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Evaluation of the importance of bacteria in the carbon flow of a small open grassland stream, the Breitenbach

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With 2 figures and 3 tables in the text

Abstract

A first estimate of annual bacterial production on the basis of bacterial biomass and heterotrophic bacterial activity was made for the Breitenbach, a small open grassland stream in Central Europe. A surprisingly high value of 750 g C/m^2/year was calculated, suggesting that the bacteria may contribute significantly to the nutrition of primary consumers in the Breitenbach.

Introduction

Classical ecological, including limnological, studies considered bacteria and fungi mainly in their function as decomposers of organic material. At the trophic levels of primary consumers, secondary consumers, etc. consumption should be accompanied by substantial production of biomass. But at the level of bacteria which also consume organic matter, formation of biomass should be very small compared to consumption.

During recent decades, it has been shown that bacterial biomass is of great importance in the food web of lakes. For example, KUSNETSOV & ROMANENKO (1966) reported that the bacterial production in the Rybinsk Reservoir surpassed the primary production. Later investigations by e.g. OVERBECK (1971, 1972, 1979 a), TILZER (1972), GRANBERG (1974), and ANDERSON & DOKULIL (1977) emphasized the importance of bacteria in lake ecosystems not only as decomposers but also as producers of organic matter. FENCHEL & JØRGENSEN (1977) explained the essential role of bacteria in detritus food chains of different aquatic ecosystems and emphasized their quantitative importance in food webs, especially in benthic systems.

It is certainly not unjustified to assume that bacterial biomass in small streams is of still greater importance than in lakes, but estimates of bacterial production in such ecosystems have, as far as I am aware, not yet been published. In this study, a first attempt is made to estimate the bacterial biomass production in the Breitenbach, a small open grassland stream in Hesse (Federal Republic of Germany).

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The Breitenbach

The Breitenbach is a small Central European stream over 4 km in length. Its source is about 350 m a.s.l. and its entry into the river Fulda about 220 m a.s.l. The upper reach is surrounded by trees, whereas in the middle stretch, considered in this study, the stream flows through grassland, about 50 m from the wooded valley slopes. Some study site characteristics are given in Table 1.

A comparison of primary production and input of coarse particulate allochthonous organic matter is presented in Table 2. Compared with the nearby Rohrwiesenbach, a small woodland stream, the input of allochthonous material is rather low. Considering that the input of dissolved and fine particulate organic matter (the latter is possibly higher than coarse particulate input) was not measured, the real allochthonous influence is certainly important in the open grassland stream Breitenbach.

Estimate of bacterial production

A first rough estimate of bacterial production in the middle reach of the Breitenbach can be made using numbers of bacteria from sediments and flow-

Table 1. Characteristics of the middle reach of the Breitenbach. Most data are from Marxsen (1980 a), some (discharge, temperature) from Brehm & Meijering (1982).

Discharge	2.6 –51 l/s
Mean width	0.35 –1.6 m
Depth	max. 0.4 m
Temperature	2 –14 °C
pH	6.5 –7.8
Conductivity	109 –124 μS_{20}/cm
Total inorganic carbon	4 –10 mg C/l
Oxygen	near 100 % saturation
Ortho-phosphate	10 –70 µg P/l
Ammonia	<1 –70 µg N/l
Nitrite	0.2 –5 µg N/l
Nitrate	0.2 –1.2 mg N/l
Dissolved organic carbon	0.5 –3.5 mg C/l

Table 2. Primary production and input of coarse particulate allochthonous organic matter (g C/m^2/year). Data from Marxsen (1980 a).

	Breitenbach	Rohrwiesenbach
Primary production of macrophytes (incl. "Aufwuchs")	70–200 (55–78 %)	–
Primary production of "Aufwuchs" (excl. on macrophytes)	11 (4– 9 %)	22 (3 %)
Input of coarse particulate organic matter	47 (18–37 %)	634 (97 %)
	128–258 (100 %)	656 (100 %)

ing water, and data on heterotrophic bacterial activity known only for bacteria from flowing water.

Number and biomass of bacteria

The numbers of bacteria were determined by the acridine orange direct count method. Samples of sandy sediments were first homogenized. By registering the volume of bacterial cells during microscopic counting, the total volume of bacteria could be calculated. Details of the methods were described earlier (Marxsen 1981 a, b, 1982).

The number of bacteria in the flowing water fluctuates from about 500,000 to 3,000,000 cells/ml during the year (Marxsen 1980 b), whereas in the upper 2.5 cm of the sandy sediment about 10^9 to 10^{10} bacteria/ml can be found. The biomass of epilithic bacteria (on gravel and stones) was assumed to be 5 % of the value in the same volume of sand. For conversion of bacterial biovolume into biomass dry weight the values proposed by Bakken & Olsen (1983) were used: a buoyant density of $1.07 \, g/cm^3$ and a dry matter content of 30 %. Assuming dry matter to contain 50 % carbon, the conversion factor from bacterial biovolume into bacterial carbon is $0.16 \, g \, C/cm^3$ or $1.6 \times 10^{-13} \, g \, C/\mu m^3$. The recently published conversion factor of Bratbak (1985) ($5.6 \times 10^{-13} \, g \, C/\mu m^3$) would give 3.5-fold higher values of bacterial biomass. For one m^2 of the stream, annual fluctuations of between 8.4×10^{12} and 8.4×10^{13} bacterial cells (suspended in the flowing water and sessile on sandy to stony particles of the upper 2.5 cm sediment layer) were calculated, corresponding to about 0.15 to 1.6 g of bacterial carbon.

Glucose assimilation and heterotrophic bacterial production

Based on uptake kinetics, extensive investigations on heterotrophic bacterial activity were performed in the Breitenbach water (Marxsen 1980 c). In the Plußsee, a lake in Northern Germany, Overbeck (1979 a, b) observed that the maximum uptake velocity (V_{max}) for glucose corresponds to about 10 % of the heterotrophic bacterial production; in other lakes of this region it can be less than 5 %. Kuparinen (1984) found a relationship of actual glucose uptake (which is lower than the maximum uptake velocity) to bacterial production of 4 to 8.3 % on an annual basis in a brackish water system at the SW-coast of Finland. Assuming V_{max} to correspond to 10 % of total bacterial production, a cautious estimate of total production can be made. Application of the lower percentages would result in higher production values.

Glucose assimilation in the Breitenbach sediment is not known. Wallis (1979) (using uptake kinetics) compared the assimilation of glumatic acid per cell by sessile and planktonic populations of stream bacteria. It was found that uptake by sessile bacteria was slightly lower, whereas Ladd et al. (1979) observed (using similar methods) a higher assimilation of glutamic acid by sessile bacteria. Until special investigations in the Breitenbach will have been performed, bacterial cells in the upper 2.5 cm of sediment are assumed to assimilate as much glucose as suspended cells.

Using these somewhat hypothetic or even speculative assumptions bacterial production in the middle reach of Breitenbach is calculated to be about 750 g C/m^2/year. Divided by a mean biomass of 0.82 g C/m^2 a P/B ratio (production per biomass) of 910/year results.

Bacteria in the food web of the Breitenbach

Conversion efficiency and carbon sources

The surprisingly high heterotrophic bacterial production value of 750 g C/m^2/year should be comparable to other parts of the food web in the Breitenbach. The first question is: How much organic matter is necessary for such high production?

In the literature, values of bacterial carbon conversion efficiency (percentage carbon incorporated into bacterial biomass/carbon used) are quite

Table 3. Carbon flow through the trophic levels in the middle reach of the Breitenbach: measured or estimated values and lacks. Primary production and input of organic matter is regarded as the first level, production by bacteria and fungi as the second and production of primary consumers as the third level. The higher levels are not considered. For sources of data see Table 2 and text. All values in g C/m^2/year.

1st level:	
Primary production, photoautotrophic (80–210)	200
Release of DOM by primary producers	?
Chemoautotrophic production	?
Input of coarse particulate allochthonous matter	50
Input of fine particulate allochthonous matter	>50
Input of dissolved allochthonous matter (surface run-off, interflow, groundwater discharge)	?
Input from the upper reach of the stream:	
particulate material	?
dissolved material	?
Total (necessary for nutrition of bacteria 3000)	>3000
2nd level:	
Production of bacteria	750
Production of fungi	?
3rd level:	
Production of insects	50
Production of *Gammarus*	20
Remaining production of primary consumers	?

variable. Percentages of more than 50 %, mostly found with labile substrates such as glucose or amino acids, are probably not valid for a natural stream like the Breitenbach, with a high portion of refractory organic matter. Newell et al. (1983) and Newell (1984) found carbon conversion efficiencies between 9 and 14 % for various detrital material into bacterial biomass in marine environments under nutrient poor conditions. These efficiencies could increase to 38 % in nutrient enriched (N, P) media. Similar carbon conversion values (19 to 64 %) were reported by Haines & Hanson (1979) for bacterial yields from saltmarsh plant debris incubated in nitrogen-rich media and by Robinson et al. (1982) from seaweed detritus (22—43 %). In the carbon flow calculations of Newell (1984) C-transfer efficiency from plant detritus to bacteria is 23 %. Therefore it seems reasonable to assume a carbon conversion efficiency of 25 % for the Breitenbach. On this basis the organic carbon needed by the heterotrophic

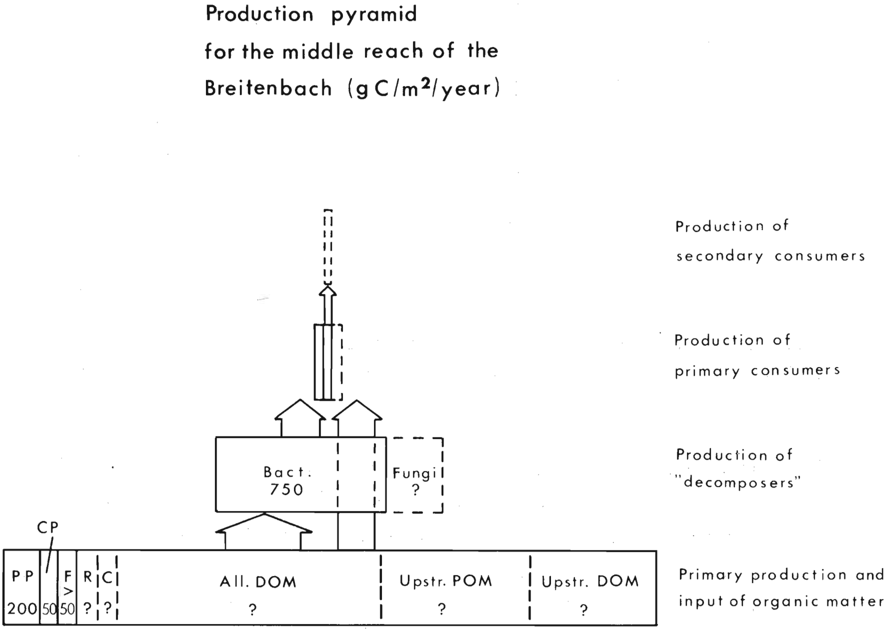

Fig. 1. Hypothetical production pyramid for the middle reach of the Breitenbach. The solid lines enclose compartments for which at least estimated values are known; no values are known for compartments which are limited by dashed lines. In this figure the detritus und grazer food chains are combined to emphasize the quantitative importance of bacteria. PP — primary production (excl. release of dissolved organic matter), CP — coarse particulate allochthonous organic matter, F — fine particulate allochthonous organic matter, R — release of dissolved organic matter by primary producers, C — chemoautotrophic production, All. DOM — allochthonous dissolved organic matter, Upstr. POM — particulate organic matter from upstream, Upstr. DOM — dissolved organic matter from upstream. For the origin of data see Table 3.

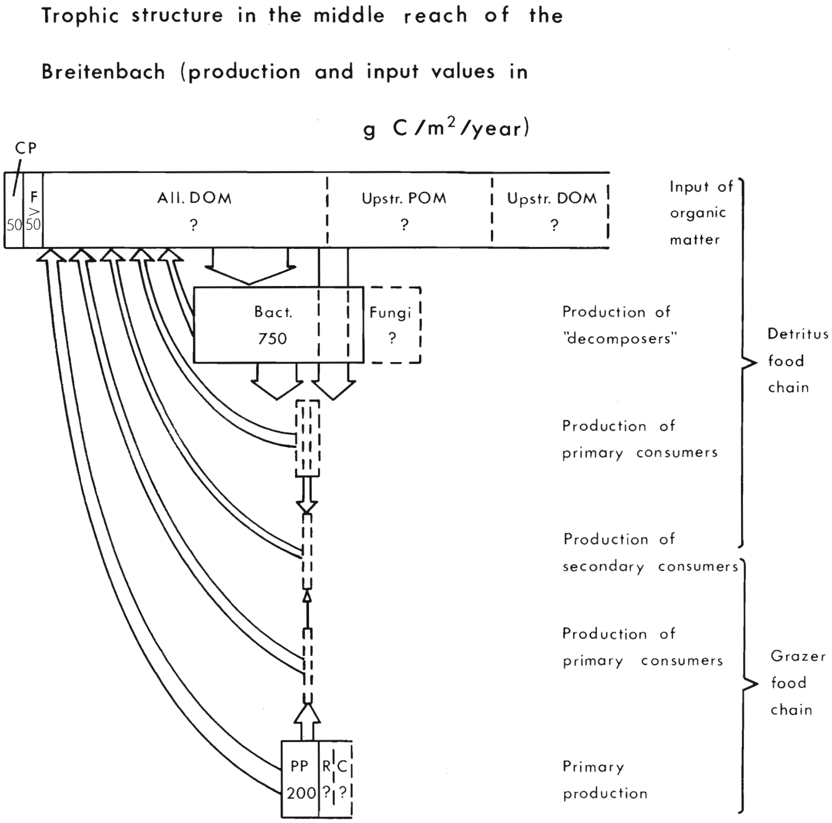

Fig. 2. Hypothetical trophic structure in the middle reach of the Breitenbach. Grazer and detritus food chains are separated, as in Cummins et al. (1966). For explanations see Fig. 1.

bacteria amounts to 3000 g/m^2/year. Assuming 10 % efficiency, 7500 g C/m^2/year are required by the bacteria, or at 50 % efficiency, 1500 g C/m^2/year.

Table 3 shows the different carbon sources for the first trophic level in the middle reach of the Breitenbach. Primary production and input of organic carbon are regarded as the first level whereas bacterial and fungal production is considered as the second level (the same is done in Fig. 1), — to emphasize the importance of bacteria in the trophic system of the Breitenbach. From the first level approximately 200 g C/m^2/year represents primary production of macrophytes and "Aufwuchs" algae (without release of dissolved organic matter) and about 50 g C/m^2/year input of coarse particulate matter from the terrestrial environment; input of fine particulate matter is presumed to be more than 50 but less than 100 g C/m^2/year. Of the remaining unknown carbon sources in that section of Breitenbach considered, it is expected that considerable amounts from the input of dissolved matter (esp. by groundwater) and from transport from the upper reach of the stream (more as particulate than as dissolved material) are used by the bacteria. The release of dissolved matter by primary producers and chemoautotrophic production are believed to be less important.

The total production and input from external sources at the first level must exceed 3000 g C/m^2/year, because the fungi also need organic carbon for nutrition, while an unknown fraction is eaten directly by primary consumers.

Consumption of bacteria by primary consumers

From the third trophic level of primary consumers, rough estimates of insect and *Gammarus* production are available. About 50 g C/m^2/year of total insect production was calculated on the basis of data from BENEDETTO (1975), who found that the biomass of emerging insects from the species *Agapetus fuscipes* (Trichoptera) was 4.0 % of annual production, and ILLIES (1982), who reported the total annual dry weight of all emerging insects as about 4.1 g dry matter/m^2, whereas the *Gammarus* production was calculated to be about 20 g C/m^2/year from the data of PIEPER (1978). Considerable numbers of young *Gammarus* live in sandy sediments of the Breitenbach, where the largest proportion of bacterial production occurs. Insect larvae, which are supposed to have the highest production among primary consumers in the stream, populate the sandy sediments in relatively small numbers (WAGNER 1985). This means that most of the presumed high bacterial production is not available for insect nutrition. In addition, the question, which insect larvae can ingest bacteria, remains. Most could have problems because of the structure of their mouthparts and their behaviour.

The main consumers of bacteria in the sandy sediments of Breitenbach must be sought among other animal groups. FENCHEL & JØRGENSEN (1977) state that protozoans "may be the most important consumers of bacteria in nature and constitute a significant link in food chains between bacteria and metazoans. Within all major groups of protozoa (flagellates, rhizopods, and ciliates), single species and larger taxons are found which are totally specialized to a bacterial diet". NEWELL (1984) also stresses the importance of protozoans in energy flow through decomposer food chains. But this group of organisms is scarcely investigated in the Breitenbach and no information on their quantitative occurrence or their feeding rates is available.

Another group living in sandy sediments is the meiofauna, which consists of benthic metazoa measuring less than 1 or 2 mm, including groups such as rotifers, turbellarians, nematodes, gastrotrichs, tardigrades, harpacticoid copepods, and small oligochaetes. Again FENCHEL & JØRGENSEN (1977) explain, that "this heterogeneous assemblage of organisms undoubtedly plays a large role as a consumer of bacteria in nature". But a complete picture of the feeding biology of those organisms is far from available. All these groups have been observed in the Breitenbach sediment, harpacticoid copepods by Klemp (1979), the others by Schwank (1981, 1985), but sufficient information on quantitative occurrence, nutrition and production of the various groups is not available.

A quantitative relationship between bacteria and microconsumers in the Breitenbach food web cannot be described. It should be mentioned that at the primary consumer level, of which insects, *Gammarus*, protozoans, and the meiofauna have been briefly discussed, several "internal food chains" exist. Thus organisms of the meiofauna feed not only on bacteria, but also on protozoans (as well as on material from the first level), while insects may feed on the same groups (including meiofauna), such that the assignment of such distinct organisms to one particular trophic level is an oversimplification, as is well known to ecologists.

Comparison with other studies on benthic bacterial production

As already stated, the estimated value for heterotrophic bacterial production in the Breitenbach seems to be rather high. It is difficult to believe that such an enormous amount of organic carbon (about 3000 g C/m^2/year) is available for bacterial nutrition in the stream section considered. To establish whether the estimated bacterial production of 750 g C/m^2/year is reasonable, comparison with other benthic systems could help. Such investigations however are very scarce.

Kaplan & Bott (1983) give indirect estimates of conversion of DOC into bacterial carbon from experiments performed with stream-bed sediments of a third order reach in Pennsylvania. Their data at different conditions ranged from 1.6 to 190 mg C/m^2/h. The annual mean of the Breitenbach from this study is 86 mg C/m^2/h.

Fenchel & Jørgensen (1977) calculated the production for a hypothetical detritus food chain in a temperate, coastal system where decomposition of detritus occurs mainly in the sediment. Their estimate of bacterial production (5 kcal/m^2/day) corresponds to about 190 g C/m^2/year.

Newell (1984) published a study on energy flow in a kelp bed community on the west coast of the Cape Peninsula, South Africa. He found the bacterial production in this system to be 6550 kJ/m^2/year, which corresponds to about 160 g C/m^2/year.

Odum (1957), in his classical study on the trophic structure and productivity of Silver Springs, evaluated bacterial production at 460 kcal/m^2/year, corresponding to about 50 g C/m^2/year. His bacterial conversion efficiency (9 %) is lower than assumed here and in the other studies mentioned, thus contributing to the low production value.

Carbon flow in the Silver Springs and in the marine systems mentioned is almost entirely based on autochthonous primary production, whereas in addition to primary production of the Breitenbach itself, this stream receives large quantities of allochthonous organic matter which enter the food chain. Thus a higher bacterial production in such a system is not impossible.

From the biomass dry weight of 4.6 g/m^2, bacterial carbon content in the Silver Springs can be estimated at 2.3 g/m^2, from which the P/B ratio of about 22/year for bacteria can be calculated. FENCHEL & JØRGENSEN's (1977) P/B ratio is about 150/year, while for the present study it is 910/year. WETZEL (1983) reports P/B ratios for bacteria from 73 to 237/year. Compared with this range the P/B ratio for Silver Springs is far too low, the ratio for the Breitenbach far too high.

Future studies on heterotrophic bacterial production, its carbon sources, and its consumption by the fauna, including measurements of carbon and energy flow, will reveal whether the assumptions on the function of bacteria in the Breitenbach discussed here provide an approximately accurate picture. However the preliminary estimates clearly suggest that the bacteria play an important role in the stream's food web and cannot be regarded simply as decomposers.

Summary

Classical limnological studies considered bacteria and fungi mainly in their function as decomposers of organic material. Whereas at the trophic levels of primary consumers, secondary consumers, etc., consumption should be accompanied by substantial production, at the level of bacteria which also consume organic matter, formation of biomass should be very small compared to total consumption. But during the last decades, it has been shown, that bacterial production is of great importance in the food web of lakes.

A first estimate of annual bacterial production on the basis of bacterial biomass and heterotrophic bacterial activity was made for the Breitenbach, a small open grassland stream in Central Europe. A surprisingly high value of 750 g C/m^2/year was calculated, suggesting that the bacteria may contribute significantly to the nutrition of primary consumers in the Breitenbach.

Zusammenfassung

In klassischen ökologischen Untersuchungen wurden Bakterien und Pilze hauptsächlich in ihrer Funktion als Destruenten organischen Materials betrachtet. Auf den Trophiestufen der Primärkonsumenten, Sekundärkonsumenten, usw. sollte Konsumption gleichzeitig Biomassenbildung bedeuten. Dagegen sollte auf der Ebene der Bakterien und Pilze, die ja auch organische Stoffe konsumieren, also Konsumenten sind, nur eine sehr geringe Biomassenbildung im Vergleich zur Gesamtkonsumption vorhanden sein. Für Seen wurde in den letzten Jahrzehnten gezeigt, daß die Bakterien mit ihrer Biomasse eine wichtige Rolle in der Nahrungskette spielen können.

Für den Breitenbach, einen kleinen Wiesenbach in Osthessen, wird hier erstmals eine Abschätzung der bakteriellen Produktion auf der Basis der bakteriellen Biomasse

und ihrer heterotrophen Aktivität vorgenommen. Dabei wurde ein überraschend hoher Wert von etwa 750 g C/m^2/Jahr ermittelt. Vergleicht man diesen Wert mit der Biomassenbildung der Primärkonsumenten, die fast eine Größenordnung niedriger liegen dürfte, so wird deutlich, daß die Bakterien zusammen mit den Pilzen in der Lage sind, einen ganz wesentlichen Beitrag zur Nahrungsversorgung der Fauna zu leisten (Tabelle 3, Abb. 1 und 2).

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