Biogeochemistry **42:** 253–283, 1998.

Lake Kinneret dissolved oxygen regime reflects long term changes in ecosystem functioning

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Key words: dissolved oxygen concentration, yearly oxygen budgets, hypolimnetic respiration

Abstract. Lake Kinneret (Israel) has undergone several prominent chemical and biological changes since 1970. Between 1970 and 1991 significant, long-term gradual increase were recorded in epilimnetic dissolved oxygen (DO) concentrations (about 20%), and in pH levels (0.2 units). Concomitantly there was a significant increase in hypolimnetic H_2S concentrations (about 75%) and a long-term gradual drop in zooplankton biomass (50%). Since 1994 these trends were reversed and the levels of the three chemical parameters have returned to those found in the 1970's and that of zooplankton to mid 1980's levels. The present study is an attempt to relate some of these long term changes by means of yearly oxygen budgets, based on fluxes of oxygen producing and consuming processes. This analysis raises the possibility that part of the long-term increase in epilimnetic DO and pH between 1970 to 1990 may be attributed to reduced inputs of organic matter from alochthonous sources and possibly to enhanced burial of organic matter in the bed sediments. However, the major cause for the observed increase in epilimnetic DO and pH is increased sedimentation of organic matter to the hypolimnion during stratification. As indicated by the amount of H_2S formed in the hypolimnion during stratification added to the amount of oxygen entrapped in this layer at the onset of thermal stratification, between 1970 to 1991 the sedimentation flux of organic matter increased by approximately 40%. It is estimated that during these two decades hypolimnetic respiration increased from ca. 8% of the annual amount of oxygen evolved due to photosynthesis during the early 1970's to ca. 12.5% during the 1980's. The shift in the layer of oxidative processes is suggested to be the result of a multi-annual decline in zooplankton grazing pressure, which led to increased sedimentation of organic matter. The reversed trends for DO, pH and H_2S since 1994 may have partially been due to the increase in zooplankton activity and partially due to changes in phytoplankton community structure.

Introduction

The concentration of dissolved oxygen (DO) in a given layer of water depends on the balance between oxygen producing and oxygen consuming processes. Oxygen generation in aquatic environments is essentially due to photosynthesis; removal mechanisms include various biological and chemical processes, notably respiration and chemical oxidation. Inputs and outputs of organic matter from and to external sources and sinks also influence the oxygen balance because the decomposition of organic matter requires oxygen. Gas exchange with the atmosphere may also affect aquatic oxygen concentrations and the direction of this flux depends on the DO saturation value. A supersaturated surface layer serves as a source of oxygen to the atmosphere whereas an undersaturated layer serves as a sink of atmospheric oxygen. The calculation of DO budgets for natural water bodies requires estimating all of the different oxygen fluxes, some of which are difficult to asses (e.g. gas exchange).

An ongoing water quality monitoring program for Lake Kinneret, initiated in 1969, generates routine limnological data which constitute the Lake Kinneret Database. In the present study we use the database in an attempt to relate observed changes in epilimnetic DO levels during 1970–1996 to long-term trends in other chemical and biological parameters. Oxygen budgets are performed in two steps; one focousing on whole lake budget and the second calculating hypolimnetic respiration. By means of annual oxygen budgets for the lake we examine the dynamics and relative importance of routinely measured oxygen fluxes (primary production, inflows and outflows of dissolved oxygen and organic matter), calculated fluxes (exchange with the atmosphere, zooplankton respiration, sedimentation of organic matter) and fluxes for which no data exist (other respiratory $_2$ consumption). We demonstrate that the observed long-term increase in epilimnetic DO concentrations and pH levels were mostly due to reduced respiration.

The study site

Lake Kinneret (32°48′N:35°37′E) plays a major role in Israel's water economy and currently supplies about 50% of the nation's drinking water. The lake lies in the Syrian-African Rift Valley, at about 200 m below mean sea level. It has a mean depth of 24 m, maximum depth of 43 m, a volume of 4100×10^6 m^3 and water retention time of 4 to 8 years. Average annual inflow is 750×10^6 m^3, of which about 65% enters via the Jordan River. The main outflow from the lake is by sub-surface withdrawal to the National Water Carrier (multi-annual average: 420×10^6 m^3); annual evaporation accounts for the loss of 260×10^6 m^3.

The lake is warm-monomictic with water temperature ranging between 12–15 °C in winter and 26–30 °C in summer (Figure 1). Homothermal period usually extends from mid-December to mid-March, but may vary between 3 weeks to 4 months. Over the remaining nine months the lake is stratified, with a distinct seasonal thermocline that deepens with time at a rate which is slow in summer, but then increases in November (Serruya 1978, Hambright et al. 1994). In May, about two months after the onset of thermal stratification, the hypolimnion becomes anoxic, and biodegradation of organic matter is then carried out by nitrate reducers followed by sulfate reducing bacteria (Hadas

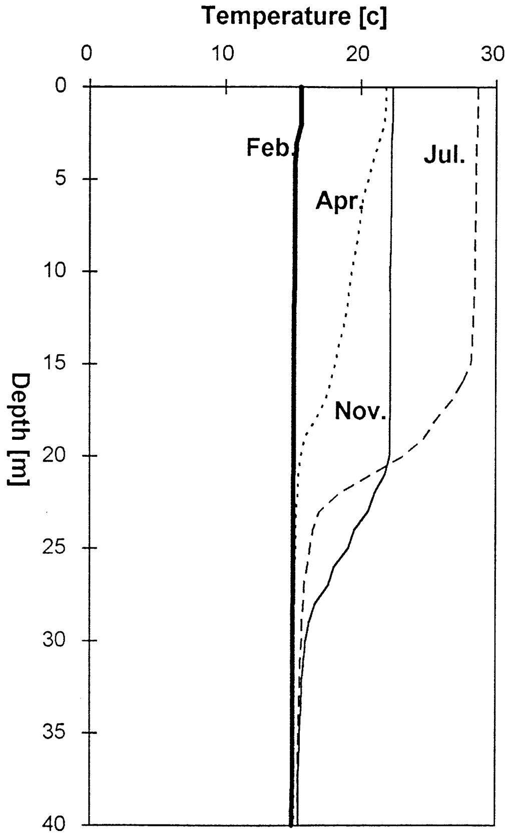

Figure 1. Representative seasonal vertical profiles of temperature in Lake Kinneret. Data are monthly mean values for 1986 taken from the Lake Kinneret Data Base.

& Pinkas 1992). These lead to hypolimnetic accumulation of H_2S, NH_4^+ and soluble reactive phosphorus-SRP (Eckert & Truper 1993; Serruya 1978) (Figure 2). Further details on the seasonal variations in the depth distribution of temperature, oxygen, pH and H_2S are given by Eckert & Hambright (1996).

The seasonal succession, abundance and distribution of phytoplankton in the lake have been described by Pollingher (1986). Generally, phytoplankton biomass is maximal ($>$200 g wet wt. m^{-2}) in late winter-spring (March–May) due to an annual bloom of the dinoflagellate *Peridinium gatunense* (Hickel & Pollingher 1988). The bloom usually crashes in May, after which the phytoplankton is dominated by a diverse and relatively low-biomass (20–40 g wet wt. m^{-2}) community of nanoplanktonic species, including chlorophytes, diatoms, cryptophytes and cyanobacteria. The seasonal pattern of primary production in the pelagic zone of the lake is characterized by relatively high

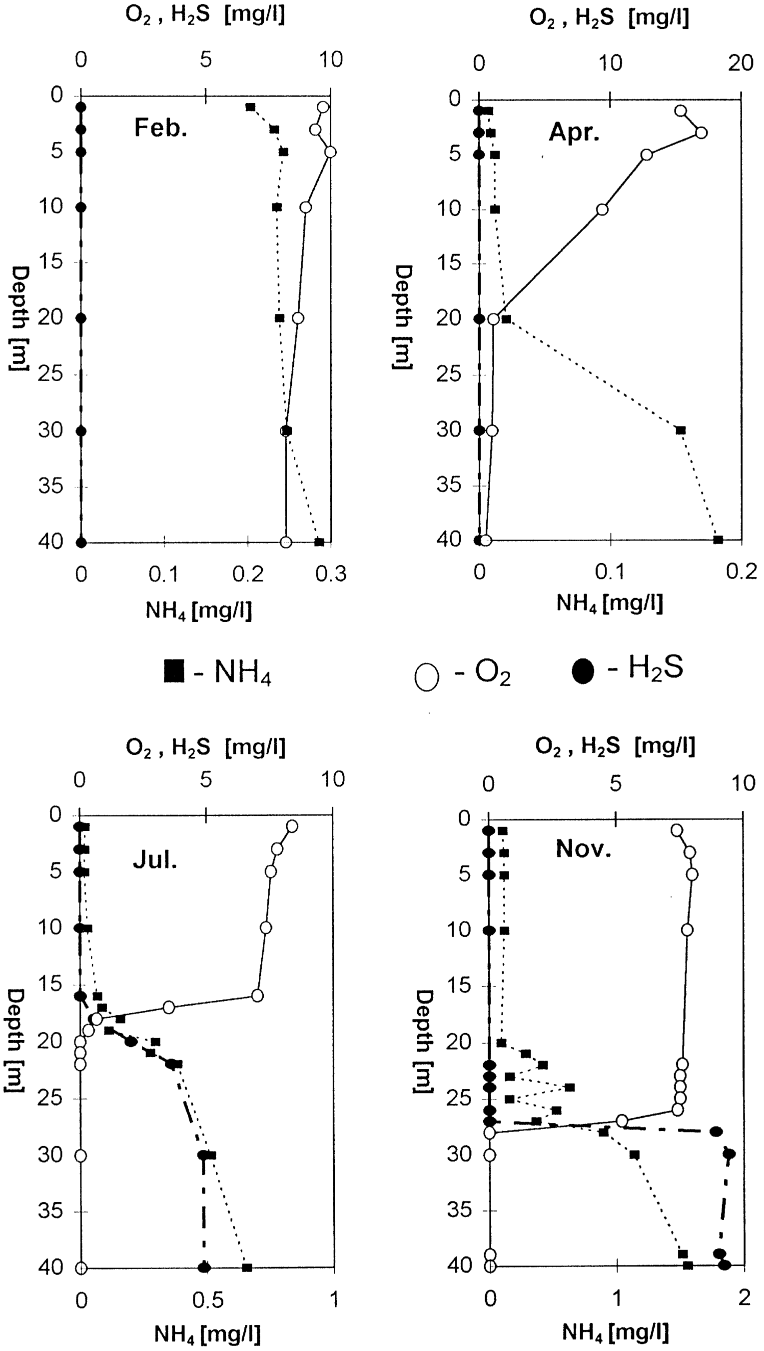

Figure 2. Representative seasonal vertical profiles for NH_4^+ H_2S and O_2 in Lake Kinneret. Data are monthly mean values for 1986 taken from the Lake Kinneret data Base.

values in spring, of about 2500 mg C m^{-2} day^{-1}, followed by a decrease from June to January (Berman & Pollingher 1974; Berman et al. 1995).

Since 1969, Lake Kinneret has undergone several prominent biological changes. A significant gradual and continuous decrease in zooplankton biomass has been recorded over this period, so that zooplankton biomass in the 1980's was only half of that recorded in the early 1970's (Gophen et al. 1990a). The long term records also reveal that around 1981 summer–fall phytoplankton biomass increased significantly, from 20 to 40 g m^{-2}, and remained at those higher levels throughout the 1980's (Berman et al. 1992). Gophen et al. (1990a, 1990b) attributed this increase to the reduction in zooplankton biomass due to increased predation by zooplanktivorous fish.

Since 1994 a series of unusual events related to phytoplankton biomass, composition and primary productivity were observed. In 1994 the biomass attained during the spring bloom of *P. gatunense* was a record high. In late summer that year the cyanobacterium *Aphanizomeon ovalisporum* bloomed for the first time in the 25-year record (Berman 1995) while in the following winter an unusual bloom of another cyanobacterium *Microcystis aeruginosa* was recorded (Zohary & Pollingher, unpublished data). Similar patterns were recorded in 1995. In 1996 and 1997 for the first time in 35 years (Pollingher, unpublished data) *P. gatunense* did not bloom. Instead a succession of short blooms of nanoplanktonic species was observed.

Methods

I. Sources of data for oxygen mass balance for Lake Kinneret

Lake Kinneret Database data (LKDB): The LKDB includes long-term (usually 1969–present) weekly or biweekly data for various biological, chemical and physical parameters (Table 1). Most samples and measurements were taken weekly from a pelagic site (station A, water depth 42 m). Water samples were collected at 09:00 ± 1 h with a Rhode sampler from 1, 3, 5, 10, 20, 30 and 40m. During the stratified period additional samples were taken at the thermocline depth (maximum dt/dZ), 1m below it and 1m above it. Samples for dissolved oxygen were collected in 300 ml BOD bottles, fixed immediately upon collection, and analyzed (Winkler procedure) within 2 to 4 h. Other chemical and biological analyses were carried out as detailed in Table 1.

Inventories of solutes in the lake were calculated in two steps: first by linear interpolation between the concentrations at the measured depths to obtain representative concentrations for each 1 m thick layer; second, the volume of each layer was computed from the hypsographic curve of Lake Kinneret and multiplied by the representative concentration.

Table 1. Lake Kinneret Database parameters* used in this study, the method of their determination, and the time periods for which data were available.

Parameter	Units	Method used and reference	Period measured in L. Kinneret
Water temperature	$^{\circ}$C	Inverse thermometer & STD depth profiles	1970–1985; 1986–1996
Wind	m S^{-1}	1970–to date	
Primary production	mgC m^{-2} d^{-1}	^{14}C uptake (1)	1972–1983; 1987–1996
Chlorophyll *a* concentration	mg m^{-2}	fluorometric (x)	1970–1996
Phytoplankton biomass & species composition	g wet wt. m^{-2}	Utermhol (1)	1970–1996
Zooplankton biomass	g wet wt. m^{-2}	microscopic counts (2)	1970–1996
Dissolved Oxygen (DO)	μM / mg L^{-1}	Winkler titration (3)	1970–1996
TOC	mg L^{-l}	Raveh & Avnimelech (4)	1976 & 1978–1996
SRP	μg L^{-1}	Molybdate reactive P (3)	1974–1996
TP	μg L^{-1}	Ascorbic acid (3)	1970–1996
PON & DON	mg L^{-1}	Vanado-molibdo-phosphoric acid (5)	1970–1996
NH_4+	μg L^{-1}	Indophenol (3)	1970–1996
NO_3	μg L^{-1}	Cd reduction (3)	1970–1996
Dissolved H_2S	mg L^{-1}	Iodimetric (3)	1970–1996
pH		(3)	1970–1996

[*] LKDB chemical data are under the responsibility of the senior author since 1987. [1]Berman & Pollingher 1974; [2]Gophen 1990a; [3]APHA 1982; [4]Raveh & Avnimelech 1972; [5]Nydall 1974.

Long term records (1969 to 1991) of wind speeds over Lake Kinneret are presented by Hambright et al. (1994). Wind speed and direction were monitored continuously next to the Kinneret Limnological Laboratory, situated at the north-western coast of the lake, with a Lambrecht mechanical anemometer between 1969 to mid 1986, and with a UVW Young type anemometer since mid 1986. In 1986 the site of these measurements was changed to a near coast location. In 1996 the measurements of this station were compared to those of a new station positioned about one kilometer off-shore and it was found that the

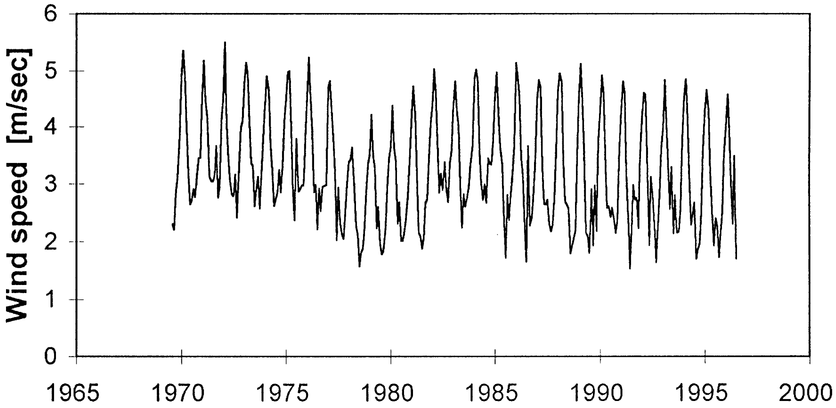

Figure 3. Long term of U_{10}, the monthly mean wind speed 10 m above the water in L.K. Data from 1986 onwards were corrected as described in the text.

near coast station is partially sheltered. According to seasonal ratios between the wind raw in both stations during 1996 the data from 1986–to date of the near-shore station was corrected by multiplying it by a factor of 1.4 for the period between May to September and by a factor of 1.18 between October and April. The wind data were also corrected for an altitude by extrapolating the data to an altitude of 10 m above the monthly mean lake level according to the procedure described below. The corrected long term record of monthly mean wind speed at 10 m height above the water, U_{10}, is shown in Figure 3.

Additional data: Loading data for total organic carbon (TOC) and total organic nitrogen (TON) entering the lake via the Jordan River (in tonnes month^{-1}) were obtained from the Mekorot water company; analytical procedures were as specified in Table 1. Jordan River inflow volumes (in 10^6 m^3 month^{-1}) and Lake Kinneret outflow volumes (by pumping and overflow) were provided by the Israel Hydrological Service.

Reconstruction of missing data: Missing data for primary production, TOC and TON were reconstructed. For primary production (^{14}C uptake method), missing data for the years 1970–1971 and 1984–1986 were “filled in” from existing chlorophyll data using significant regressions based on the long term record. Berman et al. (1995) have shown that chlorophyll levels and ^{14}C uptake rates in Lake Kinneret were well correlated both on the multi-annual and seasonal scales. Missing TOC data (1970 to 1975 and in 1977) were completed by assuming that TOC concentrations during those years were identical to the average of TOC concentrations measured in 1976, 1978 and 1979. Missing TON data (1970–1973) were completed by assuming that

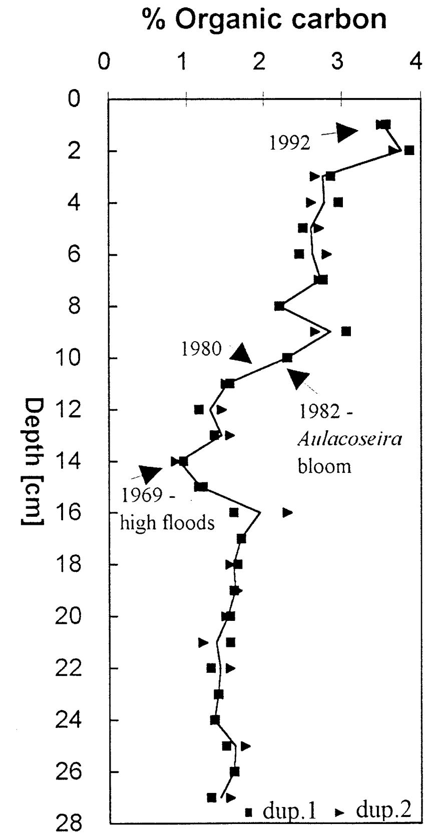

Figure 4. Percent organic carbon in the sediments along a core taken from station A, the age of sediment layers deposition assessed from ^{137}Cs activity profile and from a preserved layer of *Aulacoseira granulata* (see text).

concentrations were identical to the average concentration measured between 1974 and 1977.

New Data: Sediment core organic carbon content and dating

The long term sedimentary profile of organic carbon (oxygen equivalents) in pelagic bed sediments was determined by analyzing the organic carbon content along a sediment core, sampled by means of a piston corer at station A in fall 1992 (Figure 4). Analysis of organic carbon was made on duplicate samples by using an ANCA analyzer (European Scientific). Bulk sediment samples were dissolved in dilute HNO_3 to remove Ca-carbonate bearing minerals. An age of deposition profile for the sediments in this core was constructed by determining the age of deposition of three different horizons along a parallel core. A peak in ^{137}Cs activity at a depth of 14 cm was attributed to the increased deposition of allochthonous sediments during the extremely rainy winter of 1968/69 which was characterized by high floods in the river Jordan (Nishri & Koren 1993); A 2 mm thick layer of preserved cells of *Aulacoseira granulata* at 10 cm depth was assumed to be due to a large bloom which occurred in winter 1982 (the first since the early 1960's, Pollingher et al. 1986) and the uppermost layer (17 mm thick) represents sedimentation in 1992.

Zooplankton species composition data
Long term data for zooplankton biomass and trophic structure was taken from Gophen (1976, 1978, 1981a, b) and more recent data from the LKDB. Herbivorous zooplankters included cladocerans, rotifers, copepods nauplii and I–IV copepodite stages; Carnivorous zooplankters include: copepodite stage V and adult copepods.

II. Calculation of oxygen budgets

An oxygen budget for the whole lake was calculated between 1970 to 1990, from monthly mean and annual data using the following mass balance equation (in moles O_2 year^{-1} lake^{-1}).

$$\Delta Q/dt = (OP) + (K_{in}) - (K_{out}) - (Org) - (Zoo) - (K_c) - (Sed) - (BC) \quad (I)$$

where:

$\Delta Q/dt$ = the monthly change in the standing stock of DO in the lake;

OP = amount of photosynthetically evolved O_2;

K_{in} = input flux of DO from external sources (essentially via the Jordan river);

K_{out} = output flux of DO due to pumping and overflow;

Org = the difference between monthly inflow and outflow of organic matter;

Sed = flux of organic carbon buried in bed sediments;

K_c = net oxygen exchange with the atmosphere (positive sign represents removal from the lake);

Zoo = zooplankton oxygen consumption by respiration;

BC = unknown respiratory flux which includes bacterial, algal, fish and protozoan oxygen respiration.

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[*] parameters measured in carbon units were converted to moles O_2 assuming a $C:O_2$ molar ration of 1:1.

For several fluxes for which detailed data were available (**OP, ΔQ/dt, $\mathbf{K_{in}}$, $\mathbf{K_{out}}$, Org, Zoo** and $\mathbf{K_c}$) annual fluxes were obtained by summarizing monthly fluxes. **Sed** was attributed annual values and the unknown flux, **BC**, was calculated after solving the mass balance equation for each year.

OP was computed from primary production measured routinely by the *in situ* ^{14}C uptake method. $\mathbf{K_{in}}$ was approximated by assuming that the Jordan River water was at saturation with DO, and at a temperature of 15°C. $\mathbf{K_{out}}$ was calculated by multiplying the average monthly DO concentration in the epilimnion by the amount of water pumped through the NWC or which overflowed from the lake.

Org was obtained by subtracting the amount of organic carbon exported from the lake by pumping and outflow, Org_{out}, from the allochthonous input of organic carbon, Org_{in}. Org_{out} was calculated by multiplying epilimnetic TOC concentrations by the appropriate outflow volume of water. The underlying assumption was that allochthonous TOC undergoes decomposition in the lake, an O_2 consuming process.

Sed – Sediment organic carbon (CORG) content in the deeper zone of Lake Kinneret (depth $>$20 m; area approx. 100 km^2) ranged from 1% to 3.85% dry wt. at 14 cm and 0–3 cm depth, respectively (Figure 4). The 1970's and the 1980's are assumed to be characterized by 1.6% and 2.4% CORG, and accordingly we estimate an overall lake annual burial of 2000 and 3000 ton CORG, respectively (to be discussed below).

$\mathbf{K_c}$ – Oxygen exchange with the atmosphere depends on both wind velocity and on the degree of DO saturation at the lake surface. This parameter was evaluated according to the stagnant boundary layer model (Bolin 1960) and calculated according to Fick's law to explain diffusional transport across the liquid film, using the following equation:

$$K_c = (D_{O2}/h) \times (DO_{sat} - DO_{meas}) \tag{II}$$

Where:

D_{O2} = molecular diffusion coefficient of oxygen at the appropriate temperature, expressed in cm^{2}s^{-1} (values taken from Broecker & Peng (1974), considering the surface water temperature).

h = the thickness of the stagnant boundary layer, in cm;

$DO_{sat} - DO_{meas}$ = the difference between the monthly mean value of DO at saturation (computed from the monthly mean surface temperature) and measured DO at 1 m depth.

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h – was calculated from wind speeds as follows. Monthly mean wind speed was extrapolated to an altitude of 10 m above lake level (which varies both seasonally and annually) by the empirical relationship given by Kohler & Parmele (1967): $U_1/U_2 = (Z_2/Z_1)^n$ where U_1 and U_2 represent wind velocities at elevations (above sea level) Z_1 and Z_2, respectively. The coefficient n varies with wind field; $n = 0.15$ is a typical over water value and has been used here. The extrapolated wind velocity at 10 m height, U_{10}, (Figure 3) was then introduced into Smith's (1985) exponential regression equation relating the thickness of the stagnant boundary layer, h, to U_{10}. For Lake Kinneret, h was found to vary between 280 μm in stormy months to 530 μm during months of predominantly calm weather.

Zoo – In order to simulate seasonal changes in the temperature-dependent respiratory oxygen consumption, respiration rates and biomass parameters were subdivided into three temperature regimes: 15 °C from January to March; 22 °C for April through June and October through December; and 27 °C from July to September. Zooplankton biomass data was partially taken from previous publications (Gophen et al. 1990b; Gophen & Serruya 1990) and more recent data was taken from the LKDB). The data was subdivided into two categories according to species and development stage: carnivores and herbivores. For each group, respiration was calculated from the monthly average biomass and the relevant metabolic respiratory parameters Gophen (1976, 1981a, 1981b).

BC – the unknown combined respiratory flux, which includes whole lake (both epilimnetic and hypolimnetic annual processes), was obtained after solving the mass balance equation (I) with all other annual terms included.

Results

Observed long-term changes in the DO regime and related parameters

The long-term record shows that DO levels in the upper water layer (UWL) of Lake Kinneret gradually increased between 1970 to 1987; remained high throughout 1987–1993 and dropped again to typical 1970's levels between 1994 to 1996 (Figure 5a). The change in surface water DO saturation levels, computed from ambient temperatures, showed a similar patterns to that of DO concentrations (Figure 5b). For instance the 0–1 m depth annual average DO saturation value increased from ca. 100% during the early 1970's to ca. 120% saturation by the end of the 1980's and back to ca. 100% saturation in 1996.

Comparison between the 1970's (1970–1978) and the 1980's (1979–1990) shows that the variance in DO data for those 2 periods was different. In order

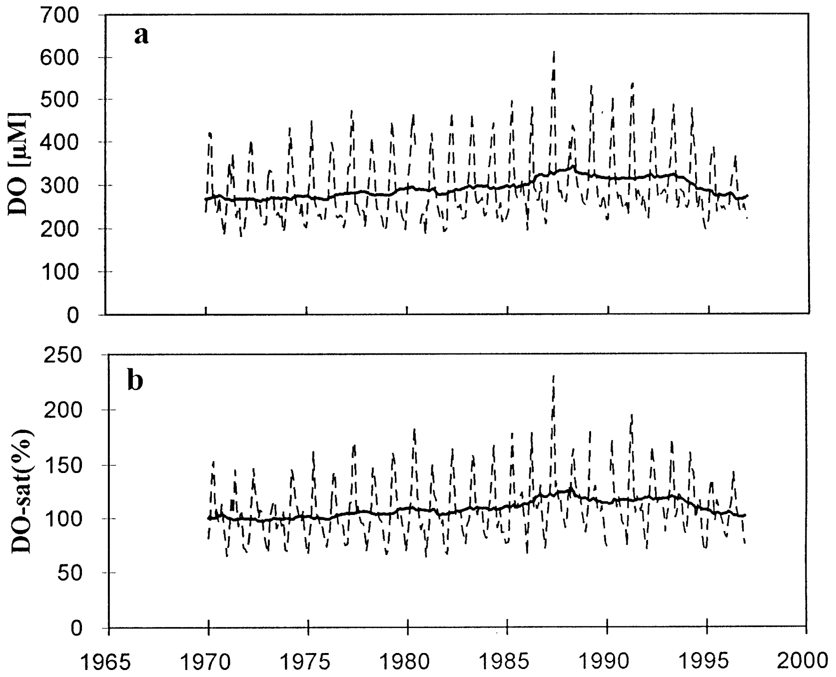

Figure 5. A. Measured long term (1970–1996) variations in monthly average dissolved oxygen concentrations (thin line) and running mean for 12 consecutive months (thick line) at 1m depth layer, B. Same for DO degree of saturation.

to homogenize the data, to obtain similar variance in each decade, a log transformation was used before performing a t-test. The difference in UWL DO levels between the two periods was significant ($p < 0.0001$). In general, DO concentrations in the UWL were higher during the 1980's than in the 1970's (Figure 6) but this difference was significant only part of the year. For example, the monthly average O_2 concentration (at 1 m depth) in April increased from an average of 350 to 460 μM and typical summer levels increased from 235 to 265 μM for the 1970's and 1980's, respectively. A t-test performed separately for each month in both periods showed that in winter (complete mixing of the water column) and in May (breakdown of the bloom) the difference between the two decades was not significant.

The total amount of DO in Lake Kinneret increased by about 20%, from an annual average of 690 to 790 $\times 10^6$ moles of O_2 during the 1970's and in the early 1980's, respectively. The error involved in the Winkler titration was estimated as 0.9% but the error of estimating the inventory is expected to be larger due to the linear interpolation performed between layers of measured DO concentration. The reproducibility of the overall

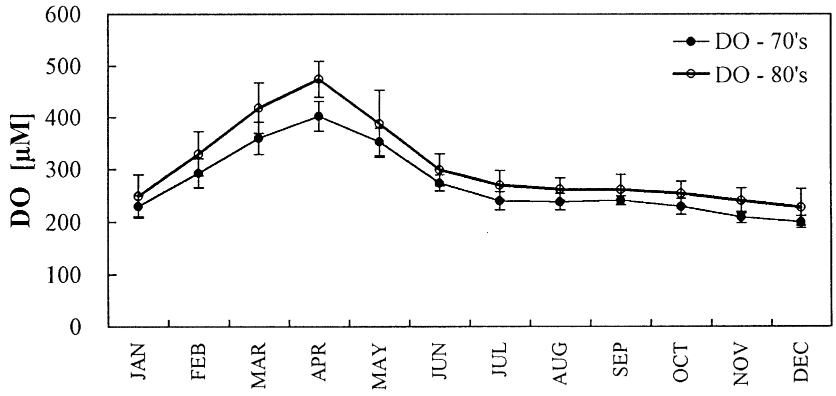

Figure 6. Measured seasonal patterns of DO at 5 m depth shown as multi-annual means for each month during the 1970's Vs. the 1980's. Error bars indicate 1 standard deviation.

procedure for estimating lake DO inventories was examined (in April 1997) by sampling three consecutive DO profiles within 40 minutes, according to the procedures described above. The overall lake inventories of DO calculated from these profiles were 34 861, 33 996 and 35 200 tones. Hence the deviations of the inventories calculated from the average were −0.6%, −2% and 1.5%, respectively. Thus the long-term increase in the inventory of DO is larger than the error of estimating the inventory.

Concomitant with long-term DO changes, between 1970 to 1990 the average pH of the surface water increased significantly ($R_2 = 0.18$, $p = 0.0033$) from ca. 8.55 to ca. 8.75 in the early 1990's. Since winter 1994, the pH dropped back to levels which were typical for the 1970's (Figure 7).

The long term profile of the hypolimnetic inventory of H_2S in fall (Figure 8) reveals a significant ($R^2 = 0.47$, $p = 0.0015$) increase between 1970 to 1990, followed by a decrease after 1994. This increase was from about 4000 tones in the early 1970's to about 7000 tones by the end of the 1990's. The long term fluctuations of the hypolimnetic inventory of NH_4^+ is shown in Figure 9.

The monitoring of TOC in Lake Kinneret began in 1978 (dissolved organic carbon was not measured). Yearly average TOC concentrations dropped between 1978 and 1989 from 3.9 to 3.1 mg L^{-1} (Figure 10). During the late 1970's concentrations of dissolved organic nitrogen (DON) in the lake also dropped, from 0.7 to 0.25 mg L^{-1} (Figure 10).

The seasonal patterns of wind (in the north-western part of the lake) and lake water temperature (Figure 11) reveal that the strongest winds prevail between June and August whereas highest epilimnetic temperatures are found in August and September.

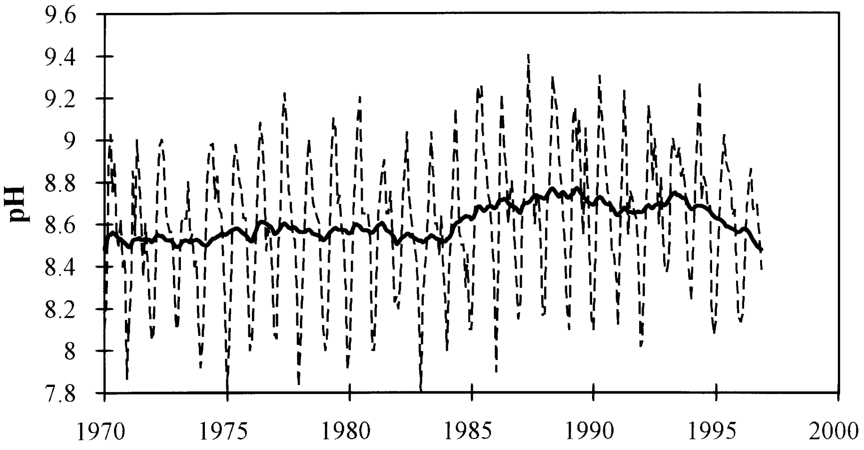

Figure 7. Measured surface water (1 m depth) pH values between 1970 to 1996, monthly averages (thin) and running averages for 12 consecutive months (thick line).

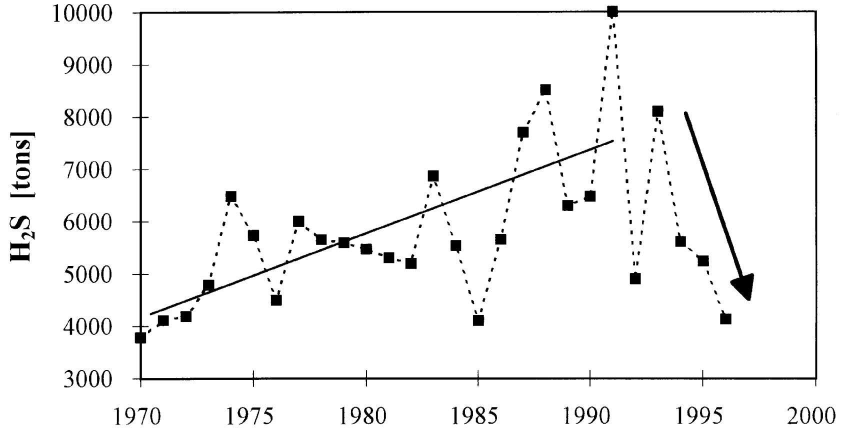

Figure 8. Hypolimnetic inventory of H_2S in fall (Sep.–Nov.). Line representing linear fit between 1970 and 1991 ($R^2 = 0.47$).

Mass balance components and their long-term variations

The long-term variations in the annual fluxes of **OP, BC, Zoo, K_c, Org, Sed** and **K_{in}–K_{out}** are presented in Figures 12 and 13. Annual fluxes of oxygen production, **OP**, varied between 6 to 13 × 10^9 moles of O_2 year^{-1} lake^{-1} and respiratory **BC** fluxes varied between 2 to 8 × 10^9 moles O_2 year^{-1} lake^{-1}. Total lake zooplankton community respiration, **Zoo**, decreased from 4 during the 1970's to 2 × 10^9 moles O_2 year^{-1} lake^{-1} by the end of the 1980's–early 1990's and then raised again to 2.4 in the mid 1990's. Net annual removal

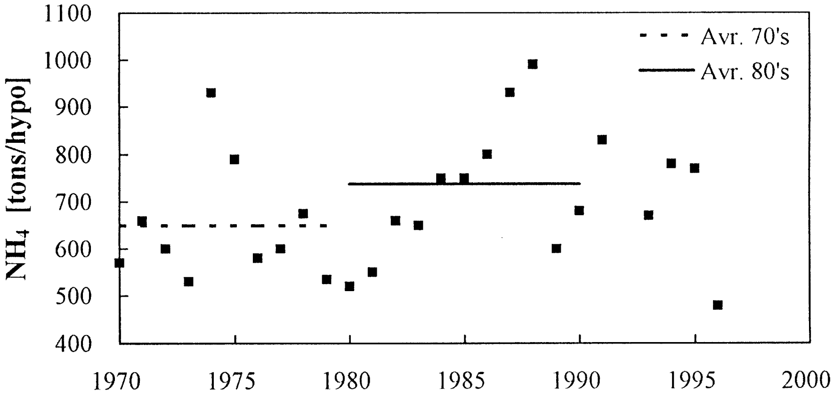

Figure 9. Measured average September–October hypolimnetic inventory of NH_4^+ (mg L^{-1}) during 1970–1996.

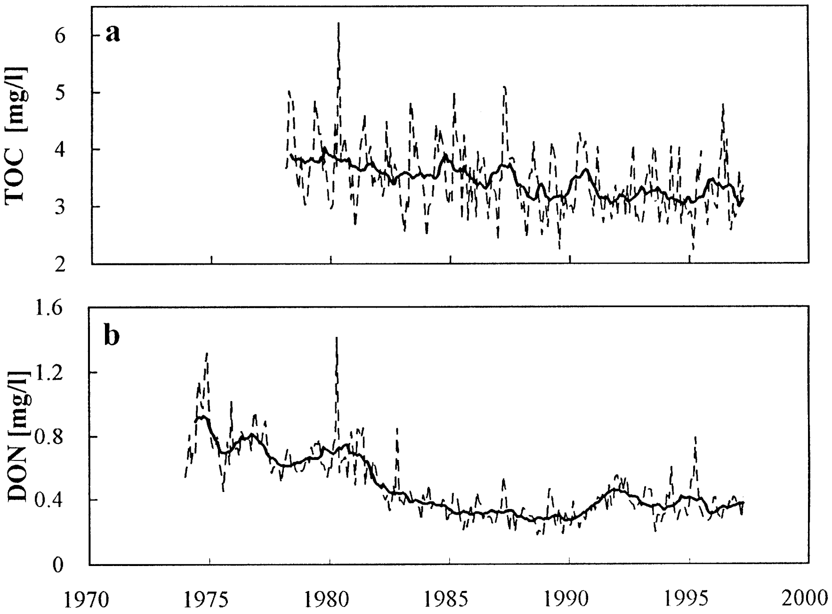

Figure 10. Measured mean water column annual concentrations (mg L^{-1}) of TOC and DON in Lake Kinneret.

of DO, over the lake surface, by gas exchange (**K$_c$**), increased from 380 × 10^6 to about 1250 × 10^6 moles O_2 year^{-1} lake^{-1} (Figure 12), as a result of higher saturation levels in the surface water layers during the 1990's. **Org**, the net influx of organic matter, decreased from 100 × 10^6 moles O_2 year^{-1} in the 1970's to 30 × 10^6 moles O_2 year^{-1} in the 1980's (Figure 13). Except

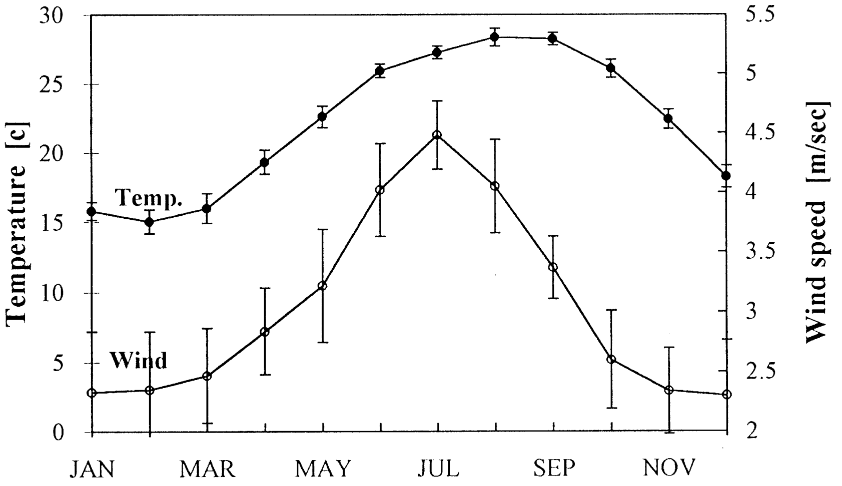

Figure 11. Multi-annual monthly mean temperature at station A, 3 m depth, and of wind speed at the eastern coastal station, based on data for 1979–1987. Error bars indicate 1 standard deviation.

for 1992 this was also the level of **Org** during the 1990’s. **Sed** flux increased, from 165 × 10^6 moles O_2 during the 1970’s $year^{-1}$ to 235 × 10^6 moles O_2 $year^{-1}$ during the 1980’s. K_{in} was relatively stable throughout the two decades whereas $\mathbf{K}_{out}$ increased, by about 0.3% of **OP**, in accordance with the rise in epilimnetic DO levels between 1970 to 1990. Consequently K_{in}–K_{out} gradually declined.

Discussion

A significant long-term increase (20%) in Lake Kinneret epilimnetic DO levels between 1970 to 1991 and a decrease after 1994 are reported here. The increase is significant only during the stratified period, suggesting that the processes leading to this change are affected by stratification.

The most prominent long-term biological changes observed between 1970 to 1991 in Lake Kinneret were a continuous decline in annual zooplankton biomass (Gophen et al. 1990a), and a 2-fold increase in summer-fall phytoplankton biomass (dominated by nanoplankton) around 1981, but not in the late winter-spring phytoplankton (*Peridinium*-dominated) biomass (Berman et al. 1992). Both observations were based on routine microscopic counts. The increase in summer-fall algal biomass during the 1980’s was not accompanied by a parallel increase in primary productivity or chlorophyll levels (Berman et al. 1995). During these two decades, the ratios between algal biomass to chlorophyll levels and primary productivity have more than doubled.

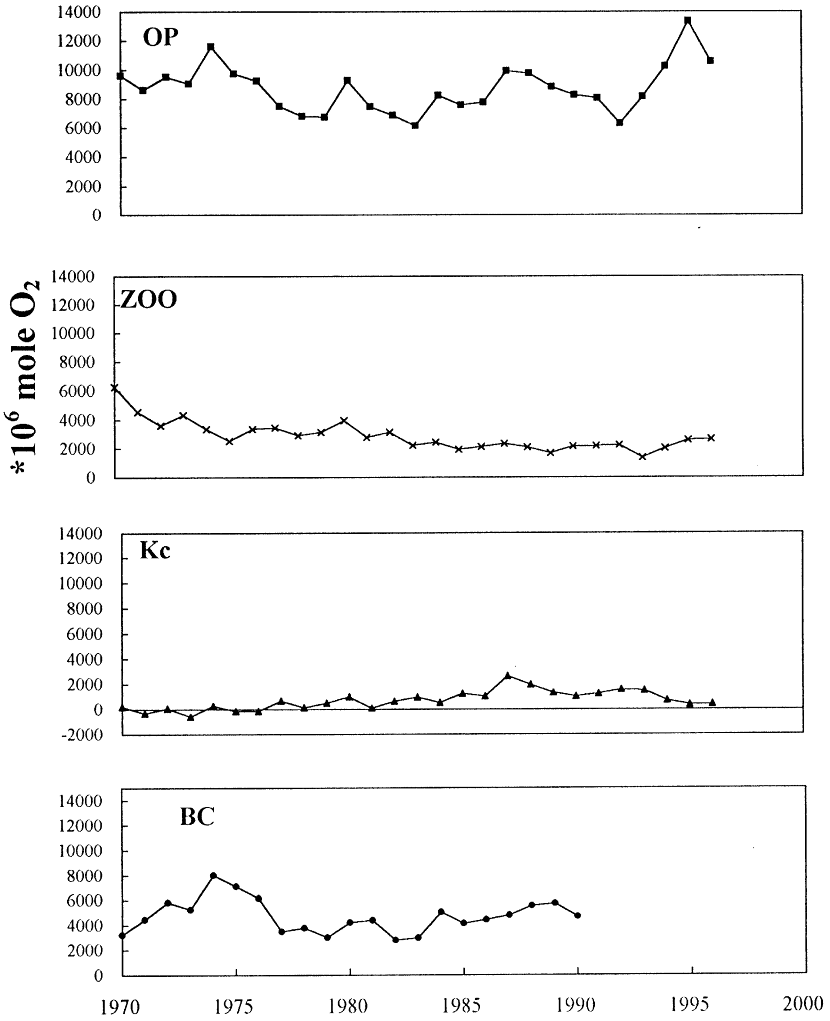

Figure 12. Measured or calculated long-term (1970–1990) annual fluxes of oxygen: **OP** production due to photosynthesis, **Zoo** – zooplankton respiration, **K$_c$**-gas exchange flux (positive values = removal from the lake) and **BC** the unknown respiratory fluxes (see text) computed from the mass balance equations.

This change could not be attributed to differences in population composition, since no significant variations in algal species composition took place during these two decades (Berman et al. 1992). We do not attempt to explain these observations here but only to point out that the rise in DO levels can not be attributed to increased productivity.

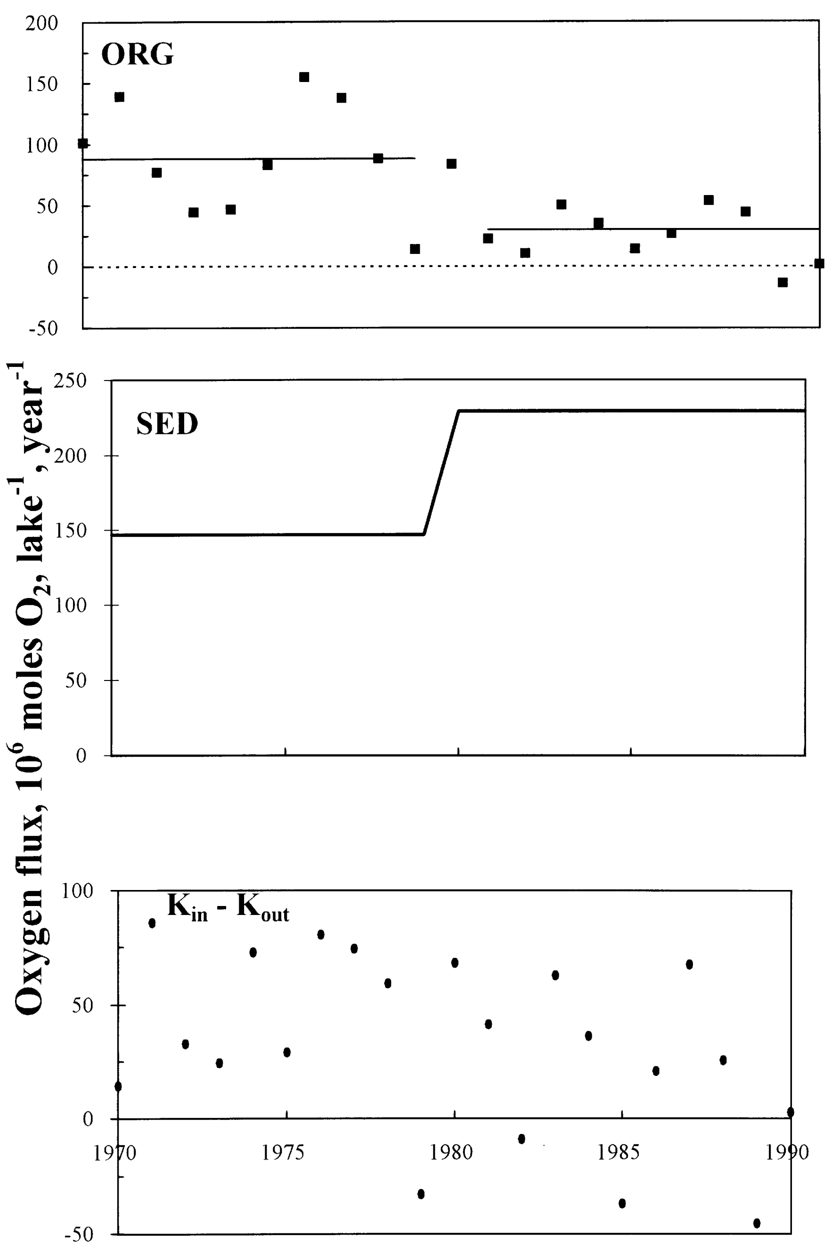

Figure 13. Long term (1970–1990) oxygen fluxes **Org**, **Sed** and **K_{in}-K_{out}**.

As expected in a lake ecosystem in which the pH is buffered by the carbonate system (Serruya 1978) and in which both total CO_2 and DO are controlled by the same processes (photosynthesis, respiration and gas-exchange), DO levels and the pH in Lake Kinneret epilimnion during the summer-fall, between 1970 to 1990, were correlated ($R^2 = 0.54$, $p < 0.0001$, $n = 210$). The long term increase in pH of the surface water was less pronounced than that of DO (Figures 5 and 7) possibly because the effect of gas exchange is different for the two gases or that pH is expressed in a logarithmic scale. In comparison to DO there is a relatively larger reservoir (2–3 mm) of total CO_2 in Lake Kinneret water (Berman-Frank et al. 1994) and smaller pCO_2 gradient between the lake and the atmosphere in comparison to that of pO_2.

A significant correlation was also observed between long-term (1970 to 1990) epilimnetic summer–fall DO levels and algal biomass ($R^2 = 0.40$, $p < 0.0001$). Again, this is expected if both parameters are affected by similar processes (photosynthesis, respiration).

It is expected (Stumm & Morgan 1976) that photosynthetic activity increases both DO and pH levels whereas oxidative processes will affect the aquatic environment in the reversed direction. In Lake Kinneret the multi-annual profile of OP is not similar to those of DO and pH. Hence, the long-term increase in DO and pH, between 1970 to early 1990's, suggests that the difference between oxygen production to consumption has increased, due to a decrease in epilimnetic respiration. In our mass balance these include **Zoo** and the epilimnetic part of the **BC** respiration.

The drop in **Org** flux (Figure 13), represents a long term decrease in allochthonous input of organic matter to the lake. The reduced organic input load is expected to result in a smaller demand for respiration processes, leading to elevated DO levels during the 1980's and 1990's [1992 is an exception because of the extremely large inflow of the river]. Sallingar (1991) reported a gradual decrease of TOC levels in the Jordan River, from 6 mg L^{-1} in 1976 to 3 mg L^{-1} in 1985. This implies that the total input of organic carbon from external sources declined from about 2800 in the 1970's to about 1400 tonnes during the 1980's and to less than 600 tonnes $year^{-1}$ during the 1990's. An additional indication for this trend was the gradual drop in the DON load through the Jordan river, from about 530 tonnes $year^{-1}$ during the 1970's to about 230 tonnes $year^{-1}$ during the 1980's and 1990's (Figure 14). These declines were due to a) a long-term decrease in the loads of peat eroded from the Hula valley situated in the drainage basin, due to anthropogenic activities (Y. Geifman pers. com.), b) a long-term, and as yet unexplained, gradual reduction in the concentration of dissolved organic compounds in some of the Jordan River tributaries starting in the mid-1970's and c) the effect of a the "Einan" settling reservoir, built upstream of Lake Kinneret in winter 1982

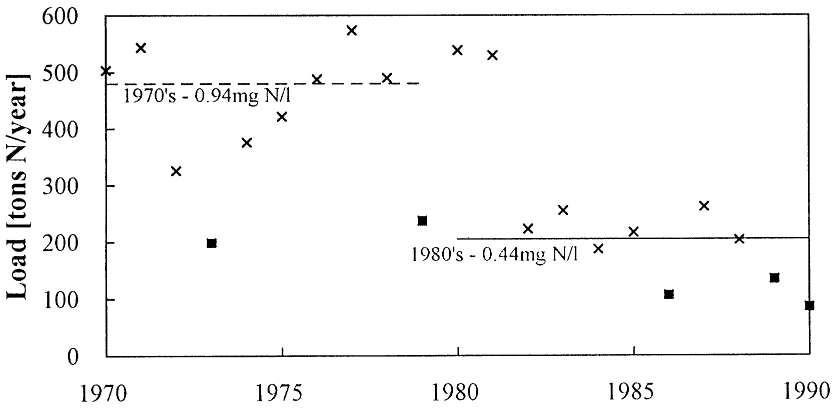

Figure 14. Measured yearly load of dissolved organic nitrogen (DON) in the Jordan River, 1970–1996. Filled squares represent years with low inflow of water.

in order to reduce inputs of fresh organic matter (from sewage and fish ponds) into the lake.

Between 1970 to 1990 the drop in the allochthonous input load amounted to 70×10^6 moles O_2 (Figure 13), or approximately 0.8% of the autochthonous production. However it is most probable that only a portion of the **Org** flux estimated here is actually available for oxidative processes within the lake, because this flux probably includes refractory organic compounds originating from the erosion of peat soils into the river channel. We, therefore, refer to this value as the maximum possible long-term decrease in **Org**.

To estimate the long term profile of the **Sed** term, the age of deposition for each sedimentary layer is required. Moreover we should know whether the organic matter content of this layer has been stabilized or whether it may still undergo early diagenetic decomposition.

The age of deposition for Lake Kinneret bed sediments was partly deduced from sedimentary ^{137}Cs profiles and our interpretation of these profiles is somewhat unusual. It is expected that peaks in ^{137}Cs sedimentary profiles represent major fallout events on the lake surface but in the case of Lake Kinneret these peaks represent major erosional events in the drainage basin that may have occurred several years after fallout, due to the high ratio between the area of the drainage basin to that of the lake (approx. 16.5) as well as due to the extreme rates of erosion observed in the basin during very rainy winters (Nishri & Koren 1993; Koren, MSc thesis 1993). The layers representing sedimentation in other years were determined by interpolation between layers for which the age of deposition was known (1968/69, 1982 and 1992). For these interpolations we assumed an average bulk sediment net sedimentation rate of 110 mg cm^{-2} year^{-1} (Nishri & Koren 1993), a specific density of 2.5 gr cm^{-3} for the dry sediment, and by taking into account measured porosity profiles published in Koren (1993).

The minimum levels of CORG at 14 cm depth are attributed to increased sedimentation of allochthonous material eroded from the drainage basin in the floods of winter 1969. An increase in the organic carbon content at the upper part of the sedimentary column is often claimed to result from incomplete early diagenetic processes. However in the sedimentary CORG profile presented here (Figure 4) the relatively stable content between 3 and 9 cm depth (a layer which represents about 8 years of sedimentation during the 1980's), which is terminated below by a sharp drop in CORG, may represent a layer in which early diagenetic processes are already completed (meaning that this layer represents CORG buried in the sedimentary column). Such an assumption, however, may have overestimated the sediment burial flux during the 1980's. Therefore, the long-term change in **Sed** flux (1% of **OP**), between 1970 to 1990, should be considered as a maximum possible change.

The error in estimating $\mathbf{K_{out}}$ is relatively small (few percent) and is similar to the error of estimating DO inventories. The long term increase in $\mathbf{K_{out}}$ is equal to 0.3% of **OP**. Thus the expected change in the inventory of DO in the lake due to long term changes in external sources and sinks between 1970 to 1990 [$\mathbf{Org{+}SED{-}K_{out}}$] should be lower than 1.5% of **OP**.

Between the 1970's to the 1980's the increase in $\mathbf{K_c}$ estimated above amounts to approx. 10% of **OP**. This increase should have been compensated for by a parallel rise in organic carbon removal to external sinks, or decline in input from external sources. However, as noted above the sum of these fluxes should be $\leq$ 1.5% of **OP**, suggesting that the 1970–1990 long term change in $\mathbf{K_c}$ calculated above is overestimated and that as a result the unknown flux of **BC** calculated through the DO budget is under estimated by 8 to 10%. The error obtained in estimating K_c could be due to: (1) wind regime data was obtained at only one station, which is not necessarily representative for the entire lake, (2) wind data used were monthly mean velocities and therefore some wind events may not have given their appropriate weight for gas exchange processes and (3) The correlation between wind regime and piston velocities was obtained by using a regression equation taken from the literature and the predictive ability of this equation is not high due to the log transformation involved.

During stratification, hypolimnion respiration first proceeds through the reduction of DO. When all oxygen is consumed, respiration continues through nitrate reduction and subsequently by sulphate reduction (Capone & Kiene 1988). These hypolimnetic respiratory processes lead to the accumulation of H_2S as well as solutes released from the mineralization of organic matter (such as NH_4^+). Removal of sulphide from the hypolimnion, by sedimentation and burial of FeS_x, is relatively small as compared to the standing stock of dissolved H_2S (Nishri, unpublished results). Destratification processes, which are indicated by the deepening of the thermocline, bring about the mixing between H_2S-containing hypolimnetic water and oxygenated surface water, leading to fast sulphide oxidation. Consequently, the fate of most of this sulphide is reoxidation to sulphate upon interaction with oxic water. For the DO budget, hypolimnetic sulphate reduction should be viewed only as a delay in the timing of oxygen consumption.

However, seasonal epilimnetic DO levels may be affected by changes in hypolimnetic respiration. Each mole of authochthonus organic carbon which sediments to the hypolimnion (and which is decomposed within this layer) leaves behind one mole of photosynthetically evolved O_2 (in the epilimnion), until the DO is utilized for oxidation of H_2S. The long-term increase in the hypolimnetic load of H_2S in fall, between 1970 to 1990, corresponds to an increase from 125 to 250×10^6 moles equivalent of O_2, respectively. We note that this increase is similar in magnitude to the annual average long-term rise in the inventory of DO in the lake.

The standing stock of H_2S in the hypolimnion in fall represents only part of the overall amount of H_2S which has been formed in this layer. Part of the H_2S (as well as NH_4^+) is transported by mixing processes across the thermocline as well as by upwelling of hypolimnetic water in the littoral zones of Lake Kinneret as a result of internal seiche activity (Ostrovsky et al. 1995). The boundaries of the hypolimnetic layer being mixed within the upper water layer are actually defined by the depth of the thermocline before and after mixing.

The sum of hypolimnetic respiratory (HR) processes in Lake Kinneret were calculated by adding the DO load in this layer, prior to the onset of stratification (Table 3) to the total amount of H_2S formed in this layer during stratification. The total H_2S formed in the hypolimnion was calculated by integrating over time the upward advective flux of H_2S, each month, until October while the rate of deepening of the thermocline increases plus the inventory of H_2S accumulated in the hypolimnion in October. The amount of NO_3 was in most cases (except for May through July 1992) negligible, the $S:O_2$ molar ratio due to oxidation was assumed to be 2:1 (Stumm & Morgan 1976) and the oxidation of H_2S in the upper oxic layer was assumed to be instantaneous.

The advective littoral flux was estimated by multiplying the monthly average concentration of H_2S in the layer immediately below the thermocline by the volume of the layer entrained in the epilimnion each month, calculated according to the depth of the thermocline. An example for this type of calculation during the stratified period of 1986 is presented in Table 2. As

Table 2. Calculation of the upward fluxes of H_2S and NH_4^+ during the stratified season of 1986 (April–October). A – monthly average depth of the thermocline (rounded values); B – the volume of water layer mixed during the previous month (exact values in $10^6 m^3$); C – the representative concentration of H_2S in the layer below the thermocline; D – same as -C- for NH_4^+; E – tons/equivalent moles of DO; F – tones of NH_4^+.

Month	Therm depth (m) (A)	Volume of layer (B)	H_2S mgS/l (C)	NH_4^+ mgN/l (D)	H_2S tons E = (B×C)	NH_4^+ tons F = (B×D)
Mar.	13		0	0.03		
Apr.	14	133.1	0	0.03	0.0 (0)	4.0
May	16	253.1	0	0.11	0.0 (0)	27.8
Jun.	17	119.6	0.60	0.15	71.7 (4.5)	17.9
Jul.	19	211.5	1.20	0.25	253.8 (15.9)	52.9
Aug.	20	97.1	2.00	0.30	194.2 (12.1)	29.1
Sep.	20	0	0.40	0.35	0.0 (0)	0
Oct.	25	225.5	4.30	0.60	969.7 (60.6)	135.1
SUM-					1489.4 (93.1)	266.8

suggested by J. Imberger (pers. com.) turbulence across the thermocline of Lake Kinneret pelagic zone is extremly small and by far most of the mixing between the two layers occures in littoral zones. We therefore ignored Eddy diffusion across the thermocline in the pelagic zone.

Using the above procedure we were able to demonstrate that the annual hypolimnetic respiration (HR), in terms of oxygen equivalents, has increased, between 1970 to 1990, from ca. 800 to ca. 1100 × 10^6 moles (Table 3, Figure 15), suggesting that the sedimentation of organic matter to the hypolimnion has increased from the 1970's to the 1980's by about 40%. This conclusion is also supported by the finding that after the onset of thermal stratification in Lake Kinneret, the DO depletion rate was faster during the 1980's than during the 1970's (Parparov 1994). The suggestion of a long term rise in sedimentation of organic matter to the hypolimnion is consistent with our previous interpretation of the sedimentary CORG profile, that the burial of organic matter increased in the 1980's.

The percentage of HR out of the photosynthetically evolved oxygen (Table 3; Figure 15) increased from an average of 8.5% during the early 1970's to about 12.5% by the end of the 1980's and back to ca. 7% since 1994. This indicates that part of the mineralization processes shifted site (layer) from the epilimnion, in the 1970's, to the hypolimnion in the 1980's and back to the epilimnion since 1994.

The concomitant changes in zooplankton epilimnetic respiration (zooplankton activity is restricted to the upper layer), **Zoo**, was from 40% of **OP**

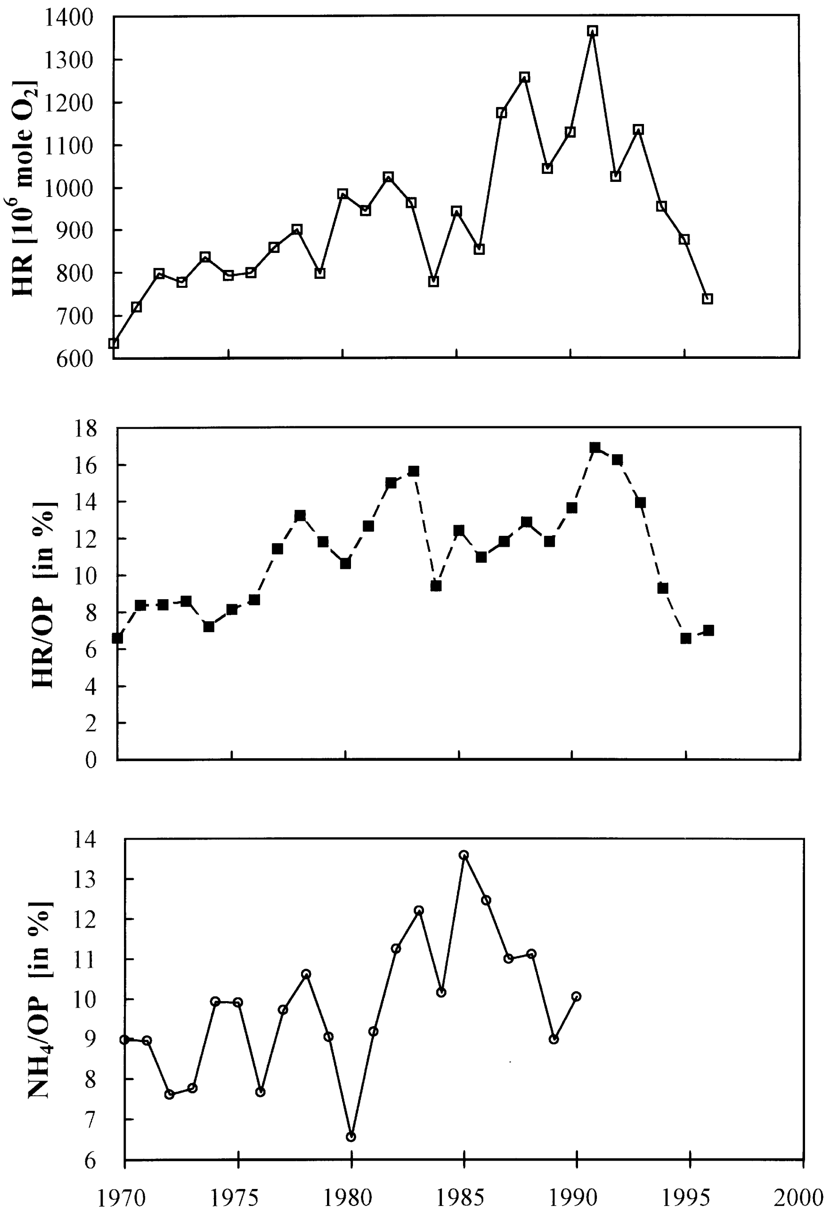

Figure 15. Hypolimnetic respiration (HR); ratios (in %) of **HR/OP** and hypolimnetic **NH_4^+** production to **OP** (**NH_4^+/OP**).

Table 3. Primary production and hypolimnetic respiration (HR) in Lake Kinneret during 1970–1990 (in 10^6 moles of O_2): (A) Inventory of H_2S in the hypolimnion in fall; (B) integrated flux of H_2S from the hypolimnion to the epilimnion during April-October; (C) The inventory of DO in the 16–42 m depth layer in March; (D) hypolimnetic respiration – HR = 2^*(A+B) + (C); (E) photosynthetically evolved DO and percentage of HR from OP, (F) = (D)*100/(E). *- primary production derived from chlorophyll.

Year	H_2S (A)	H_2S (B)	DO (C)	HR (D)	OP (E)	HR/OP (F) %
1970	118.0	21.8	355.1	634.7	9623*	6.6
1971	128.5	22.7	418.6	720.9	8609*	8.4
1972	130.8	28.8	479.2	798.4	9511	8.4
1973	149.4	36.6	405.5	777.6	9043	8.6
1974	202.4	16.5	398.2	836.1	11602	7.2
1975	179.0	19.7	395.9	793.4	9735	8.1
1976	140.4	40.1	438.5	799.4	9228	8.7
1977	187.6	32.0	418.4	857.6	7507	11.4
1978	176.2	45.8	456.7	900.8	6812	13.2
1979	174.6	36.8	374.5	797.3	6750	11.8
1980	170.7	69.6	503.7	984.4	9256	10.6
1981	165.6	53.6	505.5	943.8	7563	12.6
1982	162.0	109.4	480.0	1022.7	6823	15.0
1983	214.3	20.1	493.6	962.3	6164	15.6
1984	172.6	79.2	274.1	777.7	8258*	9.4
1985	128.2	71.4	543.6	942.8	7599*	12.4
1986	176.5	93.1	379.7	919.6	7787*	11.8
1987	240.6	44.8	601.7	1172.6	9930	11.8
1988	266.0	39.9	643.6	1255.3	9766	12.9
1989	196.7	69.3	509.4	1041.3	8828	11.8
1990	202.2	98.7	525.3	1127.1	8274	13.6
1991	312.4	81.5	576.0	1363.8	8068	16.9
1992	153.1	59.3	598.8	1023.4	6307	16.2
1993	252.8	67.9	492.4	1133.9	8158	13.9
1994	175.1	68.6	465.8	953.0	10249	9.3
1995	163.5	60.8	427.1	875.7	13360	6.6
1996	129	28.4	422.6	737.6	10537	7.0

in the 1970’s to 20% in the 1980’s and a little higher after 1993. Similar respiration estimates for the 1980’s were suggested by Stone et al. (1993). [The respective percentage for 1970 and 1971 are discarded here because OP for these two years is based on extrapolation and because this percentage is much higher then expected.] The increase in HR compensated for only a small portion of the decrease in **Zoo** and therefore other epilimnetic organisms must have replaced most of the long-term decrease in zooplanktonic respiratory activity.

Both the increase in sedimentation of organic matter and the shift in layer of the relative intensity of respiratory processes would affect not only DO levels in the epilimnion but also the hypolimnetic levels of solutes released from decomposing organic matter. One such solute which accumulates in the anoxic, H_2S enriched and low pH (7.3–7.8) L. Kinneret hypolimnion is NH_4^+. Average hypolimnetic (40m depth) NH_4^+ levels in fall (September–October) have somewhat ($p = 0.081$) increased from 0.86 mg/l during the 1970's to 0.92 mg/l during the 1980's (as presented indirectly in the form of inventories in Figure 9). The long term ratio of hypolimnetic NH_4^+ production (in oxygen equivalent terms, using Redfield ratio) to epilimnetic **OP** during stratification was examined. The calculation of the NH_4^+ production flux was similar to that used in determining hypolimnetic respiratory flux (see above) except that, instead of including the hypolimnetic inventory of DO prior to the onset of stratification, the amount of hypolimnetic NH_4^+ in March (at the onset of stratification) was subtracted from the sum of the inventory in fall and the integrated upward flux. The calculated ratio between NH_4^+ production and **OP** increased from an average of 0.087 between 1970 and 1978 to 0.105 between 1979 to 1990 (Figure 15), strengthening the suggestion of a shift to more hypolimnetic mineralization in the 1980's.

The question which then arises is what may have caused enhanced sedimentation of organic matter to lower layers during the 1980's. During stratification zooplankton activity in Lake Kinneret is restricted to the epilimnion. Herbivorous zooplankters were and still are major grazers of algae in the lake (Gophen et al. 1990c). However organic carbon ingestion levels by zooplankton, calculated for the 1970's (Serruya et al. 1980), were in the order of magnitude of primary production, suggesting that during this decade a major portion of primary productivity was ingested by zooplankton. Considering that over the two decades, zooplankton biomass has decreased to half of early 1970's levels it is suggested that the fate of algae and particulate organic carbon in the lake had changed significantly. We suggest that during the 1980's less algae were grazed by zooplankton and more by other organisms. This may have resulted in changes in the sedimentation pattern of organic detritus. In this respect there may be a difference between the role played by carnivorous to that of herbivorous zooplankton. It was documented by Wetzel (1983), Carpenter (1992) and Williamson (1991) that the activity of carnivorous zooplankton enhanced the removal of organic detritus by sedimentation of fecal pellets. In contrast, herbivorous zooplankters excrete fluffy pellets which are light and break down rapidly in the epilimnetic waters. Therefore, their role is to internally cycle nutrients within the trophogenic layer rather

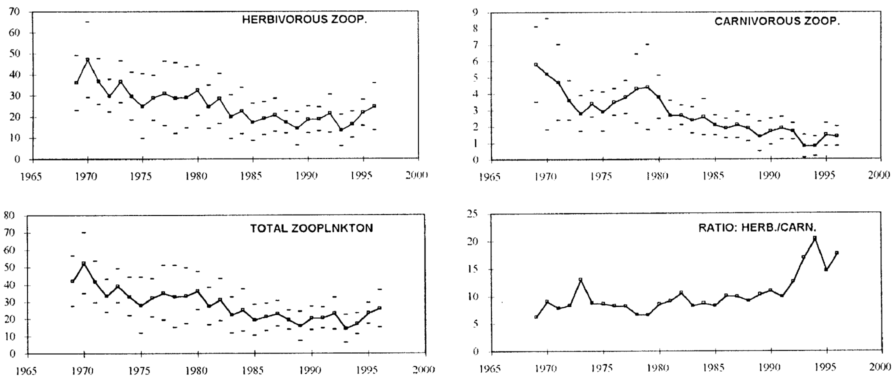

Figure 16. Long term (1970–1990) trends in the biomass of total, herbivorous and carnivorous zooplankton and the ratio between herbivores and carnivores (wet wt.) in Lake Kinneret.

than to sediment out organic particulates. Accordingly, the combined effect of the decrease in both the biomass of herbivorous and carnivorous zooplankton in Lake Kinneret between 1970 to 1990 should be taken into account. The long term record of herbivorous, carnivorous, total zooplankton biomass and the ratio between herbivorous to carnivorous (wet wt. biomass), during 1970–1996, are presented in Figure 16. It shows the decline of both herbivorous and carnivorous zooplankton biomass between 1970 to 1993 and a reversed trend for herbivorous after 1993. The changes in herbivorous zooplankton biomass during the three decades were from 40 (in the 1970's) to 20 (end of 1980's) and back to 26 g wet wt. m^{-2} (since 1994). The corresponding change for carnivorous zooplankton was from 5 (in the early 1970's) to about 1.5 g wet wt. m^{-2} (end of the 1980's). I.e., the decrease in herbivorous biomass between 1970 to 1990 was about 20 g as compared to a decrease of about 3.5 g wet wt. m^{-2} for carnivores.

Landau et al. (1988) reported that biomass of the zooplanktivorous *Mirogrex terraesanctae* (minnows), the dominant fish in the lake, have increased between 1974 and 1982. Gophen and Serruya (1990) claim that the decrease in zooplankton biomass is a result of increased predation pressure by fish. Gophen et al. (1990b) and Gophen and Serruya (1990) suggested that enhancement of fish stocking, as well as an increase of the populations of Minnows and Silver carp are the major reasons for the intensification of zooplankton predation. In support of the increased fish predation hypothesis we found that the ratio between herbivorous to carnivorous zooplankton biomass has increased significantly over the last 27 years (Figure 16-bottom), suggesting that during this period relatively less herbivorous zooplankton were grazed by carnivorous and therefore probably relatively more by fish. It is hypothesized here that the denser fecal pellets of the fish, as compared to those of herbivorous zooplankton, may have contributed to increased sedimentation of organic detritus between 1970 to the early 1990's.

The second mechanism proposed here to explain the shift in site of organic matter decomposition is related to possible changes in the chemical-physical sedimentation properties of particulates in Lake Kinneret water over the past two decades. During the crash of the *Peridinium* spring bloom, large amounts of organic aggregates are often observed (Pollingher, pers. comm.). We suggest that sedimentation of organic matter in the lake, at least during the bloom crash, is affected by aggregate abundance.

There is extensive evidence from fresh waters (e.g. O'Mellia 1987) that surface properties and colloidal stability of particles are affected by naturally occurring dissolved organic substances such as humic and fulvic acids which act to slow coagulation. The effect of particle coagulation in lakes is to increase settling velocities, thereby reducing their residence time in water. Willenmann (1986) classified several Swiss lakes into two groups, based on dissolved organic carbon (DOC) concentration. Lakes with DOC concentrations below 2 mg/l were found to have much lower particle stability (by an order of magnitude) than those with DOC concentration between 3 to 5 mg/l. Thus, changes of DOC concentration in lakes, within the range of 2 to 3 mg/l may strongly affect settling properties of particles.

In several water samples taken in summer 1991 we found that in Lake Kinneret epilimnion the ratio between DOC (filtered via 0.45 u) to TOC varied between 0.6 to 0.85, with an average of 0.75. We used this ratio to evaluate historical DOC data (between 1978 and 1990) by multiplying measured TOC concentrations by a factor of 0.75. The results indicate the possibility that annual average DOC levels in Lake Kinneret declined from about 3 in 1978 to 2.3 mg/l in 1990. Hence, the predicted drop in DOC, in Lake Kinneret is well within the range where particle stabilities may depend strongly on DOC concentration. We suggest, therefore, that the drop in dissolved organic compound concentrations in Lake Kinneret may have been a cause for the enhanced sedimentation of particulate organic matter.

Conclusions

Between 1970 to 1991 the total amount of DO in Lake Kinneret has increased by 1.1% of the annual amount produced by primary production. As compared to the 1970's the decrease in allochthonous organic carbon plus the excess amount of organic matter buried in the bed sediments during the 1980's amounted to less than 1.8% of the annual average **OP**.

Lake internal DO fluxes estimated between 1970 to 1990 suggest that enhanced sedimentation of organic matter to the hypolimnion resulted in an increase of 4.5% (of OP) in hypolimnetic respiratory processes, on the account of epilimnetic process. The effect of internal DO fluxes was more than 2.5 times larger than the effect of external fluxes. Note that enhanced sedimentation may lead to changes in both external (increased **Sed**) and internal (increased HR) fluxes. In oxygen equivalent terms the seasonal increase in hypolimnetic H_2S between 1970 to 1990 (about 125×10^6 moles) is similar to the annual average increase in DO in the epilimnion (about 100×10^6 moles). It is therefore suggested that the significant long-term increase in epilimnetic DO between 1970 to 1990 was mostly due to enhanced sedimentation of organic matter.

The 1970 to 1996 data set shows that during periods of reduced zooplankton activity, epilimnetic DO and pH levels and hypolimnetic H_2S levels were highest. We suggest that long-term fluctuations in zooplankton activity had a significant impact on the fate of algae and other organic particles in the lake. Reduction in zooplankton activity enhanced sedimentation of organic matter and hypolimnetic respiratory processes on the account of epilimnetic processes. The estimated long-term (1970–1990) decrease in DO respiration by zooplankton of ca. 15% (of OP) is larger by 10% (of OP) then the increase in hypolimnetic respiration during the 1980's. These differences suggest that zooplankton epilimnetic respiratory processes were partially compensated for by the respiratory activity of other organisms in the epilimnion. A possible cause for the long-term decrease in zooplankton activity is an increase in fish predation, suggesting the possibility of a top-down control on DO and pH levels in Lake Kinneret.

Since 1994 the algal community structure has been dramatically altered. This means that the ratio between epilimnetic to hypolimnetic respiration may now be governed by different processes and that the drop in sedimentation to the hypolimnion since 1994 should not necessarily be attributed only to the relatively small concomitant increase in herbivorous zooplankton biomass.

Acknowledgements

Sincere thanks are due to Y. Z. Yacobi, for allowing us to use his unpublished primary production data, to Mekorot Water Company for carrying out the oxygen and other chemical analyses on Lake Kinneret water and for supplying Jordan River chemical data, and to the Hydrological service for hydrological data. We also thank J. Erez who performed the sedimentary organic C analyses, and P.G. Falkowski, B. Lazar, P. Walline, U. Pollingher and T. Berman for useful discussions.

References

American Public Health Assocation (1992) Standard methods for the examination of water and wastewater, 17th Ed. APHA

Berman T & Pollingher U (1974) Annual and seasonal variations of phytoplankton, chlorophyll, and photosynthesis in Lake Kinneret. Limnol. Oceanogr. 19: 31–55

Berman T, Yacobi YZ & Pollingher U (1992) Lake Kinneret phytoplankton: stability and variability during twenty years (1970–1989). Aquat. Sci. 54/2: 104–127

Berman T, Stone L, Yacobi YZ, Shlichter M, Nishri A & Pollingher U (1995) Primary production and phytoplankton in Lake Kinneret: A long term record (1972–1993). Limnol. Oceanogr. 40: 1064–1076

Berman, T also Bull 4(1) (winter 1995) Cyanobacteria in the sea of Galilee (Lake Kinneret)

Berman-Frank I, Zohary T, Erez J & Dubinsky Z (1994) CO_2 availability, carbonic anhydrase, and the annual dinoflagellate bloom in Lake Kinneret. Limnol. Oceanogr. 39: 1822–1834

Bolin, B (1960) On exchange of carbon dioxide between the atmosphere and the sea. Tellus 12: 274–281

Broecker, WS & Peng TH (1974) Gas exchange between air and sea. Tellus 26: 21–35

Capone DG & Kiene RP (1988) Composition of microbial dynamics in marine and fresh water sediments; Contrasts in anaerobic catabolism. Limnol. Oceanogr. 33: 725–749

Carpenter SR (1992) Destabilization of planktonic ecosystems and blooms of blue-green algae. In: Mitchell JF (Ed) Food Web management – A case study of Lake Mendota (pp 461–484). Springer Verlag

Eckert W & Truper HG (1993) Microbially-related redox changes in sub-tropical lake 1. In situ monitoring of the annual redox cycle. Biogeochem. 21: 1–19

Eckert W & Hambright KD (1996) Seasonal and vertical distributions of temperature, pH, oxygen and sulphide in Lake Kinneret hypolimnion. Limnologica. 26: 345–361

Gophen M (1976) Temperature effect on lifespan, metabolism and development of Mesocyclops leuckarti (claus). Oecologia. 25: 271–277

Gophen M (1981a) The metabolism of adult *Mesocyclops leuckarti* populations in Lake Kinneret (Israel) during 1969–1978. Verh. Internat. Verein. Limnol. 21: 1568–1572

Gophen M (1981b) Metabolic activity of herbivorous zooplankton in Lake Kinneret (Israel) during 1972–1977. J. Plank. Res. 3(1): 15–23

Gophen M, Serruya S & Spataru P (1990a) Zooplankton community changes in Lake Kinneret (Israel) during 1969–1985. Hydrobiologia 191: 39–46

Gophen M, Threlkeld, S & Serruya S (1990b) Long term patterns in nutrients, phytoplankton, and zooplankton of Lake Kinneret and future prediction for ecosystem structure. Arch. Hydrobiol. 118: 449–450

Gophen M & Serruya S (1990c) Fish predation effects on plankton community structure in Large Lakes: Lake Kinneret. In: Tilzer M & Serruya C (Eds) Ecological Structure and Fauna (pp 645–660). Springer Verlag

Hadas O & Pinkas R (1992) Sulfate reduction process in Lake Kinneret, Israel. Hydrobiolgia 235/236: 295–301

Hambright KD, Gophen M & Serruya S (1994) Influence of long term climatic changes on the stratification of the subtropical, warm monomictic lake. Limnol. Oceanogr. 39: 1233–1242

Hickel B & Pollingher U (1988) Identification of the bloom forming *Peridinium* from Lake Kinneret (Israel) as *Peridinium gatunense* (Dynophyceae). Br. Phycol. J. 23: 115–119

Kohler MA & Parmele, LH (1967) Generalized estimates of free-water evaporation. Wat. Resource. Res. 3: 997–1005

Landau R, Gophen M & Walline P (1988) Larval *Mirogrex terraesanctae* (Cyprinidae) of Lake Kinneret (Israel); growth rate, plankton selectivities, consumption rates and interaction with rotifers. Hydrobiologia 169: 91–106

O'Melia CR (1987) Particle-particle interactions. In: Stumm W (Ed), Aquatic Surface Chemistry (pp 385–401). Wiley.

Nishri A & Koren N (1993) Sediment transport in Lake Kinneret. Verh. Internat. Verein. Limnol. 25: 290–292

Nydall F (1978) On the peroxidosulphate oxidation of total nitrogen in waters to nitrate. Wat. Res. 12: 1123–1130

Ostrovsky I, Yacobi YZ, Walline P & Kalikhman Y (1996) Seiche induced mixing: its impact on lake productivity. Limnol. Oceanogr. 41(2): 323–332

Parparov A (1994) Oxygen depletion in Lake Kinneret: recent events and long-term trends. Limnologica 24: 137–145

Pollingher U, Ehrlich A and Serruya S (1986) The planktonic diatoms of Lake Kinneret (Israel) during the last 5000 years – their contribution to algal biomass. In: Ricard M (Ed) Proc. 8th. Int. Diatom symposium (pp 459–470). Koeltz Scientific books, Koenigstein, F.R. Germany

Pollingher U (1986) Phytoplankton periodicity in subtrophical lake (Lake Kinneret, Israel). Hydrobiologia 138: 128–138

Raveh A & Avnimelech Y (1972) Potentiometric determination of soil organic matter. Soil Science Society of America Proceedings. 36: 967–969

Sallingar Y (1991) Geochemistry of phosphorus in Lake Kinneret watershed. PhD Dissertation, The Technion, Israel Technical Institute, Haifa, 155 pp

Serruya C, Pollingher U & Gophen M (1980) Carbon flow patterns and ecosystem management. Arch. Hydrobiol. 88: 265–302

Serruya C (Ed) (1978) Lake Kinneret. Monographiae Biologicae. Junk Publishers, the Hague, 502 pp

Smith SV (1985) Physical, chemical and biological characteristics of CO_2 gas flux across the air-water interface. Plant Cell and Environment. 8: 387–398

Smith SV, Serruya S, Geifman J & Berman T (1989) Annual mass balance of P, N, Ca and Cl in Lake Kinneret, Israel. Limnol. Oceanogr. 34: 1202–1213

Stone L, Berman T, Bonner R, Barrt S & Weeks SW (1993). Lake Kinneret a seasonal model for carbon flux through the planktonic biota. Limnol. Oceanogr. 38: 1680–1695

Stumm W & Morgan JJ (1976) Aquatic Chemistry. Wiley Interscience Publication, 789 pp

Wetzel RG (1983) Limnology: Zooplankton Productivity. pp 469–481. Saunders College Publishing.

Willenman U (1986) The role of coagulation for the removal of particles by sedimentation in lakes. Unpublished doctoral dissertation, Eidgenossischen Technischen Hochschulen, Zurich

Williamson CE (1991) Copepoda: Internal anatomy and physiology. In: Thermp JH & Covish A (Eds) Ecology and Classification of North-American Invertebrates (pp 788–790). Academic Press Inc

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