

## **Biomass allocation and carbon flow in the pelagic food web of Lake Constance**

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with 9 figures and 1 table

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**Abstract:** The seasonal succession of all major planktonic groups, i.e., phytoplankton, bacteria, heterotrophic flagellates, ciliates, rotifers, and crustaceans, was investigated during five years (1987-1991) of weekly sampling with elaborate sampling methods and microscopic countings. This allows to study the seasonal changes of the biomass and production allocation patterns within the epilimnetic food web of Lake Constance during five consecutive years. On an annual average, the contribution of phytoplankton, microbial plankton (including bacteria and protozoans), and metazoan zooplankton to the total planktonic biomass was approximately 30%, 30%, and 40%, respectively. Hence, heterotrophic biomass was on average twice as large as phototrophic biomass. In contrast, phytoplankton contributes 69% to the total production, whereas the share of microbial plankton and metazooplankton amounts to 19 and 11%, i.e., phototrophic production is twice the heterotrophic production. The seasonal biomass allocation pattern is characterized by a dominance of small organisms in early spring and of herbivorous crustaceans (mainly daphnids) during the clear-water phase and in early summer, when they contribute up to 66% of the total plankton biomass. Mass-balanced carbon flux charts could be established based on production measurements and estimates, which point to a high consistency of all measurements. However, initial production estimates of herbivorous crustaceans (calculated by the growth increment summation) during the clear-water phase and of ciliates (derived from an allometric relationship) during summer did not fit into the global network environment set up by the other measurements because of their failure to consider food limitation. The summer community exhibits a higher biomass allocation and carbon flux diversity and an increased importance of higher trophic levels as compared to the spring community. The heterotrophic biomass sustained by one unit of primary productivity in summer is twice the one in spring.

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### **Introduction**

The understanding of ecosystem dynamics and of the regulation of populations within an ecosystem requires extensive knowledge of the community structure and population interactions. Within an ecosystem, populations interact in a direct or indirect way with the outcome of certain population interactions possibly strongly modified by other populations of the food web (POLIS & WINEMILLER 1996). Furthermore, the interactions are not easily quantified by a single unit. Interactions which seem to be of minor importance based on the

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flow of energy between two populations may be of fundamental importance in terms of interaction strength (PAINE 1992, RAFFAELLI & HALL 1996) or in terms of nutrient flow. For example, bacteria are considered as a sink in terms of carbon, but can contribute substantially to the phosphorus supply of larger organisms (HESSEN & ANDERSEN 1990, HOCHSTÄDTER 1997). Additionally, the absence of an interaction between two populations at a physical scale may be a key to a better understanding of ecosystem functioning. For example, diel vertical migration of daphnids in Lake Constance, a successful predator avoidance behaviour, results in a minimization of the physical interactions between predator and prey populations. However, presence or absence of daphnids in the epilimnetic community will strongly affect the population dynamics, interactions, and carbon fluxes within the epilimnion.

Hence, a rather complete knowledge of all important taxa within an ecosystem is necessary for a thorough understanding of ecosystem functioning. Putting this idea into practise is hampered by the high diversity of living forms demanding a high diversity of sampling methods (VÉZINA & PLATT 1988). As a consequence, studies which consider all important functional groups within an ecosystem simultaneously are rare. Within the Special Collaborative Program "Cycling of Matter in Lake Constance", a large team of scientists has established such a data base for several complete annual cycles since 1987. This contribution examines the biomass allocation pattern in the pelagic zone of Lake Constance for the years 1987-1991 on a seasonal basis and extends the studies of 1987 (GELLER et al. 1991, GAEDKE & STRAILE 1994a, 1994b, GAEDKE et al. 1996) to five consecutive years. The allocation pattern can be considered as a result of all direct and indirect interactions of all interacting populations. Using carbon flow models, the energetic relationships between the different groups of pelagic organisms are examined, which also enables a consistency check of the production measurements of the individual taxa (GAEDKE & STRAILE 1994a).

## Methods

A large team of scientists sampled all relevant plankton groups ranging from bacteria to carnivorous crustaceans weekly throughout the growing season from 1987 to 1991 in the Überlinger See, the north-western part of deep ( $z_{\max} = 254$  m) and large (476 km<sup>2</sup>) Upper Lake Constance. For details on the sampling scheme regarding individual taxa see the relevant contributions in this volume (GAEDKE, HAESE et al., SIMON et al., STRAILE & GELLER, WEISSE & MÜLLER 1998). Body mass of individuals in units of carbon were established from body size and conversion factors obtained from measurements in Lake Constance or from the literature (for details see GAEDKE 1992, STRAILE 1995). Production of phytoplankton and bacteria (during 1990 and 1991) was measured with radioisotopic methods, i.e., <sup>14</sup>C-uptake of phytoplankton (TILZER & BEESE 1988) and <sup>3</sup>H-thymidine and <sup>14</sup>C-leucine uptake of bacteria (see SIMON et al. 1998). Bacterial production from 1987 to 1989 was calculated from bacterial biomass and bacterial P/B-ratios obtained in 1990/91. Growth rates of heterotrophic flagellates (HF) were measured in situ using the dilution technique (WEISSE 1991). Production of ciliates was calculated according to a multiple regression equation (MONTAGNES et al. 1988) which relates growth rate to cell size and temperature. The production of rotifers was calculated applying a modified weight-increment method assuming one weight increment from egg size to adult body size (PAULI 1991) and by calculating growth rates according to a growth-body size relationship (STEMBERGER & GILBERT 1985). Weight-increment production estimates were also used for herbivorous crustaceans and cyclopoid copepods (GELLER 1989,

WÖFL 1991). Production of the carnivorous cladocerans, *Leptodora kindtii* and *Bythotrephes longimanus*, was estimated employing P/B-ratios of 0.04 or 0.05 depending on prey concentrations (MORGAN et al. 1980). To conclude, production estimates of phytoplankton, bacteria, and HF were obtained by in situ measurements, whereas production estimates by the other groups were obtained by applying laboratory based size- and temperature-specific growth rates to the observed size structure of a group at ambient temperatures. It has to be kept in mind that the latter methods only partly account for food limitation occurring in situ.

One objective of the present study was to search for potential recurrent patterns in the seasonal changes of the plankton composition. The calendaric dates of individual events in the seasonal plankton development vary interannually owing, e.g., to differences in the timing of the vernal onset of stratification (GAEDKE et al. 1998). In order to aggregate comparable sampling dates from the different years of interest, the seasonal course was not subdivided using calendaric dates, but in up to 10 time intervals (early and late spring, the clear-water phase, etc.; for details on respective time intervals see result section) according to the actual seasonal dynamics of all available physico-chemical and biological parameters. This procedure resulted in a total of 44 time intervals within five years.

In total, more than 200 planktonic species or morphological types were distinguished within the routine sampling schemes. These organisms were allocated to seven compartments for the subsequent analyses: phytoplankton including autotrophic picoplankton, HF, ciliates, rotifers, "herbivorous" crustaceans (daphnids, *Bosmina*, *Eudiaptomus*), and "carnivorous" crustaceans (cyclopoid copepods, *Leptodora*, *Bythotrephes*). For the carbon flow models, pelagic fish (mainly coregonids) were additionally considered.

For each time interval, the carbon fluxes between the "living" compartments and the exchanges with the pool of "dead" organic matter were quantified and mass-balanced, i.e., the sum of the inputs into each compartment had to balance the sum of the outputs. Changes in standing stocks between time intervals, i.e., deviations from steady state conditions, were accounted for by the introduction of storage fluxes (GAEDKE & STRAILE 1994b). Estimates of the magnitude of individual fluxes were mostly based on the production estimates described and on some general assumptions on the diet composition of omnivores. Briefly, prey production was allocated to the respective predator compartments according to their carbon demands, which were assumed to be proportional to their production. This simple rule accounts for the omnivorous and opportunistic feeding behaviour of most pelagic predators. Omnivorous feeding behaviour was considered as the rule rather than the exception for all phago-heterotrophic planktonic compartments. Hence, the diet of "herbivorous" crustaceans consisted of phytoplankton, bacteria, HF, ciliates, and rotifers and the diet of "carnivorous" crustaceans of ciliates, rotifers, herbivorous and carnivorous crustaceans, and also phytoplankton. Feeding efficiencies on particular prey compartments may differ between predators. Given reliable evidence from the literature, the balancing routine allowed for modifications of the simple "proportional to productivity" rule. For example, HF were considered as more efficient bacterivores than ciliates, rotifers, or herbivorous crustaceans (JÜRGENS & GÜDE 1991). Carnivorous crustaceans, especially cyclopoid copepods, were regarded to prey more efficiently on ciliates than filter-feeding rotifers and herbivorous crustaceans (WICKHAM & GILBERT 1991, BURNS & GILBERT 1993, WICKHAM 1995). Hence, the diet composition of omnivores differed between the time intervals depending on the production of all potential prey compartments and the assumed efficiency of the predator to exploit them. The diet compositions calculated for each omnivorous compartment and time

interval were checked by literature data and by measurements from Lake Constance as far as possible. A detailed description of the quantification of the individual fluxes and the mass balancing procedure is provided by GAEDKE & STRAILE (1994b) and STRAILE (1995).

Non-grazing mortality was introduced to allow for sedimentation of large diatoms during summer (10% of biomass per day, GRIES 1995) and to account for viral mortality of bacteria (10% of bacterial production, HENNES & SIMON 1995). Ingestion/biomass ratios and gross growth efficiencies of compartments were calculated from the mass-balanced flux charts to control that they are within reasonable physiological bounds. A similar method to obtain mass-balanced flux charts is included in a computer program by HART et al. (1997) which is available upon request by the authors.

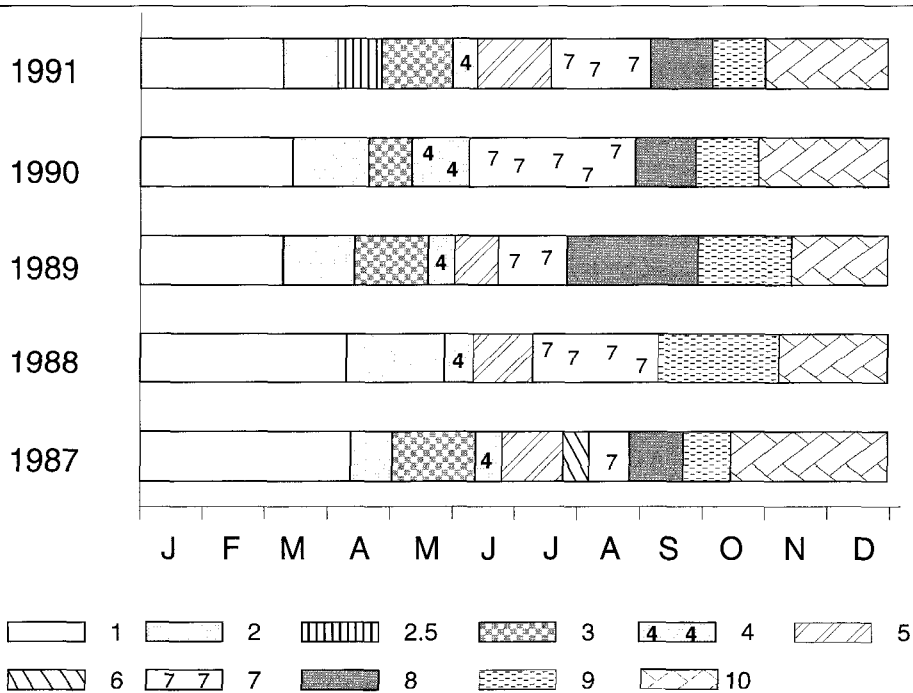
## Results

### Division of the seasonal cycle into time intervals

In the course of 1987, GELLER et al. (1991) identified 10 distinctive time intervals. Following their scheme, the subsequent four years were divided into seven (1988), eight (1990), nine (1989), and ten (1991) time intervals (TI) of unequal length lasting for two to fourteen weeks (Fig. 1). Not all seasonal events described during 1987 were encountered again during 1988 to 1991. Winter time intervals were the easiest to identify, starting after the autumnal decline of phytoplankton and lasting until the end of the year (TI 10) and from January 1st to the onset of stratification (TI 1). Spring was divided into 1 (TI 2, 1988), 2 (TI 2 and 3, 1987, 1989, 1990), or 3 (TI 2, 2.5, and 3, 1991) time intervals depending on the number of times the vernal algal development was interrupted by a re-increase of vertical mixing intensity (GAEDKE et al. 1998). The clear-water phase was defined according to Secchi-depth, chlorophyll concentration, and algal biovolume. Early summer (TI 5) may be regarded as the transition from the clear-water phase to the summer community with still high biomasses of herbivorous crustaceans and recovering biomasses of phytoplankton and protozoans. Every year, a summer peak of phytoplankton and especially ciliates could be identified (TI 7). In late summer (TI 8), biomasses of most groups were low, while in autumn (TI 9) a recovery of biomasses of phytoplankton and herbivorous crustaceans occurred. TI 6 represents a large flooding event, which interrupted the seasonal cycle in 1987.

### Biomass allocation

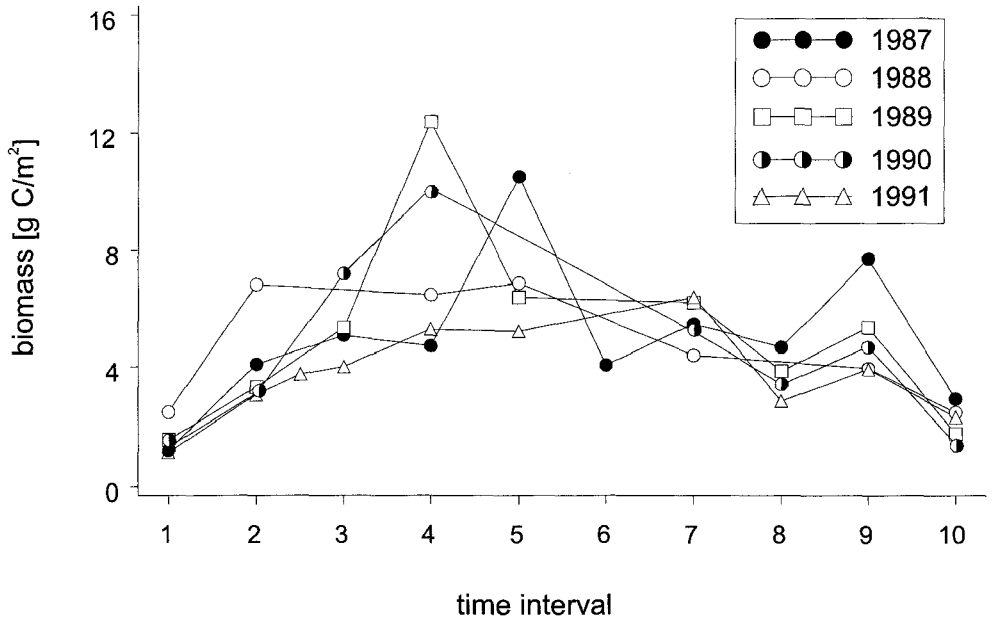
The average annual planktonic biomass in Lake Constance during the five years of study was remarkably constant at  $3.9 \pm 0.2$  g C/m<sup>2</sup>. Highest biomasses during the seasonal course were achieved during the clear-water phase and during the daphnid peak (TI 4 and 5) with the total planktonic biomass (TPB) exceeding 7 g C/m<sup>2</sup> (Fig. 2). TPB was lowest during late winter (TI 1) with approximately 1.5 g C/m<sup>2</sup>, intermediate during spring and summer, and showed a small peak in autumn (TI 9). As total planktonic biomass, the contributions of different groups to TPB reveal interannual and intraannual variability (Fig. 3). Nevertheless, a recurrent seasonal pattern is found: phytoplankton contributed as much as 50% to TPB during some spring time intervals, during the summer flooding in 1987 (TI 6), and occasionally during its midsummer bloom (TI 7, 1991). Lowest contributions (below 5%) occurred during some clear-water phases. Herbivorous crustaceans dominated planktonic biomass during the clear-water phase



**Fig. 1.** Seasonal setting of time intervals (TI) in individual years. Winter: TI 10, 1; spring: TI 2, 2.5, 3; clearwater-phase: TI 4; summer: TI 5, 6, 7, 8; and autumn: TI 9. For a more detailed description of the time intervals see text.

(TI 4) and early summer (TI 5) and in some years during autumn (TI 9). The contribution of ciliates was large in spring (TI 2-3) and again in high and late summer (TI 7-8). A succession from small ciliates to rotifers and finally to herbivorous crustaceans occurred from early spring until early summer. Maximum contribution of ciliates were found in spring during TI 2 to TI 3 (average = 13%, range: 7-24%), that of rotifers during TI 3 and TI 4 (4.5%, 1-16%), and of herbivorous crustaceans during TI 4 and TI 5 (53%, 31-66%). After the decline of herbivorous crustaceans in summer (TI 7, 8), all compartments contributed more equally to TPB, resulting in a highly diverse planktonic community. The seasonal course of 1987 was unusual in several respects. A strong winter delayed the onset of time interval 2 relative to the other years. Low temperatures in spring further dampened the seasonal development, especially of herbivorous crustaceans. As a result, biomass of herbivorous crustaceans during the clear-water phase was not as dominant and rotifer biomass was 4-fold compared to the average rotifer biomass during the clear-water phase of the subsequent four years. On an annual average, the contributions of phytoplankton, microbial and metazoan plankton to TPB were approximately 30%, 30%, and 40%, respectively (Fig. 3). Heterotrophic biomass was approximately twice the autotrophic biomass. HF and rotifers did not contribute substantially to TPB, whereas all other groups contributed on an annual average at least 10% of the planktonic biomass. The share of bacteria of approximately 10% remained remarkably constant during the seasonal course.

The ratios of heterotrophic to autotrophic biomass (H/A-ratio), metazoan to protozoan biomass (M/P-ratio), and bacterial to heterotrophic flagellate biomass (B/HF-ratio) showed



**Fig. 2.** Average total planktonic biomass per time interval in different years. For a description of the time intervals see text.

strong seasonal patterns (Fig. 4) related to herbivorous crustacean biomass. All ratios revealed increased values during the clear-water phase and in early summer (TI 4 and 5). However, besides this regularity, the ratios exhibited considerable interannual variability. HF-biomass approached bacterial biomass when metazoan biomass was small, i.e. in early spring (Fig. 4c). Biomass of herbivorous crustaceans was positively related to the B/HF-ratio ( $p < 0.01$ , Figs. 4c, 5). Herbivorous crustaceans exerted a strong predation pressure on HF, reducing thereby the predation pressure of HF on bacteria. Both effects resulted in a high B/HF-ratio. During winter time intervals, the B/HF-ratio was high despite low biomasses of herbivorous crustaceans (Fig. 5).

### Production allocation

The initial production estimates had to be corrected in some time intervals to allow for mass-balanced flux charts within meaningful physiological bounds. For example, ciliate production in summer based on allometric relationships yielded production estimates exceeding primary production in some time intervals. Likewise, production of herbivorous crustaceans during the clear-water phase as calculated by the weight-increment method had to be reduced considerably in all years except 1987.

Net primary productivity accounted for  $69 \pm 2\%$  of the total planktonic production (TPP) on an annual average and dominates TPP in all time intervals. Lowest contributions of phytoplankton to TPP were  $53 \pm 13\%$  and occurred during the clear-water phases. Due to higher specific production rates, the contribution of the smaller sized microbial plankton was

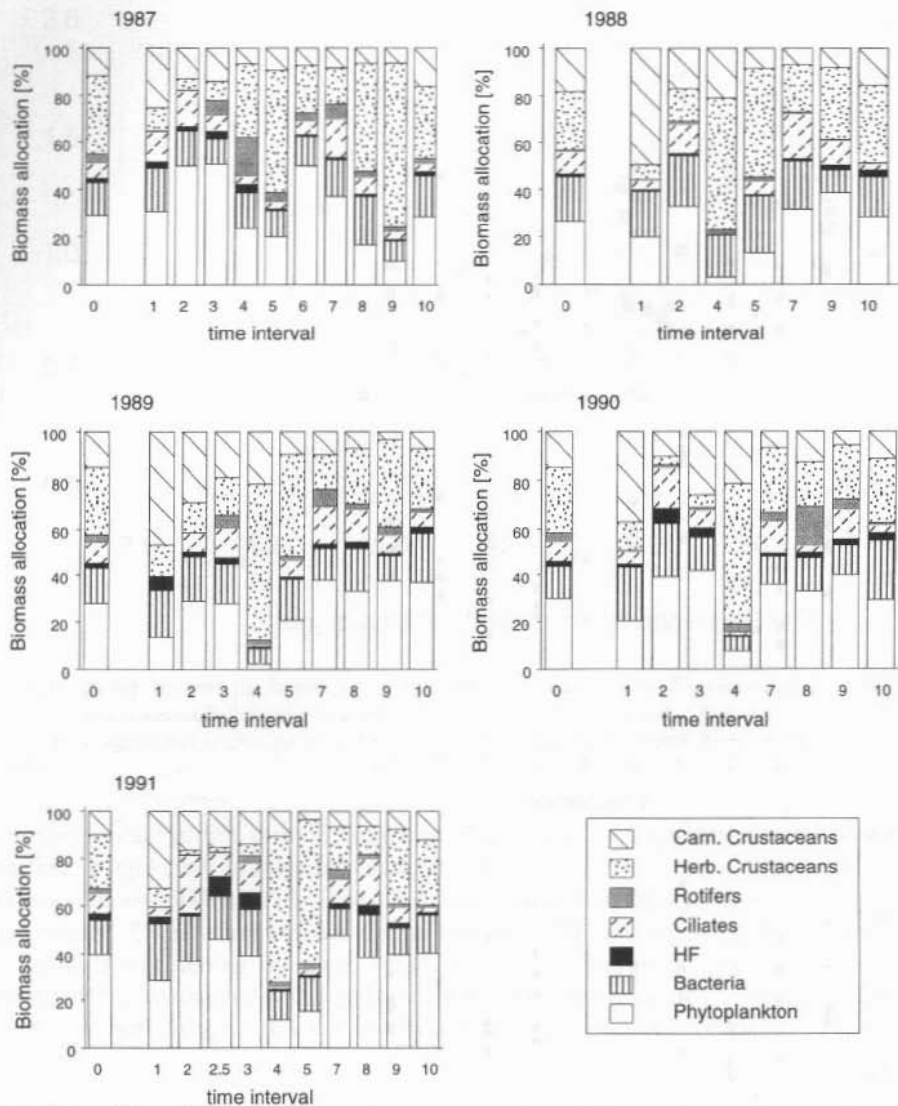
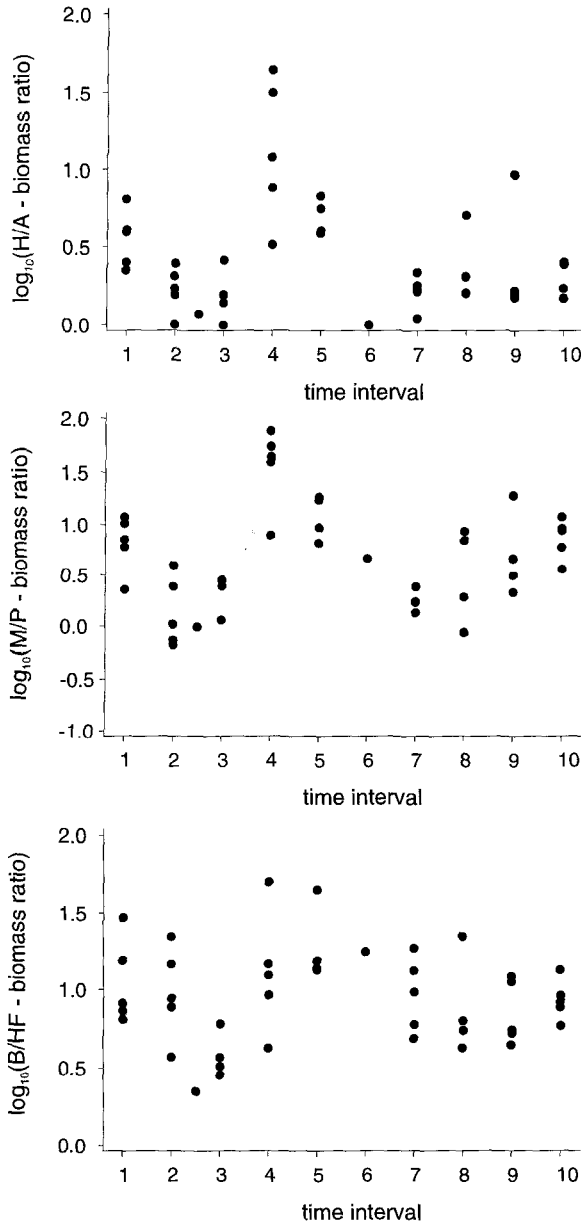


Fig. 3. Biomass allocation in different time intervals. Time intervals 0 represent the annual average.

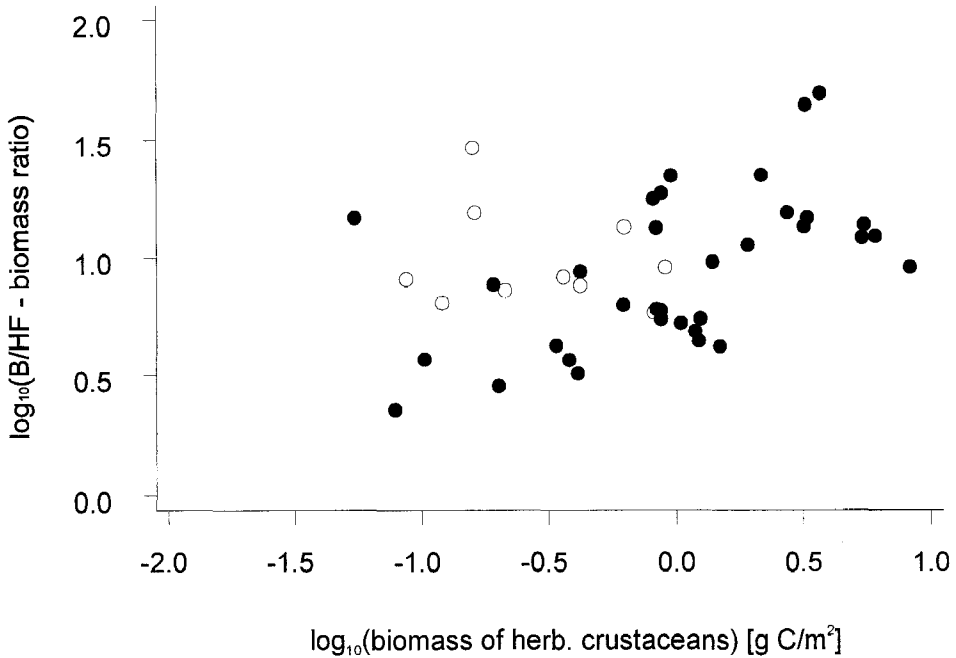
larger than the contribution of metazoan zooplankton (Fig. 6). The ratio of production between phytoplankton, microbial plankton, and metazoan plankton was approximately 69:19:11 on an annual average. The largest heterotrophic production during spring (TI 2-3) was due to ciliates. Despite the considerable reduction of maximum growth rates in summer (20% of the production estimate predicted by MONTAGNES *et al.* 1988, see GAEDKE & STRAILE (1994b), WEISSE & MÜLLER 1998, and below), ciliate contribution to plankton production was again large during high and late summer. Phytoplankton and heterotrophic flagellates exhibited the highest production to biomass (P/B) ratios (Table 1). During the clear-water phase, phyto-



**Fig. 4.** Seasonal course of biomass ratios of autotrophic vs. heterotrophic (H/A) planktonic organisms, protozooplankton to metazooplankton (M/P), and bacteria to flagellates (B/HF).

plankton biomass turned over almost once per day. Bacterial P/B-ratios reached maximum values during the clear-water phase as well. Maximum P/B-ratios of ciliates and rotifers were obtained during spring time intervals. The ciliate P/B-ratio during summer and autumn was  $0.16 \text{ d}^{-1}$ . Without a reduction to 20% of the production estimate according to MONTAGNES et al. (1988), their P/B-ratio would be  $0.8 \text{ d}^{-1}$ , i.e., larger than the phytoplankton P/B-ratio during this time. The P/B-ratio of herbivorous crustaceans during summer and autumn was lower than that of carnivorous crustaceans because the most important herbivorous species, *Daphnia*





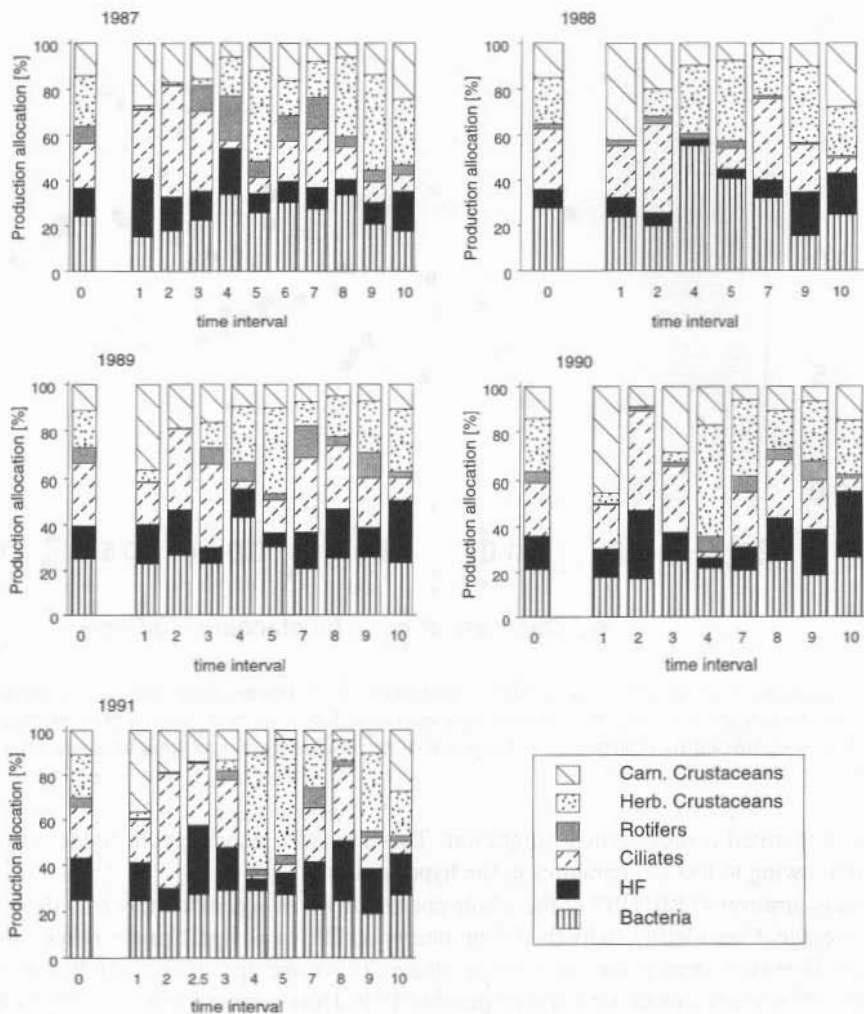
**Fig. 5.** Relationship between the biomass ratio of bacteria to heterotrophic flagellate and the biomass of herbivorous crustaceans. Circles refer to winter time intervals, dots to growing season time intervals. The relationship is significant including ( $r^2 = 0.15$ ,  $p < 0.01$ ) or excluding winter time intervals ( $r^2 = 0.29$ ,  $p < 0.005$ ).

*hyalina*, performed a diel vertical migration. This caused a considerable reduction of its production owing to low temperatures in the hypolimnion.

Biomass turnover (TPB/TPP) of the whole community was approximately four days on an annual average. Considering individual time intervals, TPB was significantly related to TPP (Fig. 7a). However, during the clear-water phase (TI 4) and in autumn (TI 9), relatively constant TPP was associated with highly variable TPB. During spring and summer, TPB was related to TPP with turnover times of four and two days, respectively (Figs. 7b, 7c).

**Table 1.** Production to biomass ratios [ $d^{-1}$ ] for individual compartments during the seasonal course.

	annual average	spring (TI 2-3)	clear-water phase (TI 4)	summer & autumn (TI 5-9)	winter (TI 1, 10)
Phytoplankton	$0.52 \pm 0.06$	$0.79 \pm 0.12$	$0.92 \pm 0.20$	$0.55 \pm 0.30$	$0.37 \pm 0.17$
Bacteria	$0.13 \pm 0.01$	$0.15 \pm 0.05$	$0.21 \pm 0.03$	$0.16 \pm 0.06$	$0.05 \pm 0.01$
HF	$0.48 \pm 0.02$	$0.47 \pm 0.13$	$0.47 \pm 0.00$	$0.58 \pm 0.11$	$0.38 \pm 0.11$
Ciliates	$0.19 \pm 0.01$	$0.31 \pm 0.08$	$0.08 \pm 0.02$	$0.16 \pm 0.11$	$0.13 \pm 0.07$
Rotifers	$0.13 \pm 0.03$	$0.15 \pm 0.04$	$0.10 \pm 0.01$	$0.12 \pm 0.03$	$0.10 \pm 0.03$
Herb. Cr.	$0.05 \pm 0.01$	$0.05 \pm 0.04$	$0.04 \pm 0.02$	$0.06 \pm 0.02$	$0.02 \pm 0.01$
Carn. Cr.	$0.07 \pm 0.01$	$0.10 \pm 0.02$	$0.04 \pm 0.03$	$0.07 \pm 0.01$	$0.05 \pm 0.01$

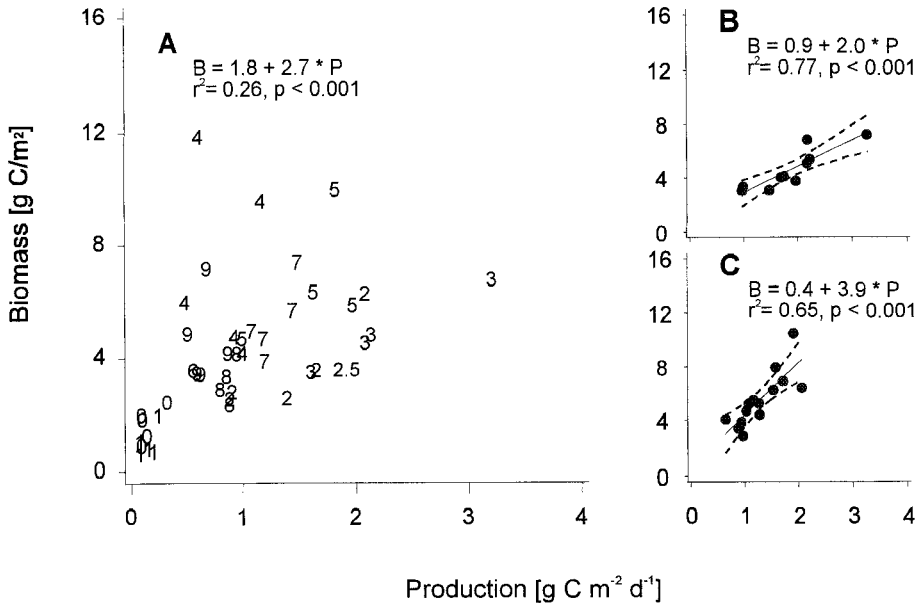


**Fig. 6.** Production allocation between heterotrophic compartments in different time intervals. Percent compositions were calculated after consistency checks of initial production estimates by means of suitability within the carbon flux environment. For details see text.

### Carbon flux charts

The relative and absolute importance of the carbon fluxes between the different planktonic groups varied greatly throughout the season (Fig. 8). During spring, ciliates dominated the grazing on phytoplankton together with so-called carnivorous crustaceans (exclusively cyclopoid copepods during this time of the year), which were able to persist in large numbers throughout winter and relied to a large extent on phytoplankton as food resource during this time. The most important heterotrophic food resource of copepods was formed by ciliates.

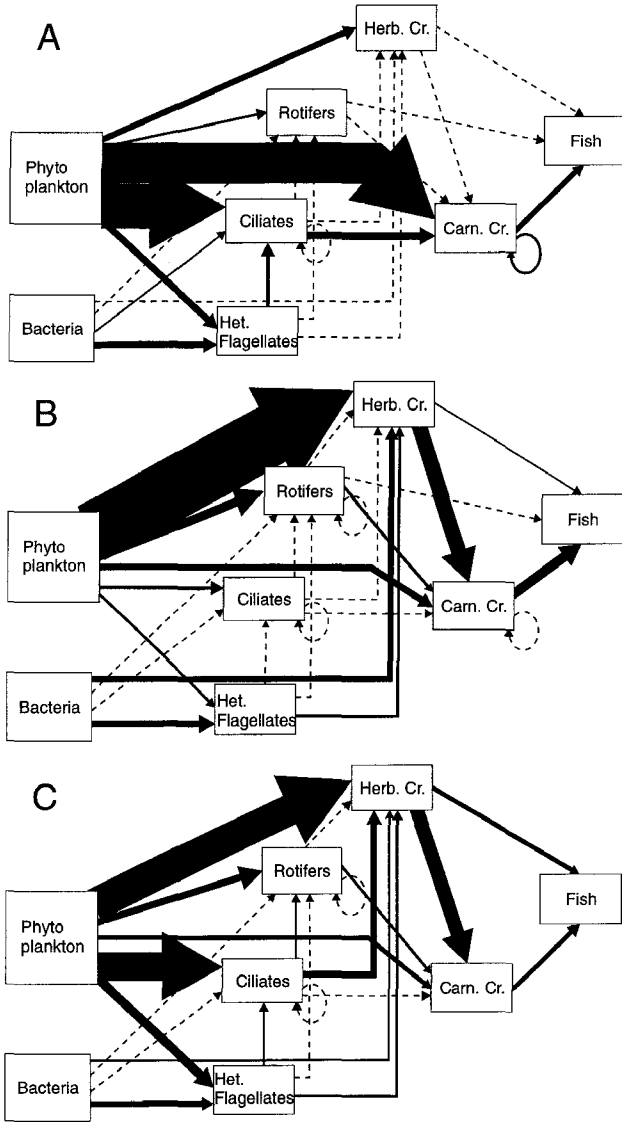
During the clear-water phase, herbivorous crustaceans, i.e. daphnids, were able to monopolise all potential food resources and to crop the majority of phytoplankton, ciliate,



**Fig. 7.** Relationship between total planktonic production and total planktonic biomass. A) All time intervals. Numbers refer to time interval numbers (see Fig. 1) except 0 which refers to time interval 10. B) Spring time intervals. C) Summer time intervals.

heterotrophic flagellate, and bacterial production. After the clear-water phase, herbivorous crustaceans lost their dominant role within the carbon flow network. Again, ciliates and during some summer time intervals also rotifers were important consumers of primary productivity. From the clear-water phase onwards, carnivorous crustaceans relied predominantly on herbivorous crustaceans as food resource, which means that enough animal food is available to allow a carnivore way of life for invertebrates. The carbon demand of carnivorous crustaceans almost approached carbon production of herbivorous crustaceans, leaving only a small part of it for fish. Fish diet consisted of approximately two thirds carnivorous crustaceans and one third herbivorous crustaceans.

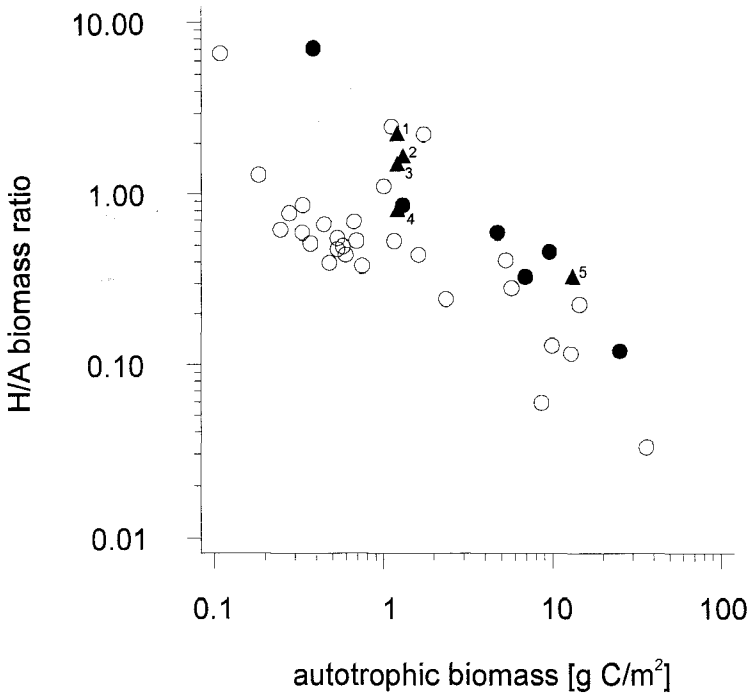
In addition to the changes in the importance of individual fluxes during seasonal succession, two overriding patterns can be recognized. First, carbon fluxes became more diverse. During spring, only 10 carbon fluxes contributed more than 1% to the overall intercompartmental carbon flux, whereas in the clear-water phase and during summer the respective numbers were 12 and 15. The second pattern may be called the "seasonal development of trophic structure": In spring, only four fluxes not originating from phytoplankton or bacteria contributed more than 1% to the overall carbon flow (i.e., fluxes from HF to ciliates, from ciliates to carnivorous crustaceans, cannibalism within the carnivorous crustaceans compartment, and the carbon flux from carnivorous crustaceans to fish). This number increased to five during the clear-water phase and to eight during summer. That is, the quantitative importance of carbon fluxes from the second to the third trophic level increased as the season progresses.



**Fig. 8.** Carbon flux charts for three selected time intervals during 1990: a) late spring (TI 3), b) the clear-water phase (TI 4), and c) high summer (TI 7). Widths of arrows indicate the percent contributions of individual flows to the intercompartmental carbon fluxes in the respective time intervals. For example, the flow from phytoplankton to herbivorous crustaceans during the clear-water phase contributed 47% to the total intercompartmental flow. Stippled arrows denote trophic links which contributed less than 1% to the carbon flux. Phytoplankton losses due to sedimentation and viral mortality of bacteria are not shown and amounted to approximately 10–15% of the production of phytoplankton and bacteria.

### Discussion

The contributions of all major components of planktonic food webs to the total plankton biomass are known for only a few lakes in the world, which prevents detailed cross-system comparisons so far. Recently, data comparable to those of Lake Constance were obtained for the summer community of 18 small lakes (surface area mostly less than 10 km<sup>2</sup>) in southern Québec (DEL GIORGIO & GASOL 1995, GASOL et al. 1995) which span 1.5 orders of magnitude in chlorophyll *a* (0.86 to 13.15 µg Chl/l). Based on this data set and additional literature data, DEL GIORGIO & GASOL (1995) concluded that with decreasing trophity the H/A-ratio increased from 0.05 within highly productive lakes up to 6 in oligotrophic lakes. This



**Fig. 9.** Ratio of heterotrophic to autotrophic biomass as a function of autotrophic biomass in limnetic and marine plankton. This figure is modified from DEL GIORGIO & GASOL (1995, their Fig. 4) and includes their data on lakes (circles) and marine sites (black dots). Deep and large lakes are represented by triangles (1 = Lake Constance (average values from this study), 2 = Königssee (BARTHELMESS 1995), 3 and 4 = North Patagonian lakes (Lago Riñihue, Lago Pirehueico, WÖFL 1996), 5 = Lake Biwa (KAWABATA & NAKANISHI 1997)).

overall trend is to be expected from the relationships between biomasses of various heterotrophic groups and autotrophs in aquatic environments. Biomasses of bacteria (SIMON et al. 1992, DEL GIORGIO & GASOL 1995), ciliates (BEAVER & CRISMAN 1989), and crustaceans (HANSEN & PETERS 1984) increased less rapidly along a gradient of enrichment than autotrophic biomass, i.e., the slopes of the relationships between heterotrophic components and autotrophs are significantly less than one. The H/A-ratios of subalpine Lakes Constance and Königssee (BARTHELMESS 1995), two subandine lakes in northern Patagonia (WÖFL 1996), Lake Biwa (KAWABATA & NAKANISHI 1997), and marine sites are high compared to lakes with similar nutrient levels sampled by DEL GIROGIO & GASOL (1995) (Fig. 9). This indicates that large and deep pelagic ecosystems support higher heterotrophic biomasses at given autotrophic biomasses than smaller lakes.

DEL GIORGIO & GASOL (1995) linked increasing H/A-ratios along a gradient of decreasing autotrophic biomass to an increasing importance of allochthonous resources in oligotrophic systems. Lake Constance as well as Lake Königssee and the Patagonian lakes represent deep lakes with steep slopes resulting in a low ratio of littoral to pelagic surface area and presumably little allochthonous inputs. Riverine input of allochthonous material in Upper Lake Constance is additionally small compared to primary productivity (GÜDE et al. 1998),

especially at our sampling site in the Überlinger See. Furthermore, production rates of phytoplankton, bacteria, and zooplankton and mass-balanced flux charts for Lake Constance indicated no need for allochthonous energetic subsidies to fulfil carbon demands of heterotrophic organisms, even with bacterial growth efficiencies as low as 20% (STRAILE 1995). Hence, it is probably safe to state, that littoral subsidies in the perialpine and periandine lakes, let alone the marine sites, are small compared to the small lakes in Québec. Following the argument of increased heterotrophic biomass due to littoral subsidies, H/A-ratios in Québec lakes are expected to exceed H/A-ratios of deep and large pelagic sites at similar autotrophic biomasses. However, the data presented in Fig. 9 imply the opposite pattern which demonstrates that H/A-ratios may be high without littoral subsidies.

One potential mechanism for increased H/A ratios in large pelagic systems may be a less pronounced top-down control of zooplankton biomass by planktivorous fish. A higher proportion of littoral habitat to total lake area within small lakes provides a larger potential for littoral-zone feeding of fishes (SCHINDLER et al. 1996), and consequently higher fish biomass per area. Increased fish biomass due to littoral subsidies will enhance predation on pelagic prey (SCHINDLER et al. 1996), which may result in decreased zooplankton biomass, i.e., decreased H/A-ratios in small compared to large pelagic sites.

Biomass allocation during spring development in Lake Constance is determined by the allometric constraints on the growth response of the different-sized taxa to the onset of phytoplankton growth. Small ciliates can react first, they are followed by larger-sized rotifers and finally by herbivorous crustaceans (MÜLLER 1989, GAEDKE & STRAILE 1994b). This succession and large contributions of protozoans to the total zooplankton biomass in spring have been observed in a large number of lakes ranging from oligotrophic to polyeutrophic conditions (ARNDT et al. 1993, MATHES & ARNDT 1994, BARTHELMESS 1995).

Herbivorous and carnivorous crustaceans are able to impose considerable top-down control on phytoplankton as well as microbial zooplankton, e.g. heterotrophic flagellates and ciliates. This is particularly evident during the clear-water phase when herbivorous crustaceans strongly dominate the biomass and carbon fluxes. Negative effects of both cladocerans and copepods on protozoans have been intensively studied in a number of in situ and laboratory investigations (WICKHAM & GILBERT 1991, PACE & VAQUÉ 1994, WICKHAM 1995). Herbivorous crustaceans (daphnids) are able to graze on bacteria (PACE et al. 1990). GÜDE (1988) suggested that during the clear-water phase daphnids contribute substantially to bacterial mortality in Lake Constance. However, as daphnids also graze on heterotrophic flagellates, they reduce the biomass of the most important bacterivores in Lake Constance (JÜRGENS & GÜDE 1991, WEISSE 1991) which results in a positive indirect effect of herbivorous crustaceans on bacteria. The positive slope of the bacteria/HF biomass ratio against herbivorous crustaceans biomass suggests that the indirect beneficial effects of herbivorous crustaceans on bacteria outweigh the direct negative effects. A similar positive effect of *Daphnia* biomass on the ratio of bacteria/HF was found by GASOL et al. (1995): Within the Québec lakes, HF-biomasses approached bacterial biomasses only during early spring when copepods dominated the metazoan biomass.

The clear-water phases, which are strongly dominated by daphnids, lasted only two to four weeks. Overexploitation of their food resources and increased predation pressure due to invertebrate predators and also fish result in a reduction of herbivorous crustaceans biomass (SOMMER et al. 1986, STRAILE 1995) which lowers the grazing pressure of herbivorous crustaceans on phytoplankton and protozoans. Furthermore, *Daphnia hyalina*, which domina-

tes biomass of herbivorous crustaceans in summer (GELLER 1989), exhibits a pronounced diurnal vertical migration. Thus, protozoans and also rotifers experience predation and competition by *D. hyalina* only during night which contributes to the diverse biomass allocation and the high flow diversity during late summer.

The summer plankton community differs from the spring community also by its turnover time, which is twice as long as in spring. This has been already pointed out for the rather unusual year 1987 by GELLER et al. (1991), but holds for all five years considered in this study. That is, 1 g C/m<sup>2</sup> carbon production per day sustained 2 g C/m<sup>2</sup> biomass during spring, but 4 g C/m<sup>2</sup> during summer. This is possible because the size structure has shifted towards larger organisms (GAEDKE 1992) with decreasing mass-specific metabolic rates. Furthermore, growth efficiencies of herbivores as well as the transfer efficiency along the size gradient increased from spring to summer (GAEDKE & STRAILE 1994a, GAEDKE et al. 1996). The increase in efficiency along with the high flow diversity and increased importance of higher trophic levels may be seen as signs of a seasonal maturing process sensu ODUM (1969). A roughly similar development of trophic structure with increasing diversity and increasing importance of higher trophic levels during the seasonal course was suggested for the marine planktonic community in the German Bight (GREVE & REINERS 1995).

Despite the overdetermination of the flow network by numerous measurements, ecologically and physiologically feasible carbon flux charts could be established with the production estimates for almost all time intervals (see GAEDKE & STRAILE 1994a, STRAILE 1995). This implies a high consistency of the underlying measurements and indicates that the balancing rules were flexible enough to account for the seasonal and interannual differences in production estimates. Despite this flexibility, the consistency check based on mass-balancing allowed the detection of inconsistencies in some production estimates which did not account for food limitation. This was most evident for ciliates after spring time intervals and for herbivorous crustaceans during the clear-water phase. Ciliate production according to MONTAGNES et al. (1988) was energetically not possible (GAEDKE & STRAILE 1994b) in the respective time intervals. For example, during high summer 1990 (TI 7, Fig. 7c), ciliate production would amount to 490 mg C m<sup>-2</sup> d<sup>-1</sup> according to the formula given by MONTAGNES et al. (1988). Net primary productivity during this time was 840 mg C m<sup>-2</sup> d<sup>-1</sup>. Even if ciliates consumed total NPP, a gross growth efficiency of 58% would be necessary to sustain ciliate production during this time interval. MÜLLER & GELLER (1993) criticized the formula of MONTAGNES et al. (1988) for overestimating even the intrinsic growth rates at high temperatures. However, using the formula of MÜLLER & GELLER (1993) which predicts higher growth rates at lower temperatures results in even higher production estimates, e.g., 570 mg C m<sup>-2</sup> d<sup>-1</sup> in TI 7/1990, given the average temperatures in the upper 20 m water column. Hence, the overestimation of ciliate production is not caused by an overestimation of intrinsic growth rates, but is due to limiting conditions which prevent ciliates from reaching intrinsic rates. In accordance with the model results, a large difference between predicted and observed ciliate growth rates was reported in a number of studies during recent years (TAYLOR & JOHANSSON 1991, WICKHAM & GILBERT 1991, LEAKEY et al. 1994, MACEK et al. 1996). In situ measurements of ciliate growth rates during 1992 in Lake Constance confirmed the food limitation of ciliate growth (WEISSE & MÜLLER 1998). According to in situ growth rates, ciliate production exceeded heterotrophic flagellate production by a factor of 2.3 during 1992 (WEISSE & MÜLLER 1998). This is reasonably close to the average value of 1.9 obtained in this study assuming that ciliates will grow after spring at only 20% of their maximum growth rates.

Furthermore, this close correspondence suggests that the network flux environment of ciliate production, which revealed this inconsistency, describes the carbon flow with some precision.

Due to low temperatures during spring 1987, the development of herbivorous crustaceans was delayed which resulted in a weak clear-water phase. Primary production during the clear-water phase in 1987 was large enough to sustain weight-increment production of herbivorous crustaceans. However, during the pronounced clear-water phases 1988 to 1991 with high biomasses of herbivorous crustaceans, low algal biomass, and low primary productivity, production of herbivorous crustaceans as estimated by the weight-increment summation was energetically not possible. Model assumptions of the production of herbivorous crustaceans during these years have to be reduced considerably in order to keep the entire flow network within reasonable physiological bounds. However, during the remaining part of the summer, the production estimate based on the weight-increment method fits into the global properties of the system.

To conclude, heterotrophic biomass in Lake Constance was large compared to lakes of similar trophic. The biomass and production allocation patterns of Lake Constance showed a recurrent seasonal scheme. Carbon flux models revealed a high consistency of production estimates when food limitation of herbivorous crustaceans during the clear-water phase and of ciliates after the spring bloom was accounted for.

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