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Seasonal changes of the quantitative importance of protozoans in a large lake. An ecosystem approach using mass-balanced carbon flow diagrams [1]

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Abstract

Based on comprehensive measurements of plankton abundance and production, quantitative carbon flow diagrams were established for the pelagic community of a large lake (L. Constance) for ten successive time intervals during the seasonal course of 1987. Using reasonable diet compositions and parameters (*e.g.* trophic transfer efficiencies in the range of 10-35%), mass-balance conditions could be fulfilled for individual compartments and the entire food web, provided that ciliate growth rates used during summer and autumn were far below the maximum rates observed in the laboratory. Ciliates, rotifers, and most crustaceans were predominantly herbivorous in our model. Ciliates played an important role in the overall carbon flow especially during the first half of the year. They constituted a substantial portion of the overall grazing pressure on phytoplankton (up to 89%, seasonal average 45%). They also formed an important part of the diet of cyclopoid copepods in spring. Thus, ciliates which are generally assigned to the microbial food web, were strongly involved in flow dynamics commonly attributed to the classical food chain. Osmotrophic bacteria derived most of their organic matter from zooplankton mediated EOC (excreted organic carbon) flows. The fraction originating directly from phytoplankton was less important. On a seasonal average, microbial production appeared to be of minor importance to the nutrition of larger plankton (*i.e.* ciliates, rotifers, crustaceans) although a tight coupling between heterotrophic unicellular and multicellular organisms was assumed. Low microbial food web efficiencies indicated that a large amount of organic carbon was respired within the microbial food web which, in turn, points to a considerable recycling of nutrients. Our model supported the hypothesis that nutrient recycling is the primary function of bacterivorous flagellates in the plankton food web of Lake Constance.

Key words: Mass-balanced flow diagram, Pelagic carbon recycling, Microbial food web, Seasonal succession, Ciliates, Network analysis.

Résumé

Variations saisonnières de l'importance quantitative des protozoaires dans un grand lac. Une approche de l'écosystème mettant en œuvre des diagrammes du flux de carbone équilibrés en masse

Basés sur des mesures détaillées de l'abondance et de la production planctonique, des diagrammes quantitatifs du flux de carbone ont été établis pour la communauté pélagique d'un grand lac (lac de Constance) pour dix intervalles

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de temps successifs pendant l'évolution saisonnière de 1987. En adoptant des régimes alimentaires et des paramètres raisonnables (par exemple des rendements de transfert trophique dans la gamme de 10 à 35%), des situations d'équilibre, exprimées en masse, pourraient être réalisées pour les compartiments individuels et pour le réseau alimentaire entier, pourvu que les taux de croissance des ciliés, utilisés en été et en automne, soient bien en dessous des taux maximaux observés au laboratoire. Les ciliés, les rotifères et la plupart des crustacés étaient essentiellement herbivores dans notre modèle. Les ciliés jouaient un rôle important dans le flux global de carbone, surtout pendant la première moitié de l'année. Ils constituaient une portion substantielle de la pression de broutage globale sur le phytoplancton (jusqu'à 89%, 45% en moyenne saisonnière). Ils formaient aussi une part importante du régime alimentaire des copépodes cyclopoïdes au printemps. Ainsi les ciliés, qui sont rangés généralement dans le réseau alimentaire microbien, étaient fortement engagés dans la dynamique des flux, couramment attribuée à la chaîne alimentaire classique. Les bactéries osmotrophes tiraient la plupart de leur matière organique des flux de carbone organique excrétés par le zooplancton (EOC). La fraction provenant directement du phytoplancton était moins importante. En moyenne saisonnière, la production microbienne paraissait être d'importance mineure pour la nutrition du plancton plus grand (c'est-à-dire les ciliés, les rotifères, les crustacés) bien qu'un couplage étroit entre les organismes hétérotrophes unicellulaires et multicellulaires soit supposé. Les faibles rendements du réseau alimentaire microbien indiquaient qu'une grande quantité de carbone organique était respirée dans le réseau alimentaire microbien, ce qui, à son tour, indique un recyclage considérable des nutriments. Notre modèle supporte l'hypothèse que le recyclage des nutriments est la fonction primaire des flagellés bactérivores dans la chaîne alimentaire planctonique du lac de Constance.

Introduction

The potential of flow analysis for ecosystem studies has been recognized for a long time since the knowledge of the flows of matter and energy within a food web is essential for the understanding of ecosystem functioning. However, flow diagrams of complex communities like those in large pelagic ecosystems have been established for only a few systems and have rarely covered extended periods of time owing to the great amount of data needed to establish reasonably realistic mass-balanced flow diagrams (Wulff *et al.*, 1989). Any simplified diagrammatic representation attempting to illustrate the carbon flux in a complex food web is easily criticized and there is a danger of misinterpretation by taking the given numbers as final facts. On the other hand, experimental studies of single process rates of individual populations are also subject to errors, and many processes are difficult to measure under natural conditions. The compilation of mass-balanced flow diagrams based on numerous measurements provides the opportunity to control the internal consistency of the underlying measurements and assumptions, and to define reasonable bounds for individual process rates which have not been measured (*e.g.* Vezina and Platt, 1988; Stone *et al.*, 1993). Thus, measurements at the population level and computations at the ecosystem level may complement each other.

The entire plankton community of large and deep, meso-eutrophic Lake Constance has been studied in detail with respect to population dynamics and seasonal changes of species composition and productivity throughout the last decade (*e.g.* Tilzer and Beese, 1988; Geller, 1989; Güde, 1990; Weisse *et al.*, 1990; Müller *et al.*, 1991). The contribution of different groups of planktonic organisms to community biomass and production has been described by Geller *et al.* (1991). Plankton biomass tended to be

approximately evenly distributed over the size spectrum ranging from bacteria to crustaceans (Gaedke, 1992). Calculations of the efficiency to transfer primary production to herbivores based on biomass size distributions and on carbon flow diagrams showed consistently an increase from low values in spring (*ca.* 10%) to relatively high summer values (*ca.* 35%) (Gaedke and Straile, in press).

The objectives of the present investigation were to present and analyse quantitative diagrams of the carbon flows within the pelagic community of Lake Constance for different times of the growing season in 1987. The flow diagrams were used to investigate major seasonal changes in the carbon cycle, and to explore the range selected parameters and fluxes may take given the numerous measurements and mass-balance constraints. Special emphasis was given to the coupling of the microbial and the classical food web. Although the importance of microbial organisms for community metabolism is well established (*e.g.* Schwaerter *et al.*, 1988), the microbial contribution to carbon cycling and the nutrition of larger zooplankton remains under discussion (Ducklow, 1991; Wylie and Currie, 1991). Thus, the following questions were evaluated: What is the role played by the microbial food web in the processing and transfer of carbon compared to larger organisms? What is the potential contribution of bacteria, heterotrophic flagellates, and ciliates to the diet of metazoans? What are the dominant DOC generative processes (*e.g.* zooplankton mediated EOC (excreted organic carbon) flows *vs.* algal exudation)?

Most topics can only be dealt with by taking the temporal organization of the system into account. Either-or answers are not to be expected in most cases but different situations are likely to prevail during the season. The number and length of cycles, the composition of trophic levels, and other network descriptors will be evaluated using network analysis in subsequent studies (*e.g.* Gaedke *et al.*, in press).

We thank all scientists who developed the biological data base. M. M. Lang provided information on the food web structure and M. Schimmele on the temperature regime. We thank Walter Geller, Hans Güde, Helga Müller, Claudia Pahl-Wostl, and Karl-Otto Rothhaupt who gave us numerous stimulating comments and detailed information. Hugh Ducklow, Hartmut Arndt and an anonymous reviewer made valuable suggestions to improve the manuscript and Stephen Barry corrected the English of an earlier version.

Materials and Methods

Study site

Lake Constance (in German: Bodensee) is a large and deep (z_{max}= 252 m), prealpine (47°50'N) lake of warm-monomictic character at the northern fringe of the Alps. It is presently undergoing reoligotrophication and can be characterized as meso-eutrophic during the investigation period (1987). Owing to its large size (476 km^2), Lake Constance has a relatively deep and well-mixed epilimnion and a true pelagic zone.

Measurements and estimates of biomass, production and other process rates

Sampling was carried out weekly (larger phytoplankton twice a week) at different depths at a 147 m deep sampling site in the north-western part of the lake (Überlingersee). Abundances of all planktonic organisms were assessed by microscopy using advanced sampling and counting techniques appropriate for the size and fragility of the organisms. Individual body sizes were established by measuring either size frequency distributions (bacteria, heterotrophic flagellates, autotrophic picoplankton (APP)), or average biovolumes of individual taxa (larger phytoplankton, ciliates, rotifers), or the individual length of the organisms in each sample (crustaceans). Original measurements of body size were converted to units of carbon using measurements from Lake Constance or from the literature. This work was performed by a large team of scientists: R. Berberovic, C. Braunwarth, R. Eckmann, A. Giani, W. Geller, U. Kenter, H. Müller, H.-R. Pauli, A. Schweizer, M. Simon, D. Springmann, H.-H. Stabel, U. Theurer, T. Weisse, and S. Wölfl (*e.g.* Geller, 1985, 1986; Geller *et al.*, 1991; Müller *et al.*, 1991; Simon, 1988; Weisse, 1988, 1991). A detailed description and a full list of references can be found in Gaedke (1992) with the following exception: the conversion factor of ciliate cell volume to units of carbon was changed from 11 to 15.4% (g C/g FW) to allow for shrinkage during fixation.

In the carbon flow model all pelagic organisms were allocated to one of the following eight trophic compartments: free-living and attached bacteria, phytoplankton including APP, small heterotrophic flagellates (mostly 1-10 µm length), ciliates, rotifers, predominantly herbivorous crustaceans (daphnids, *Bosmina*, *Eudiaptomus*), predominantly zooplanktivorous crustaceans (all life stages of cyclopoid copepods, *Leptodora kindtii, Bythotrephes longimanus*), and pelagic fish (mainly coregonids and perchs). Additionally, a non-living compartment was established which consisted of the fraction of dissolved and particulate organic matter which participates in the biotic carbon cycle.

The dynamics of the living compartments were governed by 5 different fluxes in the model food web which are partially related to each other by mass balance laws and (growth) efficiencies: a) production, b) respiration, c) ingestion, d) release of organic substances, and e) a storage flux which accounted for temporal variability of standing stocks (see below).

a) Production measurements or estimates were the most important source of information for establishing flow charts in the present study. The production of bacteria, phytoplankton, and heterotrophic flagellates was measured directly. For other plankton groups it was calculated from weight-specific growth rates and abundance measurements. The seasonal courses of bacterial production and P/B ratios have been measured with ^{3}H-Thymidine and ^{14}C-Leucine incorporation techniques at different depths and locations for several years in Lake Constance (Güde, 1986 and 1990; Simon, 1988; and unpubl.). Measurements from 1991 and 1992 were averaged for the present study yielding P/B values between 0.05 and 0.15 per day for the different time intervals. Primary production of cells larger than 0.7 µm was measured weekly, using the ^{14}C technique (4 h incubation) (Tilzer and Beese, 1988, Tilzer *et al.*, 1991). Values

obtained with this method are thought to be close to gross primary production (Dring and Jewson, 1982), *i.e.* respiration and extra-cellular release of higher molecular organic substances were subtracted to obtain potential, algal net growth. Recent measurements of algal exudation indicate mostly low rates unless oligotrophic conditions prevail which has been confirmed by Rolinski (1992) for Lake Constance. We assumed an exudation rate of 5% of primary production during winter and early spring, 10% during late spring and the clear-water phase, and 15% for the rest of the year. The net primary production of cells smaller than 0.7 µm and the growth rates of heterotrophic flagellates were determined using the dilution technique (Weisse, 1988, 1991). Non-food limited growth of ciliates was calculated according to a relationship which accounts for cell size and temperature (Montagnes *et al.*, 1988). It is based on maximum growth rates observed in the laboratory under favourable food conditions which will most probably overestimate average natural growth rates (Müller and Geller, 1993). Rotifer production was estimated by two methods. First, it was calculated using a weight-increment summation method assuming one weight increment from zero to adult body mass (Downing and Rigler, 1984). Egg development times were calculated with equations given by Herzig (1983) for various rotifer species. These production estimates were regarded as minimum values since losses of eggs occurred during fixation. Secondly, non-food limited maximum growth rates were calculated from allometric relationships (Stemberger and Gilbert, 1985). Maximum production estimates were used during spring (time intervals 1-3), and mean values obtained by the two methods during the other time intervals. Growth rates of herbivorous crustaceans and copepods were estimated in a relatively reliable way using a weight-increment method established for Lake Constance, which partially ignores the effect of food limitation (Geller, 1986). Growth rates of *Leptodora* and *Bythotrephes* were roughly estimated using P/B ratios of 0.04 or 0.05 depending on prey concentrations. The estimates of biomasses, and production and ingestion rates underlying the flow diagrams are given in Table I for selected periods of time (cp. Geller *et al.*, 1991).

b) Dark respiration of phytoplankton was taken as 20% of primary production (Fahnenstiel and Scavia, 1987). Bacterial respiration was calculated as the difference between consumption and production since excretion of organic compounds was regarded as negligible (Azam *et al.*, 1983). Respiration rates of other heterotrophs were set equal to the respective production rates which implies net growth efficiencies of 0.5 (Humphreys, 1979; Verity, 1985). This simple assumption avoided a potential bias of seasonal changes of net growth efficiencies which may derive from different temperature dependencies of growth and respiration rates established in laboratory studies by different research groups. It ensured a simultaneous reduction of growth and respiration rates under food limited conditions.

c) To satisfy mass balance laws, ingestion (including losses by sloppy feeding and interference competition) was set equal to the respective prey production as defined below (for bacteria: the summed release of organic matter) by adjusting the trophic

TABLE I. – Measurements and estimates of biomass, ingestion and production of the plankton compartments for different seasonal stages. Ingestion includes sloppy feeding, interference competition, etc. For heterotrophs, net production estimates are given. The corresponding value for autotrophs represents gross production calculated as primary production measured by the ^{14}C technique plus production of very small APP and low molecular exudation during incubation.

Parameter	*Time interval*	*Algae*	*Bacteria*	*Flagell.*	*Ciliates*	*Rotifers*	*herb. Cru*	*carn. Cru*
Biomass	early spring	2516	606	78	630	17	190	525
(mg C m^{-2})	late spring	2744	547	167	554	678	516	788
	early summer	2196	1091	78	322	556	5455	976
	high summer	2025	807	60	923	470	827	460
Ingestion	early spring	/	1315	151	1341	13	18	211
(mg C m^{-2} d^{-1})	late spring	/	1141	183	1179	366	82	187
	early summer	/	828	167	157	177	879	253
	high summer	/	381	127	367	193	214	89
Production[1]	early spring	2015	121	45	148	2	2	40
(mg C m^{-2} d^{-1})	late spring	2415	110	55	153	48	11	52
	early summer	1808	109	49	45	44	245	58
	high summer	1095	121	38	108	57	63	31

transfer efficiencies of bacteria, herbivores and carnivorous zooplankton accordingly in an iterative process. A 30% gross growth efficiency was assumed for flagellates. For simplicity, no difference was made between sloppy feeding, interference competition etc., and truly ingested material which is later released as organic substances as this had no impact on most of our results. This assumption should, however, be kept in mind when interpretating ingestion rates (*e.g.* Table I), gross growth efficiencies, and the dominant DOC generative processes. The grazeable primary production (*i.e.* net primary production minus sedimentation) was transferred to herbivores by assuming the same gross growth efficiencies for ciliates, rotifers, and herbivorous crustaceans. Differences in the exploitability of prey organisms and selectivity of predation were accounted for, *e.g.* by allowing for non-grazing mortality, and seasonal changes of diet compositions and intra-compartmental predation which were inferred from changes of species compositions.

d) The release of dissolved and particulate organic substances is influenced by different processes which are often difficult to measure *in situ*. In our food web model, we did not distinguish between the release of organic substances before and after ingestion (see above). Non-grazing mortality was modelled explicitly for phytoplankton by considering sedimentation of larger diatoms at a rate of 10% per day from the epilimnion. Fluxes fuelling the pool of dead organic carbon were calculated as the difference between ingestion (as defined above), and assimilation (respiration and production), *i.e.*, a variable fraction of prey uptake was released as organic matter which determined the trophic transfer efficiency in our model.

e) The growing season was subdivided into ten time intervals of unequal length lasting for three to six weeks which reflect different stages in plankton succession (for details see legend of Figure 3 and Geller *et al.*, 1991). For each time interval, separate flow charts were obtained by averaging biomass and production measurements over the three to six respective sampling dates. Changes of standing stocks between successive time intervals were accounted for by the introduction of a storage flux, S, for each compartment. Steady state conditions were assumed within each time interval. The storage flux acted as an additional output of the compartment if the biomass of the compartment increased, *i.e.* the grazeable net production was reduced. S was added to the production available to higher trophic levels if the biomass of a compartment decreased. The value of the storage flux S_i for time interval i with the duration of T_i days depended on the average biomass in time interval i, B_i, as well as on the biomass concentration during the previous (B_{i-1}) and consecutive (B_{i+1}) time interval:

$$S_i = (B_{i-1} - B_i)/(T_{i-1} + T_i) + (B_i - B_{i+1})/(T_i + T_{i+1}).$$

Standing stocks are given in mg C m^{-2}, fluxes including S in mg C m^{-2} d^{-1} for the upper 20 m of the water column. The uppermost 20 m correspond roughly to the relatively well-mixed epilimnetic water layer and generally include the euphotic zone to which primary production as principle energy source of the community is restricted. Since crustaceans feed mostly in the epilimnion, their total biomass was considered to be concentrated in the upper 20 m in this study, although some species migrate diurnally to greater depths.

Model food web structure, diet compositions, and mass-balance procedure

A comprehensive study on the trophic interactions of the pelagic food web of Lake Constance has been performed by Lang *et al.* (unpubl.) on which the structure of the present carbon flow model was based (Fig. 1). Some seasonal variability in our model food web structure arised from changes in the species composition or age structure of some compartments. For example, fish larvae occurring during the first half of the year established temporarily a trophic link to rotifers. All organic carbon was recycled by bacteria as there were no detritivores in our model. The nutritional value of POC ingested by eucaryotes has been omitted because it was regarded as low when compared to the energy content of attached and associated microorganisms. The biomasses and metabolic processes of the latter (including those on lake snow) have been included in the sampling and modelling approaches.

All heterotrophic compartments of the model food web were omnivorous, *i.e.* they rely on the production of at least two other compartments. Most planktonic organisms in Lake Constance exhibit a flexible and opportunistic feeding behaviour, and the species composition of most compartments changed throughout the season. We

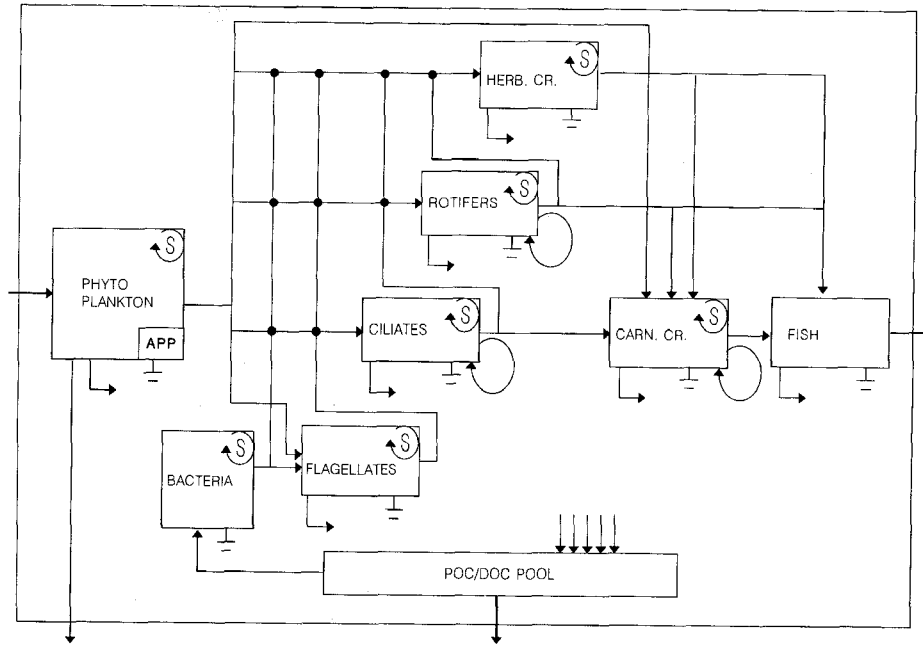


Fig. 1. Schematic carbon flow diagram of the pelagic food web of Lake Constance. The compartment labelled POC/DOC represents the pool of dead particulate and dissolved organic carbon. Herb. and Carn. Cr. stands for predominantly herbivorous and carnivorous crustaceans. $\perp$ symbolizes respiration, S the storage fluxes (magnitudes of flows are provided in Figure 2 for selected time intervals) and APP the autotrophic picoplankton.

established some simple rules to model diet compositions and relative grazing pressure: Prey production was allocated to the different consumers according to the relative contribution of each predator to total predator production. In two cases, predator productions were weighted with a factor accounting for differences in grazing efficiencies. Firstly, heterotrophic flagellates were considered as dominant bacterivores (Jürgens and Güde, 1991) which graze bacteria more efficiently than ciliates, rotifers, and cladocerans in our model (weighting factor for heterotrophic flagellates: 10; other predators: 1). Secondly, cyclopoid copepods were regarded as more efficient predators of ciliates than filter feeding rotifers and daphnids (weighting factor for copepods: 10; other predators: 1).

Food requirements of heterotrophic flagellates not satisfied by consumption of bacteria were supplemented by grazing on APP. A tight coupling between microorganisms and their predators was assumed by transferring protozoan production completely to the next trophic level. Food requirements of ciliates, rotifers, and herbivorous crustaceans which were not satisfied by grazing on microorganisms were covered by algal consumption. After allowing for algal sedimentation from the epilimnion, it was assumed that the remaining algal net production was taken up by herbivores (for justification see Discussion section). The magnitude of flow from rotifers to herbivorous crustaceans was estimated with a formula which relates the daily mortality of rotifers caused by interference competition with daphnid size and abundance (Gilbert, 1989). Carnivorous crustaceans consumed 80% of the production of herbivorous crustaceans as well as 80% of the rotifer production not taken by herbivorous crustaceans or other rotifers. Ciliates were ingested according to the contribution of carnivorous crustaceans to the total production of all ciliate predators. Fish relied on the remaining 20% of herbivorous crustacean and rotifer production, and on the production of carnivorous crustaceans. In the present model, primary production was the only external system input. System exports occurred by respiration, fish production, and sedimentation of diatoms and POC which was determined with sediment traps in 1987 (Giovanoli, unpubl.).

To summarize, production, P, and respiration, R, of each living compartment were obtained from measurements or the literature. Grazeable net production at one trophic level determined ingestion (including sloppy feeding etc.), I, on the next higher one. The release of organic substances, E, was obtained by mass-balancing: $E = I - (P + R)$. This mass-balance approach implied low P/I ratios if food supply was high and vice versa.

Results

Mass-balanced flow diagrams and seasonal changes of major carbon fluxes

The seasonal course of 1987 may be characterized by relative low temperatures in spring which probably retarded daphnid growth, and an exceptional flooding

combined with cold and rainy weather in late July/early August. The clear-water phase was relatively weak and characterized by an unusually high abundance of rotifers.

Biologically sound mass-balanced carbon flow diagrams can be obtained for all but one time interval, suggesting a high degree of consistency between the measurements and parameter estimates. However, one alteration is necessary to achieve mass-balanced charts in summer and autumn. Ciliate production as estimated by an allometric relationship, representing non-food limited growth under laboratory conditions (Montagnes *et al.*, 1988), appears much too high during this time and does not fit into the overall network environment. Firstly, it implies ingestion rates of herbivores which are higher than primary production when reasonable transfer efficiencies are used. Secondly, consumption of such a high ciliate production contradicts present concepts on the diet composition of potential predators. For example, daphnids are regarded as predominantly herbivorous but to avoid unrealistically high gross growth efficiencies they would have to rely predominantly on ciliates. A somewhat arbitrary reduction of these production estimates by a factor of five yields mass-balanced flow diagrams, with transfer efficiencies in the order of 30% and reasonable diet compositions for the predominantly herbivorous organisms (see below). Assuming higher transfer efficiencies (*i.e.* mainly P/I ratios) would imply very low respiration rates and/or the release of very small amounts of organic matter which, in turn, would imply unrealistically high growth efficiencies for bacteria. This version of the food web model will be used in the subsequent analysis since ciliates are most probably food limited *in situ* during the second half of the year.

Other inconsistencies arise during one period in autumn (time interval 9) when an extremely high abundance of *Daphnia hyalina* was observed at one sampling date. It exceeds the abundances observed on the previous and subsequent sampling date by a factor of 8 and 29 respectively. Equally high densities of *D. hyalina* have never been observed during 12 years of investigation, and especially not in autumn (Geller, in prep.) suggesting that an unusual high spatial concentration or a counting error may have occurred. It is impossible to construct a carbon flow diagram with sensible transfer efficiencies which sustains the production related to the recorded density of *D. hyalina.* The time interval will not be analysed in the following study and is omitted from the figures.

Quantitatively, the most important fluxes throughout the season are the grazing of herbivores on phytoplankton, the release of organic substances by the different herbivores and phytoplankton, and the uptake of organic matter by bacteria (Fig. 2). Individual feeding transfers within the microbial community never achieve quantitative importance to the overall carbon flow. Respiration of phytoplankton and bacteria represent the most important individual metabolic processes. At the beginning of the growing season, a continuous size-related shift occurs regarding the relative importance of herbivores (Gaedke, 1993). Ciliates are the first to react to the pulse of primary production (Müller *et al.*, 1991). In early spring, food web structure is least complex and the pelagic carbon cycle is clearly dominated by three inter-compartmental fluxes: phytoplankton grazing by ciliates, release of organic substances by ciliates, and the uptake of organic substances by bacteria (Fig. 2a). In late spring,

carbon fluxes exhibit a greater diversity (Fig. 2b). The three fluxes mentioned above remain of outstanding importance, however, rotifers also play an important role in the overall carbon cycle. Herbivorous crustaceans dominate phytoplankton grazing and related fluxes not before early summer (June/July) (Fig. 2c). Highest flow diversity is reached in high summer (August) when all groups of herbivores contribute substantially to the carbon cycle, and other plankton groups also occur in relatively high numbers. The contribution of ciliates is again remarkably high although production estimates were reduced as compared to laboratory data (see above). Primary production, representing the only energy input in the model system, reaches its highest values in spring and decreases throughout the summer (Tilzer and Beese, 1988). The magnitude of carbon flows and the total system throughput reflect this trend (notice the different scaling of the y-axes in Figure 2).

Production of ciliates, rotifers, and herbivorous crustaceans can be sustained with relatively low transfer efficiencies (*ca.* 15%) during spring and the flooding event in late July/early August. Higher values (around 30%) are required during the clear water phase, in summer and autumn (for details see Gaedke and Straile, in press). Gross growth efficiencies obtained by mass-balancing for carnivorous crustaceans fluctuate around 30%. Respective values for bacteria are between 20 and 40% which renders a severe underestimation of bacterial production unlikely unless labile allochthonous material turns out to be of unexpected importance. Some experimental evidence suggests that protozoans grow with higher efficiencies than rotifers or crustaceans (Caron and Goldman, 1990). Assuming a transfer efficiency for ciliates which is 0.1 units higher than that of other herbivores does not alter the principal model results (Table II).

Grazing pressure on phytoplankton, bacteria, and heterotrophic flagellates

Ciliates are the most important phytoplankton grazers in spring and, less pronounced, in high summer although their ingestion rates were considerably reduced as compared to laboratory measurements (see above) (Fig. 3). An increase of ciliate transfer efficiencies by 0.1 units reduces the contribution of ciliate grazing on phytoplankton from 45 to 37% (seasonal average) in our model but does not alter their temporal dominance (Table II). Daphnids dominate the herbivorous community during their mass development in early and late summer. Heterotrophic flagellates contribute 10% to the overall grazing activity although they satisfy more than 50% of their energy demands by herbivory in our model (seasonal average) (Table II). Autotrophs are the dominating food source of flagellates in autumn, winter, and during the clear-water phase whereas in early spring and high summer bacterial production is sufficiently high to cover 70-80% of the energy demand of flagellates. Phytoplankton grazing by heterotrophic flagellates is at most in the range of APP production. Strongly enhancing the relative grazing efficiency of flagellates on bacteria by increasing the weighting factor from 10 to 50 (see method section) does not alter the strong dependence of heterotrophic flagellates on autotrophs (Table II). An increase of the flagellate transfer efficiency from 30 to 40% reduces their food demands and, thus, the food requirements

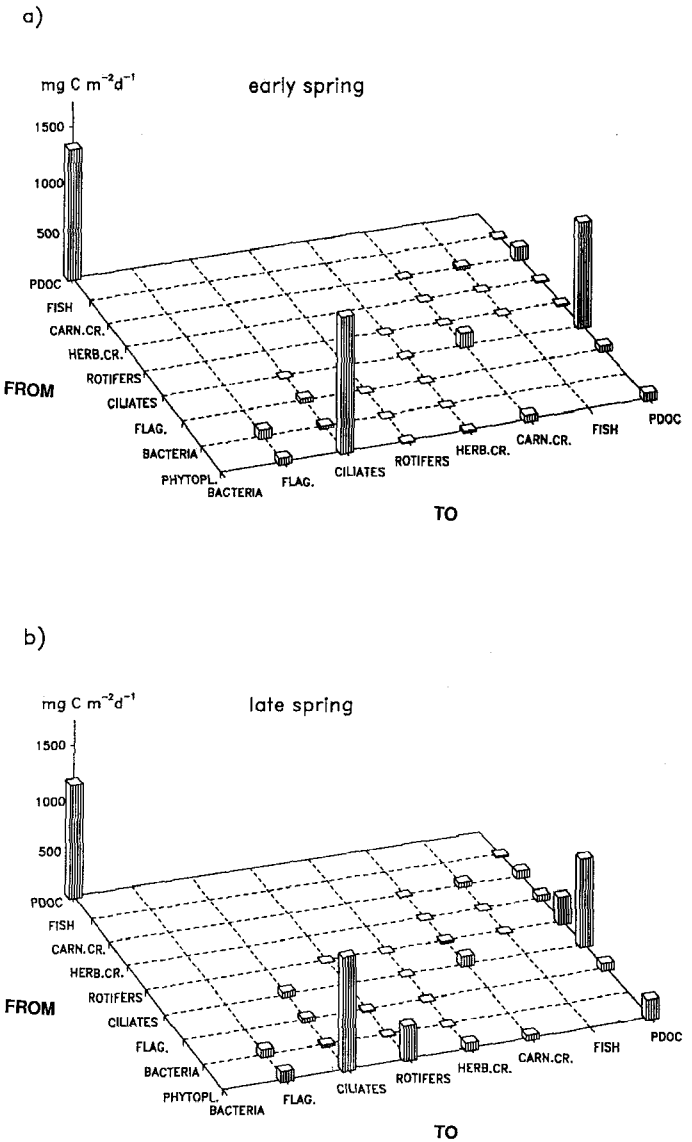
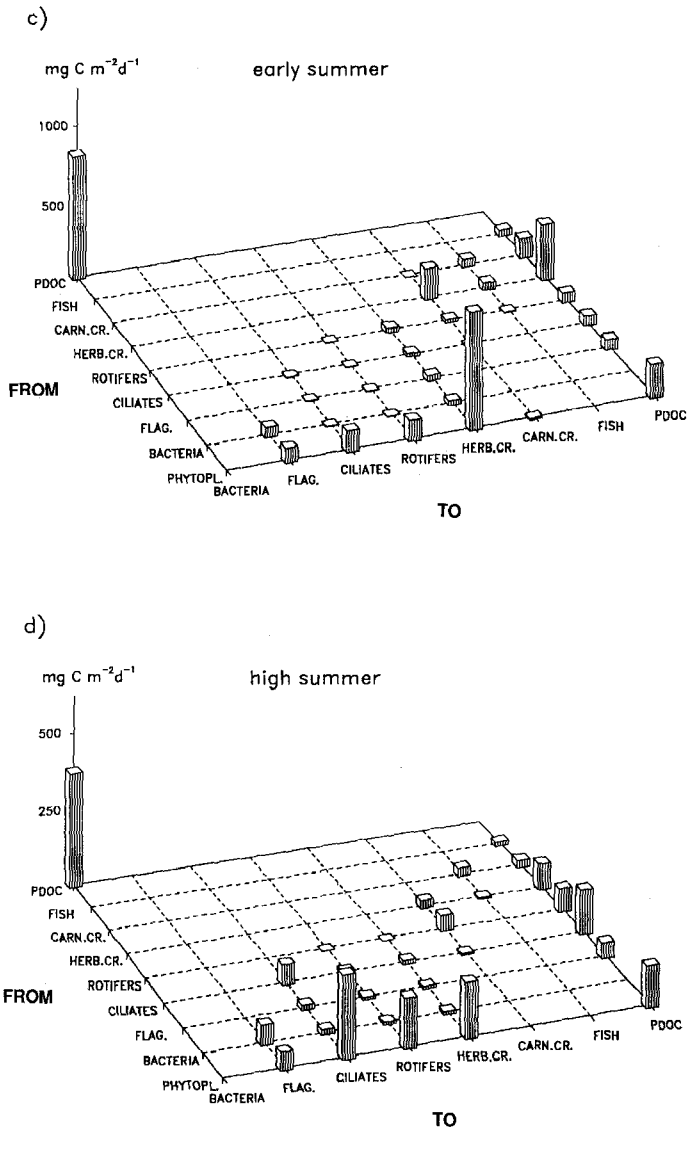


Fig. 2. Matrix of feeding transfers within the pelagic food web of Lake Constance to be read from left to right. All fluxes are given as mg C m^2 d^{-1} for the upper 20 m of the water column. FLAG: heterotrophic flagellates; HERB. CR.: predominantly herbivorous crustaceans (*e.g.* daphnids); CARN. CR.: predominantly carnivorous crustaceans (*e.g.* cyclopoid copepods); PDOC: particulate and dissolved organic carbon.



not satisfied by grazing on bacteria to 44%. In any case, heterotrophic flagellates are the principal bacterivores in our model, which consume about 75 to 95% (seasonal average 90%) of the bacterial production (Table II). Bacterivory by ciliates, rotifers, and crustaceans is of minor importance in respect to both, the grazing pressure on the prey and the nutrition of the predator. In Lake Constance daphnids are regarded as less efficient bacterivores (Geller and Müller, 1981).

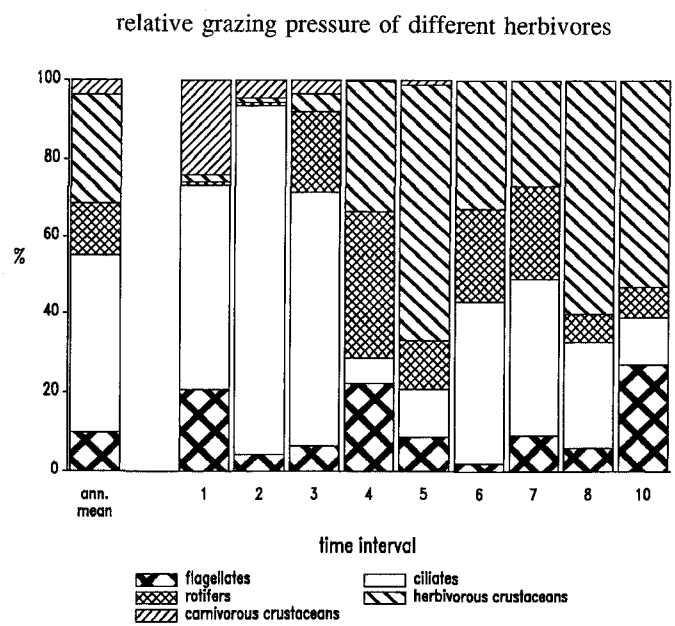


Fig. 3. Seasonal changes of the relative grazing pressure of different herbivores. The number of time intervals describes the seasonal course: # 1: late winter, # 2 and 3: early and late spring, # 4: clear-water phase, # 5: early summer with daphnid maximum, # 6: heavy flooding, # 7 and 8: high and late summer, # 10: late autumn.

In turn, heterotrophic flagellates are grazed by ciliates, rotifers, and crustaceans in our food web. The relative importance of the various consumers resembles that of phytoplankton grazers described above (Fig. 3). Heterotrophic flagellates do not contribute a substantial fraction to the diet of any of their predators since similarly sized autotrophic organisms exhibit densities which are one or two orders of magnitude higher (Gaedke, 1992).

Diet compositions of ciliates, rotifers, and crustaceans and their seasonal changes

Phytoplankton is the principal food source for small metazoan zooplankton belonging to the classical food web (*i.e.* herbivorous crustaceans and rotifers) and equally well for ciliates. The latter derive 69 to 94% (seasonal average 89%) of their nutrition from phytoplankton according to our calculations (Fig. 4) which are fairly insensitive against different assumptions (Table II). Heterotrophic flagellates provide another 3 to 15% (average 5%). Intra-compartmental predation may achieve some importance during high summer when the abundance of carnivorous ciliates is relatively high.

A food chain between bacteria, heterotrophic flagellates, and ciliates has been postulated for Lake Constance for most of the season based on inverse population developments and exclusion experiments (Weisse, 1991). Heterotrophic flagellates are the principal bacterivores in our model (see above). The consequences of a tight coupling between heterotrophic flagellates and ciliates were explored with an alternative version of the food web model by assuming that ciliates graze much more

TABLE II. – The effect of alternative assumptions on major flows and network parameters. The standard model version assumes a weighting factor of 10 for flagellate grazing on bacteria, a weighting factor of 1 for ciliate grazing on heterotrophic flagellates, equal transfer efficiencies for ciliates, rotifers, and herbivorous crustaceans, and a transfer efficiency of heterotrophic flagellates of 30%. Alternative version 1: as standard but the efficiency of ciliates is 0.1 higher than that of rotifers and herbivorous crustaceans. Version 2: as version 1 but with an efficiency of flagellates of 40%. Version 3: as standard model but with a weighting factor of 50 for flagellate grazing on bacteria (*i.e.* the flagellates are very efficient bacterivores as compared to ciliates, rotifers, and crustaceans). Version 4: as standard but with a weighting factor of 10 for ciliate grazing on flagellates (*i.e.* ciliate graze more efficiently on heterotrophic flagellates than rotifers and crustaceans). The entry "no effect" indicates that the change of underlying assumptions does not affect the process under consideration. $\bar{X}$ indicates the seasonal mean and "range" the seasonal variability. All values are given as percentages.

Effected flow or process	*standard*		*version 1*		*version 2*		*version 3*		*version 4*	
	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$	range
Bacterial contribution to flagellate diet	42	28-79	no effect		56	37-92	56	31-98	no effect	
Flagellate contribution to consumption of bacteria	69	54-87	no effect		no effect		91	86-97	no effect	
Protozoan contribution to the input of the POC/DOC-pool	46	14-82	36	10-82	33	6-82	no effect		no effect	
Phytoplankton contribution to ciliate diet	89	69-94	86	61-94	87	65-95	91	73-96	85	27-94
Flagellate contribution to ciliate diet	4.6	3-15	5.5	4-18	5.3	3-17	no effect		7.9	3-64
Ciliate contribution to phytoplankton grazing	45	7-89	37	4-89	38	4-92	46	7-90	44	2-89
Microbial food web efficiency	14	7-29	17	10-32	18	10-37	no effect		12	5-25

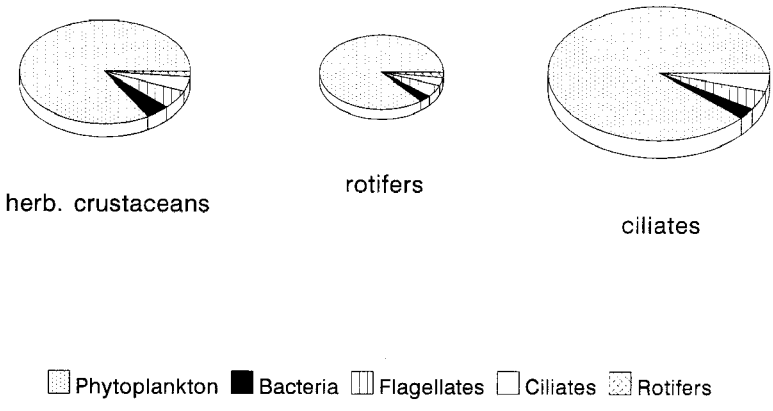


Fig. 4. Seasonal average of the diet composition of ciliates, rotifers, and herbivorous crustaceans. The area of the pies symbolizes the relative ingestion rates.

efficiently on flagellates than the other predators (weighting factor of ciliates: 10; other predators: 1, see method section) (Table II). Under this presumption ciliates graze 75-99% (seasonal average 90%) of the flagellate production (corresponding values of standard food web model: 10 to 95%, 50% on seasonal average). Nevertheless, heterotrophic flagellates only gain importance for ciliate nutrition during two time intervals but not on a seasonal average. Thus, ciliates may exert a top-down control under these assumptions but do not rely substantially on heterotrophic flagellates.

The diet composition of the compartment of predominantly carnivorous crustaceans exhibits pronounced seasonal changes (Fig. 5) which partially reflect the shift in dominance from cyclopoid copepods during winter, in spring (until June), and in late autumn to carnivorous cladocerans which contribute a large share from July to October. In contrast to the copepods, carnivorous cladocerans do not feed on phytoplankton. Nutrition of cyclopoid freshwater copepods at the beginning of the year remained under discussion since abundances of acknowledged prey species are very low. In our model ciliates constitute an important part to the diet of cyclopoid copepods in late winter and spring. The remaining fraction of copepod energy demands is covered by phytoplankton grazing which is in accordance with a recent study on limnetic copepod nutrition (Adrian and Frost, 1992). Cannibalism is only of minor importance for copepod nutrition in the model. During the clear-water phase and successive time intervals, rotifers and herbivorous crustaceans which are mostly represented by daphnids, dominate the diet of carnivorous crustaceans which are now predominantly cladocerans (Fig. 5).

To conclude, herbivory is of outstanding importance to cover the energy demands of ciliates, rotifers, and most crustaceans as compared to the contribution of bacterial and protozoan production. Ciliates are of great importance for the planktonic carbon cycle during most time of the year. Regarding time-averaged quantitative carbon fluxes,

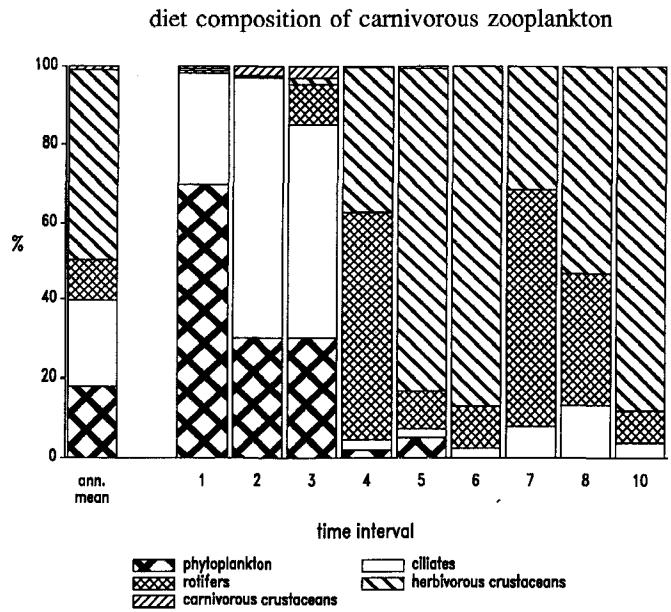


Fig. 5. Seasonal course of the diet composition of predominantly carnivorous crustaceans (*i.e.* cyclopoid copepods and zooplanktivorous cladocerans). Numbers of time intervals as in Figure 3.

ciliates, rotifers and predominantly herbivorous crustaceans have similar functions in our model. Considering the temporal organization reveals that ciliates are specialized in reacting quickly to resource pulses owing to their potentially high growth rates.

Recycling of organic matter

Decomposition of primary production may follow several routes in pelagic environments. Bacteria are directly supplied with organic carbon from phytoplankton through exudation from healthy cells, and by lysis of senescent and dead cells. This passage contributes only a minor fraction (6 to 26%, seasonal average 16%) to the organic carbon pool in our food web model (Fig. 6). It achieves relatively high values when the gross growth efficiency of herbivores is high which implies a smaller release of EOC by zooplankton, and vice versa. In contrast, protozoans are of great importance for the recycling of organic matter in the standard model, especially in spring. The share of metazoans is relevant from the clear-water phase onwards. An increase of protozoan transfer efficiencies by 0.1 units implies a reduction of their contribution to the POC/DOC pool from 46 to 33% on seasonal average (Table II).

Importance of microorganisms for the overall carbon flow

Pelagic food webs are sustained by two energy inputs, primary production and the production of osmotrophic bacteria which forms the basis of the microbial loop. As

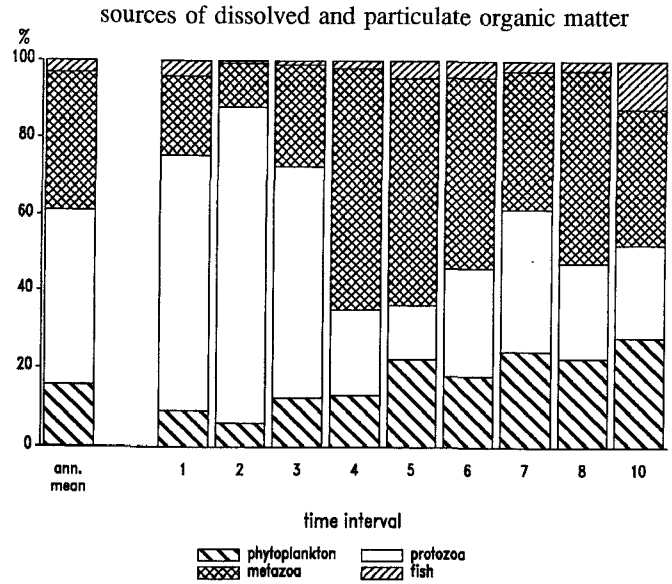


Fig. 6. Origin of dissolved and particulate organic matter and its seasonal change. Numbers of time intervals as in Figure 3.

allochthonous inputs of labile organic matter are regarded as negligible in our model, primary production is by far higher than bacterial production. The ratio between epilimnetic bacterial and autotrophic production varies seasonally between 7 and 18%. The importance of the microbial food web in relation to the classical food chain was quantified by Ducklow (1991) who introduced a measure called microbial food web efficiency which aims to quantify the link-sink issue. It reflects how much of the food uptake by microorganisms becomes finally available to macroconsumers and is defined as the ratio:

$$\frac{\text{heterotrophic flagellate and ciliate production grazed by rotifers and crustaceans}}{\text{ingestion by heterotrophic flagellates and ciliates}}$$

The microbial food web efficiency is low in spring, and during and after the summer flood. It is relatively high during the clear-water phase, and in early summer and autumn (Fig. 7). Low values may be caused by (1) low transfer efficiencies (here in spring and during the flooding event), (2) by a considerable consumption of flagellate production by ciliates which is then not available to larger zooplankton (here in spring, during flooding and in high summer), and (3) by protozoan intra-compartmental predation (here important for ciliates in high summer) and vice versa.

Discussion and Conclusions

The uncertainty of food web models that results from variable feeding behaviour, physiology, and specific model assumptions cannot be overcome. In a natural food

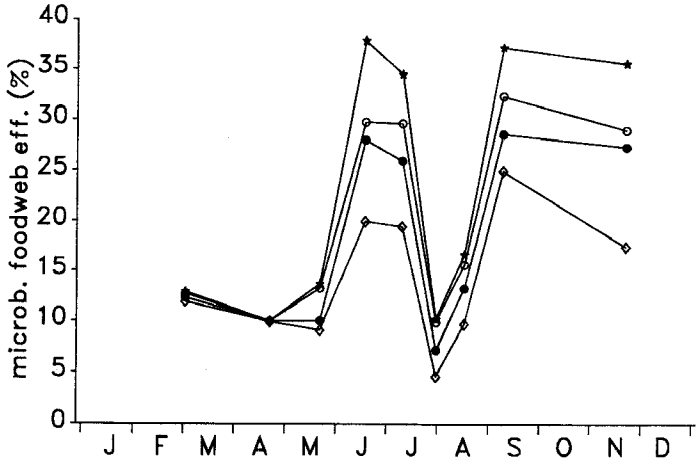


Fig. 7. Seasonal course of the microbial food web efficiency. Full circle: standard model; open circle: alternative model version 1; star: alternative version 2; rhombus: alternative version 4 (for definition of standard and alternative model versions see legend of Table II and text).

web all fluxes fluctuate in time and space. Stone *et al.* (1993) constructed a large number of different flux charts for Lake Kinneret based on the same data set by allowing for potential errors in the measurements and estimations, and for natural variability. A small amount of flux variation which is very likely to occur in a fluctuating environment, could provoke severe changes of single flows.

We tried to consider this problem in three different ways. First, we calculated time-averaged flow charts for periods of several weeks (*i.e.* sampling dates) to reduce the impact of short-term fluctuations in plankton abundances which are enhanced by physical processes at our sampling site (Gaedke and Schimmele, 1991). This procedure reveals seasonal trends which would be masked using annual averages. However, it prevents a detailed analysis of the effects that changes of the abundance and species composition of fast growing planktonic organisms may have upon carbon flows. The flow diagrams represent an average situation thought to be approximately representative for a certain period of time. The natural system is unlikely to attain the model carbon flows at any moment owing to its dynamic behaviour in time and space.

Secondly, a large body of field measurements and literature data was compiled to decrease the degrees of freedom when calculating mass balanced flow charts. The consistency of these parameters could be controlled by estimating the fluxes (*e.g.* production rates) and the efficiencies of various processes (*e.g.* growth and assimilation efficiencies) as this leads to an over-determination of the flow diagram when applying mass-balance constraints. In general, this method does not yield a unique solution but reduces the range of possible flux charts. It is remarkable on the other hand that solutions do exist which will satisfy almost all of the numerous constraints given by measurements.

Third, alternative hypotheses concerning the food web structure and transfer efficiencies, which all agree with present knowledge, were analysed to exhibit potential consequences of our uncertainty. They may all give a realistic picture of the ecosystem in Lake Constance.

The mass-balancing procedure invented for this study considers explicitly the numerous production measurements which are partially independent from biomass measurements. It does not require estimates of gross growth efficiencies which are regarded as less reliable than the production estimates in the present case study. Our procedure requires relatively little computational effort and it prevents that a mass-balancing procedure, incorporated in a software package, selects automatically unrealistic values for fluxes or adjusts weight-specific rates to unrealistic values. In other studies, alternative techniques like inverse methods (*e.g.* Vezina and Platt, 1988; Ducklow *et al.*, 1989) or linear programming (Stone *et al.*, 1993) were applied which have different advantages. Since the mass-balancing technique may influence the resulting flow charts and model results in different ways, their impact will be evaluated (*e.g.* by using linear programming) and discussed in detail (Straile *et al.*, in prep.).

Another inherent difficulty in the present, and most other modelling approaches, is of whether a "result" is largely implied by underlying assumptions or whether it represents new, independent information originating from the compilation of different data sources. We tried to reduce this problem by describing implications of assumptions and model structure in detail, and by presenting the consequences of various alternative hypotheses (*e.g.* Table II). Nonetheless, the results presented here are regarded as sufficiently reliable to support several conclusions which are subsequently discussed.

In summer and autumn, considerations of mass-balance and diet compositions point to ciliate production rates well below the potential rate established in the laboratory. This result is supported by *in situ* measurements of ciliate growth rates (Gilron and Lynn, 1989; Taylor and Johannsson, 1991) which were also considerably lower than the values provided by Montagnes *et al.* (1988). Three out of four ciliate species isolated from Lake Constance grew considerably slower than predicted by Montagnes *et al.* (1988) at high temperatures in the laboratory which demonstrated again that generalized allometric relationships provide only a rough indicator for actual growth in specific case studies (Müller and Geller, 1993). Estimates of laboratory and *in situ* growth rates are in closer agreement in spring (Müller, 1991).

In our food web model, heterotrophic flagellates cannot rely solely on bacterial production but cover an approximately equal amount of their energy demands by herbivory. The degree of herbivory may have been overestimated if either bacterial production and transfer efficiencies have been underestimated and/or flagellate biomass and/or growth rates have been overestimated, *e.g.* by the dilution technique. The latter are likely to represent maximum estimates since enhanced bacterial growth owing to filtration has to be assumed (Weisse *et al.*, 1990; Güde, 1986; Simon, 1988 and unpubl. results). The model results of the contribution of ciliates, rotifers, and crustaceans to the overall grazing pressure on phytoplankton were in reasonable

agreement with former investigations. Gaedke (1993) calculated the metabolic activity from allometric relationships for the three differently sized plankton groups based on the respective biomasses and individual body sizes. The metabolic rates showed a similar seasonal course for the relative importance of the different groups.

In analogy to their dominant prey organisms, the compartment of carnivorous zooplankton exhibited a similar shift towards larger sized species during the season. Marine copepods are known to feed on ciliates (Stoecker and McDowell Capuzzo, 1990). The relevance of this trophic interaction was less clear for Lake Constance. According to our calculations, ciliate production is important for copepod nutrition during the first part of the year as it represents the only heterotrophic production of quantitative importance available for carnivores during this time. In turn, cyclopoid copepods are the only potential predators of ciliates in early spring as fish larvae are unlikely to consume ciliates (Eckmann, pers. comm.) and abundances of other metazoans are low. Similar results were obtained from model calculation for L. Kinneret (Stone *et al.*, 1993).

Ciliates were important phytoplankton grazers and, in turn, derived most of their food by herbivory. Furthermore, they are likely to constitute a major part of the diet of cyclopoid copepods at the beginning of the year. By these means, a substantial portion of phytoplankton may reach larger zooplankton, especially if growth efficiencies of ciliates turn out to be high. Thus, ciliates which were generally assigned to the microbial food web, are strongly involved in flow dynamics commonly attributed to the classical food chain. In the present context the conceptual separation of the microbial loop and the classical food web may cloud the discussion and appears inconvenient for a further understanding of limnetic ecosystem functioning. Our findings support arguments made by Sherr and Sherr (1988) who emphasized the numerous trophic links between algae and various heterotrophs. Larger functional differences between ciliates and herbivorous crustaceans may prevail in pelagic systems where the latter are dominated by raptorial feeders which prefer larger food items than most ciliates ingest.

Calculated transfer efficiencies of herbivores were mostly high during the clear-water phase, and in summer and autumn although no nutrient limitation of algal growth was accounted for and the restricted edibility of some algal species was only considered by allowing for sedimentation of diatoms. High transfer efficiencies indicate an efficient utilization of prey production and a tight energy budget for the heterotrophic plankton community. An overestimation of transfer efficiencies for herbivores could result from an overestimation of their production. However, assuming lower production values for herbivores requires an increase of the efficiency of carnivorous crustaceans and/or a reduction of their production estimates. Both values are already at their upper and lower bounds respectively (Morgan *et al.*, 1980) which renders this hypothesis unlikely. Alternative model food web structures which *e.g.* channel a larger fraction of ciliates to carnivores, do not change this result. The transfer efficiencies of herbivores obtained from the flow diagrams are in reasonable agreement with calculations based upon biomass size distributions derived from the same data set (Gaedke and Straile, in press). According to actual knowledge such high transfer

efficiencies may only be achieved if they are close to gross growth efficiencies which suggests that losses, such as non-grazing mortality and sloppy feeding, are low.

Besides osmotrophic bacteria and carnivorous cladocerans, all planktonic heterotrophs covered a considerable fraction of their energy demands by grazing directly on autotrophs. Direct or indirect utilization of dead organic matter, representing the second input of energy into the food web, is of minor importance. Bacterial growth efficiencies indicate consistent estimates of bacterial production and the release of organic substances by the plankton community which implies that estimates of losses by respiration should be reasonable as well. The importance of herbivores for fuelling the organic carbon pool may have been overestimated by assuming that respiration equals production (*e.g.* Geller, 1985), and that all primary production which is not respired, exudated or sedimentated, is consumed by herbivores. The high trophic transfer efficiencies from the clear-water phase onwards suggest that the latter assumption is reasonable for that period of time. In contrast, our food web model may underestimate the fraction of organic matter passing directly from the phytoplankton compartment to the organic carbon pool in spring. At this time primary production is at its maximum and abundances of herbivores are still relatively low. However, the ciliate population will graze the net primary production in early spring if it has a weight-specific ingestion rate (I/B) of two (the corresponding values for other time intervals are below 0.6). I/B values (I: ingestion, B: biomass) in this range were found in a laboratory study of the numerically dominating species, *Pseudobalanion planctonicum* (Müller, 1991). Estimates of volume-specific clearance rates (Fenchel, 1986; Sherr and Sherr, 1987) indicate that the ciliate community in early spring is capable of clearing the uppermost 20 m of the water column within 2 to 20 days. Energetic considerations suggested that the upper bound of the clearance rates were required to cover ciliate energy demands in Lake Constance as under this assumption, I/B values of 1.4 were obtained in spring 1987 when considering *in situ* abundances of the dominant algal species (Müller *et al.*, 1991). Thus, ciliate ingestion rates are at an upper bound in early spring in our model. This may indicate that the fraction of particulate primary production not consumed by herbivores has been underestimated. It may become directly available for bacteria unless sedimentation from the epilimnion is too low. Alternatively, the importance of large heterotrophic flagellates may have been underestimated. When applying specific sampling techniques these organisms constituted a significant herbivore group in early spring in a large number of lakes (Arndt and Mathes, 1991).

To conclude, the amount of carbon exudated by phytoplankton appears to be small as compared to the zooplankton mediated EOC flow during most of the year independent of specific model assumptions. The potential importance of this feedback effect of herbivores on bacteria has been demonstrated also with a comprehensive chemostat experiment (Arndt *et al.*, 1992).

A non-mass balanced carbon flow diagram which relied largely on ingestion measurements or estimates (Weisse *et al.*, 1990), has been established for the same sampling location in Lake Constance for the early spring of a subsequent year (1988). Similar results were obtained in some aspects (*e.g.* the low grazing rates of metazoan

herbivores as compared to primary production) whereas different conclusions were made in others. For example, Weisse *et al.* (1990) assumed a much higher bacterial production based on measurements with the dilution technique and satisfied energy demands of heterotrophic flagellates solely by bacterivory. Bacteria were exclusively fuelled directly by primary production of which they required a large fraction although a bacterial growth efficiency of 50% was assumed. Recycling of organic matter, *e.g.* from herbivores which is of major importance in our model has been ignored in that flow diagram. Weight specific ingestion rates of ciliates were low (0.5) and only 2.8% of ciliate carbon per day was channelled to macrozooplankton. The corresponding value in our model is about 20% and lies within the range of values found by *in situ* grazing experiments with daphnids (Wickham and Gilbert, 1993)

To summarize, protozoa appear to be of minor importance for the nutrition of larger plankton. The microbial transport of bacterial carbon is a function of both, the food web structure and the transfer efficiency of the grazers. To estimate the maximum contribution of microorganisms to the diet of larger zooplankton, we assumed a food web structure with tight coupling between the uni- and multicellulars. Nevertheless, microbial food web efficiencies indicate that a large amount of organic carbon is respired within the microbial food web, and only a small amount of bacterial carbon is channelled to the classical food web via the microbial food web. However, dissipating a considerable fraction of the total carbon (*i.e.* representing a sink in respect to carbon) implies a correspondingly high recycling of nutrients. Concentrations of soluble reactive phosphorus in the uppermost 0-8 m dropped below 10 (resp. 3) $\mu g\ l^{-1}$ from May (resp. August) to October 1987 indicating a limitation of algal growth during this time (Gaedke and Schweizer, 1993). Thus, our model results suggest that the primary function of bacterivorous flagellates and other bacterivors may be nutrient recycling in the pelagic food web of Lake Constance. Enhanced nutrient recycling is likely to increase phytoplankton growth as bacteria were regarded as mostly carbon limited in Lake Constance during the period of investigation (Güde, 1990). Enhanced phytoplankton growth, in turn, would promote higher zooplankton growth rates. The potential importance of bacteria for carbon recycling and heterotrophic flagellates for phosphorus remineralisation in Lake Constance was pointed out by Güde *et al.* (1985) for the first time. Recent detailed measurements confirm this point of view (Jürgens and Güde, 1990). The cycle of phosphorus will be investigated in a similar way in a subsequent study to complement the present investigation.

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