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Original Research

Peculiarities of Pelagic Community Metabolism in Small Dimictic Lakes as Demonstrated by Daily Changes of Oxygen Vertical Distribution

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Abstract

Our paper presents daily fluctuations in the concentration of oxygen in two small moderately eutrophied lakes in the Bytowskie Lake District (northern Poland), measured with the aid of a manually operated oxygen and temperature probe. Based on the results of these measurements, gross primary production, respiration, and net production of the ecosystem were calculated. It was observed that rhythmic changes in oxygen concentrations occurred in the epilimnion and – under favorable conditions – also in the upper part of the metalimnion. However, changes in the concentration of oxygen due to biological processes in the metalimnion were compounded by fluctuations caused by internal seiches, especially in shallower sites closer to the lake shores. In May and July the reach of the production layer coincided with the isopleth of 100% saturation with oxygen and, apart from the epilimnion, also encompassed the upper part of the metalimnion. In May, when the thermocline was particularly shallow, much of the primary production and respiration took place in the metalimnion.

Keywords: daily oxygen technique, gross primary production, lake metabolism, net ecosystem production, respiration

Introduction

Well over half a century ago it was demonstrated that daily fluctuations in the concentration of oxygen in lakes could be used for evaluation of the rate of primary production and respiration in these ecosystems [1-3]. However, certain limitations to the then existing methodology meant that the free-water approach, based on changes of oxygen concentration measured directly in a lake, was used rather infrequently. Concentrations of oxygen in water were measured with a method relying on titration of discrete samples, which made measurements encompassing a whole water body excessively time-consuming. An additional obstacle was the insufficient knowledge on gas exchange between the surface layer and the atmosphere.

For a long time, measurements of primary production and respiration in water bodies were dominated by methods based on incubation of closed water samples, and mainly the oxygen method of clear and dark bottles [4, 5] or the ^{14}C method [6, 7]. In the years to follow, owing to advances in measurement techniques (polarographic and optic oxygen probes, data recorders, robotic measuring devices, etc.), *in situ* measurements attracted increasing attention [8]. The interest was additionally stimulated by our improved understanding of gas exchange in the water and air contact zone [9, 10]. Repeatedly measured oxygen and CO_2 concentrations, pH, and an increasing number of other parameters

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have proven to be a valuable source of information on the metabolism of whole water ecosystems [11-17]. What matters is also that the free-water methods do not create certain limitations of the *in vitro* methods [8, 18], first of all the so-called bottle effect [19]. However, they pose their own specific problems. For example, they are sensitive to disturbations caused by vertical motions of water. In 2010 Staehr et al. [20] published a paper in which they recapitulated the experience gained while applying the method of measuring daily changes in oxygen concentrations in lakes and suggested a standard procedure of conducting measurements and calculating gross primary production (GPP), respiration (R), and net ecosystem production (NEP).

Oxygen probes, adequately sensitive and precise, even though they are more and more commonly applied, are by no means cheap devices. Moreover, additional instruments necessary for high-frequency automatic measurements, mass recording of data, and auxiliary meteorological measurements pushes the costs even further. However, for small lakes characterized by a simple shape of lake basin and water table protected from strong winds, it seems possible to attain satisfying results at a much lower expense.

This paper presents daily fluctuations in the concentration of oxygen in two small lakes, measured with the aid of a manually operated oxygen and temperature probe. Based on the readings thus obtained, GPP, R and NEP were computed using the calculation procedure suggested by Staehr et al. [20]. With the oxygen vertical profiles it was possible to include in the calculations not only the epilimnion but also the metalimnion, in which the oxygen maximum appeared in the first half of the growing season. Gas exchange between water and the atmosphere was assessed according to the level of water saturation with oxygen, assuming – as Cole and Caraco [10] claim – that weak winds had a small effect on that process.

Material and Methods

The present study was performed on two lakes: Mały Borek and Krążno (Fig. 1, Table 1) in the Bytowskie Lake District. The landscape of this district is composed of terminal moraines. The area is rich in lakes, but they are neither very deep nor vast. Some of the lakes are classified as

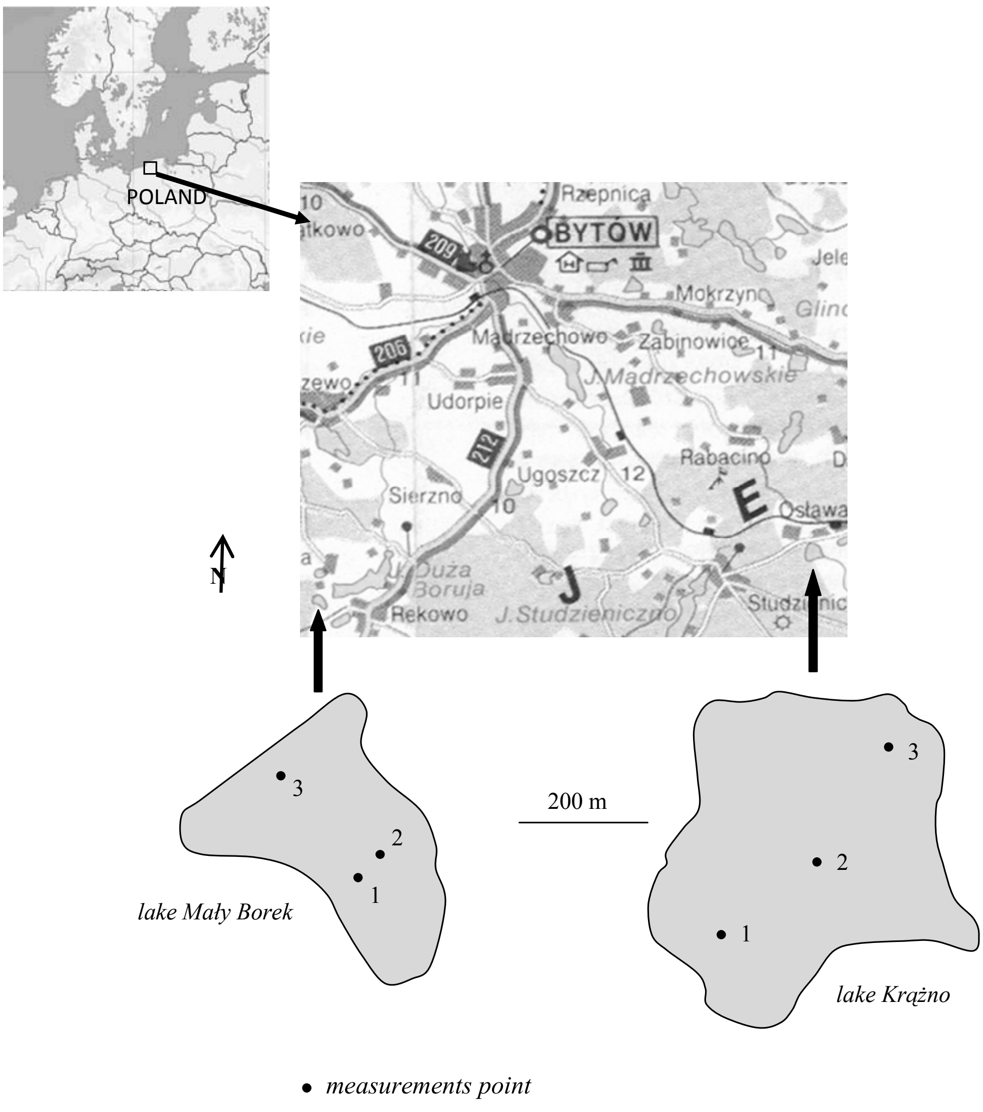

Fig. 1. Lakes Krążno and Mały Borek and the locations of measurement sites.

Table 1. Morphometric data and chemical characteristics of lakes Krążno and Mały Borek.

	Krążno		Mały Borek	
Surface area, ha	13.7		7.6	
Volume, thous. m^3	890.5		456	
Maximum depth., m	16		11	
Measurements conducted in June 2007	Surface	Bottom	Surface	Bottom
Conductivity, μS	222	327	110	119
N_{tot}, $mgN \cdot dm^{-3}$	1.01	3.02	0.79	1.10
N_{min}, $mgN \cdot dm^{-3}$	0.07	2.67	0.05	0.49
P_{tot}, $mgP \cdot dm^{-3}$	0.12	0.38	0.02	0.14
P_{min}, $mgP \cdot dm^{-3}$	0.00	0.23	0.00	0.04

the so-called lobelia lakes, which are characterized by the presence of relict post-glacial flora and some specific physico-chemical properties of water, namely a low concentration of phosphorus and calcium, low pH, and relatively high water transparency [21-24].

The two examined lakes differ in their trophy – Mały Borek is a mesotrophic lobelia lake while Krążno Lake is eutrophic. These are small, dimictic lakes, with simple shapes, as well as fairly high, woody banks that keep their water tables well protected from winds.

The field studies in Krążno Lake were carried out in three 2- to 3-day measuring series (May, July, and October), and those in Mały Borek comprised two such series (May and July) in 2007-08. On each lake, 3 measuring sites were set up in open water (Fig. 1). At those sites, using a WTW TA 197-Oxi oxygen probe, vertical profiles of temperature distribution and concentration of dissolved oxygen (every 0.5-1 m) were determined. The measurements were repeated several times (3-5 times) a day. One measuring series at all three sites took about 1 hour total. Prior to each measuring series, the electrode was calibrated in an atmosphere of saturated water vapor. The resolution of the oxygen probe was 0.01 $mgO_2 \cdot dm^{-3}$ and accuracy, as claimed by the manufacturer, was 0.5% of measured value. Simultaneously, solar irradiance was measured with a global solar radiation sensor at a wavelength of 310 to 2800 nm (Kipp and Zonen), coupled with a LAB-EL 486 recorder. The sensor was placed at a height of 5 meters above the ground, 0.5 km away from Mały Borek. Global solar irradiance doses were integrated at hourly intervals. The PAR (400-700 nm) was estimated as ~46% of total solar irradiance.

In general, the calculations of the GPP, R, and NEP were carried out in accordance with the guidelines given by Staehr et al. [20], but some modifications were introduced, such as:

1. Calculations were not limited exclusively to the mixed layer (Z_{mix}), as suggested by the above authors, but performed for the whole production layer in which a daily rhythm in the fluctuations of oxygen concentrations was observed. Thus, our calculations also encompassed the upper part of the metalimnion, in which the oxygen maximum occurred. Based on the vertical distributions of oxygen concentrations at all the test sites and on the volumes of particular water layers, the mass of oxygen contained in the production layer was calculated. Changes in the mass of oxygen in the production layer were re-calculated per lake area unit.
2. In all the calculations of the exchange of oxygen with the atmosphere, the same wind velocity was assumed at a height of 1.5 m above the water surface, equal 1 $m \cdot s^{-1}$. Cole and Caraco [10], in their experimental studies, demonstrated that within a range of low wind velocities (V_{wind} <3 $m \cdot s^{-1}$), the rate of gas exchange with the atmosphere is only weakly correlated with the wind velocity, and the gas exchange takes places even when no wind is blowing as long as the oxygen concentration in the surface water layer is different from the saturation concentration. In the small water bodies where Cole and Caraco [10] as well as Cole et al. [11] carried out their experiments, the mean wind velocity at a height of 10 m above the water table from May to November was 1.4-1.5 $m \cdot s^{-1}$, and the modal value was less than 1 $m \cdot s^{-1}$. In just 3% of the observations, the wind blew at a velocity over 3 $m \cdot s^{-1}$.

Calculations of the respiration on a given day were made based on the measurements taken the following night. According to Fukushima et al. [12], the intensity of respiration in the first phase of a night is strongly affected by the intensity of photosynthesis on the previous day, and among all the tested combinations (respiration from the beginning of the following night, from the end of the preceding night, mean respiration from the whole of the following night, etc.), the daily respiration is most faithfully reflected by mean respiration from the following night.

Results

Water transparency constantly differed between the lakes. In Mały Borek it was much higher (Secchi depth 3.2 m in May and 3.0 in July) than in Krążno Lake (in May and in July Secchi depth just 1.4-1.5 m, and in October about 3.3 m).

In May, the waters of the epilimnion in both of the analyzed lakes, which then covered just a 1.5-meter layer of water, were characterized by oxygen oversaturation, reaching 120-130% (12-12.5 $mgO_2 \cdot dm^{-3}$ in Mały Borek and 13-14 $mgO_2 \cdot dm^{-3}$ in Krążno Lake) (Fig. 2). In the upper part of the metalimnion, at a depth of 3-3.5 m, an increase in the content of oxygen (oxygen maximum) was noticed, up to the concentration of 16-17 $mgO_2 \cdot dm^{-3}$. Oxygen oversaturation in that layer reached 150% and was connected with the shallow location of the thermocline, within the limits of the euphotic zone. At greater depths the degree of oxygen saturation gradually decreased. The isopleth indicating 100% saturation was at a depth of about 5 meters in Krążno Lake and 6.5 meters in Mały Borek Lake. In July, the water in the epilimnion, which reached down to 3-4 m, was likewise oversaturated with oxygen, but to a lesser degree than in May (about 110%). As regards the metalimnion, it was only in Mały Borek that we could observe the oxygen maximum, although it shifted downwards to a depth of 5 m (Fig. 2B). At that depth, photosynthesis was possible owing to a relatively high water transparency. The 100% saturation isopleth in Krążno was determined to be 4 meters deep into the lake and in Mały Borek it was situated at a depth of 5.5 m. Rapidly disappearing oxygen at lower depths made it totally absent at 7-8 meters. In October (Fig. 2A), the oxygen saturation of waters of the epilimnion in Krążno Lake, was uniform down to 6 meters, and equalled about 90%. Between 7 and 8 meters of depth, a steep oxygen gradient appeared so that water below 8 meters was deoxygenated.

In the upper layers of lake water, fluctuations in oxygen concentrations distinctly demonstrated a daily rhythm (Figs. 3 and 4). The maximum oxygen concentrations were recorded in the afternoon hours and the minimum ones occurred in the morning. As depth increased, the daily rhythm of fluctuations in oxygen concentration became less apparent (increased values of standard deviations) and at certain depths it was no longer noticeable.

When comparing the daily changes in oxygen concentrations in both lakes, it may be noticed that the amplitudes of such changes in the epilimnion were smaller in Mały Borek and the peak concentrations fell on earlier afternoon hours than in Krążno. However, owing to its superior water transparency and deeper light penetration, the daily cycle of changes in Mały Borek Lake encompassed a thicker water layer. In the oxygen maximum layer, the amplitude of daily changes was even higher than in the surface layer. In May and July, in both lakes, the vertical range of daily fluctuations in oxygen concentrations coincided with the depth range of the water oversaturated with oxygen. Under good global solar radiations, a daily cycle of changes in oxygen concentrations was evident, but when the global solar radiations deteriorated, the daily rhythm of the changes became weaker.

As mentioned earlier, the rhythmic changes in oxygen concentrations appeared in the euphotic zone, which covered the epilimnion and – when the conditions favoured photosynthesis – the upper part of the metalimnion. However, in the metalimnion, changes in oxygen concentrations caused by biological processes were compounded by internal seiches [25, 26] in the lake. This meant higher dispersion of the measurement results and made the evaluation of the metabolism less precise. The situation is illustrated by vertical distributions of differences in oxygen concentrations between dusk and dawn, as well as between dawn and 9 a.m., as demonstrated in the graph of the measuring series completed in May in Krążno and Mały Borek lakes (Fig. 5).

In Krążno, the loss of oxygen at night and its increase in the first part of the day were most distinctly seen in the epilimnion, down to 2 meters of depth. Deeper, in the upper part of the metalimnion, down to 4 meters in depth, most of the measurements taken at night demonstrated oxygen loss and most of the measurements taken in morning hours revealed increase in oxygen concentration, but in both time

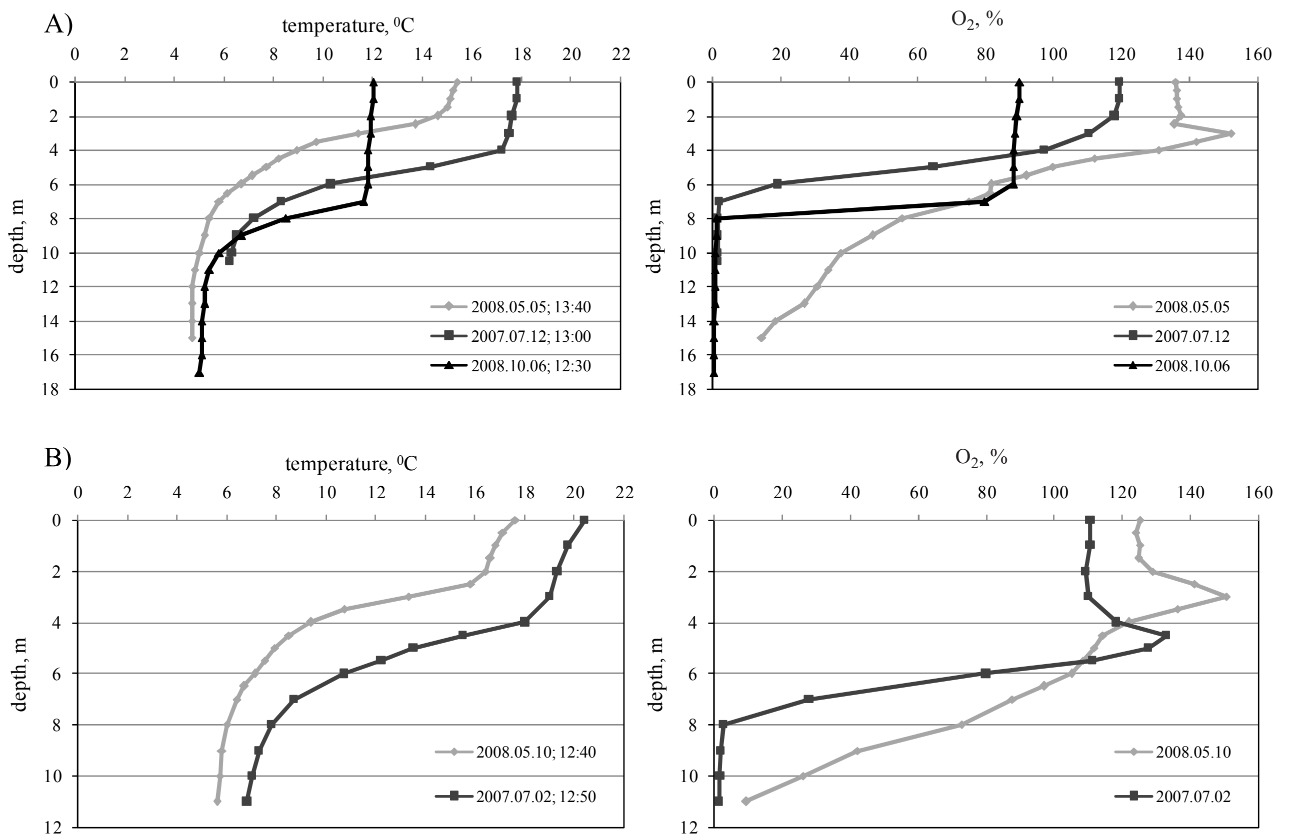

Fig. 2. Changes of water temperature and oxygen saturation: top (A) Lake Krążno, bottom (B) Lake Mały Borek at the deepest stations.

periods some of the results showed a reverse direction of changes. At night, raised oxygen concentrations were sometimes recorded and, in the morning hours, oxygen concentrations sometimes dropped. In Mały Borek the general tendency for decreasing oxygen concentrations at night and increasing ones in the morning was apparent down to 6 meters in depth, with the biggest changes occurring in the oxygen maximum layer in the upper part of the metalimnion. Analogously to Krążno, some of the results of the measurements taken in Mały Borek also showed a reverse direction of changes. Nonetheless, it could be noticed that such reversed tendencies were most frequently recorded at the peripheral stations (open symbols in Fig. 5). The amplitude of internal seiches was most probably higher at those shallower sites, closer to the shores, than in the middle of the lake, and the internal seiches in those distal parts of the lake more strongly disturbed the pattern of changes in oxygen concentrations generated by biological processes.

At lower depths, below the thermocline, changes in oxygen concentrations were apparently chaotic and not connected with a daily rhythm. There, oxygen concentration fluctuations were affected mainly by vertical water motions associated with internal seiches.

Over 100% saturation of water with oxygen implied that gross primary production prevailed over respiration. In Krążno, the layer of water oversaturated with oxygen reached from 5 m deep in May to 4 m in July, and in Mały Borek Lake it went down to 6.5 m in May and 5.5 m in July (Fig. 2). Below these depths, oxygen concentration declined rapidly. In October the saturation of water with oxygen in the epilimnion was not complete, which suggested that R prevailed over GPP in that layer as well as in the whole water column. Nevertheless, the daily rhythm of photosynthesis also was visible down to a depth of 5-6 m. Thus, it can be concluded that the production layer in those lakes comprised the upper 4-6 meters of the water column.

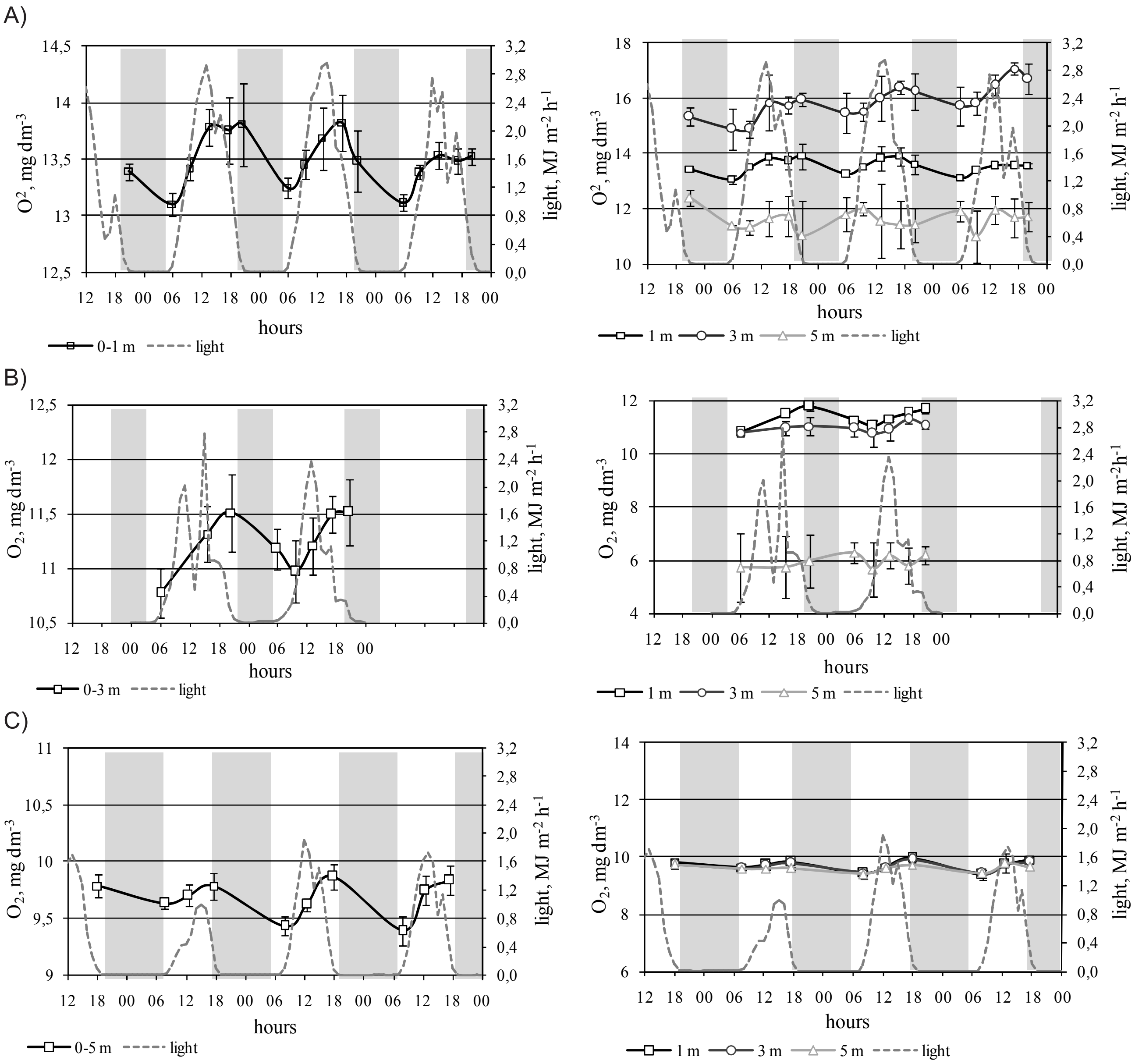

Fig. 3. Daily changes of oxygen concentrations in epilimnion (left) and of chosen depth levels (right) in Lake Krążno on the light dose background: top (A) 4-7.05.2008, centre (B) 11-12.07.2007, bottom (C) 5-8.10.2008 (mean and standard deviation).

In Fig. 6 the direction and rate of the daily oxygen concentration fluctuations in the upper 5-meter thick layer of water are presented. The bars directed upward determine an increase in oxygen content while the ones pointing downwards show a decrease. During the night hours a decrease in the amount of oxygen in the production layer was invariably observed. In daytime hours an increase in oxygen concentrations was most often observed, generated by photosynthesis, and the rate of that increase varied in particular times of a day and on particular days of measurements. In May and in July the highest rate of O_2 increase was noticed in the first half of a day (up to 0.5 $gO_2 \cdot m^{-2} \cdot h^{-1}$). The rate of the oxygen concentration increase in the afternoon hours was demonstrably lower; moreover, during the May measurements, a decline in oxygen concentrations was recorded at the end of the day in both lakes. This event was most probably connected with the depletion of assimilable forms of nutrients during the day and, consequently, inhibited photosynthesis. At night, these substances were recovered and, therefore, during the first part of a day the conditions for photosynthesis were the best. In October no repeatable differences in the oxygen concentration growth rate before and after noon were observed, which may have been associated with shorter days and longer nights in that month.

It is noticeable that declines in oxygen concentrations recorded in Mały Borek during the late afternoon hours were deeper than in Krążno. This finding also may have been related to the availability of nutrients. Mały Borek was poorer in nitrogen and phosphorus than Krążno (Table 1), and just small amounts of mineral forms of nutrients were present in the epilimnion waters during the growing season [27]. In Krążno Lake, light may have been a much more important factor limiting photosynthesis. The global solar radiations reaching the surface of the water in that lake explained from 47% of the variability in the rate of oxygen concentration fluctuations in May, up to 66% in October, and up to 81% in July. In turn, light was responsible for just 31% of this variability in Mały Borek in both May and July. It can therefore be presumed that the accessibility of nutrients rather than light was a more important factor limiting photosynthesis in Mały Borek. Higher water transparency in Mały Borek enhanced light penetration to greater depths, thus reducing the role of light as a factor limiting primary production.

Based on the changes in amounts of oxygen found in the upper 5-meter layer of water, the values of daily primary production and respiration were assessed (Fig. 7). The highest values of gross primary production were observed in May, while the lowest were in October. In May and July the respiration in the euphotic zone was lower than GPP, which meant that the net ecosystem production in those months was positive. In October, NEP in Krążno was negative.

Noteworthy are similar values of GPP in both lakes, despite the differences in their trophic states. It seems that a higher water transparency in Mały Borek largely compensated for the lower fertility of that lake.

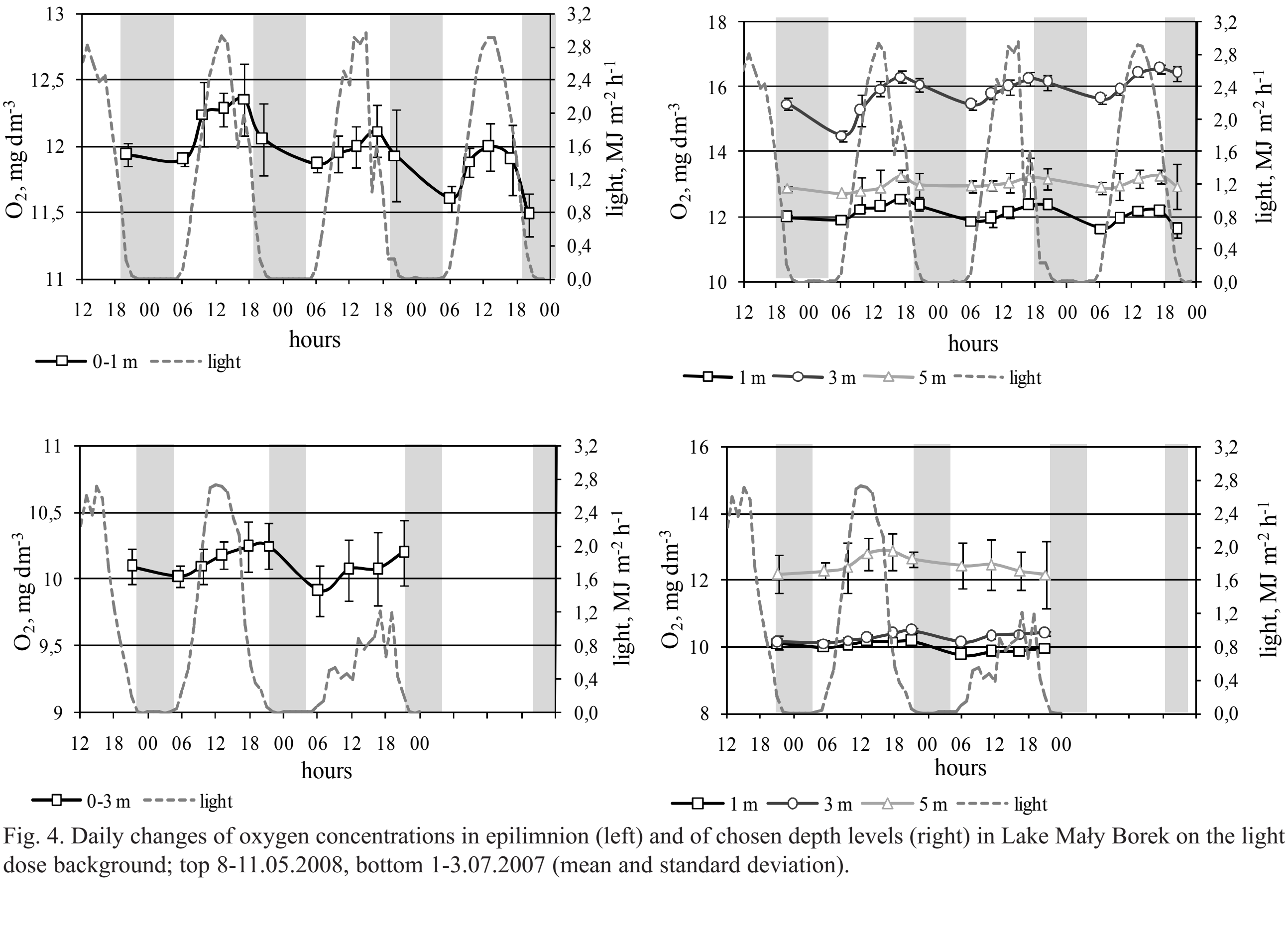

Fig. 4. Daily changes of oxygen concentrations in epilimnion (left) and of chosen depth levels (right) in Lake Mały Borek on the light dose background; top 8-11.05.2008, bottom 1-3.07.2007 (mean and standard deviation).

Discussion

In many studies on lake metabolism, based on the free-water method, changes in oxygen concentrations were measured exclusively in the epilimnion, often at just one depth level [11, 16, 28-31]. The researchers often assumed that primary production occurred only in that layer of a lake and that the amplitude of changes was identical across the whole layer.

The present study, however, shows that in small lakes, even when the water transparency is moderate, some of the primary production may take place in the metalimnion, and the amplitude of changes in oxygen concentrations in that layer can even be higher than in the epilimnion. This problem has been dealt with by Coloso et al. [32], who proved that in the clearwater lake they examined, 14-18% of GPP and 20-40% of R took place in deeper parts of the lake, below the mixed layer. The question then arises regarding to what extent neglecting that phenomenon, which occurs in small lakes with a particularly shallow location of the thermocline, affects assessment of GPP and R.

When no disturbations appear, it should be expected that as the layer of integrating oxygen measurements becomes thicker, the GPP values per lake area unit will increase, up to the depth at which photosynthesis ceases. Any further increase of the thickness of the integration

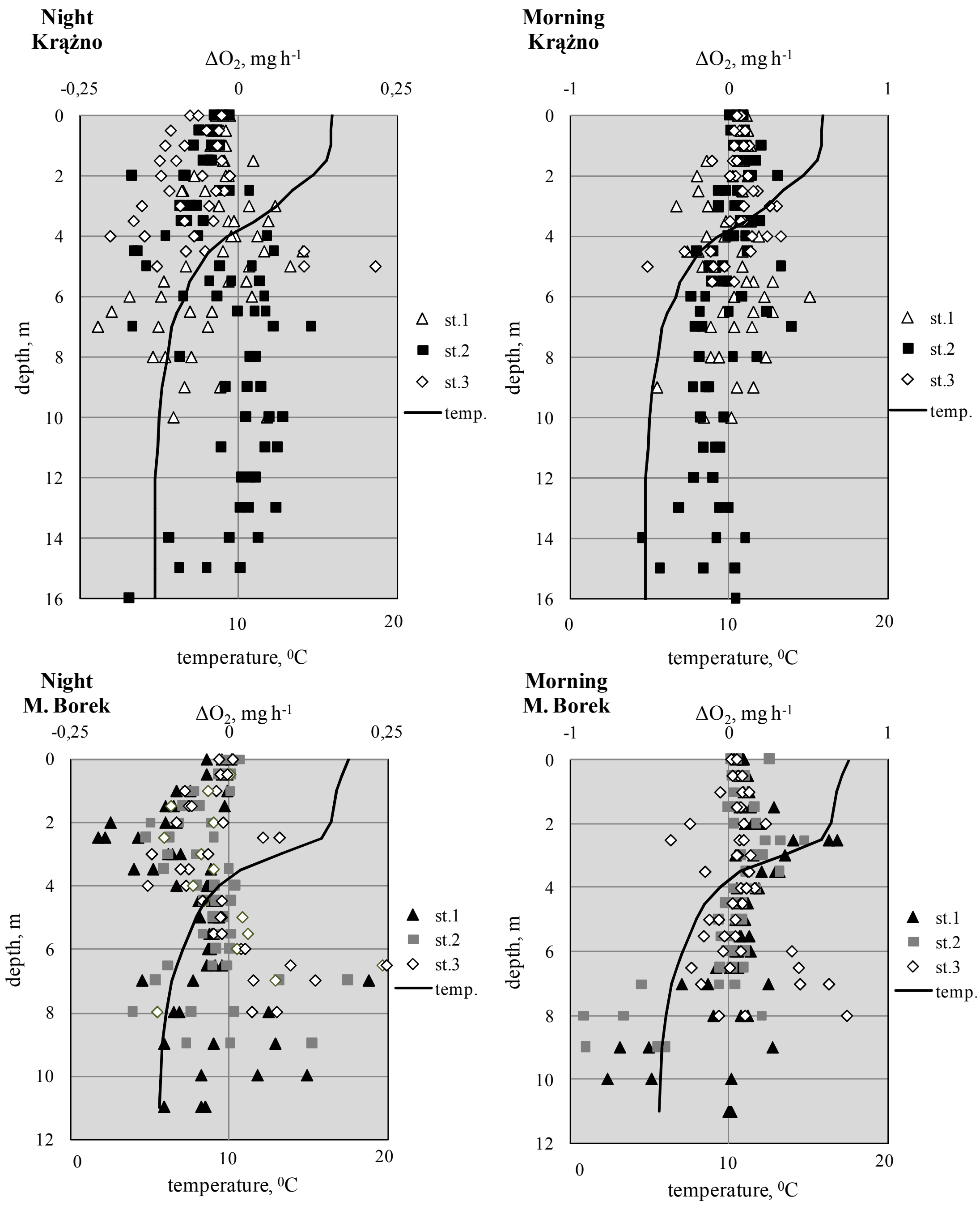

Fig. 5. Night (left) and morning (from dawn to 9 a.m., right) oxygen concentration changes in lakes: Krążno (top) and Mały Borek (bottom) in May 2008; "empty symbols" are outer stations, "whole symbols" are central stations.

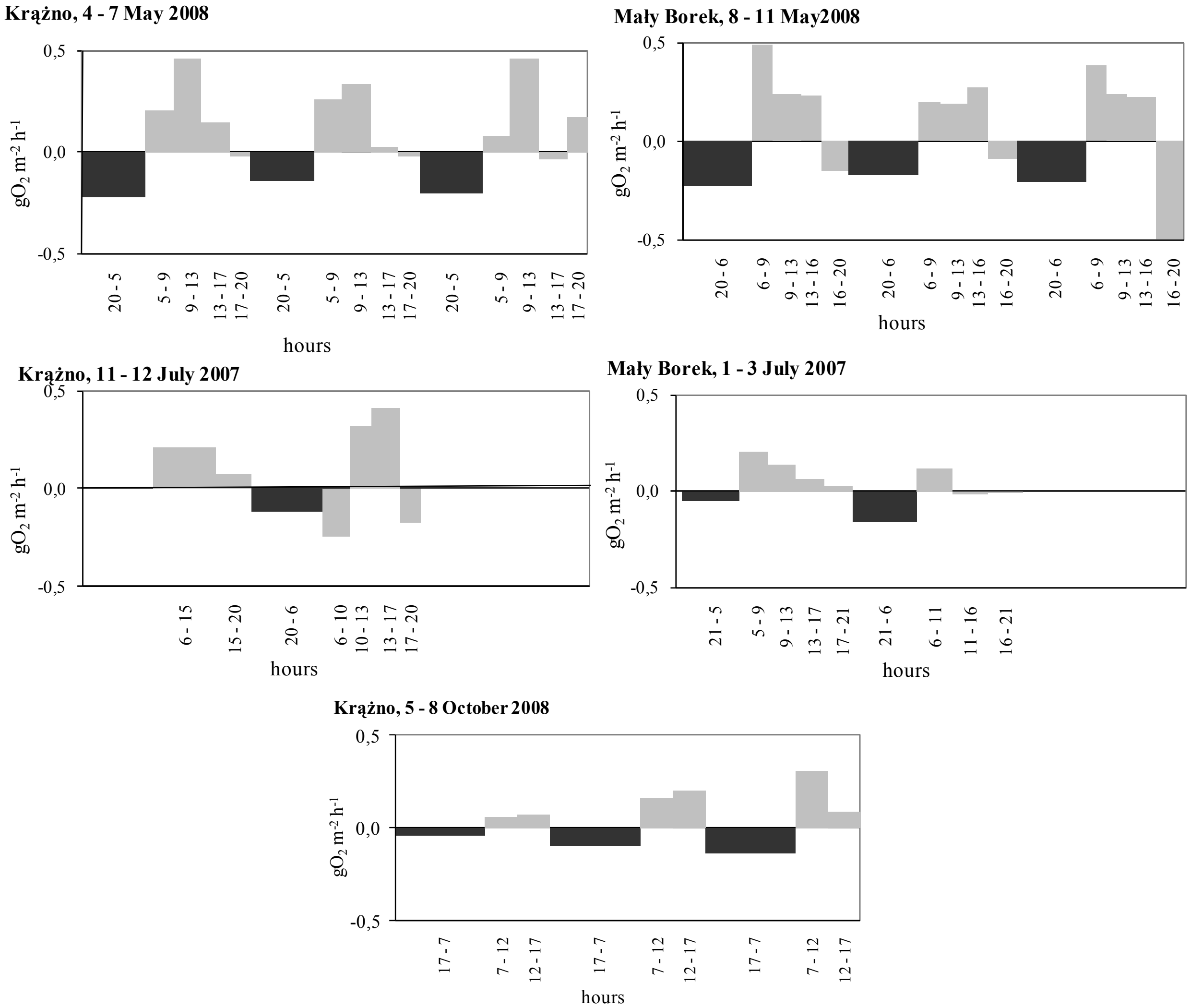

Fig. 6. Rates of oxygen concentration changes ($gO_2 \cdot m^{-2} \cdot h^{-1}$) in lakes Krążno (left) and Mały Borek (right); dark columns are night.

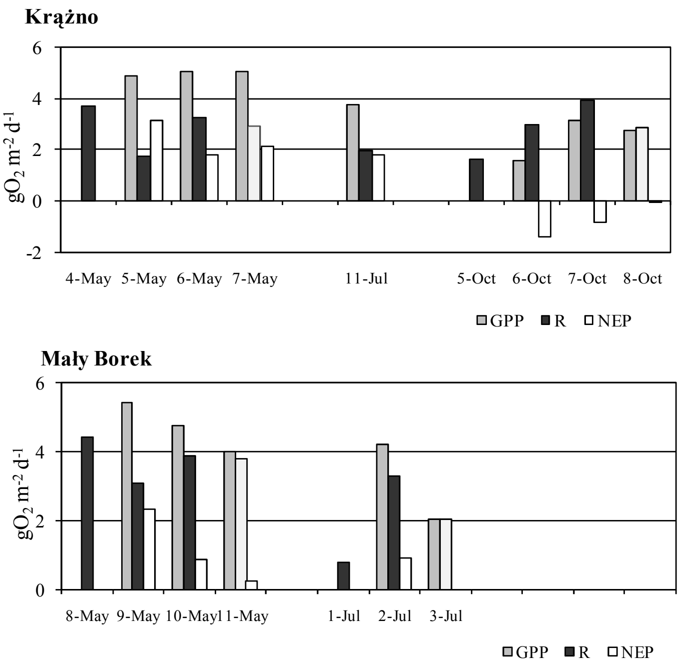

Fig. 7. Production and respiration in lakes: Krążno (top) and Mały Borek (bottom).
GPP – gross primary production, R – respiration, NEP – net ecosystem production; (May and October – data from 2008, July – data from 2007).

layer would have no effect on the GPP value, and the maximum level at which GPP was stabilized would indicate its true value. Likewise, with respect to respiration, it should be expected that the value of R per lake area unit will increase as the integration layer is thicker, but stabilization of R should not take place until the depth at which oxygen resources are depleted.

Figs. 8 and 9 show how values of GPP and R in the two analyzed lakes changed as the thickness of the data integration layer increased. The irregular shape of many curves, and especially sometimes a visible apparent decrease in the values of GPP and R with an increase in the thickness of the integration layer, reflects a strong effect of the physical factors that disturbed the picture of daily oxygen concentration changes generated by the biological processes. However, within the depth range corresponding to the production layer (in which we are particularly interested), the course of the curves reflects to a large degree the theoretical considerations. In Krążno Lake the GPP values on all the days of observations in May changed in a similar manner down to the integration depth of 4 meters, and at a depth of 4 to 5 meters they approached the level of stabilization (Fig. 8). The GPP values at that depth of integration were nearly two-fold higher (1.7-2.7-fold) than the values obtained at a depth of integration corresponding to the epilimnion layer (about 2 m). In July and October, the GPP curves reached the stabilization level at an integration depth of 4 and 6 m, respectively, which corresponded to the thickness of the epilimnion. However, no oxygen maximum appeared in the metalimnion of Krążno during those months. In Mały Borek Lake, in May, the GPP values approached the stabilization level at the integration depth of about 6 m, and in July – at 4-5 m (Fig. 9). These values were 2.8-3.6-fold in May and 1.2-1.9-fold higher in July than the GPP values obtained at the integration depth corresponding to the thickness of the epilimnion (2 and 3 m, respectively).

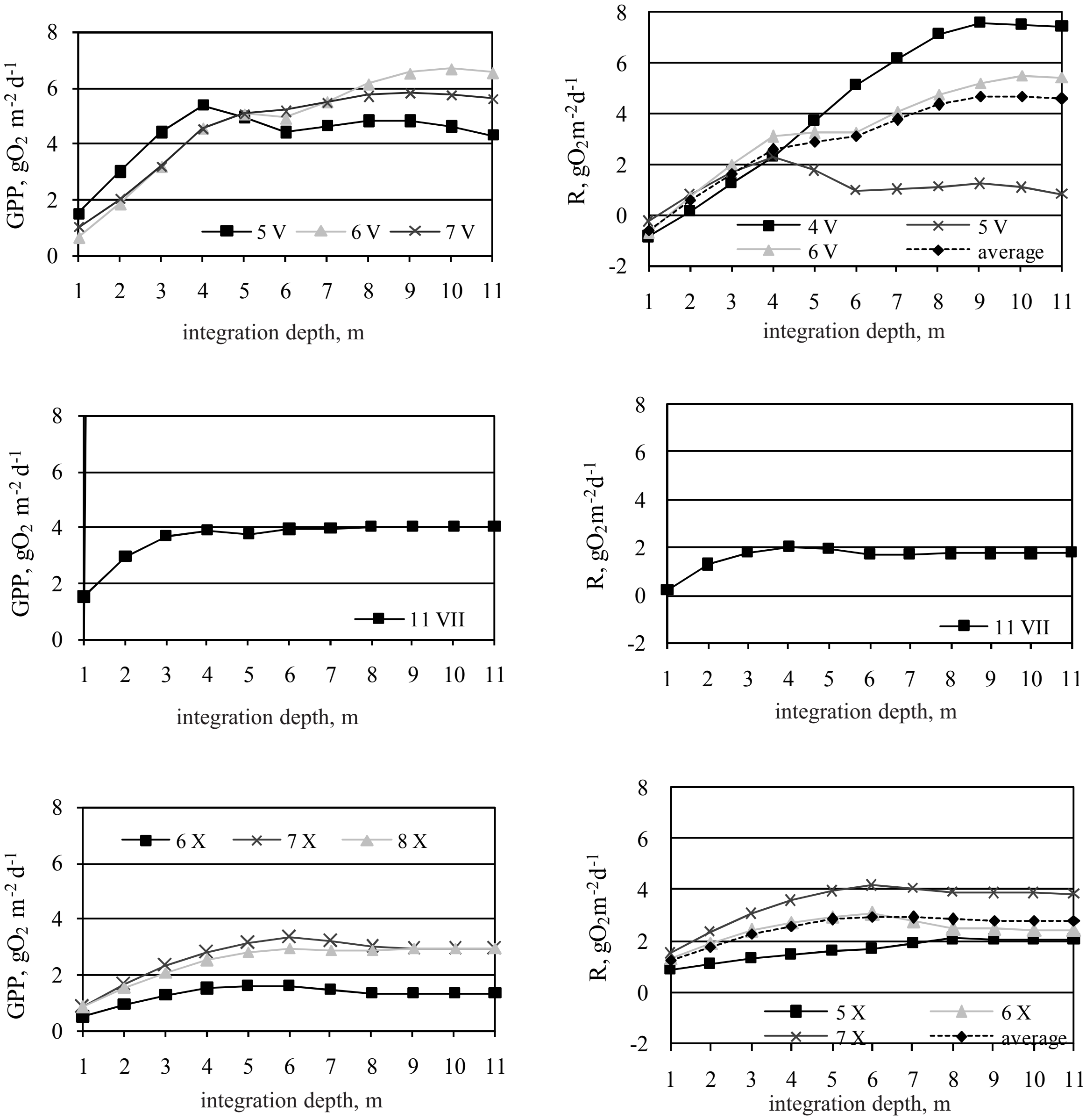

Fig. 8. Dependence of GPP and R values on the depth of data integration in lake Krążno; (May and October – data from 2008, July – data from 2007).

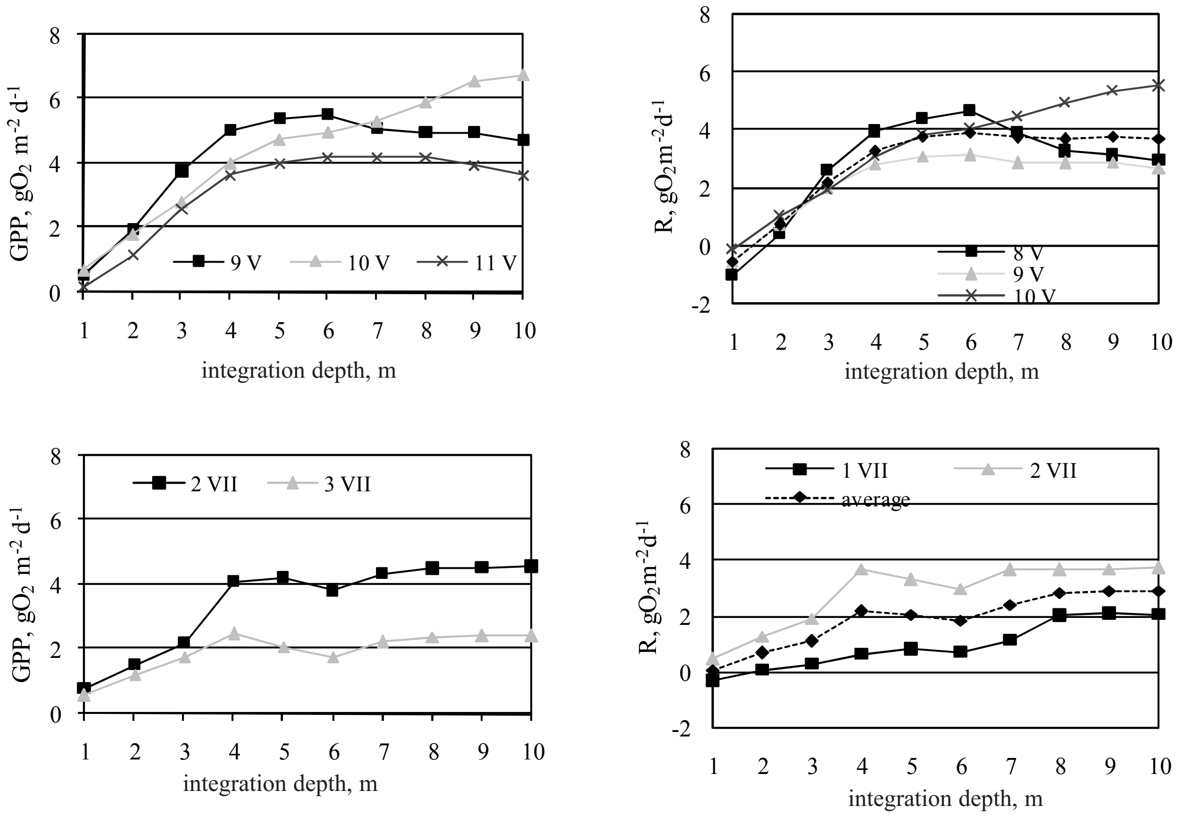

Fig. 9. Dependence of GPP and R values on the depth of data integration in Lake Mały Borek (May – data from 2008, July – data from 2007).

In all cases, stabilization of the GPP value took place when the depth of the integration layer corresponded to the thickness of the production layer, which in May and July coincided with the depth of the isopleth of 100% oxygen saturation.

With respect to respiration, the disturbances made it practically impossible to determine the depth of integration at which the value of R would be stabilized (Figs. 8, 9). However, in May the values of R integrated down to the reach of the production layer in Krążno Lake were 2- to 5-fold, and in Mały Borek Lake 4- to 4.5-fold higher than the ones integrated within the reach of the epilimnion layer. In July, an analogous difference in Mały Borek Lake was that of 1.7-1.9-fold. Thus, it becomes clear that when the thermocline lies shallow, which is fairly common in spring, much of the primary production and respiration can take place in the metalimnion.

The graphs illustrating the dependence between the value of respiration and the depth of data integration show an interesting fact, namely a negative value of R at the smallest, 1-meter deep integration depth, which occurred in May in both lakes and in July with respect to one measurement taken in Mały Borek Lake. As concentrations of oxygen in the surface layer were invariably depressed at night, this negative value could be a consequence of some overestimation of the intensity of oxygen release to the atmosphere. In such a case R would be underestimated but the error will have no effect on the estimation of GPP [20]. It is, however, possible that a negative value of respiration at a 1-meter depth of the integration layer is a calculation artefact, originating from the fact that oxygen losses from the surface layer were quickly replenished by diffusion of oxygen from deeper layers, which raised the concentration of oxygen near the water surface. This issue could be better elucidated by direct measurements of gas exchange with the atmosphere.

In 2004-05, the primary production in Mały Borek was measured using the oxygen method of clear and dark bottles [33]. The results obtained in 2004-05, compared with the present data for the same season and under similar light conditions, were very close. It is evident, therefore, that in small water bodies the free-water method as applied in this study enables us to obtain results of GPP, R and NEP comparable to the ones obtained with the traditional method. However, the metalimnion should be included in measurements, especially in the first half of the vegetative period, as a large part of primary production and respiration may take place in this water layer. Advantages of the applied method comprise whole-system measurements (in contrast to discrete sample measurements in the clear and dark bottles methods), simpler and less time-consuming procedure and elimination of distortions caused by enclosing small amounts of water in bottles. Among the drawbacks are the disturbances in the metalimnion caused by internal seiches, uncomfortable times of the day when measurements have to be taken, and the applicability of the method limited to small water bodies, in which a sufficient number of measurements can be taken within a relatively short time.

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