

## Energy flow through the algal and bacterial communities in the surface layer of bottom sediments of the River Raba and Dobczyce Reservoir (southern Poland)

Teresa BEDNARZ and Aleksandra STARZECKA

Karol Starmach Institute of Freshwater Biology, Polish Academy of Sciences,  
ul. Sławkowska 17, 31–016 Kraków, Poland

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**Abstract** – The biomass, production, respiration of algae and heterotrophic bacteria were determined in the surface layer (0.5 cm) of bottom sediments in the river above and below the reservoir, and in the backwater and littoral zone of the reservoir during the vegetation periods (April–October) in 1993 and 1994. The amounts of energy flowing (assumed as the sum of biomass, production, and respiration) through algae and bacteria communities at particular stations were respectively 64–387 and 39–142 kJ m<sup>-2</sup> d<sup>-1</sup>. From the pool of total energy bio-accumulated by heterotrophic bacteria and algae, 87–98% originated from algae, but from the pool of energy released 76–97% was due to heterotrophic bacteria.

**Key words:** bacteria, algae, biomass, production, respiration, sediments, river, dam reservoir.

**Przepływ energii przez zbiorowiska glonów i bakterii w powierzchniowej warstwie osadu dennego rzeki Raby i Zbiornika Dobczyckiego (południowa Polska).** Oznaczono biomasę oraz produkcję pierwotną glonów i biomasę oraz produkcję heterotroficznych bakterii, a także respirację tych organizmów w powierzchniowej warstwie (0.5 cm) osadów dennych w rzece powyżej i poniżej zbiornika, i w cofce i litoralu zbiornika w sezonie wegetacyjnym (IV–X) w 1993 i 1994 roku. Ilość energii przepływającej przez zbiorowiska glonów i bakterii (suma biomasy, produkcji i respiracji) wynosiły odpowiednio 64–387 i 39–142 kJ m<sup>-2</sup> d<sup>-1</sup>. Na glony przypadało 87–98% puli całkowitej energii bioakumulowanej przez heterotroficzne bakterie i glony, natomiast 76–97% energii uwolnionej pochodziło od heterotroficznych bakterii.

### 1. Introduction

The surface layer of sediments receives a particulate material in the form of detritus, i.e. organic carbon lost by non-predatory processes from any trophic level (Wetzel et al. 1972) and also, directly, by algal and bacterial production *in situ*. Recently bacteria have been recognized not only as mineralizers but also as important producers of particular organic carbon (Williams 1981a, 1981b, Riemann et al. 1982, Azam et al. 1983, Simon 1984), which, through bacterial grazing, is transported to higher trophic levels of the water ecosystem (Simon 1984, Vadstein et al. 1989, Tulonen 1993). In the surface layer of bottom sediments benthic algae

productivity is often high and may provide as much as a third of the total primary phytoplankton productivity (Van Raalte et al. 1976, Daumas 1990, Pinckney and Zingmark 1993). During photosynthesis 22–46% of the fixed carbon may be released, as dissolved organic matter, and directly utilized by bacteria in the course of their production (Azam et al. 1983, Chrost 1984, Simon 1984, Scavia 1988, Vadstein et al. 1989). On the other hand, the bacterial production supply of particulate organic matter can be high, in the range of 18–44%, an average 30% of the phytoplankton lake primary production (Vadstein et al. 1989).

The input of organic matter to the sediments is controlled by many factors: primary production, depth and transparency of the water column, force of bottom currents, and seasonal variations in input, which directly or indirectly modify biological activity in the surface layer of bottom sediments (Overbeck and Chrost 1990). In addition, exchanges in this layer also depend on bacterial activity and macrofauna burrowing (Daumas 1990).

The aim of the present work was to estimate the charge of energy flowing through the algal and bacterial benthic communities in the surface layer of bottom sediments of the River Raba and the Dobczyce Reservoir.

## 2. Study area

The investigation was carried out in the River Raba and the Dobczyce Reservoir at four stations: 1) the River Raba above the reservoir (stony bottom, depth 0.3 m); 2) the backwater (muddy-gravelly bottom, depth 0.5–0.8 m); 3) the littoral zone of the reservoir (muddy-sandy bottom, depth 0.5–0.8 m); 4) the River Raba below the reservoir (stony bottom, depth 0.3 m) (fig.1).

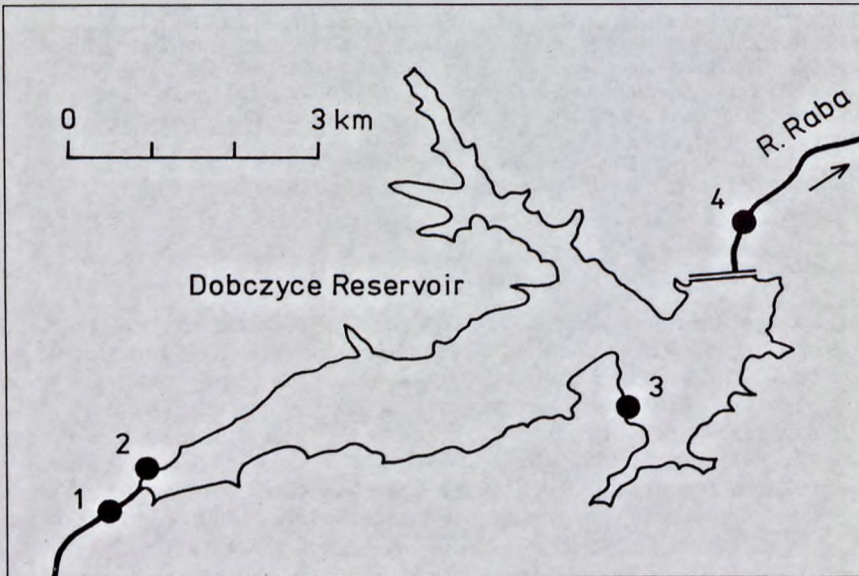


Fig. 1. Location of sampling stations (1–4) on the River Raba and Dobczyce Reservoir.



The River Raba rises in the Gorce Mountains (Carpathian Mts) at an altitude of 700 m. The Dobczyce Reservoir (49°57' N, 20°02' E, altitude 270 m) lies in the middle course of the River Raba, at the 60th km from its source. The geological base of this section of the river basin (Pogórze Wielickie Hills) is Silesian flysch (Tertiary sandstones of various age). The catchment area consists of a mosaic structure of arable fields, grasslands, and forests (Pasternak 1969). The main source of water for the reservoir is the Raba which brings in 88.6% of the total water inflow (Mazurkiewicz 1988). The volume of the Dobczyce Reservoir is  $120 \cdot 10^6 \text{ m}^3$ , surface area 1000 ha, max. depth 28 m, mean depth 11 m, and average turnover  $3.6 \text{ y}^{-1}$ . The littoral zone of the reservoir constitutes 25% of its area. The reservoir, being dimictic water body, is thermally stratified in summer and mixed twice a year, usually in April and in October.

### 3. Material and methods

Samples of the surface layer of bottom sediments were collected during two vegetation seasons (April–October 1993 and 1994) at monthly intervals. In the case of the reservoir (Stations 2 and 3) the samples of the surface layer of 0.5 cm of bottom sediments were taken by means of a tube sampler 6 cm in diameter. However, in the river (Stations 1 and 4) the samples were collected by scraping the sediments from areas marked on the stones by means of the same sampler. At each station nine sub-samples were taken and mixed, yielding a mean sample for any given station.

The ash-free dry weight of sediments was determined using the dry weight (105 °C) and organic matter content, estimated as loss on ignition at 550 °C. According to Jørgensen (1979), it was accepted that organic carbon constituted 50% of ash-free organic matter.

The primary production of algae ( $P_a$ ) in water suspension of sediments was determined by using the light-dark bottle method and a Clark oxygen electrode (100 g of fresh sediment suspended in 900 mL of water from the sampling site (the water being autoclaved to remove the non-benthic microorganisms). In order to ensure a uniform level of the content of oxygen and carbon dioxide dissolved in the sediment suspension, the samples were intensively aerated. They were exposed to light (PAR 103  $\text{mmol m}^{-2} \text{ s}^{-1}$ ) and in the dark, at 20 °C during 12–16 h. The respiration of algae ( $R_a$ ) was assumed as 20% of their photosynthesis (Hargrave 1969, Hillbricht-Ilkowska 1977).

The respiration of heterotrophic bacteria ( $R_b$ ) was calculated from amount of the oxygen taken up by the bacterial fraction isolated from the water suspension of sediments (prepared in the same way as that described above) by means of filtration through Whatman GF/C glass microfibre filters. After aeration, the filtrates were kept in the dark at 20 °C during 12–16 h. From the number of viable heterotrophic bacteria in the filtrate (determined *via* spread plates using agar media) and the amount of the oxygen consumed by them (measured by means of a Clark electrode), the respiration of one bacterial cell was calculated. Then, using the number of heterotrophic bacteria determined in 1 g of fresh sediments (using the plate method), the respiration of these bacteria in the sediments was calculated. The obtained values were multiplied by the production coefficient 0.08, according to Sorokin and Kadota (1972), and the production of heterotrophic bacteria ( $P_b$ ) in the sediments was calculated.

The biomass of algae ( $B_a$ ) was estimated on the assumption that  $1 \mu\text{g}$  of chlorophyll *a* corresponds to  $50 \mu\text{g C}$  (Jørgensen 1979). Chlorophyll *a* was determined by ethanol extraction, according to Sartory (1982). The biomass of bacteria ( $B_b$ ) was determined using the total number of heterotrophic bacteria in the sediments (estimated by the agar plate method), assuming that one bacterial cell contains  $6.05 \times 10^{-8} \mu\text{g C}$  (Watson et al. 1977). The Schrodinger coefficient (Odum 1982), expressing the ratio of respiration to biomass of bacteria ( $R_b/B_b$ ) was also calculated. All measurements were carried out in 3 replications and the results given as an arithmetical mean in  $\text{kJ m}^{-2} \text{day}^{-1}$ .

According to the equation of photosynthesis, in the calculations concerning production and respiration the assumption was that  $1 \text{ g O}_2$  is equivalent to  $0.375 \text{ g C}$  and  $14.78 \text{ kJ}$ . In calculating the algal and bacterial biomass it was accepted that  $1 \text{ g C}$  is equal to  $4.9 \text{ kcal}$  and  $20.53 \text{ kJ}$  (Cummins 1967, Hargrave 1969). The diel sum of energy utilized for bioaccumulation ( $B_a+P_a$  or  $B_b+P_b$ ) and respiration ( $R_a$  or  $R_b$ ) constituted the energy pool flowing through the algal or bacterial link. These charges were assumed as 100% for calculation of the percentage share of energy utilized by algae or bacteria in the bioaccumulation and the releasing of energy (respiration).

#### 4. Results

The mean content of organic carbon in the surface layer of bottom sediments was highest in the littoral zone of the reservoir (Station 3) and 1.4–2.2 times exceeded those at the remaining stations (Table I). The mean diel values of the investigated parameters ( $B_a$ ,  $P_a$ ,  $B_b$ ,  $P_b$ ,  $R_a$ ,  $R_b$ ) varied at particular stations. In the River Raba at Stations 1 and 4, above and below the reservoir,  $B_a$  was about 2–8 times greater than those in the reservoir (Stations 2, 3). Contrary to  $B_a$ ,  $P_a$  and  $R_a$  at Station 1 were 4–5 times greater than the values at the remaining stations. The

Table I. The characteristics of algal and bacterial communities in the surface layer of bottom sediment in the River Raba above (Station 1) and below the Dobczyce Reservoir (Station 4), and in its backwater (Station 2) and littoral zone (Station 3) in the vegetation seasons (April–October) of 1993–1994: C — total organic carbon,  $B_a$  — biomass of algae,  $P_a$  — production of algae,  $R_a$  — respiration of algae,  $B_b$  — biomass of bacteria,  $P_b$  — production of bacteria,  $R_b$  — respiration of bacteria (mean  $\pm$ SD,  $\text{kJ m}^{-2} \text{d}^{-1}$ ).

Parameter	Stations			
	1	2	3	4
C	659.2 $\pm$ 61.0	846.7 $\pm$ 47.4	1197.5 $\pm$ 111.1	556.8 $\pm$ 80.5
$B_a$	273.6 $\pm$ 81.5	45.2 $\pm$ 8.4	77.32 $\pm$ 14.7	365.5 $\pm$ 57.3
$P_a$	71.6 $\pm$ 30.9	15.7 $\pm$ 9.4	13.6 $\pm$ 6.9	18.0 $\pm$ 10.8
$R_a$	14.3 $\pm$ 6.2	3.1 $\pm$ 1.9	2.7 $\pm$ 1.4	3.6 $\pm$ 2.2
$B_b$	3.6 $\pm$ 0.9	2.9 $\pm$ 1.0	4.0 $\pm$ 2.9	3.2 $\pm$ 1.0
$P_b$	4.5 $\pm$ 1.1	6.1 $\pm$ 1.8	3.9 $\pm$ 1.8	14.9 $\pm$ 5.9
$R_b$	44.5 $\pm$ 9.4	52.1 $\pm$ 14.9	35.0 $\pm$ 15.3	124.2 $\pm$ 50.0
$R_b/B_b$	12.4	18.0	8.7	38.8
$B_a+P_a+R_a$	359.5	64.1	93.6	387.1
$B_a+P_a$	345.2	60.9	90.9	383.5
$B_b+P_b+R_b$	52.6	61.1	42.9	142.3
$B_b+P_b$	8.1	9.0	7.9	18.1



biomass of heterotrophic bacteria ( $B_b$ ) was practically equal at all the investigated stations. Conversely,  $P_b$  and  $R_b$  were greatest in the River Raba below the reservoir (Station 4) and were about 2–4 times greater than those at the remaining stations.

The greatest values of energy charges flowing through algal ( $B_a+P_a+R_a$ ) and bacterial ( $B_b+P_b+R_b$ ) links were found at Station 4 and exceeded about 2.7 times the charge of energy flowing through the bacteria (Table I). The smallest energy pool in the algal link appeared at Station 2 and in the bacterial one at Station 3. At the two stations in the Raba the amount of energy flowing through the algae was similar, but in the case of heterotrophic bacteria it was different. In the river below the reservoir it was about 3 times greater than that in the river above it. In the littoral zone (Station 3) the energy pool transformed by algae was 1.5 times greater than that in the backwater of the reservoir (Station 2). Conversely, the sum of energy transformed by heterotrophic bacteria in the backwater was 1.4 times greater than that in the littoral zone. The amount of energy bioaccumulated in the heterotrophic bacteria link ( $B_b+P_b$ ), was about 7–43 times smaller than that bioaccumulated in the algal link ( $B_a+P_a$ ), although the amount of energy released by heterotrophic bacteria respiration ( $R_b$ ) was 3–35 times greater than that of algae ( $R_a$ ).

Taking into account the percentage share of the energy bioaccumulated ( $B_a+P_a$ ) and released ( $R_a$ ) in the diel charge of energy flowing through the algal link ( $B_a+P_a+R_a$ ) it was found that 95–99% of energy was taken up for bioaccumulation and only 1–5% was released. In the case of the bacterial link the bioaccumulation of energy ( $B_b+P_b$ ) was only 15.4–18.4%, and most, i.e. 81.6–87.3% of the energy, was due to its release ( $R_b$ ) (fig. 2). The ratio of the amount of energy released as

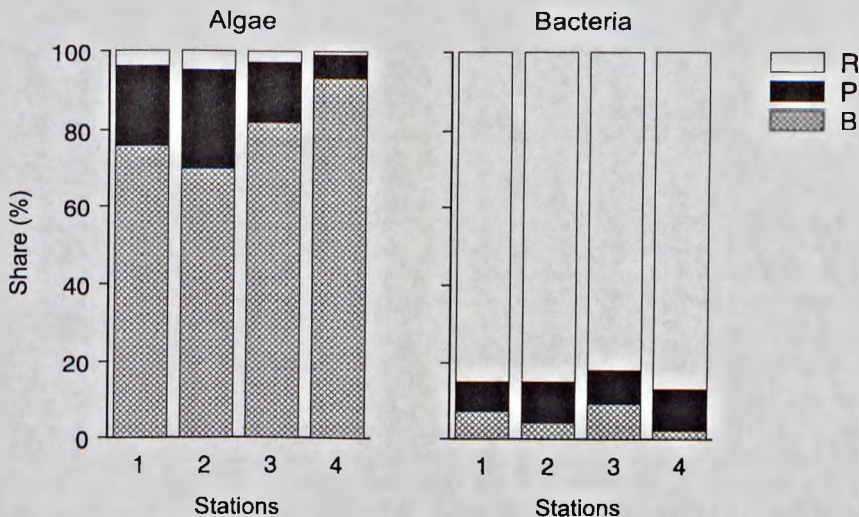


Fig. 2. Energy flow on the level of algae and heterotrophic bacteria in the surface layer (0.5 cm) of bottom sediments in the River Raba above (Station 1) and below the Dobczyce Reservoir (Station 4), and in its backwater (Station 2) and littoral zone (Station 3) in the vegetation seasons (April–October) of 1993–1994: B — biomass, P — production, R — respiration.

a result of bacterial respiration to the amount accumulated in their biomass ( $R_b/B_b$ ) indicated that the expenditure of energy per unit biomass of heterotrophic bacteria was lowest in the littoral zone of the reservoir (Station 3) and highest in the River Raba below the reservoir (Station 4). In the backwater of the reservoir  $R_b/B_b$  was double that in the littoral zone. The comparison of two stations in the Raba showed that  $R_b/B_b$  was about 3 times greater in the river below than that above the reservoir (Table I). The production of heterotrophic bacteria ( $P_b$ ) comprised 6% of algal primary production ( $P_a$ ) at Station 1 and 83% at Station 4. In the littoral zone (Station 3) and in the backwater (Station 2) the values were 29 and 39% respectively (fig. 3).

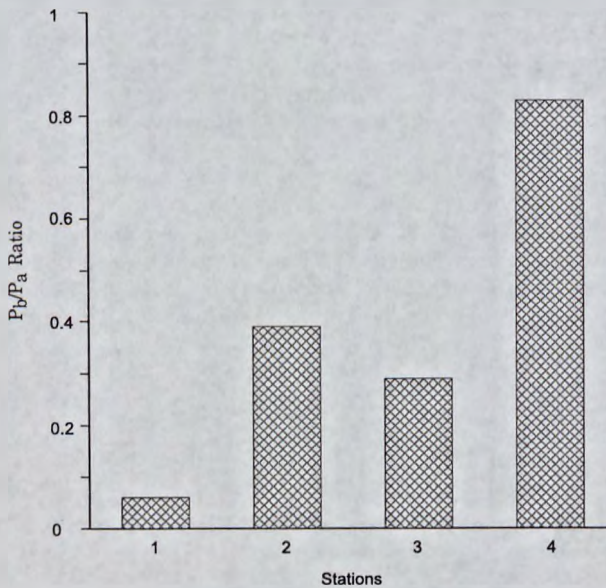


Fig. 3. The relation of bacterial production ( $P_b$ ) to primary production ( $P_a$ ) in the surface layer (0.5 cm) of bottom sediments in the River Raba above (Station 1) and below the Dobczyce Reservoir (Station 4), and in its backwater (Station 2) and littoral zone (Station 3) in the vegetation seasons (April–October) of 1993–1994.

## 5. Discussion

The differences between the activity of algae and heterotrophic bacteria at particular stations in the surface layer of bottom sediments could be elucidated by the different physiological state of these organisms, by the various availability of substrates, and the changing physico-chemical conditions, such as the temperature and light conditions requisite for algal production. For example, in the river above the reservoir the temperature of the water during the investigation period was 5–10 °C higher than that below it (G. Mazurkiewicz unpubl.), which unquestionably led to the different activity of algae and bacteria in the river above and below the reservoir. In the reservoir the water of the littoral zone showed greater



transparency (1.40–3.75 m) than that of the backwater (0.15–1.60 m) (Mazurkiewicz unpubl.). Therefore the bioaccumulation of energy on the algal level in the littoral zone was somewhat greater than that in the backwater.

The organic matter transported by the river to the reservoir was mostly deposited in the reservoir. The processes taking place in the reservoir distinctly reduced the carbon deposit in the surface layer of bottom sediments in the river below the reservoir, this also having been observed in previous investigations (Starzecka and Bednarz 1998), and lowered the trophic level of the outflowing water in comparison with the water feeding the reservoir (Bednarz 1995). The similar bioaccumulation of energy on the bacterial level in the river above the reservoir and in the backwater and the littoral zone showed a similar abundance of substrates for them. However, the different values of the energy expenditure per unit biomass of heterotrophic bacteria ( $R_p/B_b$ ) showed that the easily degradable organic matter was utilized by bacteria in the river above and in the reservoir, while only organic matter more refractory to bacteriological degradation penetrated into the river below it.

Taking the amounts of energy flowing through both algal and bacterial links together as 100% it could be said that 56–85% of energy was due to the bioaccumulation and 15–44% to the release of energy. From the pool of energy bioaccumulated by algae and bacteria together 87–98% was due to the algal link, but from the pool of energy released by them 76–97% was due to the bacterial link (Starzecka and Bednarz 1996). The obtained values clearly indicated that the algae play the greater role in bioaccumulation of energy in the surface layer of bottom sediments, but the bacteria play a greater role in energy release. The important role of bacteria in energy release was also noted in Marion Lake sediments, where 30–45% of the oxygen consumed by the benthic community was due to bacteria (Hargrave 1969). Similarly, the important role of bacteria was emphasized in observations carried out in the euphotic zone of Lake Tanganyika by Hecky et al. (1981), who found that 80–95% of community respiration was bacterial.

Bacterial production in lake water can be high, in the range  $16.5 \pm 3.5\%$  of total production in the littoral zone (Gajewski et al. 1993), with 13–50% of phytoplankton production (Hecky et al. 1981, Chróst and Faust 1983, Vadstein et al. 1989, Gebre-Mariam and Taylor 1990). In the present investigations bacterial production in the surface layer of bottom sediments ranged from 6 to 83% of algal production. Taking into account that the authors mentioned above compared the production in the whole water column, therefore similarly as the present authors in a very small layer only, the bacterial production measured by the latter should be regarded as high.

The authors are aware that the methods used in the present work give data distinctly different from those obtained by the measures carried out *in situ* in undisturbed sediments. The method used here to determine the primary production and respiration of heterotrophic bacteria gave overestimated results, *inter alia* owing to better light conditions, and facilitated access to metabolic substrates and carrying away of the final products. On the other hand, the plate method used for numeration of heterotrophic bacteria gave underestimated results (10–100 times) in comparison with the direct counting method, but permitted evaluation of the number of heterotrophic bacteria which were actually living and actively participating in the metabolic processes in the sediments. As was confirmed, many of the chemical transformations of organic and inorganic constituents in aquatic environments can only be mediated by heterotrophic bacteria because the enzyme systems required for these reactions are not found in other organisms (Chróst

1990). Besides, more than half of the total bacterial numbers in water environments using the acridine orange direct count method, is not metabolically active (Meyer-Reil 1978, Zimmermann et al. 1978, Kato 1984). Moreover, the authors' earlier observations (Starzecka and Bednarz 1993), carried out in the Dobczyce Reservoir using the same methods as in the present work, showed that 11% of oxygen consumption by epibenthic communities was due to bacteria. If one accepts only 10 times underestimation of the heterotrophic bacteria number (obtained by the plate method), their respiration would amount to 110% of total oxygen respiration of epibenthic communities, which is unrealistic. For this reason, in earlier works and the present one the authors did not accept any underestimation of the methods applied. In spite of reservations concerning the methods used in the present work, the results obtained, similarly as the indicatory data, illustrated the tendency of changes occurring in the surface layer of bottom sediments, and can be used for comparison of the investigated river with the reservoir.

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