

## The importance of *Daphnia* for zooplankton grazing in Lake Constance

By RICARDO M. PINTO-COELHO<sup>1</sup>

Limnologisches Institut der Universität Konstanz

With 5 figures and 4 tables in the text

### Abstract

The seasonal variation of zooplankton community grazing rates in pelagial of Lake Constance was examined in situ. Two size fractions were considered: P1 > 170  $\mu\text{m}$  (mesozooplankton) and 50 < P2 < 170  $\mu\text{m}$  (microzooplankton). As expected, the grazing rates were highest when daphnid biomass values reached their seasonal maximum (clear-water phase). Care was taken to include diel variations of grazing rates in the seasonal model. Comparison of grazing rates of *Daphnia* populations (PGR) and community grazing rates (CGR) as well as multiple regression analysis were applied to evaluate the contribution of these herbivores to the overall zooplankton grazing. The filtering rates of both *Daphnia* populations (PGR) controlled the basic seasonal trends as well as the magnitude of mesozooplankton grazing. Among the selected variables, the biomass of *D. hyalina* explained the highest amount of total variability of community grazing. The coupling effect between zooplankton vertical migration and diel fluctuations of grazing rates was investigated by means of the biomass specific community grazing rates. It was shown that higher epilimnetic community grazing rates at night are mostly due to biomass concentration and not to enhanced specific filtering rates. Finally, the effect of temperature and food concentration on the filtering rates of *Daphnia* were also examined. Filtering rates of *D. hyalina* were significantly affected by low temperatures in hypolimnion and by particulate organic carbon in epilimnion of L. Constance.

### Introduction

Over the past two decades several in situ investigations of zooplankton grazing have been carried out in freshwater ecosystems (see STERNER, 1989 and PETERS, 1984 for reviews). Nevertheless, many questions concerning this subject remain unsolved. Examples of such questions are: a) Are there distinct relationships between temperature, food concentration and grazing rates under field conditions? b) How are specific filtering and community grazing rates related to each other over the diel cycle? c) What role do smaller organisms, e.g. young stages of copepods and rotifers, play in the overall grazing? d) To what

<sup>1</sup> Author's address: Limnologisches Institut, Universität Konstanz, Mainaustr. 212, D-7750 Konstanz-1, Germany.

extent do food quality and selective grazing influence these rates? Many authors have dealt with these subjects, but conflicting results appear in the literature (see discussion below).

As a deep, large prealpine lake, L. Constance has a complex herbivore zooplankton community (LAMPERT, 1978; WALZ et al., 1987). Two of the major local herbivores are species of *Daphnia*: *D. galeata* and *D. hyalina*. The first lives mostly in the upper 12 m throughout the entire growing season (from late April to November), and the second species is a conspicuous vertical migrator (GELLER, 1986). These strikingly different behavioral characteristics probably induce other eco-physiological differences, which have only recently been better understood (GELLER, 1985 and 1989). When the grazing patterns of these two *Daphnia* species and other herbivores were analyzed separately, some important differences could be detected (PINTO-COELHO, 1990): *D. hyalina* and the calanoid *Eudiaptomus gracilis* (which is also a vertical migrator) exhibit higher filtering rates at night whereas *D. galeata* maintains stable filtering rates during day and night. Whether these enhanced filtering rates of vertical migrators can explain the higher community grazing rates at night is still an open question for L. Constance and probably for most lakes. Some authors (e.g. GULATI et al., 1982 and LAMPERT & TAYLOR, 1985) have postulated that the zooplankton biomass concentration near the surface would be the most important factor causing higher community grazing rates at night. Others, such as HANEY (1985), affirmed that enhanced filtering rates of *Daphnia* would be a key factor modulating those daily patterns of zooplankton feeding. Notwithstanding the differences observed in the behaviour of daphnids in L. Constance, GELLER (1989) found that these species have only slightly different cumulative annual productions ( $P_{D. hyalina} = 18$ ,  $P_{D. galeata} = 24$  g DW · m<sup>-2</sup>). His study was based on field data collected during the growing seasons between 1979 and 1982. During this period, the mean annual biomass for *D. hyalina* and *D. galeata* were 1.6 and 0.9 g DW · m<sup>-2</sup>, respectively.

Most field investigations of zooplankton grazing rates using modern equipment like the GLIWICZ-HANEY grazing chamber combined with a sensible and reliable sample processing method have been carried out in shallow and/or eutrophic lakes. This trend holds true especially for European lakes such as L. Balaton (ZÁNKAI & PONYI, 1986), Schöhsee (LAMPERT & TAYLOR, 1984 and 1985), Blelham Tarn (THOMPSON et al., 1982) and L. Créteil (MOURELATOS & LACROIX, 1990), with relatively few exceptions, such as L. Geneva (GAWLER & ANGELI, 1987).

Although daphnids play a major role in the zooplankton grazing in L. Constance (LAMPERT, 1978), no detailed information on seasonal and diel courses of grazing activities at the population level is available for this lake. Therefore, a relevant question at this point would be: Which are the relative contributions of these *Daphnia* species to the overall zooplankton grazing in L.

Constance? From November 1987 through December 1988, I measured zooplankton community grazing and specific filtering rates of herbivores in L. Constance. 210 such experiments were carried out in 33 different days, covering a large variety of environmental conditions and different times of day. To answer the above question, two different approaches were used. First, the grazing rates of both *Daphnia* populations were compared with the community grazing rates of mesozooplankton. Furthermore, a multivariate linear model was applied to evaluate "contribution" to overall grazing (in terms of percentages of explained variability of community grazing rates) of biomass of *Daphnia* spp. and other herbivores as well as the influence of water temperature and food concentration. Further objectives of this study were: a) to record the seasonal changes in the community grazing rates over an annual cycle (care was taken to include the differences between night and day measurements in this seasonal model), b) to assess the effects of changes in the biomass on the daily fluctuations of community grazing rates, and c) to investigate the effects of water temperature and food concentration on the specific filtering rates of *D. hyalina* and *D. galeata*.

## Methods

In situ zooplankton grazing measurements were conducted in Lake Constance in weekly intervals during spring bloom, clear-water phase and summer, and every two or three weeks in fall-winter. Specific filtering rates (FR) and Community grazing rates (CGR) were measured by means of short incubations with  $^{14}\text{C}$ -labelled algae. In all experiments the Chryptophyceae *Rhodomonas* sp. (Length: 6–10  $\mu\text{m}$ , volume 300  $\mu\text{m}^3$ , strain 26.80, Göttingen) was used as labelled food. Previous studies (KNISELY & GELLER, 1986) demonstrated that this alga is well grazed by most zooplankters of L. Constance. The algae were labelled by incubating 100 ml of an exponentially growing culture in WC-Medium (GUILLARD & LORENZ, 1972) with approximately 100  $\mu\text{Ci}$  of  $^{14}\text{C}$  carbonate for three days, with the same light and temperature conditions under which the cultures had been kept previously (15 °C, 250  $\mu\text{E} \cdot \text{sec}^{-1}$ , 16H + 8D hours). On the day of the experiment, the algal suspension was centrifuged and washed three times with fresh WC-Medium (isotope free). The amount of the diluted  $^{14}\text{C}$  after each resuspension and the end of the grazing experiments was always checked. Only the radioactivity (dpm) in the particulate fraction of the algal suspension was used in the calculations of grazing rates. Nevertheless, percentages of diluted  $^{14}\text{C}$  in the experimental food suspension at the end of the field experiments never exceeded 8%. The carbon content and the cell concentration in these suspensions were also determined.

A modified GLIWICZ-HANEY twin grazing chamber (10 l each half) was utilized. Each experiment lasted no more than 13 minutes. The amount of experimental food did not exceed 5% of the actual seston concentration. At the end of the experiment, the content of the chamber was filtered through a net system containing two mesh sizes: 50  $\mu\text{m}$  and 170  $\mu\text{m}$ . Two size-fractions (modified from SIEBURTH & SMETACEK, 1978) were thus obtained: mesozooplankton (fraction 1) containing all organisms larger than 170  $\mu\text{m}$  (mostly cladocerans and adult copepods). In the second fraction organisms between 50  $\mu\text{m}$  and 170  $\mu\text{m}$  were retained (rotifers, small copepodites and nauplii as well as some protozoans, especially during spring bloom).

A new procedure for further sample processing was introduced (BERBEROVIC & PINTO-COELHO, 1989): The filters were rapidly transferred to a grid in a thermic-box containing stabs of dry-ice. In less than one minute, the samples were thoroughly frozen. In the laboratory, the frozen filters were dried in a lyophilizer for at least ten hours. Individual specimens were then subjected to size measurements and radioactivity determinations. Laboratory experiments demonstrated that the isotope loss was greatly reduced with this new procedure when compared with samples preserved with sugar-formalin.

Further sample processing for liquid scintillation counting was performed according to the usual methodology (see LAMPERT & TAYLOR, 1985). FR's and CGR's were calculated using the formulas provided by HANEY (1973). For each experiment, grazing rates of *Daphnia* populations (PGR) were calculated with equation 1 using the individual measurements of filtering rates and abundance data set (animals were sorted into different size classes).

$$\text{PGR} = \sum_i^n \text{FR}_i * A_i \quad (1)$$

where  $\text{FR}_i$  is filtering rate in  $\text{ml} \cdot \text{day}^{-1}$  and  $A_i$  is abundance of individuals  $\cdot \text{l}^{-1}$  in a given size class  $i$  ( $i$  varied from 0.6 to 2.5 mm with intervals of 0.25 mm).

A seasonal model of grazing rates was constructed using both day and night measurements of CGR (and PGR). The resulting diel community grazing rate was calculated in the following way:

$$\text{CGR}_{\text{diel}} = \text{CGR}_{\text{d}} * \text{day} + \text{CGR}_{\text{n}} * \text{night} \quad (2)$$

where  $\text{CGR}_{\text{diel}}$  is the daily value for community grazing ( $\text{ml} \cdot \text{l}^{-1} \cdot \text{day}^{-1}$ ),  $\text{cgr}_{\text{d}}$  and  $\text{cgr}_{\text{n}}$  are community grazing rates ( $\text{ml} \cdot \text{l}^{-1} \cdot \text{h}^{-1}$ ) measured in day and night incubations, respectively. Day and night are respective durations (h) of the day and night.

The day length (in hours) for the location of Constance was determined according to the equation (STRASKRABA, 1980):

$$\text{day}_1 = 12 + \sin(d + 280) * 3.87 \quad (3)$$

where  $d$  is the Julian Date: 1 to 365.

Zooplankton abundance and biomass determinations were performed on samples taken from the second half of the grazing chamber in each experiment. The same size fractionation as described above was applied. Samples were fixed with 4% formalin containing Rose Bengal (50 mg/l) which made easier counting and determination procedures. Fraction 1 was counted under a dissecting microscope. Since this data set was required for biomass calculations and estimations of population grazing, each individual was measured, too. The carapace length from the top of the head (without helmets) to the point of insertion of the tail spine was considered for cladocerans. Length measurements of copepods were made from the tip of cephalothorax to the end of abdomen (without furcal rami). Subsampling using a 5.0 ml Hensen-Stempel Pipette was carried out if the number of organisms exceeded 600.

Biomass calculations for fraction 1 were done using allometric equations for zooplankters of *L. Constance* (GELLER & MÜLLER, 1985 and WÖLFL, 1990).

Weight specific community grazing rates ( $G_b$  in  $\text{ml} \cdot \mu\text{g}^{-1} \cdot \text{day}^{-1}$ ) were calculated using the equation:

$$G_b = \frac{\text{CGR}}{\text{Biomass}} \quad (4)$$

where CGR is community grazing rates in  $\text{ml} \cdot \text{l}^{-1} \cdot \text{day}^{-1}$  and Biomass refers to a specific population (i.e. *Daphnia* spp.) or the total zooplankton biomass in  $\mu\text{g DW} \cdot \text{l}^{-1}$ .

Particulate organic carbon (POC) of the fraction  $< 50 \mu\text{m}$  was determined for every grazing experiment. 500–1000 ml of lake water were carefully filtered through a MF-filter ( $8.0 \mu\text{m}$ ,  $\varnothing = 25 \text{ mm}$ ) previously covered with a layer of 1–2 mm of diatomite earth ("Kieselgur") free of any organic matter. The filters were used as support for the diatomite earth and the mesh size ( $8 \mu\text{m}$ ) was important only for regulating the water-flow rate during the filtration procedure. Particles as small as free living freshwater bacteria are normally retained (up to 90% of all bacteria) in the diatomite earth (SIMON & TILZER, 1987). The filters were dried at  $40^\circ\text{C}$  for 24 hours. The layer of "Kieselgur" was carefully transferred to porcelain vessels suitable for combustion. Each sample was allowed to combust 20 min at  $800^\circ\text{C}$  under pure Oxygen (99.999%  $\text{O}_2$ ) flow. The  $\text{CO}_2$  content of the combusted sample was determined by titration with HCl, 0.01 N. This method can detect POC concentrations as low as  $0.02 \text{ mg C} \cdot \text{l}^{-1}$  (LENARZ, 1972).

Grazing experiments were carried out in Überlingersee (north-western arm of L. Constance, depth 147 m). This is a routine sampling station for several investigations performed at the Limnological Institute, Konstanz. Thus, I had access to chlorophyll-a data sets which consists of weekly epilimnetic chlorophyll-a determinations over the entire annual cycle (M. M. TILZER, unpubl.), as well as to records of water temperature profiles from the institute's hydro-physics group (G. HEINZ & M. SCHIMMELE, unpubl.).

To investigate the possible effects of water temperature and food concentration on the filtering rates of the two *Daphnia* species, regression analyses were run with isolated data sets. Six data sets were chosen for this purpose:

- a) *Daphnia hyalina* in hypolimnion/metalimnion ( $d > 36 \text{ m}$ ) during summer, day values.
- b) *Daphnia hyalina* in lower epilimnion/metalimnion ( $20 < d < 30 \text{ m}$ ) during summer, day values.
- c) *Daphnia hyalina* in epilimnion ( $0 < d < 6 \text{ m}$ ), June 1988, night values.
- d) *Daphnia hyalina* in epilimnion ( $0 < d < 6 \text{ m}$ ), October 1988, night values.
- e) *Daphnia galeata* in epilimnion ( $0 < d < 6 \text{ m}$ ) summer I (June/July 1988), day values.
- f) *Daphnia galeata* in epilimnion ( $0 < d < 6 \text{ m}$ ) summer II (July/August 1988), day values.

### Statistical Analysis

Predictive Regressions (Least-Squares method for Model I) and functional regressions (Geometric Means method or Model II) were run for filtering rates versus length of the individuals. For a discussion of the convenience of choosing regression models I or II in length  $\times$  FR regressions of cladocerans refer to CHOW-FRASER & KNOEHEL (1985). In the literature concerning filtering rates of cladocerans, only model I has been used in most cases. Basically, the reason for introducing model II is that both carapace length and filtering rates are subject to a combination of inherent variability and measurement error and the variable's distribution is typically normal bivariate (SOKAL & ROHLF, 1981). Nevertheless, predictive regressions were also run, to allow comparisons with other literature sources. Furthermore, this regression model was the basis for other linear regression analysis used in this paper (ANCOVA, Multiple Regression).

Analysis of Covariance (ANCOVA) was applied to compare different FR versus length regressions. Interpretations of the results of this analysis were done according to SOKAL & ROHLF (1981) and calculations were performed using SAS statistical package — Proc GLM (SAS Inst., 1988). Functional regressions (Model II) were calculated with a Turbo-Pascal (Version 5.1) program.

A multivariate linear model (Model Selection: forward, Proc Reg SAS) was fitted to assess the possible interactions between community grazing rates and other variables like biomass of major herbivores, temperature, POC, chlorophyll-a and water temperature. The basic model used was:

$$\begin{aligned} \text{CGR} = & a + b \cdot B_{\text{DH}} + c \cdot B_{\text{DG}} + \\ & + d \cdot B_{\text{CAL}} + e \cdot B_{\text{BOS}} + f \cdot B_{\text{CYC}} + \\ & + g \cdot \text{POC} + h \cdot \text{Chl}_a + i \cdot \text{Temp}^2 \end{aligned} \quad (5)$$

where CGR is community grazing rates in  $\text{ml} \cdot \text{l}^{-1} \cdot \text{day}^{-1}$ ,  $B_{\text{DH}}$  is *D. hyalina*,  $B_{\text{DG}}$  *D. galeata*,  $B_{\text{CAL}}$  *E. gracilis*,  $B_{\text{BOS}}$  *Bosmina* spp.,  $B_{\text{CYC}}$  *Cyclopoida*, POC particulate organic carbon ( $\text{mg C} \cdot \text{l}^{-1}$ ),  $\text{CHL}_a$  Chlorophyll-a ( $\mu\text{g} \cdot \text{l}^{-1}$ ) and  $\text{TEMP}^2$  square power of temperature ( $^{\circ}\text{C}$ ). All zooplankton data were entered in biomass units ( $\mu\text{g} \cdot \text{l}^{-1}$ ). The polynomial intercept is "a". The values "b" through "i" are the estimates of the independent variables. The forward selection mode begins with no variables in the model. For each variable, a F-value is calculated. If the F-value is lower than an arbitrarily fixed boundary, the selected variable is not included in the final model (SAS Inst., 1988).

An important methodological question concerning the application of multivariate linear models to biological data is: What data transformation should be used? I decided not to include log transformation values of the biomass variables, as did PETERS & DOWNING (1984), for the following reason: Several regressions between FR (dependent) and length as well biomass (independent variables) of *D. galeata* were run. The results of these regressions can be seen in Table 1. It is clear that the best fit was achieved when the independent variables were the cubic power of length and weight (not log-transformed) were used. In both cases,  $R^2$  was greater than 0.8. This means that the best curve to explain  $\text{FR} \times \text{Weight}$ , in this data set, is a linear instead of a power function. This confirms the findings of CHOW-FRASER & KNOEHEL (1985) who affirmed that filtering rates of *Daphnia* relate approximately to the cubic power of carapace length. I did not include interactive terms (nested variables) since a few outliers (or extreme values) could heavily bias the regression (PETERS & DOWNING, 1984). The square of temperature tries to accommodate the nonlinear responses of filtering rates to temperature (ZÁNKAI & PONYI, 1976).

## Results

The seasonal changes in temperature, chlorophyll-a concentrations, water transparency and POC (fraction  $< 50 \mu\text{m}$ ) are presented in Fig. 1. It is possible to characterize five different seasonal stages by inspecting this figure.

Table 1. Length and biomass vs. filtering rates regression estimates of *D. galeata* in epilimnion of L. Constance in 1988.

data transformation	y = ax + b		F	R <sup>2</sup>
	a	b		
$x_1 \cdot y$	17.780	-11.450	283.298	0.7077
$x_1^2 \cdot y$	7.860	-2.627	461.715	0.7978
$x_1^3 \cdot y$	4.085	0.466	660.747	0.8496
$\log x_1 \cdot \log y$	2.447	1.543	232.989	0.6657
$x_w \cdot y$	0.460	1.599	736.306	0.8629
$\log x_w \cdot y$	4.856	-1.101	171.914	0.5950
$\log x_w \cdot \log y$	0.676	0.333	232.989	0.6557

obs:  $x_1$  = length (mm),  $x_w$  = weight ( $\mu\text{g}$ ),  $y$  = filtering rates ( $\text{ml}/\text{ind} \cdot \text{day}$ ),  $n = 125$ .

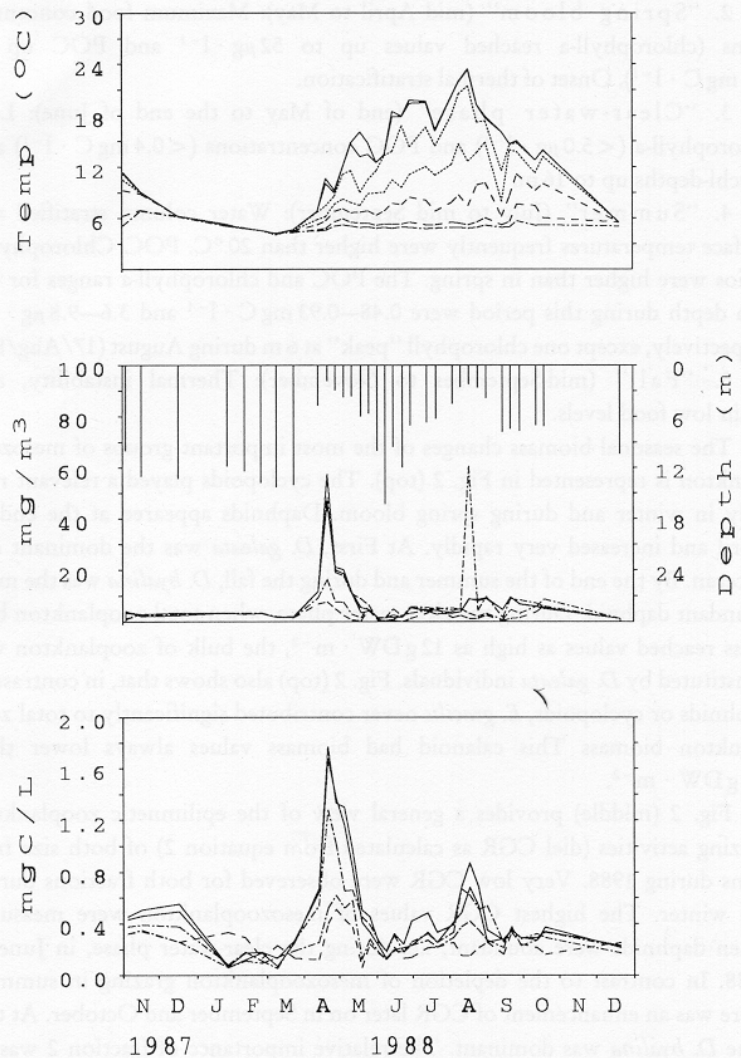


Fig. 1. Water temperatures and food conditions in Lake Constance (Überlingersee). Top panel: temperatures at 0, 2, 6, 12, 20, 36 and 50 m depth. Middle: Secchi depths (right ordinate), chlorophyll-a at 0, 2, 6, 12 and 20 m depth. Bottom: particulate organic carbon POC at 0, 2, 6, 12, 20, 36 and 50 m depth.

1. "Winter" (end of November to beginning of April): The water column is isothermic ( $0 < d < 50$  m), chlorophyll-a and POC concentrations were lower than  $5 \mu\text{g} \cdot \text{l}^{-1}$  and  $0.50 \text{ mg C} \cdot \text{l}^{-1}$ , respectively, and POC concentrations from deep layers equalled or exceeded those from near the surface.

2. "Spring bloom" (mid April to May): Maximum food concentrations (chlorophyll-a reached values up to  $52 \mu\text{g} \cdot \text{l}^{-1}$  and POC up to  $1.7 \text{mg C} \cdot \text{l}^{-1}$ ). Onset of thermal stratification.

3. "Clear-water phase" (end of May to the end of June): Low chlorophyll-a ( $< 5.0 \mu\text{g} \cdot \text{l}^{-1}$ ) and POC concentrations ( $< 0.4 \text{mg C} \cdot \text{l}^{-1}$ ) and Secchi-depths up to 16 m.

4. "Summer" (July to mid September): Water column stratified and surface temperatures frequently were higher than  $20^\circ\text{C}$ . POC: Chlorophyll-a ratios were higher than in spring. The POC and chlorophyll-a ranges for the 2 m depth during this period were  $0.48\text{--}0.93 \text{mg C} \cdot \text{l}^{-1}$  and  $3.6\text{--}9.8 \mu\text{g} \cdot \text{l}^{-1}$  respectively, except one chlorophyll "peak" at 6 m during August (17/Aug/88).

5. "Fall" (mid-September to November): Thermal instability, and again low food levels.

The seasonal biomass changes of the most important groups of mesozooplankton is represented in Fig. 2 (top). The cyclopoids played a relevant role only in winter and during spring bloom. Daphnids appeared at the end of April and increased very rapidly. At first, *D. galeata* was the dominant cladoceran. By the end of the summer and during the fall, *D. hyalina* was the most abundant daphnid. During the clear-water phase, when total zooplankton biomass reached values as high as  $12 \text{g DW} \cdot \text{m}^{-2}$ , the bulk of zooplankton was constituted by *D. galeata* individuals. Fig. 2 (top) also shows that, in contrast to daphnids or cyclopoids, *E. gracilis* never contributed significantly to total zooplankton biomass. This calanoid had biomass values always lower than  $1.0 \text{g DW} \cdot \text{m}^{-2}$ .

Fig. 2 (middle) provides a general view of the epilimnetic zooplankton grazing activities (diel CGR as calculated from equation 2) of both size fractions during 1988. Very low CGR were observed for both fractions during the winter. The highest CGR values of mesozooplankton were measured when daphnids were abundant, i.e. during the clear-water phase, in June of 1988. In contrast to the depletion of mesozooplankton grazing in summer, there was an enhancement of CGR later on in September and October. At this time *D. hyalina* was dominant. The relative importance of fraction 2 was almost always evident. On some occasions, such as immediately before clear-water phase and during some short periods in the summer, CGR of microzooplankton was comparable to or even higher than those of mesozooplankton.

The adjusted equation related to the multivariate linear model is given in Table 2. A highly significant total  $R^2$  was obtained. The F-values of POC and cyclopoid biomass were not significant and these variables were excluded from the model. The F-values of all other included variables (except *Bosmina*) were significant at the 0.05 level ( $\text{Prob} > F$ ). The relative importance of the biomass of the two *Daphnia* species in the model can be evaluated by compar-



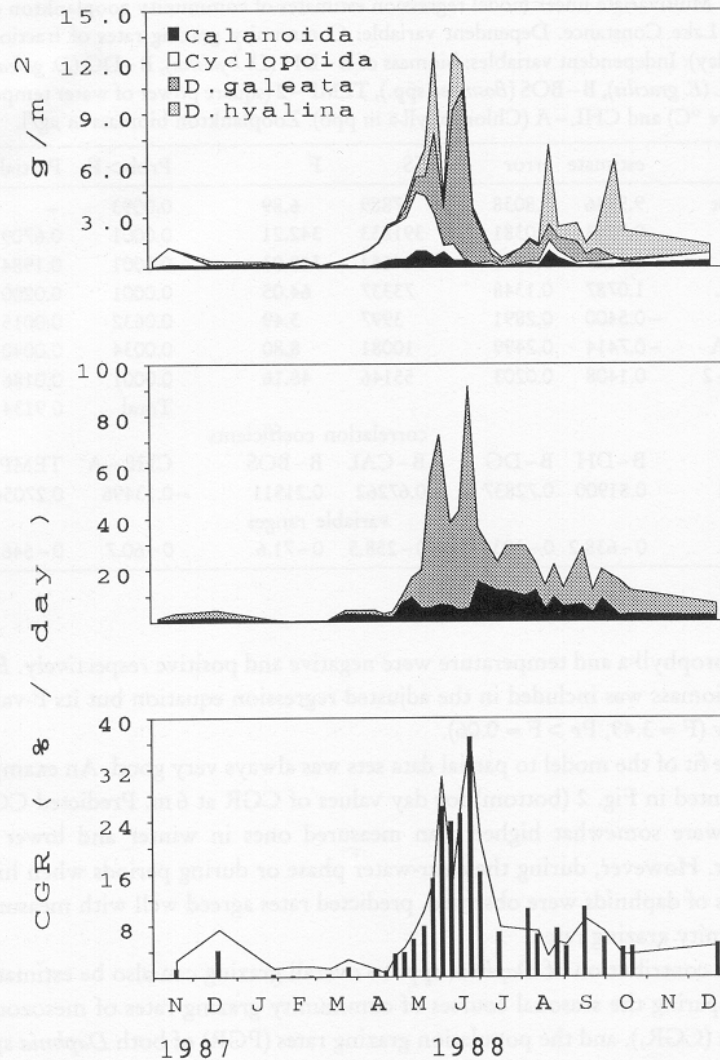


Fig. 2. Zooplankton biomass and CGR in Lake Constance. Top panel: seasonal biomass variation of major zooplankton groups. Middle: seasonal course of size-fractionated community grazing rates. Values refer to the whole diel cycle (see Equation 2). Upper polygon: mesozooplankton; lower polygon: microzooplankton. Bottom: Comparison of measured community grazing rates at 6 m, day values (black bars) with the predicted values from the multivariate model (Table 2) which are depicted by a solid line.

ing the partial  $R^2$  of independent variables. These values for *D. hyalina* and *D. galeata* were 0.6709 and 0.1984, respectively (Table 2). Temperature and Chlorophyll-a did not have high partial  $R^2$  but their estimates are nevertheless significant at the 0.05 level. As one could expect, the estimates of the parameters

Table 2. Multivariate linear model regression estimates of community zooplankton grazing in Lake Constance. Dependent variable: Community grazing rates of fraction 1 (ml/l · day). Independent variables: biomass of B-DH (*D. hyalina*), B-DG (*D. galeata*), B-CAL (*E. gracilis*), B-BOS (*Bosmina* spp.), TEMP-2 (square power of water temperature °C) and CHL-A (Chlorophyll-a in ppb). Zooplankton biomass in µg/l.

	estimate	error	SS	F	Prob > F	Partial R <sup>2</sup>
intercept	9.9846	3.8038	7889	6.89	0.0093	–
B-DH	0.7043	0.0381	391833	342.21	0.0001	0.6709
B-DG	0.3127	0.0175	364154	318.03	0.0001	0.1984
B-CAL	1.0787	0.1348	73337	64.05	0.0001	0.0200
B-BOS	-0.5400	0.2891	3997	3.49	0.0632	0.0015
CHL-A	-0.7414	0.2499	10081	8.80	0.0034	0.0040
TEMP-2	0.1408	0.0203	55146	48.16	0.0001	0.0186
					Total	0.9134
	correlation coefficients					
	B-DH	B-DG	B-CAL	B-BOS	CHL-A	TEMP-2
CGR-1	0.81900	0.72837	0.67262	0.21511	-0.13496	0.27056
	variable ranges					
0-936.1	0-638.2	0-1034.0	0-258.5	0-71.6	0-60.7	0-546.2

n = 210

for chlorophyll-a and temperature were negative and positive respectively. *Bosmina* biomass was included in the adjusted regression equation but its F-value was low (F = 3.49, Pr > F = 0.06).

The fit of the model to partial data sets was always very good. An example is presented in Fig. 2 (bottom) for day values of CGR at 6 m. Predicted CGR values were somewhat higher than measured ones in winter and lower in summer. However, during the clear-water phase or during periods when high biomass of daphnids were observed, predicted rates agreed well with measured community grazing rates.

The contribution of *Daphnia* spp. to overall grazing can also be estimated by comparing the seasonal courses of community grazing rates of mesozooplankton (CGR<sub>1</sub>), and the population grazing rates (PGR) of both *Daphnia* species (Fig. 3). The seasonal trends and the amplitude of CGR of mesozooplankton are practically the same as the summation of PGR's due to *D. hyalina* and *D. galeata*. The first species dominated before the clear-water phase and throughout the fall whereas grazing of *D. galeata* was important during the clear-water phase and immediately thereafter. The PGR mean annual values were 70.3 and 48.4 ml · l<sup>-1</sup> · day<sup>-1</sup>, for *D. hyalina* and *D. galeata*, respectively.

Fig. 4 summarizes day/night depth profiles of CGR (mesozooplankton). A clear seasonal component can be observed on these profiles. During the spring bloom, there was no difference between day and night values. Diel changes became apparent during May and were highest at the beginning of June (8/Jun/1988). During the clear-water phase, zooplankton feeding rates at surface in-

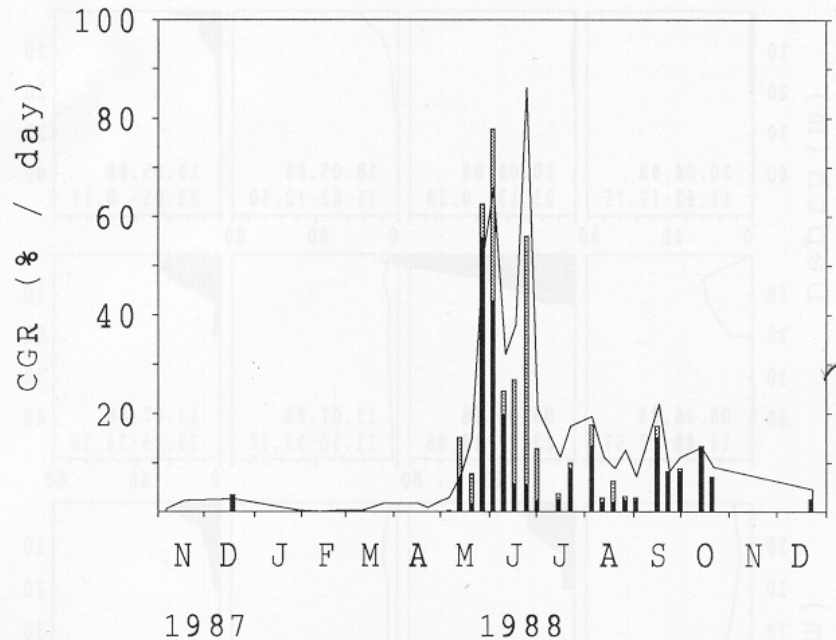


Fig. 3. Comparison of model (Equation 1) generated estimates of grazing rates of *Daphnia* populations (Black bars: PGR of *D. hyalina*; hatched bars: PGR of *D. galeata*) with the actually measured community grazing rates of mesozooplankton (solid line).

creased from day to night by a factor 30. In summer (July and August) large diel amplitudes in CGR's were again observed. Eventually, they decreased gradually in September and October.

The possible influence of higher individual filtering rates of *D. hyalina* and *E. gracilis* could not be detected at the community level (mesozooplankton). At night, biomass specific grazing activities ( $G_b$ ) in the epilimnion were equal or lower than day values (Table 3). Even during the clear-water phase (June),

Table 3. Diel variations of zooplankton community grazing:biomass ratios ( $\text{ml} \cdot \mu\text{gDW}^{-1} \cdot \text{day}^{-1}$ ) in epilimnion (0–6 m) in L. Constance (Überlingersee) during 1988.

Date	<i>D. galeata</i>		<i>D. hyalina</i>		Zooplankton	
	day	night	day	night	day	night
20. Apr. 1988	1.6	8.5	3.4	9.8	0.1	0.1
18. May. 1988	1.2	1.1	2.9	6.5	0.3	0.3
08. Jun. 1988	1.0	1.3	–	1.6	0.7	0.6
13. Jul. 1988	1.0	3.9	–	1.6	3.1	1.1
24. Aug. 1988	6.6	3.7	–	3.4	4.4	1.1
28. Sep. 1988	4.1	5.9	–	1.2	3.7	0.9
19. Oct. 1988	7.3	–	–	0.9	1.5	0.6

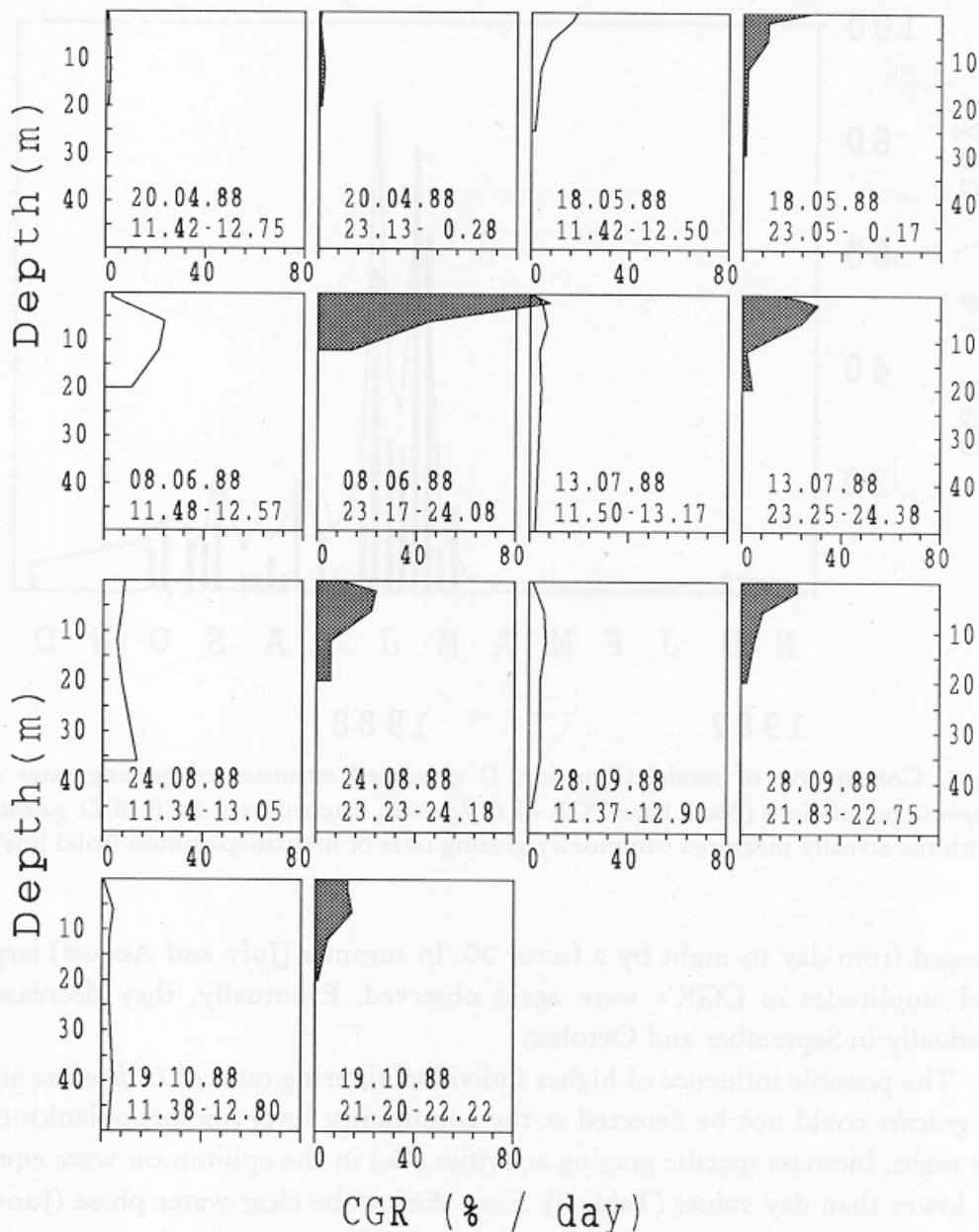


Fig. 4. Depth-profiles of community grazing rates of mesozooplankton in day and night experiments (hatched). Time (hours) in decimal units.

night  $G_b$  ratios were clearly lower than day ones. Table 3 also provides ratios calculated specifically for *Daphnia* species. Specific  $G_b$ 's were calculated using the biomass of each *Daphnia* population and CGR (Eq. 4). Higher  $G_b$ 's were found for *D. galeata* in some night incubations (e.g. April and July).  $G_b$ 's for the vertical migrator *D. hyalina* were also higher at night before clear-water phase, but day values of  $G_b$  for this species could not be calculated in most occasions since their individuals were absent from epilimnion during the day.

The effects of food concentration and temperature on the filtering rates of the two *Daphnia* species are summarized in Fig. 5. The interaction between *D.*

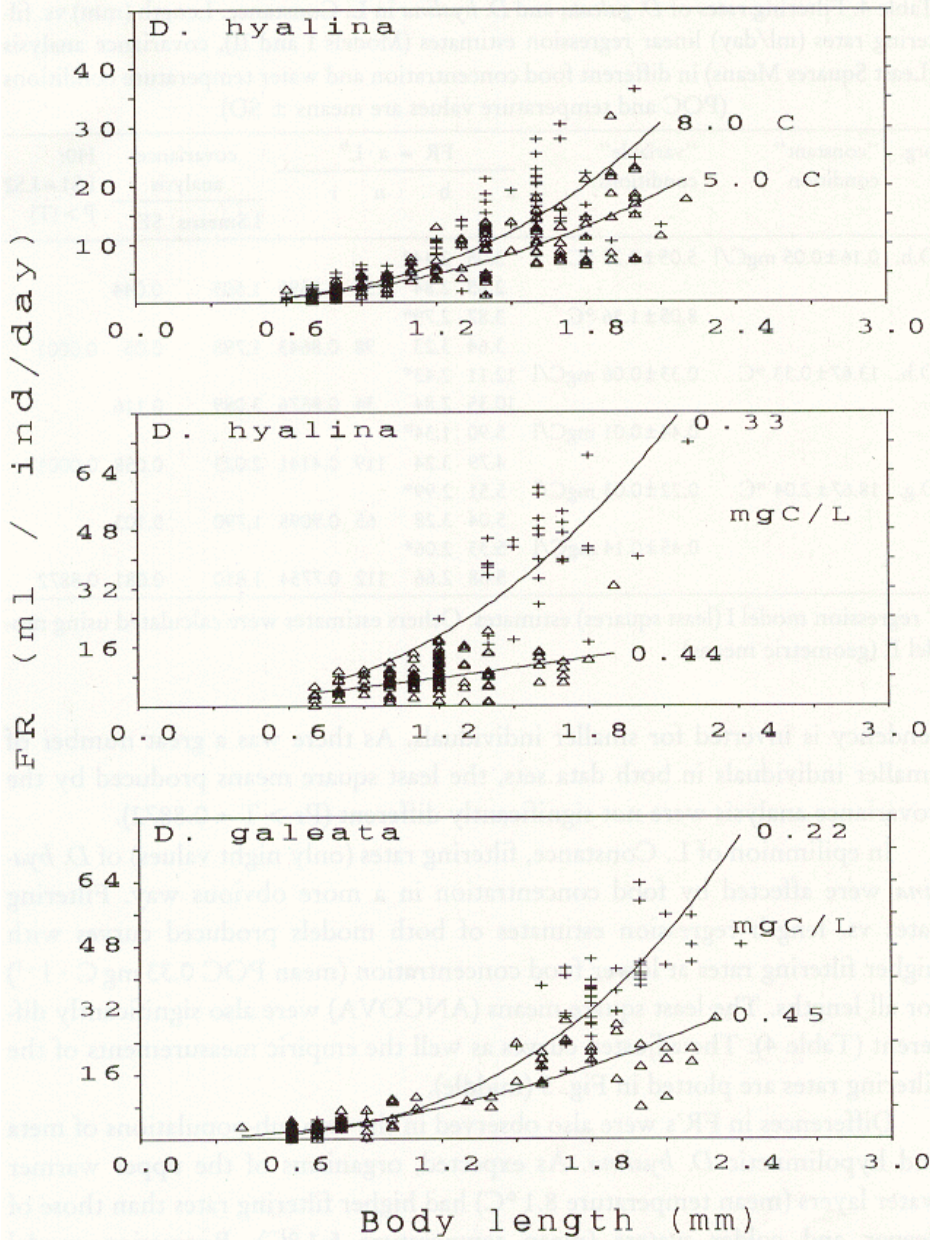


Fig. 5. Filtering rates  $\times$  Length (mm) in *Daphnia* spp. Top panel: *D. hyalina* under different temperature conditions. Crosses: 8.05 °C, Triangles: 5.05 °C. Middle: *D. hyalina* in different food conditions. Crosses: 0.33 mgC  $\cdot$  l $^{-1}$ , Triangles: 0.44 mgC/l. Bottom: *D. galeata* in different food concentrations. Crosses: 0.22 mgC  $\cdot$  l $^{-1}$ , Triangles: 0.45 mgC/l.

See Table 4 for regression statistics.

*galeata* and food concentration seems to be complex. The two data sets were constructed using very different food levels (Table 4). Only day values were included here. Fig. 5 (bottom) shows that only individuals larger than 0.9 mm filtered higher volumes of water at lower food concentration. Surprisingly, this

Table 4. Filtering rates of *D. galeata* and *D. hyalina* in L. Constance. Length (mm) vs. filtering rates (ml/day) linear regression estimates (Models I and II), covariance analysis (Least Squares Means) in different food concentration and water temperature conditions (POC and temperature values are means  $\pm$  SD).

org.	"constant" condition	"variable" conditions	FR = $a \cdot L^b$				covariance analysis		H0: LS1 = LS2 P >  T
			a	b	n	r	LSmeans	SE	
D.h.	0.16 $\pm$ 0.05 mgC/l	5.05 $\pm$ 0.28 °C	3.05	2.44*					
			2.85	2.84	153	0.8595	1.505	0.044	
		8.05 $\pm$ 1.36 °C	3.87	2.79*					
D.h.	13.67 $\pm$ 0.33 °C	0.33 $\pm$ 0.06 mgC/l	3.64	3.23	98	0.8643	1.798	0.05	0.0001
			10.35	2.84	34	0.8576	3.089	0.116	
		0.44 $\pm$ 0.01 mgC/l	5.90	1.34*					
D.g.	18.67 $\pm$ 2.04 °C	0.22 $\pm$ 0.03 mgC/l	4.79	3.24	119	0.4141	2.023	0.058	0.0001
			5.04	3.28	65	0.9098	1.790	0.103	
		0.45 $\pm$ 0.14 mgC/l	5.33	2.06*					
			5.68	2.66	112	0.7754	1.810	0.081	0.8872

\* regression model I (least squares) estimates. Others estimates were calculated using model II (geometric means).

tendency is inverted for smaller individuals. As there was a great number of smaller individuals in both data sets, the least square means produced by the covariance analysis were not significantly different ( $Pr > T = 0.8872$ ).

In epilimnion of L. Constance, filtering rates (only night values) of *D. hyalina* were affected by food concentration in a more obvious way. Filtering rates vs. length regression estimates of both models produced curves with higher filtering rates at lower food concentration (mean POC 0.33 mg C  $\cdot$  l<sup>-1</sup>) for all lengths. The least square means (ANCOVA) were also significantly different (Table 4). The adjusted curves as well the empiric measurements of the filtering rates are plotted in Fig. 5 (middle).

Differences in FR's were also observed in the two sub-populations of meta and hypolimnetic *D. hyalina*. As expected, organisms of the upper warmer water layers (mean temperature 8.1 °C) had higher filtering rates than those of deeper and colder waters (mean temperature 5.1 °C). Regression model estimates and the covariance analysis of regressions (Table 4) revealed that these sub-populations had significantly different filtering rates. A plot containing the two data sets and the adjusted curves is also provided in Fig. 5 (top).

## Discussion

### Community grazing rates and *Daphnia*

The contribution of *Daphnia* populations to the overall zooplankton grazing is thought to be of relevance in several European lakes such as L. Geneva

(GAWLER & ANGELI, 1987; BALVAY et al., 1990), L. Constance (LAMPERT, 1978), Schöhsee (LAMPERT & TAYLOR, 1985), L. Vechten and other Dutch lakes (GULATI et al., 1982 and 1985), Blelham Tarn (THOMPSON et al., 1982) and in L. Balaton (ZÁNKAI & PONYI, 1986). However, this evaluation is mostly done by visual comparisons of biomass and CGR data or it is based on determinations of *Daphnia* filtering rates applied to biomass data sets. Some authors have used multivariate models connecting CGR to environmental variables such as water temperature and food concentration (GULATI et al., 1982) but no multivariate model considering CGR and biomass at the species level is available for these lakes.

The model presented in this study clearly demonstrated the coupling effect between *Daphnia* biomass and overall grazing. Most of the observed variation was "explained" by the biomasses of the *Daphnia* species (Table 2). The biomass of the calanoid *E. gracilis* "explained" a much lower fraction of CGR variation. This agrees well with the seasonal biomass ratios between this calanoid and the two *Daphnia* (Fig. 2 top). Another important model output was that the biomass of cyclopoids had a negligible effect on the community grazing, since it did not reach the minimal requirements to be incorporated into the model. The negative estimate for *Bosmina* probably reflects the finding that these organisms were abundant in dates or depths of relatively low mesozooplankton grazing (such as just after spring bloom or in depths below 6 m).

The lower  $R^2$  for *D. galeata* ( $R^2 = 0.1984$ ) does not mean that this species always plays a secondary role when compared to *D. hyalina* ( $R^2 = 0.6709$ ). The latter probably had a greater  $R^2$  because large portions of the total zooplankton biomass was formed by its individuals when CGR was high. There was, however, one important exception: *D. galeata* was the dominant cladoceran (Fig. 2) during clear-water phase where the highest CGR value in the annual succession was measured.

The model also detected significant effects of temperature and chlorophyll-a concentrations. GULATI et al. (1982) found significant variance ratios (F) when specific feeding rates (SFR) were regressed against temperature and food concentration. They found a positive partial coefficient for temperature in Celsius degree (1.1437) and a negative one for food concentration in  $\text{mg C} \cdot \text{l}^{-1}$  (-1.451). Their data were log transformed. A more detailed analysis of the possible effects of temperature and food concentration is made below.

The lack of any clear relationship between CGR's and POC in the multivariate model was not surprising. POC and Chlorophyll-a do not always change in the same direction (see Fig. 1). It was shown that the ratio POC:Chlorophyll-a varies seasonally, and higher values of this ratio are expected to be found in summer. In contrast to chlorophyll, POC sometimes may reflect changes in numbers of bacteria, detritus and even small heterotrophs like ciliates or flagellates. On the other hand, higher partial  $R^2$ -values for chlo-

rophyll-a strengthens the relative importance of algae for the CGR's (fraction 1) in Lake Constance. LAMPERT & TAYLOR (1985) have already demonstrated that crustacean zooplankton grazing caused algal mortality rates higher than those determined for bacteria.

The comparison between CGR and PGR of *Daphnia* confirmed the basic model outputs. First, it gave clear indications that *Daphnia* is the most important organisms for mesozooplankton grazing in L. Constance. Furthermore, it was also shown that *D. hyalina* has a more preponderant influence on community grazing if the time scale is considered. This species had higher PGR on most occasions (including low winter values). However, if the absolute scale of grazing is considered, *D. galeata* plays a key role in the zooplankton community since its PGR was higher in periods of maximal grazing activities of zooplankton.

On some occasions, predicted PGR's were higher than CGR's. This could be explained by the fact that PGR estimates are based on a deterministic model (power function relating FR to body size). This model does not take into account stochastic variations in the filtering rates of individuals (which are reflected in the CGR) and, thus, it may sometimes result in overestimations. KNOECHEL & HOLTBY (1986) used a similar approach to compare CGR measured in situ and PGR of cladocerans (estimated with a multivariate model) in a small lake in Canada. Their model also provided accurate estimates of CGR over a wide range of conditions.

### Diel rhythms in individual filtering and biomass specific rates

Higher nocturnal filtering rates for the vertical migrators *D. hyalina* and *E. gracilis* were already demonstrated for L. Constance (PINTO-COELHO, 1990). However, as seen in the results, such diel rhythmic feeding behaviour did not affect community  $G_b$ 's in a measurable way. Biomass specific grazing rates were indeed comparable or even lower than the daily ratios in most night incubations. Nevertheless, this is in agreement with other grazing studies (GULATI et al., 1982; LAMPERT & TAYLOR, 1985). LAMPERT & TAYLOR (1985) suggested that the relative unimportance of diel feeding rhythms in some lakes may be due to the rather small size of the local zooplankton. This is certainly not the case in the present study, since only organisms greater than 170  $\mu\text{m}$  were considered here. It seems that the biomass contributions of other organisms such as *D. galeata* and especially cyclopoids (which migrate to the surface at night but do not affect CGR's) counterbalanced these enhanced night filtering rates of *D. hyalina* and *E. gracilis*. This would be the case during the clear-water phase, when *D. galeata*, *Mesocyclops leuckartii*, and *Cyclops vicinus* (Fig. 4 and also WÖLFL, 1990) were abundant in the lake. Table 3 shows that diel variations of  $G_b$ 's for *D. galeata* were minimal during June 1988. As



expected, night  $G_b$ 's for *D. hyalina* were always higher in all dates when it was possible calculating these coefficients during the day.

### Food concentration and in situ filtering rates of *Daphnia*

The effect of food concentration was analysed in *D. galeata* and *D. hyalina* populations which were restricted to epilimnetic (0–6 m) waters to avoid possible interactions with great temperature gradients. Furthermore, the greatest fluctuation in food concentration was found in the epilimnion (Fig. 1). For the vertical migrating *D. hyalina* only night measurements were considered.

Only large *D. galeata* individuals ( $L > 1.0$  mm) seemed to respond to different food levels. The data sets contained organisms from summer when the temperature was always higher than 18 °C (see below for further details about this temperature). The first data set was constructed with organisms collected immediately after the clear-water phase, presumably under food shortage conditions. In this particular year, there was a very pronounced clear-water phase with very high Secchi values (Fig. 1). In the second data set, animals were collected under typical summer food conditions (see Table 4). In spite of a great difference in food concentrations between the two *D. galeata* data sets (0.22 and 0.45 mg C · l<sup>-1</sup>), the FR vs. length relationships were found to be not significantly different. A possible explanation may be related to the allometric structure of the selected *D. galeata* populations. It can be easily observed in Fig. 5 (bottom) that there was a large number of small individuals (smaller than 0.9 mm) and a relative "lack" of medium size individuals (around 1.2 mm) in both data sets. As a consequence, regression estimates were biased because the smaller organisms had a different behaviour than expected (they filtered equivalent or even higher amounts of water at higher POC concentrations). Additionally, this fact indicates that the nature of the effect of food concentration on the filtering rates may vary with size.

The interaction between *D. hyalina* and food concentration was easier to demonstrate, but in a certain way, it was a surprise. The two data sets derived from night experiments which were carried out in the epilimnion in June and October. The water temperature was almost constant ( $\pm 0.5$  °C) in all selected experiments. There were two different food levels: In June, the mean concentration of POC was 0.33 mg C · l<sup>-1</sup> and of chlorophyll-a 1.2  $\mu$ g · l<sup>-1</sup>. Later, in October, POC was somewhat higher (0.44 mg C · l<sup>-1</sup>) and chlorophyll much higher (5.0  $\mu$ g · l<sup>-1</sup>). As expected, the FR's were significantly higher in June. However, these differences in FRg's might not be due only to food concentration. Very different phytoplankton compositions (dominance of poorly-edible algal populations in fall) may influence decisively the edibility of the phytoplankton (Cf Fig. 3.20 in SOMMER, 1989). Inedible algae such as gelatinous Chlorophyceae, large diatoms or filamentous blue-green algae can be a major

factor inducing lower FR's and assimilation rates, as well as increasing food rejection and respiration rates in *Daphnia* (for a review see LAMPERT, 1987).

To study the effect of food concentration on feeding rates, the first point to observe is which concentration range should be considered. Above the incipient food level (ILL), the filtering rates of daphnids decrease and the ingestion rates remain constant. Daphnids (e.g. *Daphnia magna*) have ILL levels up to  $0.2 \text{ mg C} \cdot \text{l}^{-1}$  (PORTER et al., 1982). These authors found that the highest response of *Daphnia* filtering rates to fluctuations in food concentrations were observed when these levels varied between 0.2 and  $2.0 \text{ mg C} \cdot \text{l}^{-1}$ . Furthermore, it was postulated that POC concentrations between  $0.20\text{--}0.25 \text{ mg C} \cdot \text{l}^{-1}$  could be accepted as ILL for field conditions (THOMPSON et al., 1982). GULATI et al. (1982) used POC concentrations between 0.25 and  $0.50 \text{ mg C} \cdot \text{l}^{-1}$  to study the influence of food concentration on the specific filtering rates of zooplankton in L. Vechten. Also, it seems that the range of POC concentrations used in the present study ( $0.25\text{--}0.50 \text{ mg C} \cdot \text{l}^{-1}$ ) is convenient for investigating the effect of different food levels on individual filtering rates of *Daphnia*.

Another point to consider is that food concentrations have different effects on filtering rates of different zooplankton species. It is well known, for instance, that calanoids respond to oscillations in food concentrations with less sensitivity than do cladocerans (PETERS, 1984). I thought that it would be easier to investigate FR vs. food concentration interactions in *D. galeata* because this species does not undergo any extended vertical migration in L. Constance (GELLER, 1986), thus avoiding possible overlapping temperature effects. Moreover, other aspects of the ecology of this species (GELLER, 1985) indicate that *D. galeata* would be more sensitive than *D. hyalina* to food availability in the lake. An important aspect is the threshold food level, which is the lowest food requirement for maintenance of a certain population (LAMPERT, 1977). This level is higher for *D. galeata* ( $0.60 \text{ mg DW} \cdot \text{l}^{-1}$  vs.  $0.40 \text{ mg DW} \cdot \text{l}^{-1}$  for *D. hyalina*, values from GELLER, 1985) and indicates that this species would be more sensitive to fluctuations in food level. Therefore, it was a surprise to detect "better" statistics in the migrating *Daphnia*.

The least square regression (model I) coefficients for body length vs. clearance rates of both *Daphnia* species are comparable to other literature values. The exponent  $b$  (see Table 4) varied between 2.06 and 2.99 with the exception of *D. hyalina* FR's of data set d ( $0.44 \text{ mg C} \cdot \text{l}^{-1}$ ,  $13.67^\circ\text{C}$  and  $b = 1.34$ ). Using mixtures of *Chlamydomonas* ( $0.25 \mu\text{g DW/ml}$ ) and *Aerobacter* ( $0.25 \mu\text{g DW/ml}$ ) as food suspensions, DE MOTT (1982) found similar exponents for *D. rosea* (2.41–2.98). GELLER (1975) estimated an exponent  $b = 2.40$  for *D. pulex* feeding on *Scenedesmus acutus* suspensions at  $15^\circ\text{C}$ , below the ILL ( $0.24 \text{ mg C} \cdot \text{l}^{-1}$ ).

All estimates of the exponent  $b$  using model II were higher (2.66–3.28) than least square values (model I) when the two regression models were run for

the same data set. Nevertheless, these exponents (model II) agree well with other estimates also based on this model. CHOW-FRASER & KNOECHEL (1985) found a mean slope of 3.19 in a series of in situ measurements of *Daphnia* spp. FR's (including *D. galeata*) in many lakes of Canada. They suggested that steeper slopes obtained with this model indicate that animals filter-feed in proportion to their volume rather than to surface area, as can be inferred from exponents calculated with least square regression model (see GELLER, 1975).

### Influence of temperature

The theoretical feeding response to temperature fluctuations could be described using a power function ( $Y = a \cdot X^b$ ) where  $Y$  is the feeding response,  $X$  is the temperature, and  $a$  and  $b$  are regression constants (PETERS & DOWNING, 1984). If  $b$  is the slope of the regression coefficient between natural logarithm of FR and temperature, the Van't Hoff or the more familiar  $Q_{10}$  can be expressed in the following way:

$$Q_{10} = e^{10 \cdot b} \quad (6)$$

The response of other ecophysiological functions to temperature such as respiration could also be described using this coefficients. The  $Q_{10}$  for respiration in *Crustacea* measured over a wide range of temperatures (0–30 °C) lies between 2.09 and 2.70 (IVLEVA, 1980). Since the relationship between FR and temperature is not linear, I tried many transformations of the temperature data to be used in the multivariate model. The highest partial  $R^2$  was achieved when temperatures were transformed to their square values. However, as discussed below, more interesting temperature effects on feeding rates appear when they are investigated at the species level.

Temperature effects on filtering rates of zooplankton are difficult to measure under field conditions. Acclimatization may shift temperature optima (KIBBY, 1971; GELLER, 1975) and temperature history of migrating zooplankton species in a thermally stratified lake is varied and not easily determined (HANEY, 1985). Another complicating factor is the metabolic compensation. According to this theory, animals increase their respiratory rates at unfavourably low temperatures and decrease them at unfavourably high temperatures (IVLEVA, 1980). Not surprisingly, many authors have not observed any clear relation between temperature and in situ CGR's or FR's (HANEY, 1973; HANEY & HALL, 1975; DOWNING & PETERS, 1980; CHOW-FRASER & KNOECHEL, 1985). Others have mentioned the possible temperature effect or only indirectly observed its influence on feeding rates (NAUWERCK, 1963; LAMPERT & TAYLOR, 1985). Temperature effects on field estimates of FR's and CGR's have been statistically demonstrated in only a few cases (ZÁNKAI & PONYI, 1976; GULATI et al., 1982 and BODGAN & GILBERT, 1982 and MOURELATOS & LACROIX,

1990). It is interesting to notice that the temperature ranges which produced measurable effects on FR's were frequently below 18 °C. This could also be a reason why temperature influence on feeding behaviour has been so difficult to detect, since many studies have focused on temperature gradients above this "critical" value.

In this study, the effect of temperature on filtering rates was investigated in *D. hyalina* populations living in deep waters. In meta-hypolimnion, there was a slight but rather constant temperature gradient and food concentrations at those depths (20–50 m) were quite comparable (Fig. 1, bottom). Another important reason for choosing these depths is that this species, as a diurnal vertical migrator, may be extremely sensitive to light stimuli (HANEY & HALL, 1975; RINGELBERG, 1987). In those depths there was no incident day light during the summer of 1988. Two data sets were assembled with animals collected in depths where temperature was always below 18 °C (ca. 5.0 and 8.0 °C for data sets a and b, respectively) and organisms from the colder hypolimnion (36–50 m) filtered at significantly lower rates. This does not necessarily mean that temperature effects are only present at low temperatures, but temperature related rates-of-change of many physiological processes are higher outside the temperature optimum for poikilotherms (PENZLIN, 1989).

### Final Remarks

Using two different and independent approaches, it was demonstrated that not only both *Daphnia* species play fundamental roles in controlling overall zooplankton grazing but it was also shown that these species have very different grazing activities along the seasonal course. *D. galeata* was the most important herbivore during the clear-water phase and *D. hyalina* dominated zooplankton grazing outside this period.

The multivariate model relating community grazing rates to biomass of different species of zooplankton, water temperature and chlorophyll-a can be a useful tool for studies of plankton dynamics on the pelagic community of Lake Constance since accurate estimates of zooplankton grazing can be obtained using a simple array of basic limnological parameters.

The paper also contributes to the controversial question whether there is a diel rhythm in the biomass specific community grazing rates. In spite of great diel amplitudes observed in CGR, there was no enhancement in epilimnetic grazing rates per unit of biomass of mesozooplankton ( $G_b$ ) at night. It should be kept in mind, however, that these findings rely on a methodology which has some limitations: a) Only one type of experimental food, *Rhodomonas* sp., was tested; b) the grazing experiments were run in just one period of the day (10:00–14:00 hs) and at night (21:00–24:00); c) all data for this paper were collected between November 1987 and December 1988.

It is also necessary to outline that the smaller fraction of zooplankton plays a relevant role in the overall grazing. A more detailed analysis of microzooplankton grazing during the years 1988 and 1989 in this lake will be presented elsewhere. Finally, the interactions between filtering rates, food concentration and water temperature suggest these two factors are acting simultaneously in diverse ways to control filtering rates of zooplankton in a lake. Maybe the best example was represented by *D. hyalina*. During the growing season in L. Constance, its filtering rates were modulated by temperature in the hypolimnion and by food concentration in the epilimnion.

### Acknowledgements

I thank Drs. W. GELLER, T. WEISSE, and H. MÜLLER for significant improvements on this manuscript. I also thank A. GIANI for her assistance in the field and supportive comments on earlier drafts of this paper. Thanks as well as to the captain of the RV Lauterborn K. WIEDEMANN for helping me with the sampling gear. I also appreciate the suggestions made by Dr. W. LAMPERT and two anonymous reviewers. This research was supported by the Deutsche Forschungsgemeinschaft (Sonderforschungsbereich 248) and by a personal grant of the Brazilian Education Ministry (MEC/CAPES Proc. Nr. 386/86-2). I also wish to thank Dr. G. SWEET for linguistic corrections.

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Submitted: 8 November 1990; accepted: 27 February 1991.



