Interrelationships between crustacean zooplankton and phytoplankton:

Results from 15 years of field observations at the mesotrophic Saidenbach Reservoir (Germany)

Wolfgang Horn & Heidemarie Horn
*Sächsische Akademie der Wissenschaften zu Leipzig, Arbeitsgruppe 'Limnologie von Talsperren',
Neunzehnhainer Str. 14, D-09514 Wünschendorf, Germany*

Abstract

Fifteen years of data (1975–1990) on the phyto- and crustacean plankton in the meso/eutrophic Saidenbach Reservoir were analysed to reveal correlations between these groups or members of them. The weekly or fortnightly samples were collected from different depths and times, and were integrated to form seasonal averages. For the dominant organisms, summer means of abundance were plotted against one another. Among the Crustacea, *Daphnia galeata* exerts a strong influence on nanoplankton resulting in an increased Secchi depth in years with a high standing stock of Daphnia. No such correlations were found for Eudiaptomus and the Cyclopoida, which are not able to remove such small particles. The abundance of Daphnia showed no obvious effects on Cyanophyta, colony forming Chlorophyta and *Asterionella formosa*. This implies that in the Saidenbach Reservoir, factors other than crustacean grazing are of crucial importance for the population dynamics of the latter algal groups. It is shown, that the influence of the Crustacea on the phytoplankton is evident not only for short periods, i.e. in clear-water stages, or in biomanipulated lakes, but also can be observed under 'non-manipulated' conditions for longer time periods.

Introduction

Biomass and species composition in any body of water depend on a number of factors. Most important are the resources, e.g. nutrients, light, on the growth side and the losses, e.g. grazing, predation, on the other side. All these factors exist together in any ecosystem, and are commonly referred to as bottom-up and top-down effects, respectively. In laboratory experiments, e.g. for the determination of individual filtration and ingestion rates, in situ investigations, e.g. calculation of individual or population performance as community grazing rate, enclosures and experiments with parts or whole ecosystems, e.g. experimental lakes with different or no fish stock, the influence of the zooplankton on the phytoplankton and the cycling of minerals and energy have been studied.

Numerous investigations on the interactions between phyto- and zooplankton have been performed. Mostly, they have been based on short-term experiments in enclosures, laboratory or in situ experiments. Long-term observations of these relationships are scarce, particularly in waters where, in contrast to biomanipulated lakes, the fish stock is subjected to little direct anthropogenic influence.

Description of study site

Investigations were carried out in the drinking-water Saidenbach Reservoir (Erzgebirge, Sachsen, Germany). At its maximum water-level, it holds a volume of $22.4 \times 10^6 \, m^3$, the surface area is approximately 146 ha and the maximum depth is 45 m. The mean annual air temperature is about 7°C. The water is soft, relatively nutrient rich and characterized by meso/eutrophic conditions with increasing nutrient concentrations in the tributaries and in the water of the main basin. There was a doubling of soluble reactive phosphorus (SRP) during the study period. During the growing-season,

phytoplankton development is mostly P-limited. Winter concentrations of SRP range from 10 to 15 μg l^{-1} P, while epilimnetic summer concentrations range from 0 to 4 μg l^{-1}. Occassionally, Si-limitation also occurs for short periods (see Horn & Horn, 1990); nitrate concentrations are permanently above 25 mg l^{-1} nitrate, thus indicating no N-limitation.

Methods

Phytoplankton samples were taken (during the time of ice formation and break-up longer sampling intervals were needed) from about 10–14 different depths every week or every fortnight throughout the year, with a Ruttner-sampler, while crustacean plankton were collected with a closing net (mesh size 175 μm) from five different depth ranges, extending throughout the whole water column. The values for the different depths under investigation were depth and time integrated to form seasonal averages, so that every presented summer value is the result of nearly 100 zooplankton and 300 phytoplankton samples. The summer average includes all data from the beginning of the stagnation period (when water temperatures finally rise above 4°C) to its end, if vertical temperature differences no longer exist within the water column. For the present study, the summer average for the whole water column was used and not that of the epilimnion, because the vertical distributions of the Crustacea sometimes show higher concentrations in waters below the very shallow epilimnion in early summer. The biomass or biovolume of the zooplankton species was calculated from length-weight ratios on the basis of length measurements taken on each sampling date (see Bottrell et al., 1976, and our own formulas). In the case of phytoplankton, self-ascertained standard volumes were used. The present study considers all years from 1975 to 1990 except for 1982. This year was excluded, because only monthly data from zooplankton were available.

For the well-known and expected causal connections among planktonic organisms (e.g. in food chains), and for the most important species/groups, the summer means of abundance were plotted against one another. The results were only examined for linear correlations and their significance (Grimm & Recknagel, 1985). No further statistical analyses were carried out, because the goal of this paper was to detect and to describe the prevailing processes and relationships between phyto- and zooplankton over entire growing seasons. In order to avoid the danger of deriving spurious connections

from correlations, only those relationships for which there exists a large body of evidence from experimental and field observations were investigated statistically. To avoid the impression that between the tested variables, an ultimately valid quantitative relationship exists, the calculated linear regression line was not included in the figures. The essential statistical parameters for each analysis of the non-log transformed data are presented (Table 1 or in the Figures).

Results

In Fig. 1 the annual averages of the biovolume of the dominant phyto- and crustacean plankton groups over the time period 1975–1990 are presented. There are no obvious trends concerning the total biovolume of both, but a shift in the crustacean community after 1986 may be seen: the cladocerans – dominated by *Daphnia galeata* – decreased. For the phytoplankton, the increasing dominance of blue-greens in the late 1980's is most noteworthy.

Figure 2 shows the relationships between nanoplankton, that means all species smaller than 20 μm in length, and the total crustacean biovolume, and specific constituent groups. No diminution in grazing influence on the nanoplankton can be deduced from the correlation to the pooled biovolume of the whole crustacean community (see Table 1 also). In the following diagrams, the main compartments of the Crustacea were tested. *Daphnia galeata* seems to exert a strong influence on the nanoplankton. Low nanoplankton biovolumes were found in years with high densities of Daphnia. When looking at Eudiaptomus and the Cyclopoida, quite the reverse relationship to the nanoplankton becomes apparent, as the biovolumes of both crustacean groups are positively correlated with nanoplankton biovolume.

Two species among the nanoplankton were dominant in the Saidenbach Reservoir: *Rhodomonas pusilla* and *Chrysochromulina parva*. These organisms show a clear relationship to *Daphnia galeata* (see Fig. 3) as shown previously (Fig. 2) for the whole group of nanoplankton, which again indicates the influence of the filter-feeding Daphnia on the small phytoplankton species. The relationships between these two species and the copepods were absent or showed – as in the case of the nanoplankton as whole group – the reverse tendency, i.e. a positive correlation.

However, there were no obvious interrelationships at all between the two tested net plankton groups,

Table 1. Statistical parameters from correlation analyses. Due to multiple testing the critical probability value is $p = 0.0026$ (Rice, 1989). The number of data pairs in the correlations are mostly 15, but 1) indicates that 1977 has been omitted, and 2) that data only for the last 10 years are considered. + and − indicate positive or negative slopes.

Variable 1	Variable 2	r^2	p	Figure
Crustacea	Nanoplankton	0.34	0.0225	2
Daphnia galeata	Nanoplankton	0.54-	0.0018	2
Eudiaptomus gracilis	Nanoplankton	0.59+	0.0008	2
Cyclopoida	Nanoplankton	0.65+	0.0003	2
Crustacea	*Rhodomonas pusilla*	0.10	0.2509	
Daphnia galeata	*Rhodomonas pusilla*	0.60-	0.0007	3
Eudiaptomus gracilis	*Rhodomonas pusilla*	0.21	0.0858	
Cyclopoida	*Rhodomonas pusilla*	0.58+	0.0010	
Crustacea	*Chrysochromulina parva* 2)	0.07	0.4569	
Daphnia galeata	*Chrysochromulina parva* 2)	0.70-	0.0025	3
Eudiaptomus gracilis	*Chrysochromulina parva* 2)	0.33	0.0824	
Cyclopoida	*Chrysochromulina parva* 2)	0.20	0.1950	
Daphnia galeata	Green algae (colonies)	0.19	0.1043	4
Daphnia galeata	Blue-greens	0.15	0.1538	4
Crustacea	*Asterionella formosa*	0.15	0.1538	
Daphnia galeata	*Asterionella formosa*	0.10	0.2509	4
Eudiaptomus gracilis	*Asterionella formosa*	0.00	1.0000	
Cyclopoida	*Asterionella formosa*	0.01	0.7229	
Crustacea	Secchi depth 1)	0.03	0.5538	5
Daphnia galeata	Secchi depth 1)	0.77+	0.0000	5
Eudiaptomus gracilis	Secchi depth 1)	0.11	0.2466	5
Cyclopoida	Secchi depth 1)	0.45	0.0086	5
Cyclopoida	*Daphnia galeata*	0.40	0.0114	6
Cyclopoida	*Eudiaptomus gracilis*	0.14	0.1694	
Daphnia galeata	*Eudiaptomus gracilis*	0.10	0.2509	

or *Asterionella formosa* with any zooplankton group (Fig. 4, Table 1). Neither in the case of colony forming green algae, mainly *Coenochloris polycocca, Pandorina morum*, nor in the group of blue-greens, which were dominated by *Aphanothece clathrata, Gomphosphaeria lacustris, Aphanizomenon flos-aquae*, was any interrelationship apparent.

The high filter-feeding performance of *Daphnia galeata* results in an enhanced Secchi depth in years when this species has high standing stocks (Fig. 5). The asterisk marks a year with unusually high flushing rates and therefore especially high mineral turbidity. No such correlations however can be presented for Eudiaptomus and the Cyclopoida. These organisms are not able to remove the small algae, which affect the Secchi depth to a great extent.

Discussion

It is widely known and accepted, that nanoplankton is a good ingestable food source and, therefore, is intensively grazed upon by filter-feeding crustacean plankton. In particular, cladocerans like Daphnia can use it and as a consequence, suppress nanoplankton standing stocks to a great extent in situations where there is a high stock of Daphnia. The observed strong correlation between the two groups supports the hypoth-
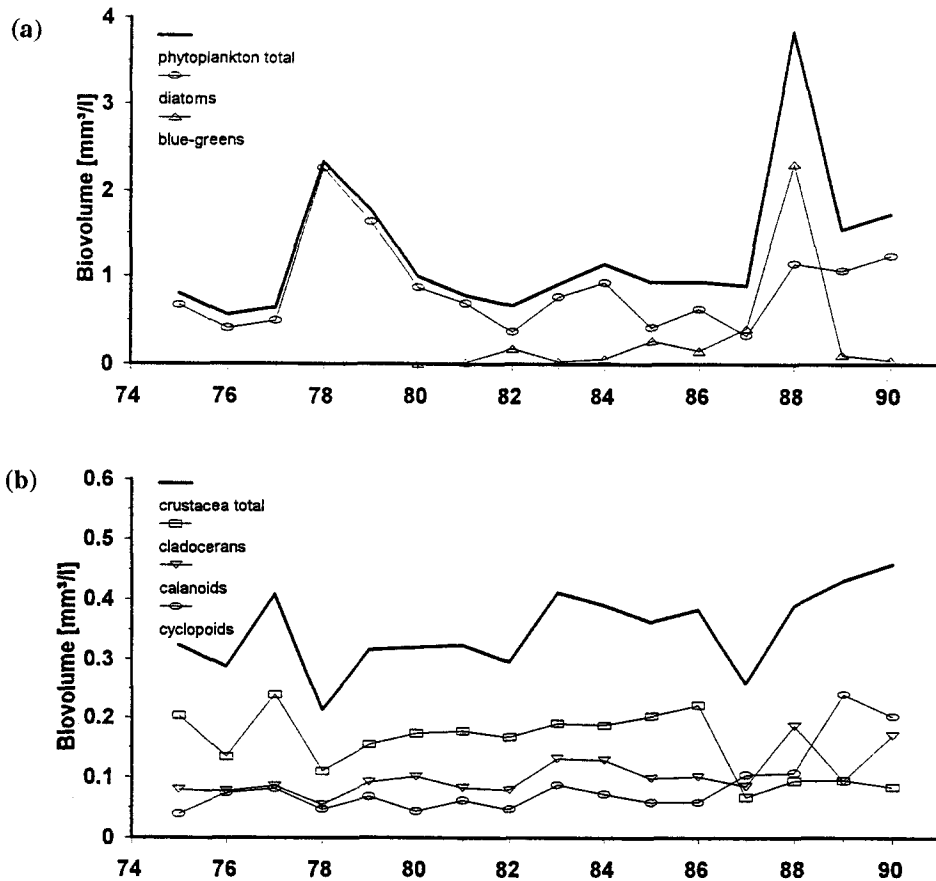
Fig. 1. The annual average of the biovolumes of the dominant groups of (a) phyto- and (b) crustacean plankton during the study period (naupliar stages were not considered in the averages).

esis that *Daphnia galeata* suppresses the nanoplankton as a whole (and certain nanoplanktonic species like *Rhodomonas pusilla* and *Chrysochromulina parva*) by grazing. Furthermore, our results support the notion that the copepods are not primarily 'micro-filter feeders', and they are not able to graze down particles as small as those filtered by Daphnia. The occassionally significant positive relation between Eudiaptomus or Cyclopoida and nanoplankton, which was caused by the simultaneously high values of these noncladocerans and nanoplankton, can be attributed to the low density of the Cladocera in these years. This suggests the existence of an indirect effect of the Cyclopoida on the nanoplankton.

From the other groups of algae, it is also known that their population dynamics can be affected directly, e.g. by grazing or non-grazing, or indirectly, for instance by elimination of competitors, and changes in nutrient conditions by the zooplankton. The colony forming green algae can take advantage of the zooplankton suppressing other competing algae and of nutrient uptake via gut passage; algae with gelatinous sheaths are protected from a herbivore's digestive enzymes and are therefore hardly digestable, but they are permeable to certain nutrient ions (Porter, 1976). This proposed scenario is not likely to persist during the whole growing season, but to exist only for some weeks, more or less exclusively during the time of crustacean population development. Also blue-greens can profit from the Crustacea, which are suppressing their competitors. Certain blue-green species may also inhibit the zooplankton mechanically or by toxins. None of these proposed effects however were observed in Fig. 4 or could be derived from it. In the Saidenbach Reservoir, further effects on blue-green algae development should not be disregarded, e.g. the increasing nutrient conditions, Si-depletion or weather conditions influencing thermal stability (Horn & Horn, 1990). This also
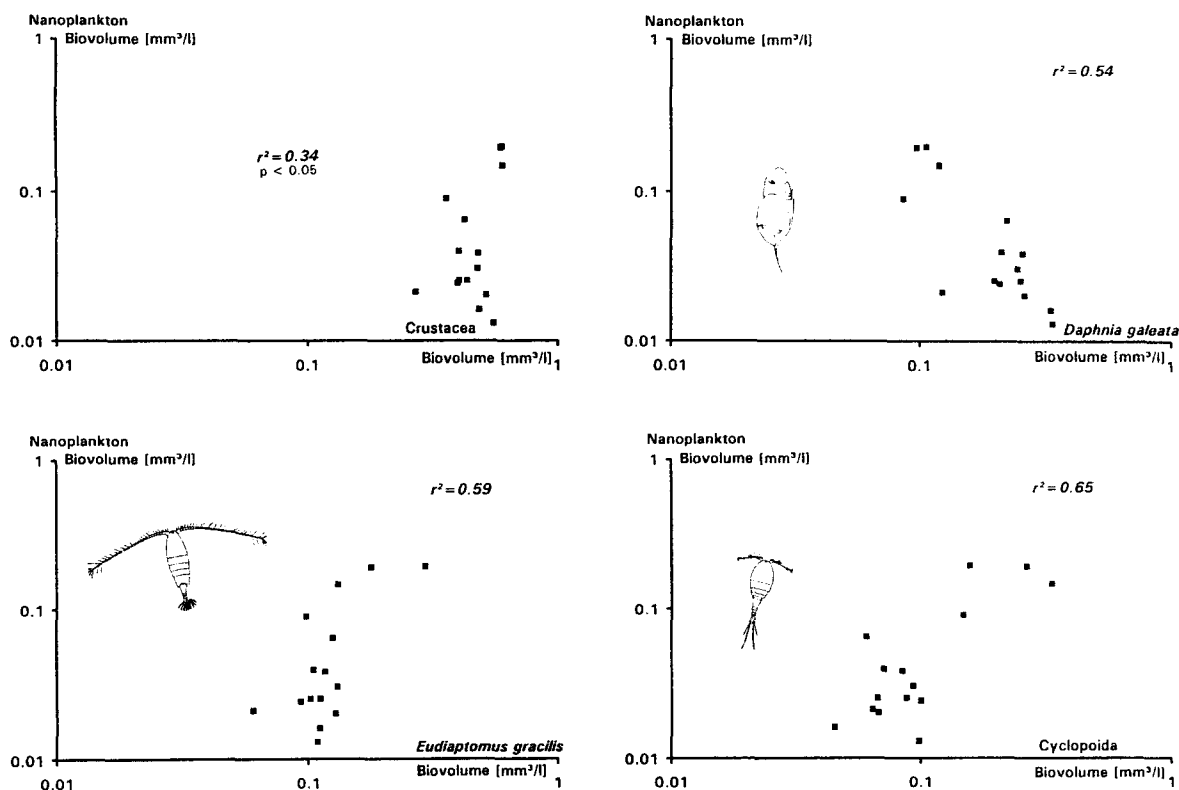
Fig. 2. The interrelationships between the summer means of the nanoplankton and the planktonic Crustacea (total), *Daphnia galeata*, *Eudiaptomus gracilis* and the Cyclopoida.

holds for the diatom *Asterionella formosa*, which was examined for possible interrelationships too. Although from our own (Horn, 1981) and other investigations (Infante, 1973; Geller, 1975), it is known that this alga can be ingested by Daphnia and in spring, the gut of the dominant Cyclops is obviously to a great extent filled with diatoms, no apparent correlation between this alga and the entire crustacean population, Daphnia and the Cyclopoida respectively, were evident (Fig. 4, Table 1). Our analysis reveals that the dynamics of this diatom species is essentially influenced by other factors. In particular, stratification conditions and sedimentary losses are very important in influencing the population development of *Asterionella formosa*. A further important but not evident fact for the diatoms is the elimination of nanoplanktonic competitors by Daphnia. This can improve the nutrient conditions for the diatoms by reducing P-competition and thus stimulates their growth. Because the diatoms are important for phosphorus export to the sediment and therefore for self-purification of the water column (Grim, 1967),

this possible alga compositional shift (as a result of Daphnia grazing) can be a desired effect.

The filter-feeding activity of the *Daphnia galeata* population exerts a great influence on the Secchi transparency values, because these filter-feeders are able to eliminate the nanoplankton to a great extent. Small particles (i.e. nanoplankton) affect the Secchi depth values to a greater extent than comparable concentrations of larger particles. These two effects result in enhanced Secchi depths in years when Daphnia occur at high densities. Because Eudiaptomus and the Cyclopoida are apparently not able to remove such small particles, no 'enhancement effect' on the Secchi depth was observed, when copepods were abundant.

Reasons for the different values of Daphnia biovolume during the study period are assumed to be caused by changes in the fish population. Sport fishermen have reported a high standing stock of zooplanktivorous fishes, mostly larvae, fingerling, small fishes – e.g. stickleback, perch, roach, for the last few years. Unfortunately, no exact data are available as far as this ecosystem compartment is concerned. But it seems that
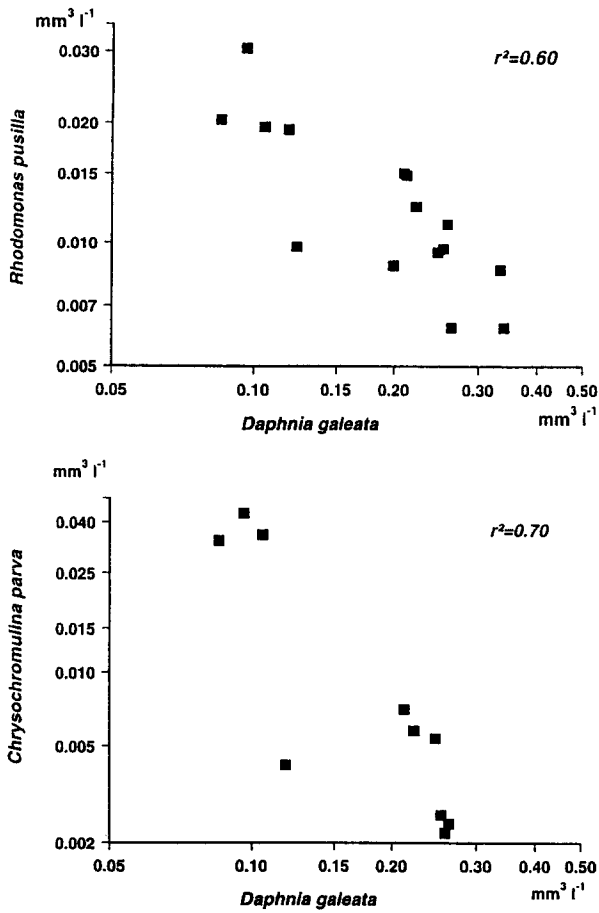
Fig. 3. The summer means of *Daphnia galeata* vs a) *Rhodomonas pusilla*, and b) *Chrysochromulina parva*.

under 'natural conditions', i.e. without anthropogenic heavy piscivorous fish stocking as in biomanipulation experiments, large fluctuations in biovolume and composition of the crustacean plankton may be normal; especially in reservoirs being subjected to large water level fluctuations with its effects on fish reproduction. Among invertebrate predators, only the cyclopoids may have an influence on Daphnia. *Leptodora kindtii* is also present, but at low abundance. However, we did not find a significant correlation between *Daphnia galeata* and cyclopoid abundances (Table 1, Fig. 6).

Conclusions

The influence of the crustacean plankton on the phytoplankton and vice versa can be observed not only in short-term experiments with extremely high standing stocks of Daphnia or in biomanipulated lakes. The
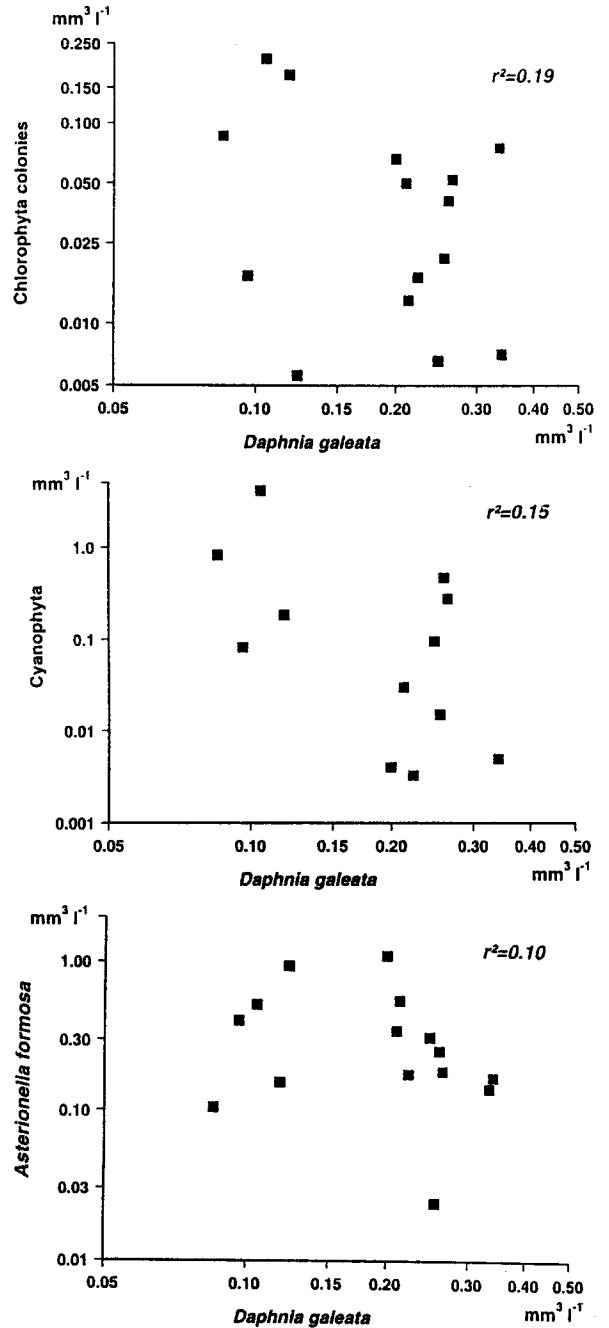

Fig. 4. The interrelationships between the summer means of *Daphnia galeata* vs colony forming a) Chlorophyta, b) Cyanophyta and c) *Asterionella formosa*.

well known and proven effects for short periods, e.g. clear water stages in ponds and lakes, also exist under 'non-manipulated' conditions for longer time periods. They can be confirmed using the summer means of long-term observations.
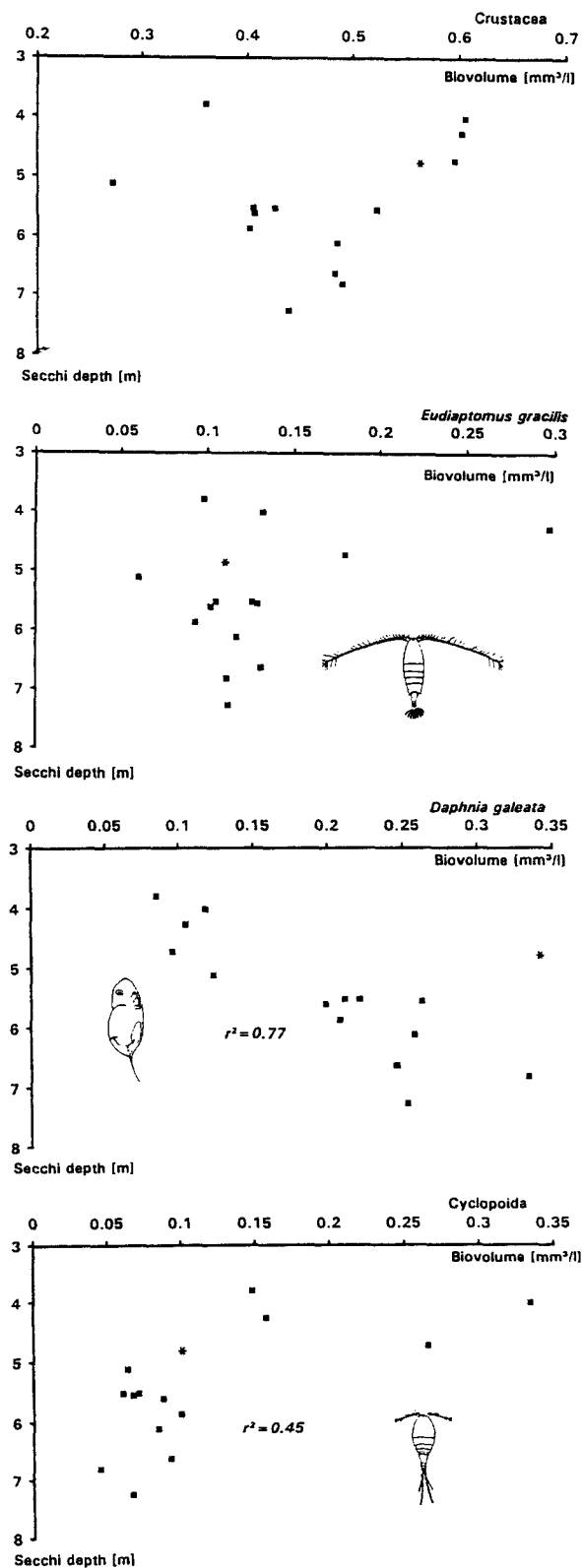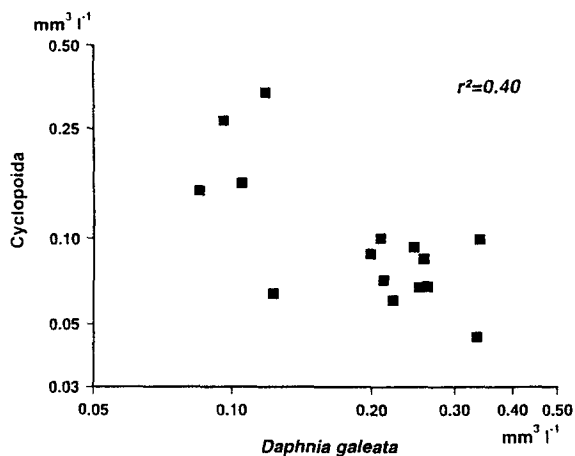
Fig. 6. The interrelationship between *Daphnia galeata* and the Cyclopoida (summer means of biovolume).

The influence of the crustacean plankton on the phytoplankton in the Saidenbach Reservoir can be demonstrated for selected groups only. *Daphnia galeata* appears to be the most important grazer. This species exerts obviously a strong influence on *Rhodomonas pusilla*, *Chrysochromulina parva* and the nanoplankton in general, and results in enhanced Secchi depths in years with a high standing stock of Daphnia. No such correlations were detected for Eudiaptomus and the Cyclopoida, which are apparently not able to graze small algae.

On the other hand, no direct influence of any Crustacea on the net phytoplankton could be derived with this method. Obviously, other factors, e.g. sedimentation, competition, seem to be more essential for the population dynamics of *Asterionella formosa*, colony forming green algae and blue-greens.

Acknowledgement

References

Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Weglenska, 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419–456.

Fig. 5. The dependence of the Secchi depth on the abundance of the planktonic Crustacea (total, without naupliar stages), *Daphnia galeata*, *Eudiaptomus gracilis* and the Cyclopoida (summer means; the asterisk marks a year with high flushing rates and therefore high mineral turbidity; this year is not included in the analysis).

238

Geller, W., 1975. Die Nahrungsaufnahme von *Daphnia pulex* in Abhängigkeit von der Futterkonzentration, der Temperatur, der Körpergrösse und dem Hungerzustand der Tiere. Arch. Hydrobiol. Suppl. 48: 47–107.

Grim, J., 1967. Der Phosphor und die pflanzliche Produktion im Bodensee. Gas- und Wasserfach (Wasser) 108: 1261–1271.

Grimm, H. & R.-D. Recknagel, 1985. Grundkurs Biostatistik. VEB Gustav Fischer Verlag, Jena, 156 pp.

Horn, W., 1981. Phytoplankton Losses due to Zooplankton Grazing in a Drinking Water Reservoir. Int. Revue ges. Hydrobiol. 66: 787–810.

Horn, H. & W. Horn, 1990. Growth of Blue-Green Algae in the Saidenbach Reservoir and its Relationship to the Silicon Budget. Int. Revue ges. Hydrobiol. 75: 461–474.

Infante, A., 1973. Untersuchungen über die Ausnutzbarkeit verschiedener Algen durch das Zooplankton. Arch. Hydrobiol. Suppl. 42: 340–405.

Porter, K. G., 1976. Enhancement of algal growth and productivity by grazing zooplankton. Science 192, No. 4246: 1332–1334.

Rice, W. R., 1989. Analyzing tables and statistical tests. Evolution 43: 223–225.