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Search for Environmental Causation of the Cladoceran Dynamics in Lake Kinneret, Israel

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Abstract

Ten years of monthly dataset of cladoceran (*Diaphanosoma* sp., *Bosmina* spp., *Ceriodaphnia* spp.) density in Lake Kinneret (spatially scattered lake sampling stations), Israel, was studied with the aim of searching impact factors controlling their dynamics. Statistical regressions indicated that out of several environmental factors (among others, non-pyrrhophyte algal biomass, invertebrate predation) only temperature factor was relevant. Additional speculative assumptions of zooplanktivore fish predation suggest this factor as a significant impact on cladoceran dynamics.

Keywords

Cladocera, Monthly, Dynamics, Temperature, Fish, Predation

1. Introduction

The spato-temporal and bathymetrical distributions, as well as the eco-physiological characteristics of Cladocera in Lake Kinneret, were widely studied by the author. Metabolic activities during 1972-1977 comprised of two cycles: 1972-1974 and 1975-1977 suggested changes of nutritional values of potential food resources [1]. The role of cladoceran organisms within the Carbon flow pattern of the Kinneret ecosystem was analyzed [2]. The impact of food availability, fish predation and temperature on their distribution was documented as well [3]. The potential impact of fish and invertebrate predation on cladoceran densities was documented [4]. The temporal changes of cladoceran metabolic traits in relation to changes in nutrient availability in Lake Kinneret were documented [5]. The impact of temperatures on the densities of cladocerans assemblages was documented [6] [7] [8]. The relation of cladoceran population dynamics to fish predation and consumed algal preferences based on annual means were documented [9]. The temporal indications in those studies were annual or several

months (seasonal) timing intervals. In the present paper, the monthly time units were considered. It makes it possible to implicate a precise insight into the temporal trend of changes of the cladoceran population.

Recent environmental changes within and around Lake Kinneret eco-system, such as, climate, hydrology, phytoplankton, and nutrients, did not have a direct impact on the cladoceran densities fluctuations. Nevertheless, an indirect impact on the cladoceran community was documented. Although climate changes of temperature increase, precipitation, river discharges and Lake-water-level decline, did not directly influenced long-term Cladoceran densities although seasonal fluctuations of temperature passively affected their dynamics. Climate changes also affected nutrient regimes in the lake. The Kinneret eco-system was shifted from P to N limited system. Phytoplankton composition was changed; hydrochemical cycles were modified as well; the metabolic trait of cladocerans were responsively changed but long-term change of density fluctuations of as a result of nutrient availability modifications was not indicated.

2. Material and Methods

The density of Cladocera in Lake Kinneret was monitored since 1969 and onwards. A decade (1975-1985) of the dataset was chosen for the analysis of monthly changes of the numerical density values (No/L) averaged for the whole lake. A program of spatial, temporal and bathymetrical sampling was previously described [2] [5] [10]. The cladoceran organisms in Lake Kinneret were grouped into three categories: *Diaphanosoma* (*D. brachiurum*: Lieven) [11]; *Bosmina* (*B. longirostris, O.F. Muller; B. longirostris Var. Cornuta, Jurine* [10]; *and Ceriodaphnia* (*C. reticulate Jurine*)) [10]. The cladocerans were separated into two age groups: 1 - 3 neonates as "Small" and 4-adults as "Large" [8].

Statistical analyses included: Fractional Polynomial (FP) Regression models which are based on functions of a continuous covariate [12]. This type of regression provides flexible parameterization for continuous variables which provide a wide range of shapes that include other shapes provided by ordinary polynomials. Data of phytoplankton and Epilimnetic temperatures were maintained from the Kinneret Limnological Data base [13]. The data presented here represent huge bulk of collected sample analyses, with spatial, temporal and bathymetrical justified cover, and therefore standard error and standard deviation values are statistically sufficient for the evaluation processes.

The estimation of population growth rate was done using the standard exponential population growth model:

$$N_t = N_o e^{rt}$$

And: $r = (\ln Nt_2 - \ln Nt_1)/(t_2 - t_1)$ (in: 30 for daily and 1 for monthly), where,

Nt_2—the population size at time t.

Nt_1—the initial population size.

r—the intrinsic rate of growth.

3. Results

The study of the relations between cladoceran densities and limnological parameters was initiated by computing Simple Correlation (Dependence Coefficient) between monthly averages of zooplankton groups and epilimnetic temperatures and Chlorophyll concentrations; results are given in Table 1.

Results in Table 1 indicate high dependence relations between zooplankton and temperature and lower dependence relations with Chlorophyl concentration. Nevertheless, Small and Large *Bosmina* and small Ceriodaphnia declined with Temperature increase; Small and Large *Diaphanosoma* and Small *Ceriodaphnia* decreased when Chlorophyll increased.

The next step of the statistical analysis was Polynomial Regressions between the Zooplankters Densities (monthly means of No/l) and Epilimnetic Temperature (°C) and Chlorophyll Concentration (µg/l). Results of Correlation Coefficient (r^2) and probability (p) values are given in Table 2.

Table 1. Correlation/Dependence Coefficients between Mean Monthly Densities (No/l) of Small (S) and Large (L) *Diaphanosoma, Bosmina* and *Ceriodaphnia* and Epilimnetic Temperature (°C) and Chlorophyll concentrations (µg/l) (Positive = Increase; Negative = Decline).

Dependent: S, L Zooplankter	Independent: Temp.	Independent: Chlorophyll
S-Diaphanosoma	0.405	−0.236
L-Diaphanosoma	0.401	−0.197
S-Bosmina	−0.055	0.228
L-Bosmina	−0.192	0.107
S-Ceriodaphnia	−0.556	−0.627
L-Ceriodaphnia	0.433	0.527

Table 2. Polynomial Regressions between Monthly means of Zooplankton (*Diaphanosoma, Bosmina, Ceriodaphnia*) density (No/l) (S = Small, L = Large) and Epilimnetic temperature (Temp.) and Chlorophyll Concentration (Chlor.). Correlation Coefficients (r^2) and Probabilities (p) values are presented. Positive r^2 = Increase; Negative r^2 = Decline; S = Significant; NS = Not significant.

Variables	Correlation Coefficient (r^2)	Probability (p)
Temperature		
S-Diaphanosoma/Temp.	0.164	<0.0001 S
L-Diaphanosoma/Temp.	0.161	<0.0001 S
S-Bosmina/Temp.	NS	NS
L-Bosmina/Temp.	NS	NS
S-Ceriodaphnia/Temp.	0.309	<0.0001 S
L-Ceriodaphnia/Temp.	0.393	<0.0001 S
Chlorophyll		
S-Diaphanosoma/Chlor.	0.056	0.0065 S
L-Diaphanosoma/Chlor.	0.039	0.0235 S
S-Bosmina/Chlor.	0.052	0.0085 S
L-Bosmina/Chlor.	NS	NS
S-Ceriodaphnia/Chlor.	0.188	<0.0001 S
L-Ceriodaphnia/Chlor.	0.278	<0.0001 S

All cladoceran parameters (S&L, *Diaphanosoma*, and *Ceriodaphnia* and large *Bosmina*) were declining with increase of Chlorophyll concentration: r^2 for *Diaphanosoma*, and small *Bosmina* and *Ceriodaphnia* (S&L) Vs Chlorophyll indicated enhancement densities with chlorophyll concentration increase. The third step was grouping monthly values of the values of Small/Large Zooplankter body Ratios. The two groups were seasonal periods: Winter: January-June and Summer: July-December. The results indicated only one significant difference between summer and winter mean ratios for *Ceriodaphnia*: Winter = 0.65, and 1.13 in summer. An insignificant difference of higher in summer for *Bosmina* and lower in summer for *Diaphanosoma* were found as well.

Several other types of statistical relations between Zooplankton parameters and algal groups or limnological features (Water Level, water inflows, Nutrient concentrations Secchi Depth, etc.) were insignificant. Polynomial Regressions between the Zooplankton body size ratios (S/L) and algal groups (Cyanophyta, Chlorophyta, Diatoms), epilimnetic temperatures, and Chlorophyll concentration were insignificant. The impact of fish predation is relevant but the available data is not monthly or seasonally accurate; therefore, it will be tentatively incorporated.

3.1. The S/L Ratio (Figure 1 and Figure 2)

High value of the ratio between Small (S) and Large (L) (S/L) body cladocerans might be an implication of three environmental parameter impacts: 1) Intensive reproduction; 2) Preferential predation of large body cladocerans by Fish; 3) Both. Results presented in Figure 1 represent high S/L monthly ratios of Ceriodaphnia during July-September. Similarly, ratios of Bosmina are also higher in summer but those of *Diaphanosoma* are low only during January and May. Nevertheless, Polynomial regressions of Large Vs. Small individual densities (No/l) (Figure 2) indicate significant ($p < 0.0001$) direct relation: r^2: *Diaphanosoma*—0.293; *Bosmina*—0.162; *Ceriodaphnia*—0.614. Results in Figure 1 and Figure 2 indicate that the directly correlated (Figure 2) two parameters of Large and Small densities caused by changes in reproduction and seasonality is affected by environmental dependence such as fish predation.

3.2. Intrinsic Rate of Population Growth (r) (Figures 3-6)

The actual size and dynamic fluctuations of the entire population are shown in Figures 3-6. Results in Figure 1 and Figure 2 are not reflected or even corre-
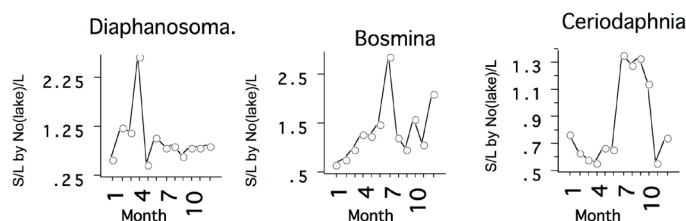

Figure 1. Monthly Lake Means of Small/Large (S/L) density (No./L) ratios of *Diaphanosoma*, *Bosmina* and *Ceriodaphnina*.
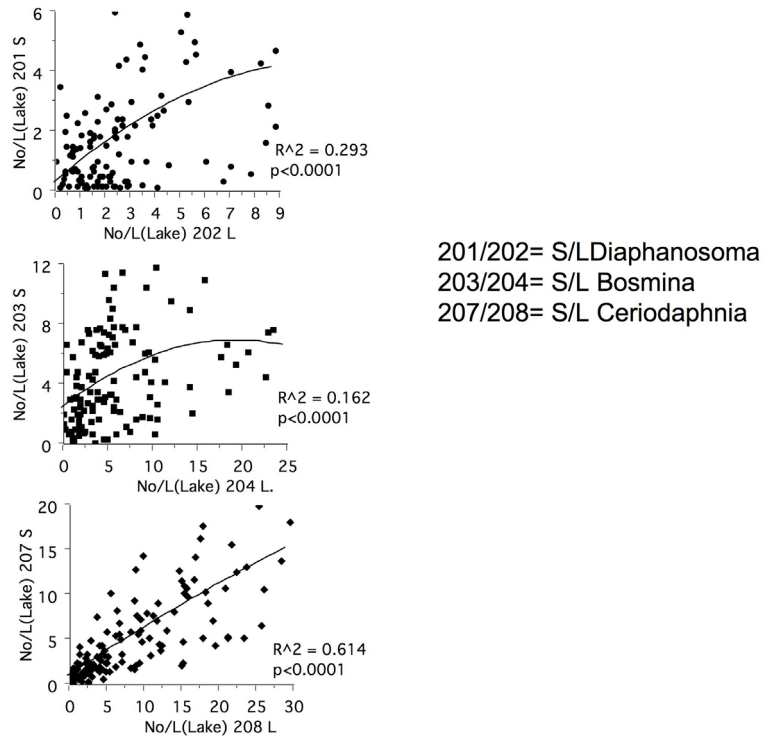
201/202= S/LDiaphanosoma
203/204= S/L Bosmina
207/208= S/L Ceriodaphnia

Figure 2. Polynomial Regressions (r² and p values are given) between lake averages of "Small" and "Large" organism densities (No./L): 201 S/202 L = *Diaphanosoma*; 203 S/204 L = *Bosmina*; 207 S/208 L = *Ceriodaphnia*.
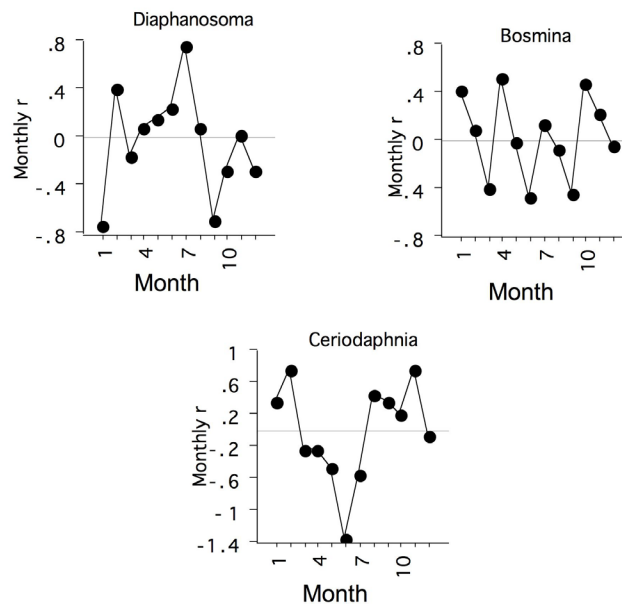

Figure 3. Monthly lake averages of the intrinsic rate of population growth (r, see text) of *Diaphanosoma, Bosmina* and *Ceriodaphnia*.

lated with results given in **Figure 3**. The population's intrinsic growth rate (r) is not dependent on S/L ratios or vice versa. Seasonal (monthly) fluctuation trait of the intrinsic rate of population growth and S/l ratios are dissimilar and therefore cannot be classified under similar impacts. All three cladocerans partly represent
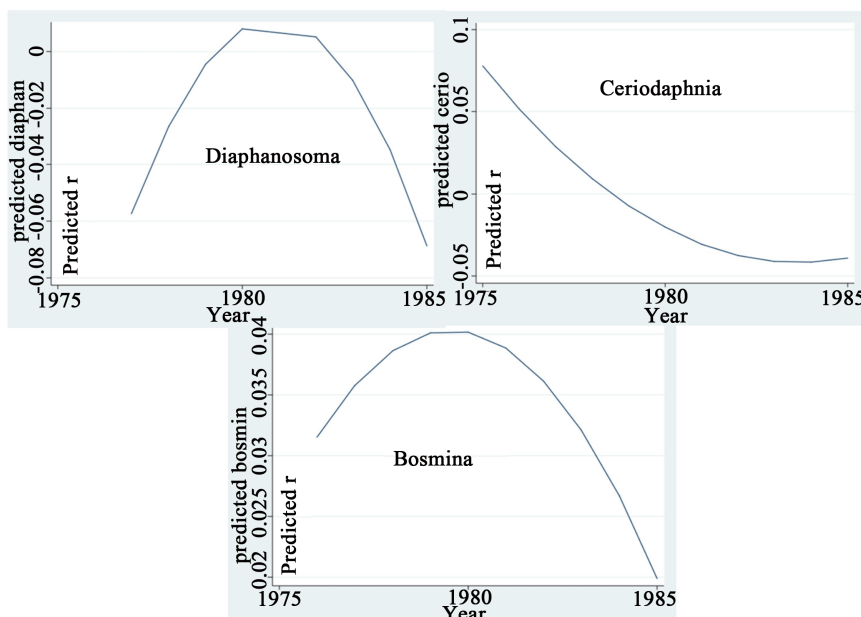
Figure 4. Fractional Polynomial Regressions between Monthly lake averages of Intrinsic Rate of Population growth (r, see text) and Years of *Diaphanosoma*, *Bosmina* and *Ceriodaphnia*.
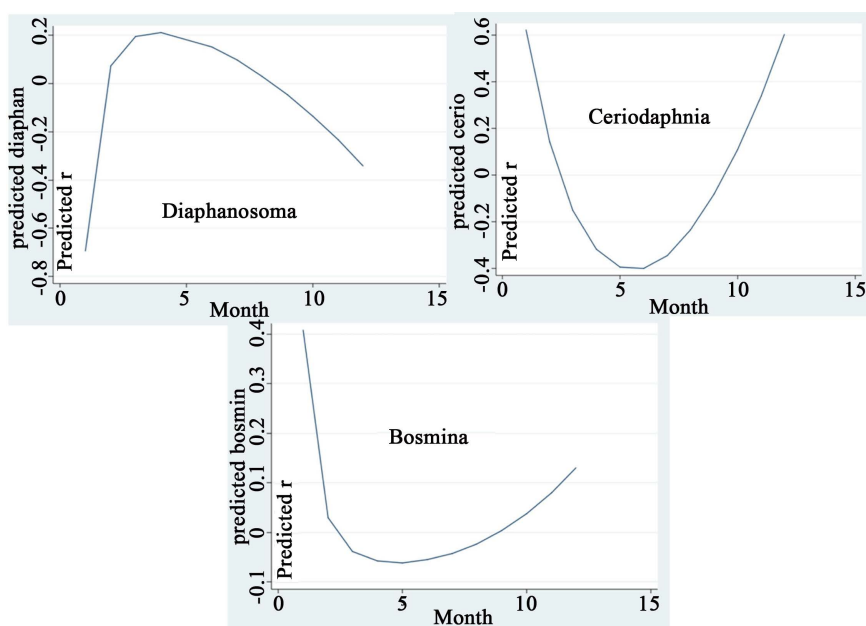

Figure 5. Fractional Polynomial Regressions between Monthly lake averages of Intrinsic Rate of Population growth (r, see text) and Months of *Diaphanosoma*, *Bosmina* and *Ceriodaphnia*.

similar annual fluctuations of r values (**Figure 4**): high in the late 1970's and declining during the early 1980's. It conclusively points to a similar impact of environmental conditions. Statistical smoothing (Fractional Polynomial; FP) of monthly r values (**Figure 5**) have shown two inverse representations between *Bosmina-Ceriodaphnia* (B-C) and *Diaphanosoma* (D): B-C Decline in late winter-spring time, and the opposite happens in D (**Figure 5**).
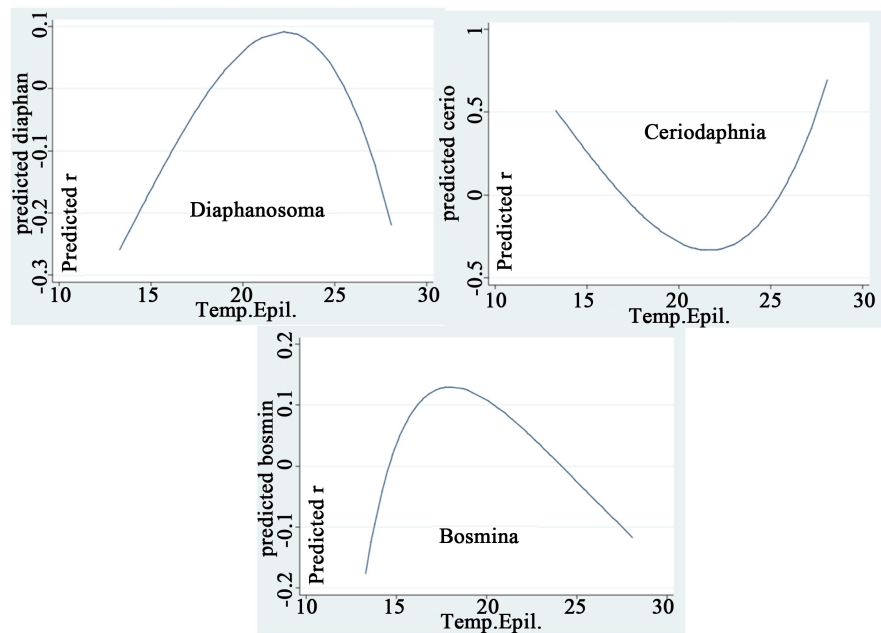
Figure 6. Fractional Polynomial Regressions between Monthly lake averages of Intrinsic Rate of Population growth (r, see text) and Monthly means of epilimnetic temperatures (˚C) of *Diaphanosoma, Bosmina* and *Ceriodaphnia*.

3.3. Epilimnetic Temperature (Figures 6-8)

Because of causative relations between most of the biological parameters and cladoceran fluctuations (monthly, annually) of densities, the Temperature parameter was tested. The impact of temperature increase on the cladocerans population rate of growth (r) is given in **Figure 6**: none of the Cladocera genera represents a unidirectional trend of relation. The optimal r values (highest rate of population growth) for *Diaphanosoma* and *Bosmina* are similar: 15˚C - 23˚C (corresponding to the Winter-Spring season; whilst for *Ceriodaphnia* two ranges: 13 - 17 and 26˚C - 29˚C (corresponding to Winter and late Summer) (**Figure 6**). **Figure 7** and **Figure 8** represent annual (**Figure 7**) and seasonal (**Figure 8**) fluctuations of epilimnetic temperatures smoothed (FP). From the early 1980's the temperature declines towards 1985; Winter 15 - 20; Summer 20 - 27.

4. Discussion

Relations between zooplankton densities and environmental conditions in lakes, either physical or biological factors, were widely studied. Lampert [14] documented zooplankton biomass build-up due to both favorable food conditions and low predation pressure followed by the development of "clear-water-phase". Manipulation of planktonic communities might be beneficial for lake restoration as water quality improvements [14] [15] [16] [17] [18]). The case study of cladoceran communities in Lake Kinneret presented in this paper is an attempt aimed at searching causative environmental parameters which control the cladoceran dynamics. It is done here, the first time, by place reliance on multiannual monthly resolution of the assemblage densities. Periodical (2 year
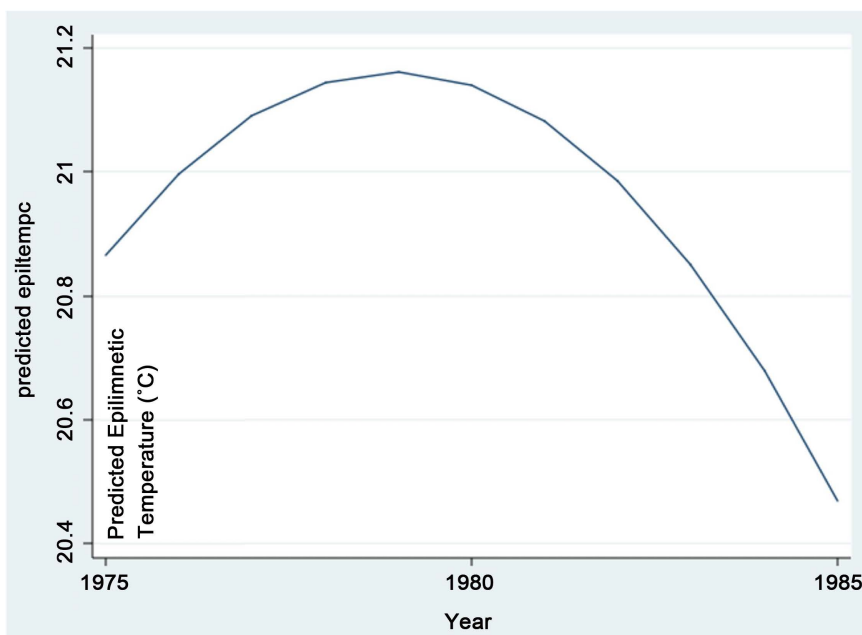
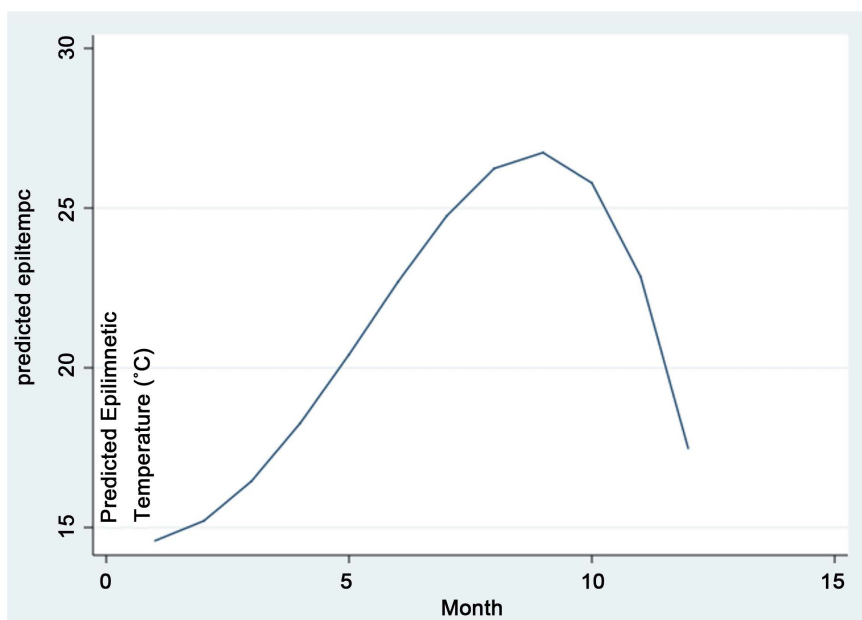**Figure 7.** Fractional Polynomial Regressions between Monthly lake averages of Epilimnetic Temperature (˚C) and Years.

Figure 8. Fractional Polynomial Regressions between Monthly lake averages of Epilimnetic Temperature (˚C) and months.

groups: 1972-1974 & 1975-1977) changes of the food nutritional value comparatively analyzed and the impact on cladoceran metabolic activity was concluded [1]. Temperature effect on the metabolism of *Ceriodaphnia* was previously documented [6]. It was found that under a temperature of 15˚C (Kinneret winter time) metabolic activities of *Ceriodaphnia reticulata* was lower by 61%, 58% and 62% in comparison with 27˚C as measured by food intake, Ammonia excretion, and respiration respectively. The production enhancement of *Ceriodapohnia* in

summer is therefore concluded as presented here (Figure 6) by the increase of r values. The opposite trend of lower production (decline of r values) of *Bosmina* and *Diaphanosoma* in summer (Figure 6) was indicated. It is suggested that the temperature elevation effect on the metabolic activity of *Diaphanosoma* and *Bosmina* is similar to *Ceriodaphnia*. Nevertheless, the summer low (*Bosmina*) or decline (*Diaphanosom*a) in "r" values (Figure 5) are due to the spring-summer increase of fish predation. These conclusions are the outcome of both experimental studies of the temperature impact on metabolic activity and the multiannual-monthly data on population dynamics presented here (see also [5]). The multiannual study, when based on annual means, [5] similarly indicated enhancement of cladoceran production in summer which supports the assumption of a significant impact of fish predation on the entire assemblages during summer conditions.

Here, an attempt was tentatively made at the implementation of experimental data to the long-term monthly record of lake population densities. Results of Polynomial Regression analysis (r^2 and p, values) (Figure 2) between young ("small") and matured life cycle stages ("Large") indicates significant relations where the highest is due to *Ceriodaphnia* ($r^2 = 0.614$) and the lowest to *Bosmina* ($r^2 = 0.162$). Consequently, it is suggested that environmental factors are similarly affecting the "small" and the "large". For example, if food condition parameter is improved and production rate enhanced, as well as intensification of visual particulate attacker fish predation pressure on "Large", the increase of S/L ration is predicted. Several other options are also relevant: cladoceran food sources deficiency followed by a lower production rate (relative decline of "small") or stock increase of filter feeder fishes which suppress the "small" higher than the "large"; also the decline of S/L ratio is predicted. The similarity of environmental impact on different groups of zooplankton is exemplified by the evaluation of the relationship between herbivorous (Young Cyclopoid stages and cladocerans) [19] and predator zooplankters (Adult Cyclopoids) (Figure 9). Figure 9 indicates a positive direct relationship between herbivore and predator zooplankton biomass, e.g. similar eco-forces pressure on both. Food composition of the zooplanktivore Bleak (*Acanthobrama terraesanctae terraesnctae, Mirogrex lissneri*) fishes, which produce the dominant stock biomass in the lake is due mostly to zooplankton, and cladoceran biomass is the major component. The ability to escape of adult predator Cyclopoids is much higher than that of herbivore cladocerans, which are therefore preyed upon more efficiently. It is suggested that fish predation (no data given) and Temperature are the dominant factors which have an impact on the cladoceran density dynamics. Figure 1 presents the multiannual monthly means of the S/L seasonal distribution which emphasizes seasonality. Figure 2 represents the proportion of the variance in the "Small" (dependent variable) group that is predictable from the "Large" (independent variable) and the significance as given by the p (probability) values of $p < 0.01$. Multiannual monthly means of Intrinsic Rate of Population Growth ("r") (Figure 3) indicates seasonality (Winter/Summer) in *Diaphanosoma* and *Ce-*
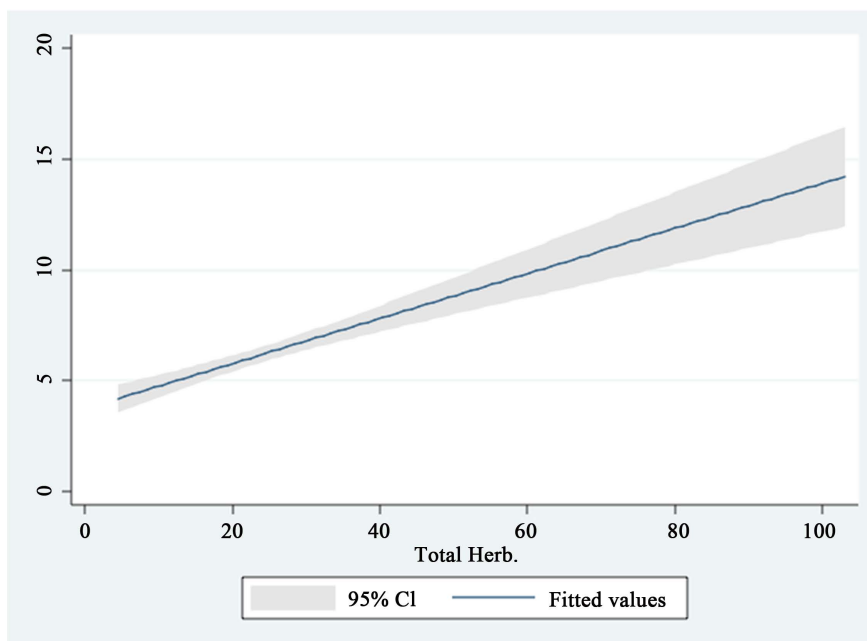
Figure 9. Polynomial Regression (shadow = 95% Confidence Interval) between monthly lake averages of biomass (g(ww)/m²) of predator (Copepodite 5 and adult cyclopoid stages) and herbivore (young cyclopoid, cladocerans and small rotifers) in Lake Kinneret.

riodaphnia and three months periodical fluctuations of *Bosmina*. Fractional Polynomial Regression Model (FP) predictions of r (intrinsic rate of population growth) (in No/l density values) in relation to years, months and temperature are presented in **Figures 4-6**. The advantage of FP is to increase the flexibility afforded by conventional polynomial models (StataCorp 2005) [20]. The fact that Coefficient of Determination (r^2) between two variables was found to be high is not necessarily a clear indication of a circumstantial relationship. The existence of a third variable as a link between the two is possible. Conclusive attribute to the r^2 level is required.

The concept of isolating related parameters of cladoceran densities and biological and/or chemical environmental parameters did not indicate strict causative variables. Even those variables which were partly validated cannot be confirmed as sole causatively correlated. Temperature impact partly confirms causation impact on a monthly basis. As known from numerous studies about Plankton-Fish relations in the Kinneret ecosystem, it is reasonable that fish predation factor plays a major role in the complicated Kinneret ecosystem aimed at cladoceran dynamics. Since detailed information on seasonal and annual dynamics of fish stock biomass is not available, inserting this parameter into a comprehensive discussion is partly speculative. It is known that the most common fish in Lake Kinneret is the Bleak Lavnun (*Acanthobrama terraesanctae-terraesanctae* and *Mirogrex lisnerri*), a zooplanktivore and Cladocera which are preferentially consumed. But seasonality and annual trend of stock biomass changes are unknown.

Usually, if from statistical evaluations a perfect answer to the search for causa-

tive parameters of the cladoceran dynamics is insufficient, a Model construction is the common solution. The modularity of complex interactions is very problematic or complicated. In a comprehensive model aimed at eco-limnological trait, there is a common option of an unwanted discord between noisy data when simulated with observed findings. A comprehensive eco-limnological (coupled physical and biological parameters) approach is commonly caused by the usage of many parameters and state variables whose validity is questionable. Several different parameter sets can produce similar dynamics. Moreover, the complexity of the food-web interaction aimed at the relevance of physical, biogeochemical and ecological coupled aspects make the validity of the model lower. Consequently, a simple model approach is more beneficial. Zooplanktivorous fish biomass impact on dynamics of nutrients and their partitioning among the ecosystem compartments linked to fish which strongly affect the nutrient dynamics and fluxes were documented by, among many others, [21]. Experimental results and the consequent computation of Carbon eliminated by a given biomass of zooplankton was estimated based on metabolic requirements (growth and grazing rates) of the grazers [2] [14] [18] [21]. Those coupled relations were used to estimate phytoplankton biomass fluctuations (Lampert, 1988). The effectiveness of two factors, fish predation and Temperature is the essence of the present study. .The raw data of cladoceran monthly stock density fluctuations is given in Figure 10 and Figure 11. All six cladocerans groups, Diaphanosoma, Bosmina,
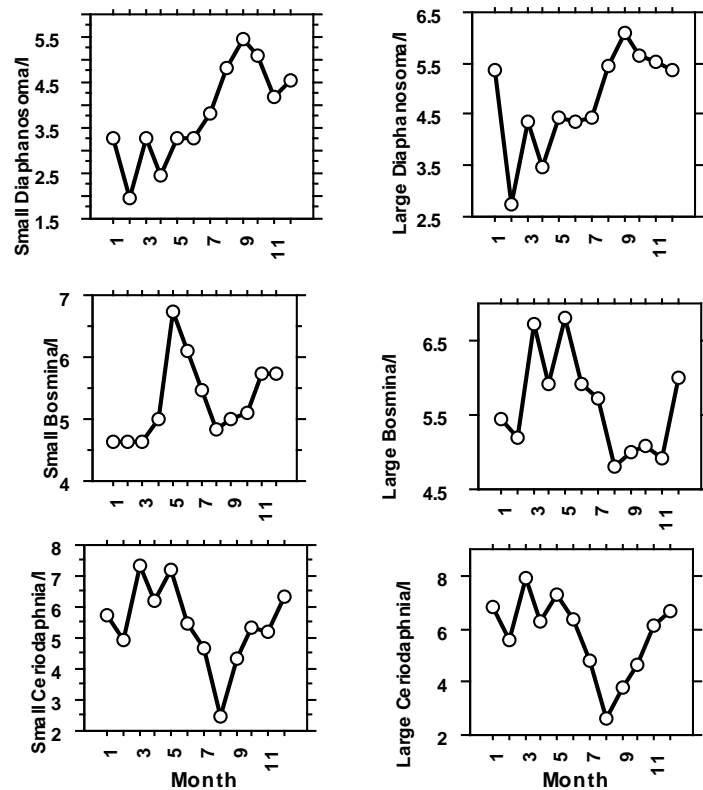

Figure 10. Monthly averages of Small (left 3 panels) and Large (right 3 panels) organisms of Diaphanosoma (upper 2 panels), Bosmina (middle 2 panels) and Ceriodaphnia (2 lower panels) densities (No./l) in Lake Kinneret (1975-1985).
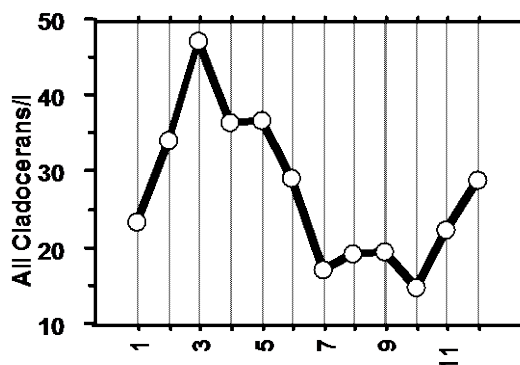
Figure 11. Monthly averages of densities (No./l) of total number of cladocerans in Lake Kinneret (1975-1985).

Ceriodaphnia, Small and Large, represent similarity of seasonal distribution pattern although slight variance were indicated: Both, Small and Large Diaphanosoma represent similarly low densities in winter and high in summer. That is a result of temperature decline and increase in winter and summer respectively. Nevertheless, in summer, fish predation is enhanced as well but the efficient escapeability of Diaphanosoma reduces their vulnerability. Not like Diaphanosoma, density trait of Bosmina, and Ceriodaphnia, Small and Large, represent slightly different combined response to fish predation and temperature: Low density in winter cold water combined with low fish predation pressure. Later, in spring, density increase is induced by Temperature elevation while fish predation is not yet intensive. Temperature increase in summer confounded by the suppression of intensive fish predation. Conclusive presentation of combined Temperature and Fish Predation impacts as averaged for the entire Cladoceran community is given in Figure 11: During winter-spring (Months: 12-1-5) the dominant impact is due to Temperature increase whilst in Summer (Months: 7 - 11) although temperature is optimal but dominance impact is due to the maximal fish predation.

The fish removal by fishery management was documented by Sondergaard *et al.* [22]. This kind of management, namely, Biomanipulation, has been used in many shallow lakes aimed at water quality improvement. They summarized two such operations with an interval of 20 years between and concluded that repeated managements of fish removal might be a relevant strategy to improve the water quality of highly external nutrient loaded lakes. It is important to account the incomplete implementation of a model constructed for temperate ecosystems to the subtropical lake Kinneret. The advantage of a model is due to its simplicity and generality. Nevertheless, wrong implications are quite common: Peridinium was a bloom forming phytoplankter comprised >50% of the annual carbon fixation in Kinneret. But this alga is not edible to zooplankton and some of the fish species in Kinneret. The ichthyofauna of Kinneret comprised mostly of planktivorous species but only one of them, the most common Bleak, consume zooplankton solely. The Kinneret Bleaks prey on Cladocera more efficiently than predator life stages of Cyclopoida. Fishing removal of Bleaks could

potentially have a significant impact on the Kinneret ecosystem (Bendorf *et al.* 1984). The food resources of Bleak is significantly different from other fish species, resulting in a degree of freedom for Bleaks removal. The grazer zooplankters preferential food are chlorophytes and diatoms; therefore, fishing removal of bleaks might improve water quality by cladoceran-mediated algal suppression. Nevertheless, as documented by Bendorf *et al.* [17], reduction of algal biomass by removal of un-wanted fish (Bleaks in Kinneret) requires Phosphorus control; otherwise, failure of Biomanipulation is predicted. During the 1969-1993, zooplankton biomass declined in Lake Kinneret and removal of about 5000 tons of Bleaks during 1994-2001 was subsidized and the biomass of zooplankton significantly increased (Figure 12). As an immediate response, zooplankton biomass was significantly enhanced but algal biomass was enhanced due to an increase of Phosphorus in the lake epilimnion. Two common modeling approaches to the study of Kinneret ecosystem dynamics aimed at the design of optimal fisheries management including zooplankton pressures were achieved: 1) The "Box Model" (Serruya *et al.* 1980) which described the major pathways of Carbon flow emphasizing the existence of two superimposed food chains: Nannoplankton-zooplankton–Bleaks and the *Peridinium-Sarotherodon glilaeus*-Detritus; 2) The "ECOPATH II" model [23] based on Biomass and Production rate of Phytoplankton, Zooplankton, Protozoa and Bacteria, and commercial fishery catches and the fish diet. Several of the ECOPATH model conclusions pointed clearly to predation on *Ceridaphnia* (*Bosmina* is not available to fish and *Diaphanosoma* is an efficient escaper) by Cyclopoid life cycle stages; most of the zooplankton production is preyed by Bleaks. Since the Kinneret food web has undergone structural modifications, discrepancies between models are predicted. Moreover, an innovated version of ECOPATH was developed the ECOSIM, aimed at temporal dynamics. It should be considered that the key initial parameters inherited from the ECOPATH are ultimately required to provide optimal simulation capabilities of the ECOSIM model. Moreover, coupled integration of ecological (zooplankton and phytoplankton) and hydrodynamics for interactive modeling of biotic and a-biotic factors probably require the usage of
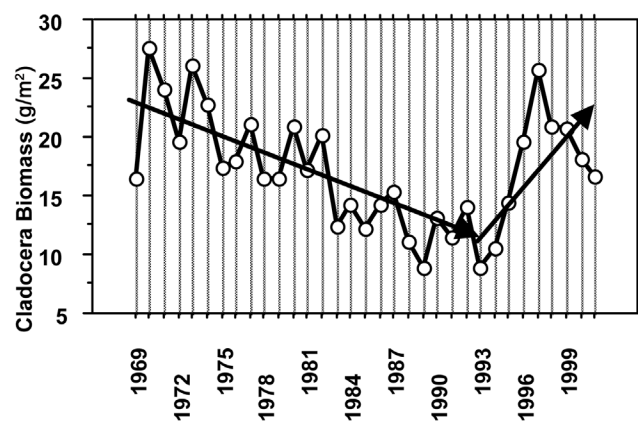

Figure 12. Annual means of total Cladoceran biomass (g(ww)/m²) In Lake Kinneret (1969-2001). Periodical decline (1969-1993) and increase (1993-2001) are arrowed.

many state variables and parameter values for the production of an adequate model. A simplified model using a low number of state variable and parameter values is more constructive and therefore recommended.

Conclusively, the cladoceran density dynamics is mostly affected by fish predation and periodical temperature changes.

5. Summary

A 10-year period of monthly record of cladoceran density (No./l) dynamic was statistically evaluated. Several indications were tested of which no direct significant relationship was identified as a major component affecting animal fluctuations. It is not impossible that food conditions and invertebrate predations are optimal. Two relevant major impacts were indicated: Epilimnetic temperatures and fish predation, mostly due to the Bleaks (*Mirogrex* sp. and *Acanthobrama* sp.). This study represents the need for indication of actually impact of the dominant ecological factors which in fact control Cladoceran reproduction and consequently their density. The present study might be therefore considered as a recommendation for future perspectives, aimed at succeeding of biomanipulation operation, *i.e.* removal of unwanted fishes.

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