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The role of plankton, zoobenthos, and sediment in organic matter degradation in oligotrophic and eutrophic mountain lakes

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Abstract

Intensity of organic matter degradation, assessed by the respiratory electron transport system (ETS) activity, was studied in microplankton, zooplankton, chironomid larvae as the dominant group of the macrobenthos, and sediment in mountain lakes of different trophic levels in summer months. The highest ETS activities per unit of surface were observed in sediments. Significantly lower activities were observed in microplankton, and lower still in zooplankton, and chironomids. The total ETS activity m^{-2} was higher in eutrophic lakes (Jezero na Planini pri Jezeru and Krnsko jezero) than in oligotrophic ones (Zgornje Kriško jezero, Spodnje Kriško jezero, Jezero v Ledvicah). The contributions of communities investigated to total ETS activity m^{-2} differed between lakes of different trophic level. Estimation of respiratory carbon loss through different components revealed that the most of the organic matter was oxidized in sediments of mountain lakes. The respiratory carbon losses were higher through zooplankton than through microplankton in all lakes. Carbon losses through plankton components and sediments were significantly lower in oligotrophic than in eutrophic lakes. The contribution of respiratory carbon loss through chironomids to total carbon loss m^{-2} was higher in oligotrophic than in eutrophic lakes. Therefore, it seems that contributions of microplankton and zooplankton to mineralization processes increase, and contributions of chironomids and sediment surface decrease with increasing trophic level of the lakes.

Introduction

To explain the structure and energy flow in an ecosystem, knowledge of population dynamics, production, respiration and feeding of the dominant species at different trophic levels is required. Estimation of the metabolic activities of the consecutive groups of organisms is central in describing the energy flux through the food chain, since most of the energy passes through as respiratory loss. In this approach, respiration is an expression of the metabolic activity. Numerous researchers have investigated metabolic activity of plankton communities (Devol & Packard, 1978; Devol, 1979; G.-Tóth, 1992; G.-Tóth et al., 1995; Rossetti et al., 2001; Simčič & Brancelj, 2001), sediment (G.-Tóth, 1992; Simčič & Brancelj, 2002 a, b), biofilm (G.-Tóth et al., 1995), and benthic communities (Hamburger & Dall, 1990; Lindegaard, 1994). It was reported that contribution of communities to total metabolic activity m^{-2} differs between aquatic ecosystems of different trophic levels (Devol & Packard, 1978; G.-Tóth, 1992, 1993; G.-Tóth et al., 1995). These studies mostly investigated the contribution of plankton, biofilm and sediment to total metabolic activity in lakes, but the contribution of benthic organisms to mineralization processes has been less frequently investigated (Lindegaard, 1994; Kurashov, 2002). Especially in shallow-water lake systems, the metabolic activity of the benthos as well as its contribution to the total (water column + sediment) mineralization is relatively higher than in deeper ones (Relexans, 1996a).

Slovenian mountain lakes are relatively small and shallow, having short ice-free period of 3–6 months (Muri & Brancelj, 2002). The structures of the pelagic community of the lakes show that Rotifera, Cladocera and Copepoda are presented with few species (Brancelj et al., 1997; Brancelj, 2002), and species of Cyanophyta and Chlorophyceae dominate the phytoplankton (Šiško & Kosi, 2002). Because of the shallowness of the lakes and low temperatures, the major part of oxidation of organic matter presumably occurs on the bottom of mountain lakes. From this point of view macrozoobenthos living on sediment of mountain lakes could contribute essentially to processes of mineralization through respiration. In high-mountain lakes, the metabolically most active zone is focused to the profundal, probably by the intensive UV-B radiation (G.-Tóth et al., 1995).

Oligotrophic mountain lakes are specific aquatic ecosystems, where low metabolic activities of organisms are expected due to low temperature and productivity. As respiration rates in these ecosystems are often below the detection limit of conventional methods, different attempts have been done to find more sensitive methods. Therefore, method based on the measurement of the activity of respiratory electron transport system (ETS) was proposed by Packard (1971). ETS is responsible for more than 90% of the biologically consumed O_2 in the biosphere (Packard, 1985). The ETS assay, based on the reduction of 2-iodo-3-nitrophenyl-5-phenyl-tetrazolium-chloride (INT), has proved to be a good tool for estimating the respiratory potential of zooplankton (Owens & King, 1975; James, 1987), microplankton (Devol & Packard, 1978), benthos (Jones & Simon, 1979; Cammen et al., 1990) and sediment (Trevors, 1984; G.-Tóth et al., 1994), in particular in that cases, when the direct measurement of the respiration rate is difficult. The main reaction is the reduction of INT into formazan instead of the reduction of the natural electron acceptor, oxygen. The activity of a complex enzyme system like ETS must be determined at the rate-limiting step. In the ETS this step is the oxidation of the coenzyme Q-cytochrome B complex (Packard, 1971). Formazan production in ETS assays has been found to be closely correlated to O_2 consumption (Kenner & Ahmed, 1975b; Owens & King, 1975; Bamstedt, 1980; del Giorgio, 1992). As ETS activity measurements show potential respiration rates they need to be converted to *in vivo* respiration rates (R) by empirically determined factors. ETS/R ratios have been published for zooplankton (Owens & King, 1975; Bamstedt, 1980; James, 1987; Simčič & Brancelj, 1997), phytoplankton (Kenner & Ahmed, 1975a), sediment (Simčič & Brancelj, 2002a) and some groups of benthic organisms (Cammen et al., 1990; Muskó et al., 1995), but none for chironomids.

The aims of this study were to determine ETS/R ratios for chironomid larvae, and biological oxidation potentials of microplankton, net zooplankton, chironomids larvae as macrobenthos and sediment surface, in order to compare the contribution of each component to total metabolic activity in mountain lakes of different trophic levels. As macrophytes are absent from lake Jezero v Ledvicah, or present in small aboundancy in lakes Zgornje Kriško jezero, Spodnje Kriško jezero and Jezero na Planini pri Jezeru (Urbanc-Berčič & Gaberščik, 2002), they were not included in the study. Additionally, respiratory carbon loss through each component at *in situ* temperatures, and relationships between respiratory carbon loss and estimation of primary assimilated carbon in the water column in lakes of different trophic levels were estimated.

Materials and methods

Samples were collected from the deepest parts of the five mountain lakes in NW Slovenia (Table 1) in August–September 2001. Water samples were taken using van Dorn water bottles (Wildco), and zoobenthos samples using a van Veen grab (Eijkelkamp). The sediment samples were collected with a Kajak corer with a 6 cm diameter plexiglass tube. Water samples were collected for analyses of chlorophyll *a* and total phosphorous at three to seven depths of the water column. Samples were transported to the laboratory at *in situ* temperature and analysed within 24 h.

Table 1. Some characteristics of the lakes studied in NW Slovenia (annual averages are represented for Secchi disc depth and total phosphorous)

Lake	Altitude (m)	Surface (ha)	Maximum depth (m)	Total phosphorus (μg P l^{-1})	Secchi disc depth (m)	Oxygen saturation at the bottom* (%)	Trophic state
Zgornje Kriško jezero	2150	0.62	9.6	10.1	Bottom	100	Oligotrophic
Spodnje Kriško jezero	1880	0.80	8.5	8.9	Bottom	100	Oligotrophic
Jezero v Ledvicah	1830	2.33	14.5	17.1	Bottom	100	Oligotrophic
Jezero na Planini pri Jezeru	1430	1.76	10.0	111.1	3.0	6.6	Eutrophic
Krnsko jezero	1383	4.96	17.6	37.2	2.2	8.0	Eutrophic

* Measured in August 2001.

Chlorophyll *a* was measured following the methods described by Jeffrey & Humphrey (1975). Total phosphorus, transparency and hypolimnetic oxygen content were used as criteria to assign a trophic state of the lakes (OECD, 1982). Total phosphorus was analysed by the standard method (APHA et al., 1998). Transparency was determined using Secchi disc. Oxygen saturation was measured using a universal instrument (MultiLine P4, WTW).

In the laboratory water samples were separated into two fractions. Zooplankton samples were prefiltered through 100 μm mesh, rinsed with filtered water to minimize bacteria and algae adhering to the body surface. After filtration, net zooplankton (i.e. planktonic crustaceans, large rotifers) were collected under a stereomicroscope using forceps and dripping-tube. Microplankton samples were filtered through glass microfibril filter (Whatman GF/C; particle retention approximately 1 μm). This fraction contains mostly phytoplankton, some protozoa and small rotifers and colonies of bacteria, while free bacteria were not retained by this filter. The volume of filtered water depended on the abundance of the organisms. The chironomid larvae, as the dominant group of the macrobenthos in all the lakes (Fig. 1), were sorted according to taxa, instars and size. Before experiments animals were rinsed with filtered water to minimize bacteria and algae adhering to the body surface, dried between two sheets of filter paper and weighed on an electrobalance (resolution 10 μg; Sartorius). As the degradation of organic matter increased with depth in the upper sediment profile in mountain lakes (Muri & Simčič, 2004), the surface layer (0–1 cm) of the sediment profile was mixed well with a glass stick. Samples of sediment (about 200 mg wet mass) were placed on pre-weighed aluminium foil and weighed on an electrobalance.

ETS activity was measured using the assay originally proposed by Packard (1971), and

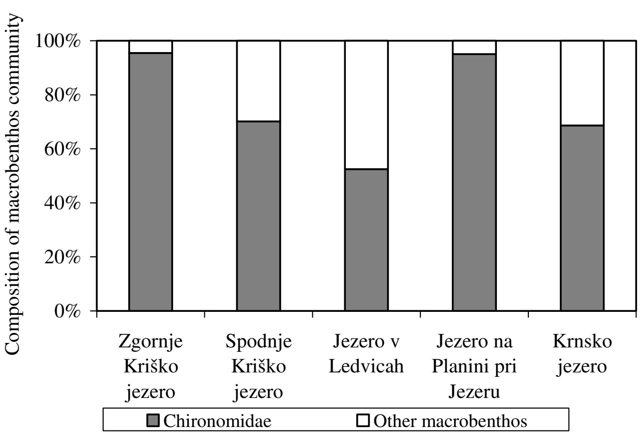

Figure 1. Proportion of chironomids in macrobenthos communities in five mountain lakes in NW Slovenia.

modified by many authors (Kenner & Ahmed, 1975a; Owens & King, 1975; G.-Tóth, 1999). Samples of zooplankton, microplankton and chironomids were homogenized immediately in 4 ml final volume of ice-cold homogenization buffer (pH = 8.4) using a glass Potter (Eurostar; Ika Labortechnik) for 3 min at 500 rpm followed by an ultrasonic homogenizer (4710; Cole-Parmer, Vernon Hills, IL, USA) for 20 s at 40 W. The sediment samples were homogenized in 4 ml final volume using an ultrasonic homogenizer for 4 min. The homogenates were centrifuged for 4 min at 0 °C at 10 000 rpm (2K15, Sigma). Within 10 min, 0.5 ml of supernatant (in triplicate) was incubated in 1.5 ml substrate solution with 0.5 ml INT for 40 min at standard (20 °C) temperature. The formazan production was determined spectrophotometrically (Lambda 12, Perkin-Elmer) by measuring $A^{490\ \mathrm{nm}}$ against the blank. ETS activity was measured as the rate of tetrazolium dye reduction, and converted to equivalent oxygen utilized per unit of mass in a given time interval as described by Kenner & Ahmed (1975a). In the mitochondrion, 2 electrons and 2 protons are used to convert 1/2 O_2 to H_2O. Two electrons are also used in the reduction of INT to formazan. Thus 2 μmol of formazan are equivalent to 1 μmol O_2. Since 1 μmol O_2 is equivalent to 22.4 μl O_2 and 2 μmol formazan ml^{-1} is equivalent to 31.8 $A^{490\ \mathrm{nm}}$, there are 1.42 $A^{490\ \mathrm{nm}}\ \mu l^{-1} O_2$. Values of ETS activity of different communities were recalculated per unit of surface using different conversion factors. The Arrhenius equation was used to convert the ETS activity at the incubation temperature to that at the *in situ* temperature:

$$\mathrm{ETS}_{in\ situ} = \mathrm{ETS}_{\mathrm{inc.}}\ \mathrm{e}^{E_a(1/T_{\mathrm{inc.}} - 1/T_{insitu})/R},$$

where E_a is the activation energy (a value of 15 kcal mol^{-1} was used; Bamstedt, 1980; Packard et al., 1975); T, the absolute temperature; and R, the gas constant.

The oxygen consumption rate of chironomids was determined following Gnaiger (1983) using a microrespirometer (CYCLOBIOS). Before respiration measurements, animals were rinsed with filtered water. After determining oxygen consumption, animals were used to determine ETS activity. Animals of different taxa were used for measurements.

Respiratory carbon loss of the organisms was estimated using ETS/R ratios of 2.0 for zooplankton (Bamstedt, 1980; Packard, 1985; James, 1987; Simčič & Brancelj, 1997), 7.0 for microplankton as phytoplankton dominated (Kenner & Ahmed, 1975b; Packard, 1985), and 2.76 for chironomids (this study). ETS/R ratios for sediments in the lakes were determined in a previous study (Simčič & Brancelj, 2002a). Respiratory carbon loss was calculated using the conversion factor 1 ml O_2 = 0.5 mg C_{org} (Lampert, 1984). In converting respiration to carbon units, a respiratory quotient (RQ) of 1.0 was assumed. Maximal depths of lakes were used in calculations of plankton metabolic activities per m^2.

Carbon productivity in the lakes was estimated using the conversion factor ^{14}C productivity/chlorophyll *a* = 16.8, calculated from published data (Devol & Packard, 1978).

A *t*-test was carried out to test for differences between oligotrophic and eutrophic lakes. The relationship between ETS activity and respiration rate in chironomids was estimated using a least square regression analysis on log–log data. All statistical analyses were performed using Microsoft Excel.

Results

ETS/R ratio for chironomids

ETS activities correlated with oxygen consumption rates (Fig. 2) according to the function:

$$\log R = 0.95 * \log \mathrm{ETS} - 0.35$$
$$(r = 0.75,\ N = 26,\ p < 0.001).$$

The ETS/R ratio was 2.76 ± 0.97 (mean ± 1 SD; $N = 26$).

ETS activity

The highest ETS activities (values ranged from 60 to 315 ml $O_2\ m^{-2}\ h^{-1}$) were observed in sediments (Fig. 3a). Significantly lower activities were observed in microplankton (0.6–19.4 ml $O_2\ m^{-2}\ h^{-1}$), followed by zooplankton (0.9–12.6 ml $O_2\ m^{-2}\ h^{-1}$), and chironomids (0.9–6.2 ml $O_2\ m^{-2}\ h^{-1}$). ETS activity in sediment was 2.3-fold higher

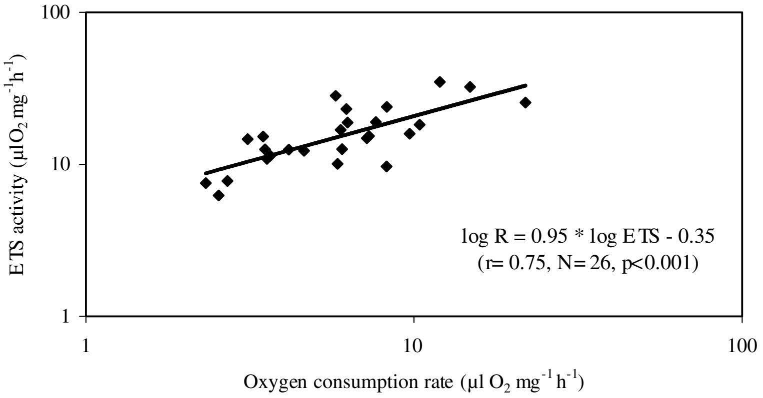

Figure 2. Relationship between ETS activity and oxygen consumption rate in larvae of chironomids.

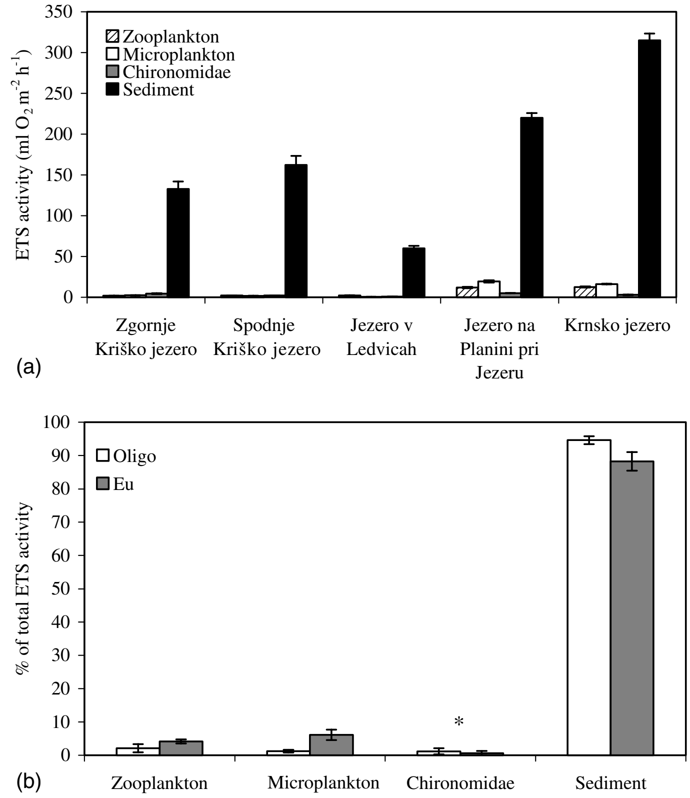

Figure 3. (a) ETS activity (ml O_2 m^{-2} h^{-1}) of zooplankton, microplankton, chironomids and sediment surface in five mountain lakes in NW Slovenia ($n = 3$), and (b) contribution of each component (%) to the total ETS activity in oligotrophic (Oligo) and eutrophic (Eu) lakes, measured at a standard temperature of 20 °C. Bars represent ± SD ($n = 9$ for Oligo, and $n = 6$ for Eu). * indicates non-significant differences.

in eutrophic (Jezero na Planini pri Jezeru and Krnsko jezero) than in oligotrophic (Zgornje Kriško jezero, Spodnje Kriško jezero, Jezero v Ledvicah) lakes. Zooplanktonic and microplanktonic ETS activities were higher in eutrophic than in oligotrophic lakes by factors of 6 and 11, respectively. ETS activities of the sediment and chironomids exceeded that of plankton by 7- to

11-fold in eutrophic lakes and by 20- to 41-fold in oligotrophic lakes. ETS activity of chironomids was higher in shallow (depth ≤10 m) lakes than in deeper (depth >14.5 m) ones (t-test, $t = 3.15$; d.f. = 13; $p < 0.01$). The total ETS activity m^{-2} was approximately 2.4-fold higher in eutrophic lakes than in oligotrophic ones.

The contributions of the communities to total ETS activity m^{-2} differed between lakes of different trophic level (Fig. 3b). The contributions of zooplankton ($t = 3.75$; d.f. = 13; $p < 0.01$) and microplankton ($t = 8.98$; d.f. = 13; $p < 0.001$) were higher in eutrophic than in oligotrophic lakes. In contrast to plankton community, sediment contributed larger proportion to total ETS activity m^{-2} in oligotrophic than in eutrophic lakes ($t = 6.11$; d.f. = 13; $p < 0.001$). Contribution of chironomids to total ETS activity m^{-2} was higher in oligotrophic than in eutrophic lakes, but values did not differ significantly ($t = 1.30$; d.f. = 13; $p = 0.22$). The contribution of zooplankton to planktonic metabolism was lower in eutrophic than in oligotrophic lakes ($t = 2.71$; d.f. = 13; $p < 0.05$).

Estimation of respiratory carbon losses

Calculation of respiratory carbon losses from ETS activity showed that the degree of mineralization was higher through zooplankton values ranged from 23.5 to 36.1 mg C m^{-2} day^{-1} than through microplankton (0.3–16.5 mg C m^{-2} day^{-1}) in all the lakes (Fig. 4a). Respiratory carbon losses were the highest through sediments (22–300 mg C m^{-2} day^{-1}). Significantly lower carbon losses through plankton components and sediments were obtained in Zgornje Kriško jezero, Spodnje Kriško jezero, and Jezero v Ledvicah than in Jezero na Planini pri Jezeru and Krnsko jezero. The contribution of respiratory carbon loss to total carbon loss m^{-2} through zooplankton ($t = 2.29$; d.f. = 13;

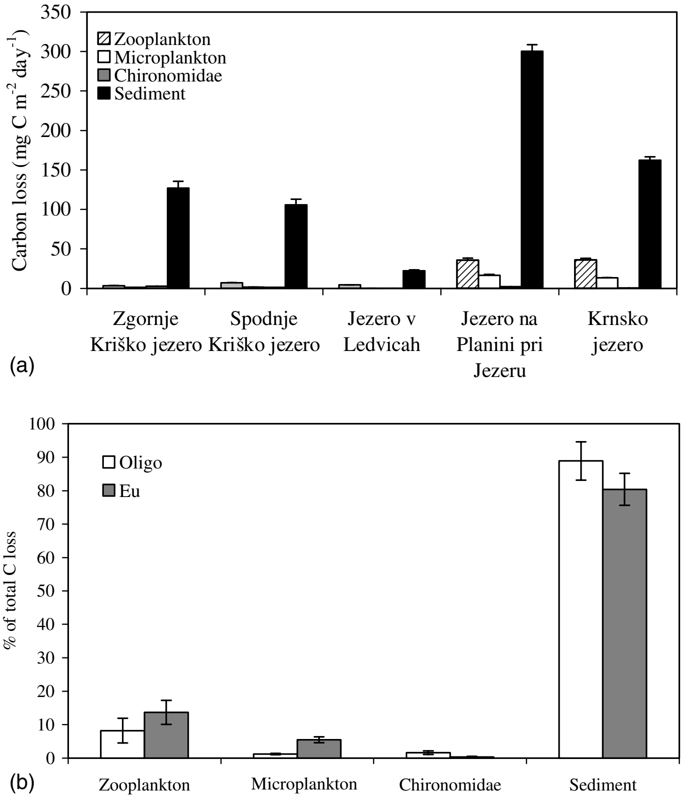

Figure 4. (a) Respiratory carbon loss (mg C m^{-2} day^{-1}) through zooplankton, microplankton, chironomids and sediment surface in five mountain lakes in NW Slovenia; converted to *in situ* temperature ($n = 3$), and (b) contribution of each component (%) to the total respiratory carbon loss in oligotrophic (Oligo) and eutrophic (Eu) lakes. Bars represent ± SD ($n = 9$ for Oligo and $n = 6$ for Eu).

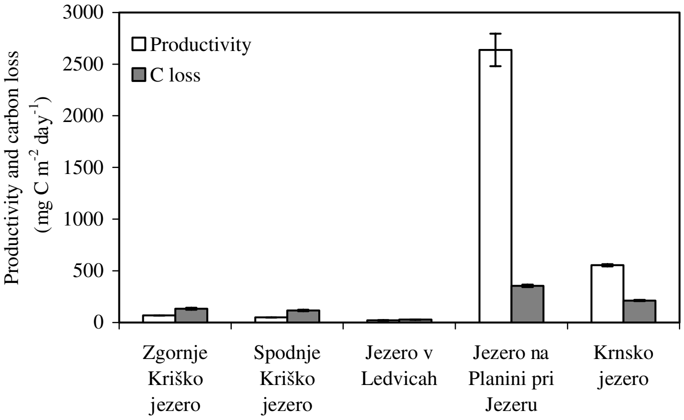

Figure 5. Estimated carbon productivity (mg C m^{-2} day^{-1}) and total respiratory carbon loss (mg C m^{-2} day^{-1}) in five mountain lakes in NW Slovenia. Bars represent ± SD ($n = 3$).

$p < 0.05$) and mikroplankton ($t = 14.24$; d.f. = 13; $p < 0.001$) was higher in oligotrophic than in eutrophic lakes, but sediment ($t = 2.98$; d.f. = 13; $p < 0.05$) and chironomids ($t = 5.53$; d.f. = 13; $p < 0.001$) contributed less to total carbon loss m^{-2} in eutrophic than in oligotrophic lakes (Fig. 4b).

Estimated carbon productivity of phytoplankton exceeded total respiratory carbon loss through plankton, chironomids and sediment in Jezero na Planini pri Jezeru and Krnsko jezero by 7.4- and 2.6-fold, respectively (Fig. 5). In oligotrophic lakes, estimated carbon productivity was much lower than total carbon demand.

Discussion

To achieve the purpose of the present study, ETS assay was used to determine metabolic potential of zooplankton, microplankton, sediment and chironomids' larvae. Although the ETS assay is destructive analyses, that is based on biochemical reaction, it has proved to be a good tool for the estimation of respiration in all investigated groups of organisms (Owens & King, 1975; Devol & Packard, 1978; Jones & Simon, 1979; Trevors, 1984; Packard, 1985; James, 1987; Cammen et al., 1990; del Giorgio, 1992; G.-Tóth et al., 1994; Muskó et al., 1995). It is, however, necessary to interpret ETS data by using one of several published ETS/*R* ratios. Otherwise, they have to be determined by researchers themselves for particular group of organisms (del Giorgio, 1992). In the present study, the ETS/*R* ratio for chironomids was determined in order to estimate their actual metabolism from ETS activity in the lakes. In these experiments, the basal metabolism and expenditure on locomotion were measured. The expenditure on filtration and specific dynamic action (SDA) was minimal, because the animals were not fed just prior to or during the experiments. The ETS/*R* ratio for chironomids (2.76) was in the range of values obtained for the other groups of animals. For zooplankton ETS/*R* ratios approach 2 (Bamstedt, 1980; James, 1987), but for benthic organisms much higher ratios are observed – 4.07 for amphipod *Corophium curvispinum* (Muskó et al., 1995), 2.38 for *C. volutator* (Cammen et al., 1990) and 11.11 for the polychaete *Nereis volutator* (Cammen et al., 1990). The latter extremely high value was explained by *N. volutator's* low activity, resulting in low oxygen consumption.

One of the purposes of the present study was to determine the biological oxidation potential in different components in lakes. The results show that the sediment has a powerful biological oxidation capacity in both oligotrophic and eutrophic lakes (Fig. 3a). Since INT can be reduced by both aerobes and anaerobes, the total microbial respiratory activity in the sediment was in fact measured (Songster-Alpin & Klotz, 1995). In the present study, ETS activity of the uppermost layer of sediment (0–1 cm of depth) was taken into account in calculating metabolic potential. Since ETS activity was also observed in deeper layers of sediment profiles (Simčič & Brancelj, 2002b; Muri

& Simčič, 2004), the reported values represent the minimum ETS activity in sediments.

Higher ETS activities of sediment were observed in lakes with higher trophic level. Because of a higher production rate in the water column of eutrophic lakes, a large amount of labile organic matter (Relexans, 1996b) accumulates at the sediment surface. This is reflected in a more intensive metabolic activity in the upper layers of the sediment profile. G.-Tóth (1992) and G.-Tóth et al. (1994) also found that in the hypertrophic Keszthely-basin of Lake Balaton, ETS activity was 3-fold higher than in the meso-eutrophic Siófok-basin.

Sediment metabolic potential greatly exceeded planktonic metabolic potential in all lakes (Fig. 3b). G.-Tóth et al. (1994) also found that sediment ETS activity exceeded planktonic activity 15- to 24-fold in Lake Balaton. What is the explanation for high metabolic potential in sediments? ETS/*R* ratios for surfaces of sediments range between 4 and 10 in the lakes studied here (Simčič & Brancelj, 2002a). These ratios indicate that sediments contain ETS-carrier factors, which contribute to ETS activity measurements but not to respiration. One of them is probably the persistence of ETS activity in dead organisms at the surface of sediment for weeks after their death, especially in the cold water of mountain lakes. James (1987), G.-Tóth (1992) and G.-Tóth et al. (1994) demonstrated that ETS fractions of planktonic and other organisms remain active for days and/or weeks after their death. Incubation of cell-free homogenates of sediment bacteria showed that ETS remains active days after the death of organisms at low temperature (G.-Tóth, 1993; G.-Tóth et al., 1994). Unfortunately, ETS assay did not distinguish between ETS of alive and dead microbial cells, as it can be determined using the redox dye 5-cyano-2,3-ditolyl tetrazolium chloride (CTC), which is an indicator of an active electron transport system in alive cells (Søndergaard & Danielsen, 2001). Benthic algae on the sediment surface additionally increase measured ETS activity, because the assay measures the activity of both respiratory and the photosynthetic electron transport systems (del Giorgio, 1992). G.-Tóth et al. (1994) supposed that both bacterial and the post-mortem ETS activity derived from the decaying organisms were stimulated by the high pH of lake water that causes rapid oxidation of the substrate in the lakes. As pH values of studied mountain lakes are high (Muri & Brancelj, 2002), mineralization of organic matter in sediments is more intensive and rapid especially during the warmer part of the year.

The contribution of microplankton to total ETS activity m^{-2} of the lake surface was greater in eutrophic lakes than in oligotrophic ones. A similar relation between ETS activity and primary production was reported for Lake Washington by Devol & Packard (1978), where the highest ETS activity in microplankton was observed during the spring bloom. The contribution of zooplankton to planktonic metabolism was lower in eutrophic than in oligotrophic lakes. G.-Tóth (1992) also reported a decreasing trend in the contribution of the net zooplankton metabolic activity to the total metabolism of the water column with increasing primary production in Lake Balaton. The results indicate that the increase in ETS activity m^{-2} with increasing trophic level of the lakes was greater in microplankton and zooplankton than in chironomids and sediment.

The results of the present study revealed that respiratory carbon losses were highest in sediments (Fig. 4a). For this reason, sediments play an important role in degradation of organic matter and nutrient recycling in aquatic ecosystems. During the decomposition of organic matter, oxygen and other terminal electron acceptors are consumed and inorganic nutrients are re-mineralized. These lakes are shallow, and it has been found that a larger proportion of total respiration occurs in the sediment in shallow lakes (Heyer & Kalff, 1998). The contribution of sediment to the total metabolic activity was proportionally higher in oligotrophic than in eutrophic lakes. These results are in accord with those of Heyer & Kalff (1998) who found that, in eutrophic lakes, the sediments account for a smaller proportion of total respiration than in oligotrophic lakes. In addition, Heyer & Kalff (1998) also reported that organic matter mineralization in littoral sediments is higher than in the profundal sediments. As sediment mineralization was estimated only in the profundal sediments of mountain lakes, probably even higher respiratory carbon losses through sediment metabolism would be obtained, if the littoral sediments were also taken into account.

The results showed that most respiratory carbon loss occurred in the sediments, but that chironimids make only a small contribution to mineralization processes (Fig. 4b). Törnblom & Pettersson (1998) found that bacterial activity constituted a large proportion of the total sediment metabolism. Nevertheless, our results showed that the contribution of chironomids to total carbon loss m^{-2} was higher in oligotrophic than in eutrophic lakes. The higher contribution of carbon respiratory loss through chironomids in oligotrophic lakes could be explained by more favourable living condition than in eutrophic lakes. Most studies have concluded that benthic algae are the primary food for chironomids (see Berg, 1995). In oligotrophic, transparent lakes, high benthic primary production is expected. Besides less qualitative food (detritus), chironomids are also exposed to seasonal oxygen depletion at the bottom of eutrophic lakes. Both factors have a negative effect on respiration rate of animals (Cammen et al., 1990; Hamburger et al., 1994). Kurashov (2002) also found that the role of profundal meiobenthos with regard to the transformation of energy flows in lake systems decreased, both with an increase in eutrophication and with an increase in the amount of organic matter in the benthal available from phytoplankton. The intensity of mineralization through chironomids was also related to the depth of the lakes. Previous studies showed that zoobenthos has a greater effect on energy flux through secondary production in the shallow lakes than in deeper ones (Jónasson et al., 1990; Lindegaard, 1994).

Higher respiratory carbon loss was observed in zooplankton than in microplankton in the planktonic communities of all the lakes. This indicates that the contribution of zooplankton to total carbon loss is not negligible as it might be expected from ETS activity data. The reason for relatively high microplanktonic ETS activity is the presence of algal photosynthetic ETS in this fraction (del Giorgio, 1992), reflected in the high ETS/R ratio of phytoplankton (Kenner & Ahmed, 1975b).

The daily respiratory carbon loss of the organisms investigated was equivalent to 13 and 38% of the estimated planktonic primary production in lakes Jezero na Planini pri Jezeru and Krnsko jezero, respectively (Fig. 5). Consequently, excess produced organic matter accumulated in the sediment. As a result of intensive mineralization through benthic metabolism and insufficient diffusion of oxygen into the bottom water layers, Jezero na Planini pri Jezeru especially exhibits seasonal anoxia. In oligotrophic lakes, estimated productivity did not exceed daily respiratory carbon loss. Actually, daily respiratory carbon loss was higher than planktonic primary production by 1.3-fold in Jezero v Ledvicah, 2.4-fold in Spodnje Kriško jezero and 2-fold in Zgornje Kriško jezero. However, these lakes are shallow and transparent to the bottom. Measurements of chlorophyll *a* content at the surface of sediments revealed a considerable quantity in both oligotrophic lakes (mean value 70 μg gDW^{-1}, gDW = gram dry weight), and in eutrophic lakes (96 μg gDW^{-1}) (Simčič, unpublished data). It is reasonable to assume that the main source of chlorophyll *a* in oligotrophic lakes is benthic algae, but in eutrophic lakes dead phytoplanktonic organisms contribute to chlorophyll *a*. Thus, the benthic algae can play an important role in primary production of the lake (G.-Tóth, 1992) and probably contribute a considerable proportion of the total primary produced organic matter in oligotrophic mountain lakes. In addition, the macrophytes can contribute to primary production in eutrophic lakes. Therefore, measuring only the planktonic primary production may underestimate the primary production of mountain lakes.

It is, however, concluded that most organic matter is oxidized in sediments of mountain lakes. It is also assumed that the contributions of microplankton and zooplankton to mineralization processes increase, and contributions of sediment surface and chironomids decrease, with increasing trophic level of the lakes.

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