

Zooplankton grazing in Lake Constance: Seasonal and day-night in situ measurements

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Introduction

One of the most interesting features of the seasonal planktonic succession in Lake Constance is the occurrence of the "clear-water" phase: A rapid late spring increase (generally between May and June) in water transparency caused mostly by a depression in algal biomass. Some authors explained this phenomenon analysing the interaction between phytoplankton production rates, climatic conditions and zooplankton grazing (LAMPERT & SCHÖBER 1978, GELLER 1980, SOMMER 1983, TILZER 1984). However quantitative in situ measurements of the grazing activities of the zooplankton community were not yet disponible till recently.

Since november 1987 I measure routinely the grazing activities in Lake Constance (Überlingersee). The objective of the this paper is to present grazing data from the 1988 annual succession. Special attention was given to the daily rhythms of food uptake (at the specific and community levels) and to the contribution of the smaller organisms (rotifers and nauplii) to the overall grazing.

Methods

A grazing twin chamber (each half has a volume of 10l) was designed by W. GELLER specially for this project. The great volume of this chamber made possible *in situ* measurements even in situations when the zooplankton abundance was as low as $16 \text{ mg C} \cdot \text{m}^{-3}$. All experiments were run using the cryptophycean *Rhodomonas minuta* labelled with ^{14}C as experimental food. Earlier studies (KNISELY & GELLER 1986) demonstrated the optimal role of this algae as food for many zooplankters. The volume from the algal suspension used as food tracer was regulated to achieve a maximum carbon input of $0.04\text{--}0.06 \text{ mg C} \cdot \text{l}^{-1}$ inside the chamber. This means that the lake seston concentration remained practically constant during the experiment.

Each experiment lasted up to 12 minutes and was terminated filtering the content of each chamber through a set of two gauze nets. Two different size fractions were thus obtained: the P 1-fraction where all organisms bigger than $170 \mu\text{m}$ were collected and the P 2-fraction with smaller organisms, mostly rotifers and small copepodites as well as nauplii ($50 \mu\text{m} < \text{P 2} < 170 \mu\text{m}$).

For further sample processing a new method was introduced (BERBEROVIC & PINTO-COELHO 1989). The nets containing the two fractions were washed with soda water and placed into a thermio-box containing plates of dry-ice. This procedure permitted rapid freezing of the organisms. At the laboratory, the samples were submitted to lyophilization for 24 hrs. Laboratory experiments demonstrated that with this new procedure, isotope loss is minimal compared to conventional methods.

Single specimens were selected from each sample for species determinations and length measurements. The remaining organisms were washed onto a GF-filter which was immediately transferred to a scintillation vial. The subsequent treatment of samples was done according to LAMPERT & TAYLOR (1985).

Results and discussion

The water temperatures at days and depths of grazing experiments in 1988 are presented in Fig. 1 A. Between periods of thermal instability of the water column (May and September) the typical summer stratification occurs with surface temperatures reaching 23°C .

In 1988 there was a very pronounced clear water-phase and Secchi depth measurements registered 18 m in June (Fig. 1 B). At that time chlorophyll-*a* concentrations in the upper 20 m were very low ($< 10 \mu\text{g} \cdot \text{l}^{-1}$). The spring bloom (20 July 1988) and a late summer algal maximum were also well illustrated by chlorophyll-*a* concentrations.

The seasonal course of the community grazing rates (CGR) are shown for the upper 10 m in Fig. 2. The two size fractions are presented separately. The annual maximum of the P 1-fraction occurred in June. During this time, the major contribution for the overall CGR values of this fraction were due to the daphnids.

The highest CGR values for the small P 2-fraction occurred prior and after the clear-water phase. Rotifers and nauplii seemingly profit of the

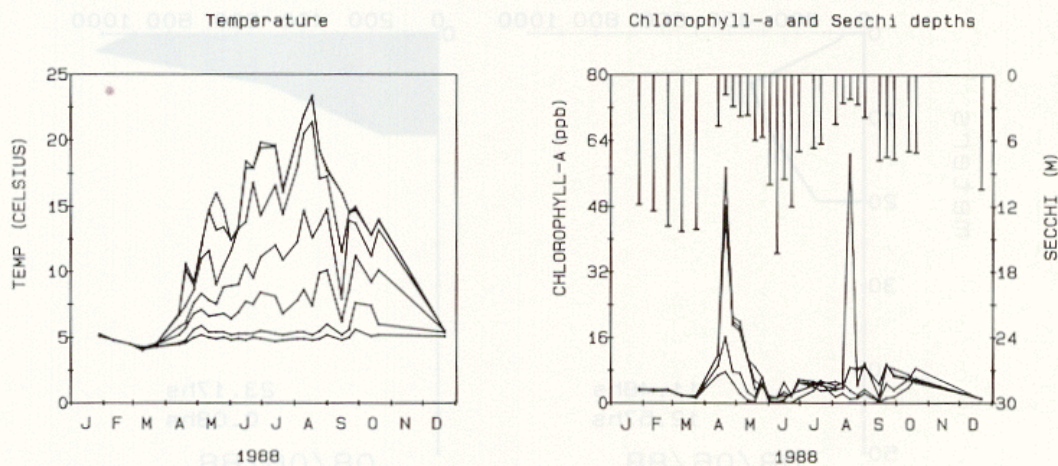


Fig. 1. A) water temperatures (0, 2, 6, 12, 20, 36 and 50 m) in Überlingersee (Lake Constance) during 1988; B) Chlorophyll-*a* concentrations (0, 2, 6, 12 and 20 m) and Secchi depths.

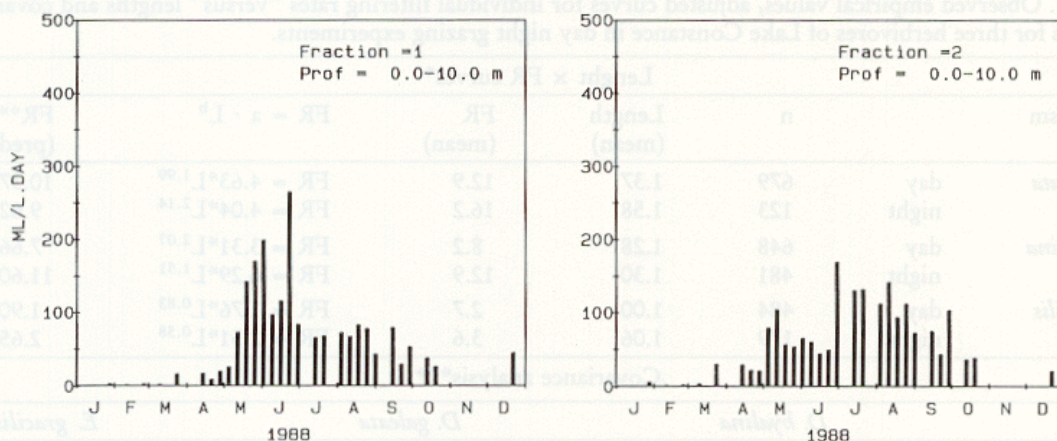


Fig. 2. Community grazing rates (CGR) in Überlingersee during 1988.

periods when daphnid populations are less abundant.

The CGR's measured in Lake Constance at daytime are comparable to those from other temperate lakes. In shallow eutrophic lakes like Hart Lake (Canada) and Schöhsee (West Germany) CGR'S are higher (HANEY 1973, LAMPERT & TAYLOR 1984). Similar seasonal data come from the unpolluted Lake Vechten (GULATI et al. 1982).

Daytime-CGR alone however give an incomplete view of the impact of zooplankton on removing seston particles. Day-values were relatively low and this tendency was strongest between May and July. Fig. 3 provides a typical example of a CGR day-night-cycle during the clear-water phase. At night, values in the upper 10 m

were five fold higher than at day. In early spring and in autumn the diel variations of CGR's tended to disappear.

TILZER (1984, Table 1) estimated the relative significance of zooplankton grazing during the spring bloom and the subsequent clear-water phase, when grazing could account to 40–80% of the overall algal loss rates. Those figures combine well with the day-data from Fig. 2. As shown in Fig. 3, however, CGR night-values were as high as $1000 \text{ ml} \cdot \text{l}^{-1} \cdot \text{day}^{-1}$ in the upper 10 m. This means that, during the clear-water phase, grazing impact in Lake Constance is considerably higher than previously estimated in the literature.

Table 1 summarizes the data of individual grazing rates of three major herbivores of the lake. The

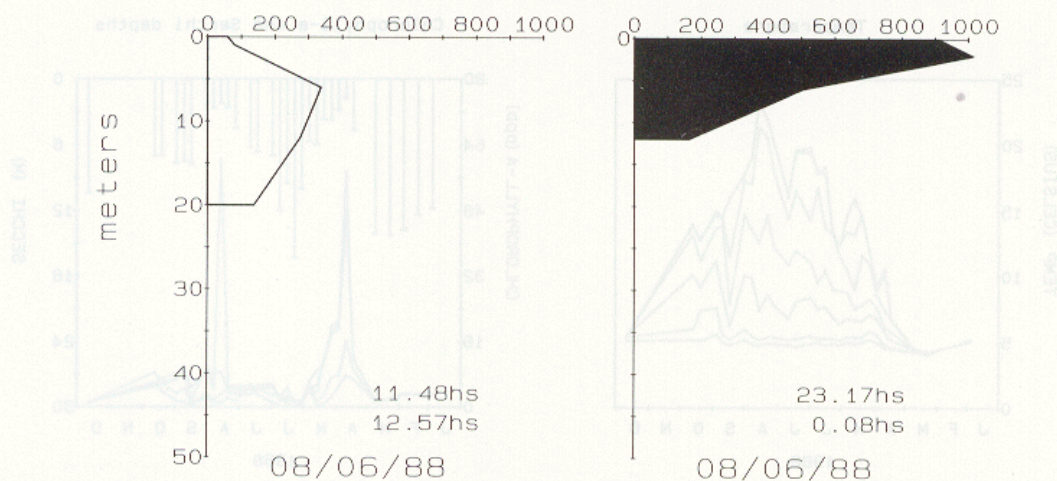


Fig. 3. Day-night grazing experiment in Lake Constance (Überlingersee) during the clear water phase in 1988. Values of CGR (P-1 + P-2) are in $\text{ml} \cdot \text{l}^{-1} \cdot \text{day}^{-1}$.

Table 1. Observed empirical values, adjusted curves for individual filtering rates "versus" lengths and covariance analysis for three herbivores of Lake Constance in day night grazing experiments.

Organism		Length \times FR curves*					
	n	Length (mean)	FR (mean)	FR = $a \cdot L^b$	FR** (predicted)		
<i>D. galeata</i>	day	679	1.37	12.9	FR = $4.63 \cdot L^{1.99}$	10.37	
	night	123	1.58	16.2	FR = $4.04 \cdot L^{2.14}$	9.62	
<i>D. hyalina</i>	day	648	1.28	8.2	FR = $3.31 \cdot L^{2.07}$	7.66	
	night	481	1.30	12.9	FR = $6.29 \cdot L^{1.51}$	11.60	
<i>E. gracilis</i>	day	484	1.00	2.7	FR = $1.76 \cdot L^{0.83}$	1.90	
	night	179	1.06	3.6	FR = $2.51 \cdot L^{0.58}$	2.65	
Covariance analysis***							
		<i>D. hyalina</i>		<i>D. galeata</i>		<i>E. gracilis</i>	
MS (adjusted)							
day-night		89.4990		0.2057		15.3026	
error		0.7902		0.9733		1.1209	
F-Value		113.2611		0.2113		13.6520	
PR > F		0.0001		0.6458		0.0002	
Adj. means		day	night	day	night	day	night
		1.5983	2.1618	2.0227	2.0675	0.5595	0.9033
Std. error		0.0349	0.0405	0.0379	0.0895	0.0482	0.0794
PR > T							
H0: day = night		0.0001		0.6458		0.0002	

* Length in mm and FR in $\text{ml} \cdot \text{ind}^{-1} \cdot \text{day}^{-1}$.

** $L = 1.5 \text{ mm}$ (*Daphnia* spp.); $L = 1.1 \text{ mm}$ (*E. gracilis*).

*** Covariance analysis with \ln -transformed data.

curves were fitted separately with data from day and night experiments, respectively. Species which conduct extended vertical migrations such as *Daphnia hyalina* and *Eudiaptomus gracilis* (GELLER 1986) filtrate significantly higher volumes of water

at night. Their adjusted means, as given by the covariance analysis, are significantly different (Table 1 B). *Daphnia galeata* shows no comparable daily vertical displacement, and its filtering rates did not vary significantly between the day and at night.

Diel rhythms in individual filtering rates of vertical migrating species may be referred to a temperature effect. Beyond animal size and food concentration, the temperature is a major parameter controlling those rates. During the summer, *D. hyalina* generally spends the days below 30 m in Lake Constance and *E. gracilis* below 15 m depth (GELLER 1986). The temperature differences between the upper 10 m water layer and those deeper layers (15–50 m) figure several celsius grades during summer (Fig. 1 A).

These rhythms in filtering rates rarely have been investigated in other lakes, and results are quite different. LAMPERT & TAYLOR (1985) did not find diel rhythms in individual filtration rates in Schöhsee, maybe due to the fact that this is a shallow lake ($z = 10.7$ m) and the temperature differences are small between the water layers where organisms are during the day and at night. Other reason might be the methods of investigation. Fixing organisms with formalin after a grazing experiment can cause isotope leakage up to 40% (LAMPERT & TAYLOR 1985). Even applying correction factors, it would be very difficult to quantify the 34% variation between filtering rates at day and at night as found in Lake Constance for *D. hyalina* in this study. In Lawrence Lake, HANEY (1985) reported night filtering rates (predicted FR values for individuals measuring 1.5 mm) for *Daphnia galeata* and *D. pulex* up to 2.9 fold higher as the day ones.

Concluding, great temporal and spatial (vertical) variations in the CGR measurements could be found. The greatest amplitude in the day-night CGR values appeared during the clear-water phase. The highest absolute CGR values were found at night in June 1988. The often neglected fraction containing small herbivores, like rotifers and nauplii, can play a relevant role to the overall grazing specially when daphnids are less abundant in the lake. In July 1988, values as high as $173 \text{ ml} \cdot \text{l}^{-1} \cdot \text{day}^{-1}$ were registered for P2-fraction in the upper 10 m layer. Finally diel rhythms could be statistically identified in filtering rates of species which are exposed to extended diurnal migration.

Acknowledgements

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