Primary production and phytoplankton in Lake Kinneret: A long-term record (1972–1993)

T. Berman, L. Stone,[1] *Y. Z. Yacobi, B. Kaplan, M. Schlichter, A. Nishri, and U. Pollingher*
Israel Oceanographic & Limnological Research, Yigal Allon Kinneret Limnological Laboratory, POB 345, Tiberias, Israel 14102

Abstract

The long-term (22 yr) record of primary production in Lake Kinneret, Israel, has been examined, together with chlorophyll and microscopically determined algal biomass, in order to discern whether there have been any significant changes in these parameters during this period. During the period 1972 through 1993, annual averages have ranged from 1,223 to 2,311 mg C m^{-2} d^{-1} for primary production, from 127 to 246 mg m^{-2} for chlorophyll, and from 39.3 to 98.5 g m^{-2} for algal wet weight. The annual peak of these parameters was in April–May. Over 22 yr, variability in primary productivity was more closely related to changes in chlorophyll than to changes in algal biomass. No evidence was found for consistently increasing long-term trends in primary production, chlorophyll concentrations, or algal wet weight biomass from 1972–1993. Although the annual and semiannual averages of algal biomass were significantly higher in the past 11 yr than those in the previous decade, this pattern could arise from a long-term cyclical but self-compensating trend. The extended record indicates that despite population growth and intense economic development around the lake and in its catchment area, there has been no extreme eutrophication of Lake Kinneret from 1972 to 1993. We suggest that this relative resiliency of the Kinneret ecosystem is due to high ambient levels of alkalinity, calcium, and pH in the lake water acting to limit phosphorus availability, which in turn restricts the outgrowth of phytoplankton.

Lake Kinneret (the Biblical Sea of Galilee) is the only large freshwater lake (~170 km^2 surface area) in Israel. In 1964, a nationwide water carrier grid was established with the lake as its principal reservoir. Since then, between 200 and 450 × 10^6 m^3 of water have been pumped annually from the lake, providing about a quarter to a third of the national water requirements. Because of the need to find solutions to the severe regional shortage of water, the lake plays a prominent role in current discussions on water reallocation in the Middle East Peace Process. In addition to its crucial role as a source of freshwater, the lake is a major and rapidly developing tourist site and supports a commercial fishery with an average catch of 1,500–2,000 t annually.

Given the obvious importance of maintaining water

[1] Present address: Zoology Department, Tel Aviv University, Ramat Aviv, Israel.

quality in this lake, a coordinated program of monitoring and research was initiated in the late 1960s. At that time it was feared that nutrient inflows into the lake, then ranging annually from 12 to 27 g N m^{-2} and 0.6 to 1.3 g P m^{-2}, were "able and likely to induce eutrophication" (Serruya 1972) and there was considerable concern about future water quality.

In order to determine the extent to which the predicted trends of eutrophication have occurred, we have examined the long-term (22 yr) record of primary production and related phytoplankton parameters in Lake Kinneret. Primary production is generally considered a key characteristic of aquatic ecosystems that determines trophic status and has major implications for water quality. Goldman (1990, p. 225) suggested that "primary production may provide the best single integration of the biological, physical and chemical factors at work in a lake."

Since the 1960s there have been extensive environmental changes in the Kinneret catchment basin and around the lake. In the watershed, there have been alterations in drainage patterns, crops, and irrigation techniques together with extensive development of lakeside and regional tourist facilities. Flow patterns within the lake have been changed by withdrawal of ~400 × 10^6 m^3 of water annually into the National Water Carrier, with only minimal outflows to the Southern Jordan River. This has brought about an increase in the amplitude of annual water level fluctuations (*see* Hambright et al. 1994). There has been an intensification of commercial fishing and fish stocking (mostly of the St. Peter's fish, *Sarotherodon galilaeus,* but also exotics such as gray mullet, *Mugil cephalus,* and silver carp, *Hypophthalmichthys molitrix*).

Among the changes observed in the lake water, we note

a sharp decline in chloride concentrations (from ~11 to 5.9–6.6 mM Cl) and in the concentrations of dissolved organic N (from ~36 to ~14 μM) and increases in hypolimnic orthophosphate (from ~0.47 to ~0.8 μM). Annual external inputs of dissolved organic N declined from ~500 to 230 t. However, total P inputs from the Jordan River (ranging annually from ~80 to 120 t) did not change significantly in the past 20 yr, although there was a rise in the relative amounts of dissolved P, from ~10 to 20% (Nishri and Schlichter pers. comm.). There has been a steady decline in zooplankton (mainly Cladocera and Copepoda) attributed to increased predation by fish (Gophen et al. 1990, pers. comm.), with average biomasses in the early 1990s being ~50% of those observed in the 1970s.

In terms of standing stock, Berman et al. (1992) showed that phytoplankton in Lake Kinneret seemed to be relatively resistant to environmental changes and that there had been no extreme long-term increase (from 1970 to 1990) in the static phytoplankton parameters (chlorophyll or microscopically determined algal biomass). Here, we examine the dynamic parameter, primary production, and address the questions: Does the primary productivity record indicate any eutrophication trends? How does variability in primary production relate to variability in the parameters of phytoplankton standing stock? Can we describe any functional relationships between environmental factors and seasonal or annual variability in primary production? To what extent can the Lake Kinneret ecosystem be defined as stable or unstable?

Lake site and methods

Lake Kinneret is a warm (13–30°C) monomictic lake in northern Israel with a maximum depth of ~42 m and a mean depth of ~24 m (*see* Serruya 1978). Winter turnover plays a decisive role in the seasonal cycle of the lake ecosystem. Full homothermy occurs from about mid-December until February–March and can last from several weeks to more than 3 months, depending on climatic conditions (Hambright et al. 1994). After stratification, the hypolimnion (initially at a depth of ~16 m) rapidly becomes anoxic, with sulfide concentrations reaching 0.15–0.23 mM. The lake water has relatively high carbonate alkalinity (ranging from ~100 to 129 mg liter) and high concentrations of Ca (0.9–1.1 mM). pH levels measured in midmorning hours in the euphotic zone range from 8.2 to 8.9. Total P (TP) concentrations in the upper water layers vary from ~0.4 to ~0.9 μM, whereas those of soluble reactive P (SRP) are usually between <0.03 and 0.15 μM. The highest concentrations (~0.3 μM) of SRP are reached in the anoxic hypolimnion toward the end of the period of strong stratification (November–December).

A prominent characteristic of the phytoplankton in Lake Kinneret is the annual development of the dinoflagellate *Peridinium gatunense* (formerly *P. cinctum*), which usually dominates the algal assemblage from midwinter (January–February) through spring (end May–beginning June). During summer and fall, the phytoplankton consists mostly of nanoplanktonic chlorophytes with some diatoms. Cyanobacteria are generally a very minor component of the assemblage (Berman et al. 1992).

Primary production has been routinely determined since 1972 using the same modified Steemann Nielsen (1952) method. The first account of primary productivity measurements in this lake (from 1969 to 1970) using the ^{14}C method with gas-flow counting was published by Rodhe (1972). Primary production was usually determined biweekly (but sometimes only monthly) from January 1972 until the present, except (due to funding limitations) for a 3-yr period from 1984 to 1986, at a central lake station (A). This site is located at the deepest part of the lake (~40 m) and is representative of the pelagic waters of the lake (Pollingher and Berman 1975).

Water was taken with a 5-liter Aberg-Rodhe sampler throughout the euphotic zone, usually at seven or eight depths from the surface to 15 m. Samples (100 ml) were placed in clear glass bottles to which ~20 μCi of [^{14}C]bicarbonate were added. After incubation for 3 h in situ, 25-ml portions were filtered under a light vacuum (max, 100 mm of Hg) on 25-mm ultra-fine glass filters (984 H Reeve-Angel) or 0.45-μm Millipore filters, rinsed with 15 ml of filtered lake water, and briefly fumed in HCl vapor to eliminate remaining traces of inorganic [14]C. The radioactivity in the particulate fraction retained on the filters was determined by liquid scintillation with quench correction. To compensate for nonbiological adsorption to filters (Williams et al. 1972), we poisoned three to five zero-time controls with Lugol's iodine for each sampling series. The total added ^{14}C dpm was also checked for each sampling series by counting triplicate 0.1-ml portions taken directly from three of the bottles. Uptake of ^{14}C in the dark, when corrected for zero-time controls, was never >5% of the integrated light profile, and therefore dark bottles were not used routinely. Conversion of 3-h [^{14}C]bicarbonate incorporation rates to daily rates was made with empirically determined conversion factors (Berman and Pollingher 1974).

Parallel water samples were taken for the determination of chlorophyll concentrations with acetone extraction and fluorescence detection (Holm-Hansen et al. 1965) and algal wet weight biomass (Utermöhl 1958 method with a Wild M40 inverted microscope) with biomass conversion factors based on size measurements of each species (Pollingher 1981).

Most of our data are based on estimates of daily areal primary production (mg C m^{-2} d^{-1}) and areal measures of chlorophyll (mg m^{-2}) or of algal wet weight biomass (g m^{-2}). These values were obtained by linear integrations of measurements at discrete depths within the euphotic zone.

Although routine measurements of the chlorophyll and wet weight algal biomass began earlier (in 1970 and 1969 respectively), in this paper we use only the data for these parameters beginning in 1972, in parallel with the primary productivity record. During this time, no changes were made in the methods used for these measurements.

TP, SRP, and total suspended solids were assayed by standard methods (Am. Public Health Assoc. 1985).

Assessing ecosystem stability

In an ecosystem at equilibrium, biological parameters such as algal populations are, by definition, in a constant state of balance and will not fluctuate unless perturbed. Such a system is termed "mathematically stable" if it tends to return to the same constant state of equilibrium after disturbance (Botkin and Sobel 1975). Several standard methods are available for assessing the stability of systems that have a single-point equilibrium (Carpenter et al. 1992; Connell and Sousa 1983); however, the situation becomes far more complicated for those systems that display little evidence of equilibrium. In Lake Kinneret, the strong seasonal fluctuations and recurring annual phytoplankton blooms lack a single equilibrium. Difficulties arise for systems that do not have an equilibrium because the standard techniques for evaluating ecosystem stability (e.g. *see* Carpenter et al. 1992) become inappropriate.

Recently developed mathematical approaches are available for assessing the stability of systems that are generally never at equilibrium but nevertheless demonstrate persistently recurring dynamic patterns (Murray 1990). Applying these approaches in the present context, we might consider Lake Kinneret a system that jumps between multiple equilibria, each equilibrium possibly being amenable to stability analysis, or a system that follows a "stable limit-cycle," oscillating in a regular fashion over time but with noise superimposed. After perturbation, the system, if stable, eventually returns to the original limit cycle. Alternatively, the system has highly complex, nonlinear, and possibly chaotic dynamics which locks onto the seasonal cycle.

A detailed treatment of the above possibilities is well beyond the scope of the present paper. Moreover, the techniques required to demonstrate or assess stability by means of field experiments are daunting, and we know of no ecological study that has convincingly proven ecosystem stability (*see* Connell and Sousa 1983).

Because of these difficulties, a less ambitious but more practical "operational" approach for assessing stability is taken here. By means of time-series analysis, we attempted to detect long-term changes in key ecological parameters (primary productivity, chlorophyll, and algal standing stocks) and to assess the qualitative nature of any apparent trends. These system parameters are considered "stable" whenever they fail to indicate any spiraling or linear runaway trends (i.e. characteristics generally indicative of an unstable system), but instead tend to converge or else oscillate in either a well-defined or a random manner about some average value.

All time-series data sets of primary productivity, chlorophyll, and algal biomass exhibited very strong visually discernible seasonal trends (Fig. 1) that conform to the well-described lake phytoplankton cycle. This marked seasonality not only has the potential to mask more important trends but also obscures the true correlations between parameters. For example, two parameters that have no real relationship of dependence between them will nevertheless appear highly correlated if they are both in-

creasing and decreasing simultaneously according to the prevailing seasonal cycle. To reveal underlying interannual trends and correlations, it is therefore necessary to suppress the masking seasonal fluctuations.

We followed the simple but effective technique described by Priestley (1984) which removes annual periodic oscillations from a multiannual data set by first passing it through a 12-month (13 point) moving average "symmetric" filter. The filtered data set (Xt') was obtained by transforming the observed time series (Xt) according to:

$$Xt' = (0.5Xt\text{-}6 + Xt\text{-}5 + \ldots + Xt + \ldots + Xt\text{-}5 + 0.5Xt\text{-}6)/12. \tag{1}$$

Results

Interannual variability and long-term trends—A general impression of the amount and variability of primary production, chlorophyll, and algal biomass in Lake Kinneret over the years 1972 to 1993 is given in Fig. 2, which shows the annual averages and standard deviations for these parameters. The lowest annual averages for primary production were recorded in 1983 (1,223 mg C m^{-2} d^{-1}) and 1992 (1,241 mg C m^{-2} d^{-1}); lowest chlorophyll averages were also noted for these years (134 mg m^{-2}) and for 1989 (128 mg m^{-2}). Maximum annual averages for both parameters were measured in 1974 (2,311 mg C m^{-2} d^{-1} and 293 mg m^{-2}). Algal wet weight biomass was minimum in 1975 (avg, 39.3 g m^{-2}) and maximum in 1987 (avg, 98.5 g m^{-2}). The ratio of highest to lowest annual averages was 1.9, 2.3, and 2.5 for primary production, chlorophyll, and algal wet weight biomass, respectively. The annual average primary production for 1972–1993 was 1,671 mg C m^{-2} d^{-1} (SD $\pm$ 287), while chlorophyll averaged 187 mg m^{-2} (SD $\pm$ 48) and wet weight algal biomass averaged 71 g m^{-2} (SD $\pm$ 16).

The time series of all monthly averages of primary production, chlorophyll, and algal biomass calculated for depth-integrated profiles from 1972 through 1993 (*see Fig. 1*) emphasize the strong seasonality of these parameters (*see above*). We filtered the data according to Eq. 1 to suppress these annual fluctuations and to uncover any important long-term trends. The resulting "smoothed" time series for all three parameters show some evidence of long-term cycling but no overall long-term linear trends (*see discussion*). In particular, the smoothed chlorophyll series shows an apparent 3- or 4-yr oscillation. Some hint of this is also shown by the series for primary production, although the continuity is marred by missing data points. The algal biomass series is probably best viewed as a cycle of a sinusoid curve, dropping over the first 4 yr, gradually rising for 10 yr, then slowly decreasing to below the initial biomass levels in the last 8-yr phase.

Our results are strikingly different from those obtained by Jassby et al. (1992), who used a similar time-series analysis and showed a consistent linear increase in the levels of primary productivity of Lake Tahoe between 1965 and 1990. They also noted that the variance of the time series increased with time proportionally to the in-
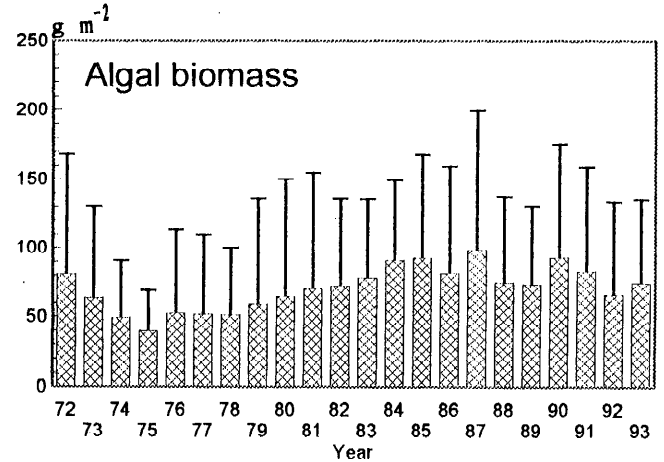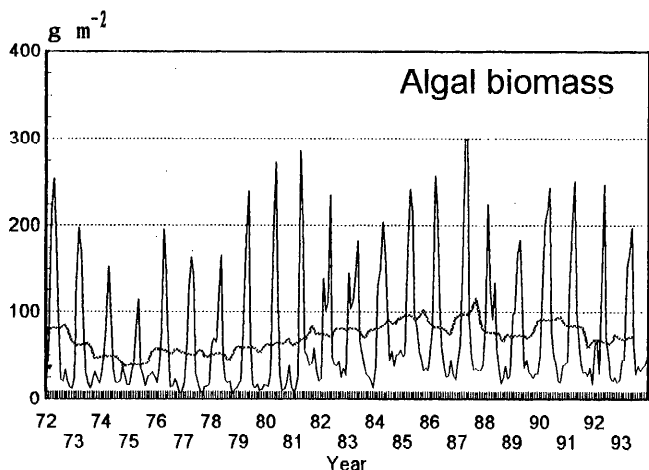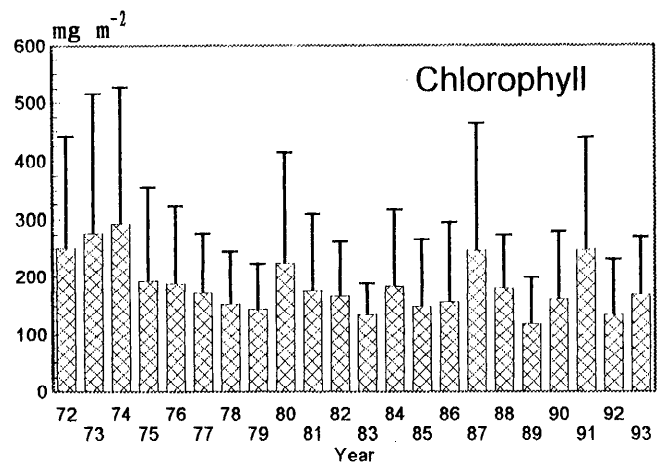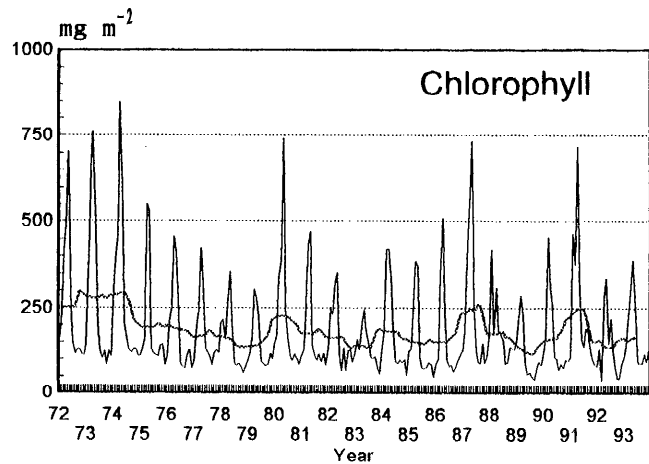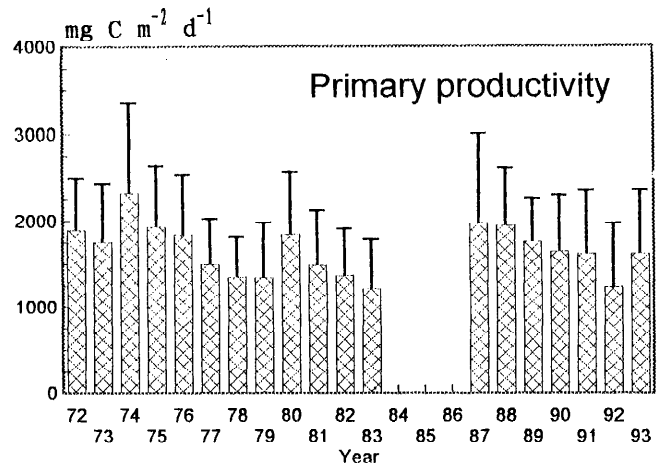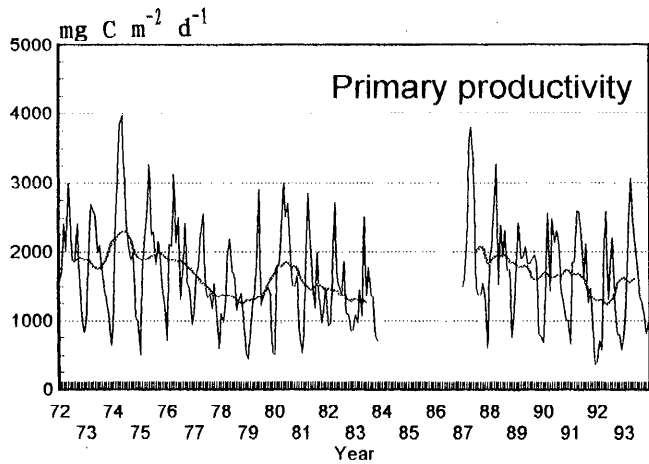
Fig. 1. Time series and 12-month (13 point) smoothed averages of all monthly averages of primary production, chlorophyll, and algal biomass, calculated for depth–integrated profiles from 1972 through 1993.

Fig. 2. Annual averages and standard deviations of primary production, chlorophyll, and wet weight algal biomass from 1972 through 1993.

creasing annual mean. We tested for a similar effect by using the same methodology but found that the variance of the primary productivity signal in Lake Kinneret was remarkably constant with time.

As an alternative check for long-term trends, we examined the time series formed by taking 6-month averages, i.e. from January to June (winter–spring) and from July to December (summer–fall), which reflect the seasons dominated by the dinoflagellate bloom and nanophyto-

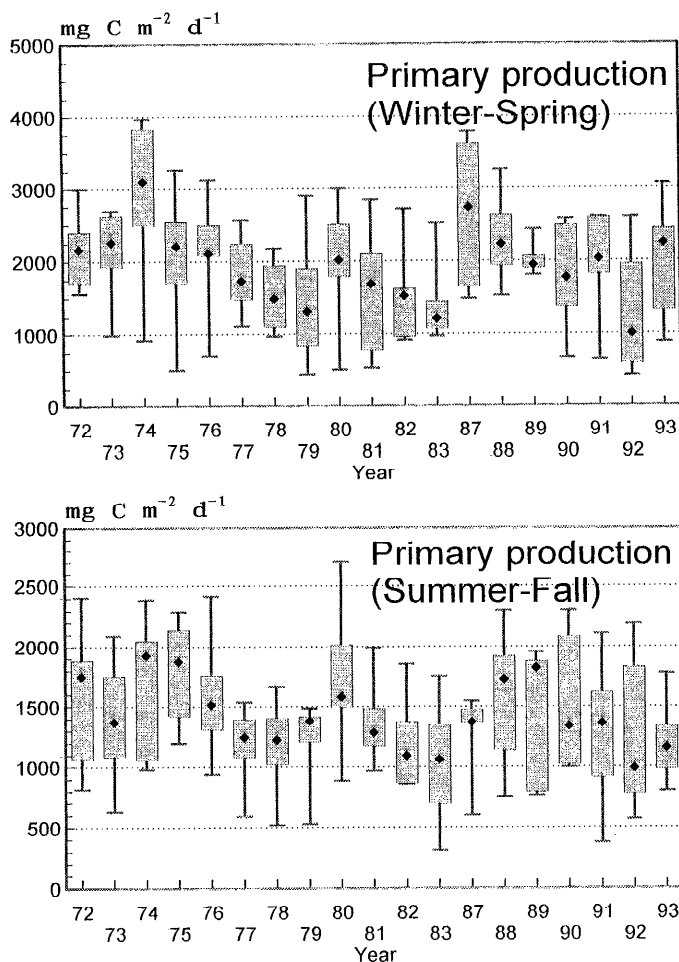Fig. 3. Semiannual (winter–spring and summer–fall) plots of median (◆), 25th–75th (box), and 5th and 95th (whisker) values of primary production for 1972 through 1993.

plankton, respectively. Isolating the time-course of individual seasons in this fashion is a simple technique that effectively removes undesirable seasonal trends.

In Figs. 3–5 we show the median, 25th–75th, and 5th–95th percentile ranges of semiannual averages calculated for primary production, chlorophyll, and wet weight algal biomass for each year from 1972 through 1993. These box-and-whisker plots illustrate the considerable variability of the 6-month averages for each parameter. For the winter–spring period, the average of primary production from 1972 to 1993 was 1,934 mg C m^{-2} d^{-1} (SD ± 412) and for summer–fall 1,400±217 mg C m^{-2} d^{-1}. For chlorophyll, the semiannual averages were 272±83 mg m^{-2} (winter–spring) and 102±18 mg m^{-2} (summer–fall), and for wet weight biomass, 113±25 and 28±10 g m^{-2}, respectively.

No obvious linear trend of increase or decrease for primary production, chlorophyll, or algal biomass is evident from the data in Figs. 3–5. Any indication of a possible linear trend would be of dubious significance considering the large amounts of variation about each median point displayed in these figures. Berman et al.
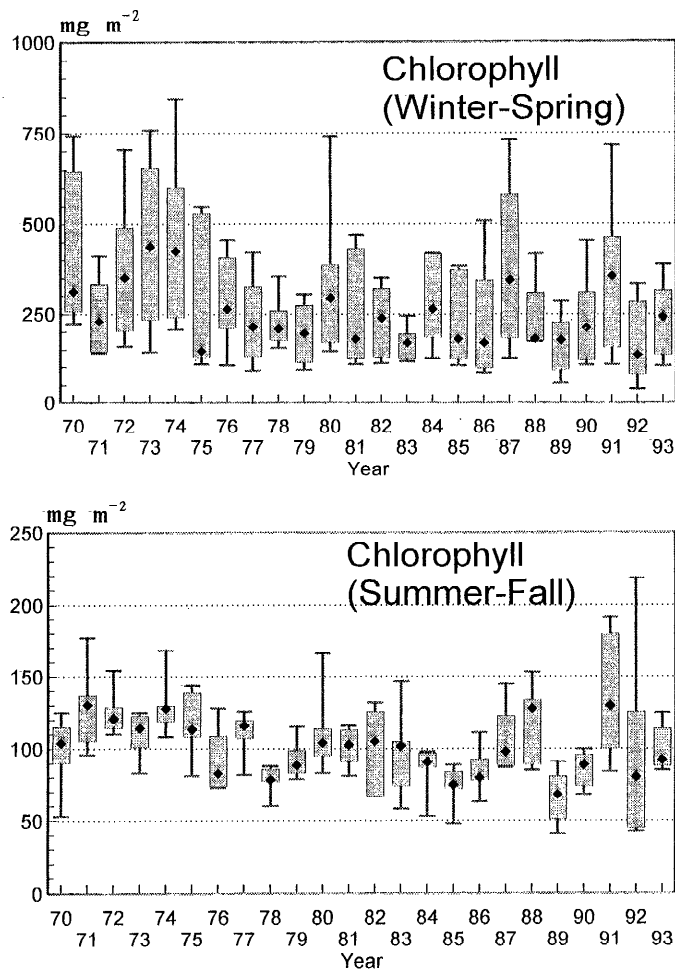
Fig. 4. As Fig. 3, but for chlorophyll.

(1992) previously noted the abrupt increase in the summer–fall algal biomass which was recorded in 1981; this level has been maintained since then (Fig. 5).

We compared annual and semiannual averages of primary production, chlorophyll, and algal wet weight biomass for two 11-yr periods (1972–1982 and 1982–1993) in order to examine whether there were perceptible differences in levels of these parameters during these periods which each span half of our total time scale (Table 1). Comparison (*t*-test) of the two 11-yr averages showed that neither primary production or chlorophyll averages differed significantly. Only the algal biomass groups differed significantly from each other, with increases of 38% for annual, 35% for winter–spring, and 60% for summer–fall averages.

As for many other lakes, phosphorus has been proposed as a critical factor in determining the levels of chlorophyll, algal biomass, and primary production in Lake Kinneret (Serruya and Pollingher 1977; Pollingher et al. 1988). We therefore examined the long-term record of TP in the euphotic zone (Fig. 6) and that of SRP (constituting almost all the TP) in the hypolimnion (Fig. 7). The higher TP concentrations recorded for each winter–spring period reflect the larger amounts of organic P sequestered in

Peridinium cells during this season. No trend was discerned in euphotic TP (as represented by 0–10-m averages) from 1972 to 1993. In contrast, SRP concentrations in the hypolimnion (averaged values August–November at 30 m) showed an increasing trend from 1972, consistent with previous reports (Smith et al. 1989; Hambright et al. 1994). This trend became readily apparent after passing the time series through a 6-yr (73 point) moving-average filter (Fig. 7). Note also that the variance of the time series increased as the trend increased.

Serruya and Pollingher (1977) proposed that changes in hypolimnic SRP (which mixes by various processes into the euphotic zone during thermocline deepening and at overturn) might be reflected by the levels of primary production or algal standing stocks in the following year. We examined this suggestion by applying standard parametric and nonparametric correlation statistics to untransformed data, but we found no significant relationships. We reasoned that the effects of the trend in hypolimnic SRP may have interfered with the analysis and obscured the true correlation. To overcome this potential problem, we suppressed the effects of slow-moving linear and cyclical trends by first-differencing the data sets (Priestley 1984). This approach allowed us to test whether the *fluctuations* of one parameter were synchronized in any way with *changes* in another parameter. We used the transformed data to obtain reasonably high correlation coefficients for linear regressions between hypolimnic SRP and the subsequent annual averages of chlorophyll ($r = 0.60$, $P = 0.004$) and of primary production ($r = 0.50$, $P = 0.04$) but not of algal biomass ($r = 0.33$, $P = 0.14$). A time-course plot of the transformed data shows a remarkable regularity of peaks of hypolimnic P followed, after a lag, by peaks of chlorophyll (Fig. 8), demonstrating that these parameters indeed fluctuated in close synchrony.

Goldman (1988) and others have shown that consistent changes in Secchi disk depths correspond closely to increases in primary production and algal standing stock
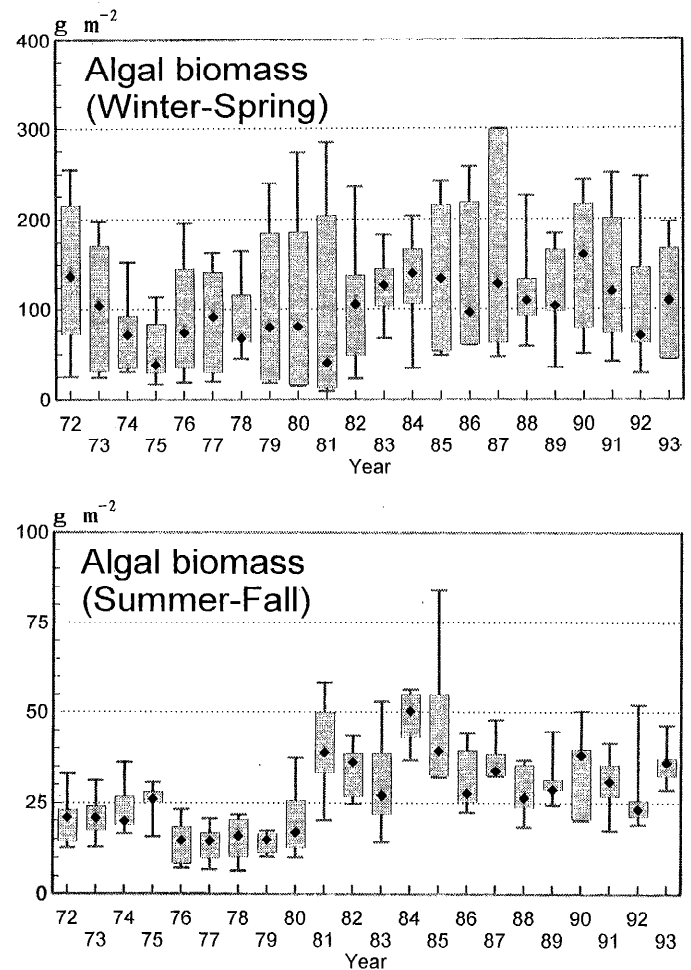
Fig. 5. As Fig. 3, but for algal wet weight biomass.

Table 1. Comparison of 11-yr annual averages of primary production, chlorophyll, and algal wet weight biomass. Two-sample t-test; primary production—mg C m^{-2} d^{-1}; chlorophyll—mg m^{-2}; algal biomass—g wet wt m^{-2}.

	1972–1982	1983–1993		
	(Avg ± SD)		t-value	Probability
Primary production				
Annual averages	1,701±313	1,628±282	0.53	0.60
Winter–spring	1,940±421	1,924±454	0.07	0.94
Summer–fall	1,450±241	1,332±188	1.20	0.27
Chlorophyll				
Annual averages	204±50	170±43	1.67	0.11
Winter–spring	300±90	245±72	1.58	0.15
Summer–fall	107±15	96±20	1.46	0.18
Algal biomass				
Annual averages	59±12	82±10	−4.83	0.0001
Winter–spring	96±22	130±17	−3.99	0.0008
Summer–fall	22±9	35±7	−3.77	0.0012

μgP liter⁻¹

TP (0 to 10 m)
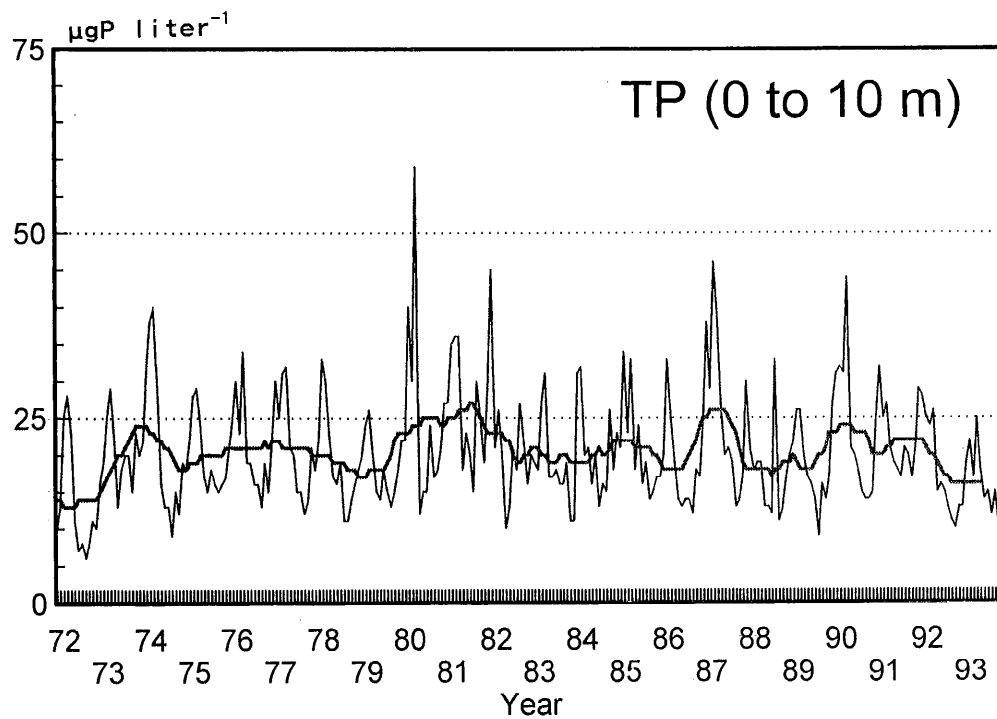
Fig. 6. Time series and 12-month (13 point) smoothed average of monthly averaged TP in the upper water layer (0–10 m) of Lake Kinneret.

that occur with eutrophication. In Lake Kinneret, the time series of Secchi depth and a related parameter—total suspended solids in the epilimnion—showed no indication of long-term trends (Fig. 9).

Seasonal variability—The general patterns of primary production, chlorophyll, and algal biomass standing stocks over the months of the year are shown in Fig. 10, which gives the median and percentile values for monthly data

μgP liter⁻¹

Hypolimnetic SRP
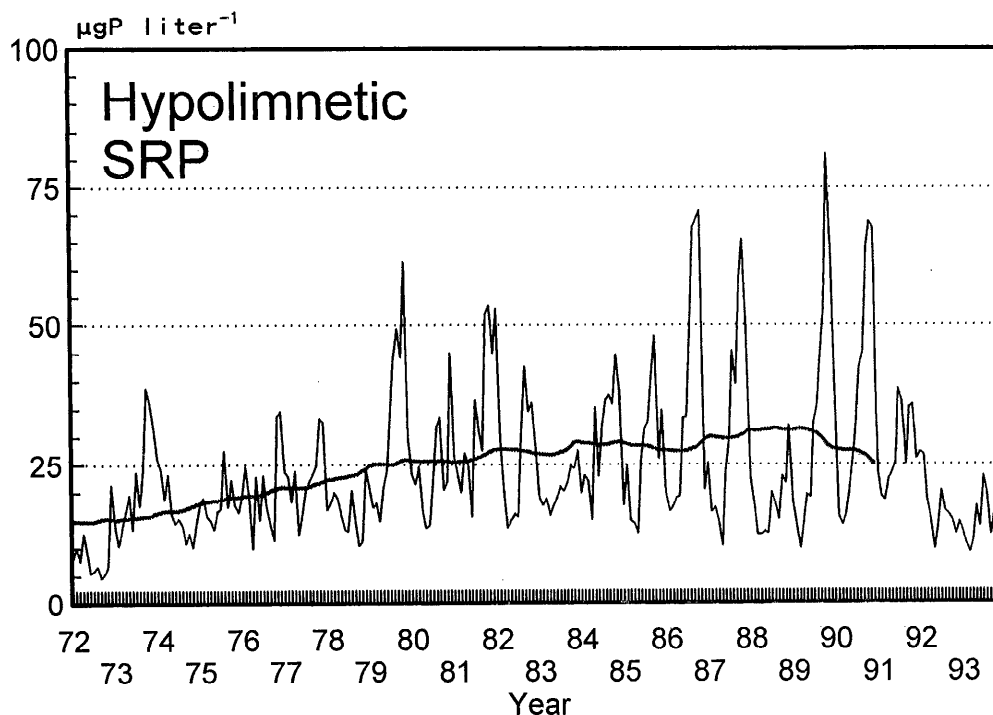
Fig. 7. Time series and 6-yr (73 point) smoothed average of SRP in the hypolimnion (30 m) of Lake Kinneret (averaged values from August through November).
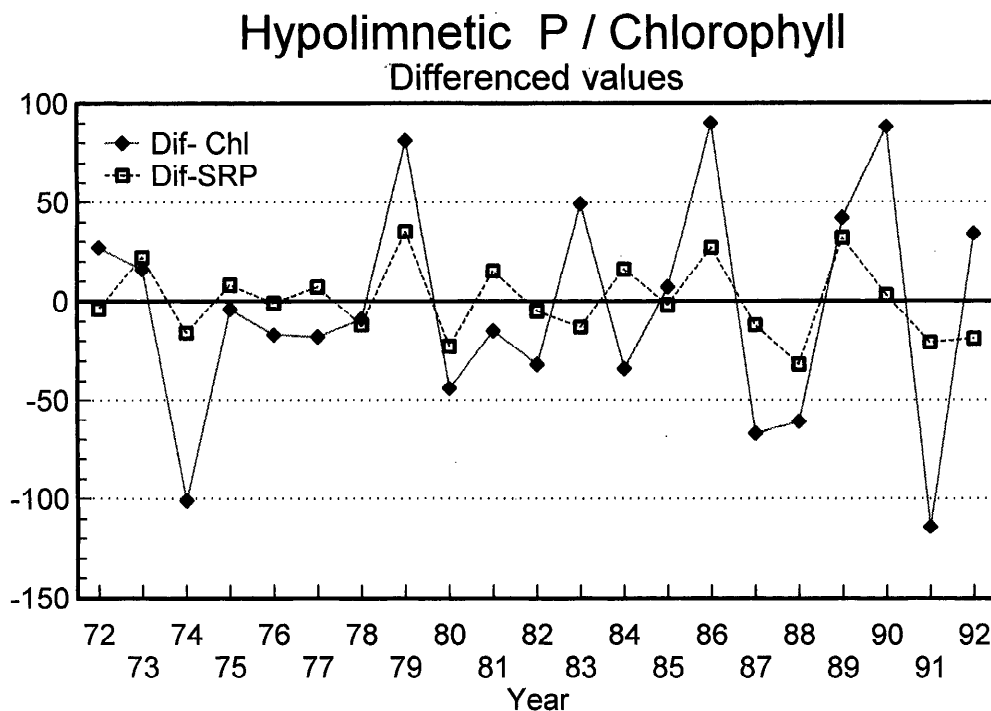
Hypolimnetic P / Chlorophyll
Differenced values

Fig. 8. Differenced values (Priestley 1984) for August–November averages of hypolimnetic SRP (Dif-SRP) and the annual averages *for the following year* of chlorophyll (Dif-Chl) from 1972 to 1993.

from 1972 to 1993. These parameters reached maxima in April and May at the peak of the *Peridinium* bloom; lowest levels were noted in December, when day length is shortest. Primary production showed the least seasonal variability (3-fold range), remaining relatively high in summer and fall despite a 5- and 8-fold maximum-to-minimum range in chlorophyll and algal wet weight biomass, respectively. The large percentile ranges in March through May (Fig. 10) reflect high sample variability caused by the very patchy distribution of the dinoflagellates during the bloom period (Berman and Rodhe 1971).

In order to reveal possible seasonal relationships, we regressed the averaged summer–fall values (*y*) of primary production, chlorophyll, or algal biomass against their averaged winter–spring values (*x*) for the same year. Significant positive correlations were found (for primary production: correlation coefficient, $r = 0.61$; $P = 0.005$; for chlorophyll: $r = 0.63$; $P = 0.002$; for wet weight biomass: $r = 0.53$; $P = 0.011$; $n = 22$). No correlations were found when summer–fall data of any given year were plotted against winter–spring values of the following year.

Interrelations among primary productivity, chlorophyll, and phytoplankton biomass—We examined the relationships among the annual or semiannual averages for integrated profiles of primary production, chlorophyll, and algal biomass using either parametric (linear regression) or nonparametric (Kendall τ) statistics (Table 2). Only the regressions of primary production on chlorophyll (annual and winter–spring averages) showed significant cor-

relations. There was a noteworthy lack of correlation between summer–fall semiannual averages of primary production vs. chlorophyll.

In addition, we compared the relationships between the "filtered" monthly data for these parameters shown in Fig. 1. Here again, significant correlations were found between primary production and chlorophyll but not between primary production and algal biomass (Table 2).

When monthly averaged primary productivity, measured at discrete depths in the upper water layer, was regressed against chlorophyll determined at the same depth, a decreasing correlation was found between these two parameters with increasing depths from 0 to 5 m (Table 3). The extent to which the changes in primary production might be explained by variability of chlorophyll ranged from 76% at 0 depth to 9% at 3-m depth. At 5-m depth, the relationship between the two parameters was not significant.

The depth dependence of the relationship between primary production and chlorophyll was also examined on the basis of monthly averages for the winter–spring and summer–fall periods (Table 3). For winter–spring months, significant regressions, although with sharply decreasing correlation coefficients, were noted for depths 0–3 m; at 5 m, the correlation was extremely poor. This pattern was similar to that obtained with all year data (*see above*). Summer–fall data had weaker correlations with a different pattern at various depths; regressions with highest *r* values occurred at 2-, 3-, and 5-m depths, and the lowest coefficient was noted at 1 m.
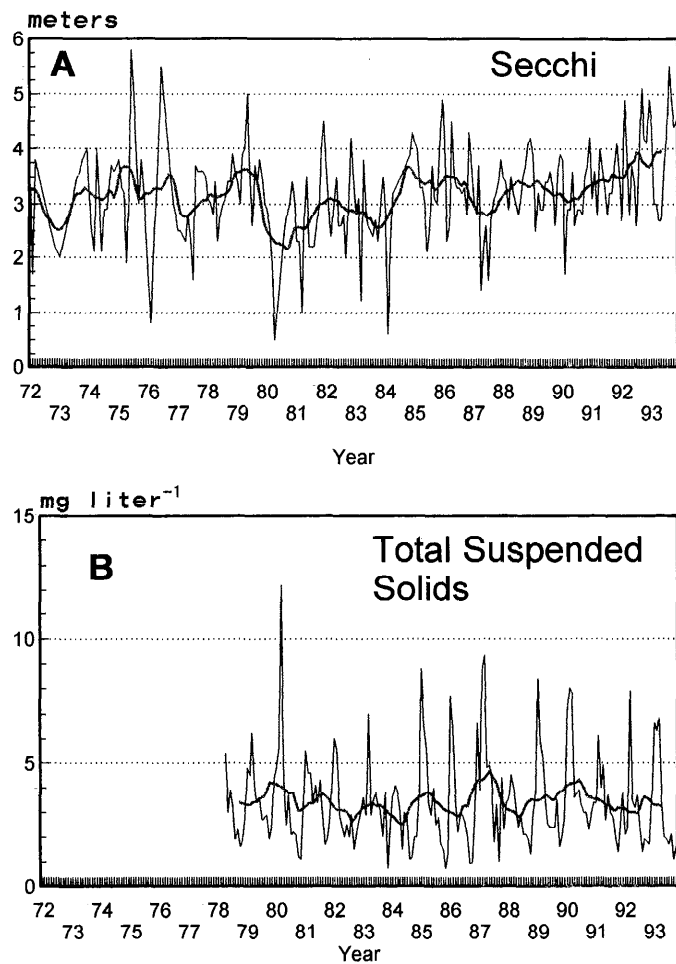
Fig. 9. Time series and 12-month (13 point) smoothed averages of Secchi depth (A) and total suspended solids, 0–10-m monthly averages (B).

Discussion

Interannual variability, stability, and eutrophication trends in Lake Kinneret—Despite population growth and intense economic development around the lake and in its catchment area, our data do not indicate that eutrophication is severe or that water quality has deteriorated within the past two decades. The long-term record, when considered over the entire period from 1972 through 1993, showed no significant upward trends in the levels of primary productivity—a key indicator of trophic state. Likewise, measures of phytoplankton standing stocks, chlorophyll, and algal wet weight biomass did not indicate consistent trends of increase or decrease.

We have shown that other parameters, such as Secchi depths, total suspended solids (Fig. 9), and epilimnetic TP (Fig. 6), which might be related to the amounts of algal standing stock also show no sign of constant increase during the period of study. Moreover, although there have been some changes of phytoplankton species with time, these have not entailed any basic alterations in overall

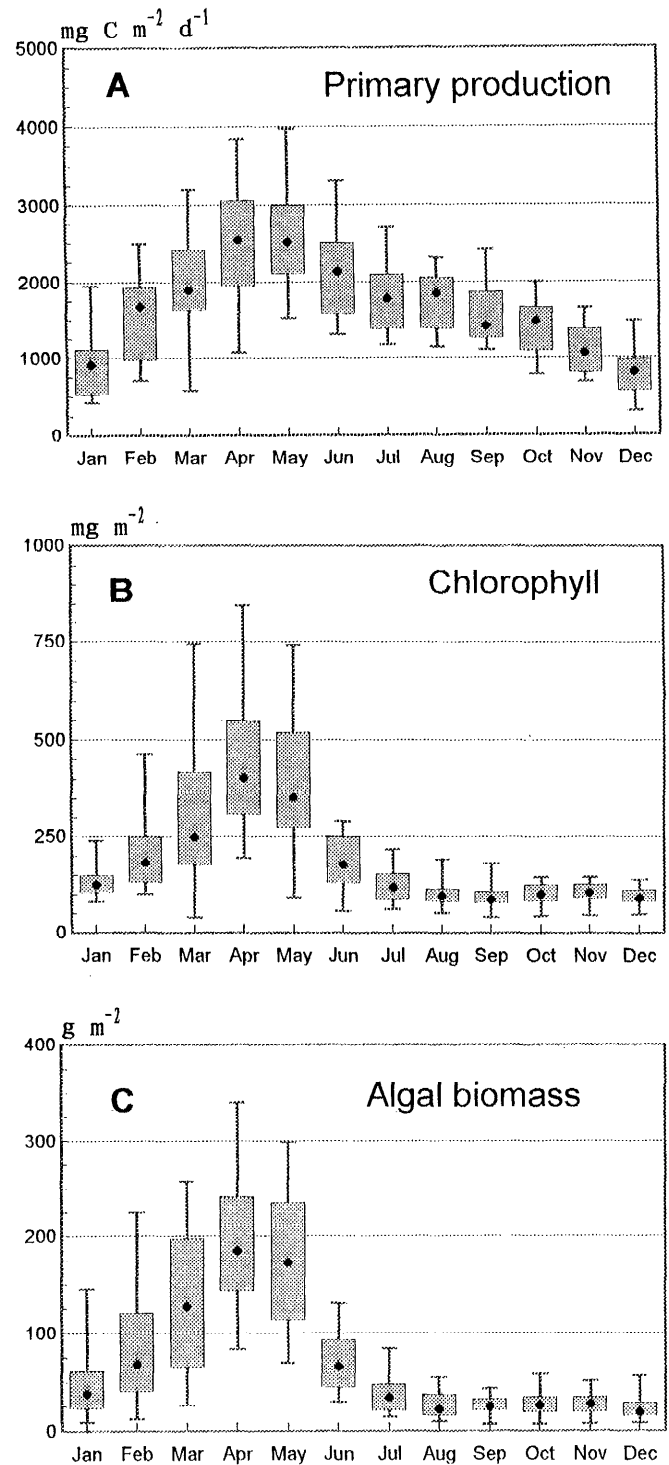Fig. 10. Seasonal pattern of phytoplankton parameters in Lake Kinneret. Monthly median (♦), 25th–75th (box), and 5th and 95th (whisker) values of primary production, chlorophyll, and algal wet weight biomass calculated for 1972 through 1993.

algal population composition (*see* Berman et al. 1992; Yacobi and Pollingher 1993).

What might be the explanation for this apparent resilience of the primary producers in the lake to change?

Table 2. Correlations between primary productivity, chlorophyll, and algal biomass for smoothed data for all months from 1972 to 1993 and for nontransformed values of annual and semiannual averages, 1972–1993. Primary productivity—mg C m^{-2} d^{-1}; chlorophyll— mg m^{-2}; algal wet weight biomass—g m^{-2}.

	Linear regression*		Kendall (t)†		
	r	P	Z	τ	P
Productivity vs. Chl					
All months 1972–1993	0.69	<0.0001	11.2	0.53	<0.0001
Annual averages	0.72	0.0007	3.13	0.53	0.0018
Jan–Jun averages	0.76	0.0003	3.60	0.60	0.0004
Jul–Dec averages	0.31	0.191	1.92	0.32	0.0600
Productivity vs. biomass					
All months 1972–1993	0.12	0.08	1.65	−0.08	0.10
Annual averages	0.05	0.82	0.17	0.04	0.86
Jan–Jun averages	0.07	0.78	−0.04	0.00	0.97
Jul–Dec averages	0.15	0.54	0.45	−0.08	0.65
Chl vs. biomass					
All months 1972–1993	0.09	0.14	1.75	−0.07	0.08
Annual averages	0.07	0.78	0.56	−0.09	0.57
Jan–Jun averages	0.04	0.95	0.25	0.04	0.80
Jul–Dec averages	0.24	0.28	0.76	−1.2	0.45

* r—Correlation coefficient; P—probability.
† Z—Kendall z value; τ—Kendall t.

Following the original ideas of Serruya and Berman (1975), Serruya and Pollingher (1977), and Smith et al. (1989), we suggest the following paradigm to describe the long-term developments of phytoplankton in Lake Kinneret. We hypothesize that the high pH, high carbonate alkalinity, and high calcium concentrations in the phototrophic zone act as a "buffer" to maintain low levels of biologically available, mainly SRP, phosphorus. Recent work by Nishri (pers. comm.) has indicated that orthophosphate tends to be stripped out of the euphotic zone by sorption onto the surface of sedimenting calcite crystals. In the hypolimnion, orthophosphate forms phosphate surface-phase complexes with calcite, [Ca$_3$(HCO$_3$)$_3$(PO$_4$)], or [CaHPO$_4$], as described by Avnimelech (1984). These processes may explain why the increasing trend in hypolimnetic SRP concentrations (Fig. 7) was not reflected by TP in the euphotic zone (Fig. 6). Intrinsically low amounts of available P, therefore, set an overall limit to the development of the phytoplankton standing stock and its photosynthetic activity in the lake.

The amounts of SRP that accumulate in the hypolimnion during the stratified period subsequently become available to the phytoplankton with the onset of homothermy in the following winter–spring and may modulate the amounts of chlorophyll and photosynthetic activity observed during the period of mixing and the *Peridinium* bloom. Variations in the amounts of hypolimnic SRP which may be caused by changes in minimum lake levels (Serruya and Pollingher 1977) may be partly responsible for the observed variability and multiyear cyclical behavior shown by chlorophyll and primary production (Figs. 1 and 8).

Additionally, we found a direct correlation between the levels of primary production and chlorophyll in winter–

spring and those in summer–fall of the same year. It seems, therefore, that whatever environmental factors determine the levels of these parameters in the winter–spring of any given year may also directly or indirectly affect their magnitude in summer and fall.

Table 3. Correlations of primary productivity (mg C m^{-3} d^{-1}) on chlorophyll (mg m^{-3}) at discrete depths for all profiles or for profiles during winter–spring or summer–fall seasons. Data based on monthly averages from January 1972 to December 1993 (1984–1986 missing).

	r^2	Prob.	n
Depth 0 m			
All months	0.87	<0.0001	319
Winter–spring	0.87	<0.0001	152
Summer–fall	0.27	0.0008	167
Depth 1 m			
All months	0.58	<0.0001	319
Winter–spring	0.73	<0.0001	152
Summer–fall	0.18	0.0204	167
Depth 2 m			
All months	0.48	<0.0001	319
Winter–spring	0.42	<0.0001	152
Summer–fall	0.37	<0.0001	167
Depth 3 m			
All months	0.29	0.0001	319
Winter–spring	0.29	0.0005	152
Summer–fall	0.32	0.0001	167
Depth 5 m			
All months	0.07	0.2260	319
Winter–spring	0.13	0.0900	152
Summer–fall	0.35	0.0001	167

Seasonal variability—Algal seasonal development in the lake follows a clear monacmic pattern with a single annual peak, typical for many lakes in the tropics and subtropics, where the factor of enhanced vertical supply of nutrients with seasonal mixing predominates (Talling 1993). Primary production showed only a moderate seasonal variation in comparison with the phytoplankton standing stock parameters (Fig. 10). This observation reflects the higher specific photosynthetic rates associated with summer–fall nanoplanktonic algae in comparison with larger net phytoplankton in winter–spring (Pollingher and Berman 1982) and also the greater penetration of photosynthetically available radiation into the water column in summer–fall (Dubinsky and Berman 1979).

The factors which most probably determine the seasonal cycle of phytoplankton in the lake have been described previously (Pollingher et al. 1988). Although phosphorus does not seem to be limiting during most of the period of the dinoflagellate peak, it may become so toward the end of the bloom. Recent studies by Berman-Frank et al. (1994) also implicate limitation by CO_2 as an important factor in terminating the *Peridinium* bloom. In summer and fall, phosphorus usually appears to limit algal standing stocks, although sometimes nitrogen may also act similarly. Zooplankton grazing is also most intense in summer and fall (Gophen and Pollingher 1985), and this is the season when the greatest extent of "top-down" control on phytoplankton might be expected.

The above scenario is consistent with our suggestion that the overall levels of primary production and chlorophyll are maintained in Lake Kinneret because of the limitation of phosphorus imposed by the indigenous lake chemistry. Within these constraints, annual variability of hypolimnetic SRP can lead to fluctuations of primary production and chlorophyll in the following year (Fig. 8). Obviously, the levels of primary production in any aquatic ecosystem are a complex function of the quantity and quality of irradiance, environmental factors such as temperature, turbulence, and mixing, amounts of photosynthetic pigment, photoadaptive capability, and the availability of carbon and other elements essential for photosynthesis. The totality of these factors may act to minimize the *seasonal* variability of primary production, whereas on an interannual scale in Lake Kinneret, primary production seems to have been restrained by overall phosphorus availability.

Interrelations among primary production, chlorophyll, and algal biomass—It is noteworthy and encouraging that our measurements of primary production were more closely correlated to chlorophyll—the pigment directly responsible for photosynthesis—than to algal biomass, which may be less tightly linked to phototrophic carbon incorporation (Tables 2 and 3). On the basis of long-term annual or semiannual averages, chlorophyll showed no correlation with algal wet weight biomass. However within any given year, when areal values of chlorophyll were regressed against algal biomass on a monthly basis, very significant correlations were obtained (*see* table 5 and

figure 6 of Berman et al. 1992), presumably because of the strong seasonal dependency of these parameters.

The differences in the winter–spring and summer–fall relationships of primary productivity and chlorophyll shown in both Table 2 and Table 3 presumably reflect the different morning vertical distribution patterns of phytoplankton during these two seasons. In winter–spring, *Peridinium* cells exhibit a diurnal pattern of depth distribution, tending to be close to the surface in the morning, moving downward in the afternoon, and becoming more or less evenly distributed in the water column at night (Berman and Rodhe 1971). Strong wind-induced mixing may interfere with this daily pattern (Pollingher 1988). The summer–fall phytoplankton usually have deeper morning maxima, and light penetration is increased. During this season, vertical profiles of primary production frequently show indications of photoinhibition in the surface and near-surface water layers (Berman and Pollingher 1974).

Methodological approach to time-series data—Our analysis demonstrates very clearly the importance of the choice of the time "window" for interpretations of long-term trends in time series. For example, in the case of the algal biomass data in Fig. 2, if a window from 1975 to 1985 is chosen, a very significant increasing trend is evident. However, if data from 1972 (or 1970, not shown) to 1993 are taken, no such trend is seen. For obvious reasons, time series of environmental parameters are almost invariably limited in their temporal range, thus making unequivocal interpretation problematic.

Another related point concerns the use and abuse of linear regression analysis. This can best be illustrated by considering the example of applying a least-squares linear trend fit to the "filtered" data of chlorophyll and algal biomass shown in Fig. 1. The equations for these linear trends are

$$[\text{Chl}] = 225 - 0.29 \times (\text{month No.})$$
$$(r^2 = 0.23, P < 0.0001) \quad (2a)$$

$$[\text{algal biomass}] = 53.4 + 0.14 \times (\text{month No.})$$
$$(r^2 = 0.37, P < 0.0001) \quad (2b)$$

where [Chl] and [algal biomass] are monthly concentrations measured from January 1972 (month No. 1).

The fact that P (the probability that the slope of the line is zero) is minuscule seems to provide compelling evidence that there is a real linear trend in these data sets. On the other hand, an examination of the smoothed data curves in Fig. 1 does not indicate any obvious long-term linear trend—certainly not what one might expect at the significance level of $P < 0.0001$. In fact, these contrary findings may be reconciled by noting that the time-course of these ecological parameters seems to oscillate over long time spans (2–5 yr for chlorophyll, ~20 yr for algal biomass) in a manner that has so far proved self-compensating.

Comparisons of the biomass data for the two periods (1972–1982 and 1983–1993) suggest that the average an-

nual and semiannual algal levels were significantly higher in the second period (Table 1). Despite the small net difference between initial and final biomass levels, the two halves of the cycle have significantly different means. Consequently, a least-squares linear trend analysis made on these data will show a significantly increasing trend, but as we have indicated this might be deceptive. For cyclical data sets, least-squares linear regressions often provide misleading conclusions and in many cases should not be applied because their underlying assumptions are rarely met. (Attempting to fit a truly nonlinear or cyclical data set to the regression line $Y = mX + c$ will never satisfy the criterion that for any value of X there must exist a real or conceivable set of normally distributed Y values of mean Y.) Although application of linear trends for analysis of time series is common, we note that nature often stubbornly refuses to be linear. For this reason, nonlinear models should be considered as alternatives to the linear fits that are frequently proposed.

Conclusions

Lake Kinneret is one of the world's most comprehensively studied warm lakes. Reports based on long-term phytoplankton records have been published for temperate-zone lakes (e.g. Goldman et al. 1993; Talling 1993; Gaedke and Schweizer 1993), but similar information from warm lakes is scarce (Talling 1986).

If we adopt the practical operational approach rather than the more exact mathematical definition of ecosystem stability (*see* assessing ecosystem stability), we can claim that Lake Kinneret has shown remarkable stability over the past 23 yr despite considerable environmental changes (*see introduction*). No significant spiraling or runaway trends of increase or decrease indicative of instability were found for major indexes of eutrophication (primary production, chlorophyll, and algal biomass). Secchi depths and total suspended solids also showed no indications of deterioration in water quality.

We propose that resource limitation of biologically available phosphorus has been the major factor responsible for restraining increases of primary production and phytoplankton in this lake. It follows that top-down control of primary production and algal standing stock by herbivores has not been a dominant factor. Within the time-frame of this study, the more or less continuous decrease in zooplankton documented by Gophen et al. (1990) was not accompanied by any concomitant increase in primary production or phytoplankton standing stocks.

The apparent stability of primary production and chlorophyll in the lake should be viewed against the background of changes that have been observed during this period. *We emphasize that the response rate for water quality parameters to these environmental changes in Lake Kinneret is not necessarily linear with time or may be on a longer temporal scale than that which we have examined.* Therefore, we stress that the apparent stability of the primary producers does not imply that increasing environmental pressures from human development on the lake can be viewed with complacency or ignored with impunity. Careful and enlightened management based on sustained monitoring and research of Lake Kinneret and its catchment area is a prerequisite to maintain or to improve future water quality.

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