The cladoceran trophic status in the nitrogen limited ecosystem of lake Kinneret (Israel)

Author Details

Moshe Gophen Migal
(*Corresponding author*)

Galilee Technology Center P.O. Box 831, Kiryat Shmone 11016, Israel
e-mail: gophen@migal.org.il

Abstract

The impact of cladocerans metabolic activities on the carbon (C), nitrogen (N) and phosphorus (P) dynamics in Lake Kinneret (Israel) is presented. The study, is based on the incorporation of field data and experimental measurements. Grazing, respiration and production rates of *Diaphanosoma* spp., *Ceriodaphnia* spp. and *Bosmina* spp. were experimentally measured at three temperatures, and the results were extrapolated to the field biomass distribution at these respective temperatures, and the total lake capacity was calculated using the following equation: consumption = respiration + production + excretion. The field capacity of consumption, respiration and production were found to be mostly correlated with biomass density, but the temporal fluctuation of the percent of excretion from consumed energy differed. The increase in P, decline in N and decrease in the TN/TP mass ratio in the epilimnion of Lake Kinneret during 1969-2004 created N limitation. An increase in C and decline in TN, with a consequential increase in the C/TN ratio were documented. TP was augmented but the C/TP ratio was only slightly increased. During 1975-2004, P was probably, a minor limitation for cladoceran growth. The positive impact of recycled P by cladocerans under the N limitation in Lake Kinneret is discussed. There is a current threat on the water quality, derived from N limitation (mostly in summer-fall) and consequent *Cyanophyta* blooms. Thus, the role of recycled P by grazers may be significant.

Key words

Introduction

The carbon (C) flux as factor of supply, relative to the demands, is significant to producers and consumers in lakes (Hessen 2005). Carbon flow efficiency through the zooplankton compartment of the food web is highly affected by the stoichiometric requirements of the organisms involved. The nutritional value of algal resources may be low, if the carbon influx (photosynthesis) coincides with nitrogen (N) and phosphorus (P) deficiencies. Low ratios of C:N and/or C:P in zooplankton, relative to algal/detritus resources, indicate N and P growth limitations for animals. The stoichiometric aspects of C metabolism and trophic transfer efficiency has been studied by Hessen (2005). This stoichiometric nutrition, with a high C level, leading to high C:N and C:P ratios and N and P limitations for primary consumers in the aquatic ecosystems have been documented by Elser *et al.* (2001) and Sterner and Elser (2002). The temporal dynamics of the metabolic activities of Cladocera, which have been investigated, based on field data and experimental measurements, in order to define their impact on the C, N and P cycles in Lake Kinneret (Israel), is presented in this paper. Bruce (2006) predicted, that on the average, 51% of the C from phytoplankton photosynthesis is consumed by zooplankton, and digestion and excretion of nutrients by zooplankton account for 3-52 and 16-57% of the phytoplankton uptake of P and N, respectively. Zooplankton play an important role in lake dynamics, as grazers in the control of algal and bacterial populations, as a food source for higher trophic levels, such as fish, and in the excretion of dissolved nutrients. Thus, understanding the role of zooplankton in the nutrient fluxes in Lake Kinneret is relevant for effective lake management. Zooplankton excretion influences the trophic dynamics in lakes by contributing inorganic N and P for primary and bacterial production (Lehman, 1980; Sterner, 1986; Vanni, 2002). Estimates of the fraction of N and P, regenerated by zooplankton and subsequently utilized by phytoplankton, range from 14-50% (Urabe *et al.,* 1995; Hudson *et al.*, 1999). One of the factors controlling this fraction is nutrient ratios in grazed and excreted substances. These factors interact dynamically, and the role of zooplankton in substance cycling is therefore significant to the nutrient flow pattern within the ecosystem.

Materials and Methods

Zooplankton studies in the Kinneret Limnological Laboratory started in 1968. The zooplankton communities have been routinely monitored by weekly and biweekly sampling at 5 - 8 stations (at 7 –

13 distinct depths) and their mass averaged by weighing the number of available samples of the entire lake. Metabolic parameters have been experimentally measured and the results have been documented in Gophen and Azoulay (2002). Routine monitoring revealed seven cladoceran species, with the three genera, *Diaphanosoma spp., Ceriodaphnia spp.* and *Bosmina spp.* being the most common (Gophen and Azoulay, 2002). Their body size was measured and incorporated into the biomass assessment of the lake (Gophen and Azoulay, 2002). Grazing, respiration and production rates that were experimentally measured at three temperatures (Serruya *et al.,* 1980; Gophen and Azoulay, 2002) were extrapolated to the field cladoceran biomass concentration averaged for the entire lake (g.m^{-2}) in order to compute the total metabolic capacities of the lake.

The cladoceran biomass has been reported in Gophen and Azoulay (2002), and the results of experimental measurements of the metabolic parameters of cladocerans may be found in Gophen and Azoulay (2002). The microscopical analysis of food preferences by cladocerans (Serruya *et al.* 1980) are 75% - nano-phytoplankton (*Chlorophyta,* diatoms), 25% detritus and bacteria. The carbon content (Serruya *et al.* 1980) with respect to zooplankton –44% of dry weight (DW) (Rachamim *et al.* 2009 documented 41-43 % of DW) and 10% of the wet weight and regarding phytoplankton –50% of DW and 40% of wet weight. The metabolic activity of *Cladocera* was calculated using the following equation: consumption = respiration +production + excretion , all expressed as gC.m^{-2}.month^{-1}. Multi-annual cladoceran total averages of production, respiration and consumption rates, calculated for the whole lake by incorporating the metabolic parameters and field data of the biomass concentration and respective temperatures, indicated the following: production – 5.0 gC.m^{-2}.month^{-1}, respiration – 9.3 gC.m^{-2}.month^{-1} and food consumption – 74.0 gC.m^{-2}.month^{-1}. The gap between food requirements and food availability was strongly positive (26 gC.m^{-2}.month^{-1}; *i.e.* intensive grazing pressure) during 1969-1982, slightly negative (-5 gC.m^{-2}.month^{-1}) during 1983 – 1993 (low grazing pressure) and slightly positive during 1994-2000. Nishri *et al.* (1998) documented zooplankton respiration to be about 15-20% of the photosynthetic production, and total zooplankton production was found to be 15% of PP. The summer season was found to be the most sensitive period for algal response to nutrient recycling by zooplankton, because external inputs were minimal (Serruya *et al.,* 1980). In this paper, I present an analysis of the metabolic activities of cladocerans in relation to phytoplankton densities and their nutrient contents (homeostasis) in Lake Kinneret.

Statistical analysis: Statistical analyses of monthly averages of data sets (KLDB 1969-2004) were done by the LOWESS (0.8) test (Stata SE 9.0). LOWESS (LOcally WEighted Scatterplot Smoother) analysis is a robust smoothing procedure of weighted regression with a level of tension of 80 to produce tight and straight curves with outlier robustness. Simple and polynomial regressions were also carried out.

Nutrient concentrations were calculated as follows (Gophen *et al.* 1999):

Particulate (Part.) P = TP – TDP;
TN = Total Kijeldhal (TKJ) + NO$_3$ + NO$_2$;
TIN = NO$_3$ + NO$_2$ + NH$_4$;
Part organic N = TKJ minus KJ Dissolved   (PON = TKJ - KJD);
TDN = KJD + NO$_3$ + NO$_2$;
Organic N = TKJ minus NH$_4$ (ON = TKJ - NH$_4$);

Results and Discussion

Temperature and Plankton: Results in figure 1 represent multi-annual changes of epilimnetic temperatures in Lake Kinneret, with a decline until the mid 1980's and an increase thereafter by 0.5°C. This corresponds to a change of 1.2%.$^{\circ}$C^{-1} of metabolic efficiencies ranging between 17.5-26°C (Gophen and Azoulay 2002). Consequently, metabolic capacities of cladoceran field populations (Fig. 2) are biomass- and not temperature-dependent. The results of annual averages, presented in Fig. 2, indicate a prominent decline in the cladoceran density of Lake Kinneret from 1970 until the early 1990's and an increase thereafter. LOWESS smoothing analyses (Fig. 3) indicated a continuous decline of cladoceran densities until the early 1990's, which leveled off later. A temporal increase in values of "small" to "large" ratios (S:L) of cladoceran densities is shown in figures 4 and 5. The abundance of the two size classes were measured in the same units. "Small" represented 1-3 neonates and "large" 3-5 neonate classes. The reason for the trend towards change was mostly due to the decline in large organisms, because the fluctuations in small cladocerans were minor (Fig. 5). Figure 6 demonstrates that the S:L ratios were below average during the 1970's and 1980's, but above average later on. Consequently, it is suggested that size frequency within the cladoceran population was affected mostly by fish predation, which was intensified, bringing about the elimination of the large organisms. It has been previously suggested (Gophen, 2004) that such trends are due to fluctuations in predation pressure produced by the zooplanktivorous Bleak fish. The increase in the S:L ratio is due
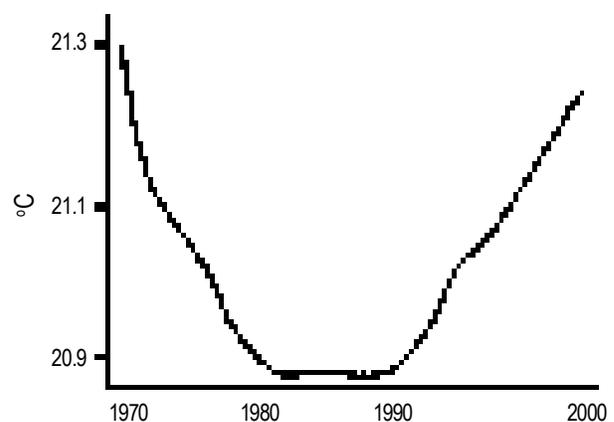

Fig. 1: Trend of changes of temperature in the Kinneret Epilimnion (0-21.5m): all dates. All depths, all stations and all day times during 1969-2004 (LOWESS 0.8)
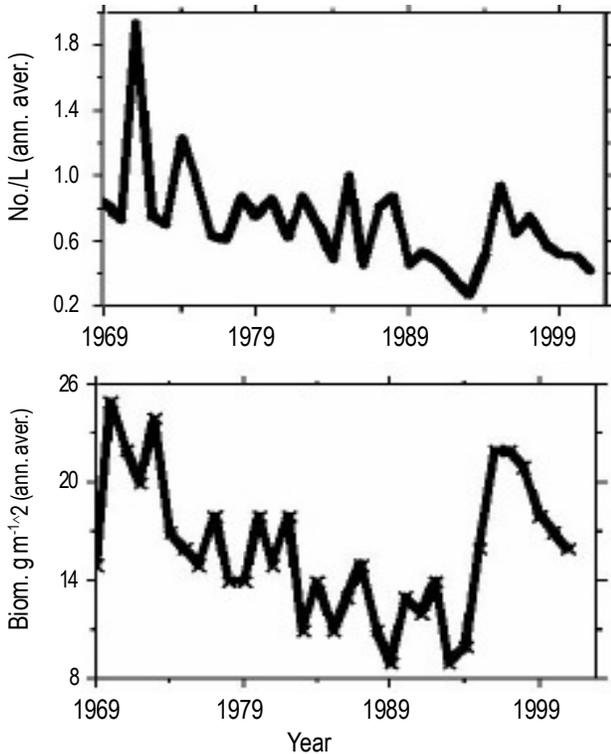
Fig. 2: Annual averages of Cladocera density in the pelagial of Lake Kinneret:all depths, all stations, all dates during 1969-2001. No.. lit^{-1} (upper) and g(ww).m^{-2} (lower)
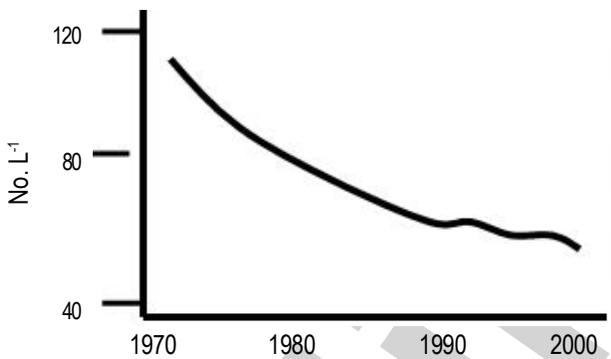

Fig. 3 : Trend of changes of Cladocera density (No.. litre^{-1}): all depths, all stations, all dates during 1969-2001. (LOWESS 0.8)
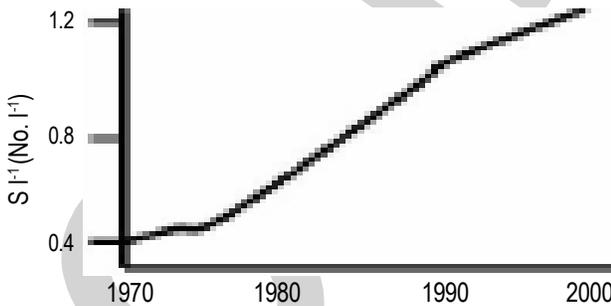

Fig. 4: Trend of changes of Cladocera Small:Large ratio (see text) (No.. litre^{-1}): all depths, all stations, all dates during 1969-2001. (LOWESS 0.8).Cladocerans as neonates 1 – 3 were counted as "Small" and 3-5 neonates as "Large"
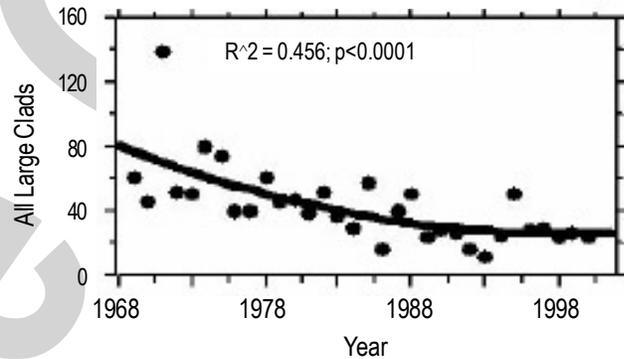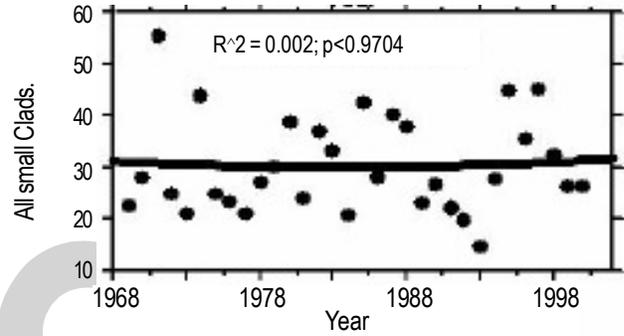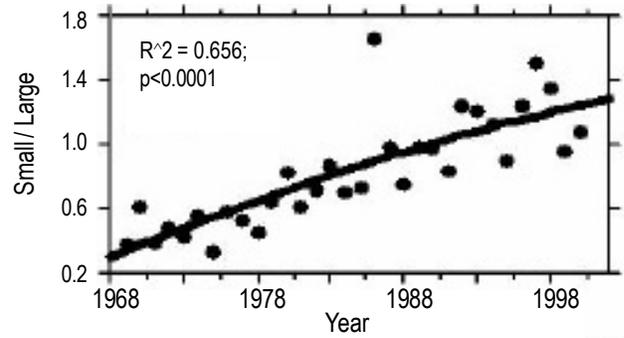

Fig. 5: Ratio between small and large cladocerans (see text): annual averages (No.litre^{-1}) (1969 – 2001). Upper – ratio; Mid – Small density; Bottom – large density
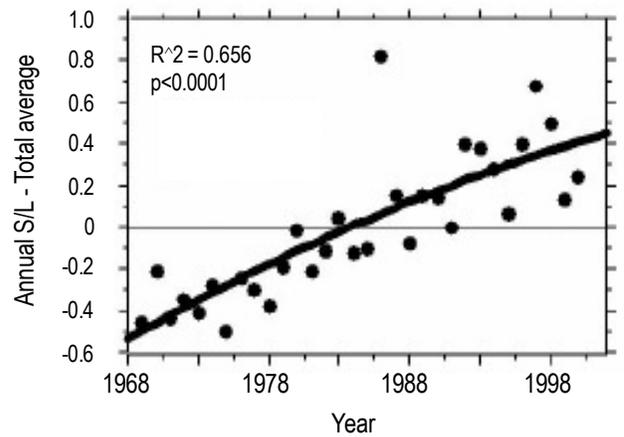

Fig. 6: Polynomial regression of the differences between multi – annual and annual averages of S/L (No.lit.$^{-1}$) of cladoceran assemblages Vs. years
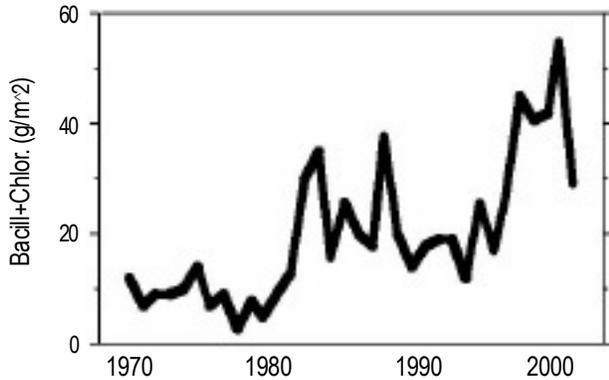
Fig. 7: Annual averages of nano–phytoplqankton (chlorophytes and diatoms) biomass(g.m⁻²)

Fig. 11: Linear Regression of Kijldhal total (upper line), and Kijldhal dissolved (lower line) concentrations (ppm) Vs. years with arrowed space of Kijldhal particulate in between based on monthly averages of all depths, all dates, all stations

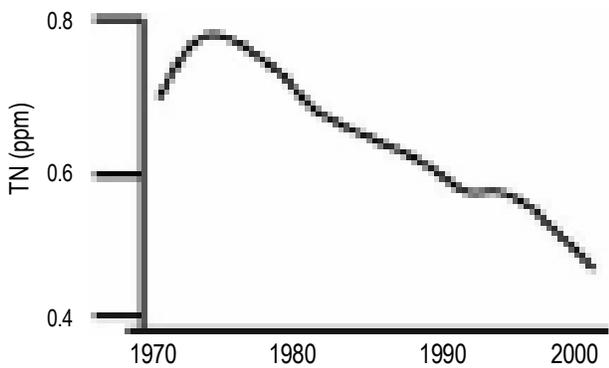**Fig. 8:** Trend of changes of epilimnetic (0 – 21.5 m) TN concentrations (ppm); all depths, all stations, all dates during 1969-2001. (LOWESS 0.8)
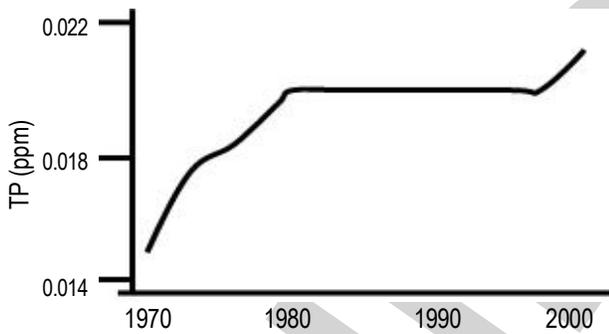

Fig. 12: Trend of changes of epilimnetic (0-21.5 m) particulate Kijldhal (see Fig.11) concentrations (ppm); of all depths, all stations, all dates during 1969-2001. (LOWESS 0.8)

Fig. 9: Trend of changes of epilimnetic (0-21.5 m) TP concentrations (ppm); all depths, all stations, all dates during 1969-2001. (LOWESS 0.8)
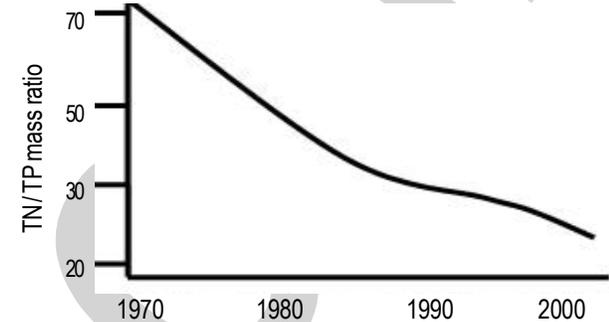

Fig. 10: Trend of changes of epilimnetic (0-21.5 m) TN:TP mass ratio; only measurements where TN and TP were simultaneously measured at all depths, all stations, all dates during 1969-2001 (LOWESS 0.8)
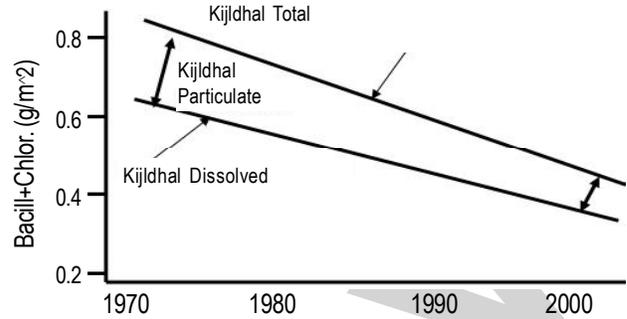
Fig. 13: Trend of changes of monthly averages of Cladocera biomass (g m⁻²) (upper panel), and assimilated energy (R + P, see text) (lower panel) (gC.m⁻².month⁻¹) during 1969-2001. (LOWESS 0.8)

Fig. 14: Trend of changes of monthly averages of epilimnetic (0 – 21.5 m) C - organic concentrations(ppm) Vs. assimilated energy (R + P; gC.m^{-2}.month^{-1}); all depths, all stations, all dates during 1969-2001. (LOWESS 0.8)
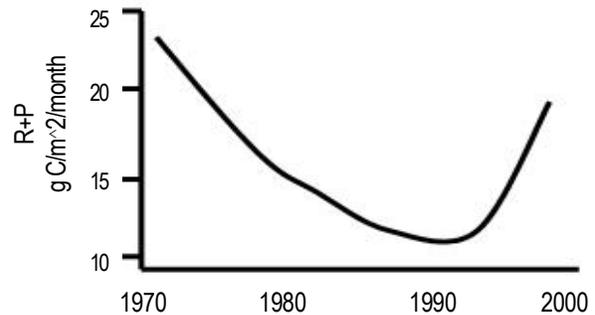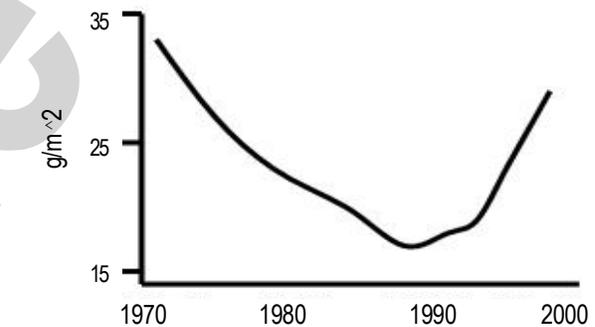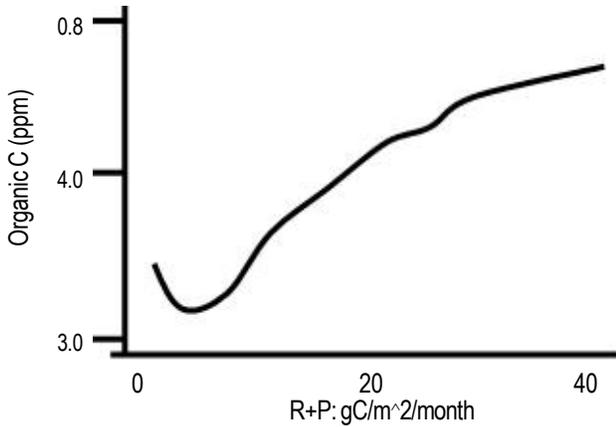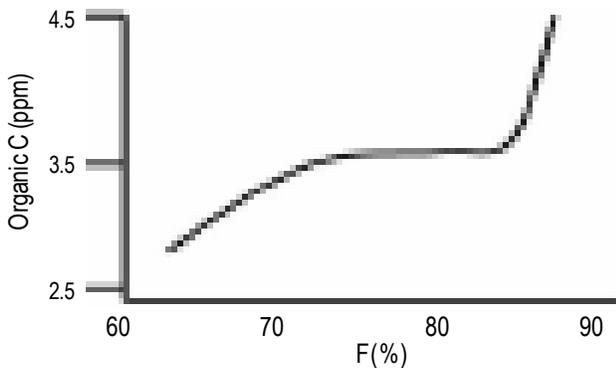

Fig. 15: Trend of changes of monthly averages of epilimnetic (0 – 21.5 m) C - organic concentrations(ppm) Vs. % of defecation (F%) from consumed energy (see text) all depths, all stations, all dates during 1969-2001. (LOWESS 0.8)
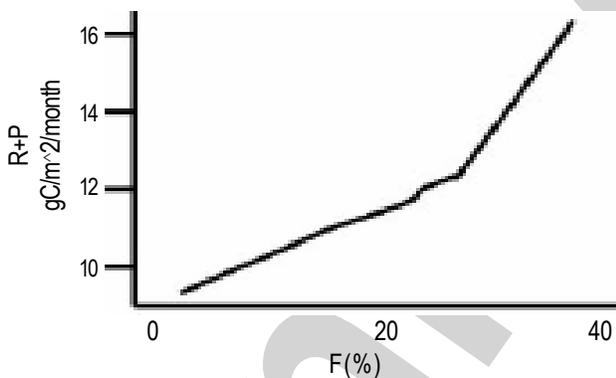

Fig. 16: Trend of changes of monthly averages of assimilated energy (R + P; gC.m^{-2}.month^{-1}) Vs. F% (see text); during 1969-2001. (LOWESS 0.8)

Fig. 17: Trend of changes of monthly averages of assimilated energy(R + P; gC.m^{-2}.month^{-1}) Vs. TN loads in the epilimnion (ton) during 1969-2001. (LOWESS 0.8)
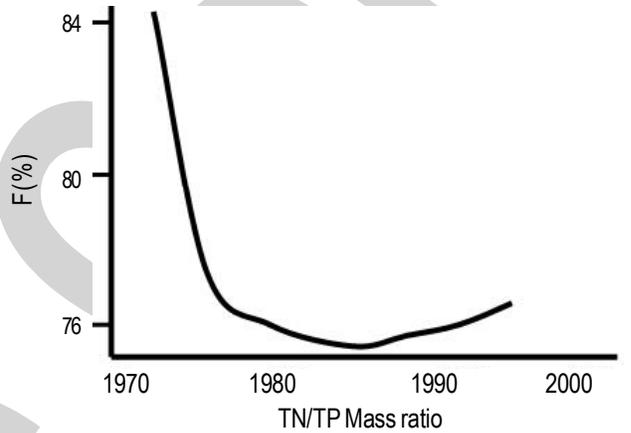
Fig. 18: Trend of changes of monthly averages of (F%) (see text) Vs. epilimnetic TN:TP mass ratio during 1969-2001. (LOWESS 0.8)
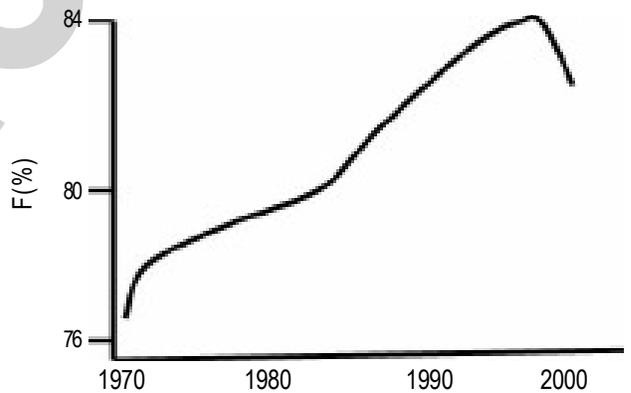
Fig. 19: Trend of changes of monthly averages of (F%) (see text) Vs. years during 1969-2001. (LOWESS 0.8)

mostly to the decline in the "large" by intensified particulate visual zooplanktivory fish feeders, since the densities of the "small" were not changed (Fig. 6). Nevertheless, the "large" probably became more productive due to the need to supply the unchanged density of "small" (Fig. 5) by lowering the number of "large". Such a change may be due to a higher availability and quality of food resources and/or increase in metabolic efficiencies.

It has previously been documented that 75% of the cladoceran food resources are chlorophytes and diatoms (Serruya *et al.,* 1980; Gophen and Azoulay, 2002). In Fig. 7, a prominent increase in nanoplanktonic food resources is shown. The decrease in the consumption of the indigestible *Peridinium* algae by *Cladocera* has been reported previously (Gophen 2004; 2008).
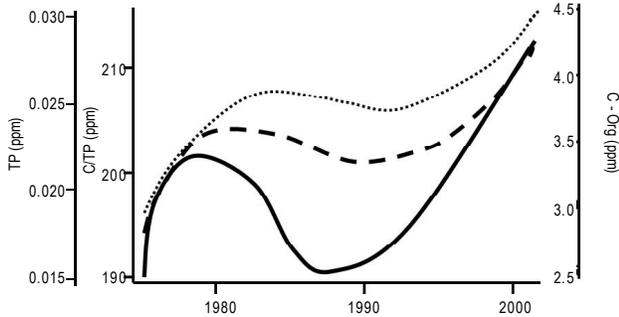
Fig. 20: Trend of changes of monthly averages of C-org (broken line), TP concentration (ppm) (dotted line) and C:TP ratio (ppm) (solid line) Vs Years during 1975-2001. (LOWESS 0.8)
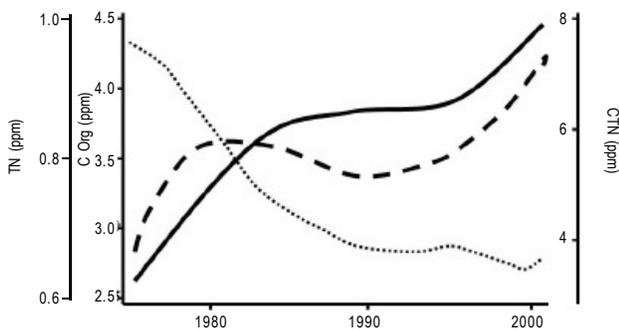
Fig. 21: Trend of changes of monthly averages of C-org. (broken line), TN concentration (ppm) (dotted line) and C:TN ratio (ppm) (solid line) Vs Years during 1975-2001. (LOWESS 0.8)

Nutrients : The increase in P, decline in N and decrease in TN:TP mass ratio in the epilimnion of Lake Kinneret during 1969-2004, which initiated N limitation, are presented in figures 8-10. The decline in the N content in the suspended particles within the Kinneret epilimnion during 1970-2001 is very pronounced in figures 11 and 12. It has been suggested that the combined effect of P limitation during 1969-mid 1980's and N limitation after 1985, encouraged nano-planktonic algal growth in the Kinneret epilimnion. Under these ecosystem conditions, cladoceran metabolism of N, C and P may have an effective role on the entire ecosystem. Consequently, metabolic efficiencies of cladoceran communities in Lake Kinneret were analyzed.

Metabolic efficiencies: Food intake, respiration and production rates were measured experimentally (Gophen and Azoulay, 2002). The defecation rate (F) was calculated from the equation: Consumption = production + respiration + F. For the computation of the capacities (consumption, production and F) in field communities, the experimental results

(mgC.mgC^{-1}.day^{-1}) were applied to the field data (g.m^{-2}) at the respective monitored temperatures. It was found that the field capacities for consumption, respiration and production were highly correlated with biomass density (Fig. 13), but the percent of F of the consumed energy was different. Fig. 14 presents the positive relation between assimilated energy (respiration + production) and the

concentration (ppm) of organic C. Therefore, the capacity of F% of the entire population was augmented with the increase in the carbon concentration, *i.e.* the more carbon that is available, the more energy that is assimilated and the larger the portion that is excreted (Figs. 15, 16). The remarkable changes in the epilimnetic N and C availabilities initiated the need to consider its relationships to cladoceran metabolic dynamics. Fig. 17 indicates an increase in the assimilated energy (respiration and production), when the epilimnetic TN load was enhanced. Nevertheless, F% declined when the TN:TP mass ratio ascended (Fig.17), and temporally (1970 – 2004) increased (Fig. 19). Figures 20 and 21 show the changes of TP, TN, C:TP, C:TN and organic C concentrations in the epilimnion of Lake Kinneret during 1975 – 2004. Organic C and TP increased whilst TN declined. C:TN was high throughout the entire period. C:TP was high only during the late 1970's and from 1987, when TP was elevated. There was an intermediate period of seven years when C:TP was low.

Hessen (2005) and Elser *et al.* (2001) documented that limiting elements are expected to be utilized for growth at a high efficiency, whilst non-limiting nutrients must be disposed off or recycled. Moreover, if there is a shortage of elements other than C, such as N, more ingested C goes to waste (Hessen, 2005). A simple regression between multi-annual monthly averages of chlorophytes plus diatoms (edible algae) vs organic C concentration in Lake Kinneret has indicated a significant relationship (R^2= 0.4; p= 0.0299). However, the relationship, of cladoceran biomass vs organic C concentrations (R^2= 0.0001; p= 0.9695) was not significant. Consequently, it has been suggested that a high level of organic C enhances algal growth; but there is probably a limiting element other than C in the case of cladocerans, which maintain a stoichiometric regulation resulting in the increased defecation of C. The C content within the algal cells is changeable, but fairly stable in the body content of cladocerans. When the organic C content within the seston particles increases, a relative portion of waste (F%) is enhanced, in spite of a higher level of assimilated energy (Figs. 16 and 17). The enhancement of energy assimilation is accompanied by a higher level of defecation (Fig. 16). Nevertheless, assimilated energy was also enhanced when the TN load was increased in the epilimnion. This may be a factor, which supports the cladoceran N limitation hypothesis. The results presented in figures 20 and 21 indicate a temporal increase of C by 50%, a TN decline of 32%, and consequently an increase in the C:TN ratio by 140%, resulting in nitrogen limitation. On the contrary, TP was enhanced by 67% and the C:TP ratio was augmented by only 12%, resulting in a very minor P limitation during the years, 1987 to 2004. Conclusively, it may be that during the entire period of 1975-2004, P was not, or was a very minor limiting factor in cladoceran growth. Hessen (2005) stated that there is a trade off between high P demands and the dietary P and/or N deficiencies. Hessen (2005) also suggested maintenance of stoichiometric metabolism by metazoans with a high C/TP ratio, when feeding on food particles with a wider range of elemental ratios, initiating constraints on their ability to utilize C. Certainly, the N stock in the epilimnion of Lake Kinneret was depleted

and that of P enriched during 1970-2004 (Figs. 8 – 12). On the other hand, these changes can not be attributed to the water level (WL) decline, because long term analysis (data not shown here) indicates the decline of TP, TDP, TN, TIN, TDN and PON simultaneously, when the WL became lower. WL decline has become a common phenomenon in Lake Kinneret during the last 40 years. The temporal decline of TN, Kijeldhal, (total and dissolved) and PON are shown in figures 11, 12 and 21. Nitrogen deficiency exists when the TN:TP ratio has become reduced below 50, accompanied by the enhancement of F%, defecation and the recycling of P. When TN:TP is above 50, F% is fairly stable, and recycled N is enhanced, but P recycling is diminished (Fig. 18). The decline in the TN:TP mass ratio in Lake Kinneret (Fig. 10) was followed by the enhancement of F%, as a result of N limitation and intensified food intake to cover N demands. Consequently, recycled P was enhanced, providing an additional P supply for nano-phytoplankton. The positive impact of cladoceran recycled P under the present conditions of C and P sufficiency and N limitation in Lake Kinneret is prominent. Considering elemental (N, P, C) algal ratios, the Kinneret ecosystem conditions shifted from one periodical situation (1969-early 1990's) to another (early 1990's – present). The first period was characterized by a low algal C:P level with a high growth rate, a pre-dominance of chlorophytes and diatoms within edible food resources of cladocerans, a negligible cyanophyte contribution and a high zooplankton grazing efficiency, *i.e.*, high rate of energy assimilation (Fig. 14). The second period was included cyanophyte enhancement, a high C:P level, a slower rate of algal growth and zooplankton feeding efficiency, where more C is channeled to detritus (Figs. 20 and 21) (Enriquez *et al.*, 1993; Cebrian 1999). Rachamim *et al.* (2009) published data on N and P excretion by Lake Kinneret zooplankton (*Cladocera* and *Copepoda*) and their elemental (C, P, N) body content. They also measured P excretion rates of 0.1-0.25 µgP.mgDW^{-1}.hr^{-1} (with two exceptions in May and June) and an N excretion rate of 0.05-0.15 µgN.mgDW^{-1}.hr^{-1} by Kinneret zooplankton (except for December) and N and P contents of 9.3-9.8% and 1.2-1.5% of DW, respectively and approximately 40% C of DW (see also Gophen, 1978; Bruce *et al.,* 2006; Gophen and Azoulay, 2002). Rachamim *et al.* (2009) calculated an elemental turnover time of N and P, excreted by zooplankton in two seasons (winter-spring and summer-fall), about 21 and 8 days in winter-spring and summer-fall for N, respectively, whilst for P it was approximately two days in two seasons. It has been suggested that the longer turnover time of N in the winter, as compared to in the summer, is due to a slower metabolic activity of zooplankton during the lower winter temperatures (Gophen and Azoulay, 2002) and a higher biomass of edible *Cyanobacteria.* However, there is a lower nutritional value in the summer in comparison to the chlorophytes and diatoms, which are common in the winter and summer. Data in figures 20 and 21 show a temporal increase in organic C, a high (190-208) C/P ratio and 4-8 C:N ratio. Rachamim *et al.* (2009) found C:N values in zooplankton that were similar to the epilimnion values (Fig. 21), but lower C:P ratios in zooplankton than in the epilimnion (Fig. 20). Epilimnetic P and C increased to a similar extent (Fig. 20), resulting in low C:P ratios. It has been conjectured

that the reason for the low demands for P by zooplankton is the high content of P in the lake and consequently a high portion of ingested P is recycled (excreted). The recycled P probably is supportive of the demands for the optimal growth of nano-phytoplankton in the lake, which may cause a deterioration in the water quality. On the other hand, epilimnetic N significantly declined and C increased (Fig. 21), resulting in the significant increase in the C:N ratio. Therefore, zooplankton N demands are high, and a major part of the ingested N is incorporated, bringing about a long turnover time of N (Rachamim *et al.,* 2009). It should be taken into account that presently, due to the N limitation, the bloom-forming dinoflagellate, *Peridinium spp*, has almost disappeared from the lake. Presently, the lake is characterized by a high biomass of *Cyanobacteria* (N$_2$-fixers and non- N$_2$ fixers). In a case like Lake Kinneret, where cyanophyte blooms threaten water quality and N is limited mostly during the summer-fall season, the impact of recycled P by zooplankton is not negligible. Therefore, biomanipulation management is worthwhile, together with P removal from watershed sources. The predation pressure of fish on zooplankton is one part of the Kinneret ecosystem dynamics and can probably be compensated by biomanipulation. The nutrient metabolism of *Cladocera,* encouraged by the shift in the ecosystem structure from P to N limitation is an independent development in Lake Kinneret. A comprehensive approach in the appropriate design of management policy should couple the two processes.

References

Bruce, L.C., D. Hamilton, J. Imberger, G. Gal, M. Gophen, T. Zohary and K.D. Hambright: A numerical simulation of the role of zooplankton in C, N, and P cycling in Lake Kinneret, Israel. *Ecol. Modell.*, **193**, 412-436 (2006).

Cebrian, J.: Patterna in the fate of productionin plant communities. *The American Naturalist,* **154**, 449-468 (1999).

Elser, J.J., K. Hayakawa and J. Urabe: Nutrient limitation reduces food quality for zooplankton: Daphnia response to seston phosphorus enrichment. *Ecol.,* **82**, 898-903 (2001).

Enriquez, Sand Sand-J.K.: Patterns in decomposition ratesamong photosynthetic organisms-the importance of detritus C:N:P content. *Oecol.*, **94**, 457-471 (1993).

Hessen, D.O.: Aquatic food webs: Stoichiometric regulation of flux and fate of carbon. Peter Kilham Memorial Lecture. *Veh. Internat. Verein. Limnol.*, **29**, 39-49 (2005).

Gophen, M.: Metabolic activity of herbivorous zooplankton in lake Kinneret (Israel) during 1972-1977. *J. Plankton Res*., **3**, 15-24 (1981).

Gophen, M. and B. Azoulay: The trophic status of zooplankton communities in Lake Kinneret (Israel). *Verh. Internat. Verein. Limnol.*, **28**, 836-839 (2002).

Gophen, M.: Water quality management in Lake Kinneret (Israel): Hydrological and food web perspectives. *J. Limnol.*, **62**, 91-101 (2003).

Gophen, M.: Hydrology and management of Lake Kinneret aimed at water quality protection. *In*: Water in the Middle East and in North Africa: Resources, Protection, and Management. Springer-Verlag. pp. 41-54 (2003a).

Gophen, M.: Ecohydrological management of Lake Kinneret: A case study. *Ecohydrol. Hydrobiol.*, **4**, 397-408 (2004).

Gophen, M.: Long term (1970-2001) Eco – Hydrological processes in Lake Kinneret and its Watershed. *In*: Climatic changes and water resources in the middle east and in North Africa. Invited Chapter (*Ed.*: H. Zereini). pp. 373-402 (2008).

LKDB: Lake Kinneret data base, (M. Shlichter manager), primary production and chlorophyll - Y.Z. Yacobi and T. Berman; Phytoplankton - U. Pollingher and T. Zohary (1969-2004).

Hudson, J.J., W.D. Taylor and D.W. Schindler: Planktonic nutrient regeneration and cycling efficiency in temperate lakes. *Nature,* **400**, 659-661 (1999).

Nishri, A., T. Zohary, M. Gophen and D. Wynne: Lake Kinneret dissolved oxygen regime reflects long term changes in ecosystem functioning. *Biogeochemistry,* **42**, 253-283 (1998).

Rachamim, T., T. Zohary, I. Berman-Frank and G. Gal: Nutrient recycling by zooplankton in lake Kinneret-Israel. Poster Presentation in ASLO Aquatic Sciences Meeting 2009. Nice, France. 25-30.1.2009; 025 (13) (2009).

Serruya, C., M. Gophen and U. Pollingher: Lake Kinneret: Carbon flowpatterns and ecosystem management. *Arch. Hydrobiol.,* **88**, 265-302 (1980).

Stata (SE 9.0): Stata statistical software: Release 9. College Station, TX: StataCorp.LP. (2005).

Sterner, R.W.: Herbivores' direct and indirect effects on algal populations. *Sci.*, **231**, 605-607 (1986).

Sterner, R. and J.J. Wand Elser: Ecological stoichiometry: The biology of elements from molecules to the biosphere. Princeton Univ. Press, Princeton, NJ. p. 439 (2002).

Urabe, J., M. Nakanishi and K. Kawabata: Contribution of metazoan plankton to the cycling of nitrogen and phosphorus in Lake Biwa. *Limnol. Oceanogr.,* **40**, 232-241 (1995).

Vanni, M.J.: Nutrient cycling by animals in freshwater ecosystems. *Annu. Rev. Ecol. Syst.,* **33**, 341-370 (2002).