

**Zooplankton grazing in Lake Constance: *In situ* measurements of temporal variations, relative contributions of size fractions and major herbivores, regulatory factors of specific filtering rates and potential impact as loss factor for phytoplankton.**

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by

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# 1 Introduction

## 1.1 The ecological significance of zooplankton grazing

One basic interaction between two trophic levels in an ecosystem occurs when one organism eats another. For an ecologist, this action can be approached on two different levels: The first level consists in describing ingestion at the individual level (autecological level). The act of consuming a food item can be divided into many phases like searching, pursuing, handling or grasping and, finally, ingesting a prey. Each one of these phases can be quantitatively described (O'Brien, 1979). The second level refers to the community level (synecological level) and, in this case, the energy- or mass-flow related to the involved trophic levels may be the major point of interest (Margalef, 1983).

The study of food web interactions in aquatic systems has many advantages over its terrestrial counterparts. The higher turnover rates of planktonic organisms allow us readily to observe the often rapid dynamics of pelagical communities or to experimentally manipulate these food webs and quickly assess the individual or systemic responses (Crowder *et al.* 1988). Furthermore, these organisms lend themselves to the testing of many ecological hypotheses, because they are small, easily cultivated, and there is seemingly reduced heterogeneity in their environment (Peters, 1984). However, as Porter (1977) claimed, the understanding of grazing in the open waters was far less complete than in terrestrial ecosystems until recently, mostly because planktonic communities have microscopic sizes and, only in the last 10-15 years, new experimental techniques have allowed to quantify these interactions in a realistic way. The possibility to conduct experiments in the field was one of greatest new methodological achievements to investigate food web interactions in aquatic systems. Two categories of *in situ* techniques have been successfully applied: a) short incubations (some minutes), usually using radioisotopes (Haney, 1971 and 1973; Gulati *et al.* 1982; Thompson *et al.* 1982; Hart and Christmas, 1984; Lampert and Taylor, 1984 and 1985; Hart, 1986; Gawler and Chapuis, 1987); and b) long-term experiments (i.e. several days or even months) using isolated portions of water columns, the so called enclosed-systems (Porter, 1972 and 1976; Anderson *et*

*al.* 1978; Lynch, 1979; McCauley and Briand, 1979, Lynch and Shapiro 1981; De Bernardi *et al.* 1982; Lampert *et al.*, 1986). The progress of all these investigations in describing the pathways in the aquatic ecosystems has been recently critically evaluated (Peters and Downing, 1984; Sterner, 1989).

A brief survey on the recent studies about zooplankton feeding will show that the determinations of individual or community feeding rates in the field or at the laboratory have been used in a wide variety of studies covering many different academic interests such as energy- or mass-flow between primary producers and herbivores (Hart, 1986), mineral cycles (Gliwicz, 1975; Lehman, 1980 a and b), competition (Gilbert, 1985; Gilbert and Stemberger, 1985), optimal foraging (Lehman, 1976; Lam and Frost, 1976; De Mott, 1989), diel rhythms (Duval and Geen, 1976; Haney and Hall, 1975; Haney, 1985), predator-prey interactions (Wilson, 1973), effects of grazing on seasonal succession and community structure of phytoplankton (Porter, 1977; Lampert, 1978; Lampert *et al.* 1986; Richman *et al.* 1990) as well as auto-ecological studies describing the feeding biology of particular herbivores (Gauld, 1951; Nauwerck, 1959; Rigler 1961; Burns, 1968 a and b; Geller, 1975; De Mott, 1982; Dagg and Walser, 1987; Lair and Ali, 1990). Nevertheless, many problems concerning basic aspects of zooplankton grazing remain unsolved. Examples of such questions are: a) what are the particular effects of biomass concentration due to diurnal vertical migration (DVM) and diel rhythms in the filtering rates of some herbivores to explain higher community grazing rates usually observed at night? b) What role do smaller organisms, e.g. young stages of copepods and rotifers, play in the overall grazing? c) To what extent do food quality and selective grazing influence these rates? d) Are there distinct relationships between temperature, food concentration and grazing rates under field conditions? Many authors have dealt with these subjects, but conflicting results appear in the literature.

## 1.2 Some considerations about zooplankton grazing in Lake Constance

As a deep, large prealpine lake, L. Constance has a complex herbivore zooplankton community (Lampert and Schober, 1978; Geller, 1980; Walz *et al.* 1987; Einsle, 1988). Two of the major local herbivores are species of *Daphnia*: *D. galeata* and *D. hyalina*. The first species 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; Berberovic, 1990 b). 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 ( $P_{D.hyalina} = 18$ ,  $P_{D.galeata} = 24$  gDW.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 gDW.m<sup>-2</sup> respectively. 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* tends to maintain similar filtering rates during day and night. It is still an open question for L. Constance and probably for most lakes whether these enhanced filtering rates of vertical migrators can explain the higher community grazing rates at night. Some authors (e.g. Gulati *et al.* (1982) and Lampert and 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<sup>1</sup> of *Daphnia* would be a key factor modulating those daily patterns of zooplankton feeding.

In Lake Constance, some weeks after the spring algal bloom, there is a rapid increase of water transparency: A clear-water phase occurs. In spite of other possible influences, like nutrient limitation, algal sedimentation or climatic factors (Lampert, 1978; Sommer, 1987 and Weisse *et al.* 1990), grazing of larger zooplankton is thought to be a key factor causing such event in this lake as well as in many other temperate mesoeutrophic lakes (Lampert, 1988; Balvay *et al.* 1990). During this period, community

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<sup>1</sup> Filtering-, grazing- and ingestion rates of zooplankton are sometimes used with different connotations in the literature. In the present investigation, care was taken in employing always this terminology in a consistent trend. A detailed description of these rates will be given in section 2.5. In this case, Haney (1985) referred to filtering rates as expressed in mL.ind<sup>-1</sup>.day<sup>-1</sup>.

grazing rates are typically the highest in the annual cycle, and zooplankton biomass is dominated by large organisms like daphnids (Haney, 1973; Gulati *et al.*, 1982; Thompson *et al.* 1982; Lampert *et al.* 1986; Zánkai and Panyi, 1986 and Pinto-Coelho, 1991). In most temperate lakes, however, the dominance of large cladocerans in the seasonal zooplankton succession is a transitory event. Soon after clear-water stage, *Daphnia* populations suffer a breakdown caused by a combination of biotic and abiotic factors (Threlkeld, 1979 and 1985; Wright and Shapiro, 1990).

On the other side, recent studies have demonstrated that zooplankton grazing can be strongly influenced if not dominated by small organisms during some periods in summer or even before the appearance of daphnids in spring (Stockner and Porter, 1988, Mazumder *et al.* 1990). Protozoans, rotifers and copepod nauplii are the most important components of the so called microzooplankton (Pace and Orcutt, 1981). Some field studies have focused on measurements of specific filtering rates of planktonic rotifers (Bogdan *et al.* 1980; Starkweather and Bogdan, 1980; Lair and Ali, 1990). Other investigations have tried to evaluate the contribution of microzooplankton to the community grazing based on *in situ* measurements (e.g. Bogdan and Gilbert, 1982; Gilbert and Bogdan, 1984, Stockner and Porter, 1988). Recently, Mazumder *et al.* (1990) demonstrated that higher levels of piscivory predation can enhance the relative contribution of microzooplankton to overall grazing. How important are these organisms as primary consumers in Lake Constance? Recent investigations indicated that microzooplankton or even smaller consumers may have a decisive role in the overall zooplankton grazing in this lake during some periods (Müller, 1989; Weisse *et al.*, 1990; Geller *et al.* 1991; Müller *et al.* 1991). Nevertheless, basic aspects concerning the feeding activities of small organisms are not satisfactorily covered even in the general literature. More complete series of measurements including daily rhythms in the seasonal trends of microzooplankton grazing are required. Simultaneous measurements of grazing of micro- and mesozooplankton under the same experimental conditions would be another point of interest since most studies have concentrated on grazing measurements of just one fraction. Additionally, there is no conclusive study demonstrating which biotic and abiotic factor(s) are more important modulating microzooplankton grazing.

### 1.3 Objectives of this investigation

Most field investigations of zooplankton grazing rates using modern equipment, like the GLIWICZ-HANEY grazing chamber (Gliwicz, 1968 and Haney, 1971) 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 and Panyi, 1986), Schöhsee (Lampert and Taylor, 1985), Blelham Tarn (Thompson *et al.* 1982) and L. Créteil (Mourelatos and Lacroix, 1990), with relatively few exceptions, such as L. Geneva (Gawler and Angeli, 1987). Thus, one of the major objectives of this study is to provide a seasonal description of zooplankton grazing derived from *in situ* measurements in a large prealpine lake. Daily rhythms of grazing will be included in the seasonal model, since those rhythms are an essential aspect of zooplankton grazing.

Another objective of this investigation is to compare meso- and microzooplankton grazing in L. Constance. Different parameters describing zooplankton feeding, such as grazing-, ingestion- and biomass specific feeding rates (Cf. section 2.5) will be applied to evaluate different aspects such as seasonal contributions of each fraction to overall grazing, daily rhythms and, finally, the impact of both fractions as primary consumers in pelagic zone of the lake. Additionally, possible regulating factors such as water temperature, quality and quantity of food as well as interactions with larger organisms will be discussed.

Earlier studies have clearly demonstrated that daphnids play a major role in the zooplankton grazing in L. Constance (Lampert, 1978; Lampert and Schober, 1978; Geller, 1980). However, no detailed information on seasonal and diel courses of grazing activities at the population level is available for this lake. Consequently the third objective of this investigation will be to evaluate the relative contributions of different *Daphnia* species to the overall zooplankton grazing in this lake. This evaluation will be done using two different approaches. First, the grazing rates of both *Daphnia* populations were compared with the community grazing rates of mesozooplankton. Additionally, a multivariate linear model was applied to evaluate the "contribution" of different herbivorous zooplankton to overall grazing (in terms of percentages of explained variability of community grazing rates) as well as the influence of water temperature and food

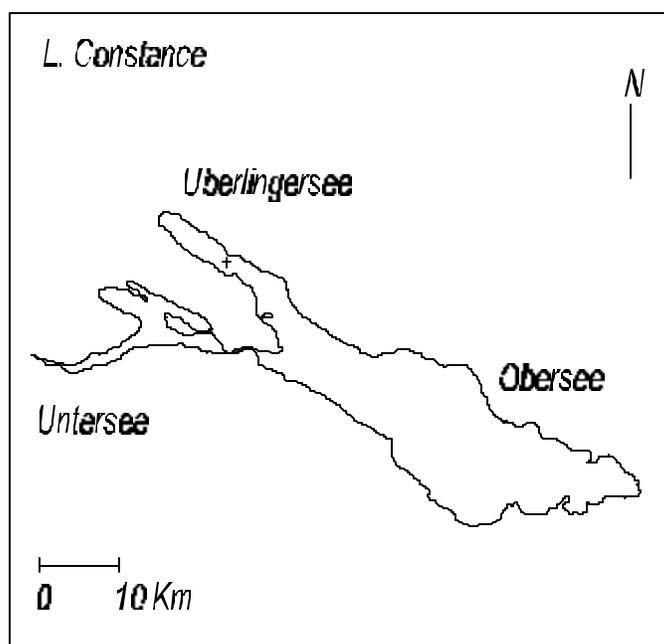
concentration on these rates.

Effects of factors such as body size, water temperature, quality and concentration of food in regulating the feeding rates of zooplankters have been intensively studied in the laboratory (Peters and Downing, 1984). However, these effects are not well understood when the feeding rates are measured *in situ*. Therefore, the investigation of these relationships in some herbivores of mesozooplankton of L. Constance was the last major objective of this study. Five factors were investigated: body size, diel rhythms, food type and concentration and, finally, water temperature. Individual measurements of filtering rates were conducted *in situ* considering all major components of mesozooplankton: *Daphnia hyalina*, *D. galeata*, *Bosmina*, *Eudiaptomus gracilis*, *Cyclops vicinus* and *Mesocyclops leuckarti*. However, emphasis will be given on *Daphnia* since these large cladocerans play the leading role in zooplankton grazing in this lake.

## 2 Methods

### 2.1 Study Area

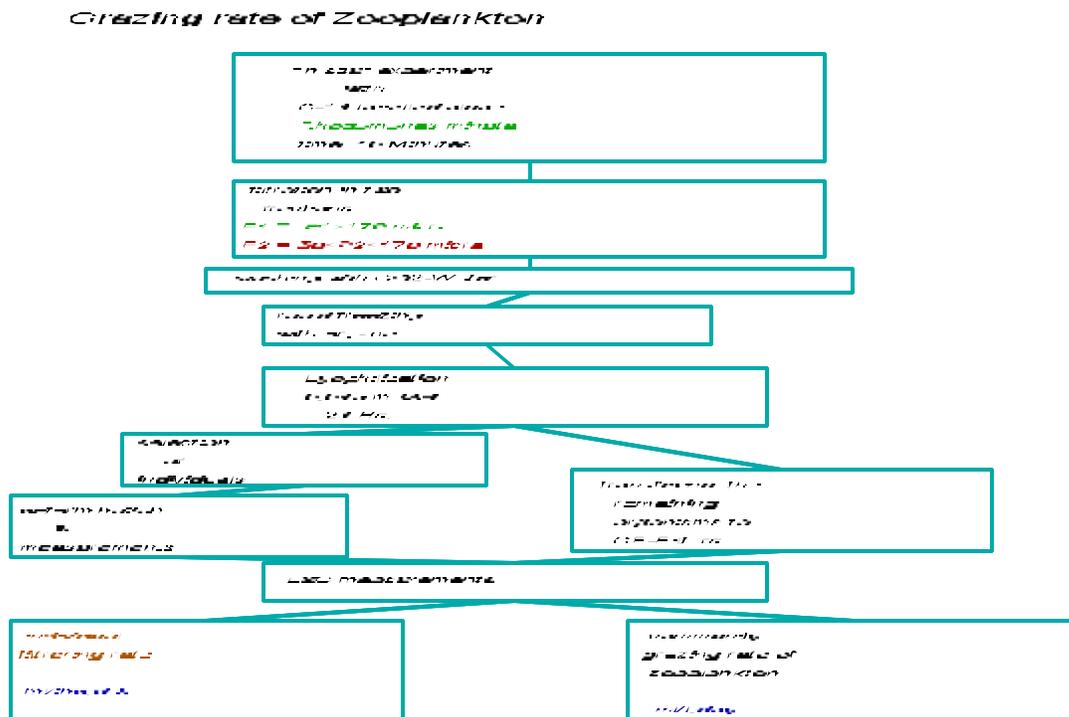
L. Constance (in German: *Bodensee*) is a temperate (Lat: ca. 47°30'- 47°50'N, Long: 8°50'- 9°45'E), warm-monomictic meso-eutrophic lake. It has ca. 550 Km<sup>2</sup>, maximum depth of 252 m. The lake has been morphometrically divided in two portions: lower lake (*Untersee*) and upper lake (*Obersee* and *Überlingersee*). The lower lake is smaller and shallower ( $A= 63 \text{ Km}^2$ ,  $Z_m= 13.2 \text{ m}$ ) and the upper lake has a mean depth of 100 m (Geller and Güde, 1989; Tilzer, 1990). The sampling station was situated in the



**Figure 1** Morphometric sub-divisions of Lake Constance. A cross indicates the sampling station where all *in situ* grazing experiments were conducted (Überlingersee).

northwestern part of the upper lake and it had a maximum depth of 147 m (Fig 1).





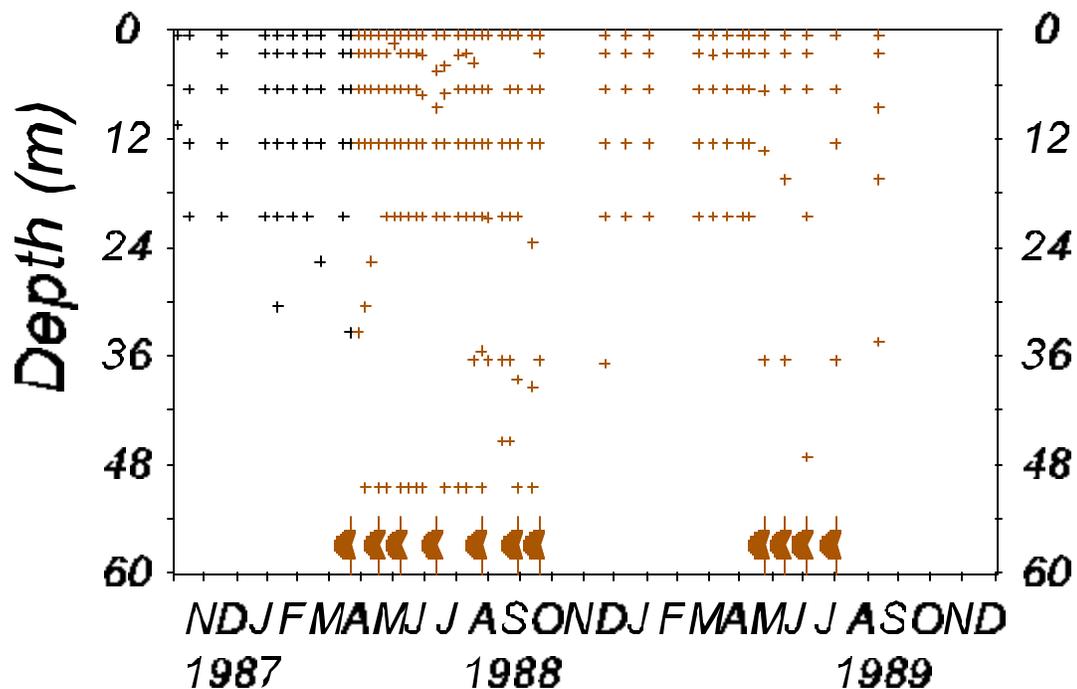
**Figure 3** *In situ* zooplankton grazing: Scheme containing the major methodological procedures.

The *In situ* determinations of zooplankton grazing were done using a twin Gliwicz-Haney grazing chamber (Fig 2). Parallel sampling (e.g two grazing experiments using different food particles) could be conducted simultaneously in the two half-chambers ( $V = 10\text{ L}$  each). The experimental food particles were labelled with  $^{14}\text{C}$  according to the technique described by Geller (1975). Two alga were used : *Rhodomonas sp.* (Length ( $L$ ) =  $12.5\text{ }\mu\text{m}$ ; Volume ( $V$ ) =  $316\text{ }\mu\text{m}^3$ ; strain 26.80, Göttingen) and *Stephanodiscus hantzschii* ( $L = 5.6\text{ }\mu\text{m}$ ;  $V = 133\text{ }\mu\text{m}^3$ ). Cell volumina and linear dimensions were calculated from stock cultures by A. Giani (pers. comm.). Both algae are important constituents of the nanoplankton in L. Constance (Sommer, 1987). Each experiment lasted up to 13 minutes. The size fractionating of zooplankton was done by sieving according to definitions of plankton size-fractions as proposed by Sieburth *et al.*(1978) modified in the following way:

'Mesozooplankton' :  $P1 > 170\text{ }\mu\text{m}$  ( $P1 = \text{fraction 1}$ )

'Microzooplankton' :  $50 < P2 < 170\text{ }\mu\text{m}$  ( $P2 = \text{fraction 2}$ )

Adult copepods and cladocerans were retained on the filters of fraction 1. Rotifers, nauplii (mostly from *Mesocyclops leuckarti*), small copepodites and in some cases, Protozoa (*Tintinnidae*) made up the bulk of biomass in fraction 2. Mollusca larvae (*Dreissena polymorpha*) were also occasionally present in the latter. The basic methodological procedures in the field and at the laboratory are summarized in Fig 3. A detailed description of sample treatment for radioactivity measurements will be given in section 2.7 .



**Figure 4** Diagram Time vs. depth showing all *in situ* grazing experiments conducted in Lake Constance (Überlingersee). Black semi-circles indicate when night incubations were done.

*In situ* grazing experiments were conducted between November 1987 and September 1989, with frequencies varying from every week during clear-water phase or summer to every two or three weeks during winter (Fig 4). These experiments usually covered the water column between 0 and 30 m (50 m during summer). Night experiment series were carried out monthly during the growing seasons of 1988 and 1989.

### 2.3 Zooplankton Biomass

In the second half of the grazing chamber, zooplankton samples were taken for determinations of

abundance and biomass. Samples were fixed with 4% formalin containing a dye, 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, each individual was measured for body size. 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 determinations of microcrustaceans were done using available allometric equations for crustacean zooplankton of L. Constance (Geller and Müller, 1985 and Wöfl, 1990).

Body volumes of rotifers were calculated from individual size measurements using modified geometric approximations as proposed by Ruttner-Kollisko (1977), and the conversion factors to dry weight (percentages of dry in fresh weight) were done using the specific conversion factors for rotifers of L. Constance (Cf. Table 2 *in*: Pauli, 1989).

## 2.4 Particulate Organic Carbon (POC)

The samples of seston < 50 : m were first concentrated by vacuum filtration over a fine suspension of diatomite-earth (*Kieselgur*) free from organic material. The C-content of these samples was measured by combustion of the air-dried filtrate in a Heraeus-furnace under pure oxygen at 800 °C. The CO<sub>2</sub> evolved was collected as bicarbonate in a solution containing 1 mL of NaOH 0.1 N and its concentration was determined by titration with 0.01 HCl. The diatomite layer retained all sestonic particles including 90% of the free living bacteria (Simon and Tilzer, 1987). Lenarz (1972) argued that C-concentrations as low as 0.02 mgC.L<sup>-1</sup> can be detected using this method.

## 2.5 Basic Calculations

Individual measurements of filtering rates (FR) were also performed in each experiment and FR were calculated according to Eq 1.

$$FR = \frac{RI \cdot 1440}{RS \cdot time (min)} \left[ \frac{mL}{ind. day} \right] \quad (1)$$

where FR is the individual filtering rate, RI is radioactivity measured in the vial containing just one specimen (dpm.ind<sup>-1</sup>), RS is the radioactivity of algal suspension in dpm.mL<sup>-1</sup>.

Zooplankton grazing at the community level can be expressed in different manners. The most common way is the community grazing rate (CGR) which is the volume (or percentage) of lake water filtrated by total zooplankton per time unit. The ingestion rate (CIR) is a measure of food uptake calculated by multiplying the grazing rate by the food concentration, usually expressed in carbon unities (POC). A third possibility would be the biomass specific grazing rate (G<sub>b</sub>), i.e. the quotient between community grazing rate and zooplankton biomass.

These parameters describe different aspects of the feeding behaviour and, therefore, it is important to understand what they mean before explaining with details how they were calculated. CGR reflects only the amount of experimental food which is ingested in a experiment. It is relatively simple to obtain since no other variable like POC or biomass of zooplankton are required for calculating it. High CGR values do not necessary mean high CIR if the real food concentration in the lake is low. Therefore, CIR is essential to build an energy flux-model between phytoplankton and primary consumers of a lake because it estimates the actual transfer rate of carbon between these communities. G<sub>b</sub>, on the other side, gives information about the physiological condition of the involved zooplankton organisms. Using this parameter, statements about daily fluctuations of grazing can be obtained. It is possible, for example, to know whether higher nocturnal community grazing rates are due to individual enhancement of filtering rates or simply to biomass concentration due to vertical migration of zooplankton to upper layers at night. Finally, we can also calculate the biomass specific ingestion rate (I<sub>b</sub>) which is the quotient between CIR and zooplankton biomass. It estimates the transfer rate of carbon per biomass unit and it can be useful to construct and validate C-

budgets at the community level. This latter parameter can also express the daily ingestion of food in percentages of carbon body weight if a factor for the conversion of body weight (DW) into C-unity is considered (Cf section 3.3).

Community grazing rates ( $CGR_n$ ) were calculated using the formula:

$$CGR_n = \frac{1}{10} \cdot \frac{RF \cdot 60}{RS \cdot T \cdot V} \left[ \frac{\% \text{ vol}}{\text{hour}} \right] \quad (2)$$

where RF is the radioactivity (dpm) of filters containing organisms, RS is the available radioactivity (dpm.mL<sup>-1</sup>) inside the experimental chamber, V is the chamber volume (L) and T is experiment duration in minutes.

One purpose of this investigation is to include diel variations of zooplankton grazing in a seasonal

$$CGR_{\text{diel}} = CGR_d \cdot D_1 + CGR_n \cdot D_2 \left[ \frac{\% \text{ vol}}{24 \text{ Hs.}} \right] \quad (3)$$

model. The diel community grazing rate was calculated in the following way:

where  $CGR_d$  and  $CGR_n$  are community grazing rates measured in day and night experiments respectively

$$day_1 = 12 + \sin(d + 280) * 3.67 \quad [hours] \quad (4)$$

(% vol.hour<sup>-1</sup>).  $D_1$  and  $N_1$  are the duration of day and night in hours for a specific date. The day length (in hours) for the location of Konstanz was calculated according to Eq 4 modified from Straskraba, 1980):

where d is the julian date.

We have seen that CGR can be expressed as a proportion of water filtered per time unity if the two volume dimensions, i.e volume of filtered water (mL) and volume of the experimental chamber (L), are conveniently cancelled ( $CGR = \% \text{ vol day}^{-1}$  or  $\% \text{ diel cycle}^{-1}$ ). In the literature (Cf. Fig 5 *in*: Lampert and Taylor, 1985) however, CGR is frequently expressed using the original absolute volume unities (e.g. mL.L<sup>-1</sup>

<sup>1</sup>.hour<sup>-1</sup> or mL.L<sup>-1</sup>.day<sup>-1</sup>). This way to express CGR will also be considered in the next three equations.

Community ingestion rates (CIR<sub>diel</sub>) were obtained in the following way:

$$CIR = CGR \cdot POC \quad \left[ \frac{\mu gC}{L \cdot 24Hs} \right] \quad (5)$$

where CGR is community grazing rates (mL.L<sup>-1</sup>.diel cycle<sup>-1</sup>) and POC is particulate organic carbon (: gC.mL<sup>-1</sup>).

$$G_b = \frac{CGR}{Biomass} \quad \left[ \frac{mL}{\mu gDW \cdot 24Hs} \right] \quad (6)$$

Eq 6 illustrates how the biomass specific grazing rates ( $G_b$ ) were obtained. Correspondingly, the biomass specific ingestion rates ( $I_b$ ) were calculated using Eq 7. CGR is community grazing rate ( $\text{mL.L}^{-1}.\text{diel cycle}^{-1}$ ), CIR is community ingestion rate in :  $\text{gC}^{-1}.\text{L}^{-1}.\text{diel cycle}^{-1}$  and Biomass refers to zooplankton biomass in :  $\text{gDW.L}^{-1}$ .

$$I_b = \frac{CIR}{\text{Biomass}} \left[ \frac{\mu\text{gC}}{\mu\text{gDW} \cdot 24\text{Hs}} \right] \quad (7)$$

Since every single individual was measured in the samples for abundance determinations and filtering rates of most herbivores were individually determined on each *in situ* incubation, these two variables could be combined to calculate the population grazing rates (PGR) of a specific herbivore on a given date. This was done to evaluate the contribution of both *Daphnia* populations in the overall zooplankton grazing. PGR

$$PGR = \frac{1}{10} \sum_i FR_i \cdot A_i \left[ \frac{\mu\text{vol}}{24\text{Hs}} \right] \quad (8)$$

of both *Daphnia* were calculated with Eq 8.

$FR_i$  is filtering rate in  $\text{mL.ind}^{-1}.\text{day}^{-1}$  and  $A_i$  is abundance of  $\text{ind.L}^{-1}$  in a given size class  $i$  ( $i$  varied from 0.6 to 2.5 mm with intervals of 0.25 mm).

Other research groups of the Limnological Institute (University of Konstanz) kindly provided additional information. Chlorophyll-a and primary production data sets used in this paper were collected and processed by primary production group (Tilzer *et al.*, unpubl.). Biovolumina of phytoplankton from 1988 and 1989 was supplied by A. Schweizer (unpubl.). Finally, water temperature records were given by the hydrophysic group (G.Heinz and M.Schimmele, unpubl.). All data sets considered here were collected at the same sampling station and dates (or the day before) when grazing experiments were conducted.

## 2.6 Statistical Analysis

Predictive Regressions (Least-Squares method or Model I) and functional regressions (Geometric Means method or Model II) were run for filtering rates versus length of the individuals. 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). For a detailed discussion of the convenience of choosing regression model II in FR vs. length regressions of cladocerans refer to Chow-Fraser & Knoechel (1985). Anyway, both regressions models were always run, to allow comparisons with other literature sources. Furthermore, model I was the basis for other statistical analyses used in this study (Analyses of Covariance - ANCOVA and multiple linear regression).

Analysis of covariance (ANCOVA) was applied to compare different regression estimates. Interpretations of the results of this analysis were done according to Sokal & Rohlf (1981) and calculations were performed using the SAS statistical package (SAS Inst. 1988, Proc GLM). Functional regressions (Model II) were calculated with a Turbo-Pascal (Version 5.1) program.

A multivariate linear model (SAS 1988, Proc Reg SAS, model selection FORWARD) 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.

$$\mathbf{CGR}_1 = \mathbf{fn}(\mathbf{B}_1, \mathbf{B}_2, \dots, \mathbf{POC}, \mathbf{Chl}_A, \mathbf{Temp}) \quad (9)$$

The basic model is illustrated in Eq 9 where  $\mathbf{CGR}_1$  is community grazing rates of mesozooplankton,  $\mathbf{B}_1, \mathbf{B}_2$ , etc. are the biomass of the microcrustaceans *D. hyalina*, *D. galeata*, *E. gracilis*, *Bosmina spp.*, and *Cyclopoida*, POC particulate organic carbon ( $\text{mgC.L}^{-1}$ ),  $\mathbf{Chl}_A$  Chlorophyll-a ( $\text{: g.L}^{-1}$ ) and  $\mathbf{TEMP}^2$  square power of temperature ( $^{\circ}\text{C}$ ). All zooplankton data were entered in biomass units ( $\text{: gDW.L}^{-1}$ ). The procedure fits a polynomial equation relating CGR to the independent variables using the least squares method (Snedecor and Cochran, 1989). The forward selection mode begins with no variables in the model.

For each variable, an F-value is calculated. If the F-value does not exceed an arbitrarily chosen boundary (default value = 0.5), the selected variable is not included in the final model (SAS, 1988).

The relationship of microzooplankton to biomass of nauplii and rotifers as well as to water

$$CGR_2 = fn(Bio_{rot}, Bio_{naup}, Chl_a, POC, Temp) \quad (10)$$

temperature and food concentration was also investigated by means of a multiple linear regression model (SAS 1988, Proc Reg). The model relating grazing of microzooplankton to these three independent variables is illustrated in Eq 10.

Table 1

Length and body weight vs. filtering rates regression estimates of *D. galeata* in epilimnion of L. Constance in 1988.

data transformation	y = a + bx		F	R <sup>2</sup>
	a	b		
x <sub>1</sub> . y	-11.450	17.780	283.298	0.7077
x <sub>1</sub> <sup>2</sup> . y	-2.627	7.860	461.715	0.7978
x <sub>1</sub> <sup>3</sup> . y	0.466	4.085	660.747	0.8496
log x <sub>1</sub> . log y	1.543	2.447	232.989	0.6657
x <sub>w</sub> . y	1.599	0.460	736.306	0.8629
log x <sub>w</sub> . y	-1.101	4.856	171.914	0.5950
log x <sub>w</sub> . log y	0.333	0.676	232.989	0.6557

obs: x<sub>1</sub>= length (mm), x<sub>w</sub>= weight (:g), y = filtering rates (ml/ind.day), n=125.

An important methodological question concerning the application of multivariate linear models to biological data is: What data transformation should be used? I decided not including log transformed values

of the biomass variables, as did Peters & Downing (1984), for the following reason: Several regressions between FR (dependent) and length as well as biomass (independent variables) of *D. galeata* were run. These regressions are represented in Tab 1. 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 the relationship FR vs. Weight, in this data set, is a linear function. This confirms the findings of Chow-Fraser & Knoechel (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 regressions (Peters & Downing, 1984). The square of temperature tries to accommodate the nonlinear responses of filtering rates to temperature (Zánkai & Panyi, 1976).

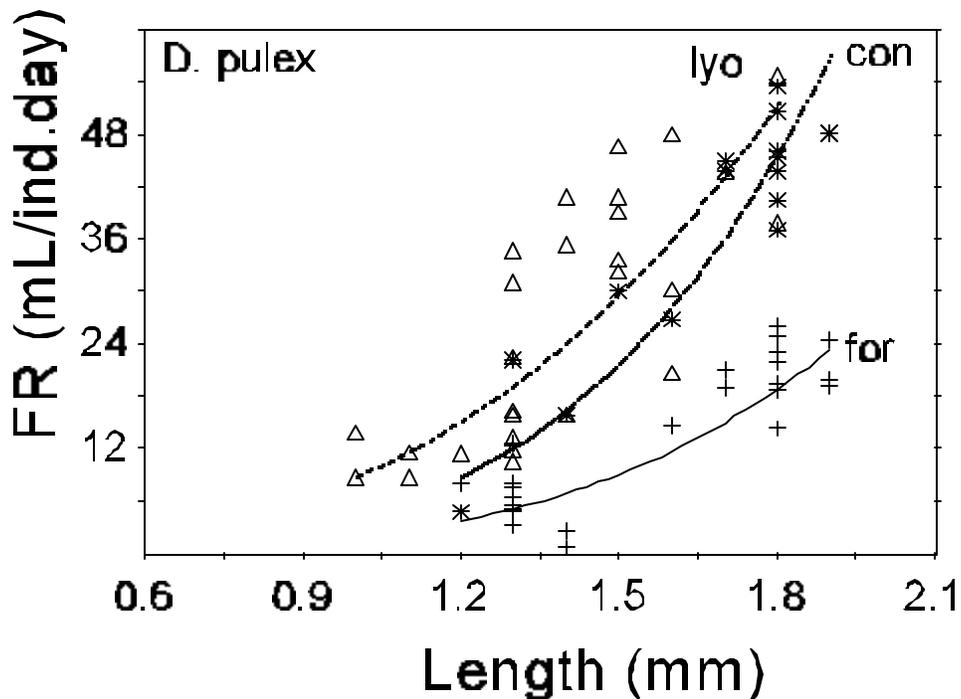
## 2.7 Methodological problems of grazing studies using radiotracers

In grazing studies with radio-tracer elements, severe losses of  $^{14}\text{C}$  or  $^{32}\text{P}$  have been reported (Lampert and Taylor, 1985). This leakage may underestimate individual filtering rates up to 70% depending on sample treatment (Peters, 1984). Two major categories of preservation have been used in recent studies: a) chemical preservation with formalin or lugol (e.g. Haney and Hall, 1975; Geller, 1975; De Mott, 1982; Gilbert and Bogdan, 1982; Haney, 1985); b) physical preservation methods such as killing organisms with boiling water followed by a rapid freezing with dry ice (Chow-Fraser and Knoechel, 1985; Sierszen and Wadras, 1987). Holtby and Knoechel (1981) argued that losses of radioisotopes in chemically preserved samples are higher than those found in samples preserved with physical methods such as killing with heat and preserving under cold conditions. However, since it is impossible to sort organisms in frozen samples, the isotope loss would appear as soon as these samples were again in aqueous medium. Lampert and Taylor (1985) showed that the isotope leakage can amount up to 50% in the first hour following the death of organisms with formalin and these losses are independent from the nature of the radioisotope which was

used. Therefore, most procedures, so far, have failed to prevent losses of radioisotopes in an efficient way.

Lyophilization was recognized early as a nearly ideal method for drying and preserving most organisms (Giese, 1967). Paerl (1984) demonstrated that deep-freezing in liquid N<sub>2</sub>, followed by lyophilization is suitable for autoradiography studies with phytoplankton. However, the adequability of this procedure for zooplankton had not yet been evaluated.

To evaluate the efficiency of lyophilization in grazing studies with radioisotopes, filtering rates of *Daphnia pulex* were determined at the laboratory. Three groups of ca. 30 animals, which were acclimated to laboratory conditions for 2 hours, were sorted in different vessels containing a suspension of 1.12-1.32 mgC/L of *Rhodomonas*. Animals were allowed to feed in these suspensions during 10 minutes (at 15 °C, 18 : E.m<sup>2</sup>.s<sup>-1</sup>). Experimental algal food was labelled with <sup>14</sup>C and the preparation of the radioactive suspensions followed the method described by Geller (1975). The radioactivity levels of these suspensions ranged between 4500 and 5800 dpm.mL<sup>-1</sup>. At the end of the experiment, the content of each vessel was gently filtered through a net (170: m). At this point, the animals collected in these filters were treated in three different ways: a) immediately measured and transferred within 20 minutes to scintillation vials ('control'); b) preserved in sugar-formalin according to Haney and Hall (1973); or c) frozen in dry ice, lyophilized and stored in a desiccator. The animals from methods (b) and (c) were measured and transferred to scintillation vials after 24 hs and 2-3 days, respectively. Once the samples were in the vials they were processed in the same way for all treatments. Animals were digested with 0.3 ml of tissue solubilizer Soluene 350 (Packard) during 24 hs at 45 °C. After that, 3 mL of the counting cocktail (Toluol-POPOP-bis-MSB) was added to each vial. Four drops of glacial acetic acid were added to avoid chemiluminescence and the samples were left at room temperature for at least 2 hours before counting them in the Beckman LS-7500 scintillator.



**Figure 5** Measured and fitted values (see Tab 2) of filtering rates of *Daphnia pulex*, gained with three different methods (see text). Figure modified from Berberovic and Pinto-Coelho (1989).

Fig 5 summarizes the results of these experiments. The highest FR's were observed in the animals which were treated with lyophilization (lyo) and the lowest values in organisms preserved with formalin (for). Larger animals from the 'control' (con) treatment had similar FR values as those of lyophilization treatment. Smaller organisms of the control group exhibited, however, lower FR's than those treated with dry-freezing. This underestimation is probably due to the fact that small animals are more susceptible to losses than larger ones and this underestimation can not be avoid even if short time intervals (40 Min.) are observed between the end of the experiment and transferring the selected organisms into the vials.

Table 2

Regression equations predicting filtering rates (FR) of *Daphnia pulex*, obtained with three different sample treatment methods.

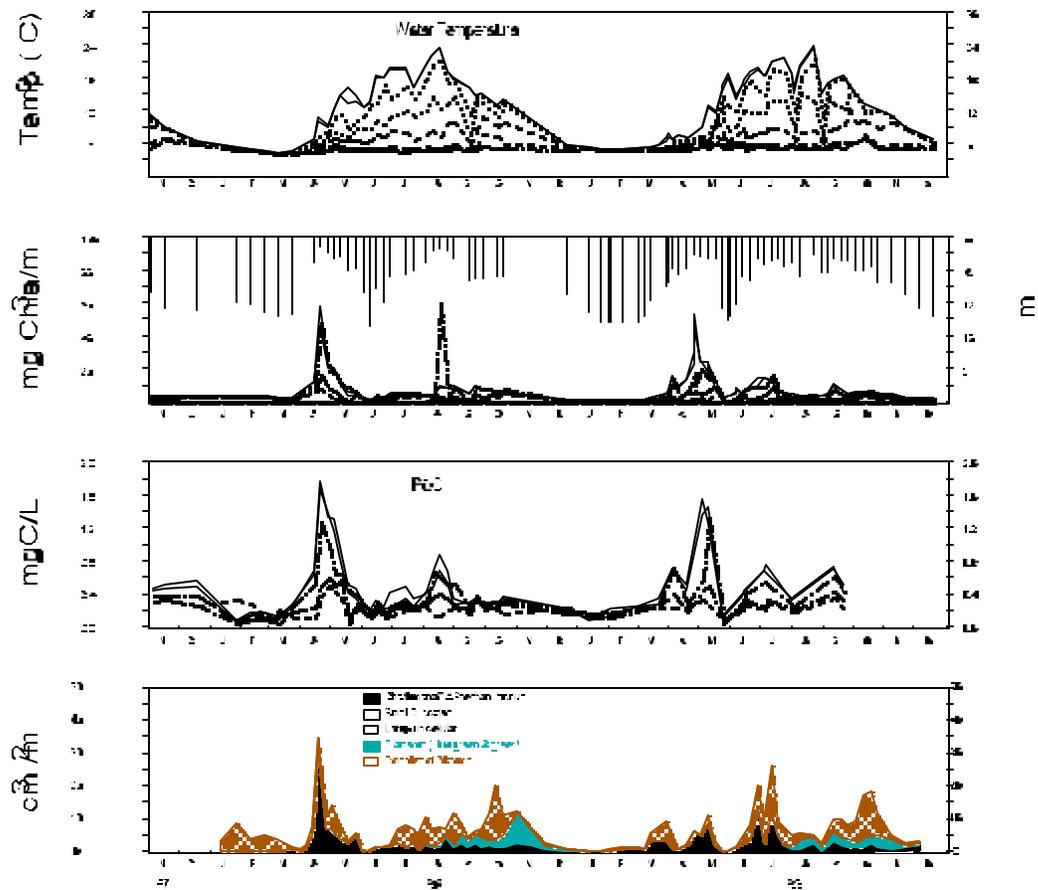
-----Class					
variable	n	FR = a.L <sup>b</sup>		pearson	
		a	b		
'control'	16	4.24	4.06	0.8994	
formalin	27	1.72	4.05	0.7324	
lyophilization	27	8.84	3.01	0.7981	
ANCOVA					
	Sum of Sqrs.	DF	MS	F	Pr>F
Length	21.91	1	21.91	96.18	0.0001
treatment	21.45	2	10.74	47.08	0.0001
Error	15.04	66	0.23	-	
	-				

Tab 2 shows that the covariance analysis (ANCOVA) with the three Length vs. FR regressions detected significant variation sources for sample treatment. The sum-of-squares (SS) due to sample treatment was comparable to the SS calculated for length. Thus, it means that distinct preservation techniques produced the same variability in FR's as did body size. The comparison of the regression estimates between sample treatments (Tab 2) allows to conclude that higher FR's were found for all size-classes treated with immediate freezing followed by lyophilization and, thus, the lyophilization significantly reduced radioisotope losses of the ingested labelled food. Bias of measured values, due to different loss rates in small and larger organisms, and thereby the artifact of distorted size-dependent rates functions were minimized as well.

## **3 Results**

### **3.1 Seasonal course of phytoplankton and water temperature**

The seasonal changes of water temperature, Secchi depths, chlorophyll-a concentrations, particulate organic carbon (POC) and biovolumina of major phytoplankton groups during the years 1988 and 1989 are represented on Fig 6. The successional development related to plankton communities in this lake may be roughly divided into five stages:



**Figure 6** Water temperatures (0,2,6,12,20,36 and 50 m), secchi disk and food availability in L. Constance. Chlorophyll-a and POC at 0,2,6,12 and 20 m and phytoplankton biovolume in epilimnion (0-20 m).

1) "Winter" (end of November to middle of March): The water column was isothermic ( $0 < z < 50$  m). During winter, there was a dominance of large colonies of diatoms but chlorophyll-a and POC concentrations were always lower than  $5 : \text{g.L}^{-1}$  and  $0.50 \text{ mgC.L}^{-1}$ , respectively. POC concentrations from deep layers equalled or exceeded those from near-surface layers.

2) "Spring algal bloom" (end of March to middle of May): Maximum food concentrations (chlorophyll-a reached values up to  $52 : \text{g.L}^{-1}$  and POC up to  $1.7 \text{ mgC.L}^{-1}$ . Nanoplanktonic algae such as *Rhodomonas spp.* and *Stephanodiscus hantzschii* reached their annual biovolume maxima. Onset of thermal stratification. Although the spring algal maximum was higher in 1988, two peaks were observed for these small algae in 1989.

3) "Clear-water phase" (end of May to the end of June): Low chlorophyll-a ( $< 5.0 : \text{g.L}^{-1}$ ) and POC concentrations ( $< 0.4 \text{ mgC.L}^{-1}$ ). Secchi depths reach 17 m.

4) "Summer" (July to mid of September): Water column stratified and surface temperatures frequently higher than  $20 \text{ }^\circ\text{C}$ . POC : chlorophyll-a ratios were higher than in spring. During 1988, POC and Chlorophyll-a concentrations ranged between  $0.48 - 0.93 \text{ mgC.L}^{-1}$  and  $3.6 - 9.8 : \text{g.L}^{-1}$ ,

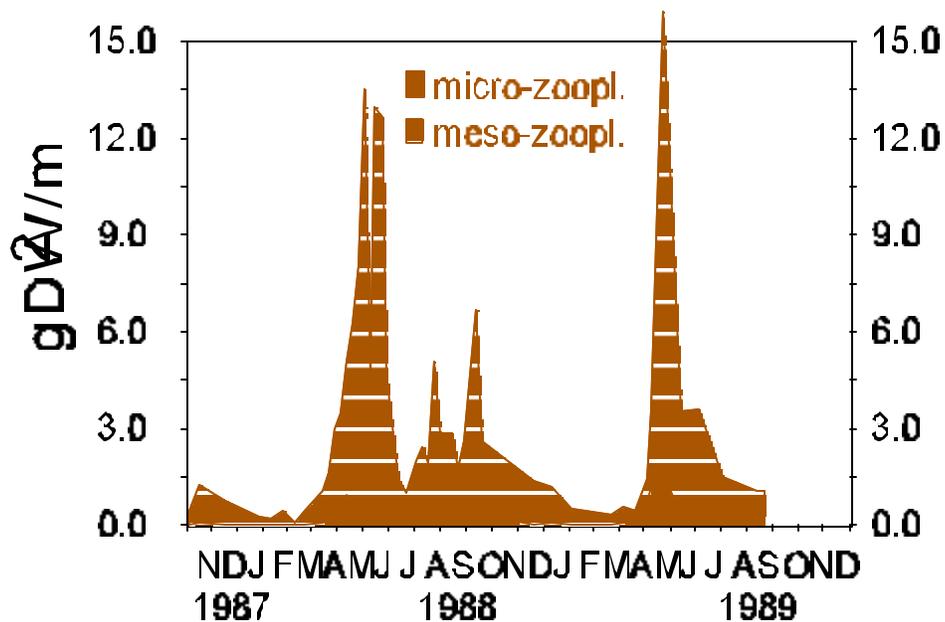
respectively, except one chlorophyll "peak" at 6 m (17/Aug/88). In both years, a second phytoplankton bloom occurred in summer. The dominant algae were large unicellular (e.g. *Peridinium*, *Staurastrum*, *Ceratium*) as well as filaments of greens (*Mougeotia* sp.) and blue-greens (*Oscillatoria* sp.). A conspicuous summer development of large unicellular algae was observed, however, only during 1989.

5)"Fall" (mid September to November): Thermal instability and again low food levels. Chlorophyll-a concentrations at surface frequently below  $10 : \text{g.L}^{-1}$ . Diatoms became dominant during autumn of both years, but absolute densities were somewhat higher in 1989.



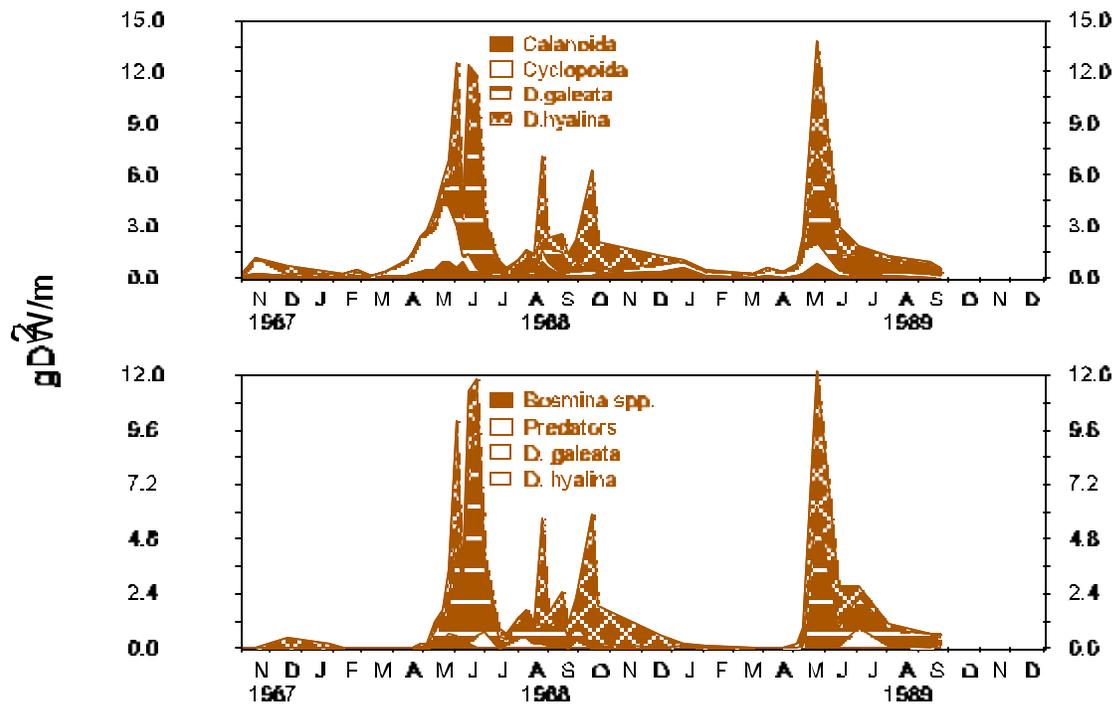
### 3.2 Seasonal course of biomass of Zooplankton

Fig. 7 illustrates the contribution of both size fractions to the overall zooplankton biomass in the epilimnion (0-10 m), as measured in the parallel samples of the grazing experiments. The mesozooplankton accounted for the highest portions of the total biomass.



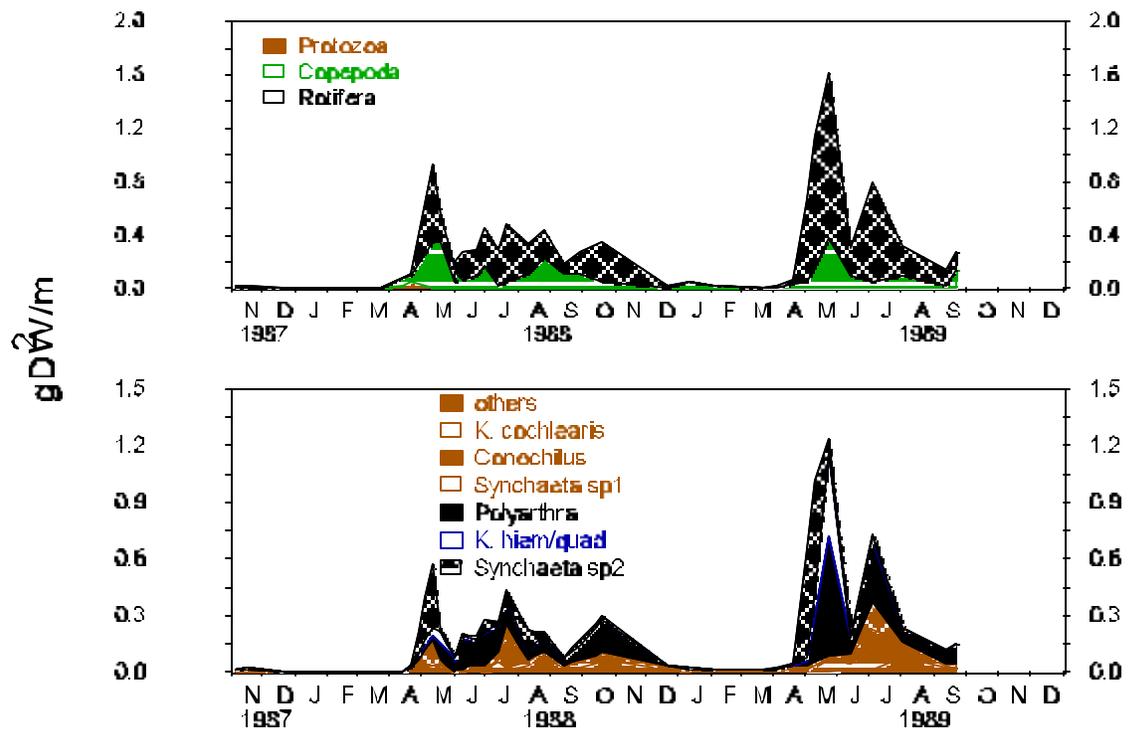
**Figure 7** Seasonal course of size fractionated zooplankton in epilimnion (0-10 m) of Lake Constance (Überlingersee). All biomass samples were taken simultaneously with grazing experiments using the second half of the twin grazing chamber.

In both years, biomass of larger organisms increased conspicuously before did microzooplankton biomass since small organisms were present in relative high numbers only at the end of April. During the clear-water phase, the biomass of mesozooplankton reached the annual maximum: ca. 12.0 gDW.m<sup>-2</sup> in 1988 and 15.0 gDW.m<sup>-2</sup> in 1989. There were always secondary "peaks" in the biomass of both fractions during summer. However, they were never so high as during the clear-water phase.



**Figure 8** Seasonal course of mesozooplankton biomass in epilimnion (0-10 m) of Lake Constance (Überlingersee). Top: *Daphnia* and copepods. Bottom: all cladocerans together.

The seasonal biomass changes of the most important groups of mesozooplankton is shown in Fig 8. Cyclopoids played a relevant role only in winter and during the spring bloom (Fig 8, top). Daphnids appeared at the end of April and increased very rapidly. First, *D. galeata* was the dominant cladoceran. By the end of summer and during fall, *D. hyalina* became more important. During the clear-water phase, when zooplankton biomass reached the annual maximum, the bulk of zooplankton was made up by *D. galeata*. *E. gracilis* never contributed significantly to total zooplankton biomass. The calanoid biomass values were always below 1.0 gDW.m<sup>-2</sup>.



**Figure 9** Biomass of microzooplankton in epilimnion (0-10 m) of Lake Constance (Überlingersee). Top: major taxonomic groups. Bottom : rotifer community.

Daphnids contributed with the highest biomass among all cladocerans (Fig 8 bottom). *Bosmina* and the predacious cladocerans *Bythotrephes* and *Leptodora* biomass never surpassed 1.0 gDW.m<sup>-2</sup>. These species had very different seasonal trends. *Bosmina* was abundant at the same time when *Daphnia* biomass peaked. The predacious cladocerans had their maximum later on, during summer.

The relative biomass contribution of protozoans, nauplii and rotifers to overall microzooplankton varied during seasons and from one year to the next (Fig 9 top). Two seasonal maxima were observed: spring and summer. Due to rotifers, higher annual biomass maximum of microzooplankton was measured in 1989. However, nauplii reached the highest biomass in summer of 1988. In both years, the biomass of smaller zooplankton was relatively low during clear-water phase. Nauplii and small copepodites had a fairly comparable biomass maximum (around 0.4 gDW.m<sup>-2</sup> epilimnion, 0-10 m) in May of both years.

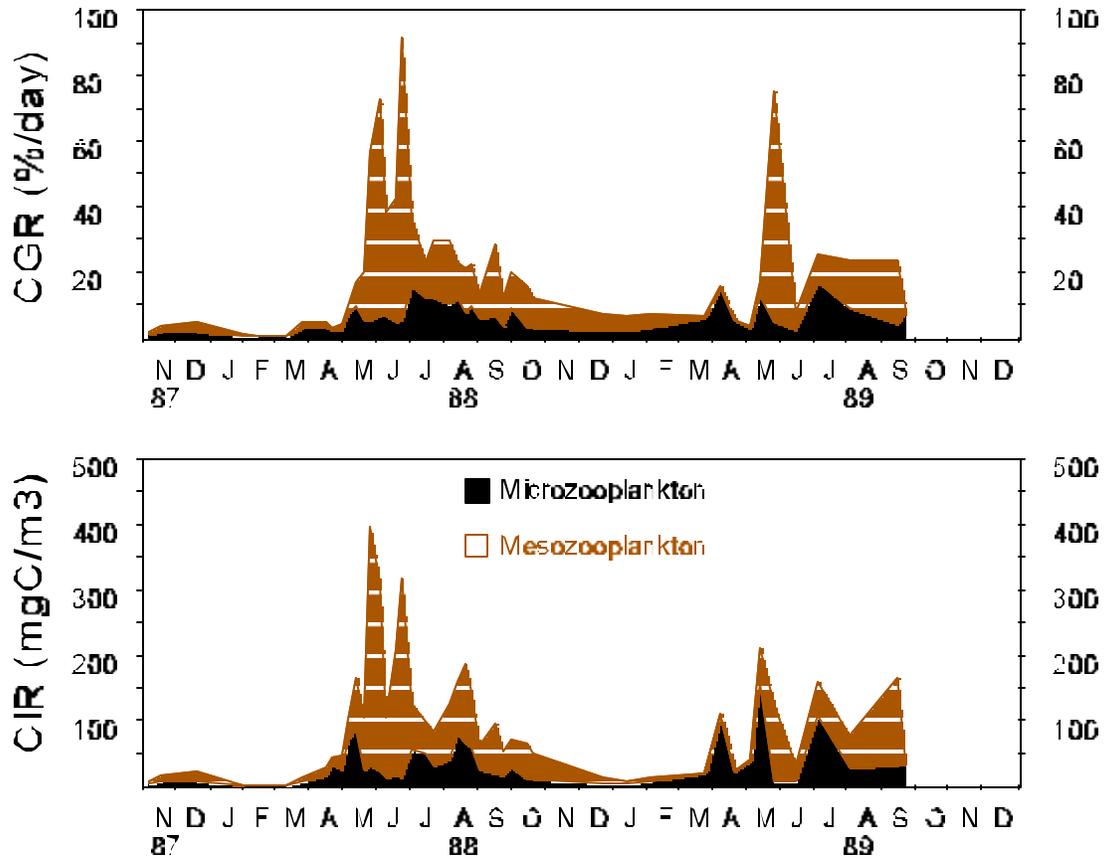
Only a fraction of all pelagical protozoans was properly preserved in the formalin-samples. However, some organisms like *Strobilidium* and *Codonella* were regularly counted. They

contributed significantly to the total biomass of this fraction in some occasions like during spring bloom of 1988.

Fig 9 (bottom) shows the seasonal composition of the rotifer community with greater detail. There were two annual maxima in their biomass: in May and July. The May peak was more distinguished in both years, but absolute densities were clearly higher during the whole growing season of 1989. Before the clear-water phase, this community was usually dominated by *Keratella hiemalis*, *Synchaeta sp.* and *Polyarthra sp.* In the warmest months, a more diverse array of rotifer populations appeared: *Keratella cochlearis*, *Pompholyx sp.*, *Conochilus unicornis*, *Polyarthra spp.* (more species of this genus were always present in summer) and *Synchaeta sp.* All these species appeared at least once with biomass higher than 0.1 g.m<sup>-2</sup>. Other species with lower biomass were, however, always present in summer: *Trichocerca spp.*, *Collotheca spp.*, *Gastropus stylifer* and *Asplanchna priodonta*. The latter is a large organism and the majority of its individuals were probably retained in the samples of fraction 1. Therefore the estimates of its biomass may be underestimated in fraction 2. In summer of 1989, compare the vigorous development of the rotifer biomass with a parallel pulse in the group of unicellular algae (Figs 6 and 9).

### 3.3 Seasonal course of *in situ* zooplankton grazing

The seasonal course of zooplankton grazing activities (CGR and CIR) is represented for both size fractions in Fig 10. Both CGR and CIR were obtained including diel variations observed on these rates (according to Eq 3 and 5). Between 23/May/89 and 1/Aug/89 only experiments using *S. hantzschii* as food particle were available. Therefore, CGR and CIR of both fractions during this time were estimated observing the ratio  $CGR_{Rho}:CGR_{Steph}$  calculated in experiments where both algae were simultaneously offered (see Cf. section 3.5). Otherwise only experiments with the cryptophyceae were considered.



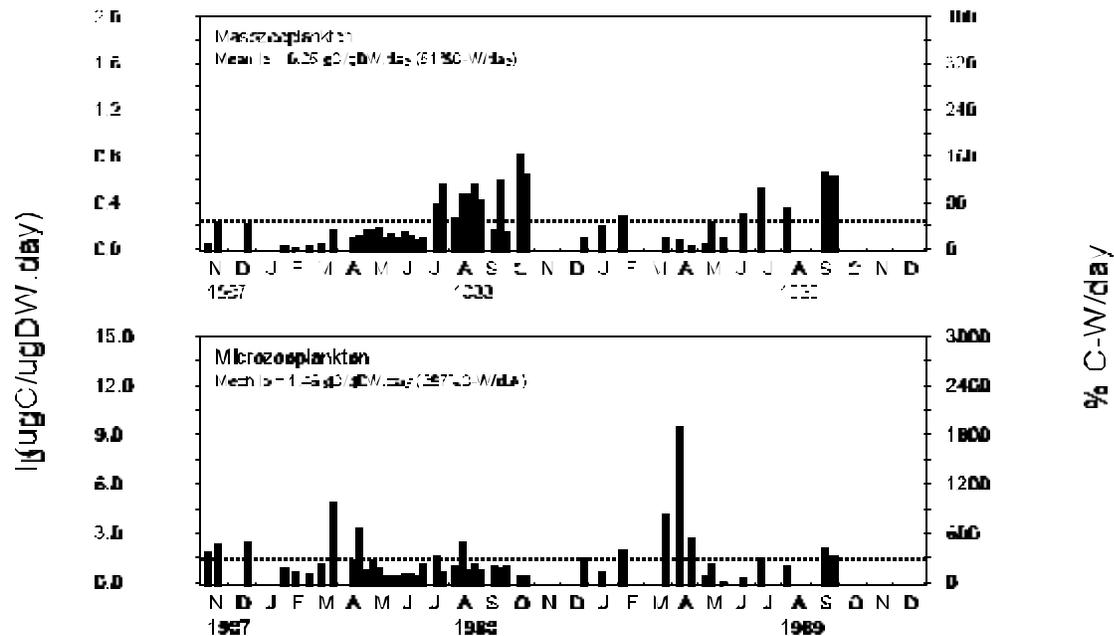
**Figure 10** Seasonal course of CGR's (top) and CIR's (bottom) in epilimnion (0-10 m) of L. Constance. *In situ* experiments using *Rhodomonas* as food particle. Diel variations were included.

Similar trends were observed for mesozooplankton in both years. As expected, the highest mesozooplankton grazing rates ( $CGR_1$ ) were measured during the clear-water phase. During this time, the differences between day and night measurements were large, since  $CGR_1$ 's were much higher at night. At 06/Jun/88 (clear-water phase),  $CGR_1$  rates for day and night incubations (2 m) were 28 and 936 mL.L<sup>-1</sup>.day<sup>-1</sup>, respectively. In summer and during autumn, diel  $CGR_1$  varied between 100 and 200 mL.L<sup>-1</sup>.day<sup>-1</sup>

(10-20 % vol.day<sup>-1</sup>).

The role of microzooplankton in community grazing was always evident. During some short periods, like before clear-water phase and during summer, the grazing rates of smaller organisms were comparable to or even higher than those of the mesozooplankton. The different patterns observed in the algal development during spring blooms of 1988 and 1989 are well reflected in the grazing response of microzooplankton (Cf. Figs 6 and 9). Maximum annual  $CGR_2$  values were usually observed in July (155 and 168 mL.L<sup>-1</sup>.day<sup>-1</sup> for 1988 and 1989, respectively). The epilimnetic (0-10 m) mean annual values for 1988 for community grazing rates were 53.6 and 149.1 mL.L<sup>-1</sup>.day<sup>-1</sup> for micro- and mesozooplankton, respectively.

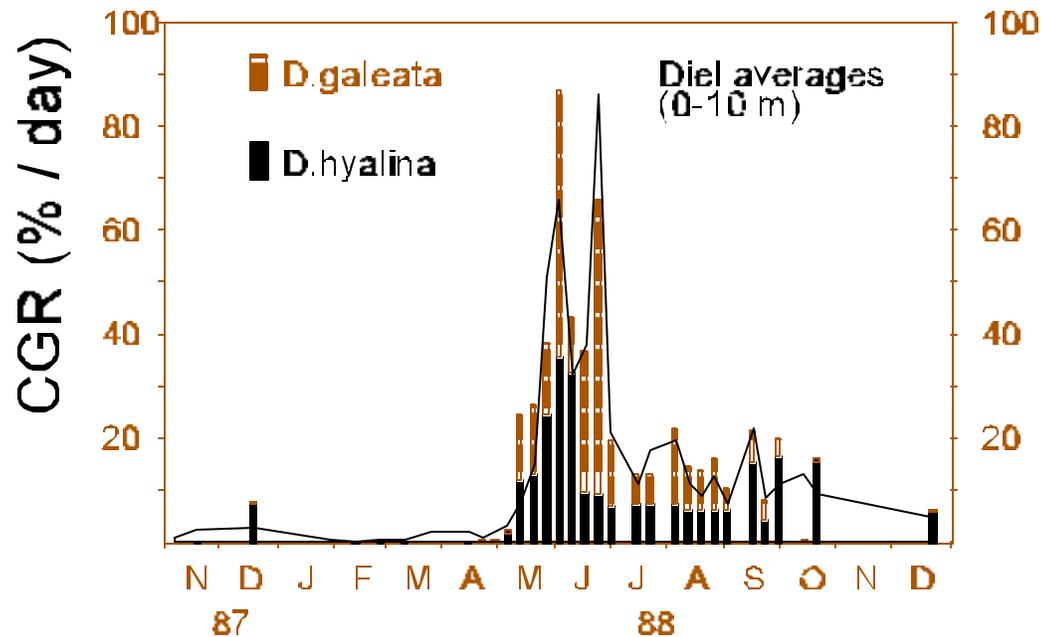
The contribution of smaller organisms to overall grazing, as can be inferred from *in situ* measurements, turns out to be still more evident if community ingestion rates are considered (Fig 10 bottom). The microzooplankton contributed with 26.4% and 27.2 % of total community grazing and community ingestion rates (mean values for 1988, epilimnion, 0-10 m), respectively. Accordingly to biomass seasonal trends, the community ingestion rates of smaller herbivores peaked during spring bloom and once again in summer. In 1989, these peaks were more elevated.  $CIR_2$  higher than 100 : gC.L<sup>-1</sup>.day<sup>-1</sup> were observed in spring of this year.



**Figure 11**  $I_b$ 's of meso- and microzooplankton in epilimnion (0-10 m) of L. Constance, expressed in :gC/:gDW.day and in percentages of C-body weight ingested per day (right). Dotted lines represent mean values (1988 and 1989 pooled).

Microzooplankton had always higher biomass specific community ingestion rates ( $I_b$ ) than larger organisms (Fig 11). Additionally, different seasonal trends can be observed by comparing  $I_b$ 's from the two size fractions. Higher  $I_b$ 's for microzooplankton usually occurred in spring whereas mesozooplankton had relatively higher  $I_b$ 's during summer. The mean  $I_b$  values were 1.49 (range 0.02 - 9.52) and 0.25 (range 0.07 - 0.83) : gC.: gDW<sup>-1</sup>.day<sup>-1</sup> for micro- and mesozooplankton, respectively (day values in epilimnion, 0-10

m, 1988 and 1989 pooled together). If a factor for the conversion C:DW of 0.50 is applied, the above given annual mean  $I_b$ 's indicate a daily ingestion of 297 % and 51 % of C-weight for micro- and mesozooplankton, respectively.



**Figure 12** Comparison of CGR of mesozooplankton (solid line) with grazing rates of *Daphnia* populations - PGR (bars) in L. Constance (Überlingersee) during 1988.

The contribution of both *Daphnia* species to overall grazing can be estimated by comparing the seasonal course of community grazing rates of mesozooplankton ( $CGR_1$ ) with the population grazing rates (PGR) for each species. Fig 12 illustrates this procedure for the year of 1988. PGR were calculated according to Eq 8. The seasonal trends and the amplitude of CGR of mesozooplankton are practically the same of the summation of PGR's due to *D. hyalina* and *D. galeata*. This fact clearly indicates the decisive

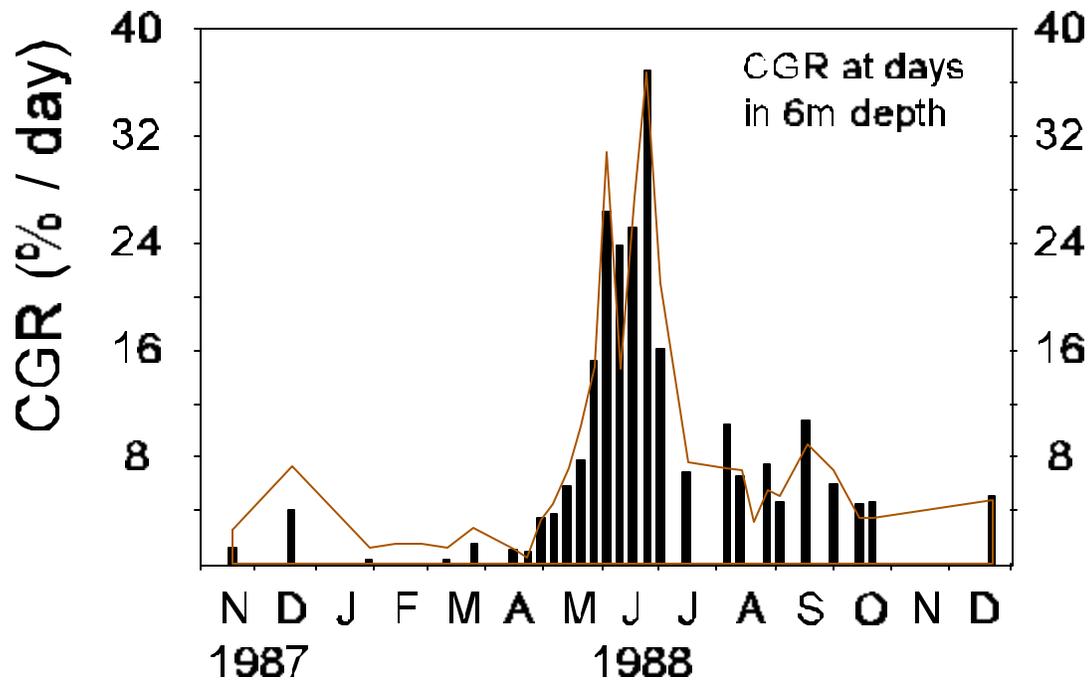
role of daphnids in determining the magnitude and seasonality of zooplankton grazing in this lake. The first species dominate before the clear-water phase and during the whole fall but grazing of *D. galeata* dominated during clear-water phase and immediately thereafter. The PGR mean annual values were 70.3 (7.3 % vol.day<sup>-1</sup>) and 48.4 mL.L<sup>-1</sup>.day<sup>-1</sup> (4.8 % vol.day<sup>-1</sup>), for *D. hyalina* and *D. galeata* respectively.

Table 3

Multivariate linear model regression estimates. Dependent variable: Community grazing rates of fraction 1 (ml/L.day). Independent Variables :  $B_{DH}$  (*D. hyalina*),  $B_{DG}$  (*D. galeata*),  $B_{AL}$  (*E. gracilis*),  $B_{BOS}$  (*Bosmina spp*),  $TEMP^2$  (square power of water temperature °C) and  $CHL_A$  (Chlorophyll a in ppb). zooplankton biomasses in :gDW.L<sup>-1</sup>.

	estimate	error	SS	F	Pr > 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
				correlation coefficients	Total	0.9134
	$B_{DH}$	$B_{DG}$	$B_{CAL}$	$B_{BOS}$	$CHL_A$	$TEMP^2$
$CGR_1$	0.8190	0.72837	0.67262	0.21511	-0.13496	0.27056
			variable ranges			
0-936	0-638	0-1034	0-259	0-72	0-61	0-546
n= 210						

The role of daphnids in the zooplankton grazing was independently confirmed by the multivariate linear model relating CGR to biomass of major herbivores and other environmental variables. The adjusted equation generated by this model is given in Tab 3. A highly significant total  $R^2$  was obtained. The F-values of POC and cyclopoid biomass did not reach the lower boundary for being included in the model. Thus, these variables were excluded from the final equation. 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 comparing the partial  $R^2$  of independent variables. These values for *D. hyalina* and *D. galeata* were 0.6709 and 0.1984 respectively (Table 3). Temperature and Chlorophyll-a did not have high partial  $R^2$ , but their estimates were nevertheless significant at the 0.05 level. As one could expect, the estimates of the parameters for chlorophyll-a and temperature were negative and positive, respectively. *Bosmina* biomass was included in the adjusted regression equation but its F-value was relatively low ( $F = 3.49$ ,  $\text{Pr} > F = 0.06$ ).



**Figure 13** Predicted values of community grazing rates (solid lines) and measured CGR (bars) for mesozooplankton in Lake Constance (Überlingersee) during 1988. See also Tab. 3.

The fit of the model to partial data sets was always very good. An example is presented in Fig 13 for day values of CGR at 6 m. Predicted values were somewhat higher than measured ones in winter and were lower in summer. However, during the clear-water phase or during periods where CGR was relatively high, predicted values had always a good conformity with measured community clearance rates.

Table 4

Multivariate regression analysis (stepwise model) between community grazing rate of and biomasses of major components of microzooplankton in Lake Constance during 1988. Temperatures in °C and rotifer biomass in :gdw.L<sup>-1</sup>.

variable	estimate	std. error	SS	F	prob>F	partial R <sub>2</sub>
intercept	9.07746	3.19483	5719.8	8.1	0.0051	-
temp <sup>2</sup>	0.23555	0.02281	75580.7	106.7	0.0001	0.5867
Rotatoria	0.99354	0.25871	10449.2	14.8	0.0002	0.0366
				Total		0.6233
simple statistics						
	n	minimum	maximum	mean	std. dev.	
cgr_2	155	0.0	269.8	46.2	43.1	
temp.	210	4.1	23.4	10.4	5.0	
Rotatoria	155	0.0	58.2	7.2	10.2	
n= 155.						

A multivariate linear model was also applied to microzooplankton grazing rates. The positive (and highly significant) effect of water temperature on grazing rates of smaller organisms

can be observed in Tab 4. Only two factors, water temperature and pooled biomass of rotifers, explained 62 % of the total variation observed on  $CGR_2$ . The F-value for these factors were also highly significant ( $Prob>F=0.0005$ ). Temperature alone explained 59% of total  $CGR_2$  variability. This table also provides the adjusted equation describing the linear relationship between biomass of rotifers, square power of water temperature and  $CGR_2$ . The variables' ranges are also represented. The model can probably be applied with greater success in the future if the values of the selected variables are kept within these ranges. Biomass of nauplii, chlorophyll-a and POC were also considered as input variables in the model, but their F-values did not reach the minimum significance level to be accepted in the final equation.

Table 5

Correlation coefficients (Pearson) between community grazing rates and biomass of major components of zooplankton as well as water temperature and food concentration in Lake Constance during 1988.

groups	Fr.	CGR-1	CGR-2	rotifera	Fr	CGR-1	CGR-2
Daphnia	1	0.89475*	0.15254	Polyarthra	2	0.22155	0.50968*
Copepoda	1	0.29044*	0.01481	K. cochl.	2	0.13720	0.44196*
Calanoida	1	0.67066*	0.02621	Pompholyx	2	0.05117	0.38667*
Cyclopoida	1	0.08066	0.00635	Synchaeta 1	2	0.01782	0.37968*
Rotatoria	2	0.26707	0.59907*	Gastropus	2	0.00385	0.36482*
Nauplii	2	0.07780	0.14094	Synchaeta 2	2	0.01595	0.38956*
Protozoa	2	-0.11314	-0.07979	K.hiem.	2	0.40680*	0.15793
Other variables:				Asplanchna	1/2	0.11206	0.16250
water temp.				Kellicottia	2	0.16103	0.13570
sqr water temp.				Conochilus	2	0.18611	0.10447
POC				Collotheca	2	0.02478	0.14436
Chloroph._a							

n=155 (CGR-2) and n=210 (CGR-1) \* : significant Prob>0.0001 under  $H_0: \rho=0$

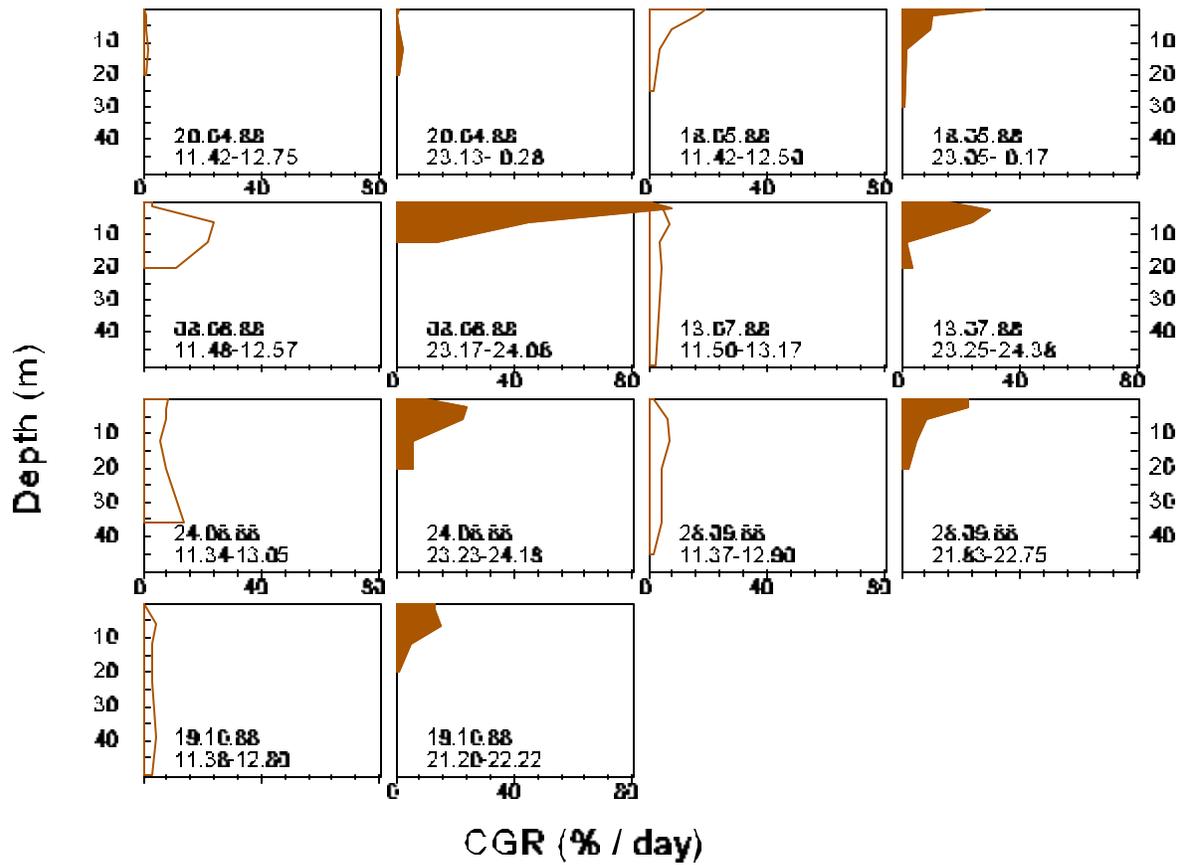
Since only the biomass of rotifers could explain significant portions of  $CGR_2$  variability, the next point would be to know which species play the most important roles to determine  $CGR_2$  rates. Tab 5 gives the correlation coefficients between grazing rates of both fractions and all zooplankton groups as well the most important rotifers. The Pearson coefficient between all rotifers and  $CGR_2$  was ca. 0.6. However, only rotifers such as *Polyarthra spp.*, *K. cochlearis*, *Pompholyx*, *Synchaeta sp1*, *Gastropus* and *Synchaeta sp2* had significant correlations with  $CGR_2$ . Most of these rotifers occurred in higher abundances during summer (Cf. Fig 9). Other rotifers, like the cold-adapted *K. hiemalis*, had Pearson-coefficients below the significance level. Note also the high Pearson coefficient between *Daphnia* and  $CGR_1$ .

Tab 5 also gives some indications about the relationships between grazing rates and environmental parameters. It was already seen that the multivariate model of microzooplankton exhibited higher partial  $R^2$  for square power of temperature. The Pearson coefficient between water temperature and grazing rates of both size fractions revealed again the same trend, i.e.,

higher values between water temperature and  $CGR_2$ . Finally, it should also be noted the low correlation values found between food concentration (POC and chlorophyll-a) and community grazing. Nevertheless these correlation coefficients, as the theory predicts, are negative (for chlorophyll-a).

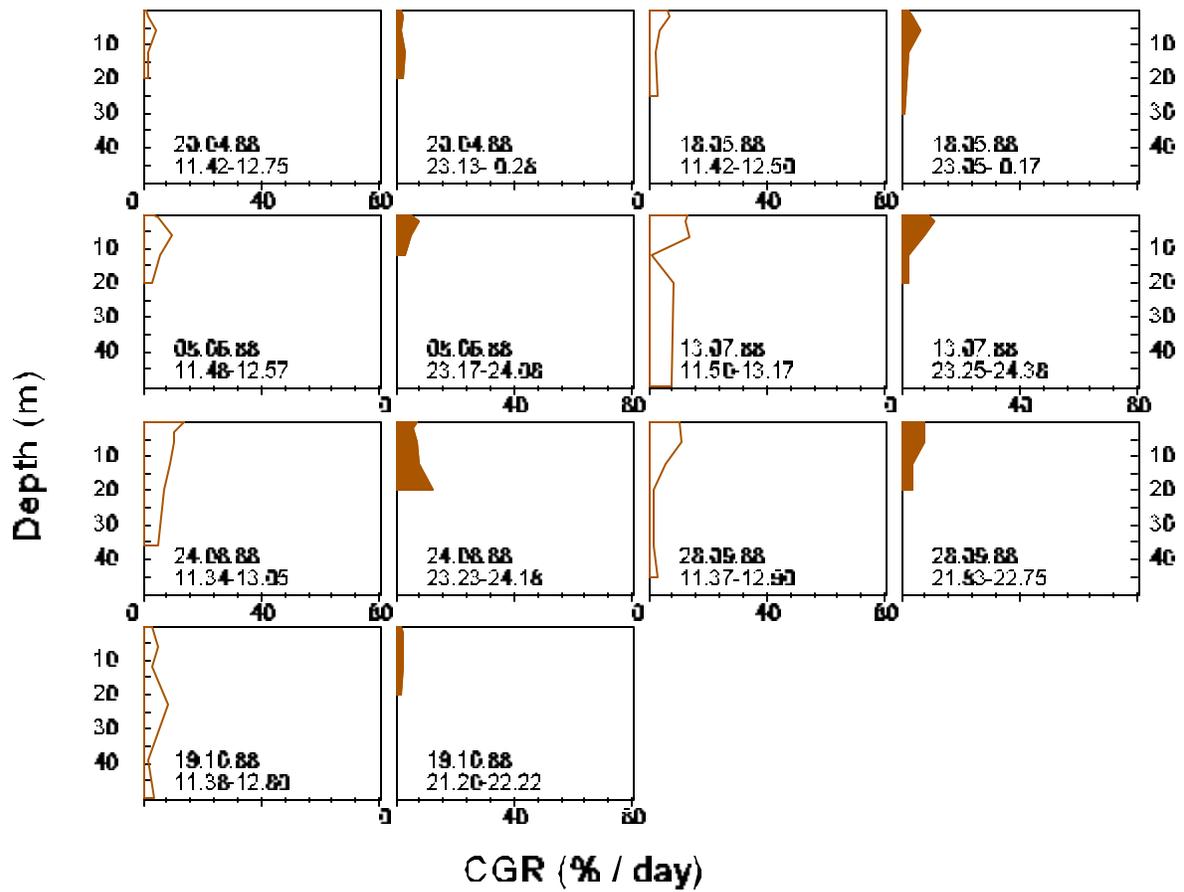
### 3.4 **Diel variations of community grazing**

In 1988, seven day/night experiment series were made covering all seasonal phases (except winter) of plankton community (these phases were described in section 3.1). The experiments were carried out at two different times of the day: between 11:00 and 14:00 (day incubations) and between 21:00 and 01:00 hs (night incubations). The nocturnal incubations were regulated by the day length so as they began as soon as the sunset had finished.



**Figure 14** CGR depth-profiles of mesozooplankton in seven day-night experiments conducted in 1988, *Rhodomonas sp.* as food particle.

Diel variations for mesozooplankton during 1988 are illustrated in Fig 14. During spring (20/Apr/88) day and night depth-profiles had basically the same outline. Diel changes were slightly apparent (especially at surface) in May and reached their maximum amplitude during the clear-water phase in June. The highest annual community grazing rates of mesozooplankton in 1988 were also measured at night ( $CGR_1 > 900 \text{ mL.L}^{-1}.\text{day}^{-1}$ , epilimnion, 0-2 m) at 08/Jun/88. In summer (July and August), night community grazing rates were always higher than during the day. In September and October diel variations were again observed, however, with lower amplitudes.



**Figure 15** CGR depth-profiles of microzooplankton. Experiments are the same as in Fig 14.

Fig 15 represents diel variations of microzooplankton community grazing during. Despite of some dates when night incubations were slightly higher than during the day (18/May/88, at 6 m and 24/Aug/88 at 20 m), most depth-profiles did not reveal any enlarged diel variation like those observed for mesozooplankton (Fig 14). Nevertheless, a seasonal component was clearly present in those experiment-series, since profiles with higher grazing rates were found during summer (June to August). In spring and autumn, these rates were lower.

Table 6  
Diel variations of zooplankton community grazing rates in Lake Constance. CGR in  $\text{mL.L}^{-1}.\text{day}^{-1}$ . Integrals (int) in  $\text{L.m}^{-2}.\text{day}^{-1}$ , from 0 to 15 m. Basic statistics of CGR and integral values are given separately for each size fraction of zooplankton.

Date	d/n	Mesozooplankton CGR-1			Int	Microzooplankton CGR-2			Int
		Min	Max	Mean		Min	Max	Mean	
20/Apr	d	6.7	14.7	10.3	132.6	12.6	38.9	21.1	311.2
	n	8.2	21.5	12.5	151.0	17.8	26.5	21.1	266.0
18/May	d	14.3	189.2	97.2	1191.9	24.0	70.8	45.2	532.9
	n	11.2	278.5	101.0	1124.4	9.3	62.4	30.1	500.7
08/Jun	d	26.1	239.1	123.9	2068.5	30.6	98.9	54.3	888.0
	n	135.5	936.1	594.9	6320.9	26.7	79.5	53.2	641.4
13/Jul	d	11.0	68.6	39.9	626.2	13.9	139.5	94.3	1283.1
	n	18.5	300.3	151.0	2292.6	22.8	115.4	67.3	918.2
24/Aug	d	55.9	136.2	84.3	865.2	52.5	136.0	92.6	1247.6
	n	54.9	241.6	135.1	2112.7	59.0	128.1	80.8	828.4
28/Sep	d	16.1	68.1	42.5	613.8	16.8	107.5	54.4	1116.9
	n	21.1	221.0	119.8	1459.5	34.8	78.6	60.5	804.2
19/Oct	d	5.2	48.2	30.6	390.3	18.4	88.2	41.6	471.3
	n	12.2	146.5	94.2	1420.3	15.0	23.0	19.1	256.3

Tab 6 gives the basic descriptive statistics related to day night experiments from 1988. Mean and integral values of community grazing rates confirmed that, contrarily to smaller



organisms, larger mesozooplankton showed extended diurnal variations in most occasions.

The next point would be to verify whether these daily oscillations of mesozooplankton grazing are due to zooplankton biomass fluctuations in the water column of epilimnion or to enhanced individual filtering rates of some herbivores like *D. hyalina* or *E. gracilis*. This can be done by comparing day and night values of biomass specific grazing rates ( $G_b$ 's). If  $G_b$ 's were higher at night it would mean that individual rhythms of filtering rates are the major factor regulating diel rhythms of zooplankton community grazing.

Table 7

Biomass specific community grazing rates ( $G_b$  in mL.:gDW<sup>-1</sup>.day<sup>-1</sup>) in epilimnion (0-15 m) of L. Constance (Überlingersee) during 1988.

date	microzooplankton		mesozooplankton	
	day	night	day	night
20/APR/88	2.9	2.9	0.1	0.2
18/MAY/88	1.9	0.9	0.3	0.2
08/JUN/88	5.2	6.3	0.9	0.6
13/JUL/88	5.5	2.4	1.1	0.9
24/AUG/88	6.7	3.9	1.1	1.1
28/SEP/88	8.7	4.9	0.6	0.9
19/OCT/88	1.9	1.4	2.1	0.6

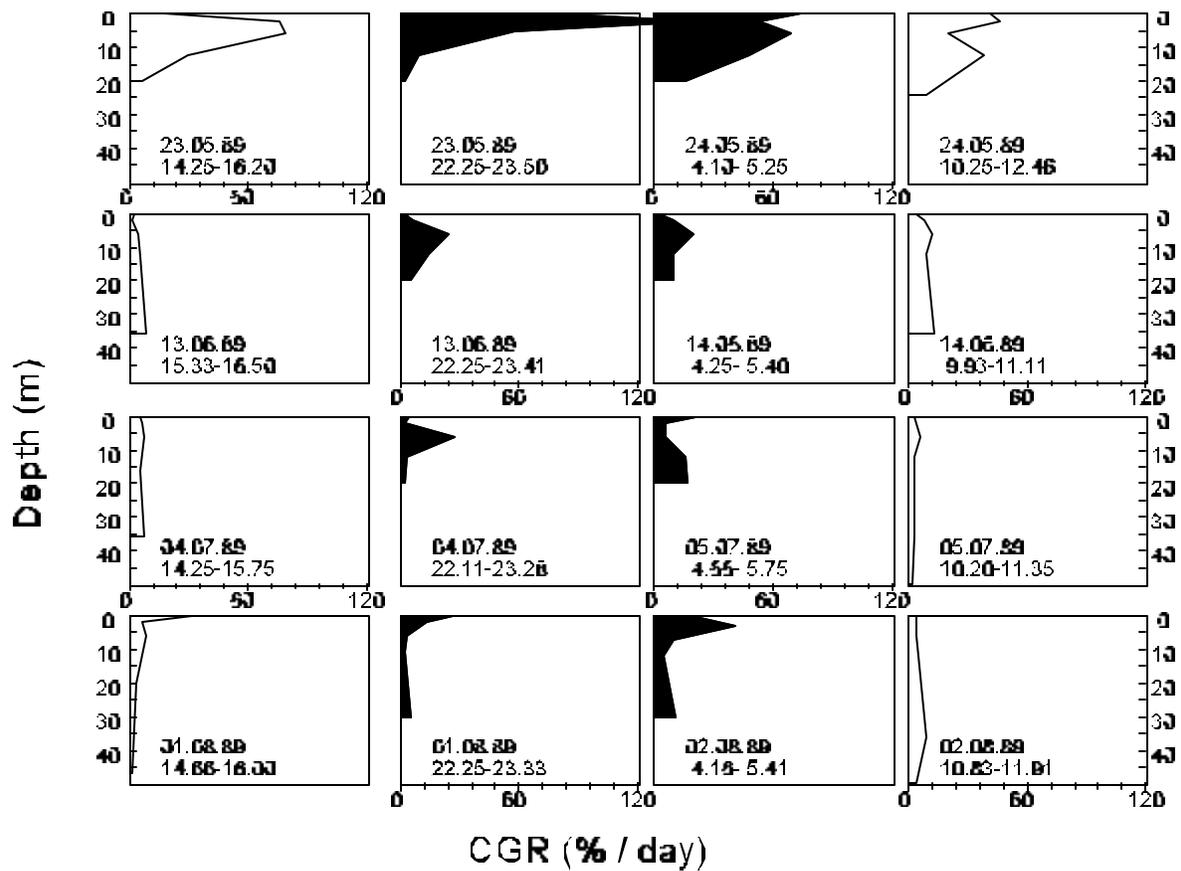
Tab 7 shows that this expectation could not be confirmed for mesozooplankton. At Night, biomass specific grazing rates ( $G_b$ ) in the epilimnion were equal or lower than day values in most experiments. Even during clear-water phase (June), when the highest CGR in the annual cycle was observed, night  $G_b$  ratios were clearly lower than day ones. Only in April and September,  $G_b$ 's were slightly higher at night. In 1988,  $G_b$ 's of larger zooplankton ranged between 0.1 and 2.1 mL.:gDW<sup>-1</sup>.day<sup>-1</sup>. Tab 7 also shows that these ratios were usually higher for microzooplankton. Additionally,  $G_b$ 's of smaller organisms were usually lower at night (excepting in June). However, it should be considered, that all nocturnal experiments of 1988 were

conducted in the first night-half. In the next paragraphs, it will be shown how important this fact is.

Table 8

Diel cycles of epilimnetic community grazing rates (CGR in  $L.m^{-2}.day^{-1}$ , integral values from 0-15 m) in Lake Constance during 1989.

Date	15-17 hs.		21-24 hs.		4-6 hs.		10-12 hs.	
	P1	P2	P1	Fractions P2	P1	P2	P1	P2
23-24/May	7271	1387	7839	1611	7239	4076	3965	927
13-14/June	498	772	1838	560	1602	2080	1124	732
04-05/July	421	3308	1592	4995	1161	8931	483	4237
01-02/August	660	1798	863	1565	2245	3352	460	2356



**Figure 16** CGR Depth-profiles of mesozooplankton in four day-night experiment series conducted in L. Constance during 1989.

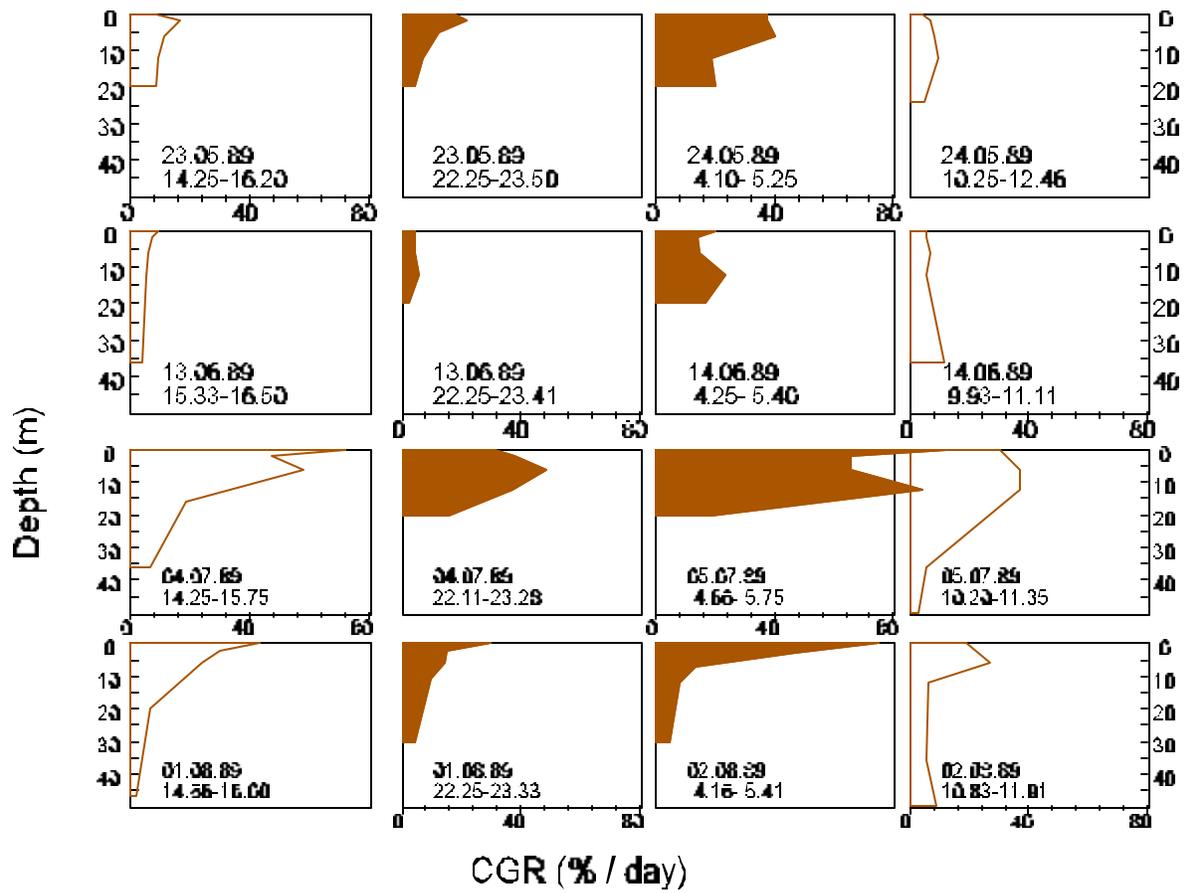


Figure 17 CGR depth-profiles of microzooplankton as in Fig 16.

Four day-night experiment series were made during 1989. The main objective of these series was to individualize possible deviations from diurnal trends observed in 1988. In each date, grazing measurements were performed in the water column (0,2,6,12 and 20 m) in four different times: ca. 15:00-17:00 hs, 22:00-24:00hs, 04:00-06:00hs and 10:00-12:00hs. The diatom *S. hantzschii* was used as experimental food in all experiments. Depth-profiles of grazing rates related to these experiments are represented for meso- and microzooplankton in Figs 16 and 17, respectively. The same trend for higher CGR of larger organisms at night was again observed. The subsequent comparison between the two night-series revealed that slightly higher grazing rates occurred during the first night half. The integral values of community grazing also confirmed this trend (Tab 8). Excepting in August 1989, mesozooplankton grazing integrals were somewhat higher in the night profiles between 22:00 and 24:00 hs.

A completely different "scenario" appears in Fig 17. One would suggest that there is little or no daily variation in these rates if the experiment series before dawn did not exist. A clear increase in the grazing rates of small zooplankters was observed during the second part of the night on all four occasions. This increase can also be observed in the integral values of CGR (Tab 8).

Table 9

Size fractionated biomass specific grazing rates ( $G_b = \text{mL.} : \text{gDW}^{-1} \cdot \text{day}^{-1}$ ) during diel cycles in 1989 in epilimnion (0-15 m) of Lake Constance.

		14-16 hs	21-24 hs	04-06 hs	10-12 hs
23-24/May	$G_1$	0.7	0.8	0.5	0.5
	$G_2$	1.1	1.7	3.6	1.6
13-14/Jun	$G_1$	0.6	0.6	0.8	1.0
	$G_2$	5.6	2.4	13.8	3.7
04-05/Jul	$G_1$	0.9	1.0	0.8	1.0
	$G_2$	11.9	10.6	24.0	12.7
01-02/Aug	$G_1$	1.1	0.5	0.9	1.5
	$G_2$	12.1	9.6	20.5	16.6

obs :  $G_1$ = mesozooplankton,  $G_2$ = microzooplankton, n=3.

Diel variations of  $G_b$ 's for the experiments of 1989 (epilimnion, 0-15 m) are summarised in Tab 9. The highest  $G_b$ 's of mesozooplankton were usually found in the first part of the night or in the morning between 10:00 and 12:00. Higher night values were detected during the clear-water phase (May) and in July. Morning  $G_b$  values were the highest ones in June and August. It is important to notice that, contrasting to microzooplankton, all  $G_b$ 's of larger organisms in the diel cycle were limited in a relatively narrow range (0.5-1.5  $\text{mL.} : \text{gDW}^{-1} \cdot \text{day}^{-1}$ ).

For microzooplankton, however, the biomass specific rates were always higher just before dawn, at the same time when highest community grazing rates were also recorded. This means, contrarily to mesozooplankton, that diel variations of microzooplankton may be strongly influenced by variations at the individual level and not only by biomass concentration during in the night.

Table 10

Diel fluctuations of mean values and standard deviations of POC (< 50 :m) concentrations, expressed in  $\text{mgC.L}^{-1}$ , in epilimnion (0-6 m ) of Lake Constance during 1989.

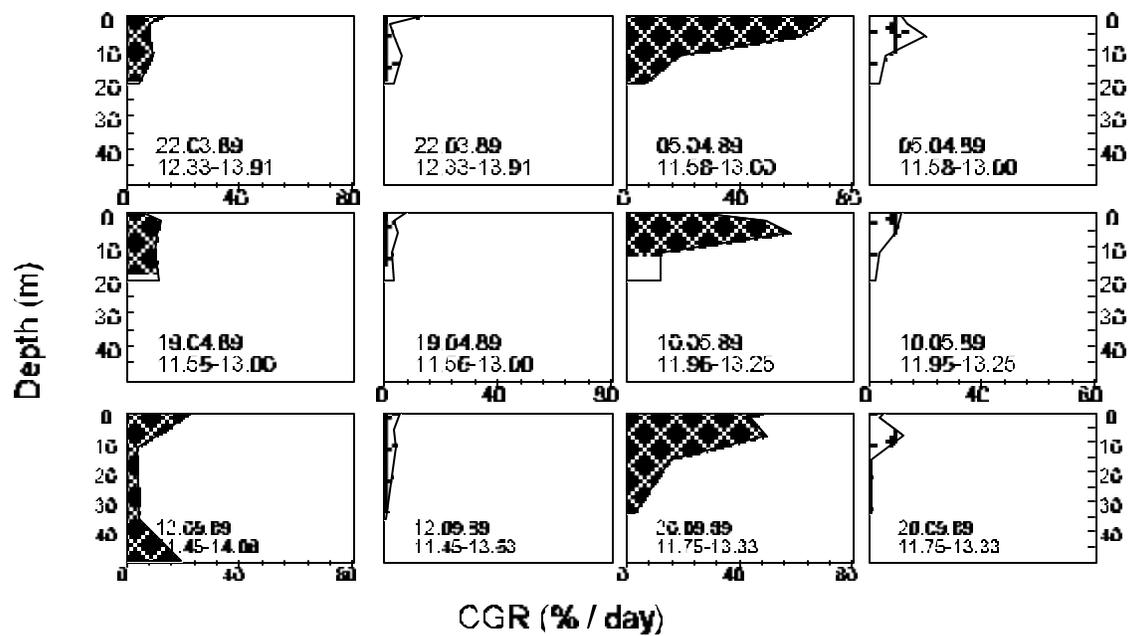
	14:00-16:00	21:00-24:00	4:00-6:00	10:12:00
23-24/May/89	0.18±0.02 (3)	0.15±0.02 (3)	0.20±0.01 (2)	0.10±0.02 (3)
13-14/Jun/89	0.36±0.04 (3)	0.42±0.02 (3)	0.49±0.03 (3)	0.42±0.01 (3)
04-05/Jul/89	0.63±0.07 (3)	0.66±0.01 (3)	0.71±0.02 (3)	0.64±0.16 (2)
01-02/Aug/89	0.31±0.03 (3)	0.31±0.07 (3)	0.33±0.02 (3)	0.28±0.08 (3)

obs : number of observations in parenthesis

Daily fluctuations in the food availability could also be observed during these day-night experiments. Tab 10 shows that POC concentrations (fraction < 50: m) were slightly higher during the second night half in all four experiments.

### 3.5 **Effects of different food types on Community grazing rates**

The twin grazing-chamber used in this study made it possible to perform grazing experiments using different food particles simultaneously. Such incubations were done before the clear-water phase, between March and May and at the end of summer, in September of 1989. Although several literature sources suggest that *Rhodomonas* is a basic item for the diet of most zooplankton organisms, some experiments were run with other algae as experimental food: the diatom *S. hantzschii*. Measurements of community grazing rates as well as determinations of specific filtering rates of major herbivores of mesozooplankton were done in these experiments. In this chapter, only the measurements at the community level will be considered. The basic objective of these experiments was to individualise possible deviations in the community grazing rates of both zooplankton size fractions when two of the most important components of the nanoplankton in this lake were simultaneously paired as experimental food particles. Thus, these experiments served as subsidies to possible generalisations (or restrictions) based on the long term experiments where *Rhodomonas sp.* was always used as food particle.



**Figure 18** Responses of CGR of microzooplankton to two different algal food particles: *Rhodomonas sp.* (dark pattern) and *S. hantzschii* (light pattern).

Contrarily to larger zooplankton, feeding responses of microzooplankton were strongly affected when different algae were offered as experimental food particles. The grazing rates from these parallel experiments are illustrated in Figs 18 (microzooplankton) and Fig 19 (mesozooplankton).

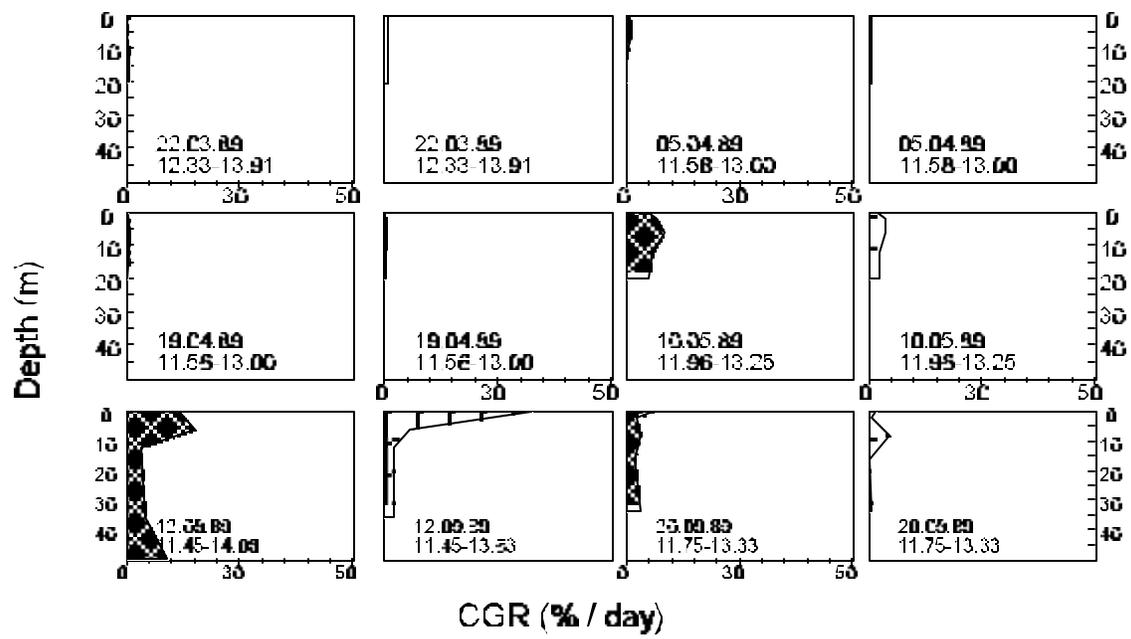


Figure 19 As in Fig. 18, for mesozooplankton.

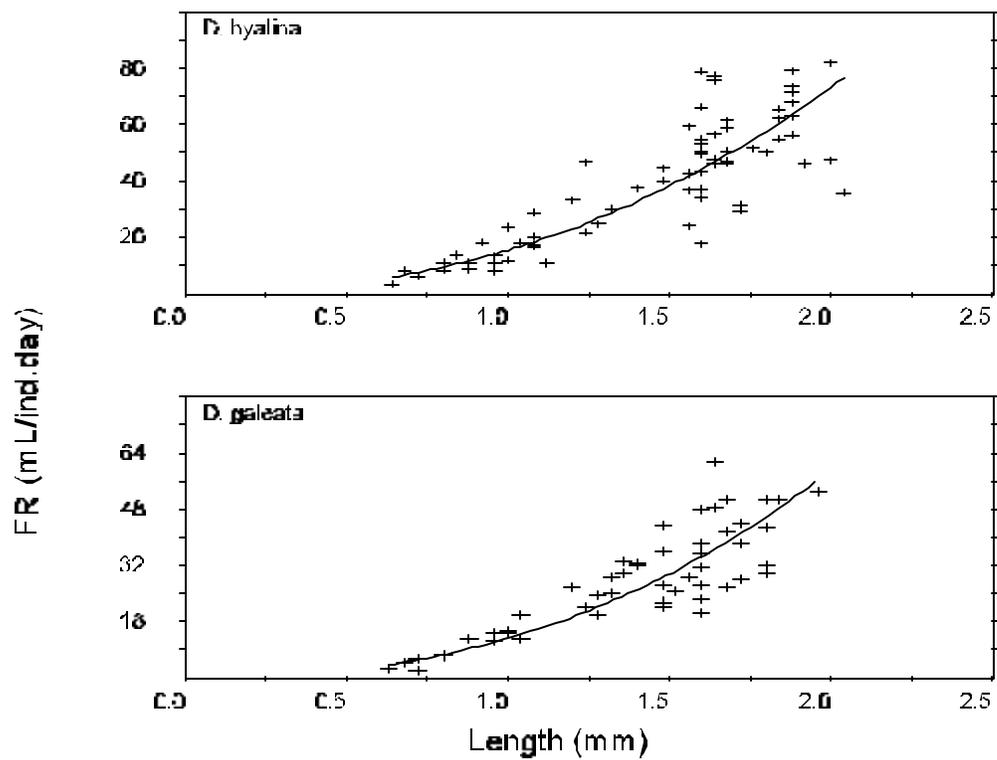
In all experiments, higher community grazing rates of microzooplankton were measured when the diatom was offered. A typical example illustrating this trend could be the experiment run in 19/Apr/89 at 2m depth, when  $CGR_2$  were 34 and 118  $mL.L^{-1}.day^{-1}$  for experiments using *Rhodomonas* and *S. hantzschii* as food particle, respectively.

Mesozooplankton grazing rates were always comparable. At 12/ Sep/89, for example, integral values (0-20 m) of  $CGR$  for larger organisms were 1366 and 1339  $L.m^{-2}.day^{-1}$  for experiments using the cryptophyceae and the diatom, respectively. The mean ratios  $CGR_{Rhod}:CGR_{Steph}$  were 0.32 for microzooplankton and 0.98 for mesozooplankton (pooled data). In section 3.6.3, it will be shown, however, that in despite of similar responses found at the community level of mesozooplankton, some organisms of this fraction had very different filtering rates when these two algal food particles were simultaneously offered in field experiments.

### 3.6 **Specific filtering rates of major herbivores**

#### 3.6.1 **Filtering rates and body size**

All zooplanktonic herbivores of Lake Constance had their filtering rates strongly affected by body size. The basic nature of these relationships depends, however, on the taxonomic group of a given organism. Cladocerans had their FR vs. body size relationships satisfactorily described by a power function. The estimates of the final equation were obtained using linear regressions on log-transformed data. In this study, two regression models were applied to calculate these estimates: least squares (model I) and geometric means (model II) method. Only model I has been considered in most studies of zooplankton filtering rates. However, there are strong arguments which recommend to use model II for linear regression estimates of *Daphnia* filtering rates based on body size measurements (Cf. section 2.6). Therefore, model II was considered for all regressions of cladoceran filtering rates. Copepods, on the other hand, had their filtering rate varying in a very specific way and different functions had to be considered for each species.



**Figure 20** Filtering rates of *D. hyalina* and *D. galeata* in L. Constance during the clear-water phase (23/May/89, night values, 0-6 m). *S. hantzschii* used as experimental food. See also Tab 11 for regressions.

Fig 20 shows typical responses of filtering rates of both *D. hyalina* and *D. galeata* to body size. The data sets come from experiments carried out in May of 1989 (night measurements) where *S. hantzschii* was used as food. Tab 11

Table 11

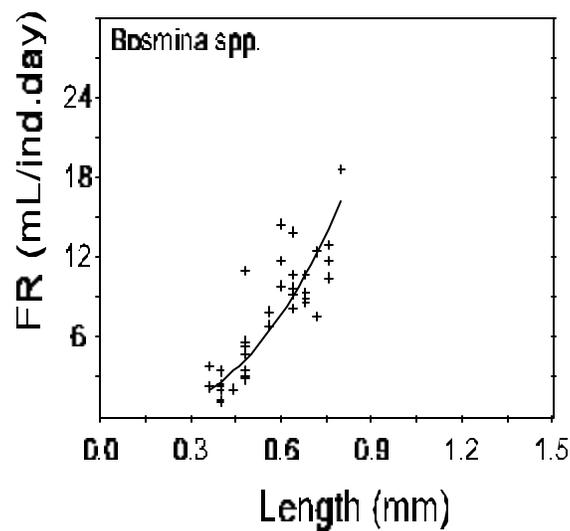
Effects of body size (mm) on filtering rates (mL/day) of *Daphnia galeata* (dg), *D. hyalina* (dh), *Bosmina* spp. (bo), *Mesocyclops leuckartii* (ml), during spring/summer of 1989 in Lake Constance.

Org	N	Length			FR			FR = a.L <sup>b</sup>		
		mean	sd	range	mean	sd	range	a	b	r
dg	63	1.39	0.35	0.63-1.96	27.9	14.6	2.1-61.5	11.11	2.41	0.9224
								10.46	2.62*	
dh	74	1.46	0.38	0.64-2.00	40.4	21.8	3.1-82.0	15.19	2.27	0.9054
								14.02	2.51*	
bo	40	0.56	0.13	0.36-0.80	7.4	4.4	1.2-18.6	28.97	2.61	0.8752
								36.60	2.98*	
ml	69	0.75	0.09	0.60-1.00	0.9	0.6	0.03-3.3	0.25	-3.93	-0.5840

Obs: Length in mm, filtering rates (FR) in mL.day<sup>-1</sup>, (\*) estimates based on model II (geometric means regression model). The pearson correlation coefficient (r) remains the same when model II is considered.

shows that body sizes in both data sets were highly correlated ( $r > 0.9$ ,  $n > 60$ ) with filtering rates. This table also shows that the regression estimates of exponent  $b$ , calculated using model II, were generally higher.

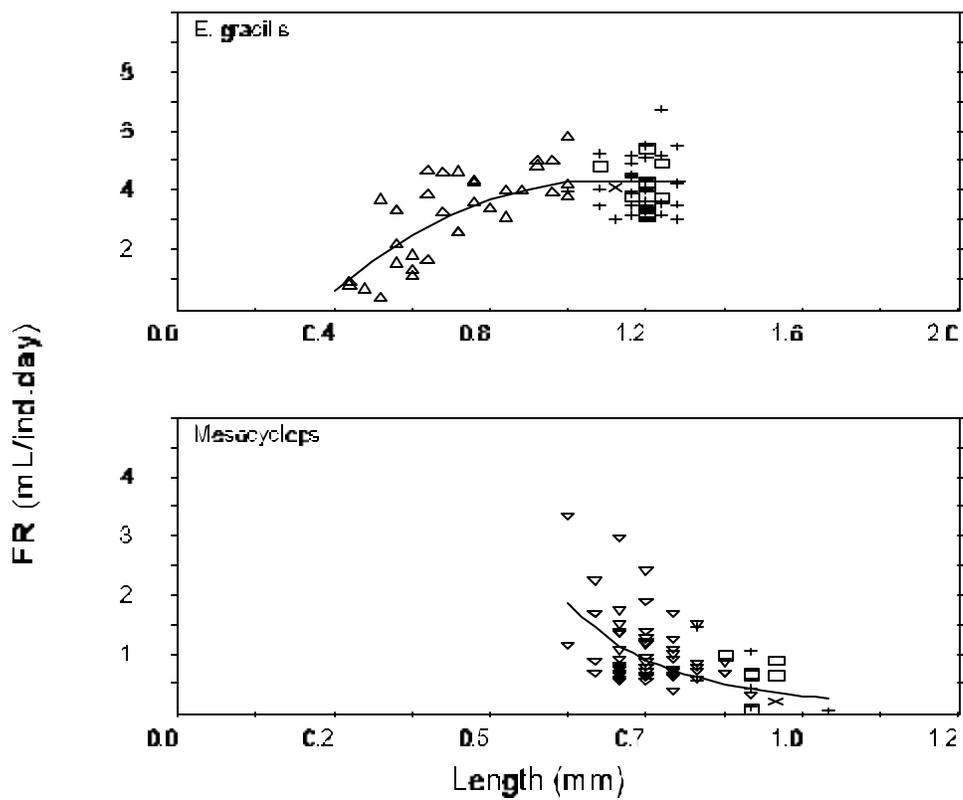
In Lake Constance, there are two *Bosmina* species: *B. longirostris* and *B. coregoni*. Their specific abundances were generally low in the experimental chamber and so I decided to merge the filtering rates



**Figure 21** *In situ* filtering rates of *Bosmina* spp. in L. Constance during clear-water phase (24/May/89, night values, 0-6 m), using the diatom *S.hantzschii* as food particle. See also Tab 11 for regression.

of these species in a single data set. Fig 21 illustrates the body size vs. FR for

bosminids during clear-water phase of 1989. Again, *S. hantzschii* was used as food particle. The Pearson correlation coefficient was again highly significant ( $r=0.8752$ ,  $n=40$ ). FR vs. body size regression estimates for this data set are also represented in Tab 11.



**Figure 22** *In situ* filtering rates of the copepods *E. gracilis* (summer 1988) and *M. leuckarti* (spring 1989). Triangles: copepodites, cross: females, squares: females with eggs and 'x': males. See Tabs. 11 and 12.

Table 12

Effects of body size, food type and time of the day on filtering rates of *Eudiaptomus gracilis* in Lake Constance during the years 1988 and 1989.

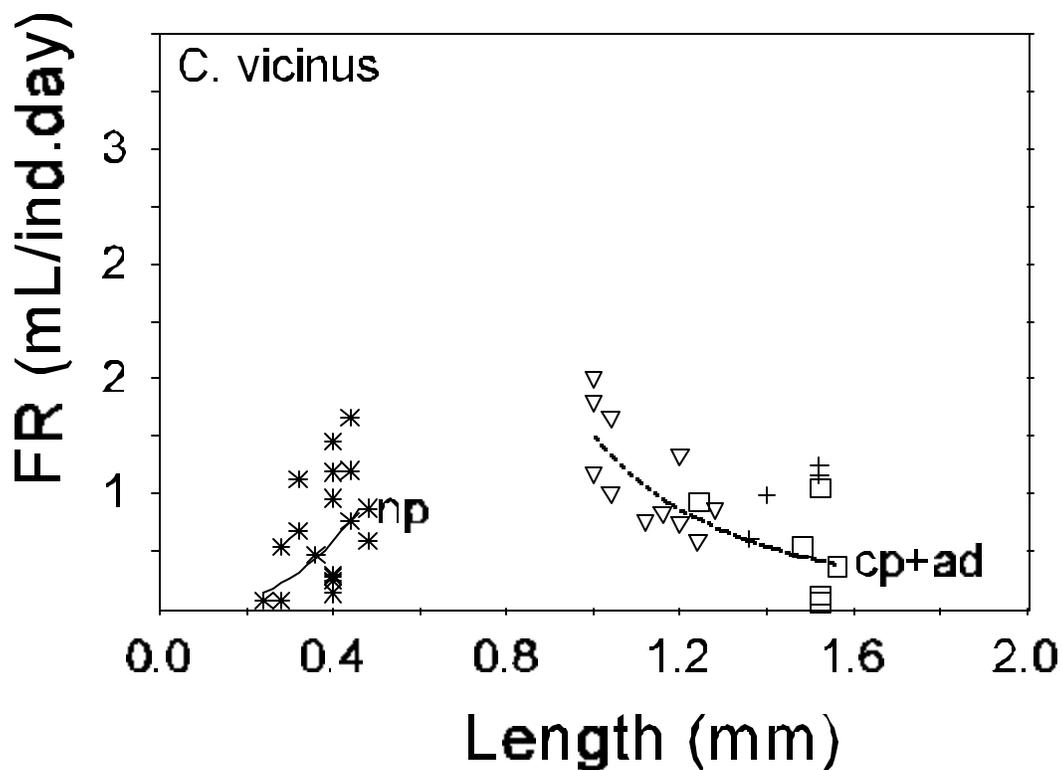
class variable	n	Non Linear			Fit	(Gauss-Newton Method)		
		a	b	c		Plateau	Regr.	Sum of Squares
-	70	-6.37	21.37	-10.77	0.99	4.23	1024	64
day	23	-4.22	12.63	-7.23	0.87	1.29	32	2
night	29	-7.81	23.47	-11.25	1.04	4.42	480	23
<i>Rhodomonas</i>	50	-8.20	22.89	-9.88	1.16	5.06	725	61
<i>Stephanodiscus</i>	31	-4.99	12.87	-4.58	1.41	4.04	172	10

Obs: Filtering rates (FR) and plateau values in mL.cop<sup>-1</sup>.day<sup>-1</sup>, Length (L) and x0 in mm.

The response of filtering rates to body size of the calanoid *Eudiatomus gracilis* during the summer of 1988 is illustrated in Fig 22 (top). The pattern of this relationship could not be described by any power function, as it was the case for cladocerans, since adult copepods have FR's which seem not to react to further increases in the body size. On the other hand, FR's of copepodites responded proportionally to body size. Therefore, the function to be fitted had to describe the increase in the FR observed for copepodites and the 'saturation-zone' observed for adults. Egg-carrying females, females without eggs and males had body sizes varying between

1.0 and 1.3 mm and in this size-range no clear increase in the filtering rates was observed. I decided to use a non-linear procedure (SAS proc Nlin, Newton-Gauss) adjusting a polynomial function with a asymptotic approximation of the saturation zone. The parameters of the fitted model are represented in Tab 12 (class variables absent). The significance of this model can be evaluated by comparing the least squares sums of regression estimates and residuals. A plot with the adjusted curve and measured FR is provided in Fig 22 (top).

Filtering rates of cyclopoids were very low. Although they were affected by body size, these organisms had a very particular filtering behaviour. Contrarily to all herbivores considered in this study, adults or older copepodites (5. copepodite) of cyclopoids filtered the selected algal food at lower rates than did younger development stages. A example of such trend is provided for *M. leuckartii* in Fig 22 (bottom). A negative power function (Tab 11) was effectively fitted in this case. Length measurements were significantly correlated with FR and, as expected, the Pearson coefficient was negative ( $r = -0.584$ ,  $n = 69$ ).



**Figure 23** *In situ* filtering rates of *C. vicinus* fed on *Rhodomonas sp.* in Lake Constance during spring of 1989. '\*': nauplii, triangles: copepodites, squares: egg carrying females, cross: females. See also Tab. 13.

Table 13

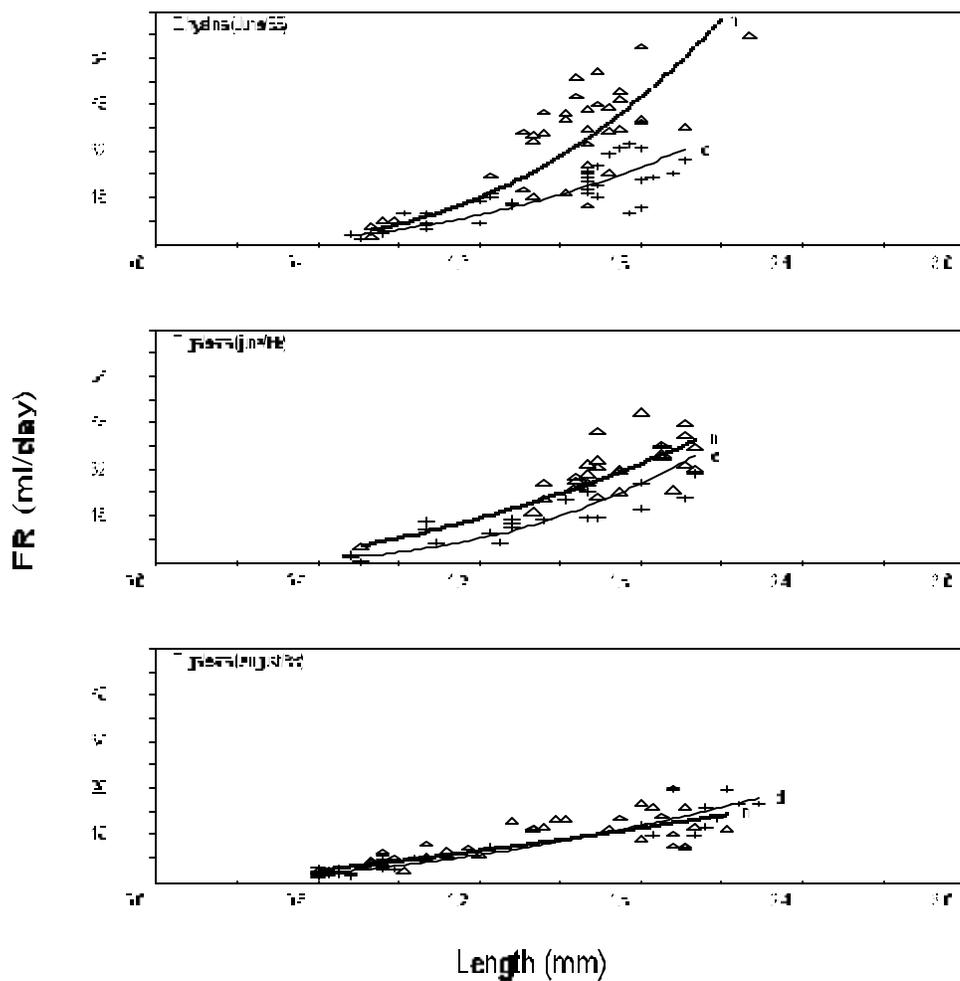
Regression coefficients describing the relationship between body size and FR ( $\text{mL.ind}^{-1}.\text{day}^{-1}$ ) in *Cyclops vicinus*.

instar	n	FR = a * L <sup>b</sup>		r
		a	b	
nauplii	18	1.79	2.79	0.5489
cop. + adults	21	1.20	-2.96	0.5556

*C. vicinus* copepodites and adults behave in a similar way as *Mesocyclops leuckartii*. However,

as a large number of nauplii instars of this species were present in spring of both years, the filtering rates of naupliar stages were also considered. Fig 23 illustrates the different relationships between body size and FR of different developments stages in this species. Older copepodites and adults filtered at lower rates than did younger copepodites. All nauplii instars, however, responded positively to body size. Tab 13 gives the regression coefficients for these relationships.

### 3.6.2 Diel variations of filtering rates



**Figure 24** Diel variations of in situ filtering rates of *D. hyalina* (June 1988) and *D. galeata* (June and August 1988) in L. Constance (0-6 m), d day, n: night. *Rhodomonas* as food. See also Tab 14.

Filtering rates of both *Daphnia* species were measured in day and night incubations. FR measurements as well as the fitted curves from some of these experiments are plotted in Fig 24. It was possible collecting individuals of *D. hyalina* in the epilimnion during the day only before the onset of DVM, like during June 1988. At that time, individuals of *D. hyalina* filtered higher amounts of water at night. *D. galeata* showed different feeding behaviours depending on which period of the year is considered. Individuals of this species showed slightly enhanced FR at night in some occasions, as during the clear-water phase. In late summer (August), however, they had comparable filtering rates in both experiment series (day and night).

Tab 14 provides the estimates of both regression models and the covariance analyses between regressions of day and night experiments for each particular species. The regressions for vertical migrators such as *D. hyalina* and *Bosmina* had always higher exponents  $b$  (in both models) at night. It is interesting to notice that the fitted model for night FR data of *D. galeata* in June caused not higher exponent ( $b$ ) but a higher intercept ( $a$ ). Observe also that exponents ( $b$ ) of model II (geometric means) were always higher than those from model I.

The covariance analysis from regression estimates (Tab 14) also

Table 14

Diel variations of filtering rates of *Daphnia galeata* (dg), *D. hyalina* (dh), *Bosmina* spp. (bo) in Lake Constance.

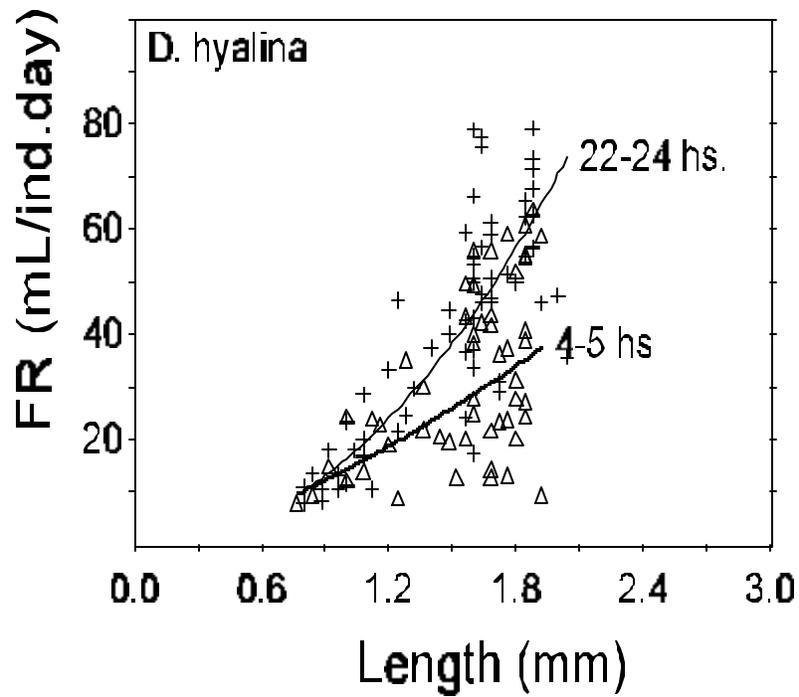
Org	class variable	n	FR = a.L <sup>b</sup>		Pearson r	covariance analysis	
			a	b		LS	SE
dg <sup>1</sup>	day	22	4.76	2.95			
	night-1	27	4.18*	3.48*	0.8485	2.67	0.110
dg <sup>2</sup>	day	31	11.21	1.93	0.8727	3.08	0.090
	night-1	35	9.72*	2.21*	0.9352	1.63	0.080
dh <sup>1</sup>	day	35	3.97	1.86	0.8202	1.83	0.070
	night-1	36	3.96*	2.00*	0.8966	2.68	0.060
dh <sup>2</sup>	day	35	5.45	1.33	0.8805	3.26	0.060
	night-1	36	5.01*	1.62*	0.8704	3.25	0.050
bo	day	13	6.38	2.42	0.6040	0.71	0.1300
	night-1	36	5.87*	2.70*	0.8687	1.76	0.0800
bo	day	13	10.19	2.76			
	night-1	36	8.85*	3.14*			
bo	day	13	16.35	2.11			
	night-1	36	14.56*	2.42*			
bo	day	13	14.85	1.43			
	night-1	36	9.36*	2.53*			
bo	day	13	6.74	1.66			
	night-1	36	13.64*	2.74*			
bo	day	13	27.72	2.48			
	night-1	36	37.51*	2.86*			

Obs: Length in mm, filtering rates (FR) in mL.day<sup>-1</sup>, (\*): estimates based on model II regression (geometric means method). dg<sup>1</sup>: June/88, dg<sup>2</sup>: August/88. dh<sup>1</sup>: June/88, dh<sup>2</sup>: May 89. night-1: after sunset, night-2: before dawn.

confirmed the different feeding behaviours of daphnids along the diel cycle. Least square means of regressions of *D. hyalina* and *D. galeata* were significantly higher at night in June (though with lower significance for the second species) but not for the data set of *D. galeata* derived from summer experiments.

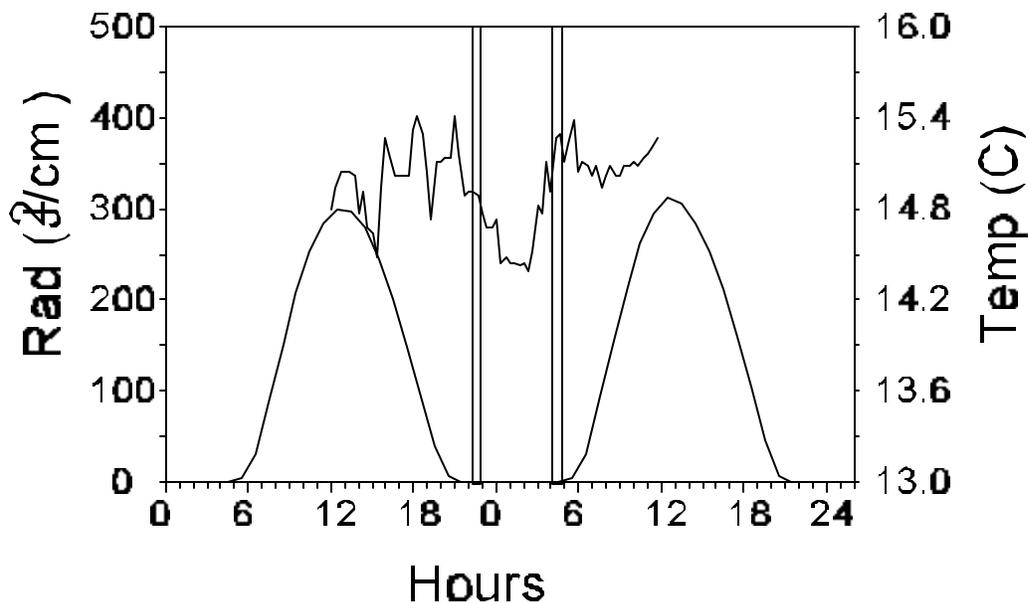
The diel variations in the FR of *Daphnia* shown in Fig 24 could not be detected by the biomass specific grazing rates ( $G_b$ ) calculated at the community level (Tab 7).  $G_b$  for larger zooplankton was higher at night only in April and September. In June, higher values of  $G_b$  were found during the day and they remained the same during the diel cycle in August for this species.

Summarising, enhanced night filtering rates of were always found for *D. hyalina*. *D. galeata* had also higher FR at night but this finding was restricted to short periods. Additionally, the difference between day and night FR's were never so conspicuous as those observed in FR's of *D. hyalina*.



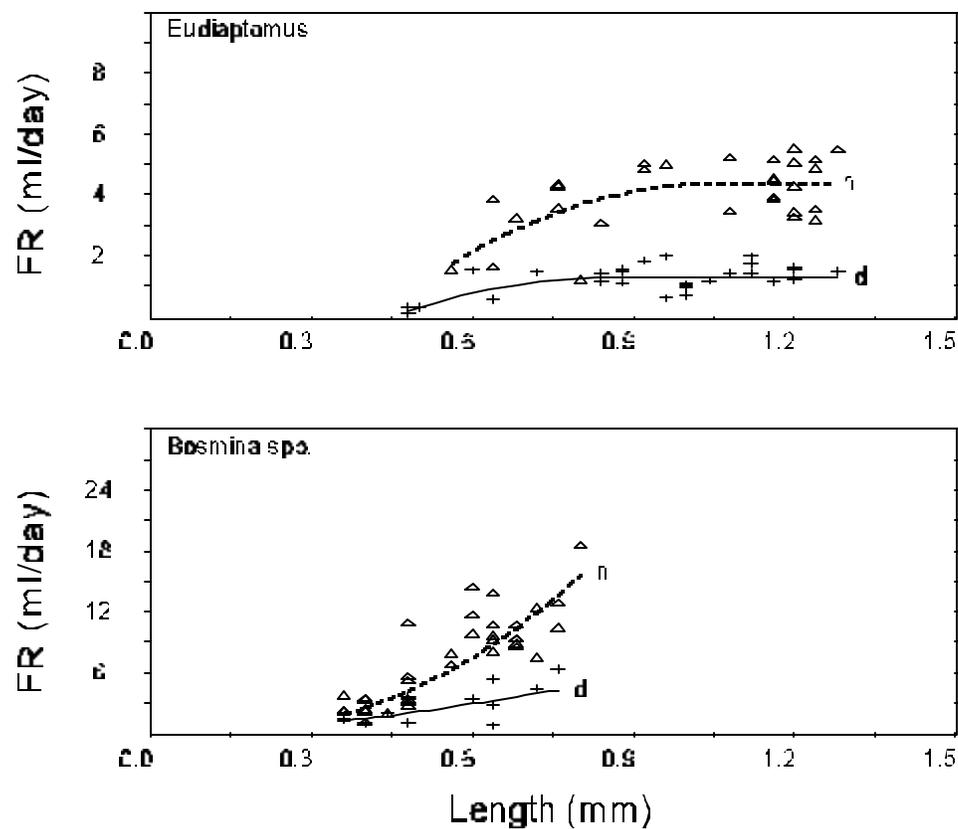
**Figure 25** *In situ* filtering rates of *D. hyalina* in Lake Constance, at night, during clear-water phase of 1989 (23-24/May, 0-6 m). *S. hantzschii* was used as food particle. Hours given as summer time.

The next point would be to investigate whether *D. hyalina* maintains comparable FR's during all the night. In 1989, grazing experiments were run just after sunset and short before dawn. As expected, night values of filtering rates for this species were higher than during the day. The two night experiment series revealed, however, distinctive grazing activities. The highest filtering rates in the diel cycle were observed for *D. hyalina* (Fig 25) in the first part of the night (22:00-24:00 hs.). These values could not be observed later in the night any more. This means that the vertical migrator *D. hyalina* has probably one or more peaks in its filtering activity at night and one of them probably occurs as soon as these organisms reach water surface, after sunset. Fig 26 illustrates the course of solar radiation and water temperature during the diel cycle of 23-24/May/89. Both experimental series were carried out in complete darkness short after sunset and before dawn. Although variations in the temperature were observed during the night, the two night series of experiments (vertical bars) were conducted under similar temperature conditions. Tab 14 shows that the least square means (ANCOVA) were significantly different between these two data sets.



**Figure 26** Diel cycles of solar radiation and water temperature (4.0 m) in Überlingersee (23-24/May/89). Radiation data provided by the Deutscher Wetterdienst. Duration of exps. delimited by vertical bars.

Diel variations of feeding activities were also examined in *Bosmina* and *E. gracilis*. Field incubations conducted in the epilimnion of L. Constance during the clear-water phase of 1989 were again considered



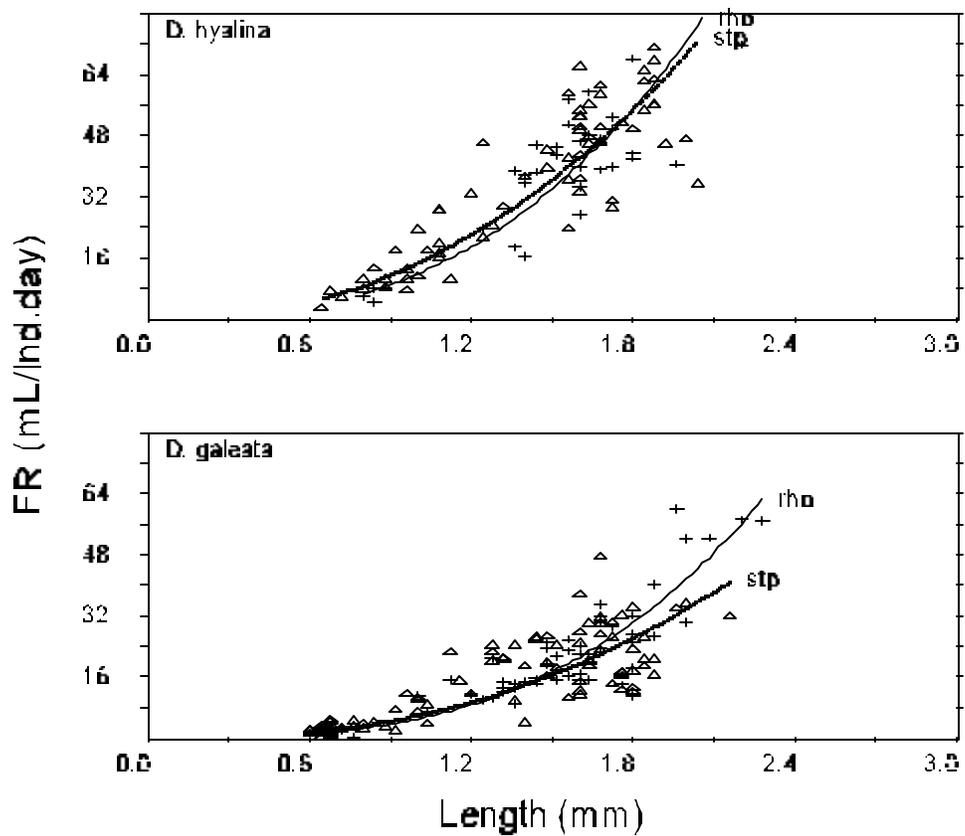
**Figure 27** Diel variations of filtering rates of *E. gracilis* (summer 1988) and *Bosmina* (clear-water phase, 1989) in L. Constance. See also Tabs. 12 and 14 for regressions' parameters; n: night, d: day experiments.

for *Bosmina*. The diatom *S. hantzschii* was the labelled food particle in all these experiments. Diel variations in the clearance rates of the calanoid *E. gracilis* were investigated during the summer of 1988 using *Rhodomonas* as food particle. Fig 27 shows that both, *Bosmina spp.* and *E. gracilis*, had higher filtering rates at night. Tabs 12 and 14 give further information about the regression estimates related to the curves as well as basic statistics for each data set, respectively. The least square mean for night FR-values (ANCOVA) of *Bosmina spp.* was significantly higher at night (Tab 14). The non-linear fit for *E. gracilis* demonstrated that night FR's for all size classes of this calanoid were also higher than during the day. Tab 12 shows that the plateau values (asymptotic approximation) were  $1.29 \text{ mL}\cdot\text{day}^{-1}$  ( $x_0=0.87 \text{ mm}$ ) and  $4.42 \text{ mL}\cdot\text{day}^{-1}$  ( $x_0=1.04 \text{ mm}$ ) for day and night experiments, respectively.

### 3.6.3 Effects of different food types on filtering rates

It was already demonstrated (Cf. section 3.5) that community grazing rates of mesozooplankton were comparable in experiments using the selected algal particles. A similar trend can be observed in Fig 28 for the most important zooplankton herbivores of L. Constance: the two *Daphnia* species. FR-data of both species came from several experiments conducted in the epilimnion during 1989 in which both algal particles (*Rhodomonas sp.* and *S. hantzschii*) were simultaneously offered. The

clusters of empiric FR-values have practically the same patterns for both algal foods and the adjusted curves have consequently similar outlines. This statement is valid not only for *D. hyalina* (top) but also for *D. galeata* (bottom). Tab 15.



**Figure 28** Effects of two algal foods (*Rhodomonas sp* and *S. hantzschii*) on FR's of *Daphnia spp.* in L. Constance (0-6 m), measured between May and September of 1989. See Tab 15 for regressions.

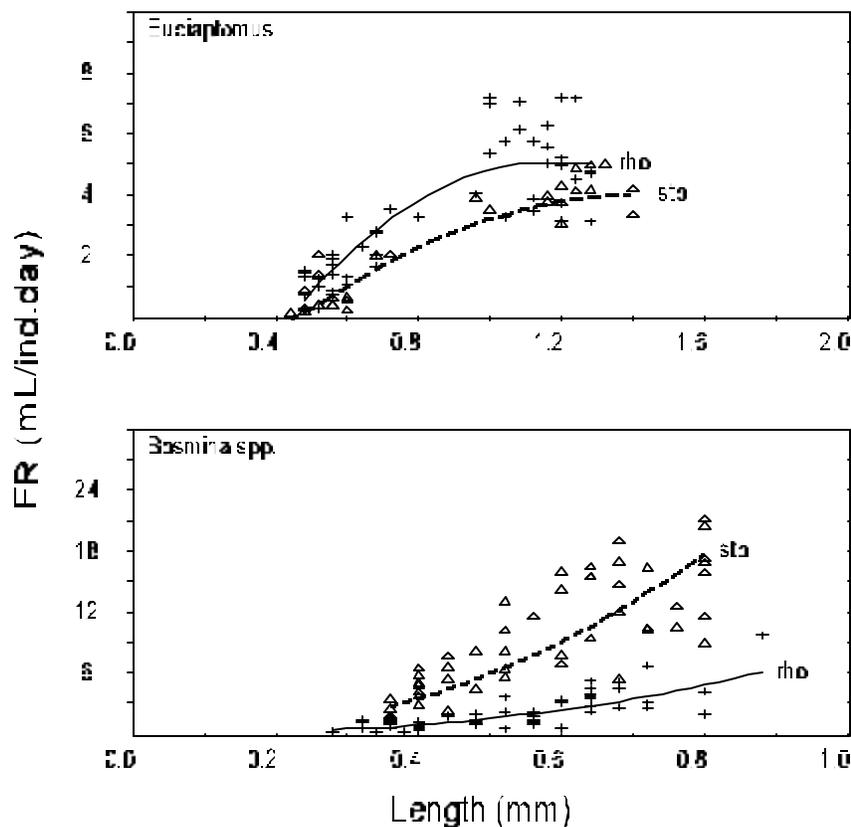
Table 15

Effects of two different food types on *in situ* filtering rates of *Daphnia galeata* (dg), *D. hyalina* (dh), *Bosmina* spp. (bo) in Lake Constance.

Org	class variable	n	FR = a.L <sup>b</sup> a	b	Pearson r	covariance analysis LS SE	Pr> T
dg	rho	54	5.01	3.06	0.8770	2.40 0.09	
	stph	89	4.23 6.43 6.10	3.49* 2.43 2.72*	0.8912	2.47 0.07	0.5554
dh	rho	32	11.69	2.64	0.9150	3.29 0.11	
	stph	66	10.64 15.17 8.85	2.88* 2.21 3.14*	0.9170	3.39 0.07	0.4372
bo	rho	54	8.43	2.54	0.7616	0.45 0.07	
	stph	52	14.70 30.13 38.56	3.34* 2.29 2.69*	0.8509	1.89 0.07	0.0001

L: length in mm, FR: filtering rates in mL.day<sup>-1</sup>, (\*): model II regression (geometric means method), rho = *Rhodomonas* sp., stph = *S.hantzschii*.

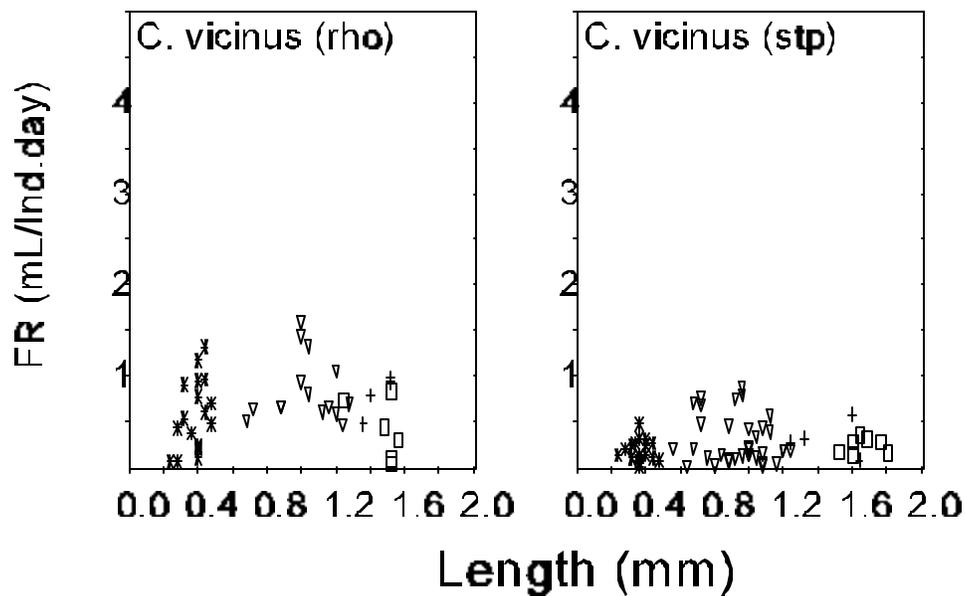
gives further confirmations of the similarities between the FR's obtained in experiments using different algal foods for both *Daphnia* species. Although all four regressions generated highly significant Pearson coefficients, the comparison between the least square means (ANCOVA) of each regression obtained using *Rhodomonas sp.* and *S.hantzschii* as algal food showed that they were not significantly different from each other. This demonstrated once again that the selected model (power function relating body size to FR) satisfactorily described the FR behaviour of daphnids and the nature of this function is not affected by different experimental treatments.



**Figure 29** Effects of two food types (*Rhodomonas* and *S. hantzschii*) on *in situ* FR's of *E. gracilis* and *Bosmina* in L. Constance, between May and September 1989, day values. See also Tabs 12 and 14.

Organisms from mesozooplankton had not always similar filtering rates when these two algae were simultaneously used. Examples of such differences can be observed in Fig 29 for *E. gracilis* and *Bosmina* spp. These organisms clearly showed preferences to one of the selected food types. The calanoid had higher filtering rates when *Rhodomonas* was offered as food particle and *Bosmina* spp. filtered *S. hantzschii* at higher rates. The least squares means and the estimates of the regression coefficients for *Bosmina* are represented in Tab 15. As expected, the LS-mean

was significantly higher in organisms fed with *S. hantzschii*. The estimate of the exponent  $b$  was higher for *Bosmina* fed with *Stephanodiscus*. The non linear fits for *E. gracilis* generated higher asymptotic approximation (plateau) for *Rhodomonas sp.* (Tab 12).



**Figure 30** *In situ* filtering rates of *C. vicinus* fed with *Rhodomonas sp* (left panel) and *S. hantzschii* (right panel) during spring of 1989 in Lake Constance (0 - 20 m).

The copepod *C. vicinus* had also different filtering rates when these two algal types were simultaneously offered as food particles. Higher filtering rates were observed when this cyclopoid fed on *Rhodomonas sp.* (Fig 30).

#### 3.6.4 Effects of food concentration on filtering rates of *Daphnia*

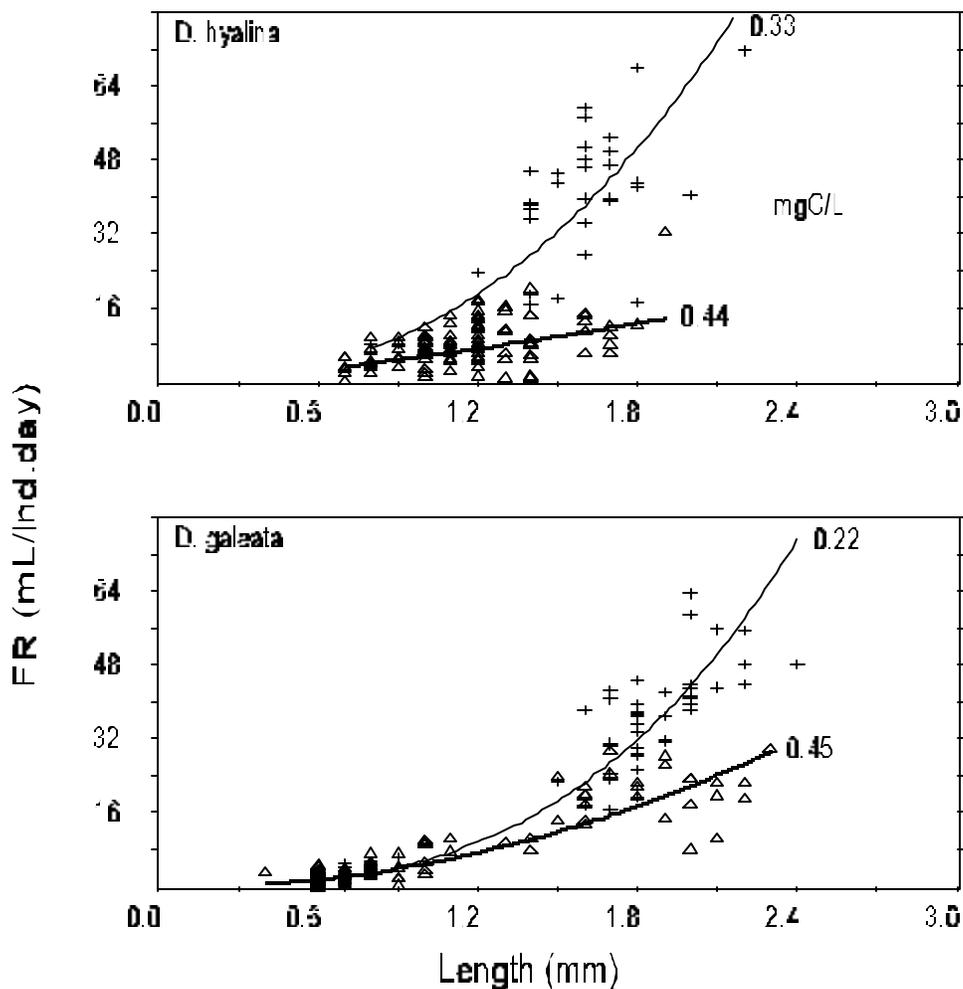
Table 16

Effects of water temperature (mean food concentration was given as the 'constant' variable) and food concentration (mean water temperature as 'constant' variable) on *in situ* filtering rates of *D. galeata* and *D. hyalina* in L. Constance. Length vs. filtering rates linear regression estimates (Models I and II), and analysis of Covariance (Least Squares Means). See text for other details.

org.	"constant" condition mean sd	"variable" conditions mean sd	a	b	n	r	LS	ANCOVA		H0: LS1=LS P> T
								SE	SE	
D.h.	0.16±0.05mgC/L	5.05±0.28 °C	3.05	2.44*	153	0.8595	1.505	0.044	0.0001	
			2.85	2.84						
D.h.	13.67±0.33 °C	8.05±1.36 °C	3.87	2.79*	98	0.8643	1.798	0.050	0.0001	
			3.64	3.23						
D.g.	18.67±2.04 °C	0.33±0.06 mgC/L	12.11	2.43*	34	0.8576	3.089	0.116	0.0001	
			10.35	2.84						
D.g.	0.44±0.01 mgC/L	0.22±0.03 mgC/L	5.90	1.34*	119	0.4141	2.023	0.058	0.0001	
			4.79	3.24						
D.g.	0.45±0.14 mgC/L	0.45±0.14 mgC/L	5.51	2.99*	65	0.9098	1.790	0.103	0.0001	
			5.04	3.28						
			5.33	2.06*	112	0.7754	1.810	0.081	0.8872	
			5.68	2.66						

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

In epilimnion of L. Constance, filtering rates of *D. hyalina* were affected by food concentration in a clear way. Only night FR values were here considered. Tab 16 shows that regression estimates of both models gave higher filtering rates at lower food concentration (mean POC 0.33 mgC.l<sup>-1</sup>) for all lengths. The



**Figure 31** Effects of different food levels (POC < 50 :m) on filtering rates of *Daphnia* in Lake Constance (0-10 m) during 1988. Experimental food particle was *Rhodomonas* sp. See also Tab 16.

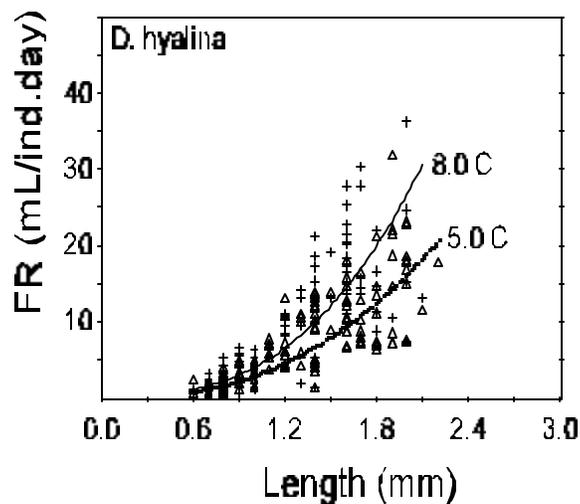
least square means (ANCOVA) were also significantly different ( $P > |T| = 0.0001$ ). This means that the two fitted equations describe significantly different

regressions. The adjusted curves as well as the empiric measurements of the filtering rates are plotted in Fig 31 (top).

Filtering rates of *D. galeata* also reacted to oscillations in the food levels under *in situ* conditions. However, different responses were observed depending on which body size is considered. The two data sets were constructed using very different food levels (Tab 16). Only day values were included in this case. Fig 31 (bottom) reveals that only individuals larger than 0.9 mm filtered higher volumes of water at lower food concentration. However, this tendency is not clear for individuals smaller than 0.9 mm. As there was a great number of young individuals in both data sets, the least square means produced by the covariance analysis were not significantly different.

### 3.6.5 Effects of water temperature on filtering rates of *Daphnia*

The effect of different temperatures on the filtering rates of *Daphnia* could be observed in two subpopulations of meta and hypolimnetic *D. hyalina*. A plot containing the two data sets and the adjusted



**Figure 32** Effect of water temperature on meta- and hypolimnetic subpopulations of *D. hyalina* in L. Constance during the fall of 1988. *Rhodomonas* was used as experimental food particle. See also Tab. 16.

curves is provided in Fig 32. As expected, organisms of the upper warmer water layers (mean temperature 8.05 °C) had higher filtering rates than those of deeper and colder waters (mean temperature 5.05 °C). Analysis of covariance between the regression estimates revealed that the curves FR vs. length are significantly different (least square means of ANCOVA in Tab 16). In the next chapter, the difficulties to observe temperature effects on field studies of zooplankton grazing will be discussed as well as the reasons explaining why these effects could be observed only in temperatures ranges outside the specific optimum range.

## 4 Discussion

### 4.1 Seasonal course of water temperature and phytoplankton community ■

#### Überlingersee

The succession of phytoplankton in L. Constance is similar to other meso-eutrophic warm monomictic lakes (Tilzer, 1990). In section 3.1, five different successional stages of phytoplankton community were identified basing on the seasonal oscillations of parameters such as water temperature, water transparency, chlorophyll-a, POC and biovolumina of phytoplankton. The community structure is strongly modified after each one of these events, and as it will be discussed later, the zooplankton is also influenced by these events or can even induce some of them. How 'typical' are these stages in the long term succession of phytoplankton in this lake? The objective of this section is to characterize the seasonal features observed in the present study relating them with other investigations in which the seasonality of phytoplankton in Lake Constance was also taken into account.

During winter mixing, phytoplankton yield is usually diatom-dominated (Tilzer, 1990). The winter dominance of diatoms could be observed in both years considered here (Fig 6). Chlorophyll-a concentrations in the euphotic zone are usually less than  $1.2 \text{ : g.L}^{-1}$  during the cold months (Tilzer and Beese, 1988). Epilimnetic chlorophyll-a concentrations were somewhat higher during the winters 87/88 and 88/89 but they remained below  $5.0 \text{ : g.L}^{-1}$ . Winter POC concentrations do not usually ascend over the  $0.3 \text{ mgC.L}^{-1}$  boundary (Geller, 1980). Fig 6 shows that similar POC values were found for the two winters surveyed in this study.

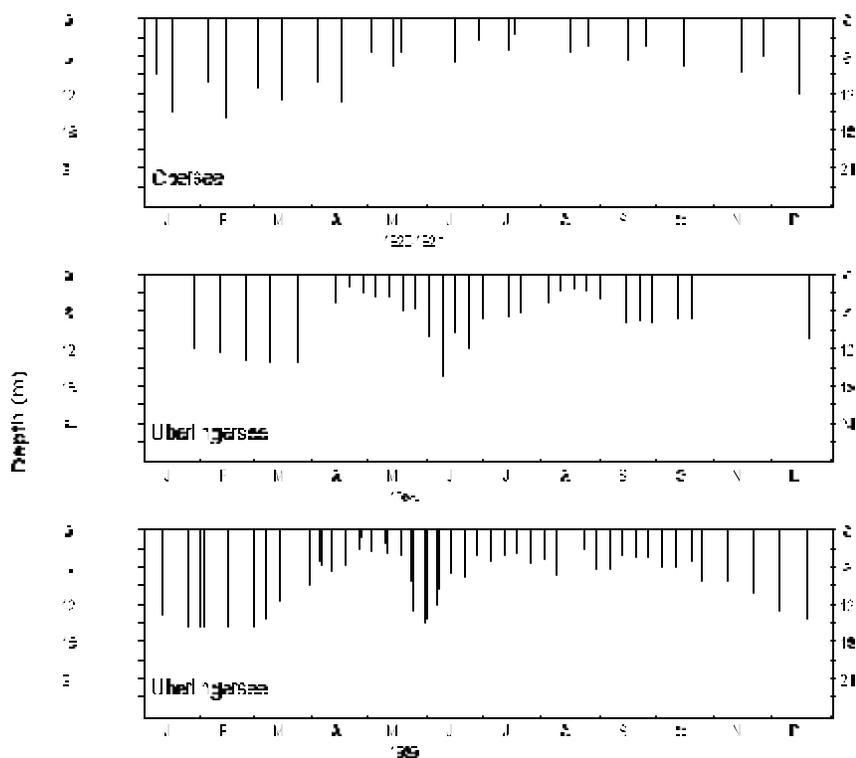
In L. Constance, surface water temperatures remain around  $5\text{-}6 \text{ }^{\circ}\text{C}$  during the winter (Fig 6) and usually do not fall below  $4 \text{ }^{\circ}\text{C}$  (Heinz *et al.* 1990). Nevertheless, these temperatures are not sufficiently low to prevent algal growth (Sommer, 1987). Thus, the effects of stratification by far exceed the direct physiological temperature-effects on regulating phytoplankton succession in this lake (Sommer, 1987). Thermal stratification influences the light-climate (Talling, 1957), nutrient regime (Parker, 1982) and

sedimentation rates (Reynolds, 1980). Thus, winter phytoplankton yield in L. Constance should be light limited, since the water temperature is not sufficiently low to prevent growth, and the nutrient levels are high enough due to greater depth of mixing (Sommer, 1985; Tilzer, 1990).

The spring-bloom occurs frequently coincident with the onset of thermal stratification and when surface temperatures reach ca. 6 °C (Sommer, 1987). Tilzer and Beese (1988) observed positive growth when the mean light flow exceeded ca. 2 mol.m<sup>-2</sup>.day<sup>-1</sup> of PAR. As soon as thermal stratification is established, the enhanced energy input leads to the establishment of the typical spring bloom algal assemblage which consists of fast growing small and edible algae. Large diatoms such as *Asterionella*, *Synedra* and *Stephanodiscus astrea* can also build up significant portions of the spring bloom algal biomass (Sommer, 1983 and 1987). Sommer (1987) called this phase as *Rhodomonas-Stephanodiscus* stage, because the spring peak of phytoplankton in Lake Constance consisted mainly of small Cryptophyceae and centric diatoms during several years. In 1988 and 1989, this statement was partially valid since the algal community was clearly dominated by these small algae during April. Nevertheless, secondary pulses for these small algae were also observed during summer (Fig 6). Biomass of phytoplankton can reach values ranging from 750 to 2500 mgFW.m<sup>-3</sup> in the euphotic zone of this lake during spring bloom (Sommer, 1983 and 1985). This biomass increase of phytoplankton during this time was well reflected by POC and chlorophyll-a concentrations as well as by low Secchi disk values (Fig 6).

During spring, the standing-stock of phytoplankton is usually limited by nutrient availability, high sedimentation rates, microzooplankton grazing and sometimes by adverse climatic conditions (Lampert and Schober, 1978; Tilzer, 1990; Weisse *et al.* 1990). Wind and colder weather can destroy rapidly this weak stratification leading to deeper mixing-zones, which in turn cause a delay of algal growth (Sommer, 1987). Therefore, deviations from the above described typical spring algal assemblage can be expected under those adverse circumstances (Sommer, 1983 and 1985).

Zooplankton grazing induces the collapse of phytoplankton biomass at the end of May or at the beginning of June: a clear-water phase occurs (Lampert and Schober, 1978, Geller, 1980, Sommer, 1983, Pinto-Coelho, 1991). There are evidences that this is a new stage of the phytoplankton succession in this lake. Auerbach *et al.* (1926) measured water transparency over four years in the earlier twenties. Their values are plotted together with more recent measurements of transparency in the lake (Fig 33). In the



**Figure 33** Seasonal courses of water transparency in L. Constance. Data from the 1920-1924 series are modified from Auerbach *et al.* (1926).

Secchi disk data of 1920-1924, no clear sign of increase in the water transparency can be noted between May and July. The clear-water phase was observed for the first time in Überlingersee in the early sixties (Lehn, 1968). This phenomenon is related to the establishment of a eutrophication process on the lake and it is characterized by phytoplankton cell volumes lower than  $200 \text{ mm}^3 \cdot \text{m}^{-3}$  near surface (Sommer, 1983 and 1985). During clear-water phase, the phytoplankton assemblage is usually dominated by large Cryptophyceae, not because of an increase of this group but mainly due to a slower decline of their biomass under intense grazing-pressure conditions and maybe to a slightly reduced edibility of these algae for juvenile zooplankton (Sommer, 1983 and 1987).

A conspicuous clear-water phase occurred in 1988 and 1989. Secchi-disk readings were higher than 12 m in both years. Lower biovolumina of phytoplankton, chlorophyll-a and POC concentrations were also observed (Fig 6).

A second algal development stage usually takes place during summer. In the warmest months, surface temperatures can exceed  $20 \text{ }^\circ\text{C}$  (Fig 6). After grazing pressure has declined and recycled nutrient have accumulated, the summer increase of phytoplankton starts with a combination of Cryptophyceae, large gelatinous and colonial green algae such as *Pandorina spp.* (Sommer, 1987). Several other groups also increase their biomass during short periods in summer: diatoms, Cyanophyta and blue greens. Fig 6 shows that population pulses of diatoms, large unicellular algae (e.g. *Peridinium*, *Ceratium* or *Staurastrum*), filaments of greens (*Mougeotia*) and blue greens (*Oscillatoria*) have successively occurred between July and September of 1988. In 1989, large unicellular algae were the most abundant group during summer. Tilzer and Beese (1988) affirmed that the summer maximum of chlorophyll-a is of a similar magnitude as the spring maximum. The concentrations of this pigment were, however, somewhat lower in summer of both surveyed years excepting a peak at 6 m in August of 1988. Chlorophyll-a:POC ratios were always lower in summer. This finding probably reflects the relative higher contribution of small heterotrophs like bacteria, HNF and ciliates or detritus to seston  $< 50 \text{ : m}$  during summer. This stage comes to an end when the increase in nutrient levels due to thermocline 'erosion' can no longer offset the effects of decreasing mean irradiance to which phytoplankton are exposed (Tilzer, 1990).

Further increase of the mixing depth and decrease of light leads to a gradual replacement of green algae by diatoms in autumn. They are the same species as those occurring during July plus *Diatoma elongatum* and *Stephanodiscus rotula* (Sommer, 1987). This diatom development in the fall was observed in October in both study years (Fig 6). The critical depth of autumnal mixing should range between 20 and 50 m (Tilzer, 1990).

Summarising, the present knowledge about phytoplankton ecology in L. Constance supports the conclusion that four major driving forces can be associated in determining the nature and seasonality of phytoplankton in the pelagial of this lake: nutrient input and availability in the euphotic zone, light conditions (mean levels of PAR), grazing pressure and indirect temperature effects (Sommer, 1987, Tilzer, 1990).

## 4.2 Seasonal course of zooplankton biomass

### 4.2.1 Mesozooplankton

A comprehensive view of zooplankton grazing is not possible without analyzing the primary phenomena occurring during the annual succession of zooplankton populations. Thus, the basic objective of the next sections is to provide an overview of these events. In some occasions, I will emphasize some facts which can facilitate the further comprehension of some important characteristics of zooplankton grazing.

#### 4.2.1.1 *Daphnia*, Cyclopoids and predacious cladocerans

*Cyclops vicinus* and both *Daphnia* species reach the highest biomass in the zooplankton but their populations have very different seasonal developments (Elster and Schwoerbel, 1970; Lampert, 1978; Geller, 1980; and Einsle, 1988). The opposed development of *Cyclops* and *Daphnia* is very characteristic for this lake and can be observed in Fig 8 for the years 1988 and 1989.

During spring, zooplankton is dominated by *Cyclops vicinus*, which is a filter feeder as copepodite but carnivorous as adult (Brandl and Fernando, 1975). In April, these organisms have their highest reproductive rate in L. Constance (Einsle, 1967). The biomass of copepodites increases rapidly till the end of May. Then, the copepodites (C-1 to C-4) of this species, triggered by day length, disappear very quickly, and migrate to the sediment, for summer diapause (Einsle, 1967). Fig 8 shows that the biomass of pooled cyclopoids decreased abruptly in early summer during both years. This fact certainly reflects the migration of copepodites of *C. vicinus* to the sediment.

Like other cyclopoids, *Mesocyclops leuckarti* also exhibits a complex seasonal pattern. During winter, there is a developmental stagnation of the fifth copepodite instar but some individuals of C-3 and C-4 can still be found (Einsle, 1988). They migrate to deep waters and can either subsist the winter on the

sediment in resting-stages or as active C-5 in the water column (Einsle, 1968). At the end of April, when the thermal stratification begins to establish, the C-5 instar moults to adult animals and the youngest copepodites instars (C-1 to C-4), originated from the first springtime generation are found some weeks later, in June (Einsle, 1968 and 1988). Only small individuals and sparse adults can be found in the water column throughout the summer and the annual biomass maximum for this species occurs usually in early autumn (Cf. Fig. 9 in Einsle, 1968). Anyway, the bulk of cyclopoid biomass in summer was practically constituted of small individuals of *Mesocyclops leuckarti* since *C. vicinus* disappears from water column and remains in the sediment (Fig 8).

*Daphnia* individuals (predominantly *D. hyalina* egg-rich females) occur relatively sparsely in spring. These populations usually begin to increase short after the spring bloom. As soon as cyclopoids have disappeared, daphnids increase very rapidly forming the largest population build up of the year (Lampert, 1978; Geller, 1980). During this initial phase of the growing season, both *Daphnia* species are found in the upper meters of water column during the day and at night (Elster and Schwoerbel, 1970; Geller, 1986; Stich, 1989). In the present study, *Daphnia* biomass values higher than 12 gDW.m<sup>2</sup> were measured in the late spring maximum. However, this is a transitory event. In many temperate lakes, *Daphnia* populations usually suffer a abrupt breakdown soon after clear-water phase, presumably due to severe food shortage conditions (Threlkeld, 1979 and Wright and Shapiro, 1990). The pattern of food fluctuations during this time is highly variable and the zooplankton has to face unpredictable changes between hunger conditions and food levels just sufficient to avoid starvation (Geller, 1989). Geller (opt. cit.) also noticed that the females of both species allocate their reproductive efforts to fewer but bigger eggs in summer, giving their offspring a better survival chance under critical food availability conditions.

*D. galeata* usually reaches the highest annual maximum in June in Lake Constance. A second peak later on seems to be rather rare for this species (Einsle, 1988). *D. hyalina*, on the other hand, has a lower spring peak which is followed by other population pulses in summer and early autumn (Einsle, opt. cit.). The above mentioned seasonal events for the two *Daphnia* species were observed during both years (Fig 8) and they will be a key factor to explain the very different contributions of these species to overall grazing (Cf.

section 4.3). From June to the autumn, *D. hyalina*, bosminids and the copepod species show a marked diurnal vertical migration, while *D. galeata* never migrates (Geller, 1986). *D. hyalina* migrates between hypolimnion during the day and epilimnion at night crossing the thermocline twice a day, with amplitude of migration exceeding 30 m (Geller, 1986 and 1988). In winter, daphnid populations are formed by a reduced number of large females (Elster and Schwoerbel, 1970)

The predacious cladocerans *Leptodora kindtii* and *Bythotrephes longimanus* have their maximum in July or August (Elster and Schwoerbel, 1970). Einsle (1988) affirmed that there has been a population increase of these organisms in the course of eutrophication in Lake Constance (Obersee). The average population density of *Leptodora* doubled from 1962/1965 to 1970/1983 though their densities never surpassed  $10^5$  ind.m<sup>-2</sup>. Furthermore, he did not notice any clear seasonal tendency for these large cladocerans. In the present study, however, a seasonal trend could be observed in both years. The populations of *Bythotrephes* and *Leptodora* always peaked short after clear-water phase in June-July (Fig 8). The values for the summer maximum of predacious cladocerans pooled together fluctuated between 0.8-1.0 gDW.m<sup>-2</sup> but mean annual biomass values for both organisms pooled together was very low (0.2 gDWm<sup>-2</sup>).

#### 4.2.1.2 *Bosmina* and *E. gracilis*

In Lake Constance, there are two bosminid species : *Bosmina longirostris* and *Eubosmina longispina* (*B. coregoni*). They have remarkably variations in their seasonal cycles from one year to another (Einsle, 1988). Müller (1985), based in a long term study (1980-1982), found that the annual maximum for bosminids usually occurred in May-June in Überlingersee. These organisms also undergo vertical migration in Lake Constance (Geller, 1986). They migrate within the hypolimnion between 20 and 40 m in a way that their populations clustered below the daphnids at any time of the diurnal cycle. Nevertheless, no vertical separation between *B. coregoni* and *B. longirostris* could be detected (Geller, 1986 and Müller, 1985). The vertical separation of *Daphnia* and *Bosmina* populations has implications on the contribution of

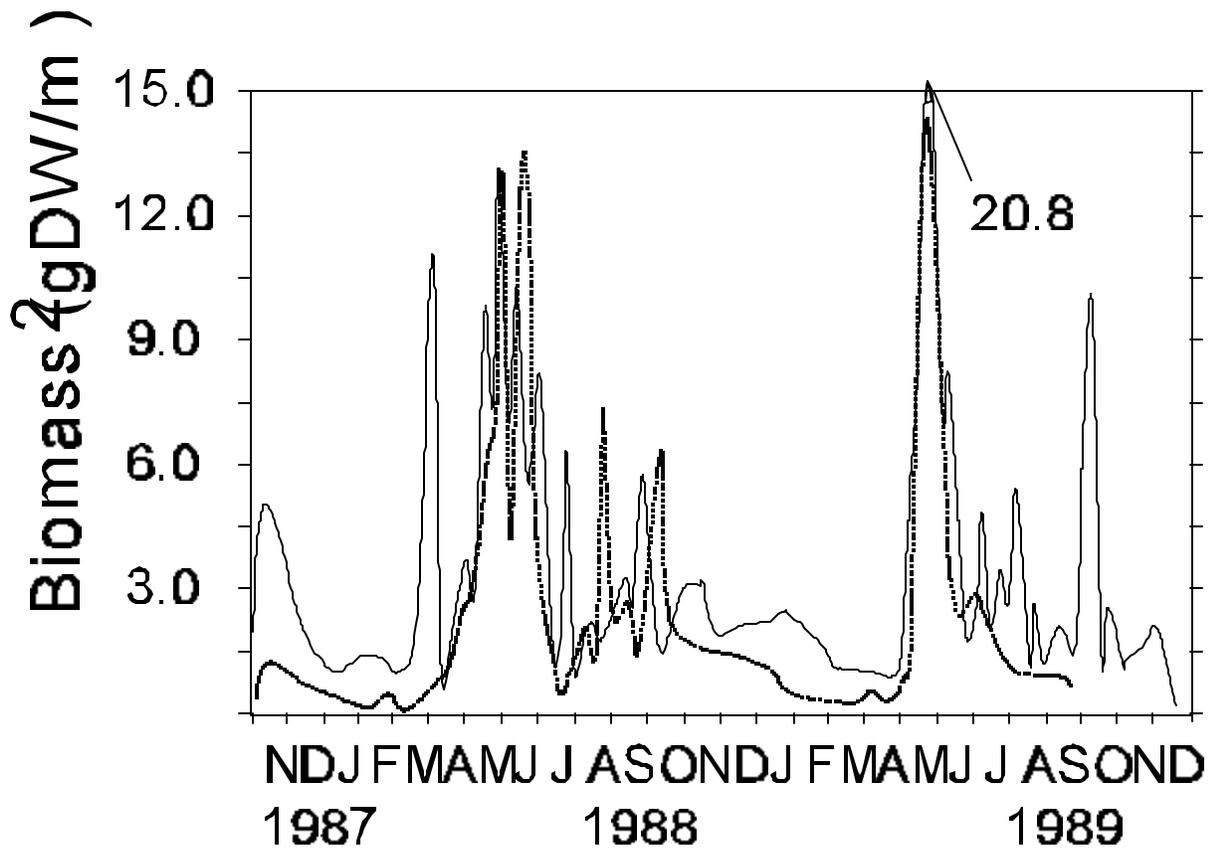
bosminids to overall grazing (Section 4.3) in a sense that their biomass maximum never coincided spatially with the highest grazing rates in the water column. Fig 8 shows that bosminids peaked in May during the years 1988 and 1989 in Überlingersee.

At least two population maxima for the calanoid *E. gracilis* usually occur in Lake Constance: in spring and summer (Geller, 1980; Einsle, 1988). An additional (but weaker) population pulse occurs sometimes in winter (Elster, 1954; see also Fig 8). In 1988, *E. gracilis* peaked in May, August and once again in December. In the next year, only the spring peak (May) was observed. The densities of the population of this copepod are predominantly regulated by food availability, predation of carnivorous cyclopoids and to a lesser degree, by the rate of reproduction (Elster, 1954 and Einsle, 1988). *E. gracilis* and bosminids had the lowest mean biomass values of all herbivores from mesozooplankton and, consequently, they contributed secondarily to overall mesozooplankton grazing (section 4.3).

#### 4.2.1.3 Comparison between two sampling techniques

A frequent question concerning seasonal variations of zooplankton is: to what extent do the numbers counted in the samples depict the real abundances of populations in the lake? Sampling and sub-sampling artifacts, counting procedures, patchiness of zooplankton, currents or other water movements like internal seiches can provoke significant discrepancies between different samples taken, for instance, with different sampling gears or in successive days.

Zooplankton samples were also taken routinely in L. Constance (Überlingersee) using the Clarke-Bumpus (C-B) sampler during the same period covered in the present study. Although the samples of these two data sets were obtained with different sampling gears and the C-B samples were usually taken the day before grazing experiments, a comparison between these data sets would be desirable since major deviations could be identified and included in the future generalisations from the conclusions of the present investigation.



**Figure 34** Seasonal course of biomass of mesozooplankton obtained with the Clarke-Bumpus sampler in vertical hauls covering 0-140 m (solid line) and with the grazing chamber (dotted line) at spot depths in the epilimnion (see Fig 4) of L. Constance.

Fig 34 compares the seasonal courses of zooplankton biomass obtained with the two sampling procedures. Although some differences can be observed (e.g. during spring of 1988 and some peaks in summer during both years), the two data sets revealed surprisingly similar trends. Differences up to factor 20 have been usually observed when two different samplers have been compared in the literature (De Bernardi, 1984). Here, it must be considered that not only different samplers were used, but also that the samples derived from grazing experiments were taken with at least 24 hs. later than those obtained with C-B sampler and these two series of samples were processed and counted by different personal at the laboratory.

The C-B data set had slightly higher values during periods of low zooplankton biomass like winter. Two reasons can explain the difference: a) the vertical haul of the Clarke-Bumpus sampler covered 0 - 140 m, whereas grazing experiments were rarely done in waters deeper than 30-35m; b) furthermore, as all towed plankton samplers, the C-B sampler concentrates the whole water column whereas the samples derived from the grazing chamber consisted of spots in different points through the water column (usually five or six spots in the 0-30 column). Therefore, it works like a plankton trap like the Schindler or Patalas trap. Zooplankton traps can underestimate vertically integrate samples in oligotrophic lakes or in periods of lower biomass, like during winter (De Bernardi, 1984). The differences observed in summer do not seem, however, to be related to underestimations due to the grazing chamber. In some occasions, higher values were observed with this chamber (summer 1988) and the C-B samples had higher values in other occasions (summer 1989). These deviations may be due to water movements and internal seiches, which probably induced day-to-day modifications in the composition and abundances of zooplankton. Gaedke and Schimmele (1991) have demonstrated that internal seiches can change the thickness of the warm and generally biologically rich epilimnion and, thus, also the areal abundance of planktonic organisms at a fixed sampling site. Seiches with amplitudes up to 12 m occur during the thermal stratification season with intervals ranging from 4 to 6 days in Überlingersee. Therefore, biomass differences would be expected to be found even in samples taken with the same sampler provided they were taken in successive days or even hours. Notwithstanding all these differences, Fig 34 shows that estimates of zooplankton biomass from both samples were well comparable. This is especially true when daphnids were abundant in the lake and, as will be discussed later, in times when the grazing activity was high.

#### 4.2.2 Microzooplankton

The microzooplankton has no taxonomic homogeneity. In this study, protozoans and a variety of metazoans were always present in very different abundances (Fig 9). Rotifers and naupliar instars of copepods were the major components of this fraction. Occasionally, protozoans were important (spring) but only those which resisted the sampling-fixation with formalin, such as tintinnids (they have a thick gelatinous layer), were usually counted. In late summer, the planktonic mollusca larvae (*Dreissena polymorpha*) were also relatively abundant.

Nauplii and young copepodites instars peaked twice in spring and during summer, though in the summer of 1989 they did not reach comparable biomass such as those observed in 1988 (Fig 9). Cyclopoids were by far the most abundant organisms since nauplii of calanoids were relatively rare. In April, most of the nauplii individuals belonged to *C. vicinus* and in summer almost all nauplii belonged to *M. leuckarti*. This agrees basically with the seasonal development of these copepods which was already extensively discussed in the latter section.

Although the species richness of rotifers in L. Constance surpasses 48 species, the numbers of total rotifers reflect frequently the densities of just two genera: *Polyarthra* and *Keratella* (Walz *et al.*, 1987). *Keratella spp.*, *Polyarthra spp.*, *Conochilus unicornis* and *Synchaetapectinata* were the most abundant rotifers during 1984 and 1985 in Überlingersee (Pauli, 1990). In the present study, the bulk of rotifer biomass (< 170 : m) was formed by six groups: *Polyarthra spp.*, *K. cochlearis*, *K. hiemalis/quadrata*, *Synchaeta sp.*, *Conochilus sp.* and a group of different species pooled together. The abundances of the first five groups, without exception, have increased one to two orders of magnitude in past thirty years, as a consequence of the eutrophication process verified in this lake (Walz *et al.*, 1987). The mean of total rotifer biomass increased since 1920's from 0.4 mgC.m<sup>-2</sup> to 138 mgC.m<sup>-2</sup> in 1977 in Obersee. In the present study, the mean total rotifer biomass was 203 mgDW.m<sup>-2</sup> for the period from November 1987 through September 1989 in the epilimnion (0-10 m) of Überlingersee (. 90-95 mgC.m<sup>-2</sup>).

*K. cochlearis* is one of the commonest members of the lake plankton in temperate regions (Hutchinson, 1967; Elliot, 1977). The population of this species in L. Constance begins to increase early in

spring, peaks before daphnids reach high densities and maintains relatively high biomass values during summer (Pauli, 1990). Individuals of this species concentrate near the surface and do not undergo any vertical migration. In Lake Erken (Sweden), the abundance of *K cochlearis* is strongly correlated with biomass of nanoplankton, especially *Rhodomonas minuta* v. *nannoplanctonica* (Nauwerck, 1963). Pourriot (1982) argued that this species, although preferring to ingest small particles (10-12: m), seems to have a diverse algal diet, being able to consume larger algal cells like *Cryptomonas* (16x48 : m).

*K. hiemalis* is one of the dominant rotifers during spring in L. Constance (Walz *et al.* 1987 and Pauli, 1990). In a similar way, I have found the highest densities for this species in May of 1988 and 1989 (Fig 9). The population maximum for this species is strongly correlated with the algal spring bloom and it seems to be an specialist in consuming *Stephanodiscus hantzschii* (Nauwerck, 1963).

In the taxonomic catalog of rotifers provided by Walz *et al.* (1987), several species of *Polyarthra* occur in L. Constance (mainly *P. dolichoptera*, *P. major* and *P. vulgaris*). They were considered as a unique group in this study. However, since every single individual was measured during counting, biomass estimates for this group could be done without large bias. The appearance of introgressive forms (e.g. *P. vulgaris* and *P. dolichoptera*) is a common characteristic in this genus and it makes sometimes very difficult sorting different specimens in preserved samples (Pejler, 1956). *P. vulgaris* occurs preferentially in summer, and, *P. dolichoptera* is a spring form (Elliot, 1977). The latter was probably the dominant *Polyarthra* during the spring maxima observed in 1989 (Fig 9). Walz *et al.* (1987) observed three to four population maxima for *Polyarthra spp.*: spring, one or two peaks in summer and one more during autumn. In each one of them, different species may be the dominant.

Excepting *S. pectinata*, all other *Synchaeta* species (e.g. *S. oblonga*, *S. truncata*) are winter-spring forms in Lake Erken, Sweden (Nauwerck, 1963). Walz *et al.* (1987) have observed, however, that *Synchaeta spp.* usually have an additional summer peak in Überlingersee but this does not occur in other parts of the lake. These organisms remain all the time near the surface due to a strong phototaxis behaviour (Nauwerck, 1963). As Walz *et al.* (1987) has already observed, I have also found two abundance maxima for *Synchaeta spp.*: spring and summer. A spring maximum, which occurred just before the maximum of

daphnids, has observed in both years and a second maximum was only noticed during summer of 1989 (Fig 9). Elliot (1977) noted that several *Synchaeta* species (*S. tremula*, *S. pectinata* and *S. oblonga*) also have their annual maximum in spring/early summer in Grasmere (English Lake District).

Both *Synchaeta* and *Polyarthra* have a virgate mastax (Koste, 1978). Rotifers with this kind of mastax have raptorial feeding habits which often means that they are omnivorous organisms ingesting small heterotrophs like protozoans, other rotifers as well as large algae (Hutchinson, 1967).

Two *Conochilus* species occur in L. Constance: *C. unicornis* and *C. uncinata* but the first one is more abundant (Walz *et al.* 1987, Pauli, 1990). These species (considered together in Fig 9) have built up a population maximum at the end of spring bloom or in summer, after biomass of daphnids had diminished. *C. unicornis* is eurytopic usually ingesting particles as small as 10 : m (Hutchinson, 1967). In other temperate lakes, they are present throughout the year (*C. unicornis*) in near surface layers. Nevertheless, a maximum can also be observed at the end of spring or at the beginning of the summer (Nauwerck, 1963, Elliot, 1977). Several other species are present in Lake Constance but their biomass is usually lower than those of the rotifers above mentioned.

The biomass of the next organisms (except *Filinia*) were grouped together as a single group in Fig 9. *Notholca* is cold stenothermic and usually has its annual maximum at the end of autumn or in December (Walz *et al.* 1987). *Kellicottia longispina* is a typical rotifer of the northern hemisphere (Margalef, 1983). It has two seasonal abundance pulses: a lower peak in spring and a second and more pronounced one during summer. *Pompholyx sulcata* lives in deeper layers (2-12 m) and its population maximum occurred between August and October. *Trichocerca* species are typical littoral forms (Koste, 1978) and usually warm-stenothermic (May, 1983), feeding on larger algae (Pourriot, 1977). Some species, however, like *T. capucina*, seem to be well adapted to pelagial waters, and peak in summer (Hutchinson, 1967). This species is present in L. Constance and it has a maximum at the end of the summer or during autumn. *T. pusilla* also occurs in Lake Constance and it has similar seasonal trends (Pauli, 1990). *Filinia longiseta* is a typical cold water adapted organism and it never occurs in high numbers (Pauli, 1990). This organism have been observed in the samples (though in low numbers) during all the winter and early spring.

The limiting factors for rotifers in most lakes are: water temperature, food quantity and quality, competition with other herbivores and predation (Walz *et al.* 1987). Several rotifers in this lake can be classified into cold- or warm-stenotherm species (Cf. Fig. 23.3 *in*: Pauli, 1990). Food quality is also an important factor, since most rotifers due, to different anatomic mandibular appendages, are food specialists (Pourriot 1977, Dumont 1977, Bodgan and Gilbert, 1982). Rotifers are also affected by competitive interactions with *Daphnia* and other herbivores (Gilbert, 1985; Schneider, 1990). Predation can also shape the seasonal abundance trends of many rotifers. *C. vicinus* and the predacious rotifer *Asplanchna priodonta* are the major predators in L. Constance and several rotifers like, *Keratella*, *Synchaeta* and *Polyarthra* are possibly under predatory pressure exerted by these organisms (Walz *et al.* , 1987). The highest predatory pressure usually occurs during spring and early summer, before *C. vicinus* migrate to the sediment and when *A. priodonta* reaches its annual maximum (Pauli, 1990). The possible influence of some of these factors controlling grazing rates of rotifers in this lake will be extensively discussed below (Cf section 4.3.3).



### 4.3 Basic attributes of zooplankton grazing in Lake Constance

#### 4.3.1 The importance of *Daphnia* and unimportance of copepods for community grazing

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 and Angeli, 1987; Balvay *et al.* 1990), L. Constance (Lampert, 1978; Lampert and Schober, 1978; Geller, 1980), Schöhsee (Lampert and 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 and Ponyi, 1986). This evaluation has been mostly done by comparisons of biomass of different zooplankton groups and CGR data (Lampert, 1988) or it is based on determinations of filtering rates of *Daphnia* and other species from laboratory experiments applied to variations of their biomass in the lake (Lampert and Schober, 1978).

Multivariate regression models have been applied to evaluate effects of body size or environmental variables such as water temperature and food concentration on the overall grazing (Gulati *et al.* 1982) or specific filtering rates measured *in situ* (Mourelatos and Lacroix, 1990) but no such model considering community feeding rates and biomass of daphnids at the species level is available for European lakes.

In L. Constance, Lampert and Schober (1978) estimated the population grazing rates of important herbivores during spring bloom and clear-water phase. They used filtering rates determined at the laboratory, such as those of *Daphnia pulex* determined by Geller (1975) and of *C. vicinus* measured by Schober (1980), combined with zooplankton abundance in the lake. They concluded that spring grazing of mesozooplankton was primarily controlled by the biomass of daphnids (Cf. Fig 5 *in*: Lampert and Schober, 1978).

The multivariate model presented in this study clearly confirmed the coupling effect between *Daphnia* biomass and overall grazing. The observed variation of CGR due to mesozooplankton was

primarily 'explained' by the variations of biomass of both *Daphnia* species. Further, this relationship was not only restricted to spring and early summer (Fig 12). The major discrepancy between the predictions made by Lampert and Schober (1978) and those presented in Tab 3 are related to the role of cyclopoids in the overall grazing. The model proposed by Lampert and Schober (1978) predicted that copepodites of *C. vicinus* would have the second highest contribution for spring zooplankton grazing after daphnids. This finding could not be confirmed by this investigation since the biomass of cyclopoids had a negligible effect on the community grazing and, thus, it did not reach the minimal requirements to be incorporated into the multivariate model. These deviations are partially explained by the specific filtering rates on which the different models are based on. Schober (1980) determined filtering rates of *C. vicinus* in the laboratory. These rates ranged between 4 and 30 mL.ind<sup>-1</sup>.day<sup>-1</sup>, for typical concentrations of spring bloom (POC = 1.17 mgC.L<sup>-1</sup>), using *S.hantzschii* as food. These values are clearly higher than the rates determined *in situ* for this species, provided in Figs 23 and 30 (range 0.1 - 2.0 mL.ind<sup>-1</sup>.day<sup>-1</sup>). This trend for lower field FR's remained unaffected even when other food particles were considered (Fig 30).

The lower R<sup>2</sup> for *D. galeata* (R<sup>2</sup>= 0.1984) does not mean that this species always plays a secondary role if compared with *D. hyalina* (R<sup>2</sup>=0.6709). The latter species probably had a greater R<sup>2</sup> 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 during the clear-water phase (Fig 7) when the highest CGR value in the annual succession was measured (Fig 10).

Lampert and Schober (1978) also maintained that the calanoid *E. gracilis* would play a minor role in the spring zooplankton grazing. This finding was confirmed by in the present study. Tab 3 shows that the partial R<sup>2</sup> of the calanoid *E. gracilis* was very low when compared with daphnids. This fact agrees with the seasonal biomass ratios of this calanoid and the two *Daphnia* species (Fig 8) and with the specific determinations of filtering rates for the calanoid (Figs 27 and 29).

The negative estimate for *Bosmina* probably reflects the finding that, although these organisms have seasonal maximum coinciding with daphnids, they live vertically separated. *Bosmina* avoids coexistence with *Daphnia* by living in deeper layers (Müller, 1985; Geller, 1986) in which lower CGR were usually observed.

Considering the basic model outputs, it may be summarised that the feeding activities of other herbivores of mesozooplankton are much less important than those due to daphnids. Recent studies in this lake (Müller, 1989; Weisse *et al.* 1990; Geller *et al.* 1991; Müller *et al.* 1991) have confirmed that microzooplankton or even smaller herbivores (e.g. protozoans) probably play the most important role in the overall grazing during the spring bloom and that this trend holds true as long as daphnids are not abundant.

#### 4.3.2 Grazing model and its verification

The use of multivariate linear models in field studies may be regarded with some caution. One of the basic assumptions of this method requires that the independent variables should not be autocorrelated with each other (Snedecor and Cochran, 1989). This criterion is very difficult to be met in environmental studies since a certain degree of autocorrelation is always present. Water temperature, for instance, may have some effect on phytoplankton growth, which influences biomass of zooplankton. Autocorrelation should increase the proportion of total variance explained by each variable and, hence, it overestimates the importance of independent variables (Peters and Downing, 1984). Nevertheless, many authors have successfully applied such multiple regression models in grazing studies provided that some cautions with data transformations are properly taken (Gulati *et al.* 1982; Peters and Downing, 1984; Knoechel and Holtby, 1986 a; see also section 2.6). In these models, body size, water temperature, food concentration have been widely used as independent variables and CGR or FR as the dependent variables. Considering these restrictions limiting the effectiveness of multivariate regression models in field studies, other independent methods had to be used in order to verify the basic model outputs. A frequent procedure is to compare the model's predicted values with the empiric values from particular situations like a subset of the whole data (Sokal and Rohlf, 1981). This comparison was done in Fig 13 using predicted and measured CGR for the depth of 6 m, day values, during the year 1988. In spite of minor differences, the predicted values clearly agreed with the measured values for this subset of CGR data.

Further evidence of the model's outcome was delivered by the comparison between community grazing (CGR) and population grazing (PGR) of both *Daphnia*. The plot (Fig 12) depicting the seasonal courses of PGR of *Daphnia* and CGR gave clear indications that *Daphnia* is the most important organism for mesozooplankton grazing in L. Constance. Additionally, it was also shown that *D. hyalina* has a more preponderant influence on community grazing if the time scale is considered because 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, the *Daphnia* 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 over- as well as underestimations. Knoechel and Holtby (1986 b) also 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: the 95 % C.I. around the mean for predicted PGR's of 10 % and 100 % day<sup>-1</sup> were about 10-13 and 90-125 % day<sup>-1</sup>, respectively.

*C. vicinus* develops considerable portions of spring zooplankton biomass but, it seems to feed on algae at very low rates under field conditions. Consequently a good question at this point would be: What are the major food resources for this species? Adults and older copepodites are carnivorous organisms (Einsle, 1967). Most Nauplii and small copepodites cyclopoids filter-feed inefficiently on small algae (Bogdan and Gilbert, 1984; Bogdan and Gilbert, 1987). The shift of food niches along the ontogenetic development was observed at the laboratory by Schober (1980) and could be confirmed in the field by this study (Fig 23). In both investigations, adults and older copepodites filtered at lower rates than did younger instars. Although the determinations of FR from Shober (1980) were always higher than my field determinations, the shape of the FR vs. Length curves were basically the same. Nevertheless, the experimental food types and maybe the duration of my experiments (. 13 min.) could probably not be adequate to measure their truly feeding rates and, hence, some underestimation may have occurred. Therefore, further research on grazing of these organisms are certainly required in this lake. In future studies, I would suggest the comparison of filtering rates obtained using the method adopted in this investigation simultaneously with short term variations of gut pigment-contents. This method has been widely used in feeding rates determinations of marine copepods (Dagg, 1983; Dagg and Walser, 1987; Simard *et al.* 1985; Bautista *et al.* 1988). These measurements require, however, time-consuming calibration procedures as well as hardware with great accuracy (Dagg, 1983).

#### 4.3.3 Impact of microzooplankton to overall grazing

Distinctive evaluations of the ecological significance of smaller herbivores for the whole zooplankton community have been done in the literature. Pace (1986) and Pace and Orcutt (1981), for example, affirmed that biomass and production of mesozooplankton are almost always higher than those of microzooplankton in many lakes, this trend being independent of lake trophy. Modern investigations conducted in L. Constance have demonstrated, however, that the above statement may not be applied for this lake. The role of microzooplankton within the zooplankton community has increased recently if comparisons among biomass and secondary production ratios between *Daphnia* and smaller herbivores, like rotifers, are made. Pauli (1990) affirmed: "The relative importance of rotifer biomass amounted to 19.1% and 13.6% of the *Daphnia* mean biomass, and to 25.8% and 22.5% of *Daphnia* productivity during 1984 and 1985 in L. Constance". Two years later, however, the mean daily productivities of pooled rotifers and both *Daphnia* species were 32 and 60 mgC.m<sup>-2</sup>.day<sup>-1</sup>, respectively (Geller *et al.* 1991). These values indicate that, during 1987, the average daily productivity of rotifers amounted up to 53 % of that of *Daphnia* in L. Constance. These authors affirmed that the microzooplankton (HNF, ciliates and rotifers) dominated the zooplankton community in terms of productivity during most phases of the growing season, reaching up to three quarters of total mean annual zooplankton productivity. The great relevance of microzooplankton for the plankton dynamics in L. Constance could be confirmed if grazing is included in the analysis. This contribution can be evaluated in two different ways. First, by comparing the CGR of both fractions along the seasons or considering them on annual basis. It was observed that, during some short periods (immediately before clear-water phase and in summer), microzooplankton grazing was comparable or even higher than grazing due to larger organisms. Additionally, the mean values of grazing rates in epilimnion (0-10m) of micro- and mesozooplankton were 58.1 and 136.3 mL.L<sup>-1</sup>.diel cycle<sup>-1</sup>, respectively (pooled data 88 and 89). This means that fraction 2 had a mean contribution of 30 % to the overall grazing in L. Constance. This contribution was more elevated if community ingestion rates are considered (33 %). Both estimates are based on diel cycles averaged over all experiments in which *Rhodomonas sp.* was used as food particle. These are certainly conservative estimates of the relative contribution of microzooplankton to overall grazing

because these percentages would be certainly higher if the trends found in the diurnal cycles of 1989 (higher  $CGR_2$  in the second night half) were included, and if the feeding rates were calculated for *S. hantzschii* as food particle. Finally, it may be observed that the term microzooplankton used in the present investigation does not include HNF and most ciliates. Müller *et al.* 1991 have demonstrated that the theoretic community grazing of all pelagic ciliates pooled together can reach up to 33 % vol. day<sup>-1</sup> during spring in L. Constance.

The second way to compare micro- and mesozooplankton grazing, and maybe a more interesting approach, would be the comparison of the biomass specific ingestion rates or  $I_b$ 's (Fig 11). It was demonstrated that microzooplankton had always higher values and this trend was unaffected by seasonal variations.  $I_b$ 's of mesozooplankton range usually between 0.2 and 1.3 : gC.: gDW<sup>-1</sup>.day<sup>-1</sup> in many lakes (Lampert, 1988) and the mean value found for mesozooplankton in L. Constance lies in the lower boundary of this range (mean  $I_b = 0.3$  : gC.: gDW<sup>-1</sup>.day<sup>-1</sup>). These rates for the smaller herbivores were higher by a factor of 5 (mean  $I_b = 1.5$  : gC.: gDW<sup>-1</sup>.day<sup>-1</sup>). Mazumder *et al.* (1990) found microzooplankton  $I_b$ 's up to 3.0 : gP/2500 : gFW.day in enclosures enriched with nitrogen and fish. This would mean a  $I_b$  of ca. 0.7 : gC.: gDW<sup>-1</sup>.day<sup>-1</sup> of microzooplankton (considering C:P= 40:1, FW:DW= 14:1 and DW:C=2:1). Similar values for  $I_b$  of microzooplankton were found in L. Constance during summer.

Higher  $I_b$ 's for smaller organisms do not necessarily contradict the size efficiency hypothesis (SHE), since many subdominant mesozooplankton taxa (i.e. cyclopoids) may contribute more to biomass than to community grazing rates (Pinto-Coelho, 1991). This theory (SEH) states that larger zooplankton organisms have higher efficiencies in removing food particles (Hall *et al.* 1976). Moreover, the higher feeding rates predicted by this theory are based on natural algal assemblages and not on grazing experiments using just one or few labelled algal particles. This discrepancy of  $I_b$  between the two fractions of zooplankton could be explained by the fact that smaller organisms have generally higher metabolic rates (Stein *et al.* 1988) and, as Dagg (1976) postulated, biomass specific ingestion rates should decrease with increasing body size in planktonic communities.

$I_b$ 's of microzooplankton were higher in spring than in summer (Fig 11). In a long term study (based

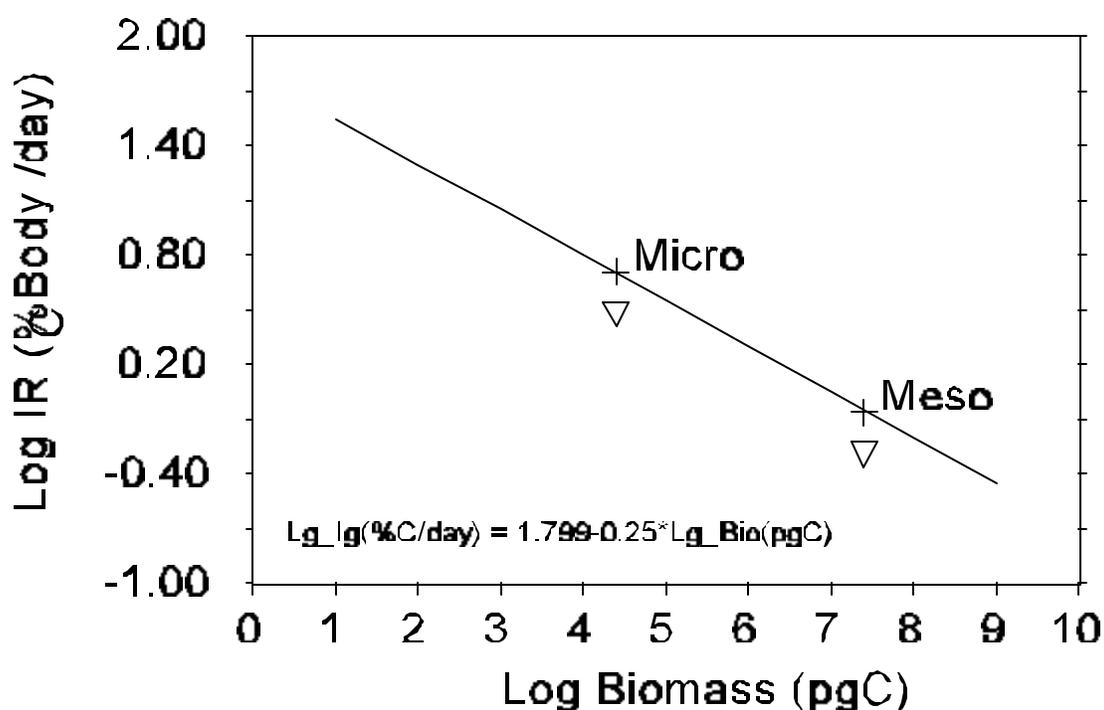
on 3-years) Müller *et al.* (1991) demonstrated that the highest biomass specific ingestion rates of ciliates in L. Constance were also consistently found in spring. During this time, a ciliate could ingest up to 152 % of its C-weight per day (Cf. Tab 4 in Müller *et al.*, 1991). This is even a conservative estimate of  $I_b$  for protozoa. Fenchel and Finlay (1983) reviewed the literature about respiration rates of free living protozoa. The respiration rates of these organisms ranged from 100 up to 2200 % C-weight.day<sup>-1</sup>. Nevertheless, higher winter or springtime  $I_b$ 's of small organisms should be regarded with some caution. During this time, biomass values may be somewhat underestimated due to methodological errors. First, the number of individuals in the samples was low (whole sample with less than 150 individuals) and, hence, the error of counting was higher than 20% (Prepas, 1984). Additionally, not all grazers were probably counted in those samples. Only protozoans with some protection (i.e. those with gelatin or lorica) such as tintinnids were satisfactory preserved with formalin. The lyophilization procedure used for preservation of samples for grazing determinations probably did not damaged soft organisms, like the majority of protozoans, and their feeding activities were probably partially detected but their biomass certainly not. Thus, overestimated  $I_b$

$$\log[\text{rate}] = a + b \log[\text{Mass}] \quad (11)$$

would appear during periods when biomass of protozoans was relatively high.

The discrepancy between  $I_b$ 's of the two size fractions of zooplankton could, however, be confirmed using another approach. General allometric equations (Eq 11) have been recently developed to compare rates of nutrient uptake, ingestion and respiration over a wide size range of planktonic organisms (Peters, 1983). These equations are simple linear regressions based on functional rates vs. biomass (both log transformed) and they have been fitted using data sets from freshwater as well marine environments (Banse, 1982; Peters, 1983). Banse (1982) demonstrated that the slope  $b$  of these regressions, in most cases, yield estimates between -0.24 and -0.26. I tried to compare the mean  $I_b$ 's obtained for both size fractions of zooplankton from L. Constance with the predicted values of this regression model since it summarises vast empirical evidences. A regression model developed specifically for filter feeders heterotrophs was used

(Moloney and Field, 1989). Before plotting the  $I_b$ 's found for zooplankton from L. Constance, they were transformed into percentages of ingested C-weight per day using a factor of 0.5 for the transformation DW:C for zooplankton (Berberovic, 1990). The transformed  $I_b$ 's had to be standardised to 20 °C, since the regression model was fitted for this temperature. A  $Q_{10}$  of 2.7 was considered (Ivleva, 1980; Lampert, 1984).



**Figure 35** Allometric model between C-weight and  $I_b$ 's of particular-feeding heterotrophs (from Moloney and Field, 1989). Crosses ( $Q_{10}=2.7$ ) and triangles ( $Q_{10}=1.0$ ) are mean  $I_b$ 's of zooplankton in L. Constance.

Fig 35 shows that the mean  $I_b$ 's calculated for both size fractions in L. Constance lie practically on the line containing the predicted values, if they are converted to the standard temperature of 20°C. Moloney and Field (1989) have also provided a plot containing a large number of empiric measurements jointly with

the regression. The untransformed  $I_b$ 's (triangles in Fig 35) are well within the range of experimental evidences provided by these authors (Cf. Fig. 2 *in*: Moloney and Field, 1989). They argued that the scatter about these regressions is frequently very high and they attributed it not only to methodological errors but also to the 'natural variability' of very different organisms that are normally considered in this kind of allometric comparisons.

#### 4.3.4 Seasonal regulation of microzooplankton grazing

The biomass maximum of microzooplankton was measured in both years short before clear-water phase (at the beginning of May). In spite of that, the highest community grazing rates of this fraction were found, in both years, later in summer. Why does microzooplankton not have a seasonal trend similar to mesozooplankton (simultaneous peaks for biomass and feeding rates)? At least four factors can potentially modulate grazing rates of microzooplankton: composition and concentration of food, composition of microzooplankton itself, and water temperature (Starkweather, 1980). Additionally, possible interactive effects with mesozooplankton should be also considered.

It is well known that the algal composition of spring bloom phytoplankton in L. Constance is mostly made up of highly palatable nanoplanktonic algae such as *Rhodomonas sp.* and *S. hantzschii* (Sommer, 1987 and see also Fig 6). In fact, due to highly favourable food conditions, there was a biomass-response of microzooplankton in spring (Fig 9). Also, we can exclude possible effects of food quality and quantity as limiting factors for feeding rates of microzooplankton during this time.

The community grazing rates of microzooplankton may also be affected by qualitative changes in its own array of species along the seasons. During the first biomass peak in May, this community was dominated by nauplii and by a simple array of rotifer populations. In summer, when the highest community feeding rates were measured, naupliar biomass was lower and the rotifer community had a more complex array of species. As already shown in the results (Tab 5), rotifers which dominated in summer had their biomass significantly correlated with  $CGR_2$  whereas cold-adapted species like *K.hiemalis* (biomass pooled together with *K.quadrata*) had no significant correlation coefficient with  $CGR_2$ . Thus, changes in the taxonomic structure have an effect on the quantitative response of microzooplankton grazing.

Although nauplii sometimes contribute notably to total biomass of microzooplankton, these organisms apparently played a secondary role in the overall microzooplankton grazing. The highest grazing rates of this fraction were measured during periods when nauplii were not so abundant in the lake (Cf. Figs 9 and 10). Not surprisingly, correlation coefficient among nauplii and  $CGR_2$  was also not significant (Tab 5) and, contrarily to rotifers, the biomass of these young larval copepods were excluded from the final equation in

the multivariate model (Tab 4). It should be noted, however, that the grazing rates of nauplii may be underestimated, due to the nature of feeding behaviour from these organisms and the method used to determine FR in this study (Cf. Sec 4.3.2).

At this point, we can reformulate the above question: Why the highest biomass of microzooplankton (though of spring-type) did not induce their maximal community grazing rates when there was plenty of good food? The two remaining reasons could explain this paradox: a) competition with larger zooplankton and b) water temperature.

*Daphnia* and rotifers have similar food niches and hence interspecific competition between them can occur. The size efficiency hypothesis (Hall *et al.* 1976) postulates that the bigger *Daphnia* would outcompete the smaller rotifers because they eat faster and more than the smaller rotifers. Furthermore, larger zooplankton should be better able to reproduce and store energy at low food concentration (Gilbert, 1985). In fact, there are experimental evidences of competitive advantage of daphnids: not only exploitative but also interference competition has been already observed between *Daphnia* and rotifers such as *Brachionus sp.* and *Keratella sp.* (Gilbert, 1985; Gilbert and Stemberger, 1985; Schneider, 1990). Also, as one would expect, the highest biomass of microzooplankton would be measured after the spring bloom (when there is plenty of suitable food) but before daphnids reached their biomass maximum. That is what I found in both years (Fig 9). CGR of microzooplankton also decreased when grazing rates of fraction 1 increased exponentially before clear-water phase (Fig 10). Unfortunately, no inverse correlation could be detected between daphnid biomass and CGR<sub>2</sub> over longer periods (Tab 5). I tried also including *Daphnia* biomass in the multivariate model of microzooplankton but the F-value was not significant.

Biomass of daphnids was never so high as around clear-water phase. The midsummer breakdown of *Daphnia* populations has already been observed in many lakes (Threlkeld, 1979 and 1985; Wright and Shapiro, 1990). Changing food conditions, increased temperature, vertebrate as well as invertebrate predation are some possible explanations for the phenomenon (Threlkeld, 1979). When daphnids were less abundant in summer, a second peak in the biomass of microzooplankton was observed and the highest grazing rates were measured for this fraction.

The next factor to be considered is water temperature. In May, when the first peak in the microzooplankton biomass was observed, surface water temperatures oscillated between 8 and 16 °C and in July-August between 16 and 23 °C (Fig 6). In spite of some cold-adapted rotifers, like *K. hiemalis*, which have their maxima earlier before clear-water phase (Pauli, 1990 and Walz *et al.* 1987. See also Fig. 9), reproductive and feeding rates of the majority of rotifers in this lake, like in many other freshwater systems, seem to respond positively to temperature (Edmondson, 1965 and Bogdan and Gilbert, 1982). The positive effect of the temperature on  $CGR_2$  was clearly demonstrated by the Pearson coefficients (Tab 5) and by the multivariate model (Tab 4). Only this factor accounted for 58% of the total variability of the community grazing rates of microzooplankton during 1988. Since no statistical evidence of *Daphnia*-rotifer interactions could be detected, it seems that water temperature may be the most important factor conditioning higher grazing rates of microzooplankton in L. Constance during summer.

#### 4.4 Diel rhythms of zooplankton feeding rates

##### 4.4.1 Mesozooplankton

Numerous diel rhythms have been described in aquatic animals and the diel vertical migration of fish and zooplankton is probably one of the most intensively studied circadian rhythms (Duval and Geen, 1976). In marine environments, this subject has been investigated mostly on calanoids, since the twenties (Marschall, 1924; Gauld, 1953). In freshwater ecosystems, diel rhythms of zooplankton grazing have been well documented in the laboratory (Starkweather, 1978, 1983) and in the field (Haney and Hall, 1975; Haney, 1985; Gawler and Angeli, 1987). Diel rhythms can affect filtering-, ingestion- and respiration rates of many freshwater organisms such as daphnids and calanoids (Duval and Green 1976; Hart, 1977; Haney 1985).

Although a clear seasonal component affected diel variations of mesozooplankton grazing, a trend for higher community grazing at night was almost always present in the experiments of 1988 (Fig 14) and 1989 (Fig 15). The differences between day and night increased from spring to summer and decreased again in late summer and autumn. An important issue at this point is to verify which effects individual variations on filtering rates have on diel rhythms of community grazing. Considering all experiments carried out in 1988 and 1989, no clear pattern indicating higher biomass specific grazing rates ( $G_b$ ) at night could be identified for mesozooplankton (Tabs 7 and 9). Day and night values were frequently near-equal or fluctuated irregularly and effects of enhanced filtering rates at night of some herbivores could be observed only in few cases like during the clear water-phase of 1989. As Geller *et al.* (1991) have already observed, diel fluctuations of individual filtering rates have little influence on community grazing of mesozooplankton and higher CGR's from night experiments were basically caused by biomass concentration near the surface.

Diel feeding patterns of zooplankton are not simple switching from day to night, but may involve fluctuations during the night (Haney, 1985). Duval and Geen (1976) have found that zooplankton community of Eunice Lake (British Columbia, Canada) has different respiration- and feeding rates during the night, with peaks just after sunset and before dawn. To investigate possible fluctuations of community grazing rates

during the night, four experiment series were carried out during 1989 covering four different periods along the diel cycle. Tab 8 shows the integral values for community grazing rates of mesozooplankton related to these experiments. Unlike microzooplankton, larger organisms had the highest grazing rates in experiments between 21:00 and 24:00 hs (excepting August). It will be discussed later (Cf. Section 4.5.2) that variations of filtering rates of some herbivores (e.g. *D. hyalina*) during the night can partially support these oscillations at night observed at the community level (mesozooplankton).

The remarkably similar vertical distributions of both grazer biomass and CGR along the diel cycles have been observed in other lakes (Gulati *et al.* 1982; Lampert and Taylor, 1985; Hart, 1986). Lampert and Taylor (1985) suggested that the relative unimportance of specific diel cycles at the community level would be caused by the rather small size of the local zooplankton. This is certainly not the case in the present study, since only organisms greater than 170  $\mu$ m were considered in the fraction called as mesozooplankton. Higher nocturnal filtering rates for the vertical migrators *D. hyalina*, *E. gracilis* and *Bosmina spp.* were already demonstrated for L. Constance (Pinto-Coelho, 1990 and Cf. with section 4.5.2). Furthermore, Fig 24 shows that higher FR's at night were also observed for *D. galeata* in some occasions. It seems, however, that the biomass contributions of other organisms such as cyclopoids (which migrate to the surface at night but do not affect CGR's) counterbalanced the enhanced night filtering rates of the above organisms. This would be especially evident in some occasions, like during the clear-water phase in 1988, when *Cyclops vicinus* and *Mesocyclops leuckarti* (Fig 8 and also Wöfl, 1990) were abundant in the lake.

#### 4.4.2 Microzooplankton

A different situation emerges when microzooplankton is considered. This is the first report about daily fluctuations on the grazing rates of microzooplankton measured under field conditions. Some researchers have indeed assumed that there are no diel variations in the clearance rates of important components of microzooplankton such as *Keratella* and *Polyarthra* (Bogdan and Gilbert, 1982 and Lampert and Taylor, 1985). It was clearly demonstrated that there was not only an increase in the community grazing rates of smaller zooplankton in the second half-night (Fig 17) but higher biomass specific grazing rates ( $G_b$ ) in this fraction were also measured just before dawn in all occasions without exceptions (Tab 9). This trend was clearer near surface waters and it indicates that diurnal rhythms of small organisms have probably a more dramatic effect than *D. hyalina* and other herbivores have on community grazing rates of mesozooplankton, since only the  $G_b$ 's of microzooplankton were affected by these fluctuations in a consistent trend. Rotifers probably play a major role in such diel rhythms since they dominated the biomass of microzooplankton in periods of greater diurnal amplitudes of  $G_b$ , like June and July of 1989 (Fig 9).

At the present moment, only speculative statements could be made suggesting possible explanations for such a phenomenon. Endogenous rhythms of phytoplankton could be an explanation. There was a slight but conspicuous increase in POC concentrations between 4:00 and 6:00 hs in all four diel cycles (Tab 10). Apparently, small organisms could have an adaptive advantage, if they could synchronize their feeding rhythms with the daily pattern of algae production in a effective way. This could be of relevance especially during food-shortage conditions which often occur in L. Constance during summer (Geller, 1986 and 1989). Unlike mesozooplankton, maximal grazing rates of microzooplankton did not occur in periods where the food availability was optimal (Cf. section 4.3.4).

#### 4.5 **Factors regulating specific filtering rates of major herbivores**

All physical and chemical factors which influence metabolic rates of any animal may be assumed to influence grazing rates of zooplankton (Peters, 1984). Body size (and different development instars), time of the day, food quality and concentration, water temperature were already in earlier investigations recognized as important factors regulating feeding rates of many zooplankters (e.g. Nauwerck, 1959; Rigler, 1961; McMahon and Rigler, 1963; McMahon, 1965; Burns, 1968 a, b and 1969; Kibby, 1971; Geller, 1975; Duval and Geen, 1976).

Another category of factors that should be considered are related to the experimental techniques. Crowding reduces the filtering rates of both copepods and cladocerans (Hargrave and Geen, 1970; Hayward and Gallup, 1976). Small experimental vessels also can originate a reduction of filtering rates of some calanoids (Corner *et al.* 1972), and recent studies have shown that copepod filtering rates can increase by an order of magnitude if vessels of several litres are used (Harris and Paffenhöffer, 1976 a; Harris and Paffenhöffer, 1976 b). Starvation may lead to rapid initial filtering rates (Geller, 1975). The age of the cell culture used in feeding experiments has been shown to influence zooplankton feeding behaviour (Ryther, 1954; McMahon and Rigler, 1963). Another important factor in experiments based on radioassays is the isotope loss in organisms preserved with formalin. These losses can produce severe underestimations of filtering rates (Berberovic and Pinto-Coelho, 1989).

In the present study, care was taken to minimize all possible influences of methodological artifacts. Our grazing chamber (10 L each half) was large enough to prevent overcrowding, the algal suspensions used in the experiments were prepared from stock cultures which were in the exponential growth-phase and animals were preserved using a new technique which minimized any loss of isotope (Cf. section 2.7).

##### 4.5.1 **Body size**

Maybe the best investigated factor affecting filtering rates of zooplankton herbivores in the field or

at the laboratory is body size (McMahon, 1965; Burns, 1968 a; Burns, 1969; Geller, 1975; Downing and Peters, 1980; Downing and Peters, 1981; De Mott, 1982; Chow-Fraser and Knoechel, 1985; Knoechel and Holtby, 1986-a; Knoechel and Holtby, 1986-b; Lampert, 1987; Mourelatos and Lacroix, 1990). In most models relating feeding rates to environmental variables, body size explains often the largest amounts of feeding rates variability (Peters and Downing, 1984; Chow-Fraser and Knoechel, 1985; Mourelatos and Lacroix, 1990).

Significative effects of body size on filtering rates were found in all herbivores considered in this study: *D. hyalina*, *D. galeata*, *E. gracilis*, *Bosmina spp.*, *M. leuckartii*, *C. vicinus*. The nature and the intensity of this relationship varies, however, strongly on what organism is considered.

Table 17

Effects of body size on filtering rates of *Daphnia*. Linear regressions (least squares model) were based on log:log transformed data. (L in mm and FR in mL.L<sup>-1</sup>.day<sup>-1</sup>).

Org.	pres. tech.	a	b	FR = a. L <sup>b</sup>	r	food type	food con.	wat. temp.	exp. type	time	ref
<i>D. pulex</i>	f	1.92	2.19	0.97	0.97	<i>Scenedesmus</i>	0.17	15	lab	day	1
<i>D. pulex</i>	f	8.64	2.35	0.94	0.94	<i>Scenedesmus</i>	1.62	15	lab	day	1
<i>D. pulex</i>	f	10.09	1.61	0.65	0.65	<i>Rhodotorula</i> <sub>2</sub>	-	24	field	day	
<i>D. catawba</i>	f	6.95	1.80	0.89	0.89	<i>Rhodotorula</i>	-	10	field	day	2
<i>D. galeata</i>	f	6.31	1.58	0.51	0.51	<i>Rhodotorula</i>	-	23	field	day	2
<i>D. rosea</i>	f	6.22	1.27	0.46	0.46	<i>Rhodotorula</i>	-	22	field	day	2
<i>D. rosea</i>	f	6.43	2.41	0.96	0.96	<i>Chlamydom.</i>	0.25	15	lab	day	3
<i>D. rosea</i>	f	5.83	2.74	0.96	0.96	<i>Aerobacter</i>	0.25	15	lab	day	3
<i>D. galeata</i>	l	4.54	2.86	0.82	0.82	<i>Rhodomonas</i>	0.15	11	field	day	4
<i>D. hyalina</i>	l	6.38	2.42	0.90	0.90	<i>Rhodomonas</i>	0.15	11	field	day	4

(1): Geller, 1975; (2): Haney (1985); (3): De Mott (1982); (4): present study; food concentration in mgC/L. f: animals preserved with formalin (4%); l: animals preserved with lyophilization procedure.

In daphnids, the relationship between individual filtering or ingestion rates and body size is usually determined by log:log regression and correlation analysis (Geller, 1975; Lampert, 1987). In most cases, the exponent (slope of the correlation) varies between 2 and 3. An increase of the filtering rate with the square of body length would be expected for a close proportionality to the area of filtering limbs. An increase according to the body weight would cause an exponent  $b$  closer to 2.5 (Bottrell *et al.* 1976). Tab 17 provides regressions coefficients for daphnids

obtained in field and at the laboratory under a wide range of conditions. Since most authors used only least square regressions (model I), only this model was considered. The exponents for *D. galeata* and *D. hyalina* found in Lake Constance usually remained between 2.3 and 3.0 (Tabs 11,14 and 15). Typical examples of FR of both daphnids of Lake Constance were somewhat higher than those found by Haney (1985) and Geller (1975). Two major reasons can explain these deviations: a) methodological features of each investigation and b) different food types.

The method to determine  $^{14}\text{C}$ -uptake in filter feeders has a well known drawback. A certain amount of incorporated  $^{14}\text{C}$  is always lost and the degree of these losses varies with the fixation procedure. The usual method for preservation of animals for radioassays has been fixation with formalin (see section 2.7). Berberovic and Pinto-Coelho (1989) have demonstrated that the lyophilization procedure adopted in this investigation greatly reduced the isotope loss. Thus, the filtering rates measured on formalin-fixed animals may have been underestimated.

The dissimilarities in the exponents  $b$  may also be related to different food types used in grazing experiments. Although it was shown in section 3.6.3 that daphnids ingest *Rhodomonas sp.* and *S.hantzschii* with relatively equal efficiencies, it may be possible that the same could not be applied when other food particles, such as the green algae *Scenedesmus*, the yeast *Rhodotorula* or the bacteria *Aerobacter* are considered. Besides food concentration and water temperature, Lampert (1987) affirmed that the exponent  $b$  can also be affected by food size. Knoechel and Holtbly (1986 b) found lower  $b$  values, for instance, when planktonic cladocerans (including *Daphnia*) were given bacteria or other very small particles. In their *in situ* measurements, the exponent  $b$  was 2.2 for the bacteria *Flavobacterium aquatile* (1.2 :  $\mu\text{m}$ , labelled with  $^{32}\text{P}$ ), 2.5 for intermediately sized yeast (6 :  $\mu\text{m}$ ) and 3.0 for *Pandorina sp.* colonies (15-28 :  $\mu\text{m}$ , labelled with  $^{14}\text{C}$ ).

Haney and Hall (1975) affirmed that the effect of body size on filtering rates varies along the diel cycle and stronger size-dependent FR relationships are expected to be found in the night. In Lake Constance, this tendency could not be observed since higher correlation coefficients for body size vs. FR at night were found only for *D. galeata* (June/1988) and *Bosmina*. However, the exponent  $b$  seems to be

affected in species which filter at higher rates at night. Higher estimates of  $b$  were found for *D. hyalina* and *Bosmina* in experiments conducted at night (See Tab 14 in section 3.6.2).

Table 18

Effects of body size on filtering rates of *Bosmina*. Least squares (model I) regression and correlation coefficients for body size (mm) vs. filtering rates, FR, in mL.day<sup>-1</sup>.

Org.	a	FR = b	a.L <sup>b</sup> r	Food type	place	rf
<i>Bosmina</i>	18.16	1.99	0.98	<i>Chlamydomonas</i>	laboratory	1
<i>Bosmina</i>	2.54	1.66	0.83	<i>Aerobacter</i>	laboratory	1
<i>Bosmina</i>	0.89	2.33	0.59	<i>Chlor.+Scened.</i>	Mt.-A Lake	2
<i>Bosmina</i>	0.90	2.69	0.63	<i>Chlor.+Scened.</i>	Brady Lake	2
<i>Bosmina</i>	28.97	2.61	0.87	<i>S.hantzschii</i>	L.Constance	3
<i>Bosmina</i>	8.43	2.54	0.76	<i>Rhodomonas</i>	L.Constance	3

references: (1) De Mott (1982); (2) Chow-Fraser & Knoechel (1985); (3) present study.

Just few models relating body size vs. filtering rates are available for *Bosmina*, since most authors have given only ranges for FR of bosminids (e.g. Bogdan and Gilbert, 1982). Some of these models are summarized in Tab 18. Chow-Fraser and Knoechel (1985) observed that FR's of single bosminids were too low (ca. 15 ingested cells during a grazing experiment) and, thus, these values would be close to the detection limits of radioassays. High isotope losses due to the preservation technique may again explain why it was very difficult to detect low FR in smaller organisms such as bosminids. The fit of FR vs. body size models would be severely restricted due to high coefficients of variation in individuals of similar size. The lower correlation coefficient (Tab 18) in the regressions found by Chow-Fraser and Knoechel (1985) may reflect this fact. In the present study, highly significant regressions between individual FR and body size of bosminids could be found. The predicted estimates for filtering rates of bosminids of L. Constance fed with *S.hantzschii* (e.g. L= 0.4 mm, FR= 2.65 mL.day<sup>-1</sup>) were similar to those found by De Mott (1982) for *Chlamydomonas* (e.g. L =0.4 mm, FR =2.93 mL.day<sup>-1</sup>). The model provided by Chow-Fraser and

Knoechel (1985) yielded lower FR values for bosminids.

In most studies on feeding rates of calanoids, no model relating body size and filtering rates is provided. Only adult females were taken into account in most models concerning feeding behaviour of calanoids (e.g. Richman *et al.* 1980; Vanderploeg *et al.* 1984). The basic difficulty here is that the easy-to-fit power function adopted for FR vs. Length in cladocerans does not work well for calanoids. In adults, sex of an individual or the number of eggs which a female is carrying may also influence filtering rates. Conover (1956) found that male calanoids graze more slowly than females. Egg-bearing *Diatomus* grazed faster than non-ovigerous females (Zankái and Ponyi, 1976). Thus, the function describing body size and FR in calanoid copepodites may not be the same for adults. For females, this relation can be satisfactorily described by a linear or just a constant function if food concentration is kept constant (Pinto-Coelho *et al.* 1988), whereas another function should be considered for younger development stages. These requirements were met using a quadratic function (Proc Nlin, SAS, 1988).

$$\begin{aligned} FR &= a + b \cdot \text{Length} + c \cdot \text{Length}^2 & \text{if } \text{Length} < L_0 \\ FR &= \text{Plateau} & \text{if } \text{Length} > L_0 \end{aligned} \quad (12)$$

Eq 12 describes the model. For values of length less than  $L_0$ , the equation relating FR and Length is quadratic (a parabola), and for values of length greater than  $L_0$ , the equation is constant (a horizontal line). The SAS procedure can fit such a function even when the joint point ( $L_0$ ) is unknown.

The filtering rates of the calanoid *E. gracilis* were described by this non-linear model fitted on empiric FR data (Fig 22). The comparison between the sum of squares of residuals and those due to the model give a measure of the model's goodness (Tab 12). The plateau values ( $= FR_{\max}$ ) for *E. gracilis* calculated with the model ranged between 1.29 and 5.06 mL.cop<sup>-1</sup>.day<sup>-1</sup> depending on what food particle or time of day was considered (Tab 12). These values agree well with other studies where FR of calanoids were determined *in situ*. The filtering rates of *E. gracilis* in Lake Balaton (Hungary) ranged between 0.01 and 3.27 mL.cop<sup>-1</sup>.day<sup>-1</sup> (Zankái and Ponyi, 1976) and between 0.25 and 2.8 mL.cop<sup>-1</sup>.day<sup>-1</sup> in Lake Erken (Nauwerck, 1963). Similar ranges for FR of this calanoid were found by Thompson *et al.* (1982) in the

British lake district. Haney and Hall (1975) observed that diel variations of FR for *Diaptomus pallidus* and *Diaptomus oregonensis* oscillated between 0.3 and 2.5 mL.ind<sup>-1</sup>.day<sup>-1</sup>. In the laboratory, adults of *E. gracilis* collected from L. Constance filtered at rates ranging from 2.4 to 7.2 mL.cop<sup>-1</sup>.day<sup>-1</sup> in food concentrations ranging from 25 to 320 : gC.L<sup>-1</sup> (Muck and Lampert, 1984).

Another descriptive function is required when cyclopoids are considered. The two most abundant cyclopoids in Lake Constance, *C. vicinus* and *M. leuckartii*, are organisms that switch their feeding habits along their ontogenetic development. Older copepodites and adults are omnivorous or carnivorous whereas younger copepodites and nauplii are filter-feeders (Einsle, 1967, 1968; Lampert and Schober, 1978; Schober, 1980). Consequently, body size vs. filtering rates should be negatively associated, at least between copepodites and adults. This complex feeding behaviour could be demonstrated for *C. vicinus* in the laboratory (Schober, 1980) and was confirmed in field incubations in L. Constance for this species and *M.leuckarti* in the present study. Filtering rates of cyclopoid copepodites were inversely correlated with body size and a negative power function could be effectively fitted. (Figs 22, 23 and Tab 13). Nauplii of *C. vicinus*, which are exclusively filter feeders, had their FR being affected positively by body size and this relationship was well described by a positive power function.

In any case, the maximum FR values of cyclopoids were very low (< 2.0 mL.ind<sup>-1</sup>.day<sup>-1</sup>) for both *C. vicinus* and *M.leuckarti*. This explains why cyclopoids played a negligible role in the multivariate model relating zooplankton biomass to overall zooplankton grazing (Cf. section 4.3.1). Low FR values of cyclopoids (algal food) have been found in other lakes, like L. Erken (Sweden), where *In situ* measurements of FR for *M.leuckarti* ranged between 0.15 and 0.9 mL.ind<sup>-1</sup>.day<sup>-1</sup> (Nauwerck, 1963).

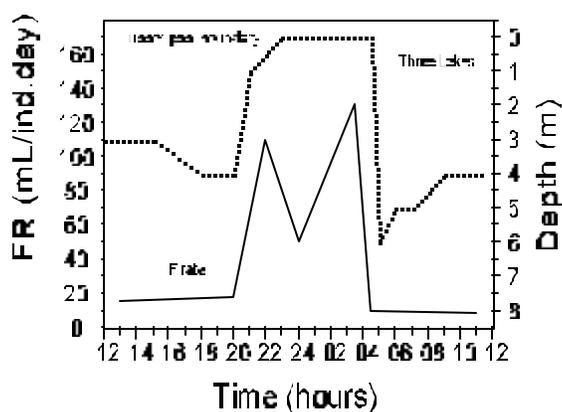
There are just few models in the literature relating body size to filtering rates of copepods (e.g. Lam and Frost, 1976). A possible reason for this shortcoming may be the distinct development of instars in the ontogeny of these organisms which often induce complex feeding behaviours. Another reason may be related to the fact that several specimens had to be sorted together for the radioactivity measurements in most studies in which FR measurements of slow filter-feeders like calanoids, cyclopoids or small cladocerans were conducted (e.g. Muck and Lampert, 1980; Schober, 1980; Knoechel and Holtbly, 1986 b). This drawback

was eliminated in the present study since all body size vs. FR relationships were based in individual measurements of filtering rates (Cf. section 2.7).

#### 4.5.2 Diel cycles in the filtering rates of planktonic crustaceans

Recent studies, some of them carried out under *in situ* conditions, have clearly demonstrated that diel rhythms are characteristic of freshwater zooplankton feeding. Haney and Hall (1975) observed consistently higher FR at night for all calanoids and daphnids in Three Lakes, Canada. Thompson *et al.* (1982) also measured higher night time filtering rates for *D. hyalina* and *E. gracilis* in two large experimental enclosures maintained in Blelham Tarn, Cumbria, UK. Starkweather (1983) investigated diel feeding cycles of *Daphnia* and other organisms of zooplankton. He found that higher FR at night are not exclusively found in daphnids and the existence of such rhythms can be demonstrated for several other cladocerans and copepods. Starkweather (1983) also compared the diel relative amplitude (night/day) of FR in many organisms. In numerous *Daphnia* species this amplitude oscillated between factor 1.5 and 3.0, excepted some extreme variations (amplitude of night/day up to factor 25.0) found by Haney and Hall (1975).

In Three Lakes, Canada, Haney and Hall (1975) observed that large *D. pulex* (2.0-2.3 mm) have a feeding pattern which is not simply switching from day to night, but may rather involve a



**Figure 36** Filtering rates of *Daphnia* in Three Lake (from Haney and Hall, 1975).

maxima shortly after sunset and just before dawn (Fig 36). Although higher FR values of daphnids in Three Lake are clearly associated with the onset of darkness and with diurnal vertical migration, Haney and Hall (1975) were unable, however, to explain what factors would trigger these two night FR-peaks. They investigated temperature and the quantity of filterable particles. These factors showed no apparent relationship to the observed fluctuations of FR.

In Lake Constance, *D. hyalina* filtered with higher intensity during the night, and the highest filtering rates were found just after sunset (Fig 25). However, only diel fluctuations of microzooplankton grazing seem to be associated to variations of food availability in this lake (section 4.4.2). No association could also be found between the higher FR's of *D. hyalina* during the first part of the night and parameters such as POC and water temperature. Therefore, the basic mechanisms regulating FR of daphnids during the night are still unknown, and this is certainly a question which demands further investigations.

The absence of diel cycles in some organisms may be as well of interest. Haney (1986) speculated that diel changes in FR should be found only in species that undergo diel vertical migration, since in the absence of other selective advantages of lower day activity (e.g. in deep layers, reduced visibility protects against predation and lower energetic costs are possible due to spending the day in colder waters), a non-migrating animal in the upper water could attain maximum ingestion by simply feeding at its highest possible rates during day and night. Haney (1986) affirmed: "Since the species here examined, at least at some time of the year, are known to migrate, this hypothesis remains untested".

Fig 24 shows that *D. galeata*, which usually does not undergo vertical migration in L. Constance (Geller, 1986; Stich, 1989), sometimes has slightly higher FR's at night but the diel amplitude of its feeding rhythms is not comparable with *D. hyalina*. Although diel variations were observed in *D. galeata* in some occasions, they were restricted to late spring and early summer. It is important to notice that during this time no DVM had begun in the lake. In summer, when *D. hyalina* was migrating, diel fluctuations in the FR were observed in the vertical migrator *D. hyalina* but not in individuals belonging to *D. galeata*. Moreover, the difference between day and night FR's of *D. galeata* becomes non-significant if all FR measurements of the experiments conducted in 1988 are pooled together (Pinto-Coelho, 1990) and, hence, the absence (or

weakness) of diel rhythms in FR's of *D. galeata* confirms the connection between diel rhythmicity of filtering rates and DVM of zooplankton.

In Lake Constance, *E. gracilis* filtered clearly higher amounts of water at night (Fig 27). However, diel rhythms in calanoid feeding seem not to be rather trivial since they have not been easily observed in freshwater ecosystems. Haney and Hall (1975) have noticed no significant differences at noon and midnight filtering rates of *Diaptomus pallidus* in their field experiments. Sometimes they found slightly higher mean FR for *Diaptomus spp.* at night. They argued, however, that this finding could only reflect an increased dominance of a species with greater filtering capacity (*D. oregonensis*) in the night samples. Duval and Geen (1976) have observed a very clear daily rhythm in the respiration rates of *Diaptomus kenai* in Eunice Lake (Canada) with the highest rates occurring shortly after sunset. Nevertheless, no data about specific feeding rates of this copepod was given by these authors. Zánkai and PONYI (1976) have intensively studied the seasonal changes of filtering rates of *E. gracilis* in Lake Balaton (Hungary). They related changes in the FR of this calanoid to oscillations in the food concentration and water temperature, but no commentary about possible diel rhythms was given. One of the few clear descriptions concerning feeding periodicity in freshwater calanoids was given by Hart (1977). He described a feeding rhythmicity along the diel cycle in the calanoid *Pseudodiaptomus hessei* (Mrázek) in the subtropical Lake Sibaya. Adult and older copepodites of this species are predominantly benthic during the day. At dusk, they migrate into pelagic waters, reaching then the highest filtering rates.

Although some diel rhythms in the feeding of calanoids have been successfully demonstrated in marine ecosystems (Duval and Geen, 1976; Simard *et al.* 1985; Bautista *et al.* 1988), other investigations have shown that such rhythms are not widely propagated in oceans, as well. As an example, Dagg and Walser (1987) could not individualize any diel rhythm in pigment gut content of *Neocalanus plumchrus* in the central subarctic Pacific Ocean.

### 4.5.3 Influence of temperature

The theoretical feeding response to temperature fluctuations could be described using a power function ( $Y=a.X^b$ ) where Y is the feeding response and X temperature, a and b are regression constants (Peters and Downing, 1984). If b is the slope of the regression coefficient between natural logarithm of FR

$$Q_{10} = e^{10 \cdot b} \quad (13)$$

and temperature, the Van't Hoff or the more familiar  $Q_{10}$  can be expressed:

The response of other ecophysiological functions to temperature such as respiration could also be described using this coefficient. 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). Lampert (1984) observed that  $Q_{10}$  values ranging from 1.5 to 5.6 have been found in the literature concerning zooplankton respiration rates but a  $Q_{10}$  near 2 has been considered appropriate in most cases. 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. It was already demonstrated that water temperature had a positive effect on CGR of both micro- and mesozooplankton, where the highest partial  $R^2$  was always achieved when temperatures were transformed to their square values. However, 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 CGR's or FR's measured under *in situ* conditions (Haney, 1973; Haney and Hall, 1975;

Downing and Peters, 1980; Thompson *et al.* 1982; Chow-Fraser and Knoechel, 1985). Others have mentioned the possible temperature effect or merely observed its indirect influences on feeding rates (Nauwerck, 1963; Lampert and Taylor, 1985). Temperature effects on field estimates of FR's and CGR's have been statistically demonstrated in only a few cases (Zánkai and Panyi, 1976; Gulati *et al.* 1982; Bodgan and Gilbert, 1982 and Mourelatos and Lacroix, 1990). The temperature ranges, over which measurable effects on FR's occurred, 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 Lake Constance, 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 6, 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 and 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, respectively) and organisms from the colder hypolimnion (36-50 m) filtered at significant 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).

#### 4.5.4 Food Selectivity in *Daphnia*, *Bosmina* and *E. gracilis*

Since the nutritional value of a food item is the result of several properties (ingestibility, assimilability, biochemical composition), only growth experiments can provide information on the ultimate utilization of a given food (Lampert, 1987). This means, for example, that different growth responses can be induced by two algae which are ingested with the same efficiencies provided they have different biochemical properties. In this section, only differences in the ingestibility of different food items will be briefly discussed since growth

experiments stay beyond the scope of this investigation.

Filtering rates of daphnids can be affected strongly when different food particles are offered but most of the selective feeding of *Daphnia*, however, is related to geometric features of the food (Burns, 1968 a). Since nanoplanktonic algae are the principal component of *Daphnia*'s natural food, most of the differential ingestibility that have been observed in daphnids were obtained when algae belonging to other size classes of plankton (i.e. larger than nanoplankton) are offered as food particle (Knisely and Geller, 1986; Lampert, 1987). It is well known, for instance, that some bacteria, filaments or colonies of blue greens or even gelatinous green algae can induce higher rejection rates and, thus, lower feeding rates (Porter, 1973 1975 and 1976; Ganf, 1983; Lampert, 1981). Anyway, these large filter-feeders can not exhibit such elaborate selective feeding such as those found in smaller cladocerans and raptorial copepods (see below). Considering these facts, one would expect minimal differences in the filtering rates of daphnids, when two small (<10:  $\mu$ m), easily assimilated (Giani, 1991) food particles were simultaneously offered under the same experimental conditions. As expected, *D. galeata* had similar body size vs. FR relationships when *Rhodomonas sp.* and *S.hantzschii* were offered as algal food under the same *in situ* conditions in Lake Constance (Fig 28). The same applied for the other *Daphnia* of this lake: *D. hyalina*. Other studies have also indicated that selective feeding behaviour of *Daphnia* is usually very restricted when different food particles from nanoplankton are compared (De Mott, 1982).

Is *Bosmina* simply a scale-down version of *Daphnia*? To answer this question, *in situ* feeding rates of bosminids were measured using the two algae above cited. These experiments revealed major differences in the feeding behaviour of bosminids (Fig 29). These small cladocerans fed highly selective and preferred the small centric diatom *S.hantzschii*. Tab 15 illustrates that the selective feeding in *Bosmina* could be statistically demonstrated. These results confirm earlier studies where *B. coregoni* preferred the smallest food particles (Gliwicz, 1977) but contrast with more recent studies in which *Bosmina* fed preferentially on flagellate *Chlamydomonas* when these motile cells were paired in a grazing chamber with aflagellate *Chlamydomonas*, *Chlorella* or yeast cells (De Mott, 1982; Bogdan and Gilbert, 1982). In all cases, *Bosmina* feeding rates seem to be affected by factors other than particle size, contrasting to most *Daphnia*

species (De Mott, 1982).

Copepods have a repertoire of actions associated with feeding: they can create scanning currents, fling and close their second maxillae to grasp large food particles individually, or they repeatedly flap this appendage to feed on small particles (Koehl, 1984). Thus, copepods are expected to have highly selectively feeding. This selectivity is not only based on food size (Gauld, 1953; Harris, 1982; Paffenhöfer, 1984) but also on food shape (Richman *et al.* 1980). Copepods may even respond to chemical cues of approaching food particles (Paffenhöfer *et al.* 1982). An actual controversy in the literature is whether copepod selectivity is due to physical properties of the animals' food-capturing sieves, or rather is due to active choice. Kerfoot (1980) referred to this controversy as "the copepod filter-feeding controversy".

In Lake Constance, *E. gracilis* showed food preferences that may be related to the different sizes of the food items that were used in the grazing experiments. *E. gracilis* had higher filtering rates when fed on *Rhodomonas* (Fig 29). Paffenhöfer (1984) demonstrated that calanoid copepods always removed algae larger than 10 : m at much higher rates than cells < 6 : m when both sizes of cells are equally abundant. The linear dimensions of *S.hantzschii* (diameter) and *Rhodomonas* (length) cultures used in our experiments were 5.6 : m and 12.5 : m, respectively and, thus, these algae belong to size categories that are probably grazed by most copepods with different efficiencies.

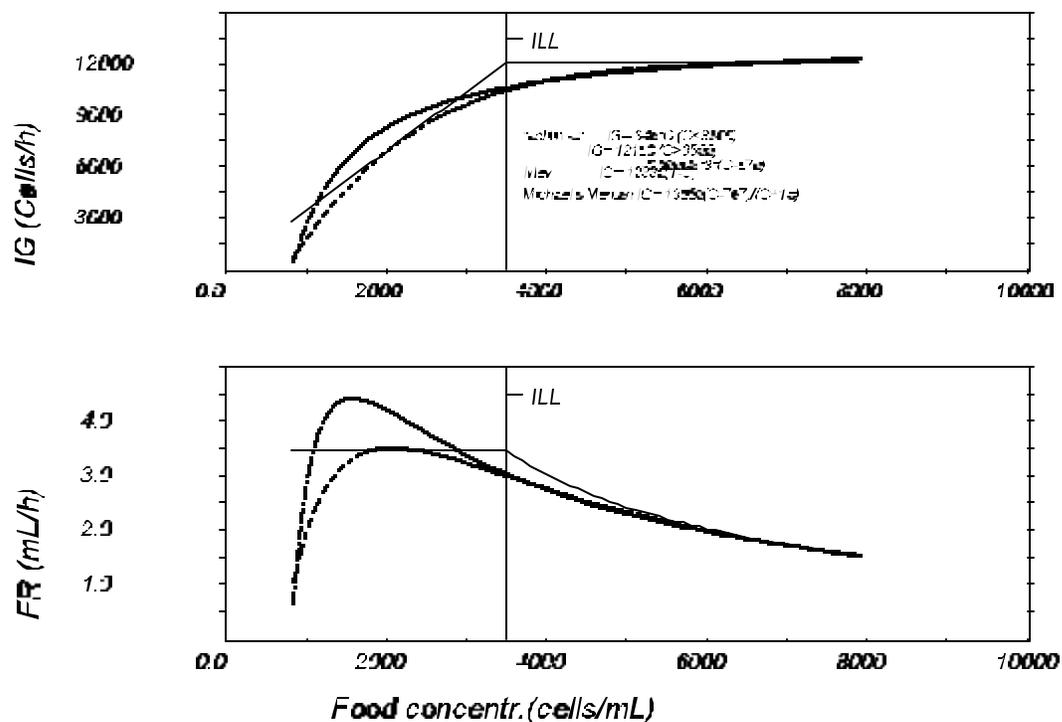
#### 4.5.5 Food concentration and *in situ* filtering rates of *Daphnia*

The effect of food concentration was analyzed in *D. galeata* and *D. hyalina* populations which were restricted to epilimnetic (0-6 m) waters. This was done to avoid possible interactions with great temperature gradients which were always present in deeper layers. Further, the greatest fluctuation in food concentration was found in the epilimnion (Fig. 6). In order to eliminate effects of diel rhythms, only night measurements were considered for *D. hyalina*.

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 above 18 °C. 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 6). In the second data set, animals were collected under 'typical' summer food conditions (see Tab 16). In spite of great differences observed in the food concentrations between the two *D. galeata* data sets (0.22 and 0.45 mgC. 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 31 (bottom) that there was a large number of small individuals (smaller than 0.9mm) 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 mgC.L<sup>-1</sup> and chlorophyll-a 1.2 : g.L<sup>-1</sup>. Later, in October, POC was somewhat higher (0.44 mgC.L<sup>-1</sup>) and chlorophyll much higher (5.0 : g.L<sup>-1</sup>). As expected, the FR's were significantly higher in June. However, these differences in FR's might not be due only to food concentration. Very different phytoplankton compositions (dominance of poorly-edible algal populations during the 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* (Lampert, 1987).



**Figure 37** Effects of food concentration on feeding rates of zooplankton. Panel modified from Mullin et al (1975). All three models are equally good to describe the data (Peters,1984).

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 limiting food level (ILL), the filtering rates of daphnids decrease and the ingestion rates (IG) remain constant. Fig 37 illustrates three different models

describing this relationship: the rectilinear model, which implies a constant FR below the ILL and constant IG above the food level. Two curvilinear models are also provided : the Ivlev and the Michaelis-Menten. Porter *et al.* (1982) fitted other non-linear models (e.g. power function) but no author was able so far to identify which model would be the best (e.g. Mullin *et al.* 1975; Porter *et al.* 1982 and Harris and Paffenhöfer, 1976).

Daphnids (e.g. *Daphnia magna*) have ILL levels up to 0.2 mgC.L<sup>-1</sup> (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 mgC.L<sup>-1</sup>. Additionally, it was also postulated that POC concentrations between 0.20-0.25 mgC.L<sup>-1</sup> 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 mgC.L<sup>-1</sup> 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 (0.25-0.50 mgC.L<sup>-1</sup>) was convenient for investigating the effect different food levels has on individual filtering rates of *Daphnia*.

Another point to consider is that food concentrations have different effects on filtering rates of different zooplankton species. Calanoids respond to oscillations in food concentrations with less sensitivity than do cladocerans (Muck and Lampert, 1984; Peters, 1984). The relationship between FR and food concentration was expected to be clearer in *D. galeata* because this species does not undergo any extended vertical migration in L. Constance (Geller, 1986; Stich, 1989), thus avoiding possible overlapping temperature effects. Moreover, the threshold food level of *D. galeata* indicates that this species would be more sensitive than *D. hyalina* to food availability in the lake. This food level, which is the lowest food requirement for maintenance of a certain population (Lampert, 1977), is higher for *D. galeata* (0.60 mg DW.L<sup>-1</sup> vs. 0.40 mg DW.L<sup>-1</sup> of edible food for *D. hyalina*, values from Geller, 1985), and it 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*.

#### 4.5.6 FR vs. body-size regressions of cladocerans: Comparison of models I

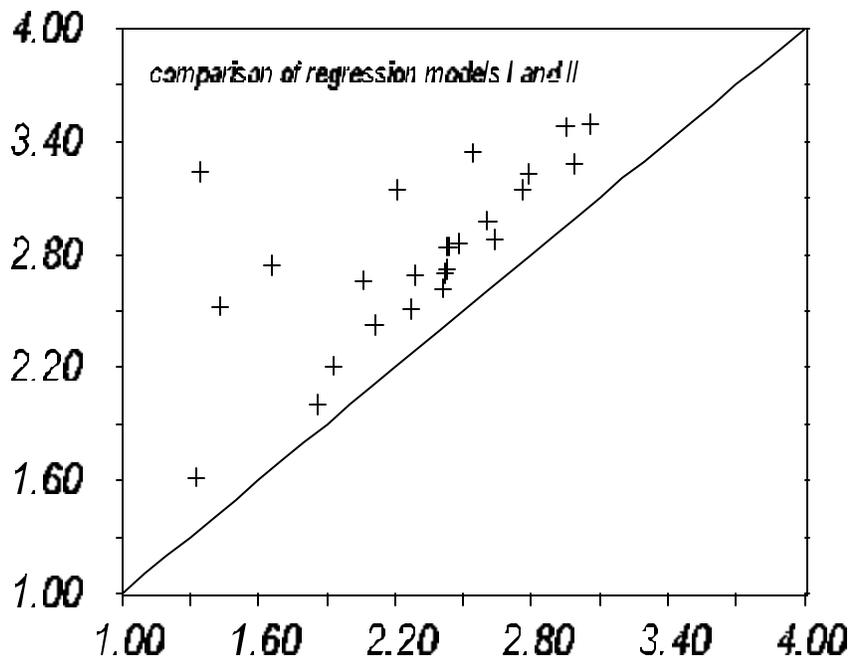
## and II

The estimates of the exponent  $b$  obtained with the geometric means (regression model II) were always higher than those generated by least squares method or model I (Tab 19). Nevertheless, the higher  $b$  values of model II agree well with other estimates also based on this regression model. Knoechel and Holtby (1986 b) obtained exponents ranging from 2.3 to 3.1 using model II for *in situ* filtering rates of cladocerans in Lake St. George, Canada. Chow-Fraser and 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.

Table 19

Comparison of the exponent  $b$  generated by two regression models relating filtering rates of cladocerans (FR in  $\text{mL}\cdot\text{ind}^{-1}\cdot\text{day}^{-1}$ ) and body size (L in mm) in the equation  $\text{FR} = a\cdot L^b$ . Model I: least square; Model II: geometric means.

	n	exponent b		range
		mean	sd	
model I	25	2.30	0.49	1.33-3.06
model II	25	2.81	0.45	1.62-3.49



**Figure 38** Comparison of the exponent 'b' in the equation relating filtering rates to body size of cladocerans ( $FR = a.L^b$ ), as calculated using regression Model I: x-axis and Model II: y-axis. See text for other details.

Although model II estimates of the exponent  $b$  were usually higher than least square  $b$  values (model I) for regressions run for the same data set, there was a good proportionality between  $b$  estimates calculated using these models (Fig 38). In some cases, however, a discrepancy between the two models can be observed. An example would be the regression of *D. hyalina* in Tab 16 (13.67 °C, 0.44 mgC.L<sup>-1</sup>, n=119,  $r=0.4141$ ), where models I and II yielded exponents  $b$  of 1.34 and 3.24, respectively. The correlation coefficient, however, is an important parameter modulating the difference between the  $b$ -estimates generated by the two regression models since the slopes of both models converge as the correlation coefficient ( $r$ ) approximates 1.0 (Knoechel and Holtby, 1986 b). Therefore, the importance of adopting model I or II is inversely proportional to the degree of correlation in the regressions relating FR vs. body size of cladocerans.



#### 4.6 Impact of zooplankton grazing on carbon-balance in the pelagial of L. Constance

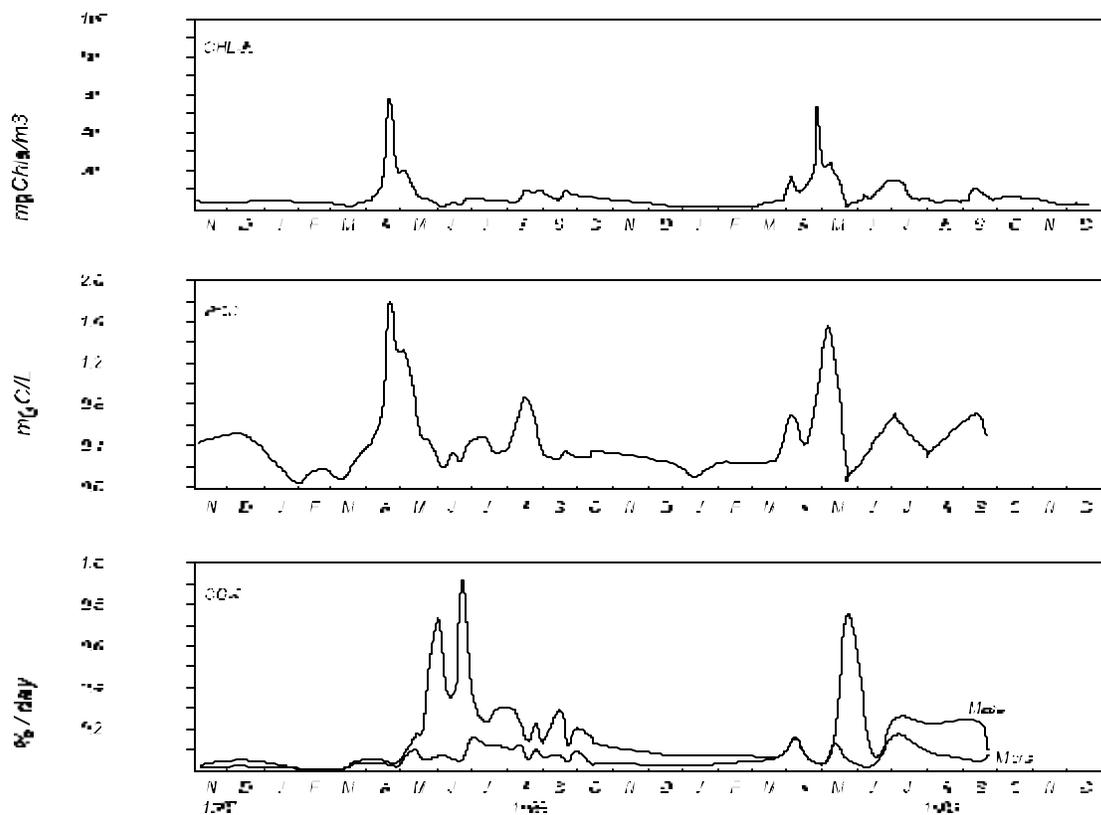
Tab 20 shows that *in situ* community grazing measurements from recent investigations have revealed that zooplankton can exert considerable pressure on the phytoplankton populations. Lampert (1988) affirmed that pelagic herbivores would be the major factor controlling losses of phytoplankton whenever its

Table 20

Maximum community grazing rates (CGR in % per day) in different lakes. Estimates based on *in situ* studies.

Lake	Year	Maximum CGR % day <sup>-1</sup>	Source
Hart Lake	1968	180	Haney & Hall, 1975
	1969	310	
Blelhem Tarn	1978	120	Thompson et al., 1982
L. Vechten	1974	40	Gulati et al., 1982
	1978	60	
L. le Roux	1983	70	Hart, 1986
Schöhsee	1983	170	Lampert & Taylor, 1985
L. Geneva	1985	175	Gawler & Angeli, 1987
L. Constance	1988	101	this study
	1989	171	

concentrations surpasses a 'critical' level. Although these levels tend to increase with lake trophy, most lakes have 'critical' values ranging between 1.5 and 4.0 gDW.m<sup>2</sup> of zooplankton biomass.



**Figure 39** Chlorophyll-a and POC (<50 :m) at 2m. Diel averages of size fractionated CGR in the epilimnion (0-10 m) of Lake Constance (Überlingersee) during 1988 and 1989.

As Hart (1986) suggested, zooplankton grazing activities can vary over several orders of magnitude within and between systems. This fact is well illustrated in Fig 39 for Lake Constance.

The figure also shows the clear inverse seasonal relationship between zooplankton grazing and concentration of food particles (POC and Chlorophyll-a) in Überlingersee and suggests that zooplankton potentially can exert considerable influence on the local algal assemblage.

The objective of this section is to evaluate zooplankton grazing as a loss factor for the phytoplankton along the seasonal succession. This will be achieved comparing carbon-intake of zooplankton (based on POC values) and C-assimilation of phytoplankton at different times of the year. Since the C-budget will be based on C-mass units, it is very important to notice that, notwithstanding some minor differences during the summer (Cf section 3.1), the seasonal courses of POC and Chlorophyll-a are very similar (especially between spring bloom and clear-water phase) in this lake. The POC values will be required to transform CGR into CIR. The carbon intake (CIR) by grazers can be obtained by multiplying the measured community grazing rate (CGR) by ambient seston carbon (POC) concentrations, on the assumption that all particles in the given volume of water filtered by animals are equally ingested. This assumption may be wrong, since zooplankton is capable to feed very selectively (Hart, 1986). Therefore, other ways must be found to validate this carbon intake by the zooplankton. The issue can be also approached by calculating the C-demand of zooplankton estimated as a fixed fraction of body C-content per day. If the C-demand is higher than C-intake over longer periods the zooplankton must be consuming food resources other than those embraced by the POC measurements. The C-demand is calculated by multiplying the C-zooplankton biomass by a factor which estimates the energetic requirements of zooplankton expressed as percentages of C-weight per day.

Zooplankton has many different size and taxonomic categories and, hence, different energetic requirements should be considered depending on the qualitative composition of zooplankton on a given date.

Table 21

Respiration rates and energetic requirements of some zooplankton organisms in temperatures ranging from 18 to 23 °C.

Organism	Resp. % C-W day <sup>-1</sup>	Req. %C-W day <sup>-1</sup>
<i>Brachionus</i>	28-60 (L)	112-240
<i>Daphnia</i>	13-25 (L)	52-100
<i>Cyclops</i>	35-38 (L)	140-152
<i>Diaptomus</i>	20-68 (L)	80-272
Protozoa	211-2200 (F)	840-8800

L: Lampert (1984); F: Fenchel and Finlay (1983).  $C_{Req} = 4 * C_{Resp}$ .

Tab 21 gives some values for daily ratios for different groups of zooplankton from recent literature reviews. For larger organisms of zooplankton, respiration rates vary between 13 and 68 % depending on the taxonomic group and temperature conditions (Lampert, 1984). Additionally, the daily energetic ratios for mesozooplankton would range between 52 and 272 % of C-Weight, considering that a certain association of zooplankton can ingest up to four times their daily C-depletion due to respiration. Tab 21 also shows that smaller organisms such as rotifers and unicellular heterotrophs have usually higher C-requirements than mesozooplankton. Protozoans, for instance, can have respiration rates as high as 92 % C-W.hour<sup>-1</sup> (. 2200 % C-W.day<sup>-1</sup>). Therefore, these relatively large ranges must be taken into account when zooplankton is considered as a unitary group.

The C-intake should be theoretically higher than C-demand for most parts of the year if POC

Table 22

Estimates of carbon intake by zooplankton assuming the unselective ingestion of all particles (particles < 50 µm), or as daily ration derived from daily carbon requirements of zooplankton in epilimnion (0-10 m) of Lake Constance (Überlingersee).

Date	biomass mgDW/m <sup>2</sup>	CGR L/m <sup>2</sup> .dc	P1/P2	CIR mgC/m <sup>2</sup> .dc	P1/P2	Energ. Requirements		
						60%	150%	300%
20/Apr/88	845	436	0.45	497	0.50	228	570	1141
18/May/88	3174	1714	2.62	846	2.79	856	2142	4285
08/Jun/88	3038	7668	7.60	1993	9.27	820	2051	4101
13/Jul/88	1028	2729	1.35	1135	1.42	277	694	1388
24/Aug/88	707	2407	1.35	1459	1.50	191	477	954
28/Sep/88	994	2738	1.87	910	2.04	268	671	1342
19/Oct/88	963	1686	3.99	696	2.11	260	650	1300
23/May/89	6499	9481	17.39	1474	17.57	1755	4387	8774
13/Jun/89	564	1142	4.38	402	4.51	152	381	761
04/Jul/89	800	3336	0.65	1793	0.61	216	540	1080
01/Aug/89	1092	2382	1.33	671	1.34	295	737	1474

Obs P1: mesozooplankton; P2: microzooplankton; P1/P2 size-fraction ratios; dc: averages over diel cycle.

concentrations reflect the food available for the zooplankton and if CGR measurements were made properly. Tab 22, shows the estimates of diel community ingestion rates (CIR) and C-requirements for zooplankton in L. Constance in day/night experiments carried out in 1988 and 1989. Considering the values given in Tab 21, three different estimates for C-requirements were considered : 60, 150 and 300 % of C-body weight per day. Requirements ranging between the two lower estimates may be appropriate for periods when mesozooplankton grazing was dominant

and ranges limited by the two higher may be appropriated for early spring or mid-summer, periods when grazing of protozoans or microzooplankton was relatively more important (Fig 36). Tab 22 shows that CIR and C-requirements had the same order of magnitude in all occasions and C-intake (CIR) values were almost always higher than the lowest daily C-requirement (60 %). As expected, CIR did not offset the lowest C-demand during the clear-water phase, when zooplankton was probably consuming all the available food in the epilimnion (0-10 m). During summer (like in August 1988 or July 1989), when the importance of microzooplankton was more evident (lower P1/P2 ratios), CIR's were even higher than the highest C-demand (300 %). Also, it seems that estimates of C-intake derived from POC-values are compatible with the energetic requirements of zooplankton and the seston < 50 : m is the most important food resource for the herbivores in the epilimnetic zone (0-10 m) of this lake. Since POC and Chlorophyll-a have similar seasonal courses and they basically reflect phytoplankton biomass, the comparison between POC derived CIR's and C-assimilation of phytoplankton can be done on a realistic base.

Tab 23 compares carbon intake of zooplankton (CIR) with primary production in L. Constance. It may be concluded, by inspecting this table, that the most important loss factor for the phytoplankton is the

Table 23

Relative significance of zooplankton grazing as loss factor for the phytoplankton community during spring bloom, clear-water phase, summer and during the autumnal phytoplankton maximum in Lake Constance.

Date	PP mg.C.m-2.day-1	CIR	CIR/PP %
19-20/Apr/88	3658	497	7.3
17-18/May/88	1037	846	81.6
07-08/Jun/88	154	1993	1294.7*
13-14/Jul/88	1392	1135	81.5
24-30/Aug/88	1117	1459	130.6
27-28/Sep/88	864	910	105.6
18-19/Oct/88	642	696	108.4
23-24/May/89	359	1474	410.6*
13-14/Jun/89	2020	402	19.9
04-05/Jul/89	1041	1793	172.2
01-02/Aug/89	649	671	103.4

\* clear water phase

zooplankton. Earlier studies have recognized the fundamental role of zooplankton grazing in L. Constance (e.g. Lampert and Schober, 1978; Geller, 1980). Tilzer (1984) estimated the relative significance of zooplankton grazing in different seasons in this lake. He argued that losses due to grazing would range between 40-80 % of overall losses. He also found that overall losses are highly correlated with the potential growth rate of phytoplankton ( $\mu$ ). In Lake Vechten, grazing induced losses on algal community can exceed primary production by a factor of four (Gulati *et al.*, 1982). Hart (1986) found that the daily carbon intake by the zooplankton amounts up to 900 % of PP in the turbid south african reservoir, L. le Roux. Tab 23 shows that ingestion rates obtained in the present investigation ranged between 7 % (spring bloom) to ca 1300 % of daily primary production (clear water-phase). The loss rates due to zooplankton grazing shown in this table are higher than those provided by Tilzer (1984). These new estimates can be justified considering two reasons: a) since night experiments were conducted in all these dates, the higher community grazing rates observed at night could always be taken into account; b) the microzooplankton was also included (excepting HNF and most ciliates) in these calculations and, as a consequence, the total zooplankton grazing remained the major loss factor in some periods outside the clear-water phase, like during summer (see, for instance, the values of July and August of 1989). Thus, the significance of zooplankton grazing in Lake Constance is greater than previously estimated, since most studies concluded that grazing would be the most important loss factor only during or before the clear water phase. The higher loss rates due to grazing calculated for summer and autumn confirm that the zooplankton community tends to utilize as much as possible of the available food during the whole growing season. Furthermore, micro- and mesozooplankton have evolved different strategies to utilize the food resources in this lake. The higher values for the ratio CIR:PP found in summer indicates that food limitation must occur frequently during this season and only organisms of zooplankton which can adapt rapidly to variations of food conditions can effectively inhabit the pelagial waters during those periods. *D. hyalina*, for instance, initiates DVM as soon as the spring bloom of phytoplankton is terminated and the thermal stratification is well stabilized in the lake. Geller (1986) demonstrated that this behaviour brings some energetic bonus for this species and, hence, it helps to offset food shortage periods. Furthermore, females tend to carry fewer but bigger eggs during summer (Geller,

1989). *D. galeata* which is not able to resist longer hunger periods (Geller, 1986) tend to disappear earlier from the pelagical zone. Rotifers and other organisms from microzooplankton, which adapt to varying food conditions very rapidly, have then an opportunity to play a key role in the zooplankton grazing.

## 5 Conclusions

### 5.1 Seasonal course of Grazing

Considering the whole annual cycle, the highest community grazing rates were always measured during the clear-water phase when absolute clearance rates of zooplankton communities (CGR) reached values higher than  $100 \text{ \%} \cdot \text{day}^{-1}$ . Carbon intake by the zooplankton (CIR) can exceed primary production by a factor of twelve during the annual maximum of grazing in L. Constance. In most occasions, however, the ratio of CIR:PP varied between 0.8 and 1.0 and, thus, it was also demonstrated not only that grazing of both zooplankton fractions is the most important loss factor for phytoplankton but also that this trend is not restricted to the clear-water phase, remaining probably unaffected during the whole growing season.

The *in situ* measurements of zooplankton grazing in L. Constance (366 incubations, conducted in 55 different occasions between Nov/87 and Sep/89) permitted to apply and test two different models which evaluated the specific contribution of major zooplankton herbivores for overall grazing. According to previous studies, these models confirmed that grazing of larger zooplankton is regulated mostly by *Daphnia* biomass in L. Constance. The relevance of daphnids in the overall grazing was demonstrated by the multivariate model and also by the comparison between PGR's of *Daphnia* and CGR's. Further, the present study quantified for the first time in L. Constance the relative contributions of both *Daphnia* species for the total grazing. *D. hyalina* populations regulate zooplankton grazing in most parts of the year, but grazing of *D. galeata* usually explains the CGR annual maximum, during the clear water-phase. Biomass of other herbivores such as *Bosmina* and *E. gracilis* seem to have a secondary effect on these rates. Contrarily to previous studies considering zooplankton feeding activities in this lake (e.g. Lampert and Schober, 1980), cyclopoids were found to have a negligible effect on community grazing. Finally, environmental variables such as water temperature and food availability (chlorophyll-a concentrations) also play significative roles in controlling CGR's of mesozooplankton.

This investigation also brought the first report concerning field measurements of microzooplankton grazing in Lake Constance. Feeding rates of smaller herbivores (50-170  $\mu$ m) were found to have always relevance for overall zooplankton grazing. Their grazing rates were sometimes even higher than those of larger organisms. This dominance of microherbivores occurred in short periods during summer, when total C-intake of zooplankton (CIR) was controlled by this fraction. As a consequence, zooplankton grazing remained the major loss factor for the phytoplankton outside the clear-water phase. Annual averages of epilimnetic (0-10 m) C-intake were 30 and 60  $\mu$ gC.L<sup>-1</sup>.day<sup>-1</sup> for micro- and mesozooplankton, respectively.

Clearance rates of smaller organisms seem to be primarily modulated by water temperature since the highest values of microzooplankton grazing occurred in the warmer epilimnion during the summer and not in periods of its maximum biomass (before clear-water phase). Contrarily to larger herbivores, biomass of different groups of microzooplankton could only explain lower percentages of CGR of this fraction. Nevertheless, rotifer biomass could still explain a significative portion of the variability found in these rates. The biomass of the second most important component of this fraction, nauplii instars, did not have any measurable effect on grazing rates of this fraction.

Recent investigations have successfully described some allometric regression models relating body size to several physiological functions such as ingestion-, respiration- or growth rates (Banse, 1982; Peters, 1983). These models enable the comparison of these functions between organisms of very different size classes. In this study, an empirical model relating body size to ingestion rates of filter-feeder heterotrophs was used in order to verify whether the biomass-specific ingestion rates ( $I_b$ 's) of both fractions were compatible with predicted values from the model. This comparison demonstrated not only the model's effectiveness in describing ingestion rates for the micro- and mesozooplankton in Lake Constance, but also justified the higher  $I_b$ 's found for smaller organisms.

## 5.2 Diel variations of community grazing

Excluding the spring bloom, when the biomass of mesozooplankton was relatively low and

dominated by cyclopoids, higher community grazing rates of mesozooplankton were always observed at night in the epilimnion. In studies related to zooplankton grazing, an actual question is which factor is responsible for higher CGR's at night. The biomass specific grazing rates ( $G_b$ 's) revealed that these nocturnal higher rates were caused basically by biomass concentration near the surface and, to a lesser degree, by enhanced filtering rates of daphnids. It was also shown that the grazer community does not maintain constant feeding rates during the whole night. Mesozooplankton CGR's were usually the highest in the first half night, and smaller organisms, in contrast, reached their maximum feeding rates just before dawn.

This is the first *in situ* investigation describing diel rhythms in small organisms of zooplankton. Microzooplankton grazing had a particular diel pattern different from those observed by larger organisms. This diel rhythm coincides with variations of food levels, since slightly higher POC concentrations were also found in the second half of the night. Contrarily to larger herbivores, the higher grazing rates of microzooplankton before dawn were consistently reflected by their biomass specific grazing rates ( $G_b$ 's). These rates followed the same diel pattern observed in the  $CGR_2$ . This means that individual fluctuations of FR's, and not biomass concentrations, modulate diel feeding rhythms of microzooplankton.

The different seasonal and diel fluctuation patterns of feeding rates of larger and smaller zooplankton reveal that microzooplankton is not just a scale-down version of larger herbivores. Both fractions are adapted to play complementary roles in the utilization of food resources in this lake. If mesozooplankton is adapted to consume the huge spring bloom algal stock, the microzooplankton is able to profit from the short pulses of suitable algal food in the summer (and partially during spring). In the diel cycle, smaller organisms seem to have developed a fine mechanism to avoid competition with larger herbivores and, further, they probably harmonize their maximum feeding rates with the daily fluctuation of epilimnetic sestonic carbon in a such way that the highest feeding rates occur simultaneously with the highest POC concentrations.

### 5.3 ***In situ* filtering rates of herbivorous mesozooplankton**

Body size influenced filtering rates of all herbivores which were considered in this investigation. The

nature of this relationship depends, however, on what species is considered. The FR's of cladocerans increased with the body size, and a power function could be satisfactorily fitted for all species.

The copepodites of the calanoid *E. gracilis* had also their filtering rates positively correlated with body length. However, filtering rates of adults did not respond to further increases of body size. A quadratic function described this relationship satisfactorily.

The cyclopoids considered in this study, *C. vicinus* and *M. leuckarti* had inverse FR vs. body size relationships when fed on nanoplanktonic algae *Rhodomonas sp.* and *S. hantzschii*. This confirmed the shift of their feeding habits from filter-feeders to carnivores as they molt into older copepodites or adults. The nauplii instars of *C. vicinus* are mainly filter feeders and consequently they increase their FR as they grow. Nevertheless, both species usually remove small (< 12 : m) food particles at very low rates when they are compared with cladocerans and calanoids.

The filtering rates of vertical migrators such as *D. hyalina*, *Bosmina* and *E. gracilis* were found to be higher at night. *D. galeata* maintained rather stable FR during night and day in most occasions; higher nocturnal FR's were found only in short periods (e.g. during clear water phase). Although *D. hyalina* had always the highest FR at night, this investigation brought some evidence that this species can also regulate its feeding rhythm during the night. They probably filter more intensively as soon as they arrive near the surface after sunset. At dawn, shortly before they descend to deeper layers, they diminish their feeding rates again. The trends of daily fluctuations in the filtering rates found for herbivores in the pelagial of L. Constance confirm the hypothesis proposed by Haney (1986), which predicts that extended daily rhythms of feeding should be found preferentially in species which undergo vertical migration.

Both *Daphnia* species filtered similar amounts of water when two different food algae (but known to have optimal nutritional qualities for most zooplankters) were simultaneously offered. These algae were: *Rhodomonas sp.* and *S. hantzschii*. Different feeding responses were found, however, when other herbivores were considered. *Bosmina* preferred the smaller *S. hantzschii* and both copepods *E. gracilis* and *C. vicinus* filtered the larger cryptophyceae at higher rates. It seems that this differential ingestibilities may be based on the ability of some herbivores (e.g. calanoids) to feed selectively on a fine-defined size

spectrum.

Subpopulations of *D. hyalina* from meta and hypolimnion had their FR's affected by water temperature. However, this effect could only be demonstrated outside the optimum range of temperatures for this species<sup>2</sup>, since FR's were significant affected only in temperature gradients below 18 °C.

Both daphnids were affected by variations in the food concentration. The intensity of this effect varied on a specific base. Contrarily to *D. hyalina*, only large individuals (>1.2mm) of *D. galeata* had their FR affected by different food levels. All size classes of *D. hyalina* had higher FR at lower food levels.

The different food preferences shown by *Bosmina* and *E. gracilis* indicate that food quality may be one important factor shaping their ecological niches in the pelagial of Lake Constance. On the other side, food concentration or water temperature may be more important variables determining the ecological niches of the larger daphnids.

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<sup>2</sup> Geller (1986) affirmed "the lower boundaries of DVM amplitudes of the migrating zooplankton species [e.g. *D. hyalina*] are controlled by the temperature". Thus, these meta and hypolimnetic subpopulations are subjected to temperature conditions which are not in the optimum range for them.

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## 7 List of Symbols and Abbreviations

ANCOVA	Analysis of covariance
C-B	Clarke-Bumpus zooplankton sampler
CGR	Community grazing (or clearance) rates [% vol. day <sup>-1</sup> ] or [mL.L <sup>-1</sup> .day <sup>-1</sup> ]
Chl-a	Chlorophyll-a [: g.L <sup>-1</sup> ]
CIR	Community ingestion rates [: gC.L <sup>-1</sup> .day <sup>-1</sup> ]
DVM	Diurnal vertical migration
DW	Dry weight [: gDW.L <sup>-1</sup> ]
FR	Filtering rates [mL.ind <sup>-1</sup> .day <sup>-1</sup> ]
FW	Fresh weight of Phytoplankton
G <sub>b</sub>	Biomass specific grazing rates [mL.: gDW <sup>-1</sup> .day <sup>-1</sup> ]
I <sub>b</sub>	Biomass specific ingestion rates [: gC.: gDW <sup>-1</sup> .day <sup>-1</sup> ]
ILL	Incipient food level [: gC.L <sup>-1</sup> ]
HNF	Heterotrophic Nanoflagellates
LS-Mean	Least-square mean
PAR	Photosynthetic active radiation [mol.m <sup>2</sup> .day <sup>-1</sup> ]
PP	Primary productivity [mgC.m <sup>2</sup> .day <sup>-1</sup> ]
P1	Mesozooplankton
P2	Microzooplankton
POC	Particulate (sestonic) organic carbon [: gC.L <sup>-1</sup> ]
SEH	Size-efficiency Hypothesis



## 8 Summary

The grazing activities of the zooplankton community as well as specific filtering rates of all major herbivores in Lake Constance (Federal Republic of Germany), were examined *in situ*. Field measurements of grazing were conducted using a modified Gliwicz-Haney twin grazing chamber. Two experimental food particles were used: the cryptophyceae *Rhodomonas sp.* and the diatom *Stephanodiscus hantzschii*. Zooplankton was divided in two size fractions: the larger mesozooplankton (>170  $\mu$ m) and microzooplankton (50-170  $\mu$ m). The diel- and seasonal variations of size-fractionated grazing were measured over the growing seasons of 1988 and 1989. Different temporal patterns could be identified. Grazing of mesozooplankton reached its maximum during the clear-water stage (May-June), and smaller herbivores had their highest community grazing during summer (July-August). The multivariate model showed that grazing rates of micro- and mesozooplankton are affected by different factors. The biomass of larger herbivores such as those of both *Daphnia* species explained the highest amount of the variability by mesozooplankton grazing rates whereas water temperature was the most important factor regulating these rates in the smaller zooplankton. Particular diel rhythms could be observed in both groups, meso- and microzooplankton. The highest community grazing rates of the larger organisms were often measured at the beginning of the evening, as soon as vertical migrators have concentrated in near-surface waters. Smaller organisms, such as rotifers, had higher community grazing just before dawn. Diel variations of filtering rates played a more important role in the community of smaller herbivores, since only the biomass-specific grazing rates ( $G_b$ ) of microzooplankton were affected consistently by these rhythms. Several factors affect the specific filtering rates of herbivores in the lake: body size, diel rhythms, food quality and quantity, and water temperature. Although filtering rates were always strongly correlated with body size, different functions had to be fitted in order to describe quantitatively these relationships for the different species. Diel rhythms affected the filtering rates of vertical migrators such as *D. hyalina*, *Bosmina* and *E. gracilis*. *D. hyalina* had preferentially higher filtering rates soon after sunset, when these organisms reach surface waters. Filtering rates of daphnids responded to different food levels, whereas bosminids and copepods had their filtering

rates strongly affected by different food types. The effects of water temperature in the filtering rates could be demonstrated only in the sub-populations of *D. hyalina* living in the meta-/hypolimnion, i.e. in regions where the temperatures were always below the optimum range for this species. The analysis of carbon intake by both zooplankton fractions demonstrated that, as soon as spring bloom is terminated, zooplankton grazing remains as the most important loss factor for autotrophs of nanoplankton in the epilimnion. This is achieved by complex temporal interactions among different size-fractions which alternate with each other during the diel cycles and seasons maximizing the carbon-flow from primary producers to grazers in L. Constance.

## 9 Zusammenfassung

Die Fraßaktivitäten der gesamten Zooplankton-Gemeinschaft und die individuellen Filtrieraten ihrer wichtigsten Organismen wurden regelmäßig im Überlingersee in zwei aufeinander folgenden Jahren (1988 and 1989) untersucht. Diese Messungen wurden mit einer modifizierten experimentellen Doppel-Kammer nach Gliwicz-Haney Art *in situ* durchgeführt. Zwei gut freßbare Futterpartikel wurden in diesen Versuchen eingesetzt: Die Cryptophyceae *Rhodomonas sp.* und die Diatomee *S.hantzschii*. Das Zooplankton wurde mit einem speziellen Filtrationsverfahren in zwei Größenfraktionen getrennt: Das Mesozooplankton (>170 : m) und das kleinere Microzooplankton (50-170 : m). Ziel dieser Messungen war es nicht nur ein umfassendes Bild über die zeitlichen (Jahres- und Tageszeitlichen) Variationen der Fraßraten dieser zwei Größ-Fraktionen zu erarbeiten, aber auch erstmals zu untersuchen, welche Faktoren die *in situ* gemessenen Filtrieraten beeinflussen können. Letztlich wurden diese verschiedenen Informationen miteinander kombiniert, um die Rolle des Zooplanktonsfrasses als Verlustfaktor für das Phytoplankton quantitativ erfassen zu können.

Unterschiedliche Tendenzen hinsichtlich der jahreszeitlichen Variationen wurden bei dem Meso- bzw. Microzooplankton festgestellt. Das Mesozooplankton hatte das Grazing-Jahresmaximum erwartungsgemäß während des Klarwasserstadiums. Die kleineren Organismen hatten dagegen ihre maximalen Fraßaktivitäten in der wärmeren oberflächlichen Wasserschichten während des Sommers. Das Multivariate-Model hat bestätigt, daß die Grazingraten von Meso- bzw. Microzooplankton prinzipiell von verschiedenen Faktoren abhängig sind. Der höchste Anteil der Variabilität der Grazingraten bei den grösseren Herbivoren läßt sich aus deren Biomasse erklären. Dagegen ist der Temperatur der wichtigste regulierende Faktor beim Microzooplankton, da dessen höchste Grazingraten nicht während des Biomassemaximums im Frühjahr sondern im Sommer aufgetreten sind. Die zwei Größenfraktionen zeigten auch verschiedene Tagesrhythmen. Die höchsten Grazingraten des Mesozooplanktons wurden fast immer kurz nach Sonnenuntergang gemessen, wenn sich eine Biomasse-Konzentration in Oberflächennähe gebildet hatte. Im Gegensatz dazu zeigte das Microzooplankton ausnahmslos deutlich höhere Raten kurz vor dem

Sonnenaufgang, d.h. in der zweiten Hälfte der Nacht. Variationen in den individuellen Filtrieraten haben wahrscheinlich eine grössere Bedeutung beim Microzooplankton, da eine entsprechende diurnale Variation der Biomasse-spezifischen-Grazingraten ( $G_b$ ) nur bei den kleineren Organismen festgestellt werden konnte.

Verschiedene Faktoren können die individuellen Filtrieraten wichtiger Zooplanktonarten beeinflussen: Körpergröße, Diurnal-Rhythmen, Futterqualität, Futterkonzentration und Wassertemperatur. Die Körpergröße hatte einen Effekt auf die Filtrieraten aller Herbivoren des Zooplanktons. Die Abhängigkeit der Filtrieraten von Cladoceren von der Körpergröße kann mit einer Potenzfunktion quantitativ beschrieben werden. Bei Calanoiden lassen sich diese Raten mit einer quadratischen Funktion beschreiben, in der nur bei den juvenilen Entwicklungsstadien eine Zunahme der Filterieraten mit der Körpergröße erfolgt. Der negative Zusammenhang zwischen der Körpergröße von Cyclopoiden und deren Filtrieraten konnte erstmals unten *in situ* Bedingungen festgestellt werden. Dies kommt dadurch zustande, daß ältere Entwicklungsstadien von Cyclopoiden Karnivoren werden und weniger Algenpartikel pro Zeiteinheit aufnehmen. Diurnale-Schwankungen in den Filtrieraten wurden bevorzugt bei solchen Organismen festgestellt, die tägliche Vertikalwanderungen durchführen. Im Tagesablauf wurden die höchsten Filtrieraten z.B. bei *D. hyalina* oft kurz nach Sonnenuntergang gemessen. Andere Vertikalwanderer, wie *Bosmina* und *E. gracilis*, hatten auch höhere Filtrieraten in der Nacht, wenn sie sich in Oberflächennähe befanden. Die Futterkonzentration hatte eine deutliche Wirkung bei Adulten beider *Daphnia*-Arten. Eine Zunahme des Futterangebotes ( $POC < 50 : m$ ) führte zu einer Abnahme der Filtrieraten. Die Parallelversuchen mit der oben genannten Algen haben gezeigt, daß die Filtrieraten anderer Herbivoren des Mesozooplanktons von Futterqualität beeinflusst werden. *E. gracilis* bevorzugte die begeißelten Algen *Rhodomonas*. Die kleinen *Bosmina*-Arten dagegen filterten höhere Mengen von *S.hantzschii*. Der Effekt der Temperatur auf die Filtrieraten konnte nur bei *D. hyalina* in den tieferen Wasserschichten beobachtet werden. Die reguläre Messung des Kohlenstoff-flusses von Primär- zu den Sekundärproduzenten im Pelagial des Überlingersees hat bestätigt, daß das Zooplankton-Grazing der wichtigste Verlustfaktor für das autothrophe Phytoplankton ist. Durch die Zusammenwirkungen von Mikro- und Mesozooplankton wird eine maximale Ausnutzung der Nanoalgen durch diese Herbivoren über die gesamte Vegetationsperiode

erreicht.



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