

Population Dynamics of Cyclopoid Copepods in Lake Kinneret (Israel)

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Abstract

Reports on the Kinneret zooplankton in general and particularly on copepods are recently dealing with numerical densities of feeding habit classes. Nevertheless, for the evaluation of the integrated role of copepod assemblages in the entire lake ecosystem, their life cycle stages fluctuations are essential. It was not done in previous reports. Therefore, long term analysis of the cyclopoid copepods life stages dynamics in Lake Kinneret was carried out. Due to information availability, two complementary methods of density concentrations were evaluated for two consecutive data sets: 1) 1969-1985 numerical (No/L) documentation of life cycle stages of nauplii (I - III and III - V), copepodites (I, II, III, IV, V) and adults; 2) 1969-2002 monthly averages of wet biomass density (g/m^2) of zooplankton major groups combined with metabolic rates. nauplii densities represent June-August peaks and older stages spring decline and high levels during summer-early winter. Polynomial Regressions between Numerical annual averages of predator and Herbivore stages as well as young vs. older life stages indicate significant relations. During winter-spring season, temperatures are optimal for cyclopoid growth as a result of the high efficiency of metabolic activity and the low pressure of fish predation. The high rate of metabolism and intensive fish predation in summer enhance low densities of adult cyclopoids.

Keywords

Kinneret, Cyclopoida, Population, Dynamics, Metabolism

1. Introduction

In 1968 the Kinneret Limnological Laboratory initiated a multidisciplinary survey of Lake Kinneret of which the author was responsible for the research and monitoring of the Kinneret Zooplankton. The total number of zooplankton species documented in Lake Kinneret is 34 of which 19 are the most common. Species inventory includes 8

species of Cladocera, 6 species of Copepoda, and 20 species of Rotifera. Multiannual and seasonal fluctuations of the biomass and ecophysiological trait of the Kinneret Cyclopoida were previously published [1]-[8]. In previous studies the analysis was related to age groups (nauplius, copepodite, adults). In the present paper indications are given to life cycle stages of cyclopoids: young (small) and older (large) nauplius, copepodite stages of I, II, III, IV, V, VI and VII and adults which were counted (monitored) separately. The innovative approach to the evaluation of Cyclopoida population dynamics presented in this paper refers to life cycle stages densities and specific biomass increment.

Mesocyclops leuckarti (Claus), the most common cyclopoid in Lake Kinneret (Israel) together with *Thermocyclops dybowskii* (Lande) produce >30% of the lake zooplankton biomass. The name of *Mesocyclops leuckarti* was modified to *Mesocyclops ogunnus* (Onabamiro). The impact of temperature and fish predation on the distribution of *M. ogunnus* in Lake Kinneret was previously documented [1] [2] [7] [9]-[12]. The impact of temperature on cyclopoid reproduction and population dynamics, food and feeding habits, diurnal migration and body size was widely studied. The present study is an attempt aimed at an insight into the role of the life stages within the mixed age composed population of the cyclopoid.

Most of the Kinneret fishes are planktivorous [12]; piscivory level among Kinneret fishes is low. Most of the Kinneret fishes prey on zooplankton intensively and only few of them (Tilapias, especially *Sarotherodon galilaeus*) consume *Peridinium* efficiently. Fish predation pressure on zooplankton is mostly due to the two endemic Bleak species *Mirogrex terraesanctae* and *Acanthobrama lissneri*. As a result of *Peridinium* decline since the late 1990's, the diet of phytoplanktivorous species like *S. galilaeus* shifted towards zooplankton consumption. Moreover, reduction in Bleaks fishery caused by low market demands increased the pressure on zooplankton which responded by massive decline [13].

2. Material and Methods

Sorting of Life Cycle Stages: Stages were classified and counted and bio-volume measured as given in [14] [15] as presented in **Table 1** [3] [4].

Two data sets were combined within the analysis of cyclopoid population dynamics: 1) Densities (No./L) of life cycle specifically sorted during 1969-1985: bi-weekly samples were averaged as monthly and 7 stations as lake representatives (similar précised documentation for later years is not available); and 2) Semimonthly (every two-weeks) averaged to monthly and 4 (A, D, G, K) stations to whole lake value to Annual means of Biomass (g(ww)/m²) densities during 1969-2002. All collected data were bi-weekly sampling in 7 stations (A, C, D, F, G, K) during 1969-1985 and 4 stations (A, D, G, K) (1969-2002) [16] from 10 - 13 fixed epi-metalimnetic depths by 5 L sampler from each depth and 1 L was sub-sampled into a bucket, mixed, and 1 L was removed from this pail, preserved by 10 ml of 10% formaldehyde of which 800 ml were filtered through 0.45 µ filter paper and all collected organisms were microscopically sorted and counted.

Table 1. Characteristics of cyclopoids life cycle stages for classification (Gophen, 1978b; Harding and Smith, 1974; Williamson and Reid, 2001).

Stage	Bio-volume ($10^6 \mu^3$)*	Number of body segments: Include: Anal segment Exclude: Caudal ramus
1 - 3 Nauplius stages	0.58	Round oval shape
3 - 5 Nauplius stages	1.21	Distal part elongated
Copepodite stage I	2.95	5
Copepodite stage II	3.88	6
Copepodite stage III	5.86	7
Copepodite stage IV	7.59	8
Copepodite stage V male	8.05	9 genital segment length = length of distal last 3 segments
Copepodite stage V female	12.55	9 length of genital segment < length of distal last 3 segments
Adult male	11.30	10 Clasping Organ (antennule tip)
Adult female	24.00	9 length of genital segment = length of distal last 3 segments

*Million cubic microns.

Number of samples collected for the first data set (1969-1985) was 1870. The routine biomass analysis was part of a long term monitoring program during 1969-2002 and included zooplankton samples treated similarly.

The following statistical procedures were used for the evaluations of the relationship between cyclopoid stages, annual and seasonal fluctuations of stage densities and physiological activities: ANOVA ($p < 0.05$), Polynomial Regressions, Fractional Polynomial Prediction, LOWESS (0.8) (STATA 9.1, Statistics-Data Analysis and Stat View 5.1, SAS Institute Inc.).

3. Results

Results in **Figure 1** indicate the positive dependence of physiological activity on temperature: in the summer period, metabolism is enhanced, whereas it clearly declines during low temperatures in the winter months of January through April. The fluctuations of total biomass and the metabolic activity of the entire population are both presented to emphasize the close relation between them. Nevertheless, there is an inverse relation between zooplankton biomass density and physiological activity: in the summer period, when temperature is high, the metabolic rate is high too, together with intensification of fish predation (top-down cascading impact), causing a decline of biomass density below 10 g/m^2 for Copepoda and an even higher decline of Cladocera and Rotifera biomass (**Figure 1**). When dynamics are analyzed on the basis of numerical density, results might differ from those resulting from Biomass density evaluation (**Figure 2** and **Figure 3**). A positive relationship of annual averages of numerical densities (nauplius, copepodite, adults) of life cycle stages (**Figure 3**) was indicated. The r^2 and p resulted values justify normal acceptance of statistical relation. Increases of monthly averages of numerical densities of nauplius and copepodite stages during spring-summer

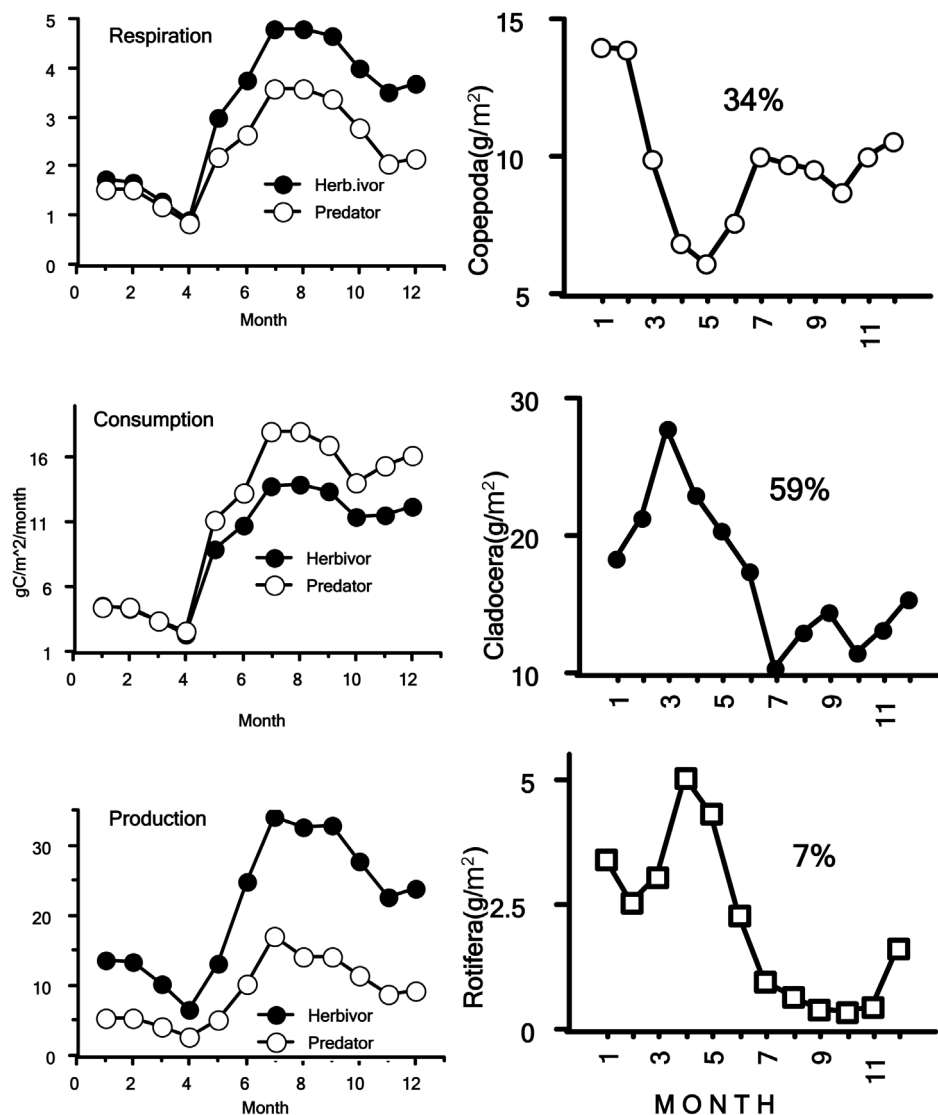


Figure 1. Left panels: monthly averages (1969-2002) of metabolic rates (gC/m²/month): respiration, food consumption and production of herbivore and predator stages of cyclopoids. Right panels: monthly averages (1969-2002) of biomass (g(ww)/m²) of zooplankton groups: copepoda, cladocera, and rotifera. % of groups is indicated.

months (May through October), but not those of adults, were documented. This prominent difference between numerical and biomass densities of population dynamics must be considered when mass balance models of lake ecosystem are constructed. Respective relation between mass and numerical densities is meaningless. It is suggested that the larger body sized adults in the mixed age of cyclopoid population are more intensively preyed on, leading to their high vulnerability.

There is a rather clear difference between the lifecycle numerical densities and life cycle stages as evaluated by Fractional Polynomial of monthly (1969-1985) averages (Figure 4 and Figure 5). Similarity of seasonal pattern was indicated within the first group of young stages of nautilus I, II, copepodite III, IV. Similarity was also indicated

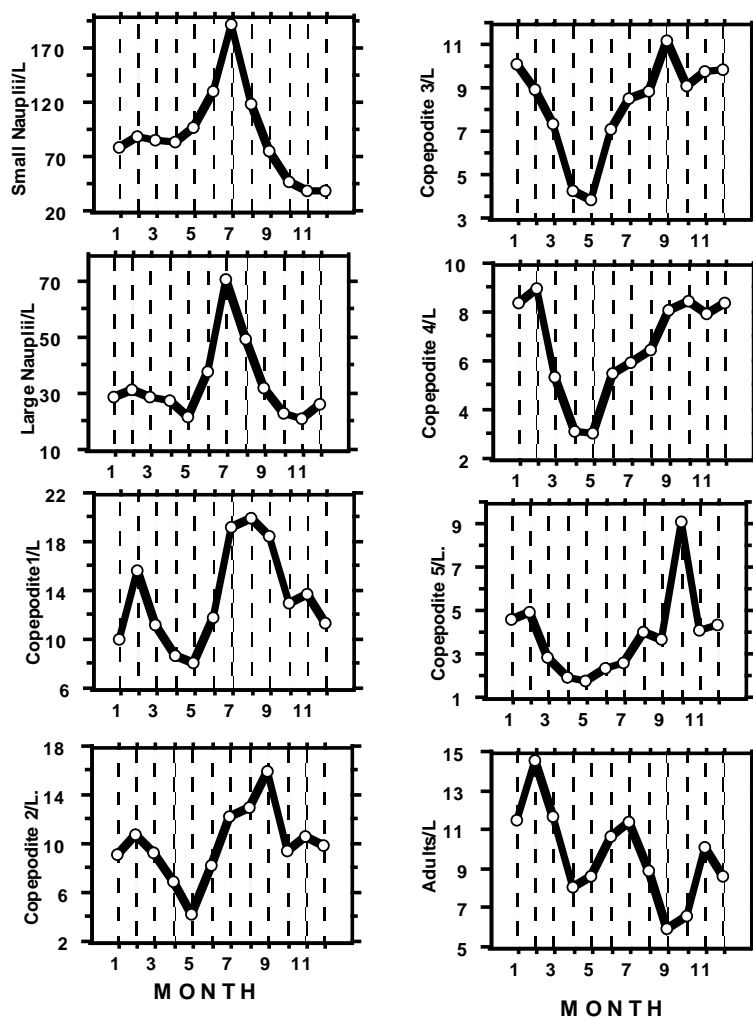


Figure 2. Monthly averages of numerical densities (No/L) of nauplii and copepodite stages and adults during 1969-1985.

for the second group of V, VI and VII stages but the pattern was different from the first group. The monthly distribution of the adults was not similar to each of the other groups. The first group predicted a winter-spring increase and a decline later on. The second group's pattern predicted a decline during winter spring period and continuous elevation afterwards. The pattern of adult distribution predicted a continuous decline from high winter values through summer-fall season.

Comparative ANOVA Test ($p < 0.05$) between winter-spring (January-May) and summer (June-December) periods of documented numerical values has indicated (**Table 2**) significant difference of copepodites and adult densities but is not significant for nauplii.

Results in **Table 2** indicate similarity of densities in two periods whilst they are lower for copepodites and higher for adults in winter-spring.

Numerical and biomass additional parameter which has an impact on zooplankton summer biomass decline is fish planktivory enhancement in summer [12]. Nevertheless,

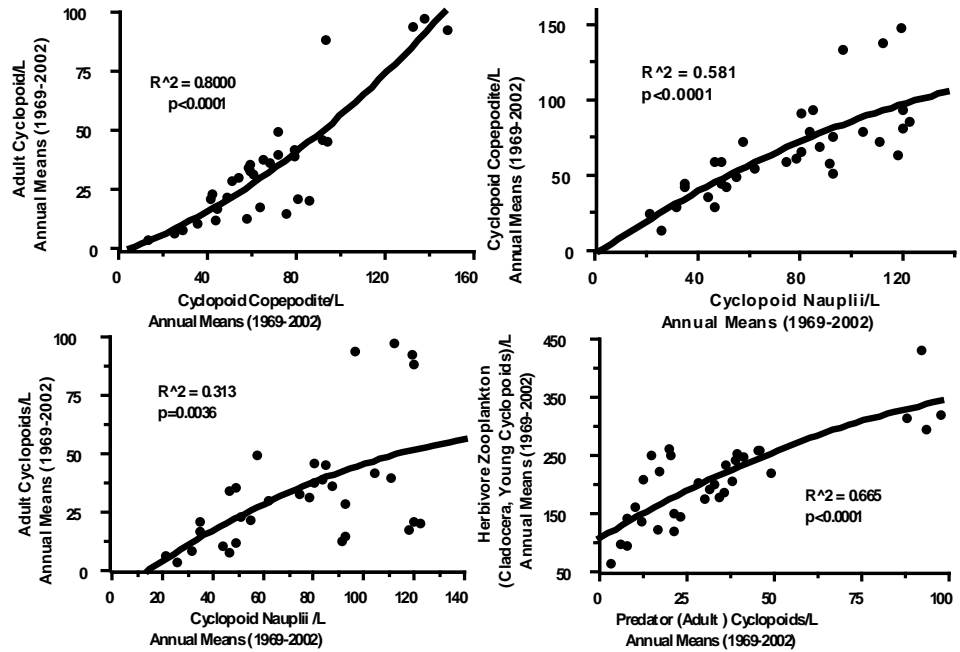


Figure 3. Polynomial regression between annual averages of numerical densities (No/L) of adults vs copepodite (left upper), adults vs nauplii (left lower), copepodite vs nauplii (right upper) and herbivores vs predator cycloids (right lower).

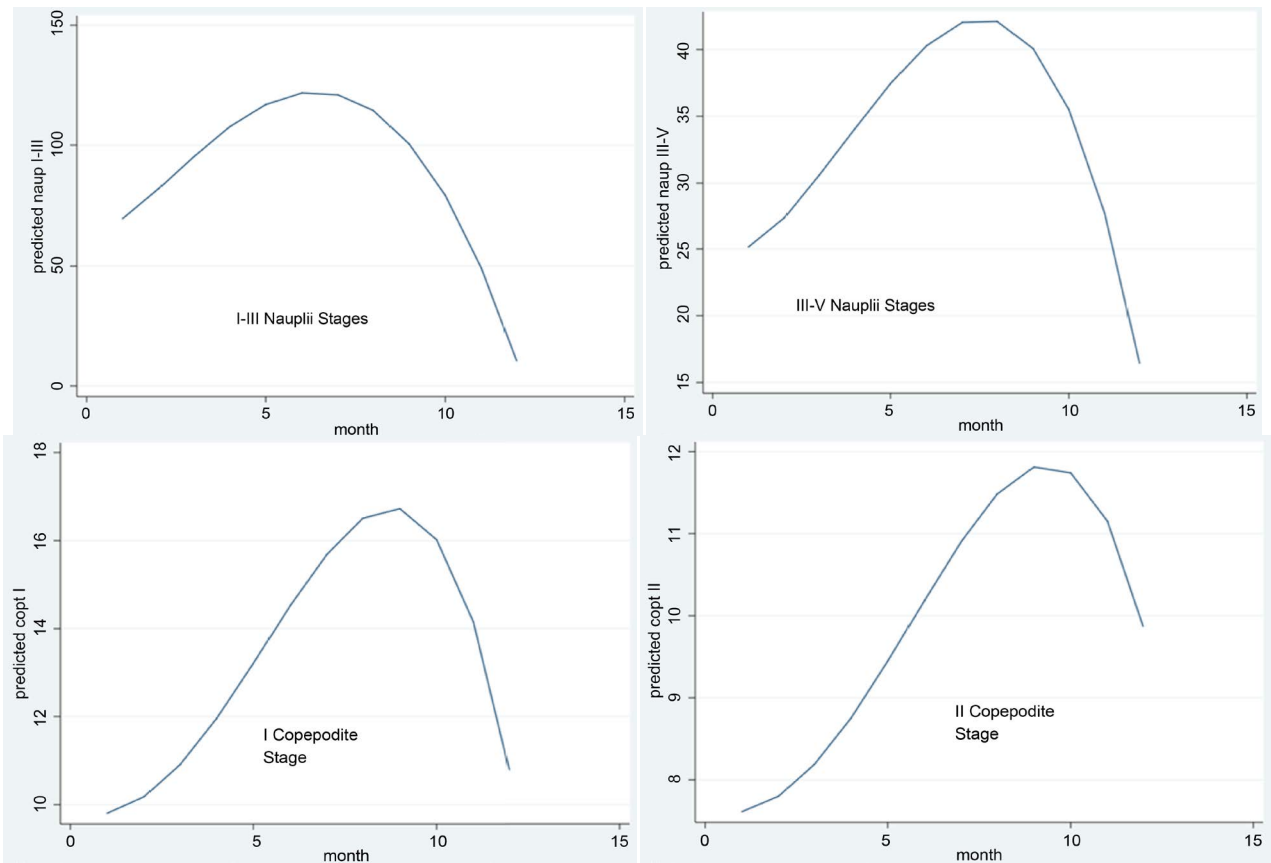


Figure 4. Fractional polynomial monthly prediction of nauplii stages (uppers) and copepodite (lowers).

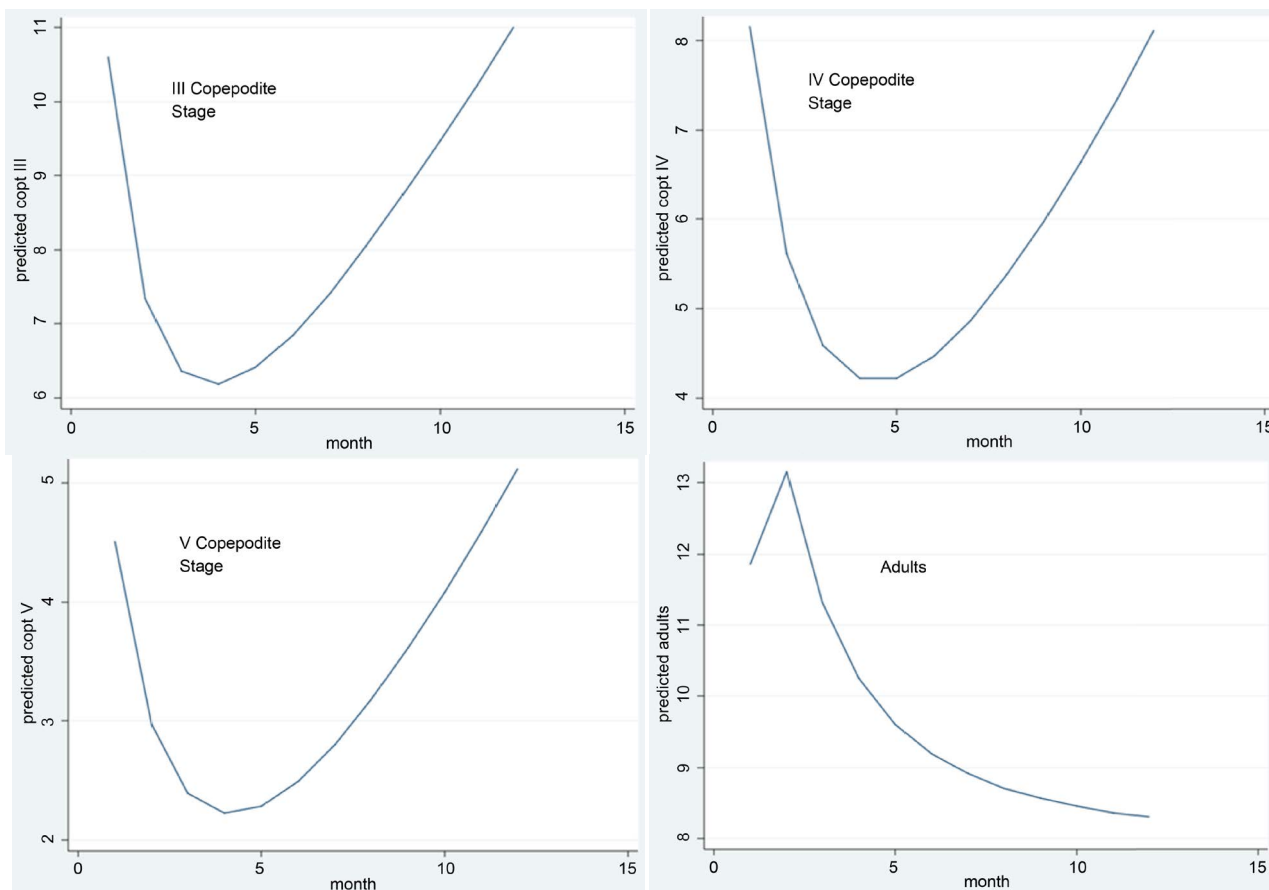


Figure 5. Fractional polynomial monthly prediction of copepodite stages (lefts and upper right) and adults (lower right).

Table 2. Results of comparative ANOVA Test ($p < 0.05$) between monthly values of numerical densities (No/L) of nauplii, copepodites and adult cyclopoids in Lake Kinneret during 1969-2002; S = Significant, NS = Not significant.

Stage	Winter-spring (mean)	Summer-fall (mean)	Probability (p)
Nauplius	118	125	0.6841 (NS)
Copepodite	35	46	0.0064 (S)
Adult	11	9	0.0241 (S)

analysis of temporal changes of cyclopoid stages distribution indicates different traits between young (nauplii, copepodite I - V) and adult stages. The patterns of seasonal distribution of nauplii and copepodites I - III represent similarity: enhancement in spring and decline later on. Copepodite III - IV show decline in spring followed by enhancement in summer. Adult stages represent an annual decline. Surprisingly, the relationship between multiannual averages of stages (nauplii, copepodite, adult) densities (No/L) represent a high level (Figure 3). Therefore, seasonal analysis of Fractional Polynomial is required (Figure 4 and Figure 5).

Another comparative analysis by ANOVA Test ($p < 0.05$) done for the difference of metabolic parameters between Herbivore (nauplii and I - IV copepodites) and Predator

(copepodite V and adult) cyclopoids is presented in **Table 3**.

Results in **Table 3** indicate a significant difference between first and second parts of the year due to the higher temperatures in summer-fall season caused by the sub-tropical climatological features of the Kinneret zone.

4. Discussion

The ecology of cyclopoid copepods in Lake Kinneret was widely studied and previously documented. Nevertheless, the parameters usage was highly diversified: numerical (by numbers) and biomass (by weight) concentrations as volume (per liter) or aerial (per m²) densities, implication of metabolic parameters to natural-field assemblages, as well as mass balances in ecological models. Nevertheless, the continuity of sampling procedures including frequencies, spatial distribution of stations and seasonal (with respect to thermal structure) bathymetrical intervals was unchanged. An attempt aimed at bridging between obstacles of different parameters is a partial objective of this paper. It is also an investigated insight into the variable available data on the biology of cyclopoid copepods in Lake Kinneret. Due to the need for combined evaluated analysis of recorded data parameters, numerical specific life cycle stages and assemblages of biomass values, two data sets were integrated: 1) during 1969-1985; and 2) during 1969-2002. The potential impact of three environmental factors was selected: availability of food sources, temperature and fish predation.

The total wet biomass (g/m²) densities of Zooplankton in Lake Kinneret and their metabolic activities (**Figure 1**) indicate opposite reciprocal results—high biomass and low metabolic rates in winter and low biomass and high metabolic rates in summer. It is likely that the metabolic rates in summer season, respiration, food consumption and growth rates are high as a result of high temperatures but the mortality is high and the total metabolic efficiency is low. Moreover, food demands of zooplanktivorous fishes in summer are high as well [12] (**Table 2** and **Table 3**) caused by intensification of top down pressure on zooplankton. Numerical densities indicate a peak of nauplii stages (**Figure 2**, top left) in July and of young copepodite a month later. It is suggested that the July-September peaks of young stages is food availability [2] and low fish predation which is due to their smaller body size. The larger size copepodite stage V and adults

Table 3. Results of seasonal comparative ANOVA Test ($p < 0.05$) between herbivore and predator metabolic activity (gC/m²/month) (see text) of cyclopoids in Lake Kinneret (1969-2002) (Gophen and Azoulay 2002). S = Significant; H = Herbivore; P = Predator; MT = Metabolic trait.

H, P, MT	Winter-spring	Summer-fall	Probability (p)
H-respiration	1.71	4.17	<0.0001
P-respiration	1.45	2.88	p = 0.0021
H-consumption	4.69	12.46	<0.0001
P-consumption	5.19	15.98	<0.0001
H-production	11.38	28.30	<0.0001
P-production	4.53	12.11	0.0004

are more vulnerable and therefore intensively preyed on in summer. The positive respective relationship as evaluated on a large scale (multiannual, 1969-2002, averages) of numerical densities clearly is prominently shown in **Figure 3**: increasing densities of nauplii. This significantly accompanied the elevation of copepodite and adults and similarly the relationship between copepodite and adult stages. Identical relationships were also documented between herbivore and predator stages of cyclopoids.

Figure 4 and **Figure 5** represent the Fractional Polynomial prediction of life cycle stages. A similar pattern of density increase is seen during January-September followed by a decline afterwards for nauplii and copepodite II and III stages. These are small size organisms and therefore lower pressure from attacking fishes is maintained and the density limiting parameter is food availability [2] and temperature. During September-December, the limiting factor is shifted from food availability to fish predation and lower rate of metabolic efficiency resulting in concentration decline. Moreover, total number of eggs produced per female increases from 27 to 93 - 100 when temperature increases from 15°C - 20°C (January-April) to 20°C - 28°C ranges. Conclusively, densities of young stages during winter-spring-early summer are increasing as a result of higher fecundity, food availability and low predation pressure. At the same period, predicted densities of copepodite stages III, IV, and V decline are caused by longer duration time of young stage development: nauplii, 15 - 28 days; copepodite, 10 - 39 days (Gophen 1978). The densities of adults are predicted to be lower during March-December as a result of fish predation, but fecundity is enhanced by temperature increase. The comprehensive consideration outcome is the following: densities prediction (Fractional Polynomial) for the III, IV, and V stages copepodites is the opposite pattern to the young stage predictions: density decline is predicted during winter-spring followed by an increase during spring-summer-fall (**Figure 4** and **Figure 5**). The specific case study of the cyclopoid copepods population dynamic in Lake Kinneret might be relevant to other limnological ecosystems aimed at evaluation of lakes functioning.

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