbon isotopic composition. During 2008 we also analyzed the carbon isotopic composition of sinking POM (POM_{traps}) and calcium carbonate ($CaCO_3$) collected at monthly intervals in sediment traps. The $\delta^{13}C$–$CaCO_3$ can be used as a proxy for $\delta^{13}C$–DIC (Emrich et al. 1970) and can thus delineate possible changes to the source of carbon in POM. These data were then compared to historical carbon isotopes and ecological data from Lake Kinneret from years when *Peridinium* did bloom. This combined dataset enabled the comparison of carbon dynamics in *Peridinium* versus non-*Peridinium* years.

Study site

Lake Kinneret, located at 35°35′E, 32°53′N and ~209 m below mean sea level, occupies a relatively large and deep basin within the Syrian–African rift series, one of the longest active tectonic features on Earth. When full, the surface area of Lake Kinneret is 169 km^2 and the volume is 4.3 × 109 m^3, with mean and maximum depths of 25.6 and 42 m, respectively (Berman et al. 2014). The lake, subjected to a Mediterranean climate with cool rainy winters and hot dry summers, is warm monomictic. It stratifies in March, reaching late summer epilimnetic temperatures of 30–31 °C. Destratification begins in the fall, culminating with holomixis around December–January when the water column cools to 15–16 °C (Rimmer et al. 2011). Winter turnover and winter inflows from the catchment provide the majority of nutrients to the euphotic zone (~15 m deep; Rimmer et al. 2008), triggering a spring algal bloom. Consequently, epilimnetic pH rises from ~8 in winter to >9 at the peak of the bloom and is then reduced by chemical precipitation of $CaCO_3$, leading to a decrease in alkalinity from ~2.7 to ~2 meq L^{-1} (Nishri and Stiller 2014).

The first 27 years of monitoring on Lake Kinneret, 1969–1995, showed a remarkable recurring annual pattern of phytoplankton dynamics. The large-celled (~50 µm diameter) dinoflagellate *Peridinium gatunense* Nygaard would produce massive spring blooms, peaking in April–May to 150–250 g wet weight m^{-2} (g WW m^{-2}) and collapsing around June each year to levels of 10–25 g WW m^{-2} (Pollingher 1986, Zohary et al. 1998). Other dinoflagellate species, including several species of the smaller-sized genus *Peridiniopsis*, usually appeared toward the end of the *Peridinium* bloom and were abundant in early summer (Pollingher and Hickel 1991). The rest of the phytoplankton (mainly nanoplanktonic) would oscillate in the background throughout the year around values of only 10–25 g WW m^{-2} (Serruya et al. 1980). This recurring annual pattern was interrupted in 1996 when for the first time on record *Peridinium* did not bloom; between 1996 and 2012 it bloomed only in 1998, 2003, 2004, 2007, and 2012 (Fig. 1). In non-*Peridinium* years the seasonal phytoplankton dynamics were inconsistent, exhibiting different bloom periods, magnitudes, modes, and species compositions (Zohary et al. 2012) and achieving spring maximum biomass generally lower than that attained in *Peridinium* years (Fig. 1). Since 1994, Lake Kinneret has been subjected to multiple invasive algal species, including bloom-forming, nitrogen-fixing, and toxin-producing filamentous cyanobacteria that make substantial contributions to total phytoplankton biomass in some years, with negative impacts on water quality (Zohary et al. 2014c, Sukenik et al. 2014a).

The zooplankton assemblage of Lake Kinneret is typical for a subtropical lake with relatively high levels of zooplanktivory. Small-bodied cladocerans (*Diaphanosoma brachyurum, Ceriodaphnia reticulata, C. rigauldi, Bosmina longirostris typica, B. l. cornuta*) and copepods (*Mesocyclops ogunnus, Thermocyclops dybowskii*) represent the crustaceans and make up the bulk of zooplankton biomass (Hambright 2008, Gal and Hambright 2014). The cladocerans and juvenile copepods are considered herbivores, whereas the adult copepods are mainly predators, feeding on the herbivores (Blumenshine and Hambright 2003). Numerous rotifers and protists, representing the microzooplankton, can constitute a major fraction of the total grazing and nutrient recycling by zooplankton (Hambright et al. 2007), but their contribution to total zooplankton biomass is small (~7%; Gophen 1978).

Chemosynthetic bacteria occupy oxic–anoxic interphases, such as the metalimnion and the sediment–water interphase, and produce organic matter with exceptionally low $\delta^{13}C$ values (about −39‰; Hadas et al. 2001).

Methods

Sampling and sample preparation for isotopic analyses

General

The spatial distribution of phytoplankton in the pelagic water of Lake Kinneret tends to be homogeneous (Zohary et al. 2014b). Furthermore, previous unpublished data of stable carbon isotopes in POM and zooplankton from Lake Kinneret exhibited negligible variability between samples collected concurrently at different pelagic sampling sites. Hence, spatial variability was considered to be minor, and our sampling was limited to a single

sampling site each month. Emphasis was placed on the temporal patterns, and sampling covered more than 2 full annual cycles.

POM of surface water (POM_{surf})

The POM of Lake Kinneret is dominated by live phytoplankton and by detritus of phytoplankton origin (Parparov et al. 2014); hence, in this study, POM was taken as a proxy for phytoplankton. In *Peridinium* years during the bloom, *P. gatunense* cells typically constituted >80% of the material collected on a GF/C filter (Parparov et al. 2014). In non-*Peridinium* years, different species bloomed in different years, as reported by Zohary et al. (2012), and the overall contribution of live phytoplankton to POM was smaller. Particulate matter was sampled at monthly intervals from November 2007 until January 2010 from 1 L of water collected from 2–3 m depth using a Rhode sampler at an open-water site ~5 km offshore from the Kinneret Limnological Laboratory. The water was filtered through a pre-combusted GF/F filter, and the filter with particulate matter was then frozen at −20 °C, freeze-dried, and kept dry until analyzed for $\delta^{13}C$, $\delta^{15}N$, and carbon and nitrogen concentrations, although only carbon isotope results are presented here.

The particulate matter collected was considered representative of POM_{surf}, even though inorganic C was not removed (explained later). A subsample of the original freshwater sample was examined under the inverted microscope and the dominant species of phytoplankton recorded. These observations were supplemented by routine phytoplankton counts and biomass estimates from the Kinneret monitoring program (Zohary et al. 2014c). The POM in Lake Kinneret may also include live bacteria and zooplankton, organic matter derived from them, and other forms of organic detritus (Parparov et al. 2014). Zooplankton was not removed from the samples by pre-filtration because it constitutes on average <10% of the seston dry weight in Kinneret water (Parparov et al. 2014). Furthermore, our unpublished C:N ratio determinations show that the samples had a mean ±SD molar C:N ratio of 9.6 ± 1.3, consistently similar to the mean of phytoplankton samples (mean C:N = 9.2 with a wide range, data not shown). Both were significantly higher than the C:N in zooplankton samples (C:N = 5.6 ± 0.7).

The filters also collected inorganic particles, mostly aluminosilicates (with no carbon) and some authigenic and allochthonous $CaCO_3$. Regular microscopic examination of the samples confirmed that $CaCO_3$ crystals were rare and comprised <<1% of the particles, and hence their impact on the isotopic composition of POM_{surf} would be negligible. The low inorganic carbon content of the particulate matter on the filters was attributed to the high sinking rate of $CaCO_3$ with specific density of ~2.5, which would quickly remove $CaCO_3$ from surface water (in contrast, $CaCO_3$ crystals were abundant in sediment trap samples). Acid treatment to remove the possible presence of $CaCO_3$ from the filters was not performed (1) to enable comparison between our results and those from earlier studies (Zohary et al. 1994, Stiller and Nissenbaum 1999) and (2) because fuming blank GF/F filters with HCl in a desiccator led to unexplained, unreasonably low background $\delta^{13}C$ values of −32 to −33‰ compared with GF/F filters that were not fumed. This isotopic composition of the fumed filters was different from that of Kinneret POM and could introduce another error.

Zooplankton

Zooplankton was collected at the same time as POM_{surf} samples using subsurface (1–2 m) horizontal hauls of 150 μm and 300 or 450 μm mesh nets. The different mesh size nets were used to ensure sufficient collection of both cladocerans and copepods. In the laboratory, zooplankton were cleaned from other particles in the net tows by letting them swim to the light (Rachamim et al. 2010). This light–dark separation process would usually last between 1.5 and 3 h and was sufficient for gut clearance prior to stable isotope analysis (Feuchtmayr and Grey 2003, Smyntek et al. 2007). The zooplankton that swam to the light (mostly cladocerans and copepods) were then collected on a 64 μm mesh net and frozen at −20 °C, freeze-dried, and kept dry until $\delta^{13}C$ analysis. Microzooplankton (rotifers and protists) were not sampled because of technical difficulties in separating them from phytoplankton and detritus. Hence, zooplankton, as referred to in this study, relates mostly to cladocerans and copepods. Because different species of crustacean zooplankton from Lake Kinneret sampled concurrently had similar $\delta^{13}C$ compositions in a previous study (Zohary et al. 1994), we treated the crustacean zooplankton as a single multi-species compartment.

POM from sediment traps (POM_{traps}) and $CaCO_3$

POM from sediment traps (POM_{traps}) and $CaCO_3$ were collected from 2 sets of sediment traps (lower and upper) positioned 1.5 and 12.5 m above the lake bottom at Station A at the deepest part of the lake. The contents of the traps were retrieved at 1–2 week intervals; for this study, only one sample each month was analyzed from January 2008 to February 2009. Each trap was made of 4 replicate PVC cylinders (53 mm diameter and 600 mm in length; Koren and Klein 2000). The deeper trap collected particles sinking into the benthic boundary layer and likely to reach the lake bottom; the shallower trap was

 DOI: 10.5268/IW-6.2.936

within the hypolimnion and collected particles settling from the epilimnion. The particulate matter was separated from the water by centrifugation and freeze-dried. The freeze-dried material was subsampled to obtain both organic (POM_{traps}) and inorganic (mostly $CaCO_3$) material separately. The organic subsample was treated with 1 N HCl to remove $CaCO_3$, dried in the hood to remove the excess acid, and stored at room temperature in a desiccator until $\delta^{13}C$ analysis was performed (Dubowski et al. 2003). The inorganic subsample was treated with diluted (1:5) NaOCl for 24 h to oxidize the organic matter. The samples were then dried at ~40 °C overnight and stored at room temperature until analysis for $\delta^{13}C$.

Carbon isotope analyses

Stable carbon isotopes are expressed by the δ notation, which stands for the relative deviation in the $^{13}C/^{12}C$ ratio between a given sample and the $^{13}C/^{12}C$ ratio of the universal standard Pee Dee Belemnite (PDB) carbonate, in parts per thousand:

$$\delta^{13}C\ [‰] = ((^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard} - 1) \times 1000. \quad (1)$$

Analyses of organic matter

One-sixteenth of the filters (POM_{surf}), or ~0.2 mg of the zooplankton and the POM_{traps} samples, was used. Isotopic analyses were performed using elemental analyzer/continuous flow isotopes ratio mass spectrometry (EA/CF-IRMS). The system consisted of a FlashEA 1112 analyzer connected to a Delta XL mass spectrometer (ThermoFisher Scientific, Germany).

All isotopic determinations were conducted in replicates; if the difference between replicates was >0.3‰, additional replicates were run. Three types of standards were routinely analyzed during each run: (1) a *Peridinium* working standard, consisting of a subsample from a single large homogeneous freeze-dried sample of *Peridinium* collected in April 1994, was run every fifth sample; (2) a sucrose standard was run after every 10 determinations, and (3) 4–5 glycine standards were run following every 50 determinations. The analytical precision on $\delta^{13}C$ standards was 0.15‰.

Analyses of $CaCO_3$

$\delta^{13}C$ was measured on duplicate samples of 0.2–0.4 g of $CaCO_3$, each using gas bench/continuous flow isotope ratio mass spectrometry. The system consisted of a GasBench III connected to a Delta XL mass spectrometer. The standard for the $CaCO_3$ was Vienna Pee Dee Belemnite; the analytical precision was 0.15‰.

Reconstructing $\delta^{13}C$–DIC from $\delta^{13}C$–$CaCO_3$

$\delta^{13}C$–DIC values for 2008 were reconstructed from our $\delta^{13}C$–$CaCO_3$ measurements using the temperature-dependent factors of fractionation between $CaCO_3$ and DIC of Emrich et al. (1970), +0.035‰ $°C^{-1}$ +1.85‰ at 20 °C, and the corresponding annual thermal data from the lake.

Data from previous studies

$\delta^{13}C$ data

$\delta^{13}C$ data from this study were supplemented with $\delta^{13}C$ data for zooplankton, POM_{surf}, and POM_{traps} from former studies (Table 1); former published data were digitized using Engauge Digitizer 4.1, and former unpublished data were collected using the same procedures as described earlier. An exception was that for collecting POM_{traps} data; the sediment traps from 1990–1995 were positioned at the same site as ours but at 17 and 28 m depth (~23 and 12 m above the lake bottom; see Discussion). The compiled dataset spanning 1991–2010 (Table 1) was used for comparing the seasonal patterns of $\delta^{13}C$ of the various components in *Peridinium* years to those in non-*Peridinium* years.

Supplementary limnological data

We used monitoring data collected routinely as part of the Kinneret monitoring program conducted by the Kinneret Limnological Laboratory, Israel Oceanographic & Limnological Research (Sukenik et al. 2014b), including weekly or fortnightly depth profiles of phytoplankton species composition and wet-weight biomass, chlorophyll *a,* primary production, and calcium (Ca) concentrations as well as water temperature, pH, and alkalinity from Station A. The data for the last 3 variables were used to calculate the carbonate chemistry variables, applying the code CO2SYS_2.1.xls for Windows originated by Lewis and Wallace (1998). The pH scale was NBS, and the constants (K1 and K2) were for salinity = 0, according to Millero (1979). Methods to determine the different variables are as specified in the respective book chapters in Zohary et al. (2014b).

Data presentation

To compare isotopic data from *Peridinium* years with those from non-*Peridinium* years, we categorized the data according to whether they originated from a year where *Peridinium* bloomed or not and plotted them along a relative annual scale, starting with turnover of 1 year (time = 0) and ending with turnover of the following year (time = 1). We chose this relative annual scale rather than Julian Day because temporal and spatial patterns are reset each year when the water column overturns and

Table 1. Sources of $\delta^{13}C$ data for particulate organic matter from surface water (POM_{surf}), particulate organic matter from sediment trap (POM_{traps}), and zooplankton from Lake Kinneret; years of data collection; and whether *Peridinium gatunense* bloomed. Published data were digitized using Engauge Digitizer software (v4.1).

Component	Years	*Peridinium*/ non-*Peridinium* year	Source
POM_{surf}	1991–1995	*Peridinium*	Unpublished, Zohary and Erez
	2004	*Peridinium*	Fig. 6; Hadas et al. 2009
	2005	non-*Peridinium*	Fig. 6; Hadas et al. 2009
	2008–2010	non-*Peridinium*	This study
POM_{trap}	1991–1995	*Peridinium*	Unpublished, Zohary and Erez
	2008–2009	non-*Peridinium*	This study
Zooplankton	1972–1973	*Peridinium*	Fig. 2; Zohary et al. 1994
	1989–1992	*Peridinium*	Fig. 2; Zohary et al. 1994
	2008–2010	non-*Peridinium*	This study

homogenizes the lake, an event that occurs in winter but not necessarily on the same calendar date each year. Therefore, the relative annual scale on the x-axis reduces associated irrelevant variation in the data, particularly because the water column overturned later than usual in winter during non-*Peridinium* years. The date of overturn each year was determined as in Rimmer et al. (2011).

Statistical analyses

To test whether the differences in $\delta^{13}C$ values between *Peridinium* and non-*Peridnium* years were significant, we performed the following analysis, as exemplified here for the POM_{surf} dataset. We first fitted 3 lines to each series of (1) the *Peridinium* years, (2) the non-*Peridinium* years, and (3) the 2 combined, using MATLAB'S polyfit function for a second-degree polynomial. The residuals of each fit (SSR: the sum of the squared deviations between the observed data and the fitted line) were then recorded (Table 2). We assumed that if no difference existed between the *Peridinium* and non-*Peridinium* series, then the SSR of the *Peridinium* years plus the SSR of non-*Peridinium* should be equal to that of the 2 combined, or total SSR. To test this assumption, the ratio (f') between the total SSR and the SRR of the 2 series was defined as:

$$f' = \text{SRR combined}/(\text{SSR } \textit{Peridinium} + \text{SSR non-}\textit{Peridinium}). \quad (2)$$

This ratio should equal 1 if no difference exists but should grow greater the more different are the 2 series. We denoted f' to distinguish it from the standard f ratio used for ANOVA, which is phrased slightly differently.

The ratio can be slightly >1, however, even if no significant difference exists between the 2 series, because the sample size is not infinite. To examine by how much this f' ratio could deviate from 1 due to the finite size of the data rather than a real difference, we performed a simulation test using MATLAB's randperm function. The bulk data were randomly recategorized into 2 pseudo groups mimicking the *Peridinium* years and non-*Peridinium* years. Pseudo group 1 had the same number of data points as the non-*Peridinium* years, and pseudo group 2 had the same number of data points as *Peridinium* years. We then fitted each group with a second degree polynomial and recorded the f' ratio:

$$f'\text{pseudo (i)} = \text{total SSR}/(\text{SSR pseudo group 1} + \text{SRR pseudo group 2}). \quad (3)$$

After repeating this procedure 10 000 times using a loop in MATLAB while recording all the resulting ratios, the 99th percentile of the resulting ratios was 1.15 (Table 2). In other words, deviations of the f' ratio from 1 by >0.15 indicates a significant difference between the *Peridinium* and non-*Peridinium* series, equivalent to p value < 0.01.

Results

All $\delta^{13}C$ data generated from samples collected in this study (POM_{surf}, POM_{traps}, and zooplankton) displayed strong seasonality (Fig. 2), with winter minima followed by late spring to early summer maxima (hereafter spring maxima). During 2008, the $\delta^{13}C$ of POM_{surf} and of POM_{traps} from both upper and lower traps fluctuated around similar values, with no apparent systematic differences. All exhibited minimum values (−31.3 to −30.2‰) in January and maximum values (−23.9 to −23.4‰) in May–June, corresponding to seasonal ranges of 6.7, 7.2, and 7.9‰ for $\delta^{13}C$ of POM_{surf}, $POM_{trap\text{-}up}$, and $POM_{trap\text{-}low}$, respectively. In the following winter (Jan 2009) they exhibited minima of −32.8, −31.7, and −30.8‰, respectively (a decrease of

 DOI: 10.5268/IW-6.2.936

9.3, 7.8, and 7.4‰, respectively, compared to the spring maxima). Zooplankton $\delta^{13}C$ (Fig. 2) revealed a slightly higher amplitude than the POM fractions during 2008, increasing from −33.1‰ in January to −22.5‰ in June (10.6‰ difference) and then decreasing the following winter to −33.7‰ (11.2‰ difference).

During 2009, however, $\delta^{13}C$–POM_{surf} ranged almost twice as high compared to 2008 (12.7‰), peaking to −20.1‰ in June. $\delta^{13}C$–zooplankton reached a peak of only −22.1‰ in July 2009 (11.6‰ range); subsequently, both dropped to −29.1 and −32.4‰, respectively, in January 2010 (9 and 10.3‰ range).

The $\delta^{13}C$–POM_{surf} values of non-*Peridinium* years seemed generally lower than those of *Peridinium* years (Fig. 3a). In particular, the spring peak values seemed lower in non-*Peridinium* years, whereas close to the time of the water column overturn in winter, the differences diminished. The same pattern was observed for $\delta^{13}C$–POM_{trap} (Fig. 3b). For zooplankton, the pattern was slightly different, with $\delta^{13}C$ values generally lower during the first one-third of the year in *Peridinium* years compared to non-*Peridinium* years but considerably higher during the next two-thirds of the year (Fig. 3c). Nevertheless, the 3 variables shared higher spring maxima of $\delta^{13}C$ values in *Peridinium* years compared to non-*Peridinium* years. To quantify by how much lower the annual peak values were in the non-*Peridinium* years, we averaged the 7 highest data points of each of the series and found the non-*Peridinium* years were lower by 3.3, 6.8, and 6.9‰ for POM_{surf}, POM_{traps}, and zooplankton, respectively.

When we calculated the f' ratio (equation 2) for the POM_{surf} dataset (Table 2), the result was 1.66, which is higher than the critical value of 1.15 given by the 99th percentile of f'_{pseudo} (see Methods). This finding indicated that ^{13}C–POM_{surf} in *Peridinium* years was significantly

Table 2. Coefficients of a second degree polynomial fit to $\delta^{13}C$–POM_{surf} vs. time elapsed since water column overturn. "Coef1" refers to the highest order coefficient followed by a descending order. Also given are R^2 of each fit and sum of squared residuals (SSR) between the observed data and the fit. "Combined" refers to the entire dataset treated as a whole, "non-*Peridinium*" to data from years in which *Peridinium* did not bloom, and "*Peridinium* years" to data from years when it did bloom (see Table 1).

Series name	coef1	coef2	coef3	R^2	SSR	f'	99th percentile
combined	−34.9	33.8	−30.0	0.48	602.8	1.66	1.15
non-*Peridinium*	−29.0	31.5	−32.5	0.86	155.6		
***Peridinium* years**	−40.4	37.2	−28.9	0.82	207.2		

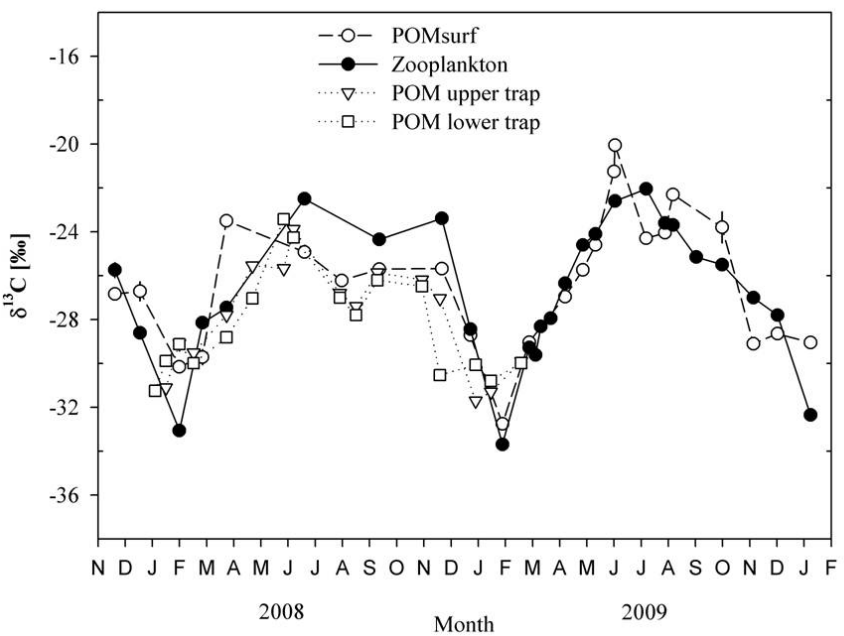

Fig. 2. Time series (Nov 2007–Jan 2010) of $\delta^{13}C$ of particulate organic matter collected from 2–3 m depth (POM_{surf}, open circles), zooplankton from horizontal net tows (filled circles), and of POM from 2 sediment traps positioned 12.5 m (triangle; POM upper trap) and 1.5 m (open squares; POM lower trap) above the sediment at Station A, Lake Kinneret. Error bars mark the range of duplicate measurements; this range was often smaller than the symbols

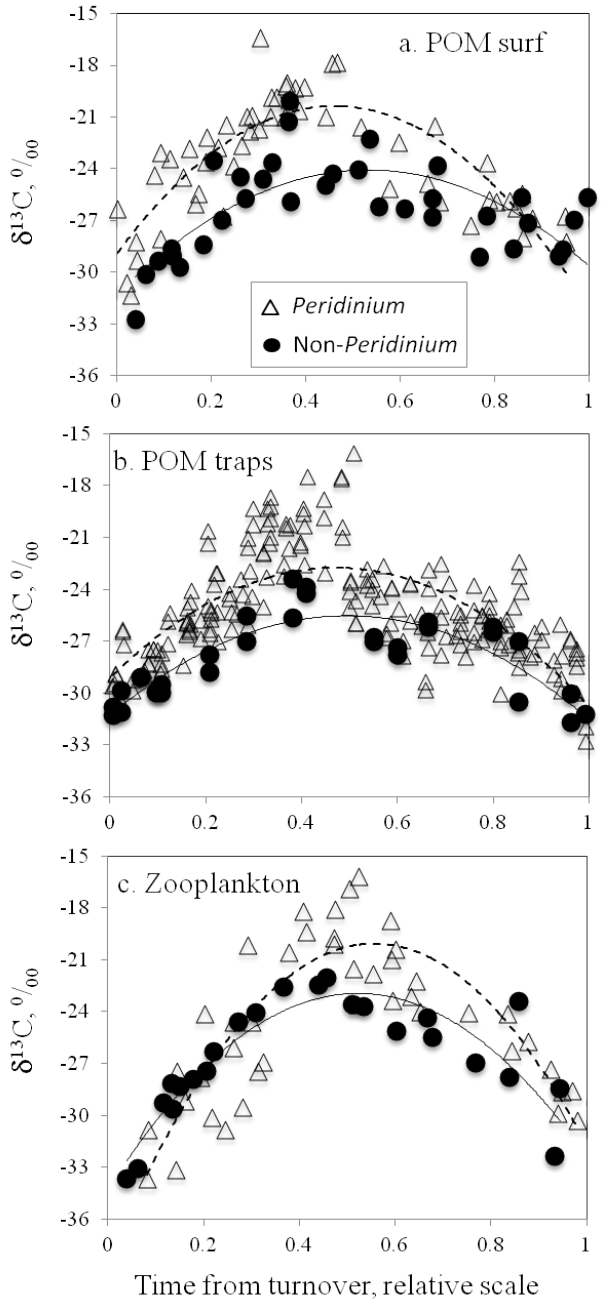

Fig. 3. The seasonal patterns of $\delta^{13}C$ of (a) POM_{surf}, (b) POM_{traps}, and (c) zooplankton in *Peridinium* years (open triangles) in comparison with non-*Peridinium* years (filled circles). The time scale along the x-axis was converted to time elapsed since water column overturn (for each year, 0 is equivalent to day of the overturn, and 0.99 approaches the day of overturn of the following year). Least squares second degree polynomial fit lines are shown for *Peridinium* years (dashed line) and non-*Peridinium* years (solid line). The parameters and R^2 values are given in Table 2. Data presented are those listed in Table 1 (i.e., both data collected during this study and data collected in previous studies). Data for the upper and lower traps were combined for POM_{traps}.

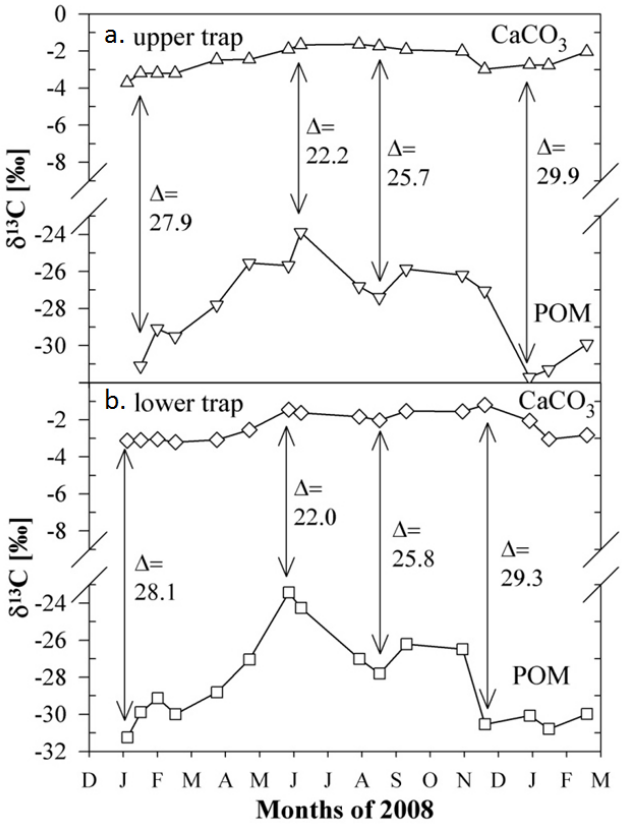

Fig. 4. Time series (Jan 2008–Feb 2009) of $\delta^{13}C$ of particulate organic matter (POM) and of $CaCO_3$ retrieved from 2 sediment traps positioned (a) 12.5 m and (b) 1.5 m above the sediment at Station A in Lake Kinneret. Data shown are means of duplicate measurements. Arrows and Δ symbols indicate the difference in ‰ between the corresponding $\delta^{13}C$ of $CaCO_3$ and POM for times chosen to represent the annual maxima and minima differences.

different from that in non-*Peridinium* years. We repeated this for zooplankton and POM_{traps} similarly showing a significant difference between the 2 series (f'>99th percentile by 0.014 and 0.067, respectively).

The values of $\delta^{13}C$–$CaCO_3$ from both upper and lower sediment traps in 2008 also exhibited a seasonal trend of minimum values in winter followed by maxima in spring, albeit with a much narrower range than that of $\delta^{13}C$–POM (Fig. 4). The $\delta^{13}C$–$CaCO_3$ in both the upper and lower sediment traps ranged between −3.7‰ (Jan) and −3.2‰ (Feb) to −1.6‰ (Jul) and −1.5‰ (May). Because $\delta^{13}C$–$CaCO_3$ can act as a proxy for $\delta^{13}C$–DIC, the difference between $\delta^{13}C$–$CaCO_3$ and $\delta^{13}C$–POM_{surf} is indicative of the extent of carbon isotopic fractionation during photosynthesis, ranging between 22.0 and 29.9‰ in 2008 (Fig. 4).

 DOI: 10.5268/IW-6.2.936

Discussion

Our objective was to examine whether the observed changes in phytoplankton species composition, namely the presence or absence of *Peridinium*, impacted the annual $\delta^{13}C$ cycle of POM_{surf}, POM_{traps}, and zooplankton and possibly gain new insights into carbon cycling. The data presented demonstrated that $\delta^{13}C$–POM_{surf} peaked to lower levels in non-*Peridinium* years (Fig. 3a). These lower peaks transferred farther up the food web to zooplankton (Fig. 3c) and to the POM exported to the sediments, as captured by POM_{traps} (Fig. 3b). We first, however, discuss the data collected concomitantly (Fig. 2), allowing us to explore possible explanations to the lower spring $\delta^{13}C$ maxima in non-*Peridinium* years (Fig. 3).

No systematic $\delta^{13}C$ differences were found among all 4 components (POM_{surf}, zooplankton, $POM_{upper\ trap}$, and $POM_{lower\ trap}$) when sampled concomitantly during 2008 and 2009 (Fig. 2). The similarity between $\delta^{13}C$–POM_{surf} (not treated to remove inorganic C) and $\delta^{13}C$–POM_{traps} (treated to remove inorganic C; Fig. 2) validates our claim that our POM_{surf} samples must have had only minute amounts of inorganic C, with negligible impact on the isotopic composition.

The similarity in isotopic composition of the different components further suggests that $\delta^{13}C$–POM approximates the $\delta^{13}C$ of the diet of zooplankton, as has been shown and discussed for this lake (Zohary et al. 1994, Stiller and Nissenbaum 1999). These data also suggest that the turnover of zooplankton biomass is faster than our monthly time resolution. Zooplankton's $\delta^{13}C$ would otherwise develop a time lag compared to $\delta^{13}C$–POM_{surf}, which agrees with a former independent estimate for the lake's zooplankton carbon residence time of 1–2 weeks (Gophen and Landau 1977).

The particulate organic matter was retrieved from the sediment traps at the end of the 1–2 week collection period, during which the traps were integrating sinking POM_{surf}. If decomposition does not occur in the traps, then the $\delta^{13}C$–POM_{traps} should exhibit the integrated value of the rapidly changing $\delta^{13}C$–POM_{surf} for each collection period. Alternatively, if decomposition is intense and material that sank early in the period does not last throughout, then $\delta^{13}C$–POM_{traps} recorded only the $\delta^{13}C$–POM_{surf} from the end of the collection period rather than an integrated value for the whole period. The difference between these 2 alternatives could potentially be used in future studies to estimate organic matter decomposition rates but would require a finer time resolution or longer duration of trap deployment.

The similarity between $\delta^{13}C$–POM_{surf} and $\delta^{13}C$–POM_{traps} (Fig. 2) also validates our comparison between *Peridinium* and non-*Peridinium* years (Fig. 3). Data retrieved from sediment traps deployed 1.5 and 12.5 m above lake sediment (Fig. 2) compared with data retrieved in part during 1990–1995 from sediment traps deployed at different depths (12 and 23 m above lake sediments; Fig. 3) was deemed valid in part by the lack of alteration of $\delta^{13}C$ with depth (Fig. 2).

The compiled sediment trap data from 1990 to 1995 also exhibited no $\delta^{13}C$ alteration with trap depths (data not shown). The notion of lack of $\delta^{13}C$–POM alteration is widely accepted (Meyers 1994); it enables the application of $\delta^{13}C$–POM from sediment cores to reconstruct past environmental conditions (Brenner et al. 1999, Dubowski et al. 2003). The lack of alteration in isotopic composition is validated in turn by the little to no carbon isotopic fractionation when organic matter is consumed (DeNiro and Epstein 1978), which would leave the remaining organic matter intact in terms of its $\delta^{13}C$.

To explore the possible causes for the significantly higher spring $\delta^{13}C$ peaks in *Peridinium* years than in non-*Peridinium* years (Fig. 3), we examined the following possible explanations: (1) a decrease with time in $\delta^{13}C$ of DIC, the source of carbon in POM; (2) a rise with time in concentrations of atmospheric CO_2; and (3) lower exhaustion of dissolved CO_2 in the absence of *Peridinium* in spring supported a higher degree of isotopic fractionation.

A potential recent decrease in the $\delta^{13}C$–DIC would produce an apparent difference between *Peridinium* and non-*Peridinium* years simply because non-*Peridinium* years are more recent. To examine this possibility, $\delta^{13}C$–DIC was reconstructed for the non-*Peridinium* year 2008 (see Methods) and compared to published $\delta^{13}C$–DIC from a *Peridinium* year in 1974–1995 (Stiller and Nissenbaum 1999). Both year types showed similar fluctuations in $\delta^{13}C$–DIC: −6 to −3‰ vs. −5 to −2.5‰ for the non-*Peridinium* vs. the *Peridinium* year, respectively, going from winter to summer. Thus, $\delta^{13}C$–DIC is not likely to explain the observed lower $\delta^{13}C$ maxima in non-*Peridinium* years.

Alternatively, atmospheric CO_2 ($CO_{2(atm)}$) rise could explain the lower $\delta^{13}C$–POM maxima; non-*Peridinium* years are more recent, and an increase of $CO_{2(atm)}$ directly translates to an increase in aqueous CO_2 ($CO_{2(aq)}$), which would increase carbon isotope fractionation in photosynthesis (Freeman and Hayes 1992, Erez et al. 1998). To test this possibility, $CO_{2(aq)}$ in equilibrium with the atmosphere was reconstructed for the non-*Peridinium* year 2008, based on the annual thermal data from the lake, $CO_{2(atm)}$ of 385 ppm and the $CO_{2(atm)}/CO_{2(aq)}$ equilibrium equation of Stumm and Morgan (2012). The reconstructed $CO_{2(aq)}$ in equilibrium changed smoothly from winter to summer following the lake's annual thermal cycle: 18.6–11.8 μmol L^{-1}. For comparison, a similar calculation was performed for *Peridinium* years from the mid-1990s. $CO_{2(atm)}$ in the mid-1990s was roughly 356 ppm, as estimated from the "Full Mauna Loa

CO_2 Record" plot (Dr. Pieter Tans, NOAA/ESRL; www.esrl.noaa.gov/gmd/ccgg/trends/), meaning that from the mid-1990s to 2008, $CO_{2(aq)}$ in equilibrium has increased by a factor of 1.08. Dividing the range found for 2008 by this factor yields $CO_{2(aq)}$ in equilibrium for the mid-1990s, which was only slightly lower: 17.2–10.9 µmol L^{-1}. In contrast, the measured $CO_{2(aq)}$ in Lake Kinneret ranges more than 14 times that value, from >100 µmol L^{-1} in winter to <2 µmol L^{-1} in spring at the height of the *Peridinium* bloom (Berman-Frank et al. 1998). $CO_{2(aq)}$ in the lake is therefore governed by intense biological processes (photosynthesis and respiration) and chemical processes (precipitation and dissolution of $CaCO_3$) and not by equilibration with rising $CO_{2(atm)}$; therefore, changes in the atmospheric CO_2 are not likely the cause for the differences in $\delta^{13}C$ between *Peridinium* and non-*Peridinium* years.

Finally, we explored whether the presence or absence of *Peridinium* itself could have caused the observed changes in spring $\delta^{13}C$ peaks. Our hypothesis was that in non- *Peridinium* years, other algae do not draw down the concentration of dissolved CO_2 as intensely as in *Peridinium* years; hence, isotopic fractionation would be greater, leading to lower $\delta^{13}C$ maxima. To examine this hypothesis, the annual patterns of ambient lake $CO_{2(aq)}$ concentrations were compared between *Peridinium* years and non-*Peridinium* years. From the long-term 1994–2012 monitoring record, we selected 6 *Peridinium* years (those with the most intense blooms in the record) and 6 non-*Peridinium* years (those with the lowest biomass of *Peridinium*). Moderate bloom years were excluded to enhance differences between the 2 types of years. For the 12 selected years, $CO_{2(aq)}$ concentrations were computed for each sampling date (every 2 weeks) and depth (1, 3, 5,

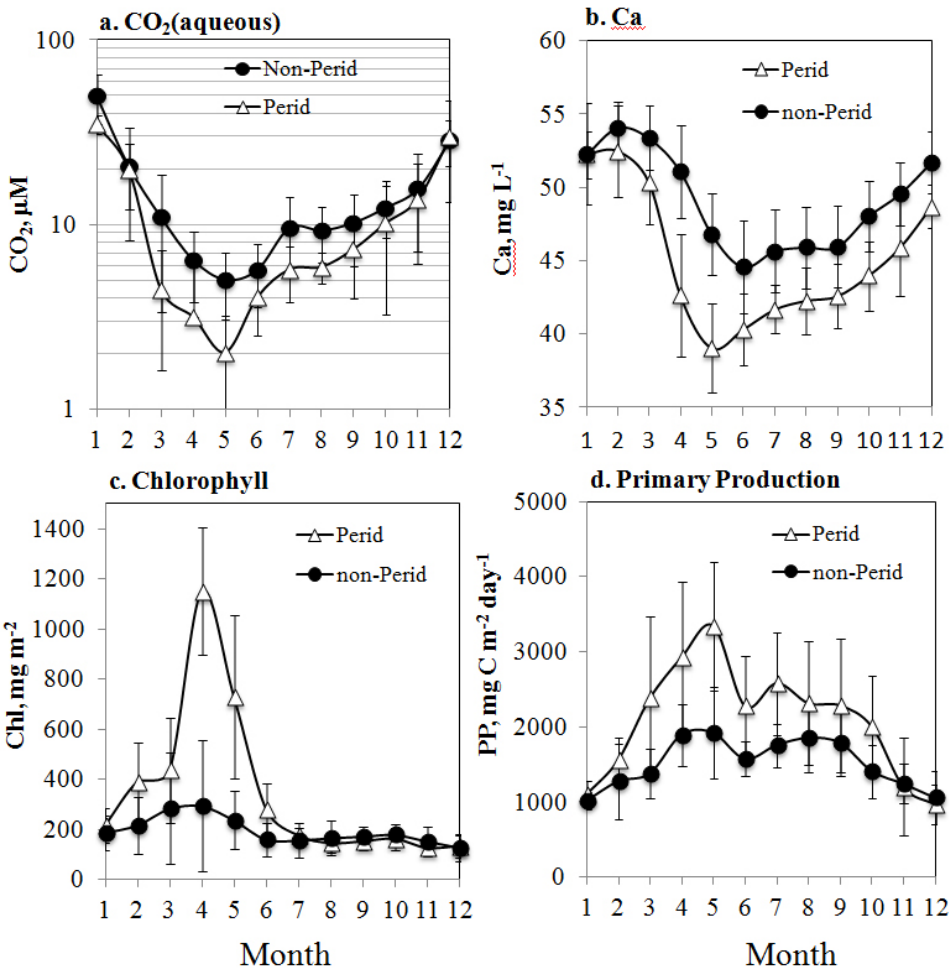

Fig. 5. Comparison of seasonal patterns (as monthly means) between 6 *Peridinium* years (Perid: 1994, 1995, 1998, 2003, 2004, 2012; open triangles) and 6 non-*Peridinium* years (non-Perid: 2005, 2006, 2008–2011; filled circles) showing: (a) 0–10 m monthly minimum $CO_{2(aq)}$; (b) 0–10 m mean Ca concentration; (c) depth-integrated (0–15 m) chlorophyll concentration; (d) depth-integrated (0–15 m) primary productivity. Error bars mark SD. All data are from a mid-lake station (Station A), collected at 2-week intervals, as part of the Lake Kinneret Monitoring Program.

 DOI: 10.5268/IW-6.2.936

10 m). Monthly averages, monthly minimum values, and SD were then computed for each month and year (usually based on 8 values per month). The minimum concentration of $CO_{2(aq)}$ reached annually would be the factor limiting isotopic fractionation. Hence, the average ±SD of the 6 monthly minimum values (one for each year) for each month and year type was then plotted (Fig. 5a).

The outcome supported our hypothesis. *Peridinium* years were characterized by lower $CO_{2(aq)}$ minima at all times of the year, with annual minima of ~2 µM in May, whereas in non-*Peridinium* years the annual minima were ~5 µM. The differences in $CO_{2(aq)}$ concentrations were largest in March, April, and May, corresponding with the annual peak of algal biomass and primary production (Fig. 5c and d). Furthermore, the length of time when CO_2 was low (<10 µM) was longer in *Peridinium* years (Fig. 5a). Berman-Frank and Erez (1996) showed that *Peridinium* from Lake Kinneret acquires a carbon-concentrating mechanism during the progression of the bloom that allows it to continue to photosynthesize when ambient $CO_{2(aq)}$ levels decline below 5 µM.

The isotopic fractionation by phytoplankton relative to the $CaCO_3$ recorded in 2008 reached maxima of 27–29‰ (Fig. 4), close to the maximum fractionation values found for the major algae groups under nonlimited CO_2 conditions (Raven 1996), further supporting that CO_2 was not fully exhausted in non-*Peridinium* years. This explanation was therefore more likely for the fractionation difference between *Peridinium* and non-*Peridinium* years. As a further implication, if $CO_{2(aq)}$ is higher in non-*Peridinium* years, the spring increase in pH will be smaller, which will in turn reduce precipitation of $CaCO_3$. In addition, if CO_2 is not exhausted as intensely, then primary production is likely lower, and possibly the export of organic carbon is lower as well, suggesting a major impact for the presence or absence of *Peridinium* on the export fluxes of both organic and inorganic carbon in this ecosystem.

The data from the Kinneret monitoring program support all these scenarios. Using the same 6 *Peridinium* years and 6 non-*Peridinium* years as for $CO_{2(aq)}$, multiannual monthly means from the euphotic zone were computed for chlorophyll, primary productivity, and Ca (as a proxy for $CaCO_3$ precipitation) and plotted for the 2 types of years (Fig. 5). The distinct spring peak of chlorophyll concentration in *Peridinium* years was nearly absent in non-*Peridinium* years (Fig. 5c); similarly, primary productivity reached distinct higher values in *Peridinium* years (Fig. 5d). The higher primary productivity during *Peridinium* years had a substantial impact on the export of organic carbon, as recorded in sedimentation fluxes of organic matter in *Peridinium* vs. non-*Peridinium* years (data not shown). The annual pattern of ambient Ca concentrations (Fig. 5b) indicates massive precipitation of $CaCO_3$ in *Peridinium* years, removing Ca from the water and drawing down Ca levels in spring. In comparison, in non-*Peridinium* years the spring drawdown of Ca was more moderate. The high ambient Ca concentrations of 40–55 mg L^{-1} are a result of carbonate rock dissolution in the catchment of the Jordan River springs, comprising the major source of water for Lake Kinneret. The increased precipitation of $CaCO_3$ in *Peridinium* years also demonstrates the impact of this single species on the export of inorganic carbon.

What prevented other algae from reaching biomasses comparable to those of *Peridinium* in the non-*Peridinium* years? Zohary et al. (2012, 2014a) concluded that the factors providing a competitive advantage for *Peridinium* were (1) its high cellular C:P molar ratios (~450:1) enabled it to attain a high biomass under P-limited conditions; (2) its large cells (~50 µm in diameter) minimized grazing losses; (3) its motility (flagellated) allowed it to maximize access to light at the surface and nutrients at depth; and (4) allelopathic abilities inhibited the growth of competitors. The combination of all these features does not exist in any other species in Lake Kinneret, such that no other species could proliferate to the extent that *Peridinium* does.

The annual blooms of *Peridinium* were interrupted in the mid-1990s following hydrological alterations in the catchment that prevented runoff from the Hula Valley peat soils from reaching Lake Kinneret except during high rainfall years. As a result, *Peridinium* blooms occur only in high rainfall years, indicating that the lack of some growth factor originating from the Hula peats inhibited *Peridinium* blooms during most recent years (Zohary et al. 2012, 2014a).

Overall, the large-celled *Peridinium* develops a dense population with low specific productivity and a long generation time of ~1–2 weeks (Zohary et al. 2014a), thus immobilizing large amounts of nutrients and slowing the overall recycling of matter within the ecosystem (Serruya et al. 1980). The major loss process to its accumulated biomass is sedimentation. In contrast, non-*Peridinium* years are characterized by lower standing stocks of smaller-celled species and faster cycling of matter, with zooplankton grazing down the primary producers and providing an advantage to non-grazed toxic species.

In summary, when present, the intensive, almost mono-specific bloom of *Peridinium* in Lake Kinneret lowers the $CO_{2(aq)}$, causing a reduction in the isotopic fractionation of the algae (higher $\delta^{13}C$ of POM_{surf}) and massive precipitation of $CaCO_3$. In non-*Peridinium* years the phytoplankton cannot deplete the $CO_{2(aq)}$ to similar levels, and hence the algae maintain a higher isotopic fractionation, leading to lower $\delta^{13}C$ maxima. These changes are reflected

higher up in the food web (zooplankton) and in sinking organic matter. The consequences for the ecosystem in non-*Peridinium* years are probably lower export fluxes of both organic and inorganic carbon, thus impacting the overall cycling of carbon.

Acknowledgements

This paper is given context and meaning by Val Smith's pioneering contributions in the scientific study of the interactions between lake biogeochemistry and phytoplankton dynamics—Val, we thank you. The authors also thank Werner Eckert and Ilia Ostrovsky for sediment trap samples, and Mark Altabet, Roi Holzman, and Ami Nishri for helpful discussions. Time series of water temperature are courtesy of Alon Rimmer; those of chlorophyll and primary production are courtesy of Yosef Z Yacobi; time series of pH, Ca, and alkalinity are courtesy of Ami Nishri, with chemical determinations conducted by Mekorot Water Company. Time series of phytoplankton biomass are original data of TZ. Funding was provided through a United States-Israel Bi-national Science Foundation grant (No. 2006211) to TZ and KDH, and through a grant from the Israel Water Authority to TZ and JE.

References

Ballot A, Krienitz L, Kotut K, Wiegand C, Metcalf JS, Codd GA, Pflugmacher S. 2004. Cyanobacteria and cyanobacterial toxins in three alkaline Rift Valley lakes of Kenya-Lakes Bogoria, Nakuru and Elmenteita. J Plankton Res. 26:925–935.

Berman T, Zohary T, Nishri A, Sukenik A. 2014. General background. Chap. 1. In: Zohary T, Sukenik A, Berman T, Nishri A, editors. Lake Kinneret: ecology and management. Heidelberg (Germany): Springer. p. 1–15.

Berman-Frank I, Erez J. 1996. Inorganic carbon pools in the bloom-forming dinoflagellate *Peridinium gatunense*. Limnol Oceanogr. 41:1780–1789.

Berman-Frank I, Erez J, Kaplan A. 1998. Changes in inorganic carbon uptake during the progression of a dinoflagellate bloom in a lake ecosystem. Can J Bot. 76:1043–1051.

Blumenshine S, Hambright KD. 2003. Top-down control in Lake Kinneret: a role for invertebrate predation. Hydrobiologia. 491:347–356.

Brenner M, Whitmore TJ, Curtis JH, Hodell DA, Schelske CL. 1999. Stable isotope ($\delta^{13}C$ and $\delta^{15}N$) signatures of sedimented organic matter as indicators of historic lake trophic state. J Paleolimnol. 22:205–221.

DeNiro MJ, Epstein S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta. 42:495–506.

Dubowski Y, Erez J, Stiller M. 2003. Isotopic paleolimnology of Lake Kinneret. Limnol Oceanogr. 48:68–78.

Emrich K, Ehhalt DH, Vogel JC. 1970. Carbon isotope fractionation during the precipitation of calcium carbonate. Earth Planet Sci Lett. 8:363–371.

Erez J, Bouevitch A, Kaplan A. 1998. Carbon isotope fractionation by photosynthetic aquatic microorganisms: experiments with *Synechococcus* PCC7942, and a simple carbon flux model. Can J Bot. 76:1109–1118.

Feuchtmayr H, Grey J. 2003. Effect of preparation and preservation procedures on carbon and nitrogen stable isotope determinations from zooplankton. Rapid Commun Mass Spectrom. 17:2605–2610.

Freeman KH, Hayes JM. 1992. Fractionation of carbon isotopes by phytoplankton and estimates of ancient CO_2 levels. Glob Biogeochem Cy 6:185–198.

Fry B. 2007. Stable isotope ecology. Springer Science & Business Media.

Fry B, Sherr EB. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib Mar Sci. 27:13–47.

Gal G, Hambright KD. 2014. Metazoan zooplankton. Chap. 13. In: Zohary T, Sukenik A, Berman T, Nishri A, editors. Lake Kinneret: ecology and management. Heidelberg (Germany): Springer. p. 227–245.

Gervais F, Riebesell U. 2001. Effect of phosphorus limitation on elemental composition and stable carbon isotope fractionation in a marine diatom growing under different CO_2 concentrations. Limnol Oceanogr. 46:497–504.

Gophen M. 1978. Zooplankton. In: Serruya C, editor. Lake Kinneret (Monographiae Biologicae). New York (NY): Springer-Verlag. p. 297–311.

Gophen M, Landau R. 1977. Trophic interactions between zooplankton and sardine *Mirogrex terraesanctae* populations in Lake Kinneret, Israel. Oikos. 29:166–174.

Hadas O, Altabet MA, Agnihotri R. 2009. Seasonally varying nitrogen isotope biogeochemistry of particulate organic matter in Lake Kinneret, Israel. Limnol Oceanogr. 54:75–85.

Hadas O, Pinkas R, Erez J. 2001. High chemoautotrophic primary production in Lake Kinneret, Israel: a neglected link in the carbon cycle of the lake. Limnol Oceanogr. 46:1968–1976.

Hajnal É, Padisák J. 2008. Analysis of long-term ecological status of Lake Balaton based on the ALMOBAL phytoplankton database. Hydrobiologia. 599:227–237.

Hambright KD. 2008. Long-term zooplankton body size and species changes in a subtropical lake: implications for lake management. Arch Hydrobiol. 173:1–13.

Hambright KD, Zohary T, Gude H. 2007. Microzooplankton dominate carbon flow and nutrient cycling in a warm subtropical freshwater lake. Limnol Oceanogr. 52:1018–1025.

Koren N, Klein M. 2000. Rate of sedimentation in Lake Kinneret, Israel: spatial and temporal variations. Earth Surf Process Landforms. 25:895–904.

Lewis E, Wallace DWR. 1998. Program developed for CO_2 system calculations. Available from: http://cdiac.esd.ornl.gov/oceans/co2rprtnbk

Martinez del Rio C, Wolf N, Carleton SA, Gannes LZ. 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biol Rev. 84:91–111.

Meyers PA. 1994. Preservation of elemental and isotopic source identification of sedimentary organic matter. Chem Geol. 114:289–302.

 DOI: 10.5268/IW-6.2.936

Millero FJ. 1979. The thermodynamics of the carbonate system in seawater. Geochim Cosmochim Acta. 43:1651–1661.

Naselli-Flores L, Barone R. 2005. Water-level fluctuations in Mediterranean reservoirs: setting a dewatering threshold as a management tool to improve water quality. Hydrobiologia. 548:85–99.

Nishri A, Stiller M. 2014. Inorganic carbon. Chap. 23. In: Zohary T, Sukenik A, Berman T, Nishri A, editors. Lake Kinneret: ecology and management. Heidelberg (Germany): Springer. p. 397–415.

Nõges P, Mischke U, Laugaste R, Solimini A. 2010. Analysis of changes over 44 years in the phytoplankton of Lake Võrtsjärv (Estonia): the effect of nutrients, climate and the investigator on phytoplankton-based water quality indices. Hydrobiologia. 646:33–48.

Parparov A, Zohary T, Berman T, Gal G. 2014. Seston and organic matter. Chap. 26. In: Zohary T, Sukenik A, Berman T, Nishri A, editors. Lake Kinneret: ecology and management. Heidelberg (Germany): Springer. p. 473–484.

Pollingher U. 1986. Phytoplankton periodicity in a subtropical lake (Lake Kinneret, Israel). Hydrobiologia. 138:127–138.

Pollingher U, Hickel B. 1991. Dinoflagellate associations in a subtropical lake (Lake Kinneret, Israel). Arch Hydrobiol. 120:267–285.

Rachamim T, Stambler N, Zohary T, Berman-Frank I, Gal G. 2010. Zooplankton contribution to the particulate N and P in Lake Kinneret, Israel, under changing water levels. Hydrobiologia. 655:121–135.

Raven JA. 1996. Inorganic carbon assimilation by marine biota. J Exp Mar Biol Ecol. 203:39–47.

Rimmer A, Gal G, Opher T, Lechinsky Y, Yacobi YZ. 2011. Mechanisms of long-term variations in the thermal structure of a warm lake. Limnol Oceanogr. 56:974–988.

Rimmer A, Ostrovsky I, Yacobi YZ. 2008. Light availability for *Chlorobium phaeobacteroides* development in Lake Kinneret. J Plankton Res. 30:765–776.

Rundel PW, Ehleringer JR, Nagy KA. 1989. Stable isotopes in ecological research. New York (NY): Springer-Verlag.

Serruya C, Gophen M, Pollingher U. 1980. Lake Kinneret: carbon flow patterns and ecosystem management. Arch Hydrobiol. 88:265–302.

Smyntek PM, Teece MA, Schulz KL, Thackeray SJ. 2007. A standard protocol for stable isotope analysis of zooplankton in aquatic food web research using mass balance correction models. Limnol Oceanogr. 52:2135–2146.

Stiller M. 1977. Origin of sedimentation components in Lake Kinneret traed by their isotopic composition. In: Golterman HL, editor. Interactions between sediments and fresh water. The Hague (Netherlands): Junk. p. 57–64.

Stiller M, Nissenbaum A. 1999. A stable carbon isotope study of dissolved inorganic carbon in hardwater Lake Kinneret (Sea of Galilee). S Afr J Sci. 95:166–170.

Stumm W, Morgan JJ. 2012. Aquatic chemistry: chemical equilibria and rates in natrual water. 3rd ed. Wiley.

Sukenik A, Hadas O, Kaplan A. 2014a. Cyanobacteria. Chap. 12. In: Zohary T, Sukenik A, Berman T, Nishri A, editors. Lake Kinneret: ecology and management. Heidelberg (Germany): Springer. p. 213–226.

Sukenik A, Zohary T, Markel D. 2014b. The monitoring program. Chap. 32. In: Zohary T, Sukenik A, Berman T, Nishri A, editors. Lake Kinneret: ecology and management. Heidelberg (Germany): Springer. p. 561–575.

Zohary T, Erez J, Gophen M, Berman-Frank I, Stiller M. 1994. Seasonality of stable carbon isotopes within the pelagic food web of Lake Kinneret. Limnol Oceanogr. 39:1030–1043.

Zohary T, Nishri A, Sukenik A. 2012. Present–absent: a chronicle of the dinoflagellate *Peridinium gatunense* from Lake Kinneret. Hydrobiologia. 698:161–174.

Zohary T, Pollingher U, Hadas O, Hambright KD. 1998. Bloom dynamics and sedimentation of *Peridinium gatunense* in Lake Kinneret. Limnol Oceanogr. 43:175–186.

Zohary T, Sukenik A, Berman T. 2014a. *Peridinium gatunense.* Chap. 11. In: Zohary T, Sukenik A, Berman T, Nishri A, editors. Lake Kinneret: ecology and management. Heidelberg (Germany): Springer. p. 191–212.

Zohary T, Sukenik A, Berman T, Nishri A, editors. 2014b. Lake Kinneret: ecology and management. Heidelberg (Germany): Springer. 683 p.

Zohary T, Yacobi YZ, Alster A, Fishbein T, Lippman S, Tibor G. 2014c. Phytoplankton. Chap. 10. In: Zohary T, Sukenik A, Berman T, Nishri A, editors. Lake Kinneret: ecology and management. Heidelberg (Germany): Springer. p. 161–190.