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The Ecology of *Keratella cochlearis* in Lake Kinneret (Israel)

Moshe Gophen[1,2]

[1]Migal-Galilee Technology Center, Kiryat Shmona, Israel; [2]Tel Hai College, Kiryat Shmona, Israel.
Email: Gophen@Migal.org.il

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ABSTRACT

A long term record of rotifers in Lake Kinneret (Israel) indicated that *Keratella cochlearis* is the most common zooplankter in it. Population dynamics parameters ("egg/female ratio" procedure) were combined with limnological data to analyze temporal fluctuations of *K. cochlearis* in the Kinneret ecosystem. Lake Kinneret is characterized by meso-oligotrophic conditions. During the winter-spring period, when the lake is completely mixed and at low temperatures, water and nutrient inputs are maximal. The lake is stratified in the summer, with an oligotrophic epilimnion; at high temperatures, nutrient and water inputs are minimal. Since the early 1990's, a decline in rainfall and water inputs and a reduction in *Peridinium*, coinciding with an ascending level of blue greens, were documented. *K. cochlearis* is affected by the water input regime, temperature, nutrient concentrations and the phytoplankton composition. The densities of individuals and egg bearing females are low in the summer and fall, and high during the late winter-spring, with E/F values being the highest during January-April. Population dynamics parameters were respectively similar. Regressions of densities of individuals and egg bearing females vs time (years) revealed a prominent long term decline.

Keywords: *Keratella cochlearis*; Lake Kinneret; Long Term; Seasonal Dynamics

1. Introduction

Keratella cochlearis (Brachionidae) is distributed worldwide. The species is common and is a constant constituent of the Lake Kinneret (Israel) zooplankton communities, although it only contributes a low biomass to the entire assemblage. The common spatial and temporal occurrence of *K. cochlearis*, coinciding with limnological changes, initiated the present study, which deals with the impact of ecological conditions on the distribution of this species. The long term data record, which was established by the Kinneret Limnological Laboratory, was the basis of the study [1,2].

Lake Kinneret, Israel, supplies 16% - 30% of the national water demands and >55% of the drinking water. The drainage basin area of the lake is 2730 km^{-2}, of which, about 200 km^{-2} is the "Hula Valley" that contributes >50% of the nutrient input. The lake is stratified from May to mid-December (with an anoxic hypolimnion) and is totally mixed from mid-December through April. The trophic status of Lake Kinneret can be classified as mesotrophic in the winter-spring season and oligotrophoic in the summer-fall period [3]. Over the last 60 years, the Kinneret ecosystem has undergone several man-made modifications: construction of a dam at the south end; diversion of salty springs and salinity fluctuations (200 - 300 ppm Cl^-); construction of the National Water Carrier (NWC) through which about 1 million m^{-3} (mcm) is pumped from the lake; exotic and native fish stocking and subsidized bleak fishing [4]. High range fluctuations of natural conditions were recorded, with seasonal ups and downs, as well as a long term decline in the water level, water inputs, plankton biomass and species composition [5]. The subtropical climate conditions of the Kinneret region are characterized by high and low levels of water and nutrient inputs in winter and summer months, respectively. The epilimnetic loads and plankton biomass present similar trends [6,7].

The lake is exploited for its fishing by ca 200 licensed fishermen, who commercially remove an average of 1832 tons of fish (108 kg/ha) per annum (1970-2005). In recent years, fishery landings have declined extremely.

A decrease in total phosphorus (TP) concentrations during the 1980's and 1990's, a decrease in organic nitrogen throughout 1970-2001 a decline in TSS and nitrates during the 1990's and a slight increase in (SRP) in the Jordan River waters have been recorded.

The following trends in the limnological processes within the Kinneret epilimnion (0 - 15 m) were recorded during 1969-2004: a positive relationship between the total nitrogen (TN) concentration and the biomass of

Pyrrhophyta, with a consequent *Peridinium* biomass suppression; a slightly increased TP concentration; a decline in TN [8]; a reduction in large cell phytoplankter (*Peridinium*) biomass, an enhancement in that of nanophytoplankton (*Chlorophyta,* diatoms and mostly *Cyanobacteria*, such as *Microcistis* and *Aphnizomenon*); a decline in the N/P mass ratio enhanced biomass of N_2-fixing cyanobacteria [9]; modification of Lake Kinneret from a P to an N limited ecosystem; a slight decline in the total biomass of phytoplankton (nano-phytoplankton dominance) under a lower water level (WL); and a decrease until 1990, with a subsequent increase, in the zooplankton biomass (92% due to Copepoda, and Cladocera). The lower water level that was followed by a decline in N and a slight increase in P accelerated the shift from a dominance of large cell algae (*Peridinium*) to that of the smaller cell size algae (nano-phytoplankton). The decline in N together with an increase in P (lower TN/TP mass ratio), with an enhanced N deficiency and a P sufficiency, resulted in cyanophyte blooming [9]. It is likely that the high biomass of small cells (particles) caused a decline in light penetration (higher reflection), as indicated by the shallower depth recorded by the Secchi measurements [8]. A decline in water temperatures during 1979-mid-1980's, with a subsequent increase, was documented [8].

The number of zooplankton species in the Lake Kinneret assemblages included: Copepoda-4, Cladocera-7 and Rotifera-35 [5]; There are 24 fish species in Lake Kinneret, of which19 are native, 5 are exotic and eight are commercially harvested. Most fishes in Lake Kinneret are planktivorous and the most common are the zooplanktivorous bleaks (*Acanthobrama sp., Mirogrex sp.*), contributing to ca. 80% of the total number of fish and more than 50% of fish biomass in the lake (Walline *et al*. 2000). In this paper, I present an analysis of the response of *K. cochlearis* populations to the temporal and seasonal fluctuations in the limnological conditions during 1972-2001.

2. Methods

Hydrological data on rain and water inputs were taken from the annual reports of the Hydrological Service Water Authority of Israel (1972-2001) (**Figure 1**). The retention time of the water in Lake Kinneret was calculated according to the relation between the inflow rates [6], and the lake volume. Water level data were provided by the Hydrological Service/Israeli Water Authority [6]. Zooplankton monitoring in Lake Kinneret was carried out during 1969-2001 with weekly and biweekly sampling at seven stations at 12 distinct depths. In the sample analyses, the total number of *Keratella cochlearis* specimens and egg bearing females were counted, and monthly averages of the number per liter were evaluated. Physical, hydrological, chemical and plankton data were collected from the Lake Kinneret Data Base [7], and expressed as monthly means (1969-2001) (for sampling procedures see [9] and [3]); professional responsibilities for the data are: chemistry-A. Nishri, phytoplankton-U. Pollingher and T. Zohary, zooplankton-M. Gophen. Herzig (1983) compiled information from several studies on temperature impact on the duration of embryonic development in brachionid rotifers. Data given in Figure 1(b) in Herzig [10], which are respectively related to the Lake Kinneret epilimnion (15˚C - 28˚C) indicate that its embryonic development value is shorter than a day. An average of 19 hours, *i.e.*, 0.8 day was used in the present study. The parameters below were employed for the analysis of population dynamics [2,11,12].

$$\mathbf{B = E/D} \quad (1)$$

where B = Finite hatching rate; E = no. of eggs per female; D = Egg development time

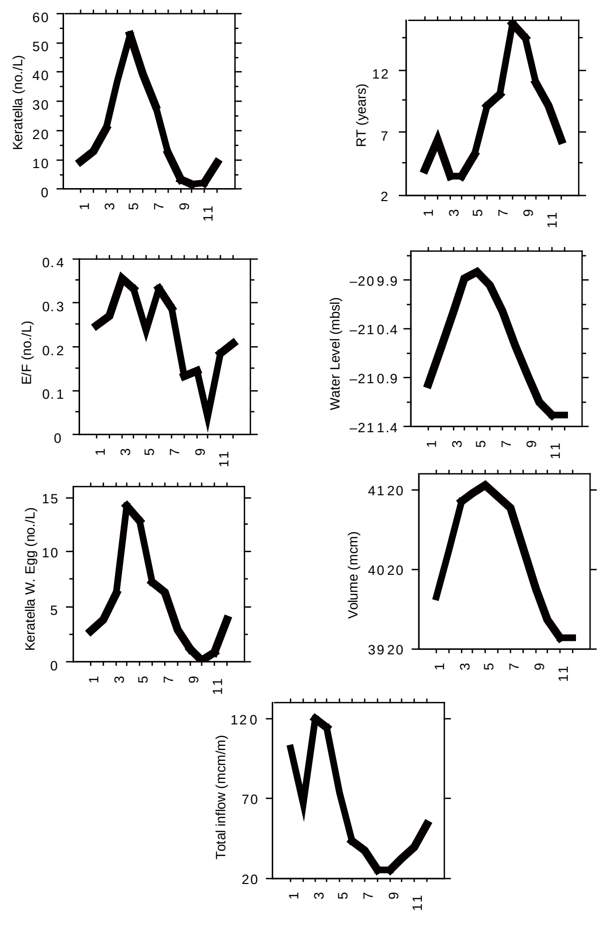


Figure 1. Monthly averaged (1972-2001) values of *Keratella cochlearis* (individuals·L^{-1}, Females carrying eggs·L^{-1} and Eggs·$Female^{-1}$) (left panels) in the epilimnion of Lake Kinneret and Hydrological data (Lake volume in mcm, Water Level in mbsl, Retention time in years, and inflows in mcm·$month^{-1}$) (right and mid panels).

$$\mathbf{1/B} = \text{Population Turnover Time} \quad (2)$$

Instantaneous birth rate,

$$b{:}\mathbf{b = \ln(E+1)/D} \quad (3)$$

Instantaneous rate of population change,

$$r{:}\mathbf{r = (\ln Nt - \ln No)/t} \quad (4)$$

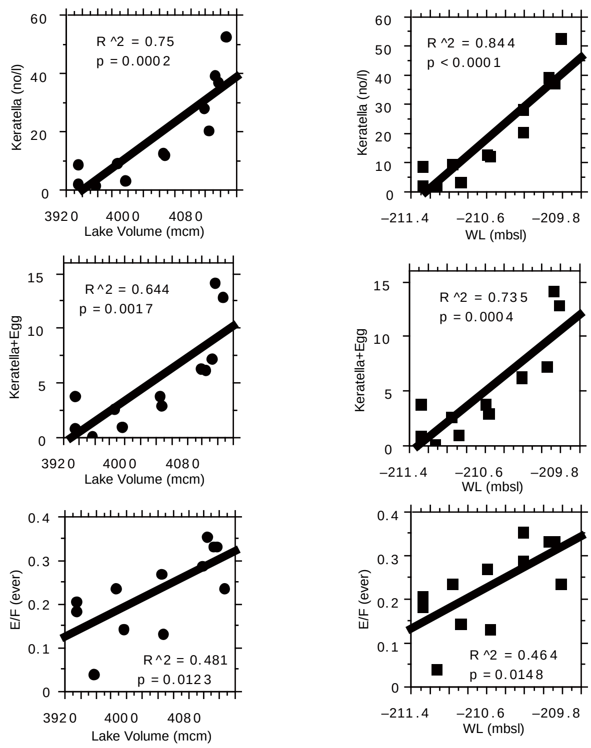
where: t = sampling time interval, 14 days, Nt = population at the end of 14 days, No = population at the beginning of 14 days; Instantaneous death rate,

$$d{:}\mathbf{d = b - r} \quad (5)$$

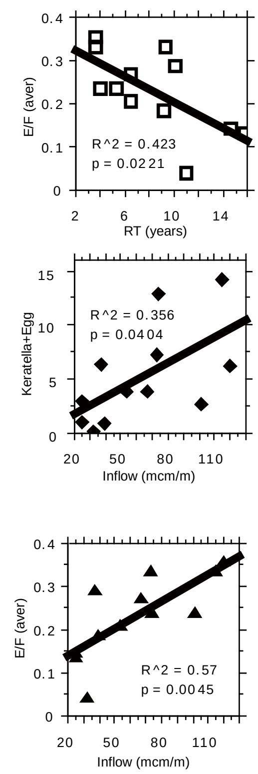
These data were collected bi-weekly and monthly averages were calculated. Annual cycles were grouped as two periodical classes: Winter: December and January-May; and Summer: June-November. Similarly, temporal classes were grouped in two classes: 1972-1985 and 1986-2001, and epilimnetic (0 - 15 m) monthly averaged temperatures were grouped as two classes: 1) 15.0˚C - 20.5˚C: and 2) 20.6˚C - 28.1˚C. ANOVA tests ($p < 0.05$) were carried out for the population dynamics parameters separately against the periodical and thermal groups.

3. Results

The population turnover time (T) and instantaneous rate of population change (r) parameters at low temperatures were found to be significantly lower than those in the high temperature class (p = 0.0426, and 0.0454, respectively): 2.8 (SD 2.5) and 4.2 (SD 5.2) months for low and high temperatures, respectively. Similar results were obtained for the periodical factors (winter vs summer): p = 0.0126 and 0.0166 for T and r, respectively; 0.012 (SD 0.104) and –0.029 (SD 0.098) for r values and 2.9 (SD 2.4) and 4.6 (SD 5.8) for T values, respectively. Instantaneous birth rates were significantly higher (p: 0.0080 - 0.0285) at temperatures above 24˚C in comparison to those at 20˚C - 24˚C. Moreover, according to the periodical distribution, there were high densities of *K. cochlearis* (**Figure. 1**) and egg bearing females between March and July. The summer and winter populations behaved differently, and the thermal range of 18˚C - 22˚C is probably optimal. Analysis of the relations between *K. cochlearis* population parameters (individual abundance, density of egg carrying females and eggs /female) and hydrological parameters (Jordan discharge [$m^3 \cdot s^{-1}$], water inputs into the lake [$m^3 \cdot month^{-1}$], lake water retention time [years], lake water level [m] below sea level and lake water volume [$million \cdot m^3$]) was carried out by simple regression (**Figures 2(a)** and **2(b)**). Significant inverse relations were indicated between egg bearing females and lake retention time. Jordan inflows vs number of individuals and E/F were significantly positive. Regressions between lake volume and the respective WL, and *Keratella*, E/F and egg bearing female densities were all significantly positive (**Figures 2(a)** and **2(b)**). These significant levels are



(a)



(b)

Figure 2. Simple regressions (R^2 and p are given) between population densities (total number, females with eggs, $Female^{-1}$) of of *Keratella cochlearis* and hydrological parameters (lake volume, water level, Inflows and retention time).

due to the rainy and cold winter season. Comparative analysis (ANOVA; $p < 0.05$) of the hydrological values vs winter (December and January-May) and summer (June-No- vember) months clearly show the higher levels of Jordan discharge and total water inputs when temperatures are colder, as well as a shorter lake water retention time in winter. The entire period (1972-2000) was divided into two terms: 1972-1985 and 1986-2000. The ANOVA test was carried out where population dynamics parameters were related to the two periods. Results demonstrated that there was a significantly higher concentration of egg bearing females and death and birth rates during 1986-2000, whilst population turnover values and the number of individuals were lower after 1985. The seasonal pattern of rate of change, instantaneous birth rate and instantaneous death rate fluctuations are presented in **Figure 4**. During the six winter months (Feb. - Apr. and Oct. - Dec.) the r values were positive and in summer (May through September) negative. The instantaneous birth and death rate values were similar, with an exceptional decline in October.

4. Discussion

It is proposed that the dry, warm summer months provide suboptimal conditions for the growth of *K. cochlearis* in Lake Kinneret. Due to the worldwide zoogeographical distribution, *K. cochlearis* has drawn the attention of zooplankton ecologists. Its feeding habits have been documented by Bogdan and Gilbert [13]; its feeding interference with *Daphnia* has been studied by Burns and Gilbert [14,15], and Gilbert and Stemberger [16]; the association of *K. cochlearis* with a predator cyclopoid and the consequent feeding interference were investigated by Gilbert and Williamson [17]; Stemberger [18]; studied the impact of spine development induction by the predator *Asplanchna*; and Walz [19-21], has documented population development of *K. cochlearis* in cultures. Not much attention has been given to the impact of diversified limnological parameters on the spatial and temporal distribution of *K. cochlearis*.

In early studies on the Kinneret zooplankton, the author partly neglected rotifer ecology because of its low contribution to the total biomass. Nevertheless, the continuous presence of *K. cochlearis* in the zooplankton records of Lake Kinneret emphasized the need to determine the impact of seasonal and long term ecological modifications within the Kinneret ecosystem. As a consequence of the geographical location of the Kinneret ecosystem within a sub-tropical region, characterized by short, cold and wet winters and long, dry and warm summers, the river runoffs are intensive in winter. As a result, the lake WL is high and obviously the lake volume is accompanied by a shorter retention time (**Table 1**; **Figures 2(a)** and **2(b)**). This probably initiates optimal conditions for *Keratella* food resources. Their availability is high and the abiotic conditions are suitable. Thus, winter populations of *Keratella* are larger and more productive (higher number of egg bearing females and E/F) (**Table 2**; **Figure 2**). The lower rates of change in winter (**Table 2**) are indicated by the higher level of stability and lower death rate values (**Table 2**). The long term analysis (**Table 3**, **Figure 3**) implies that the populations, during 1972-1985, when droughts were less frequent [6], were notably more stable, healthy and productive. The lower death and birth rate values, as well as the longer turnover time and higher densities, enhanced these features. During 1986-2000, droughts became more frequent, runoff discharges declined, and water temperature increased [6,12]. Consequently, it was suggested that food source renewal and the shift of the Kinneret ecosystem from a P to N limitation [8], with a lower productivity (a lower N content in suspended particles), caused suppression of *Keratella* communities (**Figure 1**). It is proposed that the change in phytoplankton composition, from *Peridinium* to nano-phtoplankton dominancy [8,9,12], affected the nutritional value of *Keratella* food sources. The seasonal fluctuations of the population dynamics parameters, presented in **Figure 4**, imply that the suppression of summer (May - Sep.) *Keratella* populations (Nt < No, see equation 4) is probably a result of food availability and temperature constraints. Productive and healthy assemblages were present in winter (Oct. - Dec. and Feb. - Apr.). The reason for exceptionally low values of instantaneous birth and death rates in October (**Figure 4**) is unclear.

Table 1. Comparative analysis (ANOVA) between Hydrological values (see text) and two seasons (see also Figure 4): 1) winter (12, 1 - 5) and 2) summer (6 - 11). S = significant, NS = not significant.

Hydrological parameter	Difference	Probablity
Jordan Discharge ($m^3 \cdot s^{-1}$)	1 > 2	0.0013
Retention Time	1 < 2	0.0021
Inflow ($m^3 \cdot month^{-1}$)	1 > 2	0.0100
Water Level (mbsl)	NS	
Water Temperature (˚C)	1 < 2	<0.0001
Lake Volume (mcm)	NS	

Table 2. Comparative analysis (ANOVA) between population dynamics values (see text) and two seasons: 1) winter (12, 1 - 5) and 2) summer (6 - 11). S = significant, NS = not significant.

Parameter	Difference	probability (p)
Number of Ind.	1 > 2	<0.0001
Female with eggs	1 > 2	<0.0001
Eggs/Female	1 > 2	0.0001
Rate of change	1 > 2	0.0296
Birth rate	NS	
Death rate	1 > 2	0.0174
Turnover	NS	

Table 3. Comparative analysis (ANOVA) between population dynamics values (see text) and two periods: 1) 1972-1985, and 2) 1986-2000. S = significant, NS = not significant.

Parameter	Difference	probability (p)
Death rate	1 < 2	<0.0001
Birth rate	1 < 2	<0.0001
Rate of change	NS	
Turnover time	1 > 2	0.0041
Eggs/Female	1 < 2	<0.0001
Females w. Egg	NS	
Individuals/L	1 > 2	0.0139

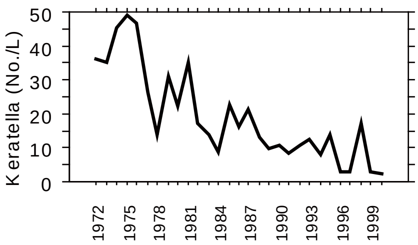


Figure 3. Annual averages (1972-2001), (No. L^{-1}) of *Keratella cochlearis* in the epilimnion of Lake Kinneret.

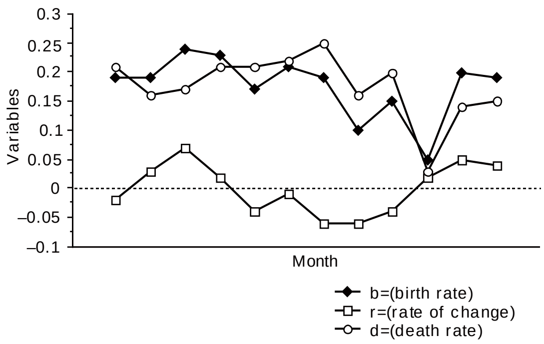


Figure 4. Monthly (January - December from left to right) fluctuations of population dynamic variables of *Keratella cochlearis* averaged for the period of 1969-2001 in Lake Kinneret.

5. Conclusion

An attempt to explain the long term and seasonal distribution of *Keratella cochlearis* in Lake Kinneret was made by analyzing the impact of biotic and abiotic conditions. The conclusion drawn was that the winter conditions are suitable for the maintenance of healthy populations, whilst droughts and/or summer conditions suppress *Keratella* assemblages.

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