

Respiration rates in shallow lakes of different types: contribution of benthic microorganisms, macrophytes, plankton and macrozoobenthos

Janusz Żbikowski · Tatjana Simčič · Franja Pajk · Małgorzata Poznańska-Kakareko · Tomasz Kakareko · Jarosław Kobak

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Abstract The determination of the metabolic activity of organisms at various trophic levels is crucial for the proper assessment of the energy flow through the ecosystem, which is the basic process determining ecosystem functioning. We estimated the respiration rate in nine shallow, eutrophic lakes (macrophyte-dominated and phytoplankton-dominated) from north-eastern Poland. Respiratory carbon loss (RCL) through bottom microbial communities, macrophytes, plankton and macrozoobenthos was estimated by measuring the Electron Transport System activity. The shares of the particular ecosystem components in

respiration processes differed among the lake types and seasons. The bottom microbial communities contributed most to the RCL (from 50% in the macrophyte-dominated lakes to 90% in the shallower phytoplankton-dominated lakes) except in macrophyte-dominated lakes in summer, where the macrophyte contribution prevailed (80%). The contribution of plankton was considerable only in the deeper phytoplankton-dominated lakes (20%). Macrozoobenthos was important (20%) only in the macrophyte-dominated lakes in spring and autumn. The RCL through bottom microbial communities was substantially higher in the shallow lakes (especially phytoplankton-dominated) than in deep, stratified eutrophic lakes. Shallow eutrophic lakes can be highly productive due to intensive organic matter mineralization at the bottom and rapid flow and cycling of carbon and nutrients resulting from their polymictic character.

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J. Żbikowski (✉) · T. Kakareko
Department of Hydrobiology, Faculty of Biology and Environmental Protection, Nicolaus Copernicus University, Toruń, Poland
e-mail: jzbikow@umk.pl

T. Simčič · F. Pajk
Department of Organisms and Ecosystems Research, National Institute of Biology, Ljubljana, Slovenia

M. Poznańska-Kakareko · J. Kobak
Department of Invertebrate Zoology, Faculty of Biology and Environmental Protection, Nicolaus Copernicus University, Toruń, Poland

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Introduction

Energy flow is one of the basic processes determining ecosystem functioning. As most of the energy leaving the ecosystem is associated with respiration (Simčič, 2005; Kominoski et al., 2018), the determination of the metabolic activity of organisms at various trophic

levels is crucial for the proper assessment of the energy flow through the ecosystem. It should be emphasized that the role of a given organism in the ecosystem depends not only on its abundance, but also on its metabolic activity, which can be estimated by its respiration rate, expressed per unit biomass (Devol, 1979; Simčič, 2005; McKinnon et al., 2015). Respiration recycles organic carbon arising from photosynthesis back to inorganic carbon and therefore affects net balances of carbon in aquatic ecosystems (Pace & Prairie, 2005). Therefore, knowledge of the intensity of metabolic processes occurring in the water column and bottom sediments is necessary for comprehensive understanding of the structure and functioning of aquatic ecosystems (Pace & Prairie, 2005; Simčič & Brancelj, 2009; Lischke et al., 2017).

It should be noted that the impact of environmental factors on the respiration rate of key biocoenotic components in lakes is still poorly known, apart from temperature (Staehr & Sand-Jensen, 2006; Simčič & Germ, 2010). So far, the role of various biocoenotic components in the metabolic process has been investigated in deep, stratified lakes, usually of low trophic level (G.-Tóth et al., 1995; Jonsson et al., 2001; Åberg et al., 2004; Simčič, 2005; Simčič & Brancelj, 2009; Simčič & Germ, 2009; Germ & Simčič, 2011; Tammearg et al., 2017). On the other hand, considerably fewer studies have been devoted to shallow, polymictic and eutrophic lakes (G.-Tóth, 1992; Brothers et al., 2013; Zimmer et al., 2016; Lischke et al., 2017). Moreover, there is still insufficient knowledge in particular on seasonal changes in metabolic activity in various biocoenotic components in shallow lakes of different types (Vachon et al., 2017). It has been demonstrated that inland waters constitute a significant component of the global carbon cycle (Tranvik et al., 2009). Therefore our knowledge of this topic should be improved to gain better insight into the functioning of such lakes.

Shallow lakes differ from deep, stratified ones in many aspects which may affect metabolic activity. The most important differences include the lack of stable thermal stratification in shallow lakes, so that the whole water column is mixed easily and frequently, increasing the impact of sediment–water interface processes on the functioning of the entire water body (Jensen & Andersen, 1992; Søndergaard et al., 2003; de Vicente et al., 2006; Filbrun et al., 2013; Martinsen et al., 2017). Scheffer (1990) has

distinguished two types of shallow lakes: (1) macrophyte-dominated lakes, with the entire bottom overgrown by submerged plants due to their high water transparency, and (2) phytoplankton-dominated lakes, with turbid water and macrophytes limited to their littoral zones. Furthermore, Żbikowski & Kobak (2007) have demonstrated that the intensity of light reaching the bottom is an important factor shaping the structure of pelophilous macrozoobenthos and physico-chemical parameters of the bottom sediments. Therefore, they further divided phytoplankton-dominated lakes into shallower and deeper lakes, depending on whether the euphotic zone reaches the bottom or not, respectively.

Given this distinctness of shallow lakes, the determination of the role of particular groups of organisms in the metabolism of organic matter in these water bodies would be a valuable augmentation of the earlier results, as the functioning of shallow lakes cannot be predicted on the basis of our knowledge of deep, stratified lakes. Respiration rate and the contributions of particular biocoenotic components in this process are likely to differ between shallow and deep, stratified lakes, as depth-dependent factors, such as thermal stratification, considerably affect near-bottom water oxygen concentrations and consequently rates of aerobic and anaerobic respiration of the microbial communities in bottom sediments (den Heyer & Kalff, 1998; Petersen & Chen, 1999; Daniels et al., 2015). Depth also affects the role of plankton due to different availability of nutrients (Devol, 1979; Simčič, 2005; Simčič & Germ, 2009), as well as that of macrozoobenthos (Jónasson et al., 1990; Lindegaard, 1994; Kurashov, 2002; Lischke et al., 2017) in metabolism of organic matter. Moreover, the share of the main groups of primary producers (i.e. macrophytes, phytoplankton and microphytobenthos) in lake metabolism is also likely to differ between shallow and deep, stratified lakes.

Respiratory carbon loss (RCL) through microorganisms in the bottom sediments and other biocoenotic components (plankton, zoobenthos, macrophytes) was estimated by measuring the Electron Transport System (ETS) activity, which is closely correlated to oxygen consumption (R) (Kenner & Ahmed, 1975a; Owens & King, 1975; del Giorgio, 1992; Packard et al., 2015). ETS activity indicates the amount of oxygen consumption that would occur if all

enzymes functioned at their maximum activity (Muskó et al., 1995). The ETS assay has proved to be a good tool for estimating the potential metabolic activity of zooplankton (Owens & King, 1975; James, 1987; Simčič & Brancelj, 1997; Hernández-León et al., 2001; Simčič & Brancelj, 2009; Osmá et al., 2016), microplankton (Kenner & Ahmed, 1975b; Devol & Packard, 1978; Packard, 1985; Simčič & Germ, 2009; Packard et al., 2015), macrozoobenthos (Muskó et al., 1995; Simčič, 2005; Simčič & Germ, 2009; Moreira et al., 2017), macrophytes (Peñuelas et al., 1988; Szabó, 2003; Simčič & Germ, 2009; Germ & Simčič, 2011) and microorganisms in sediments (G.-Tóth et al., 1994; Simčič & Brancelj, 2002; de Vicente et al., 2006; Simčič & Brancelj, 2009; Germ & Simčič, 2011; Krausz et al., 2012).

The main goal of the present study was to estimate the rate of respiratory metabolism in shallow, eutrophic lakes of various types by microorganisms in the bottom sediments and the rates of oxidation of organic matter by selected groups of organisms (macrophytes, plankton and bottom fauna), as well as to determine their importance in the process of respiration, taking seasonal changes into account. An additional goal of the study was to find relationships between the metabolic rate and selected abiotic parameters as well as some structural characteristics (density, biomass) of the selected groups of organisms. These data may help identify those parts of the ecosystems of shallow lakes which contribute most to the oxidation of organic matter through respiration, thus being crucial for their functioning, protection and conservation.

We hypothesized that (1) the RCL in the studied lakes would mainly take place on the bottom due to their shallow depth resulting in a high temperature of the sediments during the vegetation period and the lack of long-term oxygen depletions. Therefore, we expected a high impact of microorganisms from the bottom sediments on the total RCL in the lakes. We also assumed that (2) RCL should be highest in summer due to higher water and bottom temperature. Moreover, we expected that (3) macrophytes would considerably contribute to the RCL in macrophyte-dominated lakes, whereas (4) the share of RCL through plankton in phytoplankton-dominated lakes would be positively related to their depth.

Materials and methods

Study area

The study was conducted in nine shallow lakes situated in north-eastern Poland (Fig. 1). The basic characteristics of the lakes are shown in Table 1. Most of them are small water bodies, with an area of a few dozen ha, except Lakes Karaś and Hawskie. At the beginning of the study, three of the lakes were dominated by macrophytes and the other six lakes were dominated by phytoplankton. The latter can be divided into shallower (three lakes, 0.9–1.5 m of maximum depth), and deeper (three lakes, 2.5–5.7 m). However, during the study period (in summer) the status of two lakes unexpectedly changed. In Lake Zielone, which was initially dominated by vascular flora, submerged macrophytes disappeared and the lake changed its status from macrophyte to phytoplankton domination. In contrast, in Lake Gardzień, which at the beginning of the study was dominated by phytoplankton, submerged plants appeared in summer and the lake switched its status from phytoplankton to macrophyte domination. This gave us a unique opportunity to observe the changes in the proportions of the microorganisms in the bottom sediments, as well as of macrophytes, plankton and macrozoobenthos in RCL during the alteration of its alternative state. Sampling stations (one station in each lake) were located in the most representative central part of each lake determined in the previous long-term studies based on several sampling sites in each lake (Żbikowski, 2011), at a depth slightly shallower than the maximum depth. The investigated lakes had no permanent vertical stratification, as shown by the lack of considerable differences in abiotic parameters between the surface and near-bottom water (data not shown). As the lakes being studied differ from one another in depth, bottom coverage by plants and their taxonomic composition, wind exposure and catchment type (Table 1), the results can be considered generally representative for a wide range of conditions occurring in lowland, eutrophic shallow lakes.

Sampling strategy and sample treatments

The study was carried out in spring (19–21 May), summer (23–25 August) and autumn (21–23

Fig. 1 Location of the studied lakes in Poland

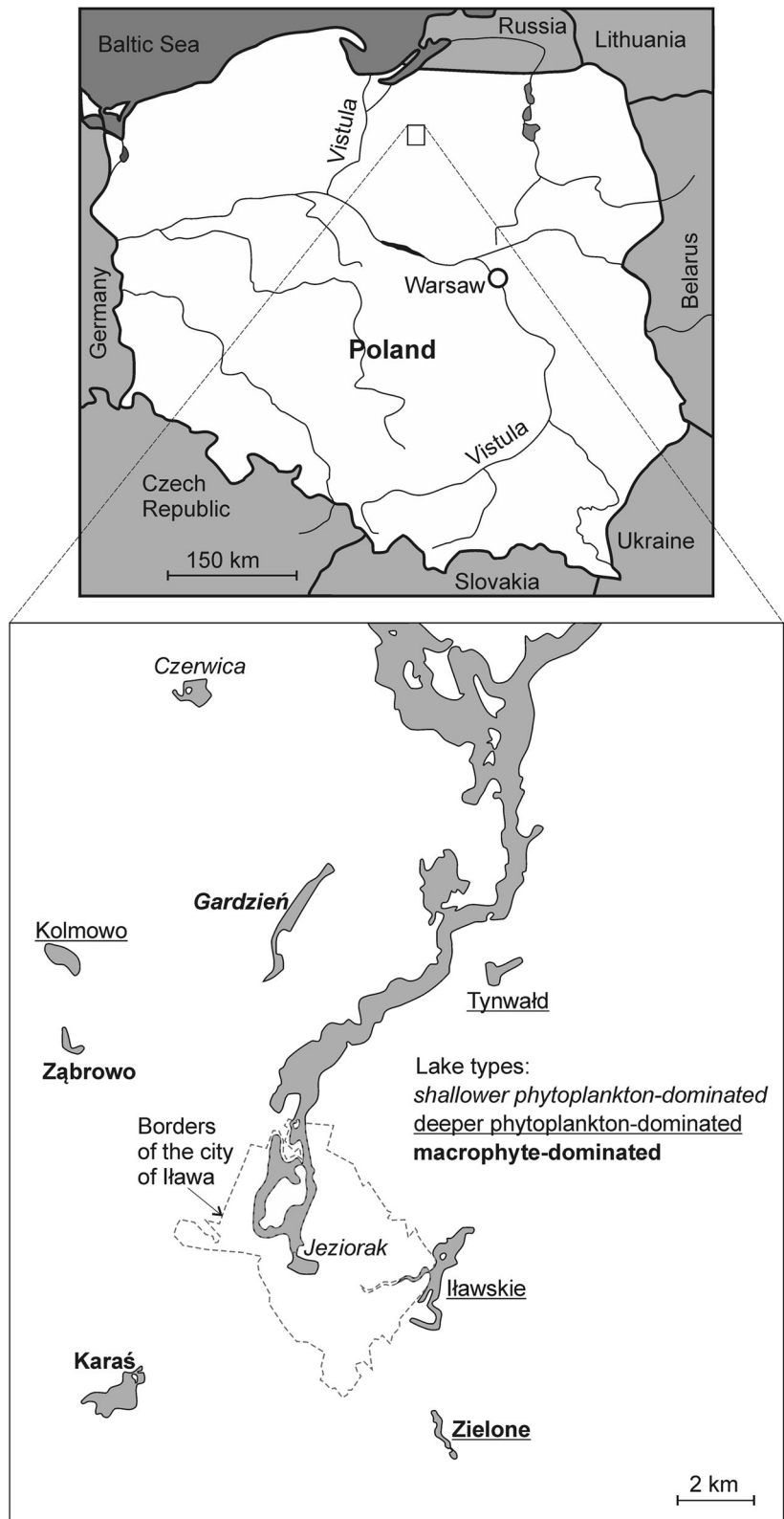


Table 1 Basic characteristics of the lakes under study

Lake name Abbreviation used in the figures	Macrophyte-dominated lakes			Phytoplankton-dominated lakes				Status-changing lakes		
	Ząbrowo Za	Karaś Ka	Jeżiorak* Je	Shallower		Deeper		Tynwałd Ty	Zielone Zi	Gardzień Ga
				Czerwica Cz	Itawskie It	Kolmowo Ko	Zielone Zi			
Surface (ha)	12.7	423.3	80.0	37.8	154.5	43.4	29.9	20.2	85.5	
Max. depth (m)	2.0	2.2	1.5	0.9	2.8	5.7	2.5	2.2	1.3	
GPS site coordinates (N/ E)	53°38'38.36"/ 19°28'21.41"	53°33'47.29"/ 19°29'28.35"	53°37'00.02"/ 19°33'08.44"	53°43'39.24"/ 19°31'00.91"	53°35'45.40"/ 19°36'57.25"	53°40'01.76"/ 19°27'39.67"	53°39'45.79"/ 19°38'05.00"	53°33'41.54"/ 19°36'37.18"	53°40'45.66"/ 19°33'31.62"	
Depth at the sampling sites (m)	1.7	2.0	1.2	0.8	2.7	3.0	2.2	1.8	1.1	
Catchment	F/A	A/M	F/T	F	A	A	A	F	F	
Wind exposure	Low	High	Medium	Low	High	High	High	Low	Medium	
Dominating submerged plants	C.d.	Ch.sp.						E.c. ^a	Ch.d. ^b	

F forest, A agricultural, M marsh, T tourist, C.d. *Ceratophyllum demersum*, Ch.d. *Chara delicatula*, Ch.sp. *Chara* sp., E.c. *Elodea canadensis*

^aOnly in the spring

^bOnly in the summer and autumn

*This is the longest lake in Poland (length: 27.4 km, surface: 3230 ha). The study was carried out in a shallowed bay part located in its oldest, southern part

November) of 2010. In spring and summer the samples were taken from each lake whereas in autumn it was not possible to take samples from Lakes Zielone and Tynwałd for technical reasons.

To determine the ETS activity of plankton, two 1.5-dm³ water samples were collected from each lake from the depth of ca. 0.5 m below the surface. In the laboratory, the samples were prefiltered through 120 µm mesh and rinsed with distilled water to minimize bacteria and algae adhering to the body surface of larger plankton that remained on the mesh (2 replicates). For ETS activity analysis, live plankton samples (predominantly zooplankton) were collected and stored in Eppendorf tubes using forceps and a dripping-tube. The water with smaller particles that passed through the mesh was filtered through a glass microfibril filter (Whatman GF/C; particle retention approximately 1 µm). Material remaining on the filter (mainly phytoplankton) was stored in Eppendorf tubes together with the filter (2 replicate samples). ETS activity was measured separately in larger- (> 120 µm) and smaller-sized (< 120 µm) plankton fractions due to further calculations of respiration rates.

Submerged vegetation biomass was sampled using a frame with a net bag (0.16 m², 3 replicate samples). The stems and leaves of the middle part of a fresh shoot were taken for ETS activity analysis and stored in Eppendorf tubes (2 replicate samples).

To collect the bottom fauna, in the macrophyte-dominated lakes we used a core sampler (catching area 40 cm², 7–10 replicate samples depending on the macrozoobenthos abundance, ca. 30 cm layer of sediments) whereas in the lakes with phytoplankton domination we used an Ekman-Birge grab (catching area 225 cm², 2–4 replicate samples). As muddy sediments of shallow lakes have high water content, the grab could penetrate them deeper than the surface layer inhabited by macrozoobenthos. Therefore the grab was covered with 0.5-mm mesh, which prevented collected organisms from escaping through the top of the device. The samples were rinsed using a 0.5 mm sieve and preserved in 4% formaldehyde for biomass assessment. For ETS activity analysis, non-preserved macroinvertebrates were stored after sieving and taxonomic determination in Eppendorf tubes.

For ETS activity determination, fresh bottom sediments (0–5 cm top layer), collected with the same core sampler as that used for collecting

macrozoobenthos in macrophyte-dominated lakes, were homogenized with a glass stick and stored in Eppendorf tubes (2 replicate samples).

All samples for ETS activity measurements were stored at – 80 °C in Eppendorf tubes until being transported in dry ice to the laboratory of the National Institute of Biology in Ljubljana, where they were analysed for ETS activity.

ETS activity

ETS activity was measured using the assay originally proposed by Packard (1971), and modified by many authors (Kenner & Ahmed, 1975b; Owens & King, 1975; G.-Tóth, 1999). Before measurements macrozoobenthos (0.1–65 mg wet mass), submerged macrophytes (16–85 mg) and sediment samples (27–58 mg) were weighed on an electrobalance (Sartorius BP 210 S, Goettingen, Germany) with 0.1 mg accuracy. Samples of plankton, macrozoobenthos and macrophytes were homogenized in 4 cm³ of ice-cold homogenization buffer (0.1 M sodium phosphate buffer pH = 8.4, 75 µM MgSO₄, 0.15% (w/v) polyvinyl pyrrolidone, 0.2% (v/v) Triton-X-100) using a Potter–Elvehjem tissue homogenizer (Eurostar; Ika Labortechnik, Staufen, Germany) for 3 min at 600 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 cm³ of ice-cold homogenization buffer using an ultrasonic homogenizer for 3 min at 40 W. The homogenates were centrifuged for 4 min at 0 °C at 10000 rpm (2K15, Sigma, St. Louis, USA). Within 10 min, 0.5 cm³ of supernatant (in triplicate) was incubated in 1.5 cm³ substrate solution (0.1 M sodium phosphate buffer pH 8.4, 1.7 mM NADH, 0.25 mM NADPH, 0.2% (v/v) Triton-X-100) with 0.5 cm³ INT (2.5 mM 2-*p*-iodo-phenyl 3-*p*-nitrophenyl 5-phenyl tetrazolium chloride) for 40 min at standard (20 °C) temperature. The reaction was stopped by adding 0.5 cm³ of stopping solution [formalin: H₃PO₄ conc. = 1:1 (v/v)]. Blanks (1.5 cm³ substrate solution and 0.5 cm³ INT solution) were incubated and treated as for the samples, followed by addition of 0.5 cm³ of homogenate (G.-Tóth, 1999). The formazan production was determined spectrophotometrically (WTW photoLab-Spectral, Weilheim, Germany) by measuring A^{490nm} against the blank. ETS activity was measured as the rate of tetrazolium dye reduction,

and converted to equivalent oxygen utilized in a given time interval as described by Kenner & Ahmed (1975b). ETS activities of larger- and smaller-sized plankton fractions were first calculated per water volume ($\text{mm}^3 \text{O}_2 \text{dm}^{-3} \text{h}^{-1}$), and then multiplied by the volume of the water column above the bottom area of 1 m^2 at the sampling stations to obtain the plankton ETS activities per unit surface area ($\text{cm}^3 \text{O}_2 \text{m}^{-2} \text{h}^{-1}$). Sediment, macrophyte and macrozoobenthos ETS activities, calculated per wet mass ($\text{mm}^3 \text{O}_2 \text{g}^{-1} \text{h}^{-1}$), were multiplied by the wet mass of 10 dm^3 of the sediments (the area of 1 m^2 and a depth of 1 cm), by the fresh biomass of macrophytes covering the area of 1 m^2 or by the number of individuals of particular macrozoobenthos species per m^2 , respectively.

The Arrhenius equation was used to convert the ETS activity at the incubation temperature ($\text{ETS}_{\text{inc.}}, T_{\text{inc.}}$) to that at the in situ temperature ($\text{ETS}_{\text{in situ}}, T_{\text{in situ}}$):

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

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

As ETS activity measurements show the potential metabolic rate of organisms, they need to be converted to in vivo respiration rates by using empirically determined factors for the respective group of organisms (i.e. ETS/ R ratio) in order to assess RCL through selected components (G.-Tóth, 1992; G.-Tóth et al., 1995; Simčič, 2005; Simčič & Germ, 2009; Packard et al., 2015). Respiratory carbon loss (RCL) of the organisms was estimated using ETS/ R ratios of 2.0 for larger-sized plankton fraction (zooplankton dominated) (Bamstedt, 1980; James, 1987; Simčič & Brancelj, 1997), 7.0 for smaller-sized plankton fraction (phytoplankton-dominated) (Kenner & Ahmed, 1975a; Packard, 1985), 2.8 for macrozoobenthos (Simčič, 2005), 4.0 for macrophytes (Peñuelas et al., 1988) and 5.0 for sediments (Simčič & Brancelj, 2002). Respiratory carbon loss was calculated using the conversion factor $1 \text{ cm}^3 \text{O}_2 = 0.54 \text{ mg } C_{\text{org}}$ (Lampert, 1984). In converting respiration to carbon units, a respiratory quotient (RQ) of 1.0 was assumed. Depths at the sampling stations were used in calculations of plankton metabolic activities per m^2 .

Respiratory carbon losses for smaller- and larger-sized plankton fractions were first calculated separately and then data for both fractions were pooled.

Abiotic parameters

Together with the collection of submerged macrophytes, plankton and macrozoobenthos samples, several abiotic parameters of water and sediments were determined. Water transparency was measured with a Secchi disc. To calculate the vertical attenuation coefficient of light under water (Scheffer, 1998: 22, Eq. 2) a Slandi LX204 (Slandi Sp. z o.o., Michałowice, Poland) luxometer was used. Temperature, conductivity and oxygen concentration at the surface and in the near-bottom water layer (2–3 cm above the sediments) were measured by taking water and sediment samples with the core sampler and analysing it with a MultiLine P4 (WTW GMBH, Weilheim Germany) Universal Pocket Sized Meter. Total phosphorus concentration was analysed spectrophotometrically as molybdate reactive phosphorus after digestion with sulphuric acid and peroxide (Lewandowski et al., 2003).

Prior to the analyses of bottom sediments, macroinvertebrates and visible plant remains were removed from the sediment samples. Water content in the sediments (WC) was measured by oven-drying sediments to a constant mass at $104 \text{ }^\circ\text{C}$ for 24 h. Organic matter content (OC) in sediments was determined after igniting dried sediments at $550 \text{ }^\circ\text{C}$ for 2 h. The latter parameter was expressed in two ways, as: (1) the percentage of dry mass of sediments (Hakanson & Jansson, 1983: 76, Eq. 2) and (2) milligrammes of dry mass per unit fresh sediment volume (10 cm^3) according to the formula:

$$\text{OCmg} = \frac{\text{DM} \times \text{OC}\%}{100}$$

where OCmg is the dry mass of organic matter in 10 cm^3 of fresh sediments in milligrammes, DM the dry mass of 10 cm^3 of fresh sediments in milligrammes, OC% the percentage of dry mass of organic matter in sediments.

The difference between these two quantities consists in the variable water content in sediments. Namely, if the percentages of organic matter in the dry mass of the sediments are equal, the sediments with the lower water content will have more

milligrammes of organic matter per unit of their fresh volume. The former value is a standard method of presenting OC in bottom sediments.

Sediment oxygen demand (SOD) was estimated by adding 300 cm³ of 100%-oxygen saturated tap water to a special dish containing 20 cm³ of fresh sediments (2 replicates). The diameter of an oxygen sensor matched tightly the outlet of the dish, which prevented the oxygen exchange with the outside. The dish walls were impenetrable to light in order to prevent the production of oxygen as a result of benthic algae photosynthesis. The oxygen uptake was measured after 1 h at 20 °C (controlled room temperature) using the MultiLine P4 multimeter and oxygen sensor WTW Cellox 325. The preliminary trials showed that the oxygen concentration did not change ca. 15 min after the end of the oxygenation process, so we assumed that oxygen losses in pure tap water would be negligible. The sediments were kept in resuspension by means of a magnetic stirrer to sustain the water flow around the membrane of the oxygen sensor.

An important aim of the study was to search for correlations between the measured ecosystem parameters presented in Table 2 and the metabolic potential of organisms at various trophic levels, expressed as RCL at in situ temperature. The only exception was SOD, which was measured at 20 °C in the laboratory, thus we correlated it with RCL at the same temperature.

Statistical analysis

We used a General Linear Model with Lake type as a between-subject factor and Season as a within-subject factor to check the differences in abiotic parameters and zoobenthos biomass. The status-changing lakes were excluded from this analysis. We applied a General Linear Model with Lake type as a between-subject factor and Season and Ecosystem component (microorganisms from the sediments, macrophytes, plankton, macrozoobenthos) as within-subject factors to test the determinants of RCL (log-transformed to reduce the departures from normality and homoscedasticity assumptions) in the studied lake types. The status-changing lakes were excluded from this analysis.

Moreover, linear Pearson correlations of RCL through vascular plants and macrozoobenthos with their biomasses were calculated. The variables

selected for the correlation analysis of the plankton and sediment RCLs are indicated in Table 2. In the Results section only statistically significant correlations are reported.

Statistical calculations were carried out with SPSS Statistics v.23 (IBM Corporation, Armonk, USA).

Results

Environmental parameters

Temperatures in the studied lakes were 15.6 ± 2.0 °C (mean \pm SD) in spring, 22.5 ± 1.3 °C in summer and 5.3 ± 0.5 °C in autumn. Obviously, temperature varied significantly with season, but not with the lake type (Supplementary Table 1), though the spring temperatures tended to be higher in the shallower lakes than elsewhere (Table 2). Other physical and chemical parameters of water and bottom sediments (Table 2) did not exhibit substantial inter-seasonal variability, except for a marginally significant effect of season on the water transparency (measured as Secchi depth, SD) (Supplementary Table 1). In most cases, these parameters did not differ clearly among the distinguished lake types, except water transparency and euphotic depth/lake depth ratio (Supplementary Table 1).

On the basis of the total phosphorus concentration (Table 2), most of the studied lakes can be classified as eutrophic or hypertrophic (Nürnberg, 1996). Water transparency was clearly higher in the macrophyte-dominated lakes (SD 1.6–2.4 m) than in the phytoplankton-dominated lakes (0.4–0.7 m). Moreover, Secchi depth values slightly increased with time, reaching 0.84 ± 0.57 , 0.91 ± 0.84 , 1.12 ± 0.66 m (mean \pm SD) in spring, summer and autumn, respectively. In Lake Zielone, SD decreased from 2.1 to 0.7 m (3-fold) after the status change from macrophyte-dominated to phytoplankton-dominated (Table 2). In Lake Gardzień, which changed its status in the opposite direction during the study, water transparency was high and similar throughout the year.

Oxygen concentration in the studied lakes ranged from 7.7 to 15.3 mg O₂ dm⁻³, pH values varied from 7.6 to 9.3 and conductivity fluctuated between 169 and 433 μ S cm⁻¹, except Lake Zielone, where it was clearly lower (82 μ S cm⁻¹) (Table 2).

Table 2 Mean values of abiotic parameters of water and bottom sediments of the studied lakes

Lake	Lake type	TS		Water ^{a,b}							Bottom			
		TP (µg dm ⁻³)	SD (m)	E (m ⁻¹)	O ₂ * (mg dm ⁻³)	pH*	Cond* (µS cm ⁻¹)	Temp ^a (°C)	Eu/D	SOD (mg O ₂ dm ⁻³ h ⁻¹)	WC (%)	OC (%)	OC (mg/10 cm ³)	
Karaś	M	Eu	48	2.4	1.8	8.4	8.1	396	14.4–22.0–5.5	1.3	3.2	94.2	42.0	228
Ząbrowo	M	Hyp	114	1.6	2.1	7.8	8.0	405	15.4–22.8–4.7	1.3	4.4	95.6	50.1	215
Jeziork	PhS	Eu	81	0.7	2.4	11.9	8.7	322	16.2–21.1–5.4	1.5	5.6	96.6	56.8	191
Czerwica	PhS	Hyp	183	0.5	5.2	13.8	9.3	248	19.2–24.7–4.7	1.5	2.9	96.9	54.0	165
Ilawskie	PhD	Eu	99	0.7	2.9	11.2	8.5	368	13.8–23.2–5.9	0.6	6.6	96.5	45.8	157
Kolmowo	PhD	Hyp	140	0.7	3.8	7.7	8.2	433	14.0–22.5–5.6	0.4	9.5	93.5	35.2	233
Tynwałd	PhD	Hyp	222	0.4	3.7	11.0	8.8	325	14.4–21.4–NA	0.6	13.2	96.2	52.6	199
Zielone ^b	M/PhD	Eu	68	1.4	2.3	9.7	7.6	82	14.5–23.7–NA	1.4	2.8	97.7	77.4	179
			60/76	2.1/0.7	3.2/1.3	11.3/8.1	7.6/7.7	76/88		2.0/0.8	2.3/3.2	97.7/97.7	77.8/77.0	181/178
Gardzien ^b	PhS/M	Eu	81	2.1	1.6	15.3	8.4	169	18.6–20.8–5.5	2.7	2.7	97.0	67.8	199
			80/81	2.3/2.0	1.3/1.7	12.1/16.9	8.7/8.3	211/148		3.2/2.5	3.0/2.6	97.3/96.9	70.1/66.6	185/207
Used for correlation analysis ^c :		P	P	P	P	P	P	P		S	S	S	S	S

Lake types: *M* macrophyte-dominated, *PhS* shallower phytoplankton-dominated, *PhD* deeper phytoplankton-dominated, *M/PhD*, *PhS/M* changing their status during the study form macrophytes-dominated to phytoplankton-dominated or the other way round, respectively

Trophic status: *Eu* eutrophic, *Hyp* hypertrophic

Parameters: *TP* total phosphorus, *SD* Secchi depth, *O₂* oxygen concentration, *E* vertical attenuation coefficient of light under water, *Cond* conductivity, *Eu* euphotic depth, *D* depth at the sampling station, *SOD* sediment oxygen demand, *WC* water content, *OC* organic content, expressed as % per unit of the sediment dry mass (%) or as milligrammes per 10 cm³ of the fresh sediments (mg)

Asterisks (*) indicate averaged values measured directly below the surface and 2–3 cm above the bottom

^aTemperature values for spring–summer–autumn samples; *NA* data not available

^bValues for particular stages of the status-changing lakes are shown in addition to means

^cVariables used for the analyses of correlation with ETS activity of plankton (P) and sediments (S)

Only in the deeper phytoplankton-dominated lakes was the euphotic depth/lake depth ratio lower than 1. SOD of the bottom sediments varied from 2.7 to 13.2 mg O₂ dm⁻³ h⁻¹. Water content of the bottom sediments was relatively high, ranging from 93.5 to 97.7%. The percentage of organic matter content per unit dry mass of the bottom sediments varied considerably among the studied lakes, ranging from 35.2 to 77.4%. Organic matter content expressed in mg per 10 cm³ of the fresh bottom sediments ranged from 157 to 233 mg.

Macrophyte biomass (Supplementary Table 2) was almost four times greater in Lake Ząbrowo (annual average higher than 3 kg m⁻²) than in Lake Karaś (annual average almost 0.9 kg m⁻²). Macrophyte biomasses in the status-changing lakes were much lower, but these results are not fully comparable: in Lake Zielone plants were present only in spring (status change from macrophyte-dominated into phytoplankton-dominated) and in Lake Gardzień only in summer and autumn (status changes from phytoplankton-dominated into macrophyte-dominated). The greatest macrophyte biomass was noted in summer. Each lake was dominated by a different macrophyte species (Table 1).

The biomass of the bottom fauna (Supplementary Table 2) was higher in the macrophyte-dominated lakes than in the phytoplankton-dominated ones (GLM: $F_{2, 3} = 13.8$, $P = 0.031$). This parameter was not significantly affected by season (GLM: $F_{2, 6} = 1.8$, $P = 0.224$) nor by its interaction with lake type (GLM: $F_{4, 6} = 1.5$, $P = 0.303$). In most lakes, chironomid larvae (Chironomidae, Diptera) dominated the macrozoobenthos community, constituting from 60% to 90% of its total biomass. Only in the two deeper phytoplankton-dominated lakes (Kolmowo and Tynwałd), was the bottom fauna represented exclusively by *Chaoborus flavicans* (Chaoboridae, Diptera) larvae, whereas Zygoptera (Odonata) larvae and Oligochaeta dominated in Lake Zielone (changing its status during the study), reaching 45% and 20% of the total macrozoobenthos biomass, respectively.

Respiratory carbon loss

Respiratory carbon losses calculated on the basis of ETS activity showed that the metabolic intensity varied in different lakes (Fig. 2). The lowest value was observed in Lake Gardzień (53.3 mg C m⁻² h⁻¹) and

the highest value (more than 4 times greater) was noted in Lake Ząbrowo (241.4 mg C m⁻² h⁻¹). There was no clear relationship between the total RCL and lake type (Fig. 2). Lower values were observed in the status-changing lakes. In all the lakes, the highest RCL values were found in summer and the lowest values occurred in autumn.

The proportions of the microbial community, plankton, macrozoobenthos and submerged macrophytes differed among the studied lake types and seasons (Fig. 3) as shown by a significant lake type × season × ecosystem component interaction in the GLM (Supplementary Table 3). In spring and autumn, the microorganisms in the bottom sediments contributed most to the RCL in all the lakes. In summer, macrophytes became the most important for the RCL processes in the macrophyte-dominated lakes, whereas the RCL in the other lakes was still dominated by the microorganisms in the bottom sediments.

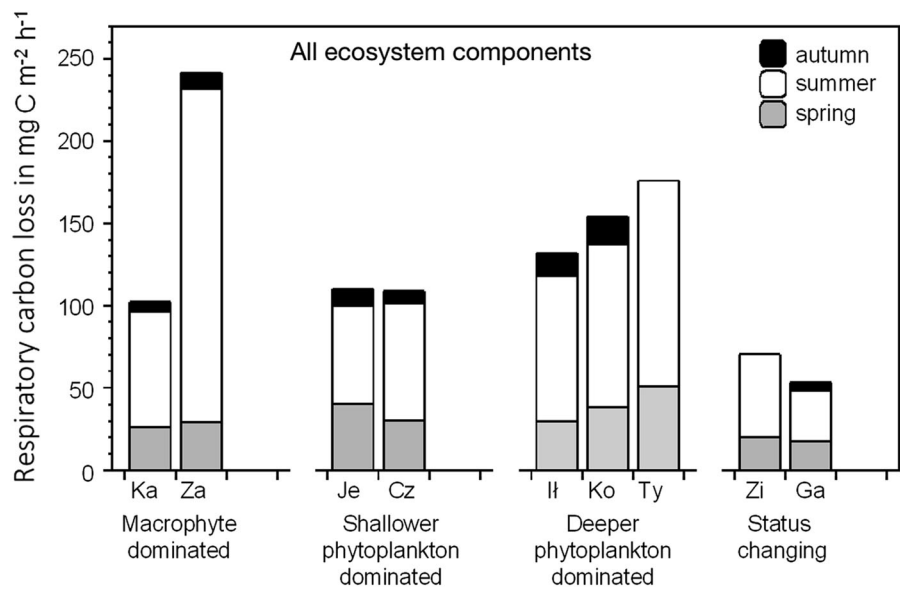
The proportion of the plankton and macrozoobenthos in the total RCL was much lower than that of the microbial communities in the bottom sediments and macrophytes (Fig. 3). Respiratory carbon loss through plankton, assessed per water area, was relatively high in the deeper phytoplankton-dominated lakes (in all seasons) and in Lake Czerwica (in summer). The role of macrozoobenthos was most important in the macrophyte-dominated lakes in spring and autumn.

Respiratory carbon loss through the microorganisms in the bottom sediments was lowest in the macrophyte-dominated lakes and status-changing lakes, higher in the shallower phytoplankton-dominated lakes and highest in the deeper phytoplankton-dominated lakes (Fig. 4). In most lakes the highest and lowest values were observed in summer and autumn, respectively. The respiratory carbon loss through the microorganisms in the bottom sediments was highly correlated with SOD ($r = 0.92$; $df = 23$; $P < 0.0001$) and the euphotic depth/lake depth ratio ($r = -0.62$; $df = 23$; $P = 0.0009$).

Respiratory carbon loss through macrophytes showed that the metabolic rate was higher in summer in the macrophyte-dominated lakes (Fig. 5). An extremely high correlation (only macrophyte-dominated lakes included, $r = 0.9965$; $df = 7$; $P < 0.0001$) was found between the macrophyte biomass and RCL.

Respiratory carbon loss through plankton showed that the metabolic rate per unit bottom surface area was clearly larger in the deeper phytoplankton-

Fig. 2 Total respiratory carbon loss in the lakes under study in consecutive seasons. No samples were taken from Zielone and Tynwałd lakes in autumn. Full lake names are given in Table 1



dominated lakes and in Lake Czerwica (Fig. 6A). However, as such a value depends strongly on lake depth, we also presented RCL through plankton per unit water volume (Fig. 6B), which enabled comparisons of the intensity of this process in the water column among lakes differing in depth. In this case, the highest metabolic rate through plankton was observed in Lake Czerwica, whereas the values in the other lakes were similar to one another. In all the lakes, the highest metabolic rates were found in summer. Plankton RCL per unit water volume strongly correlated ($r = 0.93$; $df = 23$; $P < 0.0001$) with the vertical attenuation coefficient of light under water (E). Moreover, a significant correlation between the plankton RCL and pH ($r = 0.72$; $df = 23$; $P < 0.0001$) as well between the plankton RCL and total phosphorus ($r = 0.78$; $df = 23$; $P < 0.0001$) were observed.

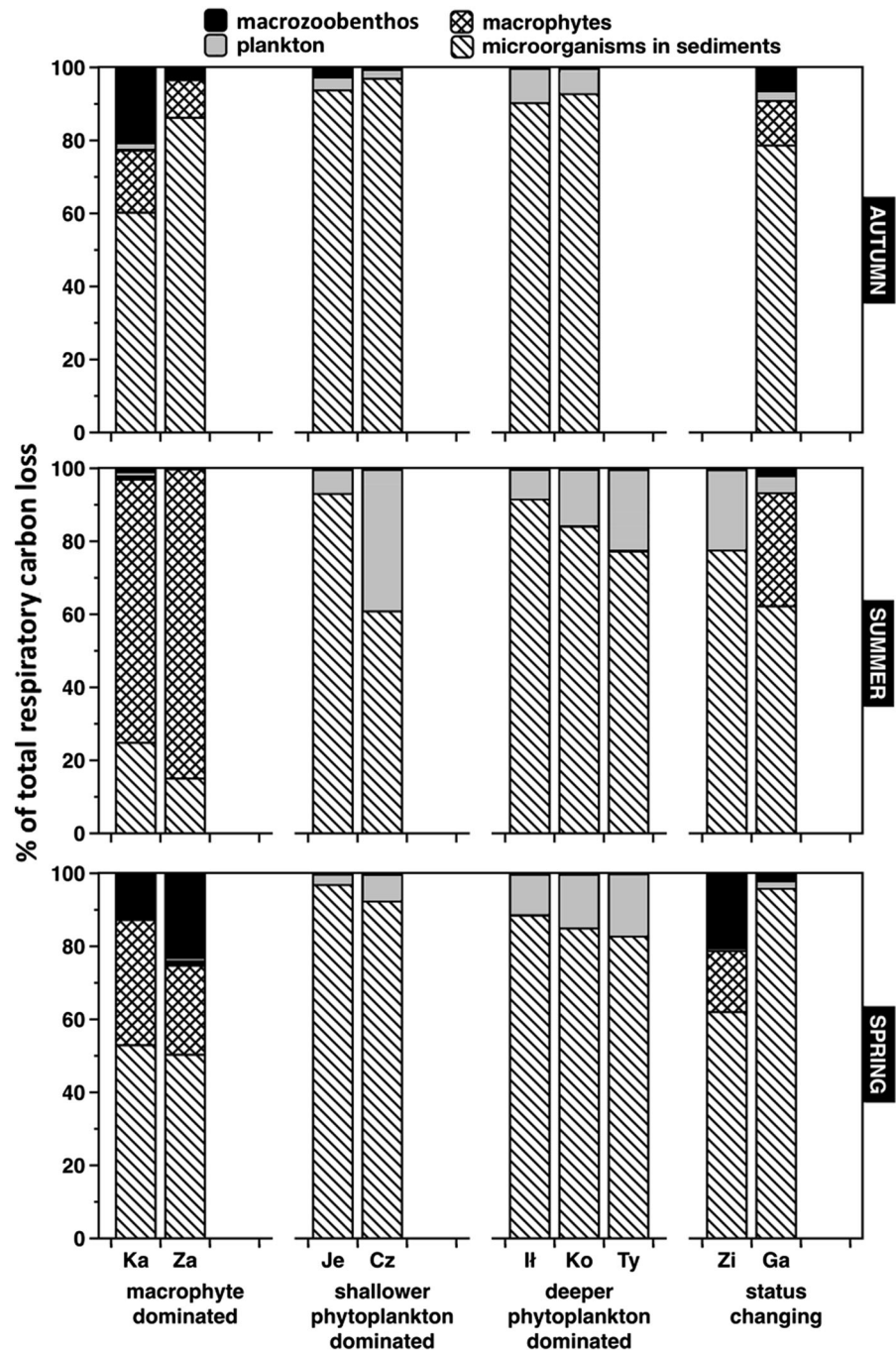
Respiratory carbon loss through macrozoobenthos showed that the metabolic rate was clearly higher in the macrophyte-dominated lakes and in the status-changing lakes than elsewhere (Fig. 7). In most lakes the highest values were found in spring. A significant correlation ($r = 0.68$; $df = 23$; $P < 0.0002$) was found between the RCL through macrozoobenthos and the biomass of this ecosystem component.

Discussion

As expected, the RCLs through the microorganisms in the bottom sediments, macrozoobenthos, plankton and macrophytes revealed their different and seasonally varying contributions to metabolic activity in various types of shallow lakes. As temperature did not vary significantly among lake types, the reasons for the differences in RCL among them must have been different. Moreover, although the spring temperature tended to be higher in shallower phytoplankton-dominated lakes, it did not translate into differences in RCL. It is worth noticing that considerable differences in the absolute values of RCLs through the studied components compared with literature data available for deep and stratified lakes were also revealed.

In agreement with the findings of the previous studies (G.-Tóth, 1992; den Heyer & Kalff, 1998; Törnblom & Pettersson, 1998; Simčič, 2005) our results showed high RCL through the microorganisms in the sediments, which constituted a significant part of the total metabolic activity also in the shallow lakes in our study. However, it is worth noticing that the RCL through the microbial communities in the sediments was substantially higher, both as a percentage share and in absolute values, in the lakes under study than in deep (> 10 m), stratified eutrophic lakes (Simčič, 2005). Nevertheless, the study by Chmiel et al. (2016) revealed that sediment organic carbon

Fig. 3 Percentage shares of particular ecosystem components in respiratory carbon loss (assessed per unit area) in the lakes under study in consecutive seasons. Full lake names are given in Table 1



mineralization contributed a comparatively small share (16%) to the CO₂ emission in a shallow humic boreal lake. They assume that the importance of sediments for the carbon budget of boreal lakes probably vary depending on basin morphometry (sediment area-to-water volume ratio), stratification

patterns and, as a consequence, temperature and oxygen regimes.

Electron Transport System (ETS) activity of bottom sediments is a measure of the respiratory activity of bacteria (Muri & Simčič, 2004), as it is mainly based on bacterial activity (Törnblom & Pettersson,

Fig. 4 Respiratory carbon loss through the microorganisms in the bottom sediments in the lakes under study in consecutive seasons. No samples were taken from Zielone and Tynwałd lakes in autumn. Full lake names are given in Table 1

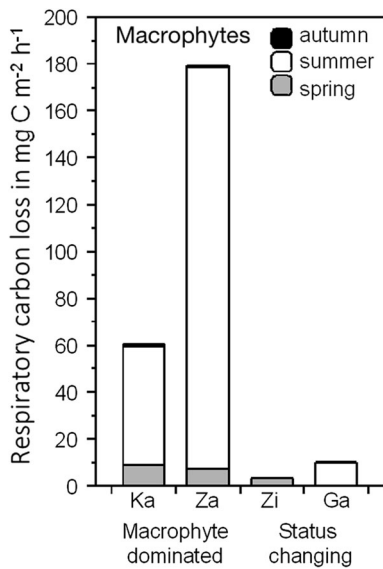
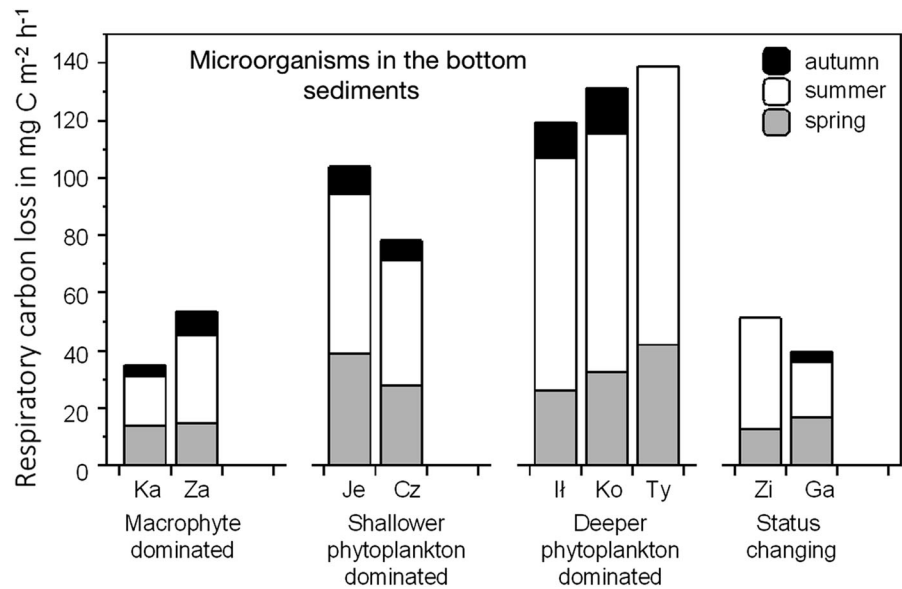


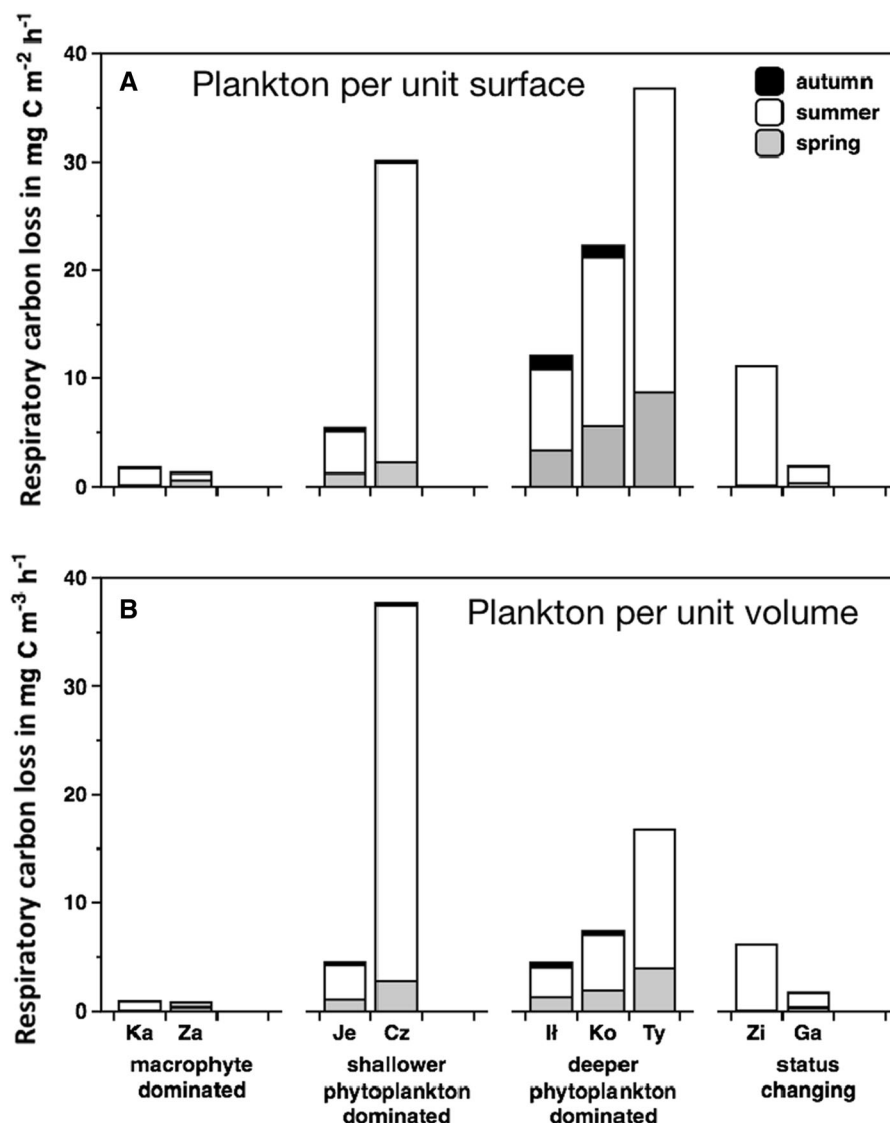
Fig. 5 Respiratory carbon loss through macrophytes in macrophyte-dominated (Ka, Za) and status-changing (Zi, Ga) lakes in consecutive seasons. No samples were taken from Zielone Lake in autumn. Full lake names are given in Table 1

1998). However, in shallow lakes, microphytobenthos can additionally contribute to the respiratory activity of microorganisms in the sediments. These organisms are able to survive and photosynthesize even under extremely low light conditions, as evidenced by McGee et al. (2008) for benthic diatoms. Moreover, mixotrophic diatoms switch their metabolism from

photoautotrophic to heterotrophic when light levels are too low for photosynthesis and can contribute to respiratory activity in the sediments (Tuchman et al., 2006). In our study only in the deeper phytoplankton-dominated lakes was the euphotic depth/lake depth ratio lower than 1, indicating that the light intensity at the bottom might be insufficient to sustain the growth of microphytobenthos. However, taking into account the above information, it is likely that microphytobenthos contributed to RCL in the bottom sediments even in those lakes. Nevertheless, we did not study microphytobenthos directly, thus we cannot confirm this assumption.

In the deep, stratified and eutrophic lakes mentioned above, low temperatures and oxygen depletions (6–8% of oxygen saturation) were observed at the bottom in summer (Simčič, 2005), and both these abiotic factors are likely to restrict the metabolic activity of bacteria as well as the rate of mineralization (Kristensen et al., 1985). The decreasing bacterial production and total sediment metabolism that coincided with the decreasing sediment redox potential in summer was also evidenced by Törnblom & Pettersson (1998) and Germ & Simčič (2011). In the present study, a positive, significant correlation between the RCL through the microorganisms in the bottom sediments and SOD also indicated a relationship between the intensity of mineralization of organic matter and dissolved oxygen concentration of the overlying water. However, in contrast to deep,

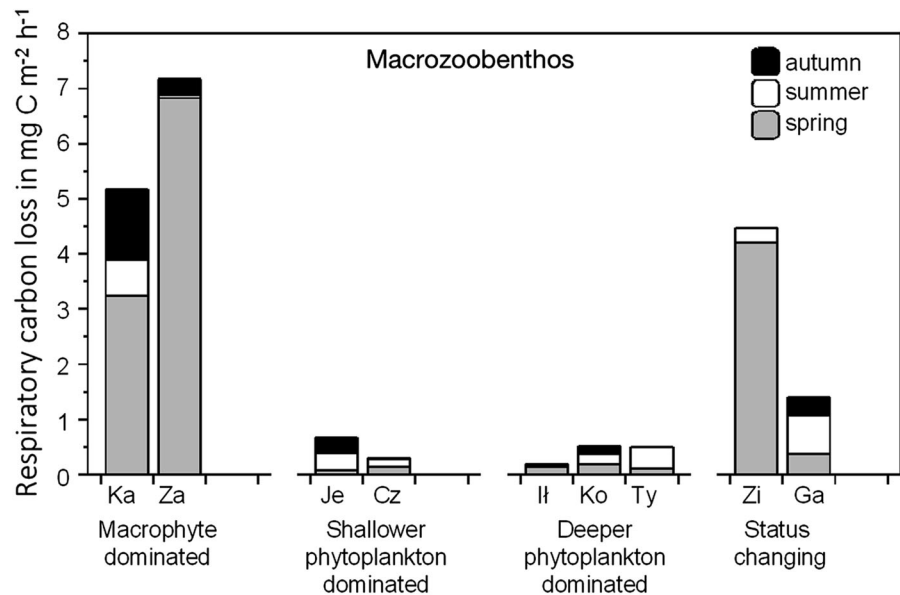
Fig. 6 Respiratory carbon loss through plankton per unit surface (water column under unit area) (A) and per unit water volume (B) in the lakes under study in consecutive seasons. No samples were taken from Zielone and Tynwald lakes in autumn. Full lake names are given in Table 1



stratified eutrophic lakes (Simčič, 2005), oxygen concentrations and water temperatures at the bottom during the vegetation season remained relatively high in all the studied lakes, enabling faster organic matter mineralization at their bottom. The reason is their shallow depth, which enables mixing of the whole water column, including a layer above the sediment surface, providing a suitable environment for microbial respiration in the sediments. Moreover, the role of oxygen and dissolved organic carbon availability in controlling nutrient release from the sediments of a shallow, polymictic Australian lake was also evidenced by Müller et al. (2016).

The present study revealed that the RCL through microorganisms in sediments differed among various lake types of the same trophic status. The higher RCL through the microorganisms in sediments of the phytoplankton-dominated lakes indicated more intense mineralization of organic matter compared with the macrophyte-dominated lakes and status-changing lakes during the presence of macrophytes. The respiratory activity in the sediments was reported to be affected by the amount and origin of organic matter and temperature (de Vicente et al., 2010; Germ & Simčič, 2011). However, in the present study the temperature could not be the reason for the observed

Fig. 7 Respiratory carbon loss through zoobenthos in the lakes under study in consecutive seasons. No samples were taken from Zielone and Tynwałd lakes in autumn. Full lake names are given in Table 1



differences, as water temperature was similar in both macrophyte-dominated and phytoplankton-dominated lakes or in some cases even lower in the latter. However, it is well known that phytoplankton detritus is labile and easily degradable, while vascular plant remains are structurally complex and therefore a longer period is needed to degrade them to forms that can be easily decomposed further by bacteria (Kristensen et al., 1995). In our study, a large amount of labile organic matter accumulated on the surface of the sediments of the phytoplankton-dominated lakes represented a better growth medium for heterotrophic bacteria. This enabled a more intensive mineralization of organic matter compared with the macrophyte-dominated lakes. Similarly, Brothers et al. (2013) found higher respiration in the sediments of the phytoplankton-dominated shallow eutrophic Lake Gollinsee than in the sediments of the macrophyte-dominated shallow eutrophic Lake Schulzensee. Interestingly, Algesten et al. (2005) reported that sediments contributed little to the total production and emission of CO₂ in boreal and subarctic lakes of low productivity during a typical summer because the source of CO₂ production is mineralization of allochthonous carbon in its dissolved form which never reaches the lake sediments even in shallow lakes. Moreover, a lower benthic respiration (28.1–237.1 mg C m⁻² day⁻¹) compared to the rates from our study (from 416 mg C m⁻² day⁻¹ in Karaś

to 2324 mg C m⁻² day⁻¹ in Tynwałd in summer) was recorded in 15 small, shallow unproductive boreal or alpine lakes in northern Sweden (Ask et al., 2012). However, we can conclude that the carbon and nutrient cycling in shallow, highly productive, especially phytoplankton-dominated lakes is driven by the rapid degradation and mineralization of the labile autochthonous organic matter.

The microbial communities in the sediments in all studied types of lakes contributed to the largest extent to the total RCL in spring and autumn, while in summer the massive presence of submerged plants in the macrophyte-dominated lakes led to the high areal RCL through macrophytes, as well as to their high contribution to the total areal RCL. The respiratory carbon loss through macrophytes was highly correlated with their biomass, regardless of their taxonomic composition. This indicates that the dominant macrophyte species had similar mass-specific metabolic activity. Extremely high respiration of macrophytes in summer, apart from being correlated with higher water temperature, is also related to additional energy requirements during their intensive growth and development in order to build structural components (Germ & Simčič, 2011). In previous studies, it was shown that the high productivity and biomass turnover of macrophytes in fertile ecosystems, similar to Lakes Ząbrowo and Karaś in the present study, contributed to the high rates of nutrient mobilization from the sediments

(Smith & Adams, 1986; Kleeberg et al., 2010; Camacho et al., 2016). Brothers et al. (2013) also found that macrophytes considerably contributed to the total carbon loss in the macrophyte-dominated shallow eutrophic lake. In contrast to the shallow eutrophic lakes, significantly lower values of the macrophyte RCL, up to $0.4 \text{ mg C m}^{-2} \text{ h}^{-1}$ in summer, was observed in the littoral of the deep, oligotrophic Lake Bohinj (Simčič & Germ, 2009), despite similar biomasses of macrophytes in the compared lakes. For comparison, Martinsen et al. (2017) who studied ecosystem metabolism in five small, shallow, oligotrophic lakes dominated by charophytes on the nutrient poor plains of Öland (Sweden) found high rates of production and respiration during spring–summer period as a result of the high charophyte biomass and shallow mixed surface layer. Thus, it is suggested that the macrophytes have an essential role in the cycling of carbon and nutrients in shallow, highly productive lakes.

As expected, the percentage shares of plankton in the total RCL in the lakes being studied were very low, with the exception of the deeper phytoplankton-dominated lakes, where relatively high values were found due to the higher water depth (larger water volume) and high abundance of algae. Theoretically, the considerable role of plankton in these lakes could have been exaggerated by overestimation of its abundance due to collecting samples from the 0.5-m surface water layer. However, high dynamics of water (as a consequence of wind action) was noted in the studied deeper phytoplankton-dominated lakes (minor differences between surface and near-bottom temperatures) resulting in the lack of vertical stratification. It is the consequence of a good exposure of the studied lakes to wind (Table 1). Therefore, it can be assumed that plankton was evenly distributed in the entire water column of the studied lakes. On the other hand, in the macrophyte-dominated lakes and the status-changing one after its switch to macrophyte domination the phytoplankton abundances were very low due to the presence of submerged plants and their mechanisms limiting phytoplankton growth (Scheffer, 1998). It is worth mentioning that the RCL through plankton in summer in Lake Czerwica was relatively high. The explanation is the very high total phosphorus concentration in water, which in conjunction with high temperature and good light conditions (the shallowest lake) provided a favourable environment for the

intensive phytoplankton development in the whole water column. Thus, plankton can be a crucial biocoenotic element in the RCL in summer even in a very shallow lake provided that it is dominated by phytoplankton.

For the lakes with phytoplankton domination the differences were observed in the RCL through plankton per unit surface area as well as per unit water volume among lakes of various trophic status and depth. For example, within the shallower phytoplankton-dominated lakes, considerably higher RCL through plankton was observed in the hypertrophic Lake Czerwica than in the eutrophic Lake Jeziorak. Similarly, among the deeper phytoplankton-dominated lakes, total phosphorus concentration was positively correlated with RCL through plankton. Higher metabolic activity of plankton, noted in the lakes with higher trophic level are in accord with the findings of G.-Tóth (1992), who found higher plankton ETS activity in the hypertrophic Keszthely-basin ($179.3 \text{ cm}^3 \text{ O}_2 \text{ m}^{-2} \text{ h}^{-1}$) than in the meso-eutrophic Siófok-basin ($58.3 \text{ cm}^3 \text{ O}_2 \text{ m}^{-2} \text{ h}^{-1}$) of Lake Balaton. Significant correlation between total phosphorus concentration and pelagic respiration was also reported for late summer–autumn in small, shallow seepage lakes located in nutrient-rich, calcareous moraine soils in North Zealand (Denmark) (Sand-Jensen & Staehr, 2007).

Calculation of RCL per unit surface area of a lake is sufficient to assess the role of plankton in this process relative to the other biocoenotic elements. However, it can be assumed that in deeper lakes the role of plankton in the metabolism of organic matter should be greater than in shallow ones, due to the greater abundance of plankton in the entire water column in the former. Thus, to compare the intensity of RCL only through plankton in lakes of various depth, a recalculation per unit volume should be made. That is why in the present paper both approaches are presented, showing a difference in the case of the shallowest Lake Czerwica, where the intensity of RCL through plankton calculated per unit volume was the highest among the studied lakes, whereas the values calculated per unit surface area were similar in Lake Czerwica and in one of the deeper phytoplankton-dominated lakes (Tynwałd).

As for the sediments of deep, stratified lakes, much lower values of RCL through plankton (more than 10-fold), up to $2 \text{ mg C m}^{-2} \text{ h}^{-1}$ or $0.2 \text{ mg C m}^{-3} \text{ h}^{-1}$,

were also reported from deep, stratified eutrophic lakes (Simčič, 2005) compared to the studied shallow ones. The differences are likely to result from higher temperatures and better light conditions in most of the water column and greater availability of nutrients for phytoplankton due to the lack of thermal stratification in the shallow lakes, compared to deep, stratified ones. Interestingly, relatively high pelagic respiration rates (27.4–546.0 mg C m⁻² day⁻¹) were reported for small, unproductive Swedish lakes (Ask et al., 2012), compared to the RCL through plankton in lakes from our study, in which RCL varied from 15 mg C m⁻² day⁻¹ in Ząbrowo to 676 mg C m⁻² day⁻¹ in Tynwałd.

Since the respiration rate of organisms increases with the higher environmental temperature (Törnblom & Pettersson, 1998; Simčič & Germ, 2009; Laas et al., 2012), the highest RCL through almost all studied elements of the biocoenosis was observed in summer and the lowest values were measured in autumn, except for the macrozoobenthos component in the macrophyte-dominated lakes and the status-changing Lake Zielone before a regime shift, where the highest values were obtained in spring. The main reason for the lower RCL through macrozoobenthos in summer is its lower abundance rather than lower metabolic activity, as our results revealed a significant correlation between the RCL through macrozoobenthos and the biomass of this ecosystem component. The lower abundance of macrozoobenthos in summer was probably caused by the increased predation by fish (Gerking, 1994), resulting from higher water temperature increasing fish metabolic rate and thus stimulating their foraging. Moreover, emerging insects could also reduce the abundance of macrozoobenthos in summer (Armitage et al., 1995). Relatively high RCL through macrozoobenthos in the macrophyte-dominated lakes and the status-changing lakes during their macrophyte-dominated state (Lake Zielone in spring and Lake Gardzień in summer) indicated the relatively important role of that component in the metabolism of organic matter, which was exclusive for this lake type. Nevertheless, the role of zoobenthos in these lakes was still lower than that of the microorganisms in the sediments and macrophytes. The results of our study are in accord with those of Brothers et al. (2013), who found lower carbon losses through macrozoobenthos in a phytoplankton-dominated lake (0.9 mg C m⁻² h⁻¹) in comparison to a lake with macrophyte

domination (3.1 mg C m⁻² h⁻¹). Moreover, RCL through macrozoobenthos found in our study was similar to that observed by Brothers et al. (2013) in a shallow, eutrophic, macrophyte-dominated lake, but substantially higher than in deep, stratified eutrophic lakes, where the values below 0.1 mg C m⁻² h⁻¹ were reported (Simčič, 2005).

Interestingly, the lowest total RCL was observed in the two status-changing lakes. This was due to the relatively low mineralization rate at the bottom, which also confirms the lowest SOD (< 3 mg O₂ dm⁻³ h⁻¹) in the status-changing lakes, and in the water column, resulting from the relatively small amount of detritus reaching the bottom and low phytoplankton abundance, respectively (transparent water). Moreover, the biomass of macrophytes in the status-changing lakes was relatively small compared to the lakes dominated by macrophytes throughout the year.

An interesting issue is the alternative status change that took place during our study in two of the lakes: Lake Gardzień that turned from a phytoplankton-dominated status into a macrophytes-dominated status and Lake Zielone that changed in the opposite direction. Factors inducing alternative status changes have been comprehensively discussed by Scheffer (1998). However, in this particular case it is difficult to find a definitive cause of the observed phenomenon. We did not observe any changes in the lake watersheds, their use and/or chemical regimes. Despite the relatively short distance between the two lakes (ca. 15 km in straight line), they changed in the opposite directions, which suggests the importance of local factors. On the other hand, taking the unique character of particular lakes into account, we cannot exclude that the same factor induced different changes in each of them. Anyway, further detailed studies on lakes and their watersheds are needed to determine exact mechanisms of the phenomenon of alternative status changes.

Conclusions

The role of particular components in the total RCL varied with the type of a shallow lake and season. High carbon losses through respiration of microbial communities in sediments, especially in phytoplankton-dominated lakes, contributed substantially to the mineralization of organic matter and recycling of

carbon and nutrients in shallow lakes of a high trophic level. The respiratory carbon loss through the studied organisms was the highest in summer with the exception of benthic macroinvertebrates due to their very low biomass at the time. Moreover, high RCL through macrophytes in macrophyte-dominated lakes during the vegetation period confirmed the importance of vascular plants for the functioning of shallow lakes. Plankton respiration per unit water volume did not differ between both types of phytoplankton-dominated lakes, which resulted in the higher impact of this component in deeper lakes. It is therefore suggested that the shallow, highly eutrophic lakes can be extremely productive ecosystems due to intensive mineralization of organic matter at the bottom and rapid flow and cycling of carbon and nutrients due to their polymictic character. The observed strong correlations between SOD, macrophyte biomass, vertical attenuation coefficient of light under water and RCL through microbial communities in sediments, macrophytes and plankton, respectively, suggest that these parameters could be considered as good predictors of RCL in shallow lakes.

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