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Changes to the phytoplankton assemblage of Lake Kinneret after decades of a predictable, repetitive pattern

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SUMMARY

1. Phytoplankton abundance and species composition in Lake Kinneret, Israel, have been monitored at weekly or fortnightly intervals since 1969. This paper summarises the resulting 34-year phytoplankton record with a focus on the last 13 years of new data, and reassesses an earlier conclusion that the lake phytoplankton shows remarkable stability despite a wide range of external pressures.
2. The Kinneret phytoplankton record can be split into two major periods. The first, from 1969 till 1993, was a period of distinct stability expressed by a typical annual pattern revolving around a spring bloom of the dinoflagellate *Peridinium gatunense* that repeated each year. The second period, starting around 1994 and ongoing, is characterised by the loss of the previously predictable annual pattern, with both 'bloom years' and 'no-bloom years'.
3. In the second period, deviations from the previous annual pattern include: the absence of the prevailing spring *P. gatunense* blooms in some years and increased variability in the magnitude of the bloom in others; intensification of winter *Aulacoseira granulata* blooms; higher summer phytoplankton biomass with replacement of mostly nanoplanktonic, palatable forms by less palatable forms; new appearance and establishment of toxin-producing, nitrogen fixing cyanobacteria in summer; increase in the absolute biomass and percentage contribution of cyanobacteria to total biomass; and fungal epidemics attacking *P. gatunense*.
4. The 34-year record serves to validate Schindler's (1987) assessment that phytoplankton species composition will respond to increased anthropogenic stress before bulk ecosystem parameters.

Keywords: annual pattern, *Aphanizomenon ovalisporum*, *Aulacoseira granulata*, long-term phytoplankton, *Peridinium gatunense*

Introduction

The deterioration of ecological systems in general and of lake ecosystems specifically, because of anthropogenic stress and pollution, is occurring at a global scale (Vitousek *et al*., 1997; Wetzel, 2001). In many cases, the stress is low level, building gradually over long periods of time, and the impacts are not immediately evident. Therefore, it is crucial to be able to identify the danger to ecosystems at an early stage, when proactive management strategies are still an option. Schindler (1987) argued that at early stages of ecosystem deterioration, variables reflecting ecosystem functioning such as primary production, nutrient levels, and respiration are not altered, and are thus poor indicators of early stress; only at advanced levels of ecosystem deterioration does the response of these bulk parameters become evident. Schindler further suggested that among the earliest responses to stress would be changes in species composition of small, rapidly reproducing organisms with wide dispersal

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powers, such as phytoplankton, and disappearance of sensitive organisms from aquatic communities. Schindler stressed the need for long-term records in order to learn about the response of ecosystems to natural versus anthropogenic perturbations.

Such a long-term record exists for Lake Kinneret, the only natural freshwater lake in Israel. The ongoing Kinneret monitoring program initiated in 1969 revealed that, despite a range of man-induced perturbations, bulk ecosystem parameters (such as primary production, chlorophyll, total nitrogen and total phosphorus concentrations) showed no apparent responses. Based on such observations, managers tended to conclude that 'water quality remains good' and that there is no major reason for concern. However, examination of the long-term phytoplankton record in the light of Schindler's hypothesis regarding early signs of ecosystem deterioration suggests otherwise.

Based on the earlier part of the Kinneret record, the seasonal dynamics of the phytoplankton in Lake Kinneret were described (Pollingher, 1981, 1986; Berman, Yacobi & Pollingher, 1992) as being of a stable annual pattern, repeatable from year to year, with minor deviations. In particular, Berman *et al.* (1995) concluded that the period from 1969 to 1993 represented a period of distinct stability in the phytoplankton. Stable did not imply static, as there were underlying dynamics, but was expressed in a typical, predictable annual pattern. Citing those studies, Reynolds (2002) referred to Lake Kinneret as 'one of the best known and attested examples of year-to-year similarity in abundance, distribution and composition of the phytoplankton'.

Nevertheless, two major perturbations to the Kinneret ecosystem took place shortly afterwards: (i) in 1993 the fishery of the dominant fish, the Kinneret Bleak, collapsed as a result of over-fishing and a major decline in fish body-size (Hambright & Shapiro, 1997); (ii) in 1994 the dried peat-soils of the Hula Valley in the lake's catchment were re-flooded, leading to changes in amounts and contents (nutrients, heavy metals and organic matter) of water flowing into the lake. During the years that followed, the ecosystem was further stressed by a continuous reduction of water levels below natural levels (details in study site section). Could the phytoplankton community maintain its documented pattern of stability despite those additional perturbations? Phytoplankton species composition data from 1990 onwards, presented here in detail for the first time, suggest that this stable pattern was actually lost after 1994.

The objective of this paper is to document the complete 34-year phytoplankton record (1969–2002), with a focus on the newer part of the record (from 1990) and on whether the well-documented stable pattern of 1969–93 was maintained in later years, despite the 1993–94 perturbations. I assess the resulting patterns in light of Schindler's (1987) hypothesis.

Material and methods

Study site: Lake Kinneret and its phytoplankton, as described by Pollingher (1981, 1986)

Lake Kinneret is a meso-eutrophic, warm monomictic lake, stratified from April till December, in the Syrian-African Rift Valley, at 32°50′N and 210 m below sea level. At full capacity the lake covers 170 km^2, contains 4300×10^6 m^3, has a maximum depth of 43 m and a mean depth of 25 m. Due to the Mediterranean climate it is subjected to cold wet winters and hot dry summers. This lake was a focus for intense studies for >3 decades as summarised in Serruya (1978) and in a comprehensive publication list (Hambright & Hershcovitch, 1998).

For many years, and as documented since the 1940s, the most salient feature of the Kinneret phytoplankton was the high-biomass winter-spring bloom of the thecate dinoflagellate *Peridinium gatunense* Nygaard (henceforward: *Peridinium*) (Komarovsky, 1951; Pollingher & Kimor, 1970; Pollingher & Serruya, 1976; Pollingher & Berman, 1982; Pollingher, 1986; Berman *et al.*, 1992). The bloom declined sharply in May to June, shortly after the establishment of thermal stratification. The summer-autumn seasons were characterised by a low-biomass, high diversity assemblage of mostly nanoplanktonic species (Pollingher, 1981, 1986), a feature reported already in the mid-1960s (Pollingher & Kimor, 1970). The general patterns of the phytoplankton seasonal dynamics were followed closely by chlorophyll concentrations and primary production, being always higher during the first half of the year and lower during the second, while Secchi depth showed the reverse pattern (Berman *et al.*, 1995). Pollingher (1981) pointed out that 'the annual succession at the species level has been an almost constant event in

the lake for many years' and described four typical stages of this annual pattern:

1 October and November – progressive destratification enriching the epilimnion with nutrients – small species predominate, typically of the genera *Erkenia* (=*Chrysochromulina*), *Rhodomonas* (=*Plagioselmis*), *Cryptomonas*, *Cyclotella*, *Crucigenia*, *Chodatella*, *Tetraedron*.

2 December to February – holomixis – resuspension of *Aulacoseira* filaments and *Peridinium* cysts; small chlorophyte coenobia and unicells (*Pediastrum*, *Coelastrum*, *Scenedesmus*, *Tetraedron*) co-existing with larger forms (*Aulacoseira*, *Closterium*, *Peridinium*, *Microcystis* colonies).

3 March to May – early stratification – dominance of *P. gatunense*, a large motile dinoflagellate with specialised life cycle and the capacity to store nutrients, with other dinoflagellate species as subdominants. The end of the *Peridinium* bloom coincided with the onset of stable thermal stratification, nutrient depletion and high temperatures.

4 June to September – stable summer stratification – predominance of species able to grow at high temperatures (up to 30 °C) and low nutrients, mostly species belonging to chroococcoid cyanobacteria (*Microcystis* spp, *Radiocystis germinata*), coenobial chlorophytes (*Pediastrum* spp., *Coelastrum* spp., *Scenedesmus* spp.) and nanoplanktonic forms of *Tetraedron* spp. *Cyclotella* spp., *Cosmarium laeve*, *Chroococcus* spp.

Pollingher noted that in unusual years with extended periods of mixing, species belonging to phase II continued to develop and, as a result, the *Peridinium* bloom was delayed and reduced in its intensity. Examples were the years 1971, 1975, 1982 and 1983.

Anthropogenic impacts on Lake Kinneret since the 1930s

Human impact on lake hydrology was probably minor until 1932, when the Jordan River outflow was dammed and the lake was functionally converted into a reservoir (Hambright *et al*., in press). Since the early 1970s, up to 12% of the lake volume is pumped annually into the National Water Carrier system. The resulting and most noticeable change to Lake Kinneret has been the increased fluctuations and overall reduction of its water levels, from natural conditions with 1.3 m fluctuations between ca −210.8 and −209.5 m (Hambright, Zohary & Eckert, 1997) to annual fluctuations of >4 m and a lowest-ever minimum of −214.9 m in November 2001 (Fig. 1). In addition, the Kinneret salinity was reduced (by diversion of saline springs) from natural levels of approximately 250–300 mg Cl L^{-1} to a minimum of 192 mg Cl L^{-1} in May 1988, but droughts and overpumping increased the salinity to >280 mg Cl L^{-1} by autumn 2001 (Fig. 1; Rimmer, 2004).

A drastic change to the Kinneret catchment was the draining of Lake Hula and its adjacent swamps in the 1950s. This natural shallow lake upstream of Lake Kinneret contained dense macrophyte stands and functioned as a natural pre-impoundment, filtering the Jordan River water. The drained Hula Valley became a major source of nitrates and sulphates into Lake Kinneret (Serruya, 1978). In 1994 a small (1 km^2) shallow lake, Lake Agmon, was created in the drained peat soils, a network of connecting canals was dug, and the water table of the Hula valley was elevated (Hambright & Zohary, 1998). With completion of engineering plans in 1998, the outflow from the Hula Valley to Lake Kinneret was restricted, contributing to a noticeable reduction in sulphate and nitrate loading into Lake Kinneret. Other actions taken to minimise

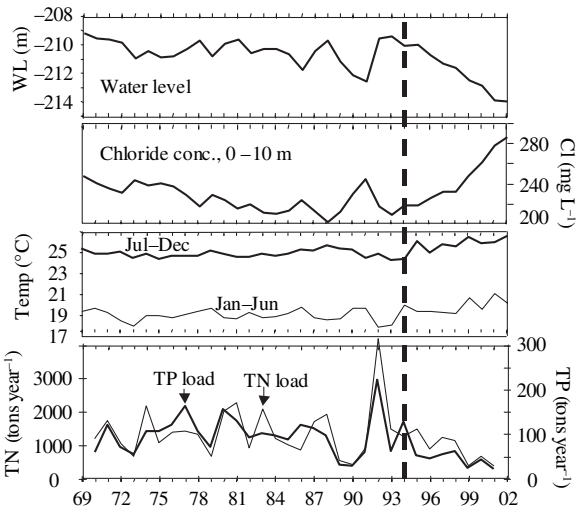

Fig. 1 Annual mean values for some forcing parameters in Lake Kinneret, 1969–2002: Water level (WL, in metre above sea level); chloride (Cl^-) concentration of the upper 0–10 m layer; water temperature of the upper 10 m layer in summer-autumn (July to December) and in winter-spring (January to June); annual load from the Jordan River, of total nitrogen (TN) and total phosphorus (TP). Data are from the Lake Kinneret Data Base, courtesy of a Mekorot water company (nutrient loading, chemical analyses) and A. Nishri.

nutrient loading included restrictions on fish ponds, treating of sewage and agricultural effluents, the construction of the Einan Reservoir in 1983 to contain low quality agricultural run-off water. As a result, the loads of total nitrogen (TN) and total phosphorus (TP) into Lake Kinneret have not increased with time, and during 1994–2002 the loads have been particularly low (Fig. 1), partly because of a series of low-precipitation years with reduced inflows.

A commercial fishery existed on the lake for generations. Since the 1950s, fishing techniques have improved, and the catch increased to a plateau in the 1970s at 1600–2000 t of fish per year, of which about 1000 tons were of the zooplanktivore Kinneret Bleak, *Acanthobrama terraesanctae* (Ben-Tuvia *et al.*, 1992), the dominant fish species. Over-fishing (harvesting of most of the large size individuals) led to a shift in the size structure of the population and to the collapse of the bleak fishery in 1993 (Hambright & Shapiro, 1997), yet bleak population density has more than doubled (Ostrovsky & Walline, 2001). This collapse led to a controversial 'bleak dilution program', a subsidised harvest of up to 1000 t of subcommercial size fish annually, that continued for a decade. Also, during the exceptionally low water level years of 2000–02 over-fishing led to a severe decline of mean body size of other commercial species like the native cichlids, *Sarotherodon galilaeus* and *Oreochromis aureus* by 2002 (J. Shapiro, pers. comm.; Ilia Ostrovsky, pers. comm.).

Over the last decade, the average temperature of the upper 10 m layer in both summer-autumn (July to December) and winter-spring (January to June) have increased significantly, by about 1 °C (Fig. 1; see later Table 3).

Field measurements and sampling

As part of an on-going routine monitoring program for Lake Kinneret initiated in January 1969, phytoplankton samples were collected at weekly or bi-weekly intervals from station A, situated at the deepest part of the lake at the node of most seiche activities. Depth profiles of water temperature were recorded at the time of sampling. Water samples for phytoplankton cell counts (and also for chlorophyll, primary production and chemical determinations) were taken with a 5-L vertical Rodhe sampler from 0, 1, 2, 3, 5, 7, 10, 15, 20, 30 and 40 m. When the lake was stratified, based on the temperature profile, three additional samples were taken from the centre of the thermocline (usually around 15 m depth) and 1 m above and below it. Phytoplankton samples were preserved in 1% acid Lugol's solution.

Phytoplankton analyses

The method for counting phytoplankton has remained largely unchanged since 1969. Microscopic counts were conducted according to the sedimentation chamber technique (Utermöhl, 1958), using an inverted microscope (Wild 40: 1969–95; Zeiss Axiovert M135: 1996–02). For the nanoplanktonic species, 10-mL subsamples were sedimented for 24 h and all phytoplankton cells in five arbitrary strips of 2 mm^2 each, making up 2% of the total chamber area, were counted at 320×. For large species, 1-mL samples were sedimented for 24 h in 1 mL chambers, and the large cells in the entire chamber were counted at 160 or 80×. Using this method, usually at least 100 'natural units' (cells, colonies or filaments) of the abundant species were counted. Starting in January 1977, small species for which fewer than five natural units were counted were recorded as present but excluded from the calculation of biomass and further data processing. Thus the detection limit was 1 mL^{-1} for large species and 25 mL^{-1} for small species. Cells appearing dead (e.g. empty shells, colourless cells) were excluded. Phytoplankton were identified and counted according to species, and for species of variable cell size (like *P. gatunense*) also according to size categories. Both the number of cells and the number of 'natural units' were recorded. Biomass was calculated by multiplying the number of cells per millilitre by the average biovolume of a cell of that species and size category, according to the most suitable geometric shape (Hillebrand *et al.*, 1999) and by assuming a specific density of one. Biovolumes were based on linear measurements made microscopically, with an eyepiece micrometer in the earlier years and later with CAPAS image analysis software (Hambright & Fridman, 1994). Biomass data were expressed as $\mu g_{wet\ wt}\ mL^{-1}$ or $g_{wet\ wt}\ m^{-3}$.

The discrete-depth biomasses were depth-integrated to give a water-column value. The depth-integrated biomass, *IB* ($g_{wet\ wt}\ m^{-2}$), was calculated according to the equation:

$$IB = \sum_{0}^{i\max} B_i W_i$$

Where B_i is the biomass ($g_{wet\ wt}\ m^{-3}$) at depth i, W_i is the weight for depth i (d_i), and is determined for different values of i, ranging from 0 to i_{max}, denoting the maximum depth for integration, according to:

$$\begin{aligned} &\text{if } i = 0 \quad &&\text{then } W_i = d_{i+1}/2, \\ &\text{if } i = i_{\max} \quad &&\text{then } W_i = (d_i - d_{i-1})/2, \\ &\text{else} \quad &&W_i = (d_{i+1} - d_{i-1})/2. \end{aligned}$$

During stratification, the depth-integration was only to the mid-thermocline depth, usually between 15 and 20 m. Phytoplankton biomass values quoted are monthly mean depth integrated values in $g_{wet\ weight}\ m^{-2}$, hereafter g m^{-2}, unless stated otherwise.

Shannon's diversity index, H', was computed for each sampling date based on the depth-integrated biomass of each species, as:

$$H' = \sum_{i=1}^{n} P_i \mathrm{Log}_2 P_i$$

where P_i is the relative biomass of species i (depth-integrated biomass of species i divided by depth-integrated total biomass) and n is the total number of species. The diversity was based on biomass rather than cell densities according to recommendation by Duarte *et al*. (1990).

In order to examine whether the well-documented stable pattern of 1969–93 was maintained in later years, despite the 1993–94 and consequent perturbations, the 34-year dataset was divided into two subsets (1969–93; 1994–2002) for statistical comparisons of a range of forcing and response variables, using routing monitoring data from the Lake Kinneret Data Base. ANOVA was used to test whether the mean values for each of the two subsets of years were significantly different.

Results

The record of phytoplankton biomass and species composition from Lake Kinneret is based on approximately 11 300 counted samples (average of 10 depths per sampling date, 25–50 sampling dates per year, 34 years), making it one of the most intensive and detailed existing phytoplankton databases.

Total phytoplankton biomass and major taxonomic groups

Annual mean depth-integrated phytoplankton biomass in Lake Kinneret has been reasonably stable over time (Fig. 2a), ranging from 39.4 g m^{-2} (1975) to 156.4 g m^{-2} (1998) with a multi-annual mean of 75.7 g m^{-2}. The years since 1994 tended to have wider fluctuations in annual mean biomass than in the earlier years: the multiannual average for the period 1969–93 was 70.9 g m^{-2} with SD of 15.6 g m^{-2}, the multiannual average for the period 1994–2002 was 88.9 g m^{-2} with a considerably larger SD of 32.2 g m^{-2}, mostly because of the exceptionally high biomass year of 1998, the year of highest annual mean biomass in the 34-year record, and exceptionally low biomass year of 1996.

On an annual basis, dinoflagellates contributed most of the biomass, with chlorophytes, diatoms, cyanobacteria and cryptophytes contributing practically all the rest (but see later about additional minor contributions) and in that order of relative

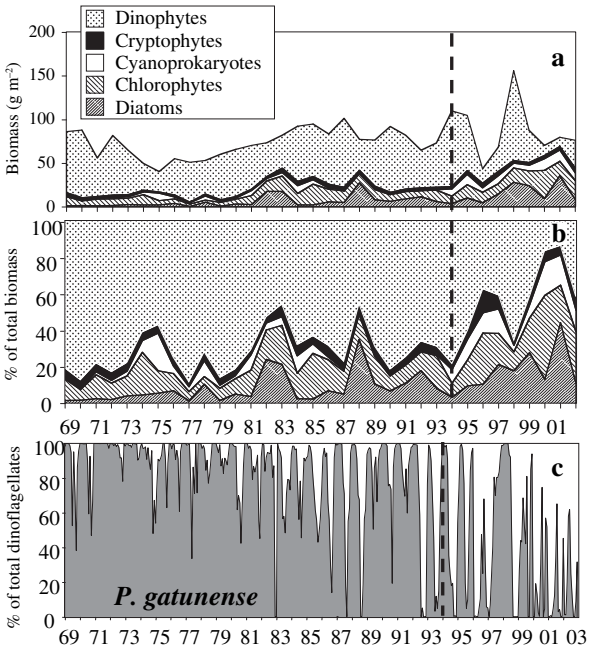

Fig. 2 (a) Annual mean depth-integrated biomass of phytoplankton, split between five main taxonomic groups and (b) the percentage contribution of each of those five groups to the total phytoplankton biomass. (c) Monthly mean percentage contribution of *P. gatunense* (grey area) to total dinoflagellate biomass. Dashed line in 1994 splits the long-term record into two periods of seemingly different phytoplankton dynamics.

contribution (Fig. 2b). A steep trend of declining contribution of dinoflagellates is apparent since 1994, while both the absolute and relative contributions of diatoms, chlorophytes and cyanobacteria increased.

The characteristic seasonal pattern of phytoplankton biomass previously described by Pollingher (1981, 1986 was repeated yearly until the early 1990s (Fig. 3): phytoplankton biomass increased in winter, peaked in spring, declined in early summer and remained low throughout the summer and fall. Slight variations to the pattern were years with winter biomass peaks preceding the spring peaks (e.g. 1982, 1983, 1988). Prior to 1993, the spring biomass peak of those years was relatively low, but this variation did not change the overall pattern.

Since 1995, the annual progression of total phytoplankton biomass has been different every year, and in most of the years has deviated from the regular pattern of the earlier years. The absence of the characteristic spring biomass peak is notable in 1996, 1997, 2000 and 2001, years in which *Peridinium* failed to bloom (see below). Substantial winter biomass peaks occurred in 1995, 1997, 1998, 1999 and 2001.

Biomass by taxonomic groups and dominant species

Dinoflagellates. The well-documented spring bloom of the dinoflagellate *P. gatunense* is evident from Fig. 3.

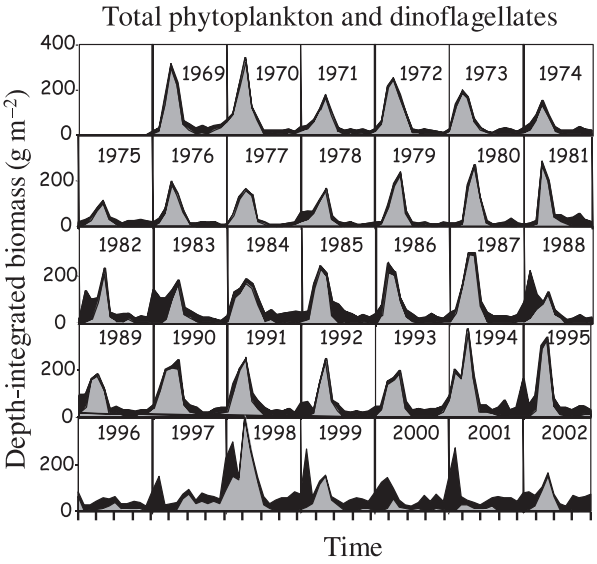

Fig. 3 Monthly mean depth integrated total phytoplankton biomass (black contour line) in Lake Kinneret, 1969–2002, showing the contribution of dinoflagellates (grey area) and all other phytoplankton taxa (black areas).

This dinoflagellate bloomed every single year from 1969 till 1995, reaching peak biomass in March, April or May with a monthly mean of about 200 g m^{-2} (range: 105–371 g m^{-2}), and dominating total phytoplankton biomass. During those years, this large dinoflagellate (average biovolume: 70 000 μm^3) typically comprised >95% of total dinoflagellate biomass (Fig. 2c), making the contribution of co-occurring dinoflagellate species (Pollingher & Hickel, 1991) rather minor. Hence, for the period 1969–95 total dinoflagellate biomass was a good proxi for *Peridinium* biomass.

However, after 27 years of recorded constancy, the years since 1996 were strikingly different: *Peridinium* did not bloom in 1996, 1997, 2000 and 2001 (Fig. 3). In 1996 a bloom started to develop relatively early, reaching 125 g m^{-2} on 7 January, but crashed to 0.4 g m^2 by 21 January (specific date values, not shown in Fig. 3) and did not recover that year. In 1997, the bloom failed to develop all winter and spring, although *Peridinium* cells appeared in the water column in June, increasing in early July to 100 cells mL^{-1}, sufficient to dominate total phytoplankton biomass in July (Fig. 3). In spring 2000 *Peridinium* contribution to total phytoplankton biomass did not exceed 20 g m^{-2}, in spring 2001 it remained below 1 g m^{-2}. In those years, other dinoflagellates became the major contributors to the total dinoflagellate biomass (Fig. 2c) but did not develop the characteristic spring blooms.

In contrast with those no-bloom years, the monthly mean biomass attained during the 1998 bloom, 411 g m^{-2}, was the highest ever recorded. An unusually high epilimnetic TP concentration was associated with this peak *Peridinium* bloom biomass: the average TP in April to May 1998 was 62.5 $\mu g\ L^{-1}$, more than double the typical concentrations at this time of year. In 1999 and 2002 a *Peridinium* bloom did develop, albeit to below-average peak biomasses.

Diatoms. Diatoms comprised only a minor component of the Kinneret phytoplankton in the 1970s (Figs 2 & 4) but since the early 1980s their relative biomass has gradually increased, with conspicuous winter (January to February) peaks in excess of 100 g m^{-2} occurring in some of the years. Those peaks are noticeable in the total biomass time series (Fig. 3) as distinct winter peaks preceding the spring *Peridinium* peaks. As with the *Peridinium* blooms, these winter diatom

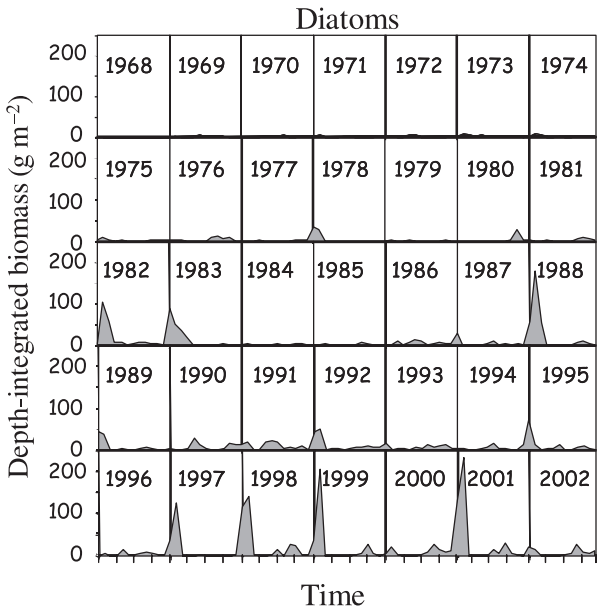

Fig. 4 Monthly mean depth-integrated biomass of diatoms in Lake Kinneret, 1969–2002. Peak biomass values occurring in winter (December to February) are always because of *Aulacoseira granulata*.

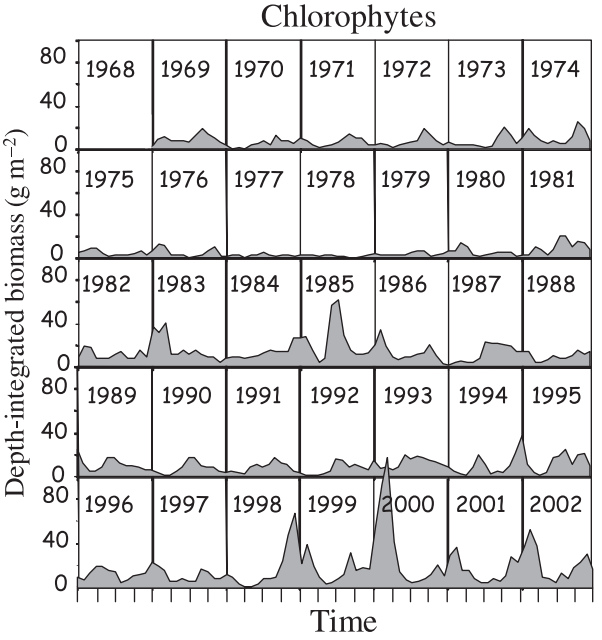

Fig. 5 Monthly mean depth-integrated biomass of chlorophytes in Lake Kinneret, 1969–2002.

blooms were attributed to a single species, *Aulacoseira granulata* (Ehrenberg) Simonsen. While winter *A. granulata* blooms were recorded in the 1980s, they have intensified in the more recent years (Fig. 4), and contributed to the altered annual pattern in the years since 1995. Until 1994, the peak *Peridinium* biomass tended to be lower in *Aulacoseira*-bloom years (1982, 1983, 1988, 1989; see Fig. 3). Since 1995, this relationship no longer held, and years with a winter *A. granulata* bloom were followed by either extensive (1995, 1998), low (1999) or no (1997, 2001) *Peridinium* blooms.

The small peaks in diatom biomass at other times of year (Fig. 4) were mostly because of *Cyclotella polymorpha* Meyer and *Synedra* spp. Other genera of pennate diatoms also occurred at low biomass densities.

Chlorophytes. The Kinneret phytoplankton is characterised by a diverse assortment of chlorophytes with relatively modest but significant contribution to total phytoplankton biomass at all times of the year (Fig. 5), and with no distinct dominant species. Pollingher (1978) listed 123 species and taxonomic varieties of chlorophytes, of which 26 species were considered common. These common species, belonging to the genera *Ankistrodesmus*, *Botryococcus*, *Chodatella*, *Closterium*, *Coelastrum*, *Cosmarium*, *Crucigenia*, *Dictyosphaerium*, *Elakatothrix*, *Oocystis*, *Pediastrum*, *Tetraedron* and *Scenedesmus*, remained common until the mid-1990s. Chlorophyte biomass has increased since the early 1980s (Fig. 5). A distinct chlorophyte peak was recorded in June to July 1985, when *Oocystis lacustris* bloomed. Since 1998, chlorophyte peaks are of unprecedented biomass values and with distinct dominants. A biomass peak in November 1998 was because of *Closterium aciculare*, in February 2000 because of *Pediastrum tetras* and *Coelastrum microporum*, and in January to February 2002 because of *Scenedesmus* spp. and *Tetraedron* sp. An unusually dense but short-lived (few days) bloom of *Carteria cordiformis* was recorded in February 1996 and of *Botryococcus braunii* in January 2000. Both events, recorded by photographs, were missed by our routine sampling, demonstrating that even weekly intervals are insufficient for capturing some of the major events in plankton dynamics in lakes.

A filamentous chlorophyte, *Debarya* sp. (Zygnematales), appeared in May 1998 and persisted till August (Table 1). This marks the first-ever record of a filamentous chlorophyte in the Kinneret phytoplankton.

Table 1 Species of phytoplankton that have been recorded in Lake Kinneret for the first time since 1994, the timing of their first record, and notes regarding their continuous presence over time

Species	Taxonomic group	First record	Current situation
Aphanizomenon ovalisporum Forti	Cyanobacteria, Nostocales	September 1994	Blooms or common in summer-autumn
Planktolyngbya sp. Anagnostidis et Komárek	Cyanobacteria, Oscillatoriales	Fall 1996	Common in summer-autumn
Staurastrum manfeldti Delponte	Chlorophyta, Desmidiales	May 1997	Common in autumn
Debarya polyedrica Skuja	Chlorophyta, Zygnematales	May 1998	Infrequent occurrence in summer
Staurastrum contortum G.M. Smith	Chlorophyta, Desmidiales	July 1998	Common in autumn
Tetraedron minimum var. *minimum* Kovácik (new morphotype)	Chlorophyta, Chlorococcales	November 1998	Common in winter-spring
Cylindrospermopsis cuspis Komárek et Kling	Cyanobacteria, Nostocales	Summer 2000	Common in summer-autumn

In the following summers, *Debarya* was rare, but it bloomed again in summer 2004.

Cyanobacteria. During the early 1970s cyanobacteria were a minor component of the Kinneret biomass, usually contributing <5 g m^{-2} to the total phytoplankton biomass. From 1975 to 1985 there were several years of higher cyanobacterial biomass (usually up to approximately 20 g m^{-2}) than in the earlier years, mostly because of peaks in *Microcystis* spp and *Chroococcus minutus*, with *R. germinata* and *Cyanodictyon imperfectum* being common (Pollingher, 1991). These years were followed by a sequence of 8 years, 1986–93, in which cyanobacterial contribution to total biomass declined to barely detectable levels (Fig. 6). Since 1994 cyanobacterial biomass increased substantially (Figs 2 & 6).

A prominent feature of the 1969–93 record is that Chroococcales species dominated the cyanobacterial biomass. N_2-fixing cyanobacteria, belonging to the Nostocales were rare (Pollingher, 1991) although they did occur in the early 1970s, with an annual mean contribution of 0.1–1.5% to total phytoplankton biomass (Fig. 6). This contribution declined to below detection limit for the following two decades. An abrupt change occurred in summer 1994, when *Aphanizomenon ovalisporum* Forti appeared and bloomed for the first time in Lake Kinneret (Pollingher *et al*., 1998; Hadas *et al*., 2002, Table 1). From then on, total cyanobacteria have increased in both their absolute biomass and their relative contribution to total phytoplankton biomass (Figs 2b & 6). Filamentous forms, some of them toxin-producers and N_2-fixers, are now important components of the summer-autumn assemblage. These new species did not replace the existing species but are occurring in addition to those, and generally the biomass of both groups is greater than during the pre-1994 era.

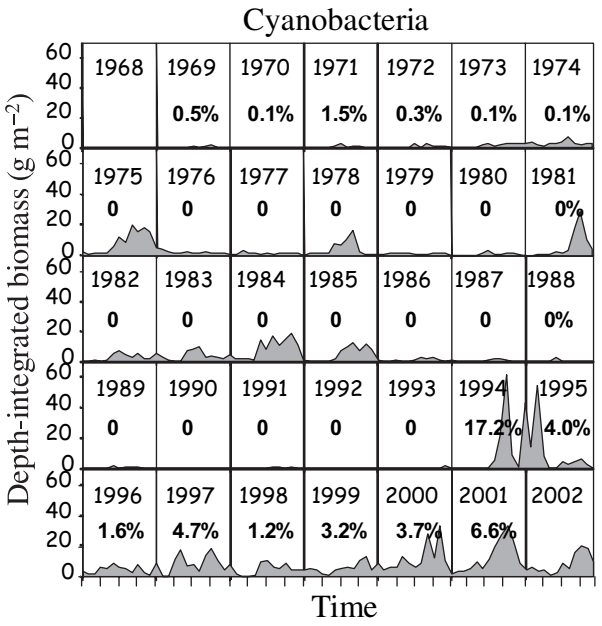

Fig. 6 Monthly mean depth-integrated biomass of cyanobacteria in Lake Kinneret, 1969–2002. Numbers below the year indicate the annual average percentage contribution of potentially N_2-fixing genera (*Aphanizomenon*, *Anabaena*, *Cylindrospermopsis*) to total phytoplankton biomass (0 indicates below detection limit). Biomass peak in fall 1994 was due to the first-ever bloom of the *Aphanizomenon ovalisporum*, and in winter 1995 because of a bloom of *Microcystis aeruginosa*.

Cryptophytes. Cryptophytes are the only group that did not show in recent years major deviations from the long-term pattern (Fig. 7). The main contributors to this group were *Plagioselmis* (=*Rhodomonas) minuta*,

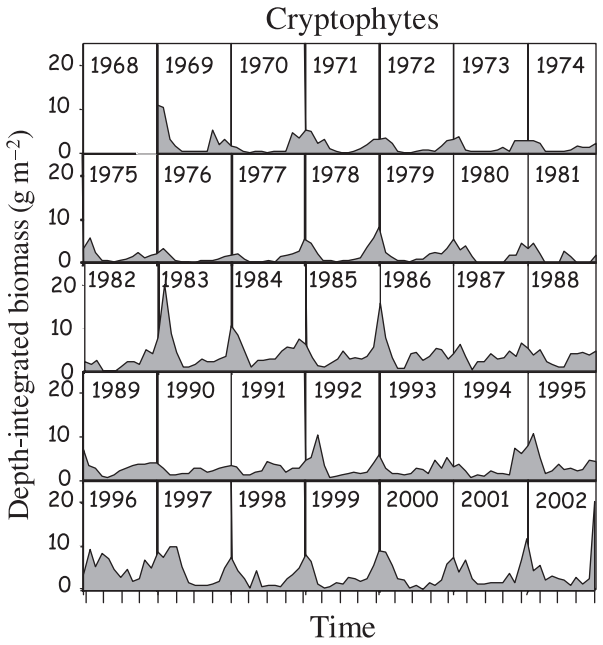

Fig. 7 Monthly mean depth-integrated biomass of cryptophytes in Lake Kinneret, 1969–2002.

P. minuta var nanoplanktonica, *Cryptomonas erosa* and *Cryptomonas ovata*. Typically, cryptophytes increased in abundance in autumn, peaked in winter, preceding the *Peridinium* bloom and declined to lower abundances in summer. Throughout the long-term record, they maintained a stable biomass of approximately 1–5 g m^{-2}, with the winter peaks usually not exceeding 10 g m^{-2} (but exceptionally high peaks >10 g m^{-2} occurred in January 1969, January 1983 and December 1985). Cryptophytes were more abundant than usual throughout the no-*Peridinium* years of 1996 and 1997, but this was not evident in the no-*Peridinium* years of 2000 and 2001.

Other photosynthetic taxa. Phytoplankton belonging to other taxa also occur in Lake Kinneret but their contribution to total biomass is minor due to their small cell size or because they are rare. Of the small sized taxa, the haptophyte *Erkenia* (=*Chrysochromulina*) *subaequiciliata* (3–5 μm diameter) is particularly common and occasionally reaches densities of 5000 cells mL^{-1}. Picocyanobacteria reach densities of 10^5 cells mL^{-1} in summer-autumn (Malinsky-Rushansky, Berman & Dubinsky, 1995). Photosynthetic bacteria, mostly *Chlorobium* spp. produce a dense metalimnetic layer in summer-autumn (Bergstein, Henis & Cavari, 1979). Of the large but rarely occurring taxa, the euglenophyte genera *Trachelomonas* and *Euglena* are recorded occasionally, the first more often than the second. Colonial chrysophytes are practically absent, although on 17 May 1998 *Uroglena* colonies occurred. These taxa will not be further discussed here.

Fungal epidemics

The lack of a *Peridinium* bloom in 2001 was associated with an epidemic of a chytrid fungus parasitic on *Peridinium* that took place at the onset of bloom development, in December 2000, with infection prevalence reaching 70% (i.e. up to 70% of host cells were found infected with the fungus, A. Alster and T. Zohary, unpublished data). This was the first time that a fungal epidemic was noticed in Lake Kinneret. Within 2 weeks of the initial infection *Peridinium* densities declined by three orders of magnitude, so that a bloom could not develop in the following spring. Since then, chytrid fungi infecting *Peridinium* were observed again: a second epidemic was recorded in August 2001; additional moderate-level fungal infections were observed throughout the summer of 2002.

Shifts in species composition

The most prominent change to the Kinneret phytoplankton in terms of species composition is the different composition of the summer assemblage in the more recent years. Table 2 lists species contributing more than 1% to the multi-annual late summer (August, September and October) average phytoplankton biomass at 1 m depth during at least one of the periods 1982–93 and 1994–2001. The data prior to 1982 were excluded from this comparison because it was impossible to reconstruct the entire dataset replacing previous taxonomic names with current ones and to separate unequivocally taxonomic semantics from actual changes in the species present. The following taxa were key biomass contributors during the first period but their relative contribution was significantly lower in the second period: *Anoemoneis*, *Chlamydomonas* spp, *Cosmarium lavae*, *Golenkinia radiata*, *Monoraphidium arcuatum*, *Scenedesmus* spp, *Gymnodinium albulum*, *Cryptomonas* spp. With the exception of the elongated *Monoraphidium*, all these taxa have a rounded form, are typical nanoplanktonic

Table 2 Summer-autumn (August, September and October) average ± SD percentage contribution of the major biomass contributing species in Lake Kinneret, station A, 1 m depth for the periods 1982–93 and 1994–2001. Species with multi-annual average biomass exceeding 1% of total biomass for at least one of the two periods are included.

Period	1982–1993 [average (SD)]	1994–2001 [average (SD)]	Significance
Group 1: average percentage contribution doubled or more			
Aphanizomenon ovalisporum	0 (0)	17.4 (21.6)	**
Microcystis spp.	2.1 (1.6)	5.4 (5.4)	*
Planktolyngbya sp.	0 (0)	3.6 (5.6)	**
Synedra spp.	0.2 (0.6)	14.3 (15.7)	**
Closterium aciculare var. *subpronum*	3.4 (7.5)	7.6 (7.5)	ns
Staurastrum contortum	0 (0)	1.3 (1.8)	*
Staurastrum manfeldti	0 (0)	1.7 (4.5)	ns
Peridiniopsis cunningtonii	1.8 (2.2)	4.3 (2.7)	*
Group 2: average percentage contribution halved or less			
Anoemoneis spp.	3.7 (2.6)	0.8 (1.3)	**
Chlamydomonas spp.	4.3 (2.2)	0.8 (1.7)	**
Coelastrum microporum	1.7 (2.0)	0.2 (0.3)	ns
Coelastrum reticulatum	1.7 (2.8)	0.8 (2.1)	ns
Cosmarium laeve	6.3 (2.9)	3.0 (3.5)	*
Golenkinia radiata	1.8 (1.5)	0.3 (0.4)	*
Monoraphidium arcuatum	2.9 (5.8)	0 (0)	*
Scenedesmus spp.	3.2 (1.5)	1.2 (1.5)	**
Gymnodinium albulum	1.9 (1.6)	0.7 (0.5)	*
Cryptomonas spp.	7.8 (4.5)	2.8 (1.3)	**
Group 3: no major change in average percentage contribution			
Chroococcus spp.	8.1 (9.6)	4.8 (5.5)	ns
Cyclotella polymorpha	12.0 (8.9)	8.0 (8.5)	ns
Chodatella spp.	1.6 (1.4)	1.0 (1.1)	ns
Oocystis spp.	7.3 (4.9)	4.5 (2.8)	ns
Tetraedron spp.	0.8 (0.2)	1.1 (0.8)	ns
Peridiniopsis borgei	2.1 (2.8)	2.4 (2.0)	ns
Peridiniopsis elpatiewskyii	4.1 (2.6)	3.1 (3.2)	ns
Peridinium gatunense	13.9 (9.2)	13.0 (12.2)	ns
Plagioselmis minutus	2.3 (1.0)	1.7 (1.5)	ns

Species are grouped according to three categories: Group 1: average percentage contribution during 1994–2001 was double or more of that during 1982–93, Group 2: average percentage contribution during 1994–2001 was half or less of that during 1982–93; Group 3: average percentage contribution during 1994–2001 ranged between ×0.5 and ×2 of that during 1982–93. *t*-Test was used to determine whether the averages for the two periods were significantly different (*$P < 0.05$; **$P < 0.01$; ns, not significant).

species, and are generally considered as potentially good food for zooplankton.

Conversely, taxa that have at least doubled their contribution to the summer assemblage since 1994, with this change statistically significant, are *A. ovalisporum*, *Microcystis* spp, *Planktolyngbya* sp., *Synedra* spp, *Staurastrum contortum*, *Peridiniopsis cunningtonii* (Table 2). All these are needle-shaped unicells, spiny forms, long filaments, or too large to be grazed by zooplankton. Thus, the most conspicuous feature of this species change is a shift from an assemblage dominated by more palatable forms prior to 1994, to an assemblage dominated by less palatable forms in more recent years. Rounded forms that are still prominent in recent summers are mostly chroococcoid cyanobacteria (*Chroococcus* spp., *R. germinata*, *C. imperfectum*, *Microcystis* spp.). Chlorophyta are still represented by a variety of nanoplanktonic taxa, especially *Chodatella*, *Oocystis* and *Tetraedron*, but these are no longer the dominant group.

There are various examples of new species of existing genera appearing in Lake Kinneret and replacing the old species of the same genus, *Staurastrum tetracerum* was a common desmid in the 1970 and 1980s. Since 1997 it is rarely seen in Kinneret samples but two new species, *S. manfeldti* Delponte and *S. contortum* G.M. Smith (Table 1) have replaced it as common components of the plankton. Five species of *Tetraedron* usually co-existed in the summer assemblage of Lake Kinneret: *T. minimum*, *T. trigonum*,

T. regulare, *T. quadratum*, *T. caudatum*. All these species still exist but their abundance has declined while a new morphotype, *T. minimum* var. *minimum* Kovácik, never recorded in the past (Table 1), has become the dominant *Tetraedron*. *Synedra acus* (several varieties) was abundant in the past, *S. rumpens* Kützing appeared in 1997 and is abundant since.

In the absence or lower abundance of *Peridinium* in some years since 1996, the relative and absolute abundances of five species of the genus *Peridiniopsis* (*Ps. borgei*, *Ps. cunningtonii*, *Ps. elpatiewskyii*, *Ps. penardiforme*, *Ps. polonicum*) and other dinoflagellates (*Ceratium hirundinella* and the non-pigmented *Entzia acuta*) has increased (Fig. 2c). In particular, *Ps. cunningtonii* and *Ps. elpatiewsyki* increased in abundance relative to pre-1994 (Pollingher & Hickel, 1991) whereas *Ps. borgei*, that was the second most abundant dinoflagellate in the earlier years, became less abundant more recently.

Of the diatoms, besides *A. granulata*, *C. polymorpha* Meyer et Håkansson occurred at all times of the year with highest abundances in June to July. *Cyclotella* was particularly abundant in the mid-1990s with summer cell densities usually exceeding 1000 cells mL^{-1} and at peak abundance reaching 5000 cells mL^{-1} . Because of the relatively small cell volume of *C. polymorpha* (110–940 μm^3), this high abundance was not accompanied by biomass domination. Since 1997 *C. polymorpha* abundance has greatly declined, and pennate diatoms, especially *Synedra ulna* and *S. rumpens* replaced it as main components of the summer assemblage (Table 2), with peak abundances also in the order of 1000–5000 cells mL^{-1}.

Of the cyanobacteria, in addition to the toxin-producing *A. ovalisporum* (Banker *et al.*, 1997), the filamentous, N_2-fixing *Cylindrospermopsis cuspis* Komarék et Kling appeared for the first time in fall 2000 and occurred every fall since then (Table 1). Nitrogen fixing cyanobacteria did occur in Lake Kinneret in the early 1970s (Fig. 6) but disappeared to below detection limit till 1994. In the Kinneret phytoplankton species list published by Pollingher (1978) *Aphanizomenon flos aquae*, *Anabaena planktonica*, *A. spiroides* and *Anabaenopsis circularis* are listed. During 1969–77 *A. planktonica* and *A. spiroides* occurred occasionally at low densities, after which their densities were below the detection limit most of the time. *Anabaena* sp. was sporadically recorded in August 1992, July 1993, and in September and October 2000. *A. flos aquae* was common from May to August 1971, causing the 'peak' of 1.5% in annual mean contribution of N_2 fixing species to total biomass reported that year (Fig. 6), but was never recorded again after 1974. *Anabaenopsis circularis* was observed in water samples but never counted. The non-heterocystic filamentous cyanobacterium *Raphidiopsis mediterranea* appeared for the first time in February 1987. It was recorded in six of ca 1000 samples analysed during 1987–90, and was not reported again until 1998. Since then, it has been common in summer-autumn (Table 1). In addition, *Planktolyngbya* sp. Agnostidis et Komárek, previously unrecorded, has been common in recent years.

Diversity index

As a result of changes in species dominance, species diversity has also changed in recent years (Fig. 8). During the period 1969–93, a typical annual pattern was associated with the development and decline of the *Peridinium* bloom. Shannon's diversity index was low during the bloom, when a single species comprised >95% of the phytoplankton biomass, and high during summer and fall, when many species co-existed. Since 1996, the annual pattern of the diversity index has disappeared, and diversity is relatively high throughout the year, as is typical of assemblages subjected to disturbances of intermediate intensity (Padisak, Reynolds & Sommer, 1993). A noticeable exception is low diversity during the intense 1998 *Peridinium* bloom.

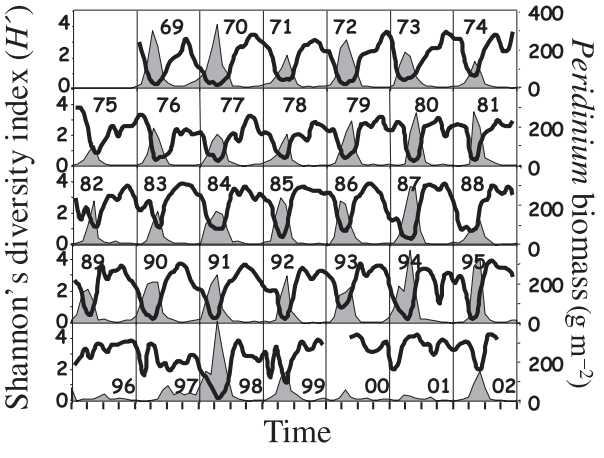

Fig. 8 Shannon's diversity index for Lake Kinneret phytoplankton, 1969–2002. The biomass of dinoflagellates (g m^{-2}, grey areas) is plotted on a second *y*-axis.

Discussion

As detailed earlier, anthropogenic stress on Lake Kinneret has been substantial since the 1930s, diverse in its nature, and accumulated over time. Nevertheless, for many years the lake ecosystem and particularly its phytoplankton maintained astonishing stability, expressed as a predictable annual pattern that revolved around a winter-spring *Peridinium* bloom. From 1994 onwards only some of the years were '*Peridinium* bloom years' whereas in other, 'no-bloom years', the phytoplankton seasonal dynamics were different and unpredictable. Furthermore, the summer assemblage of both bloom years and no bloom years after 1994 was substantially different from that typical of the lake prior to 1994, with increasing contribution of cyanobacteria. It seems that at about 1994 a critical turning point was reached, after which changes to the phytoplankton became more evident than in the pre-1994 years.

Three important features of the 34 year record for Lake Kinneret serve to validate Schindler's (1987) theory, that phytoplankton will respond to anthropogenic stress on a lake ecosystem before bulk parameters. (i) The period 1994–2002 was subjected to significantly different forcing than the preceding period, 1969–93 (Table 3). In particular, during the second period average water levels were lower, water temperatures and chloride concentrations were higher, and TP loading was smaller (Fig. 1). During this period the lake was also subjected to a 'bleak dilution program' followed by over-fishing of other commercial species, further impacting top-down influences. (ii) No significant responses of bulk ecosystem parameters to those changes in forcing could be detected. Specifically, ambient concentrations of TP,

Table 3 Long-term mean values based on annual averages (±SD and number of years in brackets) of some primary forcing and response parameters in Lake Kinneret for two periods: I. 1969–93, the period of phytoplankton stability, and II. 1994–2002, the period in which phytoplankton dynamics exhibited deviations from the previously repetitive pattern.

Parameter	Period I: 1969–1993	Period II: 1994–2002	Significance
Forcing parameters			
Water level (m a.m.s.l.)	−210.4 ± 0.9 (25)	−211.9 ± 1.5 (9)	**
Total incident solar irradiance (cal cm^{-2} min^{-1})	0.28 ± 0.01 (7†)	0.29 ± 0.03 (9)	ns
Temp, avg 0–10 m, January to June (°C)	19.0 ± 0.5 (25)	19.9 ± 0.7 (9)	**
Temp, avg 0–10 m, July to December (°C)	24.9 ± 0.4 (25)	25.7 ± 0.7 (9)	**
TP load-normalised (mg m^{-3} $year^{-1}$)	24.2 ± 10.4 (24)	13.5 ± 7.8 (8)	*
TN load-normalised (mg m^{-3} $year^{-1}$)	352 ± 187 (24)	241 ± 98 (8)	ns
Nitrate load (tons $year^{-1}$)	1012 ± 674 (24)	742 ± 331 (8)	ns
Chloride, avg 0–10 m (mg L^{-1})	225 ± 13 (25)	244 ± 25 (9)	**
Response parameters			
Secchi depth (m)	3.0 ± 0.5 (25)	3.0 ± 0.2 (9)	ns
Chlorophyll *a*, 0–15 m (μg m^{-2})	190 ± 48 (24)	227 ± 96 (9)	ns
Primary production, 0–15 m (mg C m^{-2} day^{-1})	1674 ± 332 (20‡)	1782 ± 425 (9)	ns
TP, avg 0–10 m (μg L^{-1})	19.6 ± 3.5 (25)	21.1 ± 3.4 (9)	ns
TN, avg 0–10 m (μg L^{-1})	702 ± 197 (25)	542 ± 71 (9)	ns
Oxygen, avg 0–10 m (mg L^{-1})	8.9 ± 0.8 (25)	8.6 ± 0.3 (9)	ns
pH (arithmetic mean), avg 0–10 m	8.6 ± 0.1 (25)	8.5 ± 0.1 (9)	ns
TSS, avg 0–10 m (mg L^{-1})	3.4 ± 0.5 (16§)	3.6 ± 0.8 (9)	ns
Phytoplankton biomass (g m^{-2})	70.9 ± 15.6 (25)	88.9 ± 32.2 (9)	*
Zooplankton biomass (g m^{-3})	1.52 ± 0.46 (25)	1.64 ± 0.25 (9)	ns
Percentage cyanobacteria	3.8 ± 4.7 (25)	12.5 ± 6.44 (9)	**
Percentage N_2-fixing cyanobacteria	0.1 ± 0.3 (25)	5.3 ± 5.12 (8)	**

Last column indicates whether the averages are statistically different, based on ANOVA (ns, not significant; *$P < 0.05$; **$P < 0.01$). TP, total phosphorus; TN, total nitrogen; TSS, total suspended solids.
†1986–93; ‡excluding 1982–85; §1978–93.

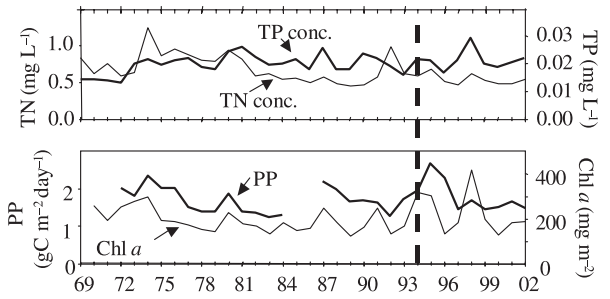

Fig. 9 Annual mean values for some bulk parameters in Lake Kinneret, 1969–2002: upper panel – TN and TP concentrations of the 0–10 m layer; lower panel – depth-integrated (0–15 m) primary production (PP) and chlorophyll *a* (Chl *a*). Data are from the Lake Kinneret Data Base, courtesy of a Mekorot water company (chemical analyses), A. Nishri (TN, TP) and T. Berman and Y.Z. Yacobi (Chl, PP).

TN, chlorophyll *a* and primary production (Fig. 9), dissolved oxygen, pH and Secchi transparency were not significantly different between the periods (Table 3). (iii) Phytoplankton species composition *did* exhibit significant differences between those two periods (Figs 2–8, Tables 2 and 3 and as detailed below).

Period I (1969–93) – repeatable patterns and stability

Berman *et al.* (1995) analysed the temporal changes in phytoplankton bulk parameters (total biomass, chlorophyll, primary production) as well as other indices of eutrophication (Secchi depth, total suspended solids) for the period 1972–93 and concluded that, until 1993, the ecosystem was stable. Besides the ecological stability, water quality was considered by them to be good. The bloom-forming *Peridinium* is non-toxic, and although it does cause taste and odour problems when in large densities, it is easily removed from drinking water by chlorination. Other symptoms of eutrophication, such as anoxia, surface scum formation and toxic blooms were rare or absent. Thus, from both water quality and ecosystem stability points of view, the *Peridinium*-dominated early state of the Kinneret ecosystem is considered a 'good' or 'desirable' state.

The phytoplankton data presented here for 1969–93 confirm Pollingher's (1981, 1986) early statements about a typical annual pattern of phytoplankton species composition and succession in Lake Kinneret, repeatable from year to year. Using Reynolds' (1997) trait-based associations of freshwater phytoplankton and his alphanumeric classification, Pollingher's (1981) four succession stages could be summarised as: $X_2 \rightarrow P$ & $J \rightarrow L \rightarrow J_2$, where X_2 is an association with *Plagioselmis/Chrysochromulina* as the key members, typical of the Kinneret autumnal progressive destratification, P is the winter *A. granulata* – dominated association, J is a chlorophyte dominated assemblage (*Pediastrum*, *Coelastrum*, *Scenedesmus*), L represents the spring *Peridinium*, and J_2 is a tentative abbreviation I gave the assortment of Kinneret summer nanoplanktonic species for which Reynolds does not have a specific abbreviation.

Period II (1994–2003) – loss of predictable patterns

While bulk parameters remained unchanged over this second period (Table 3), phytoplankton species changed markedly. A suite of deviations from the early *Peridinium*-dominated state took place since approximately 1994–96. The summarised pattern of $X_2 \rightarrow P$ & $J \rightarrow L \rightarrow J_2$ no longer held, each year was different from the other, and thus unpredictable. The most evident deviations from the typical, pre-1994 pattern included: (i) complete absence of a spring *Peridinium* bloom in some years, and increased variability in the magnitude of the bloom in others (Figs 2 & 3); (ii) intensification of *Aulacoseira* winter blooms (Fig. 4); (iii) significantly higher summer phytoplankton biomass (Table 3) with altered species composition (Table 2) suggestive of a shift from potentially more palatable forms to less palatable forms; (iv) increase in the abundance and relative contribution of cyanobacteria (Figs 2 & 6; Table 3); (v) invasion and establishment of N_2-fixing cyanobacteria (*A. ovalisporum*, *C. cuspis*) (Table 1; Fig. 6); and (vi) parasitic fungal epidemics. This new unpredictable state is considered less desirable than the earlier state, mostly because of the dangers arising from higher incidence of toxic cyanobacterial blooms.

It could be argued that the higher diversity index typical of the post-1995 years (Fig. 8) is in conflict with the last statement. However, using alternative stable-state terminology (Scheffer *et al.*, 1993; Beisner, Haydon & Cuddington, 2003), the data for the recent years suggest that the Kinneret system has not yet reached a new stable-state, and is still fluctuating between the *Peridinium* dominated state and a yet undefined new alternate-state without a *Peridinium*

bloom. If this is the case, the high diversity is only transient, and will likely change once a new stable-state is achieved.

Possible underlying mechanisms promoting the change

Although the major changes in phytoplankton dynamics and species composition followed two key perturbations to the lake, the 1993 collapse of the bleak fishery and the 1994 re-flooding of the Hula peat soils, cause-and-effect relationships cannot be automatically inferred. Quantitative analyses of the contribution of various environmental factors to the changes in the Kinneret phytoplankton species composition and annual dynamics are the focus of a follow-up study, but here a brief preliminary qualitative assessment is presented of likely relationships between the perturbations and the recorded changes.

Of the various changes that occurred in the recent history of Lake Kinneret, the most noticeable were water level and salinity variations (Fig. 1). However, in most cases these could not be linked directly with the observed changes to the phytoplankton. For example, no-bloom years occurred in both near-average (1996, 1997) and exceptionally low water level years (2000, 2001). This does not exclude possible indirect effects of extreme and fluctuating water levels, but these are not further discussed here.

The substantial declines (volume-corrected) of 28 and 44% in TN and TP entering the lake from the Jordan River between the two periods (Fig. 1; Table 3) were not translated to reduced in-lake concentration (Table 3). Rather, ambient TN and TP remained at relatively constant levels since the early 1980s, of about 20 μg P L^{-1} and 500–600 μg N L^{-1} with some interannual variation (Fig. 9). If external inputs declined, the lack of decline of in-lake concentrations implies that internal loading and recycling rates have increased and/or other, non-quantified sources of external nutrients have increased. Shifts in the major sources of nutrients, their availability and recycling rates can affect the relative advantage some species have over others, as well as various feedback mechanisms operating in a complex ecosystem.

The replacement of the summer phytoplankton species assemblage by grazing-resistant forms suggests that food web feedback mechanisms were operating. By 1993, the over-harvest of the Kinneret Bleak has yielded large populations of small body size fish that per unit biomass exert higher predation pressure on zooplankton than larger individuals, and prey on smaller zooplankton (Hambright & Shapiro, 1997). Subsidised 'bleak dilution' conducted since 1995, in which sub-commercial size bleak are removed from the lake, continued the heavy pressure on the larger size fish, as even the with smaller mesh nets used for this 'dilution' the larger size fish are harvested whereas the smallest individuals escape through the nets.

Analysis of the long-term zooplankton record indicates that the average body size of Kinneret zooplankton has been declining since the early 1980s, with smaller-bodied species and individuals becoming more abundant at the expense of larger-bodied species and individuals (K. D. Hambright, pers. comm.). These changes likely reflect growing predation pressure by fish. Thus the overall shift in body sizes toward smaller individuals in the dominant fish and subsequently in zooplankton may have indirectly increased grazing mortality on the smaller palatable phytoplankton taxa and contributed to the relative increase in non-edible forms.

Furthermore, the species shifts in the Kinneret zooplankton assemblage, towards increasing domination by smaller cladocerans *(Bosmina* and *Chydorus*) and cyclopoid copepods (*Thermocyclops*) may have impacted nutrient dynamics. These species generally have relatively high body N : P and therefore tend to recycle N and P at comparatively low ratios compared with large species (such as *Daphnia*) with low body N : P (Sterner, 1990; Sterner & Elser, 2002). In this way, zooplankton may be contributing to the increased success of cyanobacteria (Elser, 1999). Recent analyses of nutrient excretion rates by Kinneret zooplankton indicate that mass-specific, bulk zooplankton assemblage N : P remineralisation is approximately 15 : 1 (mole : mole) for macrozooplankton (>150 μm) and <10 : 1 for microzooplankton (K.D. Hambright & T. Zohary, unpublished data).

Regarding changes in the catchment, Berman, Pollingher & Zohary (1998) speculated that the reflooding of the formerly dry horizons of peat soils released micronutrients and other 'growth factors' (e.g. iron and other trace metals, chelators, various organic substances), which had previously not reached the lake. Supporting evidence for this idea was that *P. gatunense* was never recorded in the Hula

Valley and does not occur in the newly created Lake Agmon (Zohary *et al*., 1998).

Our observation of massive fungal infection of *P. gatunense* in December 2000, followed by its disappearance from the water column with no bloom development in the spring that followed, instigated the hypothesis that fungal infection may have caused the 'no bloom' phenomenon. Parasitic fungi are usually host species-specific so infection of one species favours the proliferation of other species and thus can alter the outcome of inter-specific competition and shift the course of phytoplankton succession (Ibelings *et al*., 2004). Sommer, Wedemeyer & Lowsky (1984) attributed discrepancies between potential and realised growth rates of *C. hirundinella* in Lake Constance to fungal parasites, and Heaney *et al*. (1988) attributed lower abundance of *Ceratium* in Estwaite Water and Blelham Tarn in some years to fungal parasitism. However, a series of laboratory controlled host-parasite experiments conducted on isolates of *P. gatunense* and the chytrid fungus infecting it in Lake Kinneret have shown unequivocally that this particular parasite infects only dead or senescent host cells (A. Alster & T. Zohary, unpublished data). Thus, the more likely explanation is that a different, yet unknown factor stressed *P. gatunense*, which then became more susceptible to fungal infection.

Implications

The winter of 2002/03 was unusually wet. Higher than average precipitation led to a 4.8 m rise in water level (maximum water level of −209.70 m was recorded in May 2003). The filling of the lake was accompanied by an intense *A. granulata* bloom in January to February 2003 (mean February biomass: 140 g m^{-2}) followed by a massive *Peridinium* bloom in spring (mean May biomass approximately 450 g m^{-2}), similar to 1998 in both dynamics and magnitude. It is conceivable that additional nutrients entering the lake that year, both from the catchment and from dense shoreline vegetation that developed during the low water level years and was inundated that winter, enabled this massive bloom formation. 2004 is developing to be yet another massive *Peridinium* bloom year, similar to 1998 and 2003. While the return of the *Peridinium* bloom years may suggest a return to the stable-state, the second and third occurrences of exceptionally high standing stock biomasses (Figs 2 & 3) may suggest that the ecosystem is entering a new stage – where bulk parameters are starting to respond too. Thus, the present lake seems delicate and particularly sensitive to additional human intervention.

If Schindler's (1987) hypothesis is correct, the suite of changes in phytoplankton dynamics in Lake Kinneret in recent years, and especially following more than two decades of recorded constancy, should be interpreted as early responses to increasing stress at the ecosystem level. In particular, the appearance and establishment of toxin-producing species in the country's main drinking water supply is considered an undesirable change. In addition, the appearance of fungal epidemics, the shift to dominance of less-grazed species in summer, and the loss of previously predictable annual pattern, should be viewed as a cause for concern.

Acknowledgments

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