Seasonal changes of trophic transfer efficiencies in a plankton food web derived from biomass size distributions and network analysis

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Abstract

The trophic transfer efficiencies in the planktonic food web of large, deep, and meso-eutrophic Lake Constance were derived independently from biomass size distributions and from mass-balanced carbon flow diagrams based on comprehensive data for biomass, production, and food web structure. The main emphasis was on the transfer of primary production to herbivores since this process dominates the flow of matter within the food web. Biomass size distributions offer an ecosystem approach which relies only on measurements of biomass and a few general assumptions, whereas network analysis is predominantly based on production estimates and requires more detailed knowledge of the ecosystem. Despite these differences, both approaches give consistent results for both the absolute values of the transfer efficiencies and seasonal trends. Estimates of the seasonally averaged transfer efficiency (dominated by the utilization of primary production by herbivores) range from 0.20 to 0.27. They are considerably lower in late winter and spring (0.05 to 0.21) than in summer and autumn (0.25 to 0.38, extreme values: 0.20 and 0.42).

Key words: Biomass; Food webs; Network analysis; Plankton; Seasonality

1. Introduction

The efficiency with which organic matter is transferred from a lower to a higher trophic level (here called trophic transfer efficiency) is of great importance for both practical and theoretical ecosystem analysis (e.g. Ducklow, 1991). For example, the trophic efficiency influences food web structure and fish yield, and it is

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taken as an indicator of the level of ecosystem organisation by theoretical ecologists. Despite their importance, trophic efficiencies in complex natural ecosystems have only occasionally been quantified. Such investigations require comprehensive knowledge and extensive data sets for the ecosystem under consideration, they are potentially subject to many errors, and they are frequently complicated by very complex and highly variable feeding interactions.

The present investigation provides a case study from a large pelagic ecosystem (Lake Constance) which has been studied in detail within the collaborative program "Cycling of matter in Lake Constance". Results obtained from Lake Constance may be regarded as representative for large open-water ecosystems owing to the size, depth, and morphology of the lake.

Trophic transfer efficiencies cannot be assessed directly by in situ measurements, they represent theoretical quantities which are calculated based on conceptual models. We used two different ecosystem approaches to estimate trophic transfer efficiencies and their seasonal changes in order to improve the reliability of our investigations, and to test the consistency of the results obtained by the two concepts.

The first approach is based on biomass size distributions which are constructed by allocating all organisms into logarithmically spaced size classes according to their individual body mass, and computing the total biomass per size class. Thus they are exclusively based on observations of standing stocks and cell sizes, and the factors required to convert abundances to biomass. Both kinds of data are well accessible to measurements and are well established for the pelagic zone of Lake Constance. Biomass size distributions have previously been used to analyse structural and functional aspects of the plankton community in Lake Constance (Gaedke, 1992a,b). The slope of a size spectrum can be used as an indicator for the trophic transfer efficiency since it reflects the biomass ratio between different size classes which may represent different trophic levels in pelagic ecosystems. Roughly speaking, a prey biomass which is high compared to the biomass of the predator points to a low efficiency, and vice versa. A method has been suggested to quantify trophic efficiencies from the slopes of (normalized) biomass size distributions (e.g. Platt and Denman, 1978; Gaedke, 1993) which posits (1) that the predators are larger than their prey and that average predator–prey weight ratios can be estimated, and (2) that the weight-specific metabolic rates (e.g. P/B ratios) of the component organisms follow allometric relationships. The coefficient of proportionality of the latter is only assumed to remain constant along the size gradient whereas the scaling exponent has to be specified. It was set to the commonly accepted value of 0.25 (Peters, 1983; Moloney and Field, 1989) in the present study.

These assumptions are reasonably well fulfilled for the plankton ecosystem under consideration, except for bacteria which grow much slower than expected by allometric analysis, and which derive organic substances from organisms which are larger than themselves (Güde, 1990a). They have been excluded from further analysis by restricting the size spectra to larger sized organisms. To summarize, biomass size distributions are close to the form in which the raw data are obtained
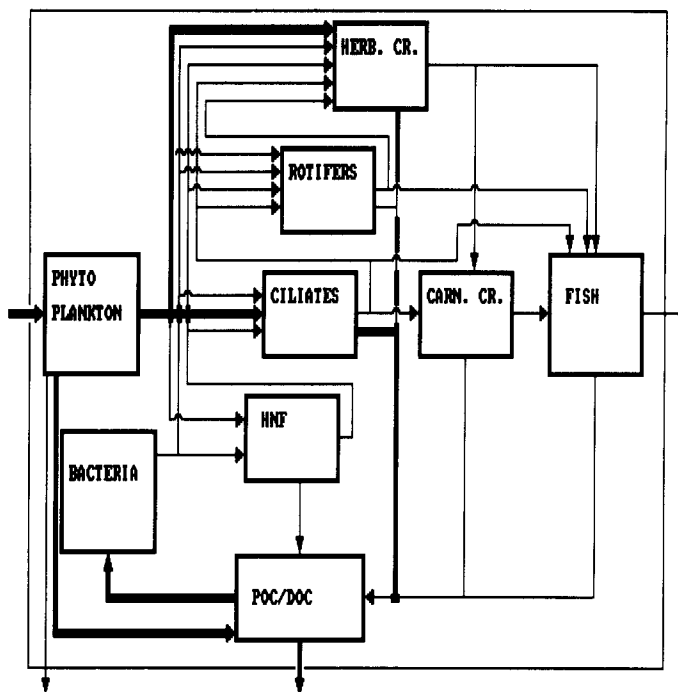
Fig. 1. Schematic diagram of the flow of matter in the pelagic food web of Lake Constance. The compartment labelled POC/DOC represents the pool of particulate and dissolved organic matter. Thick arrows indicate flows which are quantitatively important throughout the season.

and provide an estimate of the flow of matter from small to large organisms based on a few general assumptions at the expense of detailed information.

The second approach is based on mass-balanced carbon flow diagrams which were studied using network analysis. It involves much more detailed considerations of the community structure, feeding habits and interactions, and metabolic processes like production, respiration, and exudation (e.g. Baird and Ulanowicz, 1989; Wulff et al., 1989; and literature cited therein). In the present case study, a schematic diagram of the flow of matter was established between eight living and one non-living compartments to which the pelagic organisms were allocated (Fig. 1). The transfer efficiencies were directly derived from the inter-compartmental flows between autotrophs and herbivores. This improves the comparability with results obtained from size distributions and ensures a straight-forward interpretation of the ecological meaning of the computations.

Relatively low bacterial production and growth efficiencies have been suggested for Lake Constance (Güde, 1990a,b; Simon, pers. commun., 1993) suggesting that the contribution of the microbial loop to the diet of larger zooplankton is of minor quantitative importance on seasonal average when compared to the flows from autotrophs to herbivores. The analysis of numerous carbon flow diagrams which

were established by assuming different yet feasible food web structures and growth efficiencies support this point of view (Gaedke and Straile, 1994).

2. Methods

Lake Constance (German: Bodensee) is a large (476 km^2) and deep (mean depth 100 m, $z_{max} = 252$ m) meso-eutrophic lake of warm-monomictic character at the northern fringe of the Alps (47°50′N) in Central Europe. The sampling site is located in the fjord-like north-western arm of the lake. All groups of plankton organisms were sampled at least weekly during the growing season of 1987 (23 March to 16 November) at various depths by a large number of scientists. Abundances and body sizes were assessed by microscopy using different sampling and counting techniques which were appropriate for the size and fragility of the organisms (for production measurements see below). Although some questions are left open by the resulting data set, it is of outstanding quality regarding its completeness and temporal resolution as compared to other lakes or marine systems. Details on measurements and computation of biomass size spectra are given by Gaedke (1992a) and references cited therein.

The size spectra under consideration extend over the size range which consists mostly of autotrophs and zooplanktonic organisms covering their energy demands mainly by grazing on phytoplankton (i.e. ciliates, rotifers, and most crustaceans). The two largest plankton species found in Lake Constance are the zooplanktivorous cladocerans *Leptodora* and *Bythotrephes*. They are of minor importance with respect to biomass and metabolic activity, and have been excluded from the analysis to facilitate the comparability between the two approaches and the interpretation of the results. Average predator and prey sizes were computed by weighting the mean body mass, w_i, of each size class, i, with the relative metabolic activity, M_i of the prey resp. predators. The metabolic activity is calculated as $M_i = B_i^{-0.25}$, where B_i represents the biomass of size class i. This approach accounts for the higher weight-specific activities of small organisms.

Size distributions and predator–prey weight ratios were calculated repeatedly based on somewhat different yet feasible assumptions to evaluate the impact of the underlying assumptions on the overall result (Table 1). Three versions comprise the biomass of all plankton organisms within the given size range, whereas two are completely restricted to the biomass of autotrophs and herbivores which facilitates estimation of predator–prey weight ratios. Herbivorous biomass was calculated by estimating for all omnivores the fraction of the diet supplied by phytoplankton and weighting their biomass accordingly. Thus, trophic transfer efficiencies obtained from the size distributions reflect mostly or entirely the efficiency of transferring primary production to herbivores, although the contribution of other trophic interactions is included in three cases. In one version computation of average prey size is based on the assumption that only some groups of algae are grazeable and that the others are not edible at all, whereas other scenarios assume that all algae

Table 1
Assumptions underlying the computation of biomass size distributions and predator prey weight ratios (for details see text)

Version	Depth interval	Size range	Predator size	Prey size
1	0–100 m	$2–3 \cdot 10^7$ pg C	average of ciliates, rotifers, and crustaceans	average of all algae > 2 pg C
2	0–100 m	$2–3 \cdot 10^7$ pg C	average of ciliates, rotifers, and crustaceans	average of palatable algae > 2 pg C only
3	0–100 m	$2–3 \cdot 10^7$ pg C	average of herbivors > 2 pg C	average of all algae > 2 pg C
4	0–100 m	$0.1–3 \cdot 10^7$ pg C	average of all herbivors	average of all algae > 0.1 pg C
5	0–20 m	$2–3 \cdot 10^7$ pg C	average of ciliates, rotifers, and crustaceans	32 pg C constant throughout the season

are grazed with equal efficiency. In this and the other cases reality is likely to be best reflected by a middle course. Hence most probable values of the transfer efficiencies are expected within the envelope defined by the different versions.

Mass-balanced carbon flow diagrams were established based on the measurements of standing stocks and especially production estimates which were made for each plankton group for the uppermost 20 m of the water column. Trophic interactions and the diet composition of omnivores were derived from grazing experiments (e.g. Knisely and Geller, 1986) and a detailed study of the qualitative trophic interactions in Lake Constance (M.M. Lang et al., unpubl.). Allocation of prey production to different omnivorous predators was mostly based on the relative share of individual consumers to total predator production. Production estimates were either derived from measurements (bacteria, autotrophs, heterotrophic flagellates), or computed from temperature- and size-dependent growth rates obtained from the literature (for more information see Geller et al., 1991; Gaedke and Straile, 1994; and literature cited therein). For rotifer production, additional measurements of egg ratios indicating the state of nutrition were considered (Rigler and Downing, 1984). Exudation increased from 5% of primary production in winter and early spring to 10% in late spring and during the clear-water phase. A corresponding value of 15% was assumed for the rest of the season. Algal dark respiration was assumed to be 20% of primary production. Bacterial respiration was calculated as the difference between consumption and production. Respiration of other heterotrophs was set equal to production. Ingestion equalled prey production to maintain mass balance between trophic levels, i.e. non-grazing mortality was not modelled explicitly except for larger diatoms which sedimentated at a rate of 10% per day. A variable fraction of ingested prey items was released as organic matter. This fraction was calculated as the difference between ingestion, and the sum of respiration and production. This approach provokes that the release of organic matter is relatively high when prey concentrations are high, and that it is low under food-limited conditions (for details see Gaedke and Straile, 1994). Resulting growth and assimilation efficiencies were compared to previous studies (Morgan et al., 1980; Gulati et al., 1982; Le Borgne, 1982).

In order to concentrate on the dominant processes and to get consistent results from both approaches, the trophic transfer efficiency was calculated from the flow diagrams as the ratio between total production of ciliates, rotifers, and herbivorous crustaceans, and the sum of their prey production. The prey production consists of the net primary production (i.e. ^{14}C-measurements reduced by respiration, exudation, and sedimentation) and the fraction of the production of microbial organisms (i.e. bacteria, heterotrophic flagellates, ciliates, rotifers) which is grazed by ciliates, rotifers, and crustaceans. Both approaches include potential non-grazing mortality, e.g. by sedimentation.

The investigation period was divided into ten time intervals of unequal length representing different stages in the seasonal plankton development (i.e. late winter, first and second spring bloom, clear-water phase, first daphnid maximum, rainy period with heavy flooding, high and late summer, early autumn with second daphnid maximum, late autumn; for details see Geller et al., 1991) for which separate biomass size spectra and flow diagrams were computed to describe the seasonal changes in ecosystem structure.

3. Results

The trophic efficiencies as obtained from the biomass size distributions vary between 0.20 and 0.27 on seasonal average (Fig. 2a). Estimates based on the entire eukaryotic community averaged over the total water column (0–100 m) are lower (0.20–0.22) than those based on average epilimnetic values (i.e. the uppermost 20 m of the water column). The latter result is influenced by the assumption that all crustaceans are located and feed in the epilimnion. The different versions (Table 1) exhibit similar seasonal trends with low values in late winter and spring, and high values in summer and autumn. A pronounced increase in the transfer efficiencies occurs from early spring (first phytoplankton bloom) to early summer (first daphnid maximum). No systematic differences exist between the efficiencies estimated from size distributions comprising all organisms or those which are restricted to autotrophs and heterotrophs, indicating that pigmented and non-pigmented organisms are utilized with similar efficiency.

During one period in autumn most versions suggest transfer efficiencies which appear unrealistically high according to present knowledge. During this period, an extremely high abundance of *Daphnia hyalina* was recorded on one sampling date (5 October 1987). This abundance exceeds the ones observed during the previous and following week by a factor of 8 and respectively 29 (Geller, pers. commun., 1992). Equally high abundances of *D. hyalina* have never been observed during 12 years of almost weekly observations, especially not in autumn, which suggests that the exceptionally high abundance may be caused by unusual spatial heterogeneity or a counting error. Omitting the period under discussion is thought to provide a more representative impression on the seasonal course of the transfer efficiency (for further evaluations see below) (Fig. 2b).

Network analysis reveals that the major flows between living compartments
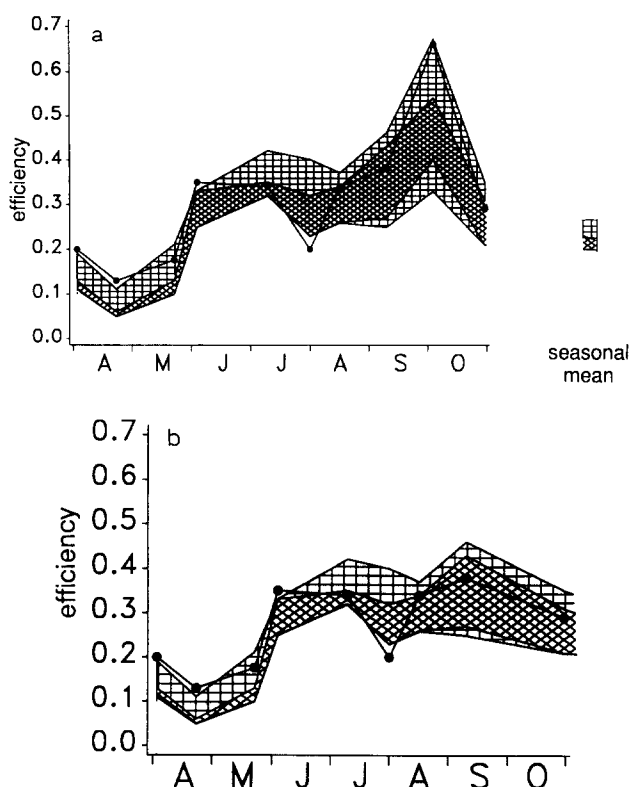
Fig. 2. Seasonal changes of the transfer efficiencies. The area defined by hatching indicates the envelope derived from the different versions of the biomass size distributions. The versions defining the darkly hatched envelope are regarded as more reliably. The line with dots represents the estimate derived from the network analysis. (a) all values included. (b) A period in autumn has been omitted which is dominated by one measurement of exceptional high concentrations of *Daphnia hyalina* (for details see text).

occur between phytoplankton and predominantly herbivorous zooplankton groups (i.e. ciliates, crustaceans) on seasonal average (Fig. 1). Other flows of quantitative importance are the release of dead organic material by autotrophs and herbivores and its uptake by bacteria (for details see Gaedke and Straile, 1994). The largest single metabolic processes within the network are primary production which represents the only system input, and the respiration of phytoplankton and bacteria. Constraints imposed by mass balance considerations strongly support the conjecture that the extremely high daphnid concentration recorded on one sampling date in October does not represent a population density which can be sustained for a longer period of time. Using reasonable diet compositions and growth efficiencies, the network cannot be balanced during that period (Fig. 2a).

The flow diagrams suggest relatively low transfer efficiencies during late July and early August. This time interval was characterized by cold and rainy weather

combined with extreme flooding of the lake. Total plankton biomass decreased during this time and the community structure changed. Transfer efficiencies derived from network analysis are relatively low since the production of herbivores and thus their energy demands, are more strongly reduced than primary production during this time interval. Some versions of the size distributions point to higher efficiencies than the carbon flow diagram because the effect of more negative slopes caused by the decrease of herbivorous biomass is partially compensated by relative small predator–prey weight ratios owing to changes in the community structure. The latter originate predominantly from a smaller contribution of daphnids to the total herbivorous biomass.

4. Discussion

The results obtained from biomass size distributions and mass-balanced carbon flow diagrams agree well with respect to both absolute values and seasonal changes of the transfer efficiencies. The values derived from network analysis are somewhat higher in spring than those obtained from biomass size distributions. However, the estimates based on network analysis are also subject to uncertainties which are introduced, e.g., by production or respiration estimates and the ambiguity of the food web structure. We do not regard the differences between the two approaches as significant unless more years are analysed in the same way (see below). A former estimate of trophic transfer efficiencies made for selected time intervals using size spectra and a rough and seasonally constant estimate of average algal cell size (Gaedke, 1993) falls within the range established in this study.

Biomass size distributions and network analysis represent non-dynamic ecosystem descriptions. The dynamic behaviour of the system under consideration has been accounted for in several ways. The season has been subdivided into ten time intervals to which the assumption of steady state conditions is restricted. Within single time intervals, fluxes are generally much higher than changes of standing stocks which may justify this assumption. Changes of average biomasses between time intervals were accounted for by introducing a storage term for each compartment of the flow diagrams. The spring estimates of the trophic efficiencies derived from size spectra are likely to somewhat underestimate the true values owing to changes of standing stocks whereas estimates for early summer and October are expected to represent maximum values for the same reason.

Despite all uncertainties involved in the quantification of the transfer efficiencies, it can be stated that there is a continuous increase of the efficiencies from early spring to early summer, and that the traditional rule of thumb of 10% transfer efficiency between adjacent trophic levels underestimates true values in summer in the planktonic food web of Lake Constance. The onset of stratification provides suddenly excellent growth conditions for small algae which quickly reach high biomasses and production rates. The larger sized herbivores have longer generation times, which causes a time-lag in the spring development between the

two trophic levels and may prevent an efficient use of the resources (for details see Gaedke, 1993; and literature cited therein). More generally, transfer efficiencies appear to be low if the ecosystem is strongly influenced by abiotic factors (e.g. onset of stratification, extreme flooding).

The absolute values of the transfer efficiencies in summer are mostly high, indicating a tight coupling between both trophic levels. This result is in agreement with the idea that herbivores are food limited during summer in Lake Constance. Direct evidence for a severe food limitation during the clear-water phase and in summer is available for several species of rotifers from the egg ratio, and for daphnids from the clutch size, length–weight relationship, and age structure of the population (Geller, 1989) as well as from their elemental composition (Berberovic, 1990). Ciliates are most probably also food limited from the clear-water phase onwards (Müller et al., 1991). Summer transfer efficiencies are in the range of gross growth efficiencies (i.e. the ratio of production to ingestion) reported for plankton organisms from laboratory studies (Fenchel, 1987; Urabe and Watanabe, 1991) which also indicates low non-grazing mortalities. Primary production has been measured weekly with an elaborate ^{14}C technique (Tilzer and Beese, 1988). However, the knowledge on the relationship between gross and net primary production under natural conditions is small as compared to the outstanding quantitative importance of this process for the overall carbon flow and the calculation of transfer efficiencies from the flow diagrams. A pronounced overestimation of the latter by assuming too large differences between gross and net primary production is unlikely since conservative estimates for dark respiration, exudation, and sedimentation were used.

Trophic efficiencies obtained in other studies are mostly similar or below the seasonal average of Lake Constance. Results from the IBP-program suggest in general low values (Morgan et al., 1980), however, the consumption and production by microzooplankton has mostly been ignored. Cross-system comparisons are complicated by differences in the quality of the data base and the assumptions involved in balancing the flow diagram. Additionally, they are strongly affected by the way of computation of the trophic efficiency (Kozlovsky, 1968). Within the framework of network theory new concepts have been suggested to describe the flow and cycling of matter within an ecosystem (e.g. Lindeman spine (Ulanowicz, 1994), trophic unfolding (Burns et al., 1991)). These concepts were not applied in the present case since the results cannot be compared directly with those obtained from size spectra.

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