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Indicators of Changes in the Phytoplankton Metabolism in the Littoral and Pelagial Zones of a Eutrophic Lake

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1. Introduction

Gross primary production (GPP) is defined as the total autotrophic conversion of inorganic carbon to organic forms, independent of its fate. Ecosystem respiration (R) is the total oxidation of organic carbon to inorganic carbon by both the heterotrophic and autotrophic organisms. Net ecosystem production (NEP) is the difference between GPP and R, and reflects the balance between all anabolic and catabolic processes [26]. Ecosystems in which photosynthesis exceeds total respiration (P>R) are net autotrophic. They are net sinks for CO_2 and net producers of O_2 and organic matter. Inversely, wherever respiration exceeds photosynthesis (P<R) ecosystems are net heterotrophic. They are net sources of CO_2 and net consumers of organic carbon [2].

There are many reports about the role of phytoplankton, macrophytes or benthos in total metabolic activity [16–18, 21, 22, 31], but the contribution of a single component to total metabolic activity in a littoral zone or the relationship between contribution of littoral and pelagial zones to the whole lake's metabolism have been less frequently investigated [23]. The littoral is an important place where water self-purification takes place, and it also acts as a buffer for the pelagial, protecting it from pollution [3, 11]. The littoral is also the zone where intensive processes of phytoplankton primary production occur, and this freshly produced

organic matter can stimulate metabolic activity not only in the littoral zone but also in a whole lake. Thus, understanding the dynamics of phytoplankton metabolism in both the littoral and pelagial zones and the factors responsible for these changes can be essential to the control of lake trophic status, especially under conditions of climate change [9]. Currently, one of the most severe threats to water quality is uncontrolled growth of phytoplankton, specially toxic cyanobacterial algae. Warmer spring and summer, the occurrence of windless periods and lack of ice cover might intensify shifts in the taxonomic structure and phytoplankton growth rate, thus affecting the pace of successional changes in lake water. Long-term studies on seasonal changes of Kortowskie Lake's phytoplankton have revealed that the algal taxonomic structure and progressing phytoplankton development in the epilimnion of this lake have shifted. The community of blue-green algae limited the development and stability of other plankton groups, induced an earlier regression of diatoms in spring and their weaker development in autumn, and successfully competed with the remaining phytoplankton taxa in summer [14].

Aquatic ecosystem metabolism has been determined with a variety of methods: diel O_2, TCO_2, oxygen isotopes, ecosystems budgets and incubations. All these methods vary widely in precision or temporal/spatial scale and differ in their capability to measure gross or net processes. There is no perfect single method, but the variety and flexibility of the methods make them applicable to research on streams, rivers, lakes, estuaries and oceans [5, 26]. New statistical and modeling approaches based on the diel O_2/DIC technique have been used to account for the mixing of O_2 due to tides, wind or flow and to estimate metabolic properties [4, 10, 13]. The diel variation of DO or CO_2 measured with *in situ* sensors may not distinguish plankton metabolism from non-plankton and/or non-biological processes, such as photochemical oxidation of dissolved organic matter or epilimnetic sediment respiration [1]. To avoid any such misinterpretations, we have used the light-and-dark bottle method to estimate the phytoplankton primary production, respiration and P:R ratio.

The aim of this study has been to describe how phytoplankton metabolism varies from day to day and between the littoral and pelagial zones of a eutrophic lake. Another goal has been to determine meteorological and hydrochemical variables which control the dynamic of PP

and R processes. These comparisons can provide unique information about the factors which induce rapid growth of phytoplankton, especially toxic cyanobacterial blooms.

2. Material and methods

2.1. Study site

Kortowskie Lake is located in the agglomeration of Olsztyn, in the Masurian Lake District (Poland), and is one of the most thoroughly investigated lakes in Europe. Selective withdrawal of hypolimnetic water, the first lake restoration method in the world, was started in this lake in 1956. The surface outflow was dammed and a pipe was laid at the bottom of the lake. Its inlet was located in the deepest, southern part of the lake, and its outlet – at the outflow from the water body [8] (Fig1). The restoration of Kortowskie Lake is continued, and multiyear studies supply very important data to analyze the changes in aquatic ecosystem. The surface of the lake is 89.7 ha and the maximum depth is 17.2 m (Tab. 1). The catchment area of the lake is 35.5 km^2: 48.4% – forest, 32.3% – agricultural land, 7.4% urban land, and 11.9% water [19].

Tab. 1. The morphometric and limnological characteristic of Kortowskie Lake
Tab. 1. Charakterystyka morfometryczna i limnologiczna Jeziora Kortowskiego

Parameter	
Surface area (ha)	89.7
Volume (mln m^3)	5.323
Maximum depth (m)	17.2
Maximum length (m)	1.660
Maximum width (m)	715
Shoreline length (m)	4.800
Limnological type	Dimictic

2.1. Sampling

Samples were collected daily on Kortowskie Lake, between 31 July and 12 August 2010 from the littoral – in the zone of emergent plants) (station 1) and pelagial – in the deepest part of the lake (station 2). Both stations were located in the same part of the lake in order to ensure similar environmental conditions (Fig. 1). A 4-liter (50 cm length) sam-

pler was used to collect water from 0.5 m depth. Immediate, for each sample the triplicate light- and dark-glass bottles were filled by siphoning from the sampler and placed in situ by hanging from the buoy at 0.5 m depth in the littoral and pelagial zones. Water samples for chemical analyses, in polyethylene 2-liter containers, were transported to the laboratory within no longer than 2 h.

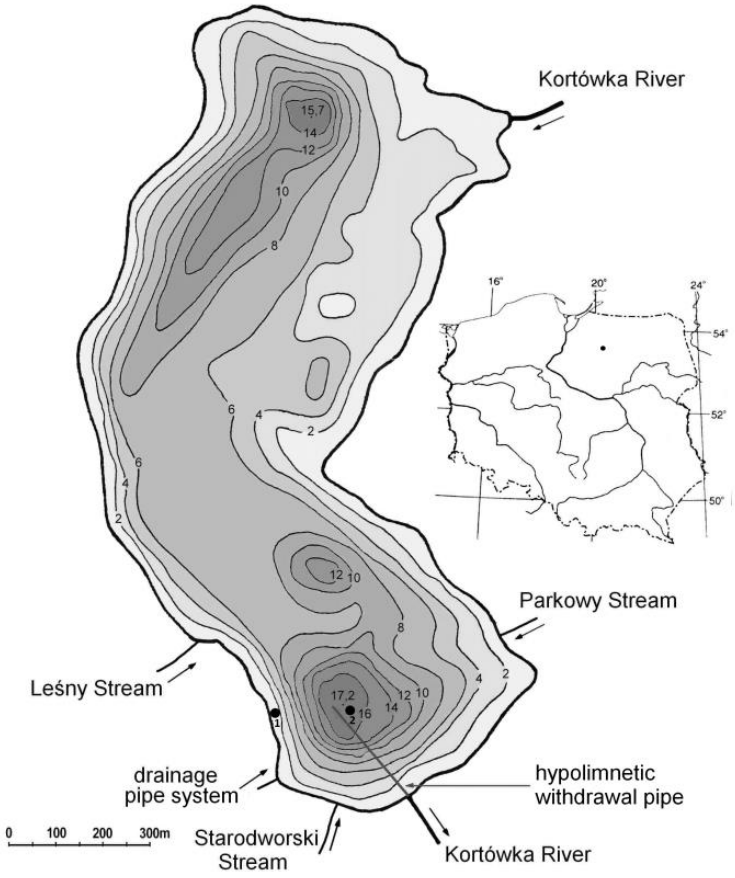

Fig. 1. Kortowskie Lake with marked the stations of metabolism measuring: station 1 – littoral zone, station 2 – pelagial zone
Rys. 1. Jezioro Kortowskie z zaznaczonymi stanowiskami pomiaru metabolizmu: stanowisko 1 – strefa litoralu, stanowisko 2 – strefa pelagialu

2.2. Primary production and respiration

Phytoplankton primary production and respiration were determined by the dissolved oxygen method described by Strickland & Parsons [28] in 300-ml triplicate light- and dark-glass bottles. Samples were incubated for 24 h *in situ* at 0.5 m in the sites where the water had been collected. The time-zero samples, which provided a measure of initial oxygen concentration, were fixed immediately. The oxygen concentrations were measured using a YSI 58 oxygen probe. The primary production rates were calculated using the formula for gross production rate given in Strickland & Parsons [28]:
P = [(light bottle) – (dark bottle)] / time and expressed as g $O_2 \cdot m^{-2} \cdot d^{-1}$.

2.3. Other measurements

Unfiltered water samples were analyzed for total organic carbon (TOC) content, and water filtered through a 0.45 μm Millipore filter was analyzed for DOC. Particulate organic carbon (POC) was calculated as the difference between TOC and DOC. Analyses were done by high-temperature combustion (HTC) using a Shimadzu TOC 5000 analyzer [7]. Total phosphorus (TP) and nitrogen (TN) were determined according to Standard Methods [27]. Colorimetric analyses were conducted on a Shimadzu UV 1601 spectrophotometer. Chlorophyll a was marked by spectrophotometry with correction for pheopigments (PN-86/C-05560/02). Temperature and dissolved oxygen (DO) were recorded *in situ* by a YSI 58 oxygen probe. pH was measured with an Orion pH meter of the Ross type.

Meteorological data were collected near Kortowskie lake, at a weather station operated by the Institute of Meteorology and Water Management.

2.4. Statistical analyses

To assess normality of data distribution, Shapiro-Wilk test was employed. Variance homogeneity was tested with F test. Data sets meeting both above conditions were tested for statistically significant differences with parametric t-test. Mann-Whitney U test was used for the other. Significance level of $p < 0,05$ was used. Simple relationships between metabolic rates and meteorological and chemical variables were

evaluated using Pearson's correlation analysis. Correlations were tested as significant at $p < 0.05$.

3. Results

3.1. Variation in primary production and respiration rate

The rate of gross primary production (GPP) in the littoral zone varied from 8.12 to 20.51 g $O_2 \cdot m^{-2} \cdot d^{-1}$ and in the pelagial from 9.19 to 20.98 g $O_2 \cdot m^{-2} \cdot d^{-1}$. The lowest rate was observed on the eleventh day of the experiment in the littoral and on the eighth day in the pelagial, while the highest rate, respectively: on the second and on the first day. In respect of the mean values for the whole study period, significantly higher rate of GPP was observed in the pelagial zone than in the littoral (respectively 15.20 and 11.61 g $O_2 \cdot m^{-2} \cdot d^{-1}$) (t-test, $p < 0.05$). In the littoral, the production rate significantly decreased during the first four days, and then remained on a relatively equal level. In the pelagial, GPP increased slightly on the second day and then, until the end of the study period varied sinusoidally, on average every two days (Fig. 2).

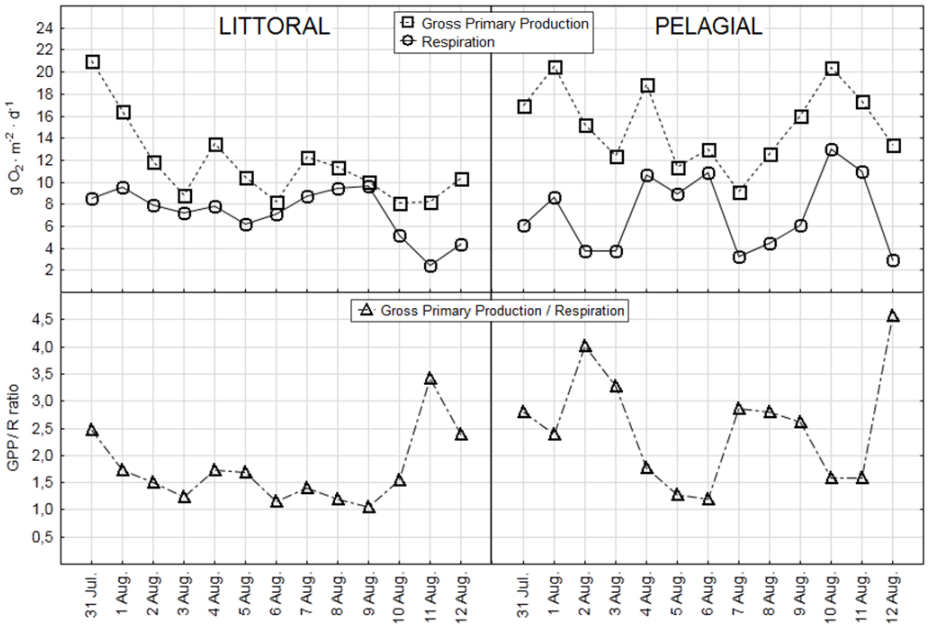

Fig. 2. Daily variability of gross primary production and respiration
Rys. 2. Dobowa zmienność produkcji pierwotnej brutto i respiracji

The rate of respiration (R) during the study varied in the range from 2.42 to 9.68 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in the littoral and from 2.94 to 12.96 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in the pelagial. The minimum value was determined on the twelfth day of the experiment in the littoral and on the thirteenth day in the pelagial. The highest respiration was observed on the tenth and ninth day. The average values in both zones were similar, respectively: 7.25 and 7.19 g $O_2 \cdot m^{-2} \cdot d^{-1}$. Although, mean respiration in the littoral and pelagial for the whole study period was not statistically significant (t-test, $p < 0.05$), daily fluctuations were higher in the pelagial zone (Fig. 2).

The ratio of GPP to R was less changeable in the littoral and oscillated around 1.0–1.7, except the twelfth day of the experiment, when it reached 3.4. In the pelagial GPP/R ratio varied dynamically (from 1.2 to 4.6) and was much higher than in the littoral (Fig. 2).

3.2. Variations in organic carbon concentration

The total organic carbon (TOC) concentration varied in the range from 11.37 to 14.79 mg·dm^{-3} in the littoral and from 10.64 to 12.65 mg·dm^{-3} in the pelagial. The lowest value was found on the first day of the experiment in the pelagial and the highest one – on the seventh day in the littoral. Although, mean TOC, DOC and POC values measured in the littoral were not statistically significant comparing to those found in the pelagial zone (U-test, $p < 0.05$), the fluctuations of organic carbon from day to day were higher in the littoral zone. Higher TOC values were observed on the first, fourth, seventh and the last two days of the experiment. In the pelagial, the concentrations remained on a similar level and oscillated around 12.0 mg·dm^{-3} (Fig. 3).

The dissolved organic carbon (DOC) concentration in the littoral ranged from 8.26 mg·dm^{-3} (the third day of the experiment) to 10.30 mg·dm^{-3} (fifth day), and in the pelagial from 8.19 mg·dm^{-3} (third day) to 9.60 mg·dm^{-3} (thirteenth day). The daily variability of DOC concentrations were higher in the littoral than in the pelagial (Fig. 3). A similar variation was also found in the particular organic carbon (POC) concentration. The lowest value of POC (2.06 mg·dm^{-3}) was observed on the last day of the experiment in the pelagial and the highest (5.78 mg·dm^{-3}) on the eleventh day in the littoral. The average POC content in the littoral was 3.69 mg·dm^{-3}, which accounted for 30% of the TOC, and in the pelagial 3.07 mg·dm^{-3} (35% TOC). The changes of POC concentration in

the littoral during the studied period had the cyclical character (the values increased, and then decreased at 3–4 days intervals) (Fig. 3).

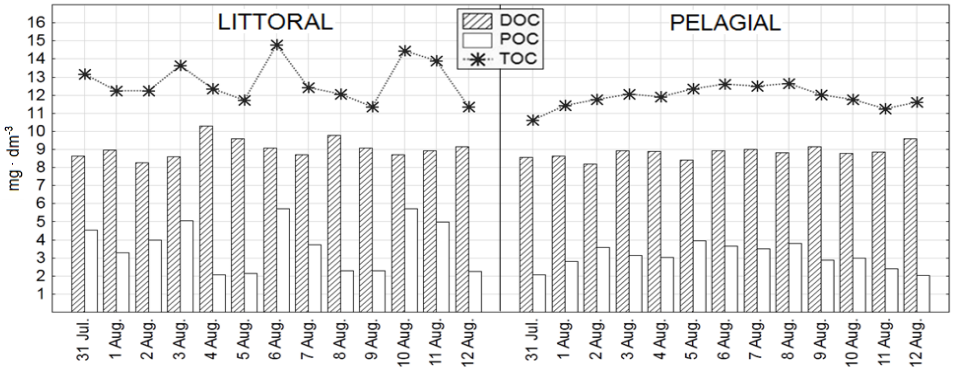

Fig. 3. Daily variability of TOC, DOC and POC concentration
Rys. 3. Dobowa zmienność stężeń TOC, DOC i POC

3.3. Variations in chlorophyll and nutrients concentration

Total chlorophyll content (chlorophyll *a* + pheophytin) ranged from 19.44 to 40.17 mg·m^{-3} in the littoral and from 20.60 to 40.14 mg·m^{-3} in the pelagial. Pheophytin dominated in both zones, making up approximately 70% of the total chlorophyll. In the littoral, the lowest values were observed on the second and seventh day of the experiment, respectively 5.2 mg·m^{-3} and 7.9 mg·m^{-3}, and the highest ones appeared on the fifth and ninth day (respectively, 27.4 and 27.5 mg·m^{-3}). In the pelagial, pheophytin concentration varied from 10.1 mg·m^{-3}on the third day to 34.5 mg·m^{-3} on the ninth day.

The average content of pheophytin during the studied period was 18.9 mg·m^{-3} in the littoral and 22.3 mg·m^{-3} in the pelagial. Chlorophyll *a* concentration varied in the range from 4.0 mg·m^{-3} (day 12) to 21.5 mg·m^{-3} (day 2) in the littoral and from of 5.7 mg·m^{-3} (day 9) to 17.0 mg·m^{-3} (day 5) in the pelagial. The average content of chlorophyll *a* in the littoral was 9.7 mg·m^{-3} and 7.0 mg·m^{-3} in the pelagial. In both zones, a very high variability of chlorophyll *a* and pheophytin was observed. Values increased and then decreased at intervals of 2–3 days (Fig. 4). Mean chlorophyll *a* and pheophytin values measured in the littoral were not statistically significant comparing to those found in the pelagial zone (t-test, $p < 0.05$).

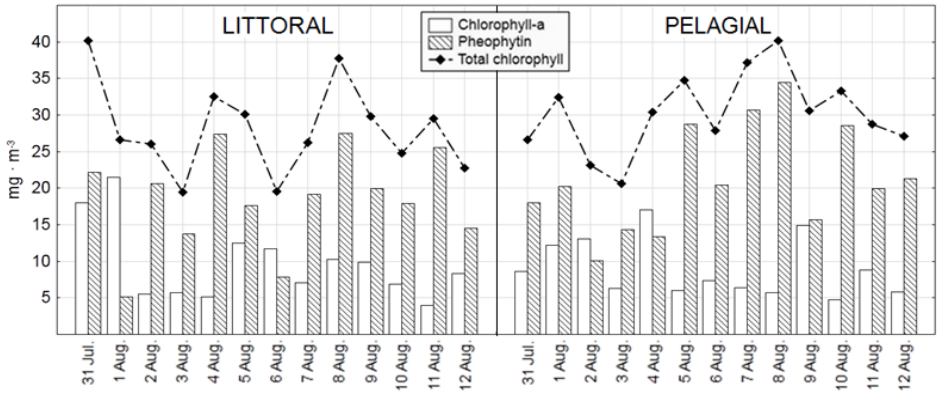

Fig. 4. Daily variability of total chlorophyll, chlorophyll-a and pheophytin concentration

Rys. 4. Dobowa zmienność stężeń chlorofilu całkowitego, chlorofilu a oraz feofityny

Total nitrogen concentration varied in the range from 1.89 to 2.76 mg·dm^{-3} in the littoral and from 1.25 to 2.90 mg·dm^{-3} in the pelagial (Fig. 5). In the littoral, minimum values were determined on the fourth and seventh day and maximum ones – on the ninth and eleventh day. In the pelagial, the lowest and the highest values were recorded on the sixth and the eleventh day, respectively. The daily variability of total nitrogen concentrations was similar in both zones with the exception of the sixth day, when the concentrations decreased rapidly in the pelagial and increased in the littoral. The average total nitrogen content in both zones was almost identical (in the littoral – 2.34 mg·dm^{-3} and pelagial – 2.22 mg·dm^{-3}).

Total phosphorus concentration in both zones varied in the same range (from 0.08 mg·dm^{-3} to 0.15 mg·dm^{-3}) (Fig. 5), but the distribution of concentrations on each day was different. In the littoral, the lowest value was determined on the eleventh day, and in the pelagial on the first day; the maximum values were detected in both zones on the ninth day of the study. Greater daily variability was observed in the pelagial. TP concentrations increased and decreased at intervals of 2–3 days. In the littoral, TP concentration gradually increased until the ninth day, than the concentration rapidly decreased on the eleventh day and then kept increasing again until the end of the study (Fig. 5). Mean TN and TP concentration were not statistically significantly different in both examined zones (t-test, $p < 0.05$).

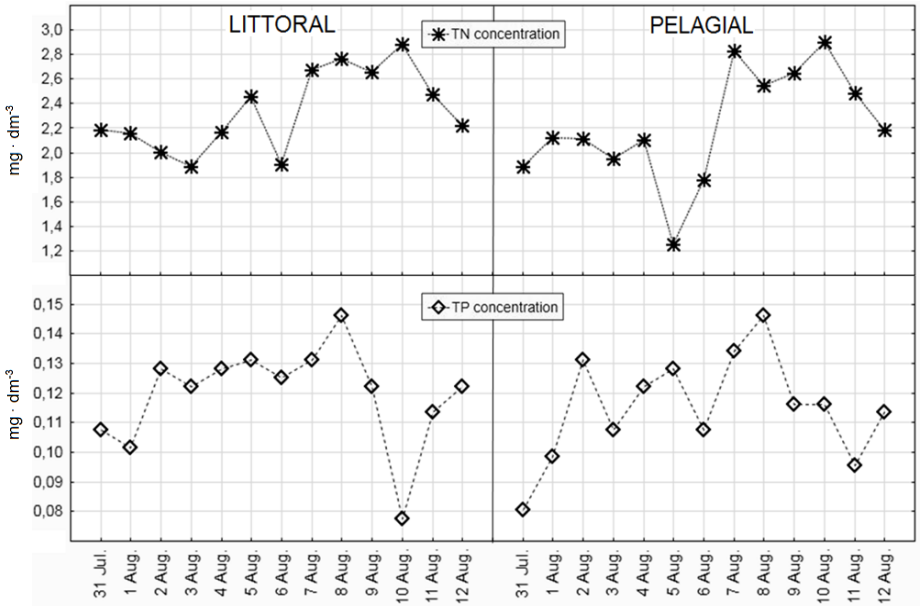

Fig. 5. Daily variability of total nitrogen and phosphorus concentration
Rys. 5. Dobowa zmienność stężeń azotu i fosforu całkowitego

3.4. Variations in pH, temperature and oxygen concentration

pH in both zones changed in an almost identical range (respectively from 7.82 to 8.37 in the littoral and from 7.91 to 8.36 in the pelagial). pH increased significantly on the second day and then remained on a similar level until the tenth day. Slightly higher daily variability was observed in the littoral. In the pelagial, during nearly all the period, the pH value oscillated around 8.3 (Fig. 6).

Temperature in both zones was very similar. The lowest temperature was found at the beginning of the study (22.5ºC in the littoral and 22.2ºC in the pelagial). On the fourth day, temperature reached the maximum value (24.1ºC in both zones), but decreased rapidly during the next two days, and then remained on a relatively stable level, oscillating around 22.5–23.5ºC (Fig. 6).

Dissolved oxygen concentration in both zones was similar and ranged from 9.17 to 11.35 $mg \cdot dm^{-3}$ in the littoral and from 9.30 to 11.73 $mg \cdot dm^{-3}$ in the pelagial. The lowest dissolved oxygen concentration was observed during the first day of study, and the highest occurred on the seventh day. The dynamics of dissolved oxygen concentration changes in

the both zones was similar. The biggest difference between the littoral and pelagial was found on the third day, when it reached 1.5ºC (Fig. 6).

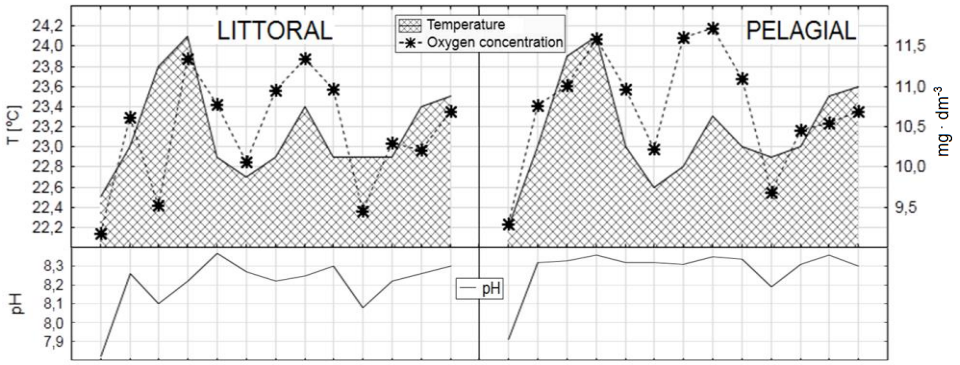

Fig. 6. Daily variability of pH, temperature and dissolved oxygen concentration
Rys. 6. Dobowa zmienność pH, temperatury i stężeń tlenu rozpuszczonego

4. Discussion

The distinct daily variability of the phytoplankton primary production and respiration rate in the littoral and pelagial zones of Kortowskie Lake showed a high dynamics of metabolic processes in the whole lake. Slightly but significantly higher primary phytoplankton production was found in the pelagial comparing to the littoral zone, where the respiration processes were also more dynamic. These differences were confirmed by statistical analysis (t-test, $p < 0.05$).

With high nutrient availability in both zones of Kortowskie Lake, no factors limiting phytoplankton growth were present. No statistically significant relationship between GPP and water chemical indicators and meteorological data was observed. In the pelagial zone, more important was the amount of organic carbon (correlation between GPP and TOC was $r = -0.62$, $n = 13$, $p < 0.05$). Numerous studies confirm that released organic carbon may constitute from 1 to 70% of primary production [20, 24, 30], and the most important mechanism of enrichment is intravital secretion of intermediates and end-products of photosynthesis [25]. Furthermore, the amount of dissolved organic carbon may regulate the primary production by direct impact on live organisms (especially algal cells), e.g. by changing the cellular membrane structures, affecting active transport and stimulating

the production of storage substances [4, 12, 15, 18]. Strong correlation between the GPP daily variability and TOC concentration verifies that organic carbon in the pelagial is possibly among the best indicators of metabolic processes. Organic matter produced as a result of high phytoplankton activity at the beginning of the study caused the TOC concentration increase in the following days. Fresh (labile) organic matter was immediately mineralized. As a result, CO_2 re-intensified the photosynthetic process. This was confirmed by the primary production increase with a simultaneous TOC decrease. Production and degradation processes in the pelagial were cyclical (the changes followed every 5 days). Presumably, the dynamics of metabolism in the pelagial will be more strongly determined by the amount of released easily available organic matter derived from primary production rather than by the nitrogen ($r = 0.2$, $n = 13$, $p < 0.05$) and phosphorus ($r = -0.47$, $n = 13$, $p < 0.05$) availability. The studies by Tank et al. [29] confirm that the metabolic balance in ecosystems is sensitive to inputs and outputs of organic matter.

In turn, the respiration rate in both zones of Kortowskie Lake depended on different factors. In the littoral zone it was the wind direction ($r = 0.57$, $n = 13$, $p < 0.05$). This effect was assumed to have been related to the amount of autochthonic organic matter which was produced in the pelagial and drifted to the south-western part of the lake, where the sampling station was located. Thus, the amount and rate of respiration in the littoral of Kortowskie Lake depended largely on the primary production volume in this zone and pulsating delivery of organic carbon from the pelagial. The rate of respiration in the pelagial zone was determined by the air temperature ($r = -0.57$, $n = 13$, $p < 0.05$) and precipitation ($r = 0.61$, $n = 13$). Daily changes in air temperature are one of the most important factors affecting the vital functions of organisms and chemical reactions, and thus may regulate the organic carbon cycle in a water column [6, 11, 12], which was confirmed by this study.

In Kortowskie Lake, the rates of primary production and respiration changed by more than 40% overnight, while the content of TOC remained on a fairly constant, even level. This relationship can be used for water quality monitoring. The measurement of phytoplankton primary production with the light- and dark-glass bottles method during one day does not show the actual metabolic processes in a whole lake. This result reflects only GPP and R at a given moment and place of water sampling. Thus, TOC can be a better and more stable indicator of the daily variabil-

ity of phytoplankton metabolism. Any substantial change of TOC concentrations in the pelagial in combination with meteorological data should be a signal to undertake broader research in order to capture changes responsible for the rapid phytoplankton growth, especially toxic cyanobacterial blooms. In the littoral zone, chlorophyll *a* content is a better indicator of metabolic changes (correlation between GPP and chlorophyll *a* was $r = -0.67$, $n = 13$, $p<0.05$). Comperative studies across nutrient regimes and latitudes of different climates, may allow us to prepare a model of daily pytoplankton metabolic balance, which could be used in programmes of water protection engineering.

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Wskaźniki zmian metabolizmu fitoplanktonu w strefie litoralu i pelagialu jeziora eutroficznego

Streszczenie

Badania przeprowadzono na eutroficznym Jeziorze Kortowskim położonym w granicach administracyjnych miasta Olsztyn (Pojezierze Mazurskie). Próbki wody do analiz pobierano codziennie w okresie od 31 lipca do 12 sierpnia 2010 roku w strefie litoralu (w pasie roślin wynurzonych) oraz w strefie pelagialu (w najgłębszej części jeziora). Badania obejmowały wielkość produkcji pierwotnej oraz respirację metodą jasnych i ciemnych butelek. Dodatkowo analizowano parametry fizyko-chemiczne wody oraz dane meteorologiczne. Wyraźna dobowa zmienność tempa produkcji pierwotnej fitoplanktonu i respiracji w obu badanych

strefach świdczyła o dużej dynamice procesów metabolicznych zachodzących w całym jeziorze. Nieco wyższą produkcję pierwotną fitoplanktonu stwierdzono w pelagialu, tutaj też procesy respiracji były bardziej dynamiczne. Przy dużej dostępności substancji biogennych w pelagialu Jeziora Kortowskiego o dynamice produkcji pierwotnej w większym stopniu decydowała ilość uwolnionej łatwo przyswajalnej materii organicznej, pochodzącej z produkcji pierwotnej, aniżeli dostępność azotu ($r = 0,20$, $n = 13$, $p < 0,05$) czy fosforu ($r = -0.47$, $n = 13$, $p < 0,05$). Brak istotnych statystycznie zależności pomiędzy GPP a wskaźnikami chemicznymi wody czy danymi meteorologicznymi świadczył, że w jeziorze nie było czynników ograniczających rozwój fitoplanktonu. Produkcja pierwotna fitoplanktonu dominowała w całym okresie badawczym. Czynniki zewnętrzne miały natomiast większy wpływ na wielkość i tempo respiracji. W litoralu istotne znaczenie miała pulsacyjna dostawa labilnego węgla organicznego, w pelagialu zaś temperatura powietrza oraz wielkość opadów atmosferycznych. Interesujący jest fakt, że w Jeziorze Kortowskim z dnia na dzień tempo produkcji pierwotnej i respiracji zmieniało się nawet o ponad 40%, natomiast zawartość TOC utrzymywała się na dość stałym, wyrównanym poziomie. Zależność ta może być wykorzystana w monitoringu jakości wód. Pomiary produkcji pierwotnej fitoplanktonu metodą jasnych i ciemnych butelek w danym dniu nie odzwierciedlają rzeczywistych procesów metabolicznych w całym jeziorze. Jest to wynik adekwatny do danej chwili i miejsca poboru próbek wody. Zatem lepszym i bardziej stabilnym wskaźnikiem nawet dobowej zmianności metabolizmu fitoplanktonu może być TOC. Każda istotna zmiana stężeń TOC w pelagialu w powiązaniu z danymi meteorologicznymi powinna być sygnałem do szerszych badań w celu uchwycenia zmian odpowiedzialnych za gwałtowny rozwój fitoplanktonu, a szczególnie uciążliwych zakwitów sinicowych. Przeprowadzenie tego typu badań porównawczych w regionach różniących się ilością substancji biogennych oraz w różnych strefach klimatycznych, umożliwiłoby opracowanie modelu dobowej równowagi metabolicznej fitoplanktonu, który mógłby być wykorzystany w programach ochrony wód.