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Lake Constance, Characterization of an ecosystem in transition

Daphnids: Keystone species for the pelagic food web structure and energy flow. – A body size-related analysis linking seasonal changes at the population and ecosystem levels

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with 6 figures and 2 tables

Abstract: Seasonal changes of the impact of daphnids on the plankton biomass size distribution, the biomass within individual size ranges, the average predator-prey weight ratios, and the efficiency to transfer matter and energy from small to large organisms are analysed in large and deep Lake Constance based on comprehensive long-term observations. A comparison of daphnid biomass and production with those of other herbivorous groups (i.e., ciliates, rotifers, herbivorous crustaceans) reveals that in early spring daphnids play a minor role in relative and absolute values as compared to small fast-growing ciliates. During this time, small algae and ciliates dominate which gives rise to a decreasing Sheldon-type size spectrum, low predator-prey weight ratios, and a low transfer efficiency along the size gradient. Around June, daphnids reach maximum abundances and become keystone species for the shape of the biomass size distribution, the food web structure, and the energy flow. They accumulate biomass in their size range one order of magnitude above the average. The slope of the normalized biomass size spectrum is less negative and positively correlated with daphnid biomass if the latter exceeds about 200 mgC/m^2. This indicates a more efficient transfer along the size gradient with high predator-prey weight ratios and high trophic transfer efficiencies. The coefficients of determination of regression lines fitted to size distributions decrease with daphnid abundance, i.e., the size spectra become more irregular when daphnids dominate. In midsummer, daphnids lose their dominance and co-exist with other herbivores (especially ciliates) in a highly diverse plankton community. The latter gives rise to a relatively smooth and almost flat Sheldon-type size distribution, lower predator-prey weight ratios, and a slightly reduced transfer efficiency along the size gradient. In late spring/early summer, negative relationships are found between daphnid biomass and the biomasses in the size ranges of autotrophic picoplankton, small phytoplankton, heterotrophic flagellates, and small and medium-sized ciliates (0.06-32 pgC and 100-30,000 pgC). In mid- and late summer or on an annual average, hardly any of these relationships existed. This cannot solely be attributed to lower daphnid abundance, but points also to a more diverse control of small plankton organisms including nutrient limitation in summer. Ciliates influence the slope and shape of the size distribution much less than daphnids although they are at least of equal importance as daphnids in respect to herbivory and related fluxes in Lake Constance on an annual average. The findings on the impact of daphnids on the energy flow within the plankton food web derived from size distributions are compared to and are consistent with results obtained by mass-balanced carbon flow diagrams.

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Introduction

Filter feeding daphnids are frequently regarded as keystone species in limnetic food webs, i.e., as species of outstanding importance for the entire food web structure and dynamics beyond their sheer biomass effect (e.g., GÜDE 1988, PACE et al. 1990, JÜRGENS 1994, HORN & HORN 1995). This motivated also numerous studies concentrating on daphnid physiology, nutrition, behaviour, and life history (cf. LARSSON & WEIDER 1995). The present study aims to complement these investigations by analyzing the role of daphnids in the well-studied pelagic food web of large and deep Lake Constance from an ecosystem perspective based on comprehensive long-term measurements. It evaluates how daphnids affect system properties such as the shape of biomass size distributions and transfer efficiencies along the size gradient and the trophic gradient. Furthermore, it aims to identify properties of daphnids which give rise to their strong impact on the biomass size distribution and food web structure and functioning.

Two closely related daphnid species, *Daphnia hyalina* and *D. galeata*, co-exist in large and deep Lake Constance (GELLER 1989). They have almost identical predator and prey species (GELLER 1985, KNISELY & GELLER 1986), but differ in respect to diurnal vertical migration during summer and their seasonal dominance. *D. hyalina* dominates in midsummer and migrates strongly into deep, dark, and cold water layers during day-time. Under these conditions, it has considerably slower metabolic rates than *D. galeata* which remains always in the warm epilimnion (STICH & LAMPERT 1984, GELLER 1989). Since processes occurring within one day are not considered explicitly in the present analysis, both species were combined. In addition, two other small herbivorous crustaceans occur in Lake Constance, the cladoceran *Bosmina longirostris* and the filter feeding calanoid copepod *Eudiaptomus gracilis*. They achieve some (relative) quantitative importance when daphnid abundances are low in winter and spring (STRAILE & GELLER 1998).

Biomass size distributions provide insights into the structure of plankton communities and into the energy flow along the size gradient without the necessity of defining distinct trophic levels or distinguishing taxonomical groups (SHELDON et al. 1972, BORGMANN 1982, RODRIGUEZ & MULLIN 1986, GAEDKE 1992a, 1992b, 1993, 1995). Allometric relationships between body size and weight-specific process rates enable a rough prediction of metabolic properties of (parts of) the entire community from size spectra (e.g. PLATT et al. 1984). For Lake Constance, a reasonable agreement was found between seasonal changes of the metabolic activity of the eukaryotic plankton community derived by this method and of more direct production estimates (e.g. ^{14}C-technique) (GAEDKE 1993).

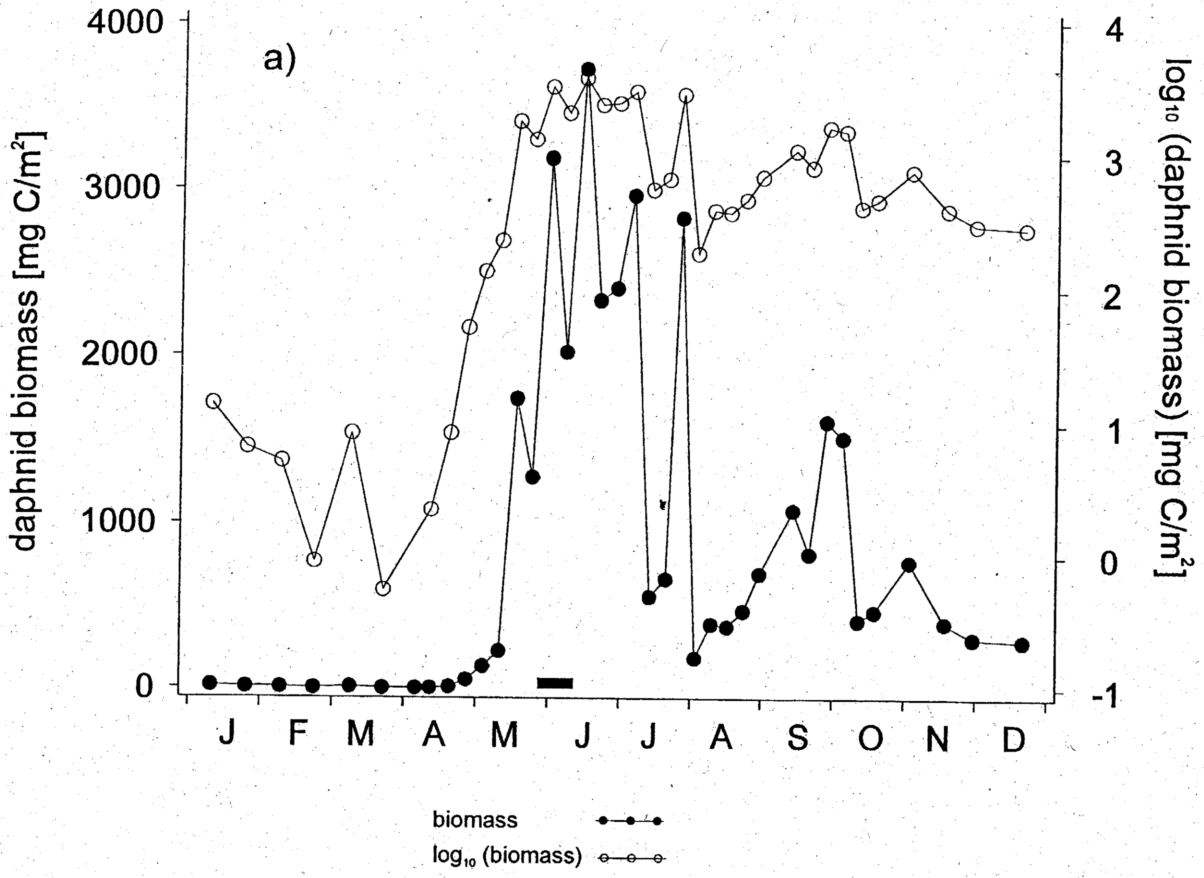
The objective of the present study is to search for relationships between processes at the population and system level and to trace the consequences of specific properties of non-selective filter feeding daphnids for the overall food web structure and functioning which is mostly inferred from size distributions. First, basic measures such as biomass, production, and the grazing impact of daphnids are compared to those of other herbivorous plankton groups, such as ciliates and rotifers. Then, their impact on the slope and shape of the plankton biomass size distribution, on individual size ranges, and on the transfer efficiency along the size gradient and between trophic levels is evaluated by comparing periods with very different daphnid abundances. The findings obtained from size distributions are related to information gained from trophic food web models (mass-balanced carbon flow diagrams) (STRAILE 1995, 1998). This study focuses on the effects of daphnids on energetical properties of the food web, for their impact on nutrient cycling see Hochstädter (1997), and for details on the binary food web structure see Lang (1997).

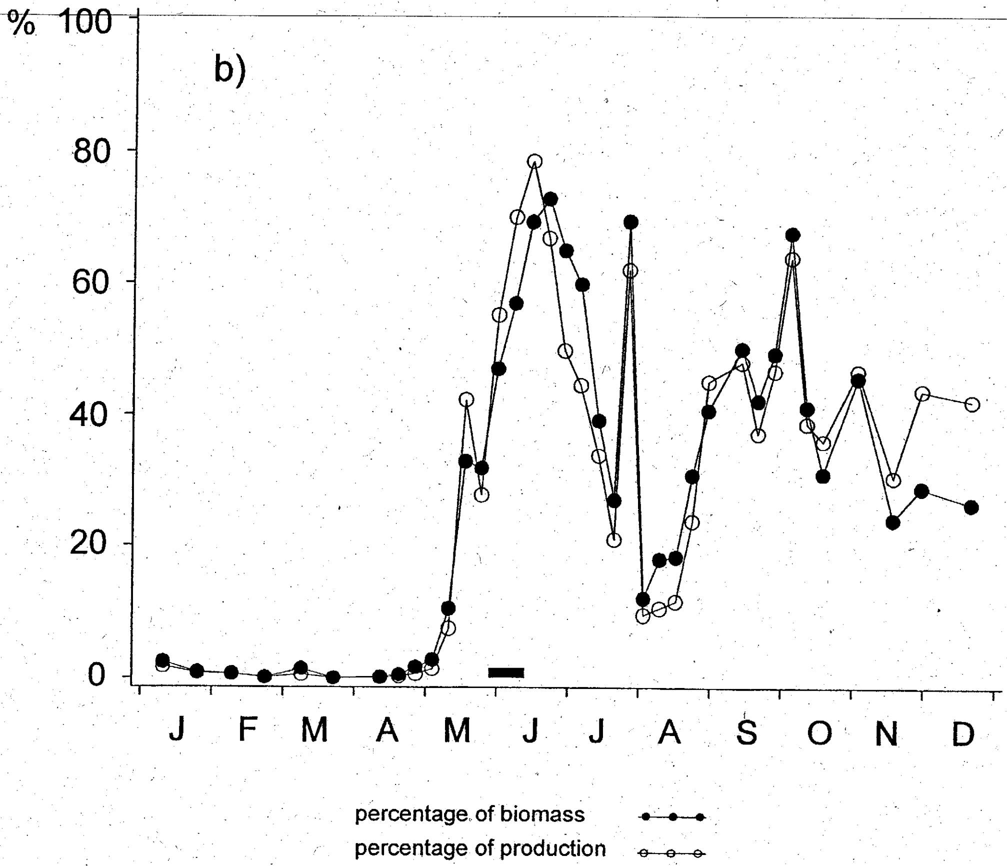
Methods

Upper Lake Constance (in German: Bodensee-Obersee) is a large (472 km^2), deep (mean depth 101 m, z_{max}=253 m), mesotrophic lake situated on the northern fringe of the Alps. The sampling site is located at the north-western part of the upper lake (Überlingersee, z_{max}=147 m), i.e., in an area with presumably little allochthonous inputs which are directly available for the plankton community. Further details on Lake Constance are provided by Güde et al. (1998).

Phytoplankton and crustacean zooplankton sampling was done weekly during the growing season and about biweekly in winter from 1979 onwards (data are lacking for the second half of 1983). Since 1987, abundances of all plankton organisms were assessed by microscopy with the same frequency which enables to apply ecosystem approaches such as biomass size distributions from this time onwards. Numerous different sampling and counting techniques were used which are appropriate for the size, abundance, and fragility of the organisms. For small organisms, such as bacteria, autotrophic picoplankton (APP), and heterotrophic flagellates (HF), size frequency distributions and their seasonal changes were established. For medium-sized organisms (larger phytoplankton, ciliates, rotifers), 30-120 morphologically different forms were distinguished, respectively. Size measurements were carried out regularly for each taxon. Analyses performed during restricted periods of time and by another institution (Stabel, unpubl.) showed that autotrophic biomass in the size range of small phytoplankton which is larger than APP, but does not sediment quantitatively in the Utermöhl chamber (i.e., cells between approximately 2 and 4 µm in length) is underestimated by these routine measurement techniques. Consequently, the five size classes -2 to 2 on a $\log_2$ scale with $2^{-2} = 0.25$ to $2^2 = 4$ pgC nominal weight are partially omitted from subsequent analyses. Size distributions of herbivorous crustaceans were inferred from measurements of 2-5 ontogenetic size categories for each species and converted to units of dry weight with length-weight relationships established for Lake Constance. For the zooplanktivorous cladocerans *Bythotrephes longimanus* and *Leptodora kindti*, ranges of body mass were taken from the literature. Original measurements of body size were converted to units of carbon using data from Lake Constance or from the literature as described in Gaedke (1992b), except that a carbon to biovolume (FW) ratio of 22% for APP and 15% for larger phytoplankton was assumed. All phytoplankton species were classified as either highly edible or net phytoplankton (Milanesi 1995, Gaedke 1998, Sommer, pers. comm.) according to their empirically established or presumed susceptibility to grazing (e.g. Knisely & Geller 1986). Highly edible algae are mostly smaller (predominantly falling into size classes 1 to 9, i.e. 10-3,500 μm^3) than less edible net phytoplankton (mostly size classes 5 to 13, i.e. 200-55,000 μm^3), but both groups overlap in size (Gaedke 1992b).

One way to construct Sheldon-type biomass size distributions is to place each organism into a size class according to its individual body weight and to sum up the biomass in each size class which are spaced logarithmically (cf. Figs. 2a, 2b). Normalized biomass size distributions may then be obtained by dividing the biomass of each size class, B, by the width of that size class. Since the latter corresponds approximately to the weight, w, of the


a)
daphnid biomass [mg C/m^2]
4000
3000
2000
1000
0
log$_{10}$ (daphnid biomass) [mg C/m^2]
4
3
2
1
0
-1
J F M A M J J A S O N D
biomass
log$_{10}$ (biomass)


b)
% 100
80
60
40
20
0
J F M A M J J A S O N D
percentage of biomass
percentage of production

organisms when using a $\log_2$-scale as done in this study, a size frequency histogram of abundance of organisms per logarithmic size class, N=B/w, and body weight (classified on a $\log_2$-scale) is obtained (cf. Fig. 2c; for details see PLATT & DENMAN 1978, VIDONDO et al. 1997). The slope of a normalized biomass size spectrum is obtained by fitting a straight line. It summarizes the steepness of the size distribution whereas the coefficient of determination of the regression line, r^2, quantifies the goodness-of-fit of the normalized biomass size spectrum to a straight line, i.e., whether the shape of the size spectrum is rather smooth or bumpy (cf. Fig. 2c). A slope of a normalized biomass size spectrum of -1 corresponds to a flat Sheldon-type size spectrum, i.e., biomass per logarithmic size class neither increases nor decreases with body size. If the slope is steeper than -1, biomass per logarithmic size class decreases with size and vice versa, slopes of less than -1 indicate an increasing Sheldon-type size spectrum. Further details and references on plankton measurements and computations of biomass size spectra are given by GAEDKE (1992a) and STRAILE (1995, 1998). The present analysis is based on average abundances across the uppermost 20 m of the water column which roughly corresponds to the maximum euphotic depth (cf. HÄSE et al. 1998) and the epilimnion (but see BÄUERLE et al. 1998). Some crustaceans perform extended diurnal vertical migrations and were sampled at day-time with vertical hauls down to 140 m depth. However, when calculating size spectra and flow diagrams, their total biomass was allocated to the uppermost 20 m ("night situation") because the majority of food is obtained from this stratum.

Estimates of predator-prey weight ratios were based on the feeding relationships among 22 trophic plankton guilds to which all plankton organisms of Lake Constance were allocated to (LANG 1997) and the size range covered by the individual trophic guilds. Average predator-prey weight ratios of the plankton food web were computed by weighing the predator-prey weight ratios of the individual feeding links according to the relative quantitative importance of the fluxes. The latter was roughly estimated from the relative share of the individual guilds to the total metabolic activity. For eukaryotes, the metabolic activity was derived from the $\log_2$-scaled size spectra using allometric relationships with an exponent of 0.15 for phytoplankton and heterotrophic flagellates and 0.25 for ciliates, rotifers, and crustaceans (MOLONEY & FIELD 1989, GAEDKE 1993, unpubl.). The relative share of bacterial production was inferred from the measured ratio between primary and bacterial production.

In this study, we distinguish between the trophic transfer efficiency which represents the ratio between predator and prey production and the transfer efficiency along the size gradient. The latter quantifies how efficient small prey items are repackaged into larger organisms and was also called "particle size conversion efficiency" by BORGMANN (1982).

Fig. 1. Seasonal development of a) daphnid biomass (full dots belong to the left linear scale, open circles to the logarithmic scale at the right) and b) the contribution of daphnids to the overall biomass (full dots) and production (open circles) of all predominantly herbivorous plankton groups (i.e., ciliates, rotifers, daphnids, *Eudiaptomus, Bosmina*) in 1988 (raw data from STRAILE 1995 and unpubl.). The horizontal bar indicates the duration of the clear-water phase proper. During 1988, weather conditions in spring changed very suddenly from unfavourable to favourable in early April which gave rise to a single pronounced spring algal bloom and an uninterrupted spring development of herbivores. Except of that, daphnid abundance in 1988 is mostly typical for other years as well.

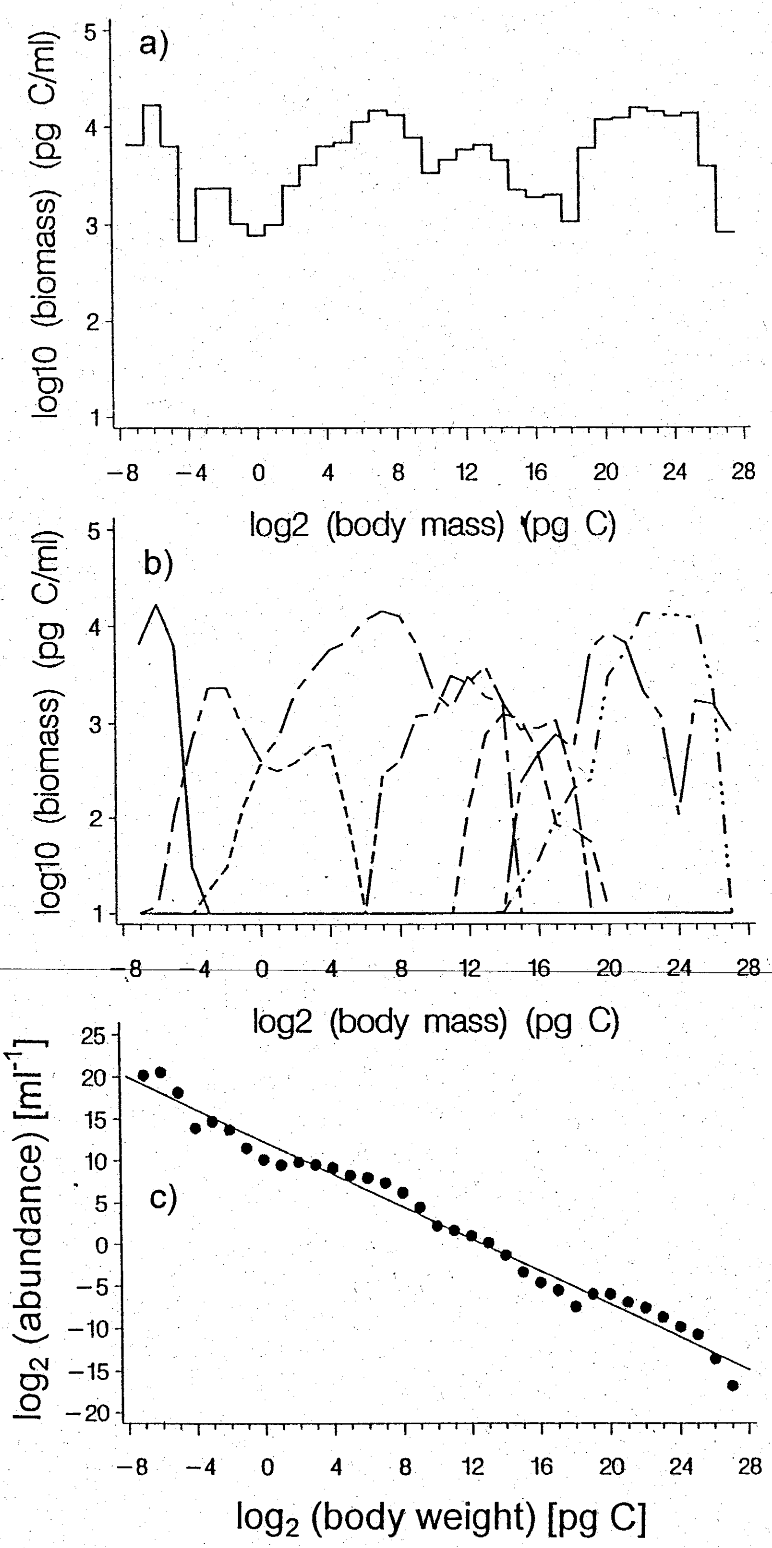


Fig. 2. Biomass size spectrum of the plankton community of Lake Constance averaged over the years 1987-93 and the depth of 0-20 m (i.e., all crustaceans are allocated to the uppermost 20 m). a) Cumulative Sheldon-type size spectrum of all plankton organisms. b) Sheldon-type size spectrum resolved for major groups of organisms (——————) bacteria, (—— — ——— — ———) autotrophs (APP and larger phytoplankton), (------------------) heterotrophic flagellates, (—— – – ———— – – ———) ciliates, (– – – – – – – – –) rotifers, (—— ··· —— ··· —— ···——) herbivorous crustaceans dominated by daphnids, and (———— — ———— — ———— — ————) carnivorous crustaceans including cyclopoid copepods and their herbivorous juvenile stages. c) Corresponding normalized biomass size spectrum (dots) with fitted regression line with a slope of -0.97.

Results

Population dynamics of daphnids

The biomass of the predominantly herbivorous crustaceans (daphnids, *Bosmina, Eudiaptomus)* exhibits recurrent seasonal changes by around 2.5 orders of magnitude. The biomass of daphnids increases during spring even more strongly from low late winter values (several mgC/m^2 or less) until it reaches, with little interannual variability, maximum values of several 1000 mgC/m^2 during or shortly after the clear-water phase in early summer (Fig. 1a; cf. STRAILE & GELLER 1998, their Fig. 7). During midsummer (i.e. around July and August), standing stocks of daphnids were lower by a factor of about ten in most years under consideration. The decrease towards autumn and winter is often interrupted by a second, less pronounced mass development in early autumn. The fast changes allow to compare situations with low and high daphnid abundances within one lake under roughly similar conditions in order to investigate their impact on the food web structure and functioning.

A comparison of daphnid biomass with those of other herbivorous zooplankton groups (i.e., ciliates, rotifers, herbivorous crustaceans) shows that daphnids are in relative and absolute values of minor importance in winter and early spring (Fig. 1b; cf. STRAILE 1995, 1998, his Fig. 2). With the onset of favourable growth conditions in early spring, autotrophs and herbivores start growing. However, the mostly large differences in generation times between autotrophs and their grazers related to differences of body weight by up to five orders of magnitude may cause pronounced variations in response times. Small herbivores such as some ciliates react almost simultaneously to the phytoplankton development and quickly build up high biomasses (MÜLLER et al. 1991), whereas peak abundances of daphnids follow about 6-8 weeks later (Fig. 1; GAEDKE et al. 1998). Subsequently, in late May and/or June, daphnid abundances increase to such an extent that the phytoplankton community is strongly suppressed causing the "clear-water phase". At this time, HF, ciliates, and rotifers occur in low densities as they are subject to intense predation by and/or competition from daphnids which strongly reduce common resources such as edible algae (cf. STRAILE 1998). Thus, daphnids clearly dominate the plankton community during and often also shortly after the clear-water phase (Figs. 1, 3b). They lose this role in midsummer (generally from late June or early July onwards), probably owing to food limitation and increasing predation by carnivorous cladocerans and fish, and co-exist with other herbivores (especially ciliates) in a highly diverse plankton community (Figs. 1b, 3c). The impact of daphnids on food web dynamics in summer is likely to be lowered beyond the biomass effect because a large proportion of the daphnids performs a pronounced diurnal vertical migration at that time. Residing in deep water during day-time reduces their growth rates and the grazing pressure on the epilimnetic community considered in the present analysis as feeding in the surface layer is restricted to the night.

Considering production rather than standing stocks as a measure of the metabolic activity and of the impact on flow dynamics reveals that daphnids dominate production of all herbivores around the clear-water phase and during many years also temporally in autumn, but not otherwise (Fig. 1b).

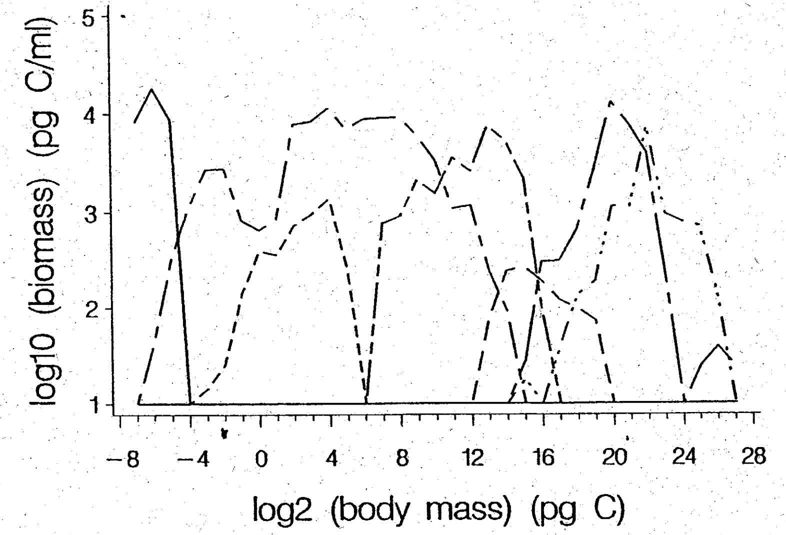
Impact of daphnids on the plankton biomass size distribution

The impact of daphnids on the food web structure and the flow of matter and energy can be evaluated using various ecosystem approaches such as biomass size distributions to begin with. In Lake Constance, no gaps (i.e., size ranges without detectable biomass) are observed within the Sheldon-type biomass size spectra (Figs. 2, 3). Furthermore, in a first approximation, plankton biomass is roughly evenly distributed over all logarithmically scaled size classes ranging from bacteria (10^{-14} gC/cell) to carnivorous crustaceans (10^{-4} gC/ind.) based on seasonal averages (Fig. 2a). Along a size gradient of almost 11 orders of magnitude, maximum and minimum biomasses per size class differ by a factor of 24 in a size spectrum averaged over seven years of investigation (size classes -2 to 2 omitted). Especially when considering individual phases during the seasonal development, some deviations from the roughly equal distribution of biomass across logarithmic size classes are found. High biomasses per size class frequently occur in the size ranges of bacteria, large net phytoplankton, and daphnids (Fig. 2b). The trough between bacteria and larger phytoplankton in the size range of small autotrophs (size classes -2 to 2) may partially be an artefact of counting techniques and will not be further evaluated (see method section). A second trough occurs in a range where very large ciliates, large rotifers, and copepod nauplii overlap in size (Fig. 2b, size classes 15 to 18). The large ciliate and rotifer taxa were assessed with low accuracy owing to relative small counting volumes. Averaged over the season, the normalized biomass size spectrum (Fig. 2c) fits closely to a straight line with a slope near to -1.

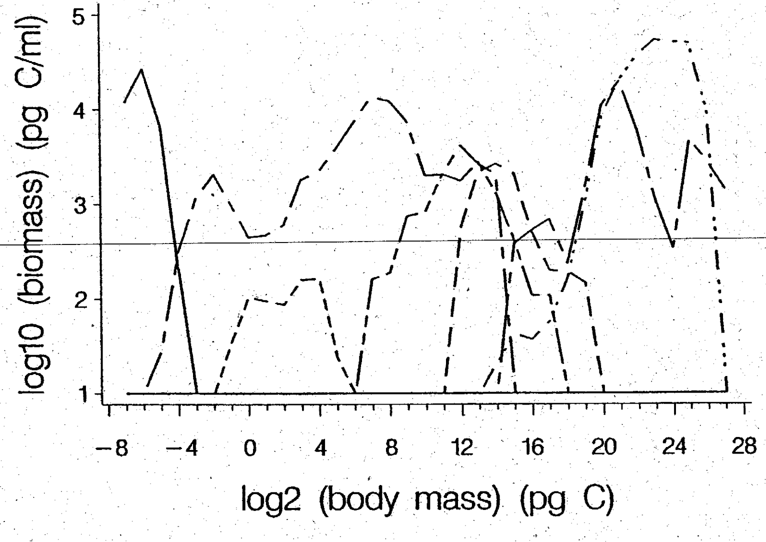
The shape of the size distributions exhibits recurrent seasonal changes in Lake Constance. In early spring, small organisms such as small phytoplankton and small ciliates dominate, whereas abundances of the largest crustaceans are frequently below the level of detection which gives rise to a more irregular size spectrum (Fig. 3a, note the logarithmic scale on the y-axis). During and after the clear-water phase, a completely different picture is found with few small and many large organisms (Fig. 3b). The latter, which are mostly represented by daphnids, form a dominant fraction of the total plankton biomass, whereas the preceding size range and that of small, highly edible algae are depleted. At this time, the size spectrum is most irregular as judged by the goodness-of-fit of a straight line to the normalized biomass size spectrum (see below). In contrast, in midsummer, the most regular size distributions are observed with an approximately equal biomass in all size classes except for algae and no dominance of a consumer group or a certain size range (Fig. 3c). This can also be inferred from the goodness-of-fit of a straight line to the normalized biomass size spectrum, which often reaches maximum values in midsummer followed by sampling dates in late spring (cf. Fig. 4b). The ratio between minimum and maximum biomass per size class amounts to ten in midsummer (seven-year average, size classes -2 to 2 omitted). Most pronounced deviations from a uniform distribution of biomass across logarithmically scaled size classes occur within the size range dominated by phytoplankton during this time. Small and mainly highly edible algae have relatively low biomass, whereas biomass accumulated in larger phytoplankton which can mostly not be as readily consumed by herbivores.

Seasonal changes of the steepness of the size distribution originate to a large extent from the pronounced seasonal variability of crustacean biomass since bacterial abundance varies relatively little throughout the year and interannually. Regression analyses was used to evaluate potential relationships between daphnid biomass (representing two single populations) and the slope and shape of the size distribution (representing the entire plankton food web) (Fig. 4). The slope of a straight line fitted to the normalized biomass size spectra was positively and highly significantly related to the logarithm of the biomass of daphnids ($r^2=0.67$, $n=240$), of all herbivorous crustaceans ($r^2=0.75$), and of all crustaceans ($r^2=0.69$). The slightly lower coefficient of determination of the regression with daphnid biomass originates from the

a) early spring



b) clear-water phase



c) midsummer

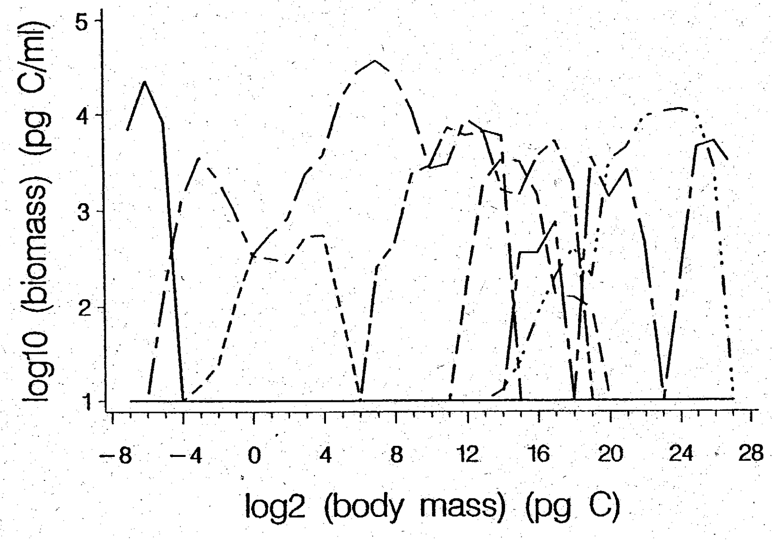


Fig. 3. Seasonal changes of the plankton biomass size spectrum in Lake Constance averaged over the years 1987-93 and 0-20 m. a) Early spring, b) during and after the clear-water phase when daphnids reach maximum densities, c) midsummer (for further details, see legend of Fig. 2b). Note the logarithmic scale of the y-axis and the extremely low biomass of the largest crustaceans in early spring.

negligible impact of daphnids in late winter and early spring. Below a daphnid biomass of about 200 mgC/m^2 which is typical for late winter and early spring, slopes vary independently of daphnid biomass at a medium or low level. At higher daphnid concentrations, a close correlation exists between daphnid biomass and the slope. The latter reaches the least negative values when daphnids are at their maximum (Fig. 4a), and no steep slopes occur at high daphnid abundance. For a given abundance of daphnids, slopes are considerably steeper in early spring when a first phytoplankton bloom builds up than in late winter when, e.g., algal and ciliate abundances are lower (Fig. 4a). The latter is one example for the fact that the slope reflects properties of the entire plankton community which cannot simply be derived from daphnid or crustacean biomass, especially during periods when these organisms are not dominating.

A pattern similar to the dependence of the slope on daphnid biomass is found when considering the coefficient of determination (r^2) of a straight line fitted to the normalized biomass size spectrum which indicates the smoothness or bumpiness of the size distribution. The value of r^2 varies between 0.93 and 0.98 independent of daphnid abundance when the latter is below 200 mgC/m^2 (Fig. 4b). Highest values of r^2 are found when daphnids co-exist with numerous other plankton organisms at medium densities in midsummer which gives rise to a rather smooth size distribution (Figs. 3c, 4b). They decrease with increasing daphnid abundance and may fall well below minimum winter levels when daphnids become very abundant during or shortly after the clear-water phase (Fig. 3b). Hence, mass developments of daphnids entail more irregular distributions of biomass across size than those found in winter.

The relative contribution of daphnids to total plankton biomass represents another measure than the absolute amount of daphnid biomass to quantify the potential impact of daphnids on the plankton food web. In agreement with the results given above, the logarithm of the relative contribution of daphnids, or of all herbivorous crustaceans, to total plankton biomass explains 69 and 76%, respectively, of the seasonal and interannual variability of the slope. Again, a weak or no correlation was found when the share of daphnids (or herbivorous crustaceans) is low, whereas a close relationship exists when daphnids contribute a large proportion to plankton biomass. The impact of daphnids on the slope originates on the one hand from the accumulation of biomass in some large size classes (about 5 out of 35) and on the other hand from the depletion of biomass around the size range of edible algae. To conclude, daphnid abundance strongly influences the slope and shape of the plankton size spectrum directly and indirectly, the functional consequences of which will be discussed below.

The impact of daphnids on the biomass within individual size classes varies along the size gradient and throughout the season. For all sampling dates at which daphnid biomass exceeded 200 mgC/m^2 (cf. Fig. 4), linear regression lines were fitted to the relationship between the logarithm of daphnid biomass and the logarithm of the biomass within each size class. Fig. 5 shows an example for size class 4. The slopes and the coefficients of determination of the regression lines belonging to the individual size classes were plotted along the size gradient (Fig. 6) in order to identify potential temporal covariations between daphnid biomass and the biomass within certain size ranges smaller than the body mass of daphnids (i.e., size classes -7 to 19). Biomasses in most of these size classes were negatively related to daphnid biomass. However, the scatter within the individual relationships and the variability between consecutive size classes were high when considering all data with daphnid biomass exceeding 200 mgC/m^2. Only the biomass of ciliates in the size range of 100-130,000 pgC (except for one size class) decreased highly significantly with daphnid biomass ($n = 154$, $p < 10^{-4}$-10^{-5}, data not shown).

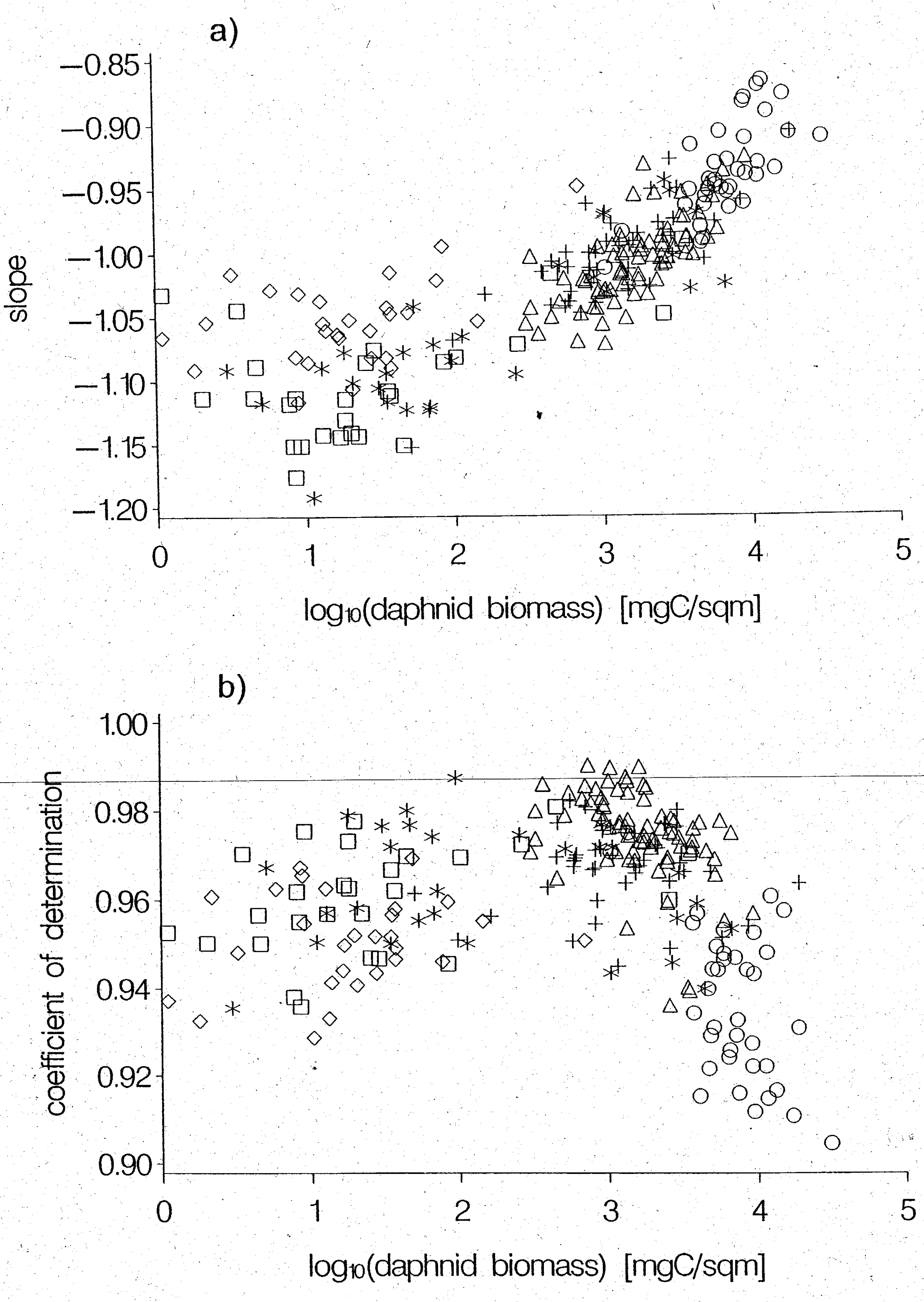


Fig. 4. Relationship between daphnid biomass (expressed in mgC/m^2 on a logarithmic scale) and a) the slope and b) the coefficient of determination (r^2) of a straight line fitted to the normalized biomass size distribution established for individual sampling dates ($n = 247$). The annual cycle is subdivided into different phases: diamond – late winter, square – early spring, star – late spring, circle – clear-water phase and subsequent period of mass abundance of daphnids, triangle – mid- and late summer, cross – (late) autumn and early winter (for details of phase definitions, see GAEDKE & STRAILE 1994, STRAILE 1998).

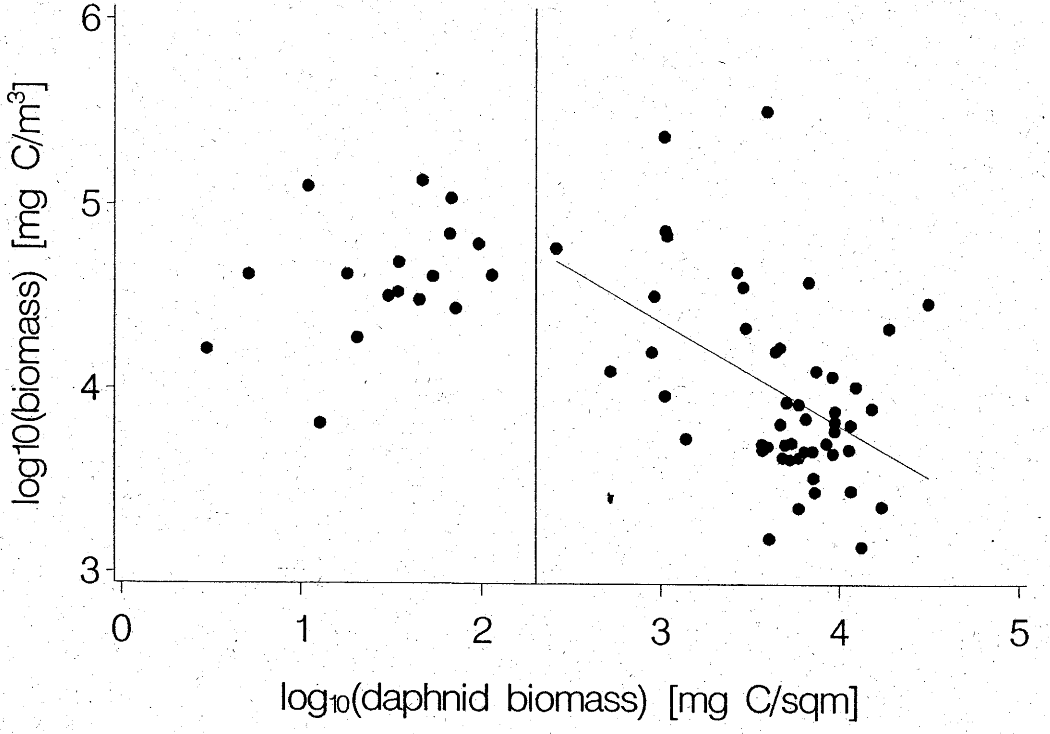


Fig. 5. Relationship between daphnid biomass (expressed in mgC/m^2 on a log$_{10}$-scale) and the biomass (expressed in mgC/m^3 averaged over the depth of 0-20 m on a log$_{10}$ scale) of all organisms falling into size class 4 on a log$_2$ scale (i.e., with a body weight of $2^{3.5}$-$2^{4.5}$ = 11-22 pgC) during late spring, the clear-water phase, and the subsequent period of mass abundance of daphnids. A typical species falling into this size class is the highly edible algae *Rhodomonas minuta*. Potential covariations between daphnid biomass and the biomass within individual size classes were evaluated by fitting a regression line to all observations with a daphnid biomass of more than 200 mgC/m^2.

More distinct patterns were found when including only sampling dates (n = 50) during the period from (late) spring, when daphnid biomass has increased to at least 200 mgC/m^2, until the end of daphnid mass abundance during or shortly after the clear-water phase. During this late spring/early summer period, the non-migrating *Daphnia galeata* dominates, and nutrient depletion is less severe and the plankton community is less diverse than during the subsequent period in mid- and late summer. In late spring/early summer, the size classes -7 and -6 on a log$_2$ scale which represent small bacteria with cell sizes of 0.006-0.02 pgC were not related to

Table 1. Seasonal changes of average predator-prey weight ratios and of the relative contribution of feeding links with predator-prey weight ratios above 10^6:1 to all feeding relationships within the plankton community of Lake Constance.

time interval	mean predator-prey weight ratio	contribution of links with ratios > 10^6 : 1
early spring	400 : 1	2%
clear-water phase/daphnid maximum	6000 : 1	15%
midsummer	1000 : 1	6%

daphnid biomass (Fig. 6a). In contrast, negative relationships were found between daphnid biomass and the biomass in the subsequent size classes (-4 to 5, i.e. 0.06-32 pgC). In the following size range, the slopes of the regression lines remained negative. However, the variability explained by daphnid biomass was mostly low and only a few of the relationships were statistically significant (Fig. 6a). When performing the same procedure for all sampling dates during mid- and late summer with a daphnid biomass exceeding 200 mgC/m^2 ($n = 98$), hardly any significant relationships were found between the biomass in individual size classes and daphnid biomass.

The impact of daphnids on individual size ranges can be further analysed by considering individual plankton groups separately. During late spring/early summer, small autotrophs falling into the size classes -6 to 5, i.e., autotrophic picoplankton with cell sizes from 0.01 pgC onwards and small eukaryotes up to 32 pgC, were often strongly negatively influenced by daphnids ($p = 0.00004$ to 0.01), whereas larger net phytoplankton and small bacteria (size classes -7 to -6 or -5) were not (Fig. 6b). In mid- and late summer, hardly any statistically significant relationships were found. Heterotrophic flagellates in the size range of about 0.1-32 pgC correlated negatively with daphnid abundance in late spring/early summer ($p < 10^{-4}$) (Fig. 6c) and on an seasonal average, but not in mid- and late summer. A similar pattern was found for ciliates in the size classes 8 to 15 (200-30,000 pgC). Especially biomass of medium sized ciliates correlated negatively with daphnid biomass in late spring/early summer ($p = 0.001$-0.05) (Fig. 6 d) but not in mid- and late summer. The size class specific biomasses of rotifers did not covary with daphnid biomass. It should be repeated that the coefficients of determination of these relationships are generally low (cf. Figs. 5, 6) which indicates that daphnids may represent only one out of several potential factors influencing biomass of small plankton organisms.

Impact of daphnids on average predator-prey weight ratios

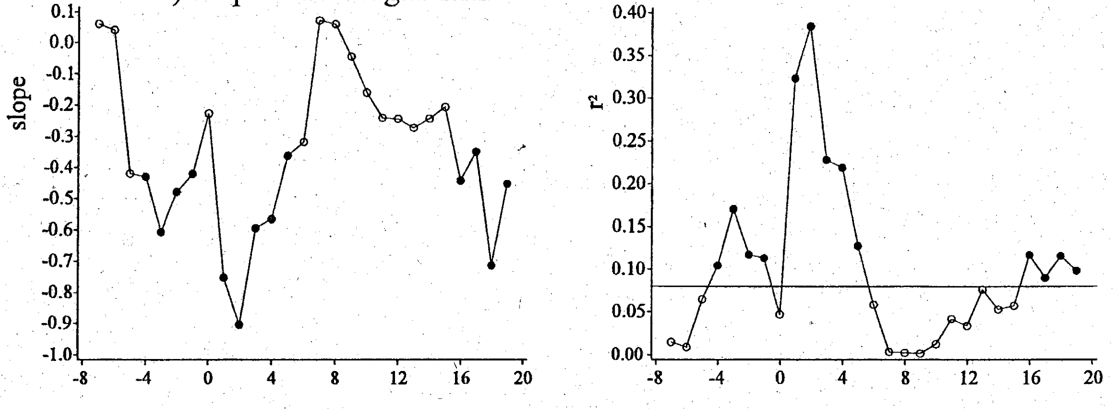
Average predator-prey weight ratios within the plankton food web quantify the “step size” by which primary and bacterial production is transferred along the size gradient from small to larger-sized organisms by trophic interactions. Larger predator-prey weight ratios imply a lower number of “steps” (i.e. feeding relationships) to transfer primary production to large top predators in pelagic food webs. The number of steps is important for energetic considerations as each trophic interaction involves losses by, e.g., respiration and excretion. Mean predator-prey weight ratios within the plankton food web of Lake Constance vary seasonally (Table 1). In early spring, small consumers (Fig. 3a) and low weight ratios prevail. Largest values are found during daphnid peak abundances and intermediate ones during midsummer. The contribution of feeding links with predator-prey weight ratios larger than 10^6:1, i.e., of filter feeders taking extremely small particles, to the total energy flow within the food web closely follows the relative importance of daphnids (Table 1).

Discussion

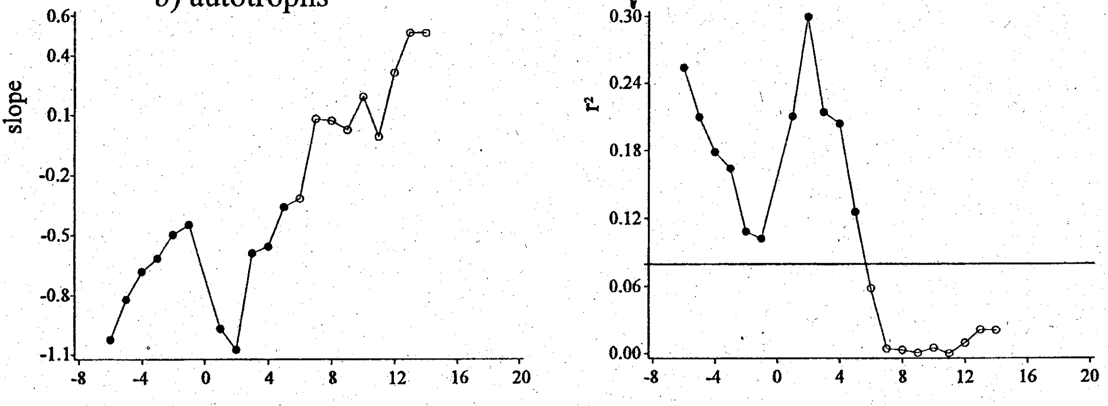
Population dynamics of daphnids

A simple inspection of standing stocks and production rates of the plankton community in Lake Constance revealed that daphnids are a major component of the pelagic food web of Lake Constance on an annual average, and that they dominate zooplankton biomass and activity

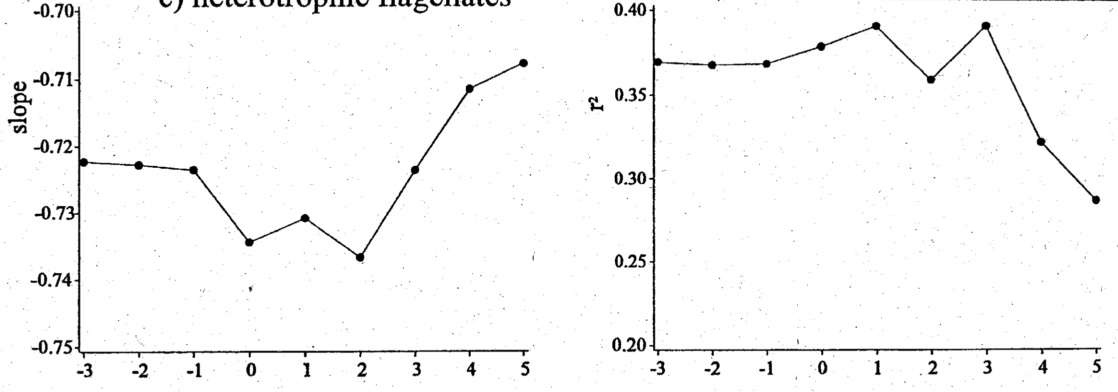
a) all plankton organisms



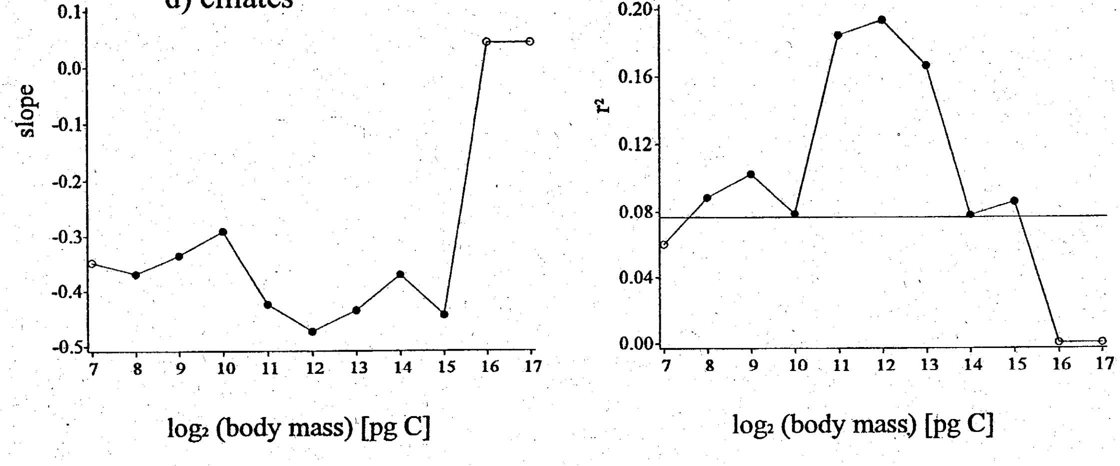
b) autotrophs



c) heterotrophic flagellates



d) ciliates



during several weeks in late spring/early summer and often also in autumn, but not otherwise. Remarkably, on an annual basis, ciliates may consume more phytoplankton than daphnids (Gaedke & Straile 1994a). However, they do not cause features comparable to the clear-water phase which is the most prominent event of biological origin in the seasonal cycle. It may be speculated that systems ruled by a keystone species exhibit a higher sensitivity to external changes affecting this species (e.g., stocking of planktivorous fish, weather conditions) than other systems with a larger variety of interconnected feeding pathways. In accordance, a striking relationship between the timing of the clear-water phase and the water temperature in winter and spring was found which is most probably caused by the temperature sensitivity of daphnids (Gaedke et al. 1998, Straile & Geller 1998). Weight specific metabolic rates of daphnids are lower than those of the small plankton organisms such as algae and ciliates dominating in spring. This results in a decline of the ratio between production and biomass of the entire plankton community from early spring to summer (cf. Straile 1998).

Impact of daphnids on the plankton biomass size distribution and on individual size ranges

On an annual average, a continuous and almost flat size distribution with high accumulations of biomass per size class in the size ranges of bacteria, net phytoplankton, and daphnids was observed (Fig. 2). Similarly shaped size spectra were found when considering the entire water column of Lake Constance rather than the uppermost 20 m (Gaedke 1992a, or open marine systems (e.g., Sheldon et al. 1972, Rodriguez & Mullin 1986), but not in a small, shallow lake (Echevarría et al. 1990). They were supposed to arise from specific properties of the pelagic food web and habitat (Sheldon et al. 1977). Potential reasons for biomass accumulations in certain size ranges which cause or enhance deviations from the overall regularity may be inferred from specific properties of the groups of organisms falling into the respective size ranges. High biomasses in the size range of bacteria may be related to observations that a substantial fraction of the particles allocated to the group of free-living bacteria is metabolically almost inert and subject to little grazing pressure (Jürgens & Güde 1994, Gasol et al. 1995). A predominant flow of matter and energy from small to large organisms may be assumed for pelagic systems. In this context, biomass accumulation in the size range of net phytoplankton may be attributed to a less efficient flow of matter towards larger organisms owing to their higher grazing resistance. An explanation for the capability of daphnids to build up a relatively high biomass in their size range emerges from a comparison of prey size ranges within the plankton community. Daphnids exploit an exceptionally wide prey size range which includes extremely small prey organisms such as small algae (e.g.,

Fig. 6. The impact of daphnids on differently-sized organisms inferred from the slopes (left panel) and coefficients of determination, r^2, (right panel) of regression lines fitted to the relationship between daphnid biomass and the biomass within individual size classes observed in late spring/early summer 1987-93. An example is provided in Fig. 5. The size classes 20-25 comprise daphnids and were excluded to avoid auto-correlation. Slopes of regression lines with r^2-values above the horizontal lines in the right panel are significantly different from zero at least at the 5-% level (for details see text). a) all plankton organisms, b) autotrophs (lacking reliable measurements, size class 0 was neglected, see method section), c) heterotrophic flagellates (all relationships are significant at more than the 0.01% level), d) ciliates. Note the different scales on the y-axes.

Bern 1994, Hansen et al. 1994) which have high weight-specific rates. The latter provide an energetic potential for a high biomass accumulation of predators which are much larger and, consequently, have considerably lower weight-specific energy demands. Other effects of the wide prey window of daphnids which are likely to enhance their monopolization of biomass are that they prey upon competitors for resources such as ciliates and small rotifers, i.e., beyond exploitation competition they exert intra-guild predation and/or interference competition (Gilbert 1989, Jack & Gilbert 1993, Wickham & Gilbert 1993, Wickham et al. 1993). Biomass accumulation per size class in the size range of daphnids may also be enhanced by predator avoidance by diurnal vertical migration which additionally reduces metabolic demands owing to low ambient temperatures.

The analysis of the temporal covariation of daphnid biomass with the biomass within individual size classes of all plankton organisms or selected groups suggested an impact of daphnids on organisms in the size range of about 0.06-32 pgC and on ciliates up to 30,000 pgC during late spring/early summer (Figs. 6a, 6d). This period is characterized by a dominance of well-edible phytoplankton (Gaedke 1998, her Fig. 7) and frequently by relatively high, but declining abundances of heterotrophic flagellates, ciliates, and rotifers (Weisse 1991, Weisse & Müller 1998). Phosphorus depletion is less pronounced than in mid- and late summer (Güde & Gries 1998) and C:P-ratios of phytoplankton indicate only a moderate P-limitation (Hochstädter 1997). Daphnids have increased from low winter values to maximum abundances and predominate the herbivorous plankton during most of this time (Fig. 1).

All relationships discussed here were statistically significant at the 5-% level and most of them are significant at a much higher level, i.e., overall results remain significant after accounting for the large number of regression analyses performed. Nevertheless, the coefficients of determination were mostly low (Figs. 5, 6b) which indicates that daphnid biomass explained at most a moderate fraction of the entire variability of the biomass per size classes. This prevented us from comparing in detail the extent of covariation of specific size classes with daphnid abundance and reminds us that a covariation of two quantities does not proof a direct causal relationship between them. The present analysis is restricted to one lake and enables only a temporal comparison between sampling dates with different daphnid abundances (s. below). However, besides daphnid abundance, numerous other factors change seasonally which potentially influence the plankton composition as well. This study covers 247 sampling dates and 7 years of investigation during which weather conditions varied greatly. The latter, in turn, influenced, e.g., autotrophs and daphnids in different ways (Gaedke & Weisse 1998, Gaedke et al. 1998, Straile 1998). This reduces the covariation of plankton groups by external forcing and enhances our ability to identify the impact of daphnids.

No covariation was found between daphnid biomass and the biomass of the smallest size classes (-7 to -5, i.e. ca. 0.006-0.04 pgC) which comprise mostly bacteria. This finding is in accordance with laboratory studies showing that daphnids do not graze the smallest bacteria (Knisely & Geller 1986, Jürgens & Güde 1994) and with concepts on the functioning of the planktonic food web. High abundances of daphnids may exert a grazing pressure on larger-sized bacteria but also on their predominant predators, the heterotrophic flagellates (Güde 1988, Weisse 1991). Hence, a trophic cascade going from daphnids via heterotrophic flagellates to bacteria may cause a positive indirect effect of daphnids on bacteria. For Lake Constance, the validity of this mechanism was supported by the pronounced negative relationship between daphnid biomass and that of heterotrophic flagellates (Fig. 6c) and by the positive relationship between the biomass of herbivorous crustaceans (dominated by daphnids) and the ratio between the biomass of bacteria and heterotrophic flagellates (Straile 1998).

In contrast to bacteria, biomass in the size range dominated by APP covaried inversely with daphnid biomass in late spring/early summer, but not later on during the season. This finding agrees with a study of the long-term population dynamics of picocyanobacteria dominating APP in Lake Constance which indicates an inverse temporal covariation of daphnid and picocyanobacterial abundance around the clear-water phase, but not later on (Gaedke & Weisse 1998, their Fig. 4). The coincidence of low biomass of small eukaryotic algae (mostly size classes 2-5, i.e., 4-32 pgC, 20-200 μm^3 cell volume) and of small heterotrophic flagellates of about 0.1-32 pgC (0.4-150 μm^3 cell volume) with high daphnid biomass is in accordance with numerous laboratory studies on the feeding ecology of daphnids (e.g., Hansen et al. 1994, Jürgens 1994, cf. Larsson & Weider 1995).

Our *in situ* observations suggest that small and medium-sized ciliates may be depressed by daphnids at least in late spring/early summer. This indicates that numerous ciliates may be more vulnerable to high daphnid abundances than most equally-sized autotrophs under natural conditions. The largest ciliates exhibiting an inverse covariation with daphnid biomass had cell sizes of 8,000-33,000 pgC (up to 130,000 pgC when considering the entire season) corresponding to about 52,000-200,000 (800,000) μm^3 cell volume and roughly 40-80 (120) μm ESD. As this cell size is beyond the preferred food particle size of daphnids (e.g., Knisely & Geller 1986, Bern 1990, 1994, Hansen et al. 1994), other mechanisms than direct predation are likely to cause the more pronounced covariation of daphnids with ciliates than with equally-sized autotrophs. In contrast to autotrophs, ciliates may be adversely affected by daphnids by exploitative competition for common resources and by interference competition (Duncan 1989, Wickham & Gilbert 1993).

Remarkably, no relationships between daphnid and rotifer biomasses in the respective size classes were found. This contradicts observations that high abundances of daphnids may suppress rotifers by exploitation and interference competition and some species also by direct predation (Duncan 1989, Gilbert 1989, Wickham et al. 1993). However, the latter is supposed to be less important than for most ciliates, and interference competition is mostly restricted to daphnids of more than 1.2 mm in length (Burns & Gilbert 1986). A considerable fraction of the daphnids at Lake Constance are below this size especially in late spring/early summer. Our present approach of relating daphnid and rotifer biomasses to each other at individual sampling dates is presumably less sensitive to detect the effect of exploitation competition than direct predation as the former acts on a larger temporal scale.

To conclude, for late spring/early summer, our in situ study of the size ranges of organisms exhibiting a covariation with daphnid biomass delivers results which are comparable to laboratory studies on the size selectivity of daphnid feeding. It indicates for this period a dominant role of daphnids among the potential factors influencing natural plankton dynamics which enables an extrapolation of laboratory studies to field conditions. Our field data suggest that ciliates, but not equally-sized autotrophs were negatively affected by daphnids, probably owing to a lower grazing resistance and to exploitation competition besides direct predation. In mid- and late summer, hardly any relationships between daphnid biomass and biomass per size classes were found. Since daphnids may achieve relatively high abundances during this time as well (Figs. 1, 4), this points to a more diverse control of the potential prey organisms including increased bottom-up effects owing to the more severe nutrient depletion (Hochstädter 1997).

The impact of daphnids on size distributions can be investigated by either comparing periods with different daphnid abundances within one lake or by cross-lake comparisons as both approaches have their advantages and limitations. Biomass size distributions of three lakes where daphnids (and carnivorous cladocerans) play a less important role or are absent year round exhibit also biomass accumulations in the size range of bacteria and (net) phytoplankton on an annual or seasonal average and relatively low biomasses in the size range following large phytoplankton (oligotrophic Lake Königssee, Barthelmess 1995; South Chilean oligo- and oligo-mesotrophic L. Pirehueico and L. Rinihue, Wölfl 1995). Consequently, these patterns appear to be independent of daphnid abundance which is within the line of arguments provided above. In accordance with the present study, investigations of the seasonal cycle of the plankton community in a rather small, highly eutrophic lake and of individual samples from 28 oligo-mesotrophic to hypertrophic lakes in Northern Germany revealed a high impact of daphnids on the shape of the plankton size distributions (Tittel 1997, Tittel et al. 1998). The slopes of these spectra were positively related to daphnid abundance whereas the coefficient of determination decreased with increasing daphnid abundance. Details of the relationship between slope and daphnid abundance may differ between these small lakes and Lake Constance. During daphnid mass developments, "empty" size classes were found in the preferred prey size window of daphnids (5-30 µm ESD which corresponds approximately to 2^3-2^{11} pgC and is mostly represented by nanophytoplankton, heterotrophic flagellates, and ciliates) or less frequently in the size range of potential competitors (40-160 µm ESD, ca. 2^{12}-2^{18} pgC, rotifers, nauplii). Hence, the influence of daphnids on the size distributions in the small and often eutrophic lakes was qualitatively similar, but presumably more pronounced than in large L. Constance. Communities with low daphnid abundances did not always exhibit smooth size spectra whereas communities with moderate daphnid densities occasionally had fairly regular ones (Tittel 1997, Tittel et al. 1998). The threshold daphnid biomass above which daphnids exerted a dominant impact on the size spectra amounted to about 0.5 mg FW/l. This value corresponds to ca. 190-340 mgC/m^2 within the epilimnion which is similar to the value found in the present study (Tittel 1997, Tittel et al. 1998).

The impact of daphnids on the trophic transfer efficiency

The slope of a straight line fitted to a normalized biomass size spectrum and the deviations from this line provide useful measures to characterize the shape of the size distribution. Above of that, the slope contains valuable information about the efficiency to transfer matter and energy within the food web underlying the observed biomass size distribution (Gaedke 1993, Gaedke & Straile 1994b). Flat size spectra and an approximately equal size range (on a log scale) covered by each trophic level (i.e., roughly equal biomass of predator and prey) indicate that size-related differences in weight-specific metabolic rates of autotrophs, herbivores, and carnivores compensate the losses implied by the transfer of energy from one trophic level to the next (Sheldon et al. 1972). Such spectra are approximately observed on seasonal average and in midsummer in Lake Constance (Figs. 2, 3, for biomasses of individual trophic levels compare Straile 1995, Gaedke et al. 1996). The steepness of a size spectrum's slope reflects the efficiency to transfer biomass from small to larger-sized organisms. A more negative slope, such as it is observed during the vernal phytoplankton bloom, implies that a relatively large amount of small organisms (autotrophs) supports only a relative small biomass of larger ones (mostly herbivores). This indicates that the efficiency of transferring biomass along the size gradient by trophic interactions is low. This efficiency depends on (1) the trophic transfer efficiencies involved in each predator-prey interaction, and on (2) the average predator-prey weight ratios which determine the "step size" by which biomass is transferred along the size gradient (Borgmann 1982). The trophic transfer efficiency is the ratio between predator and prey production and depends on the exploitation and growth efficiencies which, in turn, may depend on food concentrations (Straile 1997). If predators are only moderately larger than their prey items, a larger number of trophic interactions is required to transfer, e.g., bacterial production to large crustaceans as compared to food chains dominated by filter feeders with large predator-prey weight ratios. Consequently, the transfer efficiency along the size gradient (or "particle-size-conversion efficiency", Borgmann 1982) tends to be higher when filter feeders dominate. To summarize, a rough estimate of trophic transfer efficiencies may be derived from the slope of biomass size spectra which indicate the transfer efficiency along the size gradient if average predator-prey weight-ratios can be estimated (Sprules 1988, Gaedke 1993).

Steepest slopes are found in early spring (Figs. 3a, 4a) when a high primary production by small algae is presumably incompletely consumed by small herbivores occurring at relatively low densities (Gaedke & Straile 1994a). Around June, high daphnid abundances give rise to the least negative slopes of the normalized biomass size spectrum and corresponding Sheldon-type size distributions exhibit a biomass increase with size (Figs. 3b, 4a). This indicates maximum transfer efficiencies along the size gradient. They are partially achieved by very high predator-prey weight ratios (Table 1). Furthermore, the finding of high transfer efficiencies along the size gradient implies that the losses involved in each trophic transfer are low, i.e., that trophic transfer efficiencies are high. During midsummer when daphnids occur among smaller herbivores at medium abundances, average predator-prey weight ratios within the plankton community are lower (Table 1). As expected, observed slopes become more negative (Figs. 3c, 4). The moderate decrease of slopes by about 0.06-0.07 units (maximum 0.09) from the maximum daphnid abundance to midsummer despite declining predator-prey weight ratios indicates that the trophic transfer efficiency remains consistently high throughout summer during all years of investigation (cf. Gaedke & Straile 1994b, Straile 1995). The finding of maximum transfer efficiencies along the size gradient during maximum daphnid development is in agreement with measurements by Wylie & Currie (1991). They found a considerably higher efficiency to transfer picoplankton production to crustaceans when cladocerans dominated rather than copepods which was explained by the capability of cladocerans to bypass intermediate trophic levels. Some indirect evidence for an increased transfer efficiency to larger-sized organisms at high *Daphnia* abundances is also provided by Pace et al. (1990) who found a strong dependence of the fate of bacterial production and that of other small organisms on the composition of bacterial consumers (e.g. flagellates, daphnids).

Comparison with other ecosystem approaches

The findings on the role daphnids obtained by direct comparisons of biomass and production of different plankton groups and from biomass size distributions can partially be supplemented and controlled by other ecosystem approaches, such as mass-balanced flow diagrams (trophic food webs) and binary food webs (Lang 1997). Both approaches have been applied to the pelagic food web of Lake Constance. Analyses of trophic webs (Gaedke & Straile 1994a, Straile 1995, Gaedke et al. 1996) revealed that daphnids monopolize the carbon fluxes between living components of the pelagic food web of Lake Constance during their mass development and contribute 65-80% to the total grazing pressure on phytoplankton during and shortly after the clear-water phase (cf. Straile 1998, his Fig. 1). The flux diversity within the food web decreases owing to the dominance of a few very large fluxes.

The mass-balanced flow diagrams confirmed the hypothesis derived from the size distributions that trophic transfer efficiencies are low in early spring and high from the mass development of daphnids onwards throughout summer (Gaedke & Straile 1994b), i.e., trophic transfer efficiencies do not covary with daphnid abundances as closely as the transfer efficiency along the size gradient inferred from the slope. This supports the point of view that trophic transfer efficiencies depend more strongly on food concentrations than on the type of consumers and the predator-prey weight ratio (Straile 1997).

The finding derived from the slope of the size spectra that daphnids increase the efficiency of the transfer of matter and energy along the size gradient is also confirmed by a comparison between the trophic positions and average body weight of the predominantly herbivorous groups in Lake Constance during different seasonal stages (Straile 1995). Trophic positions of omnivorous consumers may be computed from flow diagrams and reflect the average number of trophic transfers food items passed before being eaten by the given consumer. They are calculated as the weighted average of the lengths of a population's various feeding pathways (Wulff et al. 1989). In early spring, dominant herbivores (i.e., ciliates and omnivorous copepods) are (considerably) smaller than daphnids and trophic positions increase more strongly with size than during the clear-water phase (Table 2). The relationship between body size and trophic positions in pelagic food webs (Gaedke et al. 1996, their Fig. 1) represents

Table 2. Relationships between the seasonal changes of the dominant herbivores, their trophic position (Straile 1995), their body weight, and of the trophic transfer efficiency (TTE) (Gaedke & Straile 1994b, Straile 1995). The trophic position represents the average number of trophic transfers food items passed before being eaten by the given consumer. The TTE represents the ratio between predator and prey production. Assuming that the size of the predominantly grazed autotrophs remains constant, the seasonal changes of body weight of the predominantly herbivorous organisms having similar trophic positions show that the step size by which autotrophic production is transferred along the size gradient varies seasonally. The step size, in turn, determines in concert with the TTE the seasonal changes of the transfer efficiency along the size gradient (i.e., the "particle-size-conversion efficiency", Borgmann 1982). The TTE varies seasonally as well. However, these changes are presumably more attributable to differences in resource supply than to the type of herbivores or the predator-prey weight ratio (Gaedke & Straile 1994a, 1994b, Straile 1997).

period	dominant herbivorous group	trophic position	mean body weight (pgC)	TTE
early spring	ciliates	2.2	$5*10^3$	10-20%
	copepods	2.2-3.1	10^6	
clear-water phase/ daphnid maximum	daphnids	2.2	10^7	at least 20-35%
midsummer	ciliates	2.2	10^4	at least 20-35%
	daphnids	2.4	10^7	

one of their outstanding regularities not found in the food webs of other habitats. The low trophic position of daphnids in relation to their large body size introduces scatter into this first order regularity (Table 2).

To summarize, biomass size spectra represent highly aggregated models which appear capable of explaining the major energy flows (VEZINA 1986, GAEDKE & STRAILE 1994b) without considering structural details of the food web (BORGMANN 1982). Advantages of this more holistic approach include that only a moderate amount of measurements and a few general assumptions are required to estimate energy fluxes (GAEDKE 1995). A disadvantage of size spectra is that details of the food web structure can hardly be analysed. This hampers the recognition of potential mechanistic explanations of the processes which may underlie observed changes of the energy flow. For example, changes of the relative contribution of the grazing and detritus chain (i.e., of the fluxes based on primary and bacterial production) may pass unnoticed unless other techniques are applied additionally.

Comparison with other ecosystems

Non-selective filter feeding daphnids represent one out of several types of feeding modes found in pelagic systems. The present analysis demonstrates that filter feeders with broad feeding abilities and a high reproductive potential may build up mass developments during which they shape the food web structure and functioning. This is clearly reflected in system attributes, such as the shape and slope of the size distribution and the flow of energy. In marine systems, the crustacean zooplankton is dominated by calanoid copepods which cannot graze as efficiently as daphnids on small organisms and which have lower reproduction rates. However, some kinds of gelatinous zooplankton may represent a marine analog of daphnids in several respects. They have some, but not all physiological and ecological properties in common with daphnids (LEHMAN 1988). For example, tunicates are also characterized by the ability to grow rapidly and to achieve high filtration rates on a wide range of sizes and kinds of particles including cells which are too small to be used by most other grazers (ALLDREDGE & MADIN 1982). During tunicate mass developments, apparent exclusion of competing herbivores is found, mostly by mechanisms discussed for daphnids as well, such as high reproduction, intraguild predation, and suppressing food sources below the level of sustainable growth of the competitors. However, the fragile gelatinous body structure and patchy distribution greatly complicates the study of these organisms as compared to crustaceans and much less is known about their role in marine food webs (ALLDREDGE & MADIN 1982). This has so far prevented a rigorous and detailed analysis of their impact on entire food web attributes.

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