Asian Fisheries Science 5(1992):291-302.
Asian Fisheries Society, Manila, Philippines

https://doi.org/10.33997/j.afs.1992.5.3.003

Long-Term Changes of Plankton Communities in Lake Kinneret, Israel

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Abstract

During the 1980s changes were observed in the Lake Kinneret ecosystem. Biomass and production of planktonic grazers declined. Copepod nauplii, *Keratella* spp. large body *Diaphanosoma* sp., *Ceriodaphnia* spp., *Bosmina* spp. and adult copepods became less abundant relative to small individuals. An increase of particulate P (PP) in lake water was observed, while particulate-N (PN) decreased. As a result, the TN/ TP (wt/wt) and atomic ratio (AR) of PN/PP in the epilimnion (0-10 m) decreased from 42-63 (wt/wt) and 76-117 (AR) during the 1970s to below 29 (wt/wt) and 25-70 (AR) in the 1980s. Fish predation and the change of nutritional value of particulate food sources for zooplankton affected their community changes. The decline of zooplankton grazing capacity and the improved conditions of nutrients, together may have contrib- uted to the increase of the algal biomass of Chlorophyta in the lake. Implications on other algal groups and lake management are considered.

Introduction

Lake Kinneret is a subtropical, warm (15-28°C, range of monthly average epilimnic temperatures), monomictic water body (170 km^2) with a monthly 24 m average depth and 42 m maximum depth. The lake is stratified during May to mid-December and mixed from mid-December through April. Winter-spring and summer-fall trophic conditions of the lake are very different: the winter-spring is a nutrient rich and productive period, whilst in summer-fall, oligotrophic conditions prevail in the epilimnion. Total-P concentrations during winter homothermy vary between 20 and 50 ppb, whilst during summer, epilimnetic total-P is depleted to 5-15 ppb (data from Limnological Laboratory annual reports 1969-90, Israel

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Oceanographic and Limnological Research (IOLR), Haifa). Nevertheless, available P (soluble reactive phosphorus and/or total dissolved) concentrations are low in the epilimnion (0.5-6.0 ppb-SRP and 6.0-18.0 ppb-total dissolved). The dinoflagellate *Peridinium* produces heavy blooms in late winter-spring. *Peridinium* cells are not grazed upon by zooplankton but are intensively consumed by fish. Epilimnion conditions during five summer months are characterized as steady-state with P and N deficiencies for algal communities and food limitation for secondary and tertiary producers (Serruya et al. 1980; Pollingher 1986; Pollingher et al. 1988).

There are 24 fish species in Lake Kinneret of which 15 are commercial, yielding annually about 100 $kg \cdot ha^{-1}$. Among the commercial species, four (two bleaks and two tristramellids) are endemic to Lake Kinneret, three (grey mullets and silver carp) are exotics and *Oreochromis aureus* (blue tilapia) was very rare prior to its "introduction." The most abundant genera are the zooplanktivorous bleaks (*Mirogrex* sp. and *Acanthobrama* sp.). The majority of the Kinneret fishes are planktivorous, several are benthic feeders and the level of piscivory is low (Gophen 1987). Fish (exotic and native) have been stocked in the lake since the early 1960s. During 1960-86, about 123 million fingerlings (37% *Sarotherodon galilaeus*, 26% *O. aureus*, 11% silver carp and 26% grey mullets) were planted in the lake. In spite of food sources segregation, most of the Kinneret fish species consume zooplankton, several of them throughout all seasons, and some mostly during summer-fall (Gophen 1987). Predation pressure of fish on zooplankton is heavier during summer-fall compared to winter and produced by both filter and particulate feeders. Winter zooplanktivory by bleaks larvae was recently described as well as increase of this zooplanktivorous fish stock biomass in the lake after the 1960s (Landau et al. 1988; Landau 1991). Zooplanktivory by silver carp (mostly in summer-fall) and *O. aureus* was documented by Spataru and Gophen (1985) and Spataru and Zorn (1978). Changes of fish community structure with increasing broodstocks of silver carp, *T. aureus* and bleaks and planted fingerlings were followed by intensification of zooplanktivory. Analysis of cladoceran and copepod size-class distribution and long-term (1969-89) records of zooplankton stock biomass indicated an increase of predation pressure by fish (Gophen 1987, 1988).

Kinneret is the only natural freshwater lake in Israel. Top priority of lake utilization is given to water supply: about 450 x 10^6 m^3

(25% of national demands) are pumped from the lake annually. The lake and its watershed area have been studied since 1968 by a team from the Kinneret Limnological Laboratory (IOLR) and the Mekorot Watershed Unit (Water Supply Company). During 1969-89 several changes in the ecosystem structure were observed. This paper describes these changes and analyzes their interrelationships. Consequent management recommendations are made.

Methods

Nutrient (particulate and total P and N) mass contents of the epilimnion (0-10 m depth) (Table 1) were calculated for the whole lake area based on chemical data measured by the Watershed Unit, and stored in the Lake Kinneret Database.

Phytoplankton data were collected by Pollingher and published in the annual reports of the IOLR.

Zooplankton data were collected by Gophen and published in annual reports of the IOLR. Temporal changes of plankton and nutrients and interrelationships between variables were analyzed.

Table 1. Annual (1974-89) averages of mean atomic ratios (AR) between particulate -N (PN) and particulate -P (PP) mass contents in the epilimnion (1-10 m) of Lake Kinneret.

Year	PN/PP-AR
1974	100
1975	117
1976	87
1977	76
1978	89
1979	52
1980	107
1981	62
1982	35
1983	70
1984	52
1985	50
1986	35
1987	29
1988	25
1989	46

Results

Correlation coefficients (r) and probabilities (p) of linear regressions of zooplankton and nutrient variables vs. time (years) and phytoplankton groups were calculated. The results are presented in Table 2.

Zooplankton vs. Time (Table 2 and Fig. 1)

The biomass of Copepoda, Rotifera and total zooplankton significantly ($P=0.01$) declined during 1969-85. Densities of adult

Table 2. Correlation coefficients (r - = inverse relation) of regressions between variables of zooplankton (Gophen 1969-85), phytoplankton (Pollingher 1972-85) and years: S*=(P=0.01); S=(P=0.05); NS=not significant; Chl.=Chlorophyta; Cya.=Cyanophyta; Non.=nonPyrrhophyta; Tot.=total phytoplankton; S/L=small/large ratio.

Variable	Year	Chl.	Cya.	Non.	Tot.
Copepoda biomass	-0.73 S*	-0.85 S*	-0.54 S*	-0.85 S*	-0.59 S
Cladocera biomass	-0.67 S*	NS	-0.53 S	-0.55 S	NS
Rotifera biomass	-0.66 S*	-0.64 S	NS	-0.56 S	-0.70 S*
Nauplii	-0.50 S	NS	-0.63 S	NS	NS
Adult copepods	-0.84 S*	NS	-0.62 S	NS	NS
Diaphanosoma S/L	0.77 S*	0.67 S	NS	0.67 S	0.71 S
Ceriodaphnia S/L	0.66 S	0.61 S	NS	NS	0.68 S
Bosmina S/L	0.79 S*	0.69 S	NS	0.67 S	0.76 S
Keratella	-0.74 S*	NS	NS	NS	-0.70 S*
Small rotifers	NS	-0.57 S	NS	NS	-0.73 S*
Total P	0.66 S*	NS	NS	NS	NS
Total N	NS	NS	NS	-0.54 S	-0.76 S*
N/P (wt/wt)	-0.79 S*	-0.59 S	NS	-0.65 S	-0.74 S*

copepods and *Keratella* (P=0.01), nauplii and *Bosmina* (P=0.05) were also significantly reduced during this period. The ratios of small (I-III neonate) to large adult *Diaphanosoma*, *Bosmina* (P=0.01) and *Ceriodaphnia* (P=0.05) were positively correlated with time (1975-85), i.e., densities of small relative to large cladocerans increased.

Phytoplankton vs. Time

The biomasses of nonPyrrhophyta (P=0.01), Chlorophyta and total phytoplankton (P=0.05) were positively correlated with time r=0.68; r=0.64 and r=0.62, respectively; i.e., their biomass increased in Lake Kinneret, whereas the biomass of Pyrrhophyta, Cyanophyta and Bacillariophyta did not change significantly during 1972-85.

Nutrients vs. Time (Table 2)

Total-P increase and TN/TP (wt/wt) ratio declines were significant. During 1974-85, total nitrogen (TN) significantly (r=-0.83; P=0.0017) declined in the lake. The atomic ratio (AR) between particulate N (PN) and particulate P (PP) significantly (P=0.01) declined during 1974-89 (r^2=0.7) (Table 1).

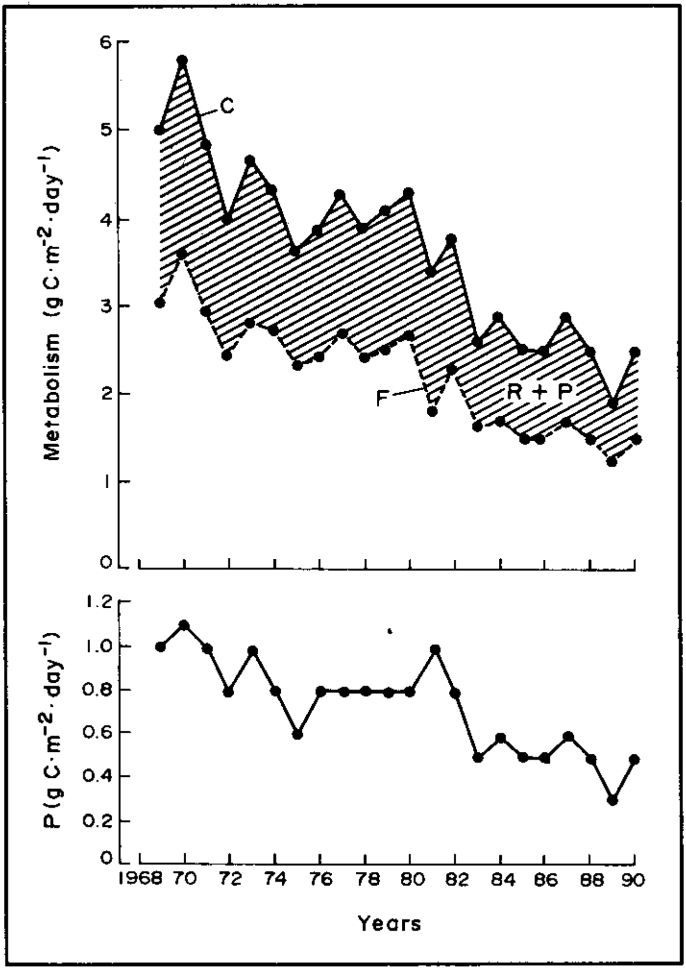

Fig. 1. Annual averages of metabolic activities (C=R+P+F; where: C=food consumption; R=respiration; P=production; F=defecation) of zooplankton communities in Lake Kinneret, during 1969-90 in g C·m^{-2}·day^{-1}.

Zooplankton-Phytoplankton Relations (Tables 2 and 3)

Copepoda and Rotifera biomass were negatively correlated with phytoplankton variables except with Pyrrhophyta and Bacillariophyta, and except Rotifera with Cynanophyta. Cladocera biomass was inversely correlated with Cyanophyta and nonPyrrhophyta.

Densities of adult copepods and nauplii were negatively related to Cyanophyta; *Bosmina* was inversely related to nonPyrrhophyta; *Keratella* was negatively related to total phytoplankton and nonPyrrhophyta. Small rotifers (all species excluding *Asplanchna* spp. and *S. pectinata*) indicated inverse relations with Chlorophyta and total phytoplankton.

The relations between phytoplankton and zooplankton were further evaluated using a dataset of monthly (1970-89) biomass values ($g_{w.w.}/m^2$). Regressions between running (five-month) averages of phytoplankton and time (months) and zooplankton (z) were calculated and the results are given in Table 3. Regressions between ratios of phytoplankton (total and each group), zooplankton and time indicated positive and significant relations, i.e., phytoplankton biomass became significantly higher relative to the biomass of zooplankton (and/or *vice versa*). Significant inverse relations were indicated between Cyanophyta, Chrysophyta and Chlorophyta and zooplankton, whereas it was positive for Pyrrhophyta and zooplankton (Table 3).

Table 3. Five-month running averages of monthly means of phytoplankton (P=total, Pyr.=Pyrrohophyta, Chr.=Chrysophyta, Cyano.=Cyanophyta; Chl.=Chlorophyta) biomass during 1970-89 (DF=233; y=a+bx) NS=not significant; Z=zooplankton.

Parameters	r	P	a	b
(P/Z) vs. (time)	0.6	<0.0001	0.7278	0.0142
(Pyr/Z) vs. (time)	0.4	<0.0001	0.7626	0.0077
(Cyano/Z) vs. (time)	0.2	0.0135	0.0722	0.0004
(Chr/Z) vs. (time)	0.5	<0.0001	-0.0974	0.0027
(Chl/Z) vs. (time)	0.6	<0.0001	-0.0170	0.0034
(P) vs. (Z)		NS		
(Pyr) vs. (Z)	0.3	<0.0001	20.8087	0.9466
(Cyano) vs. (Z)	-0.4	<0.0001	6.3383	-0.1154
(Chr) vs. (Z)	-0.1	0.05	9.6384	-0.1227
(Chl) vs. (Z)	-0.4	<0.0001	18.0485	-0.2721

Phytoplankton-Nutrients (Table 2)

Phytoplankton variables were insignificantly correlated with total-P but significantly inversely related to the TN/TP (wt/wt) ratio. Nevertheless nonPyrrhophyta and total phytoplankton were inversely correlated with total N.

Zooplankton Metabolism

The metabolic activities, food consumption (C), respiration (R), production (P) and defecation (F) of zooplankton communities in the lake during 1969-90 were calculated (for method see Gophen 1981) and the results are presented in Fig. 1. The decline of food consumption, respiration, reproduction and defecation capacities of zooplankton assemblages in Lake Kinneret during 1969-90 is prominent. The production of Cladocera during 1969-85 significantly ($P=0.01$) declined ($R=-0.74$) as well as copepod ($P=0.01$; $R=-0.72$). Moreover 95% of zooplankton production in Lake Kinneret (i.e., Copepoda and Cladocera) was inversely, significantly related to nonpyrrhophytes biomass. The decline of N/P ratio (enhancement of N-limitation) was significantly ($P=0.01$) and positively related to Copepoda production and total zooplankton biomass ($P=0.01$; $R=0.62$).

Discussion

The impacts of top-down forces (fish cascading effects) on lake water quality were intensively studied during the last three decades (Zaret and Paine 1973; Drenner et al. 1984; Reinertsen and Olsen 1984; Benndorf 1987; Carpenter 1988; Van-Donk and Gulati 1989; Gulati et al. 1990; He and Kitchell 1990). Several studies indicated the importance of bottom-up forces (nutrients) on phytoplankton density relative to top-down effects in freshwater ecosystems (McQueen et al. 1986; Benndorf 1987; Drenner et al. 1990; Carpenter 1988).

The Kinneret water quality, particularly summer densities of nanoplankton, is one of the major concerns for managers of drinking water supply from the lake.

The results presented here indicate a density decline of large copepods and cladocerans as well as of the small organisms, nauplii and *Keratella*. This zooplankton suppression was partly enhanced by an increase of fish predation pressure in the Kinneret ecosystem (Serruya et al. 1980; Gophen 1986, 1987, 1988).

Zooplankton reduction was accompanied by an increase of the biomass of total phytoplankton and nonPyrrhophyta, particularly Chlorophyta. Changes of nutrient contents occurred simultaneously: total P increased during 1969-85 and total N declined between 1974 and 1989. As a result, the TN/TP (wt/wt) ratio was lowered from values of 42-63 during the early 1970s to below 29 during the mid-1980s. It is also expressed as lower level of particulate-P/particulate-N, atomic ratio (AR) during the 1980s compared to the 1970s (Table 1). The impact of TN/TP variations on the phytoplankton assemblages was presented by Niemi (1979), McCarthy (1980), Tilman et al. (1982), Smith (1983), McQueen and Lean (1987) and Trimbee and Prepas (1987). It was reported by Smith (1983) that blue-green algal blooms occurred only, but not necessarily, when epilimnetic TN/TP (wt/wt) ratios were below 29. The effects of TN, TP, temperature, light availability and the different N form sources, in the relative biomass of Cyanobacteria were also analyzed (Smith 1986, 1990; McQueen and Lean 1987; Trimbee and Prepas 1987). Schindler (1977) and Niemi (1979) hypothesized that low N/P ratio of loads should result in N limitation for phytoplankton growth and should therefore be associated with blooms of N-fixing Cyanobacteria in lakes. Several investigators concluded that absolute P concentration rather than N/P ratios may be the dominant factor influencing the success of planktonic Cyanobacteria (Reynolds 1986; Pick and Lean 1987; Trimbee and Prepas 1987).

During the 1980s there was a decline of N/P ratios in the Kinneret seston composition. On the other hand, the availability of measurable P for algal production was not enhanced. The relative increase of P content in the seston is therefore reflecting a higher flux from P sources (external and/or internal) to algal cells (major part of the seston). It was probably accompanied by enhancement of P recycling compared to N regeneration by zooplankton (Andersen and Hessen 1991).

It is also suggested that changes of N/P ratios in the epilimnetic seston of Lake Kinneret (i.e., zooplankton food resources) (Tables 1-2) may have a metabolic effect on zooplankton communities. Andersen and Hessen (1991) analyzed nutrient metabolism in zooplankton (homeostasis) and documented that N-limitation prevailed in communities dominated by cyclopoid copepods. It is not impossible that enhancement of N-limitation improved the nutritional conditions for small cyclopoids (*Thermoclyclops* sp.).

Algal indices (ln (% algae group/(100 - % algae group))) (Trimbee and Prepas 1987) for the annual (1972-85) averages of each phytoplankton group (Pyrrhophyta, Cyanophyta, Chlorophyta and Bacillariophyta) were calculated. These annual values as well as log biomass of phytoplankton groups were analyzed by linear regressions versus logs of TP, TN and TN/TP ratios. Results of significant (P=0.01) relations are given in Table 4. Consequently, I suggest that long-term alterations of bottom-up forces (as presented by the variables of TN, TP and TN/TP; PP, PN and PP/PN-AR) in Lake Kinneret during 1972-85 positively affected (enhanced) densities of Chlorophyta. Moreover, the positive relations between indices of Chlorophyta and Cyanophyta might give a precautionary signal for predicted enhancement of Cyanophyta in the lake.

Table 4. Significant (P = 0.01) relations found between algal indices and biomass and log TN and log TN/TP; B = biomass; I = index; Chl = Chlorophyta; Cyano = Cyanophyta; TN = Total nitrogen; TN/TP = wt/wt ratio between total N and total P.

Variable	r^2	Regression
Chl. I vs. Cyano. I	0.64	Chl. I = 0.5694 + (0.4400 x Cyano. I)
Chl. log B vs. log (TN/TP)	-0.62	Chl. log B = 3.3668 - (1.5952 x log (TN/TP))
Chl. I vs. log TN	0.61	Chl. I = 2.7494 - (1.6963 x log TN)

If the observed enhancement of N limitation in Lake Kinneret during the 1980s will continue, accompanied by increasing level of P availability, flourishing of Cyanobacteria might be realistic. Nevertheless, increased level of available P is mostly affected by the chemical properties of the Kinneret waters (Serruya et al. 1980).

Smith (1990) suggested that the impact of N/P ratios on the growth of Cyanobacteria differs across an enrichment gradient and the magnitude of their effect will vary at different concentrations of TP. The effect of P supply on N fixation in lakes was suggested by Howarth et al. (1988) and confirmed by Smith (1990). Drenner et al. (1990) presented results of experiments where nutrient supply (N and P) and fish effects were not independent of each other for TP, secchi depth and filamentous blue-greens.

Nanoplankton (mostly chlorophytes) enhancement in Lake Kinneret was simultaneously affected by both top-down and bottom-up forces: increasing particulate-fish predation suppressed large copepods and cladocerans and filter-fish planktivory reduced the small nauplii and *Keratella* spp. (Gophen 1987, 1988). As a result, grazing pressure of zooplankton on nanoplankton was lowered and the density of algae was enhanced; the increase of total P, decrease of total N and therefore decline of TN/TP ratio, probably favored chlorophytes, and thus contributed also to the enhancement of these phytoplankters.

The positive relations indicated between Pyrrhophyta and zooplankton is in agreement with previous observations on nongrazeability of *Peridinium* by zooplankton (Gophen 1981). The inverse relations between zooplankton and all other algal groups is indicating trophic relations (i.e., predator-prey) and/or nanoplanktonic food limitation for zooplankton in Lake Kinneret.

The increase of soluble-P and decrease of organic-N loads in the Jordan inflows during the 1980s were documented by Geifman et al. (1987). It is suggested that decline of N content in the seston was mostly affected by lowering of external supply of N during the 1980s and the increase of particulate P in lake waters was at least partly enhanced by the loads.

To prevent a future enhancement of nanoplankton in Lake Kinneret, two parallel operations are recommended: 1) stop the decline of TN/TP ratio either by reduction of available P loads and/or modify the regime of N supply; and 2) reduce fish predation pressure on zooplankton (biomanipulation). Benndorf (1987) stated that the efficiency of biomanipulation in the improvement of water quality by algal biomass reduction is highly dependent on a decrease of P content. I assume that this is also relevant to the Kinneret management policy.

Howarth and Marino (1990), in a commentary paper, stated that Cyanobacteria gain a competitive advantage by fixing N only when the ratio of available N to available P is low (Tilman et al. 1982), and that the N/P loading ratio appeared to be a reasonable predictor of whether N fixation by plankton would occur in lakes. They concluded that P is one important control on planktonic N fixation but not the only one. Therefore, I suggest that N/P effects on Kinneret water quality require a wide spectrum of investigations.

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Manuscript received 6 February 1989; revised ms received 18 December 1991; accepted 15 May 1992.