FACTORS CONTROLLING PELAGIC PRODUCTION AND RESPIRATION IN A SHALLOW POLYMICTIC LAKE

ABSTRACT: Shallow lakes, defined as ‘non-stratifying,’ polymictic water bodies are usually eutrophic and highly productive, and more turbid than deeper lakes due to bottom sediment resuspension. Gross primary production (GPP) and total planktonic community respiration (TCR) were measured in a very shallow (on average 1.2 m deep) and large (area 25 km²), polymictic, eutrophic Lake Gardno (Baltic coastal lake, Northern Poland) with the light-and-dark bottle method. The aim was to compare GPP to TCR ratio in the pelagic zone in a course of a year and identify factors governing these processes. Identified factors governing GPP were light conditions and temperature, with Q₁₀ = 2.23 in the 2–24.5°C temperature range, whereas TCR was driven by water temperature (Q₁₀ = 2.15 in the same temperature range) and by organic matter content in water. TCR was correlated with total suspended matter (effect of bottom sediment resuspension due to wind action in a very shallow lake), however not with chlorophyll content. During two-year measurement period (years 2006 and 2007), annual GPP amounted to 402 and 471 g C m⁻², and TCR amounted to 192 and 223 g C m⁻² respectively. Lake Gardno pelagic system seemed to be net autotrophic on annual basis; GPP to TCR ratio = 2.1. Part of the organic matter produced in pelagial is probably deposited in bottom sediments decomposed there. Wind induced resuspension increases matter content in water (measured here as TSM content) and thus contributes to pelagic respiration processes (TCR).

KEY WORDS: primary production, respiration, shallow lake, Lake Gardno

Most of shallow lakes, defined as ‘non-stratifying,’ polymictic water bodies – in which due to frequent resuspension bottom sediments support primary production in the euphotic zone – are eutrophic and highly productive (Padisak and Reynolds 2003, Scheffer 2004). They are more turbid than deeper lakes due to bottom sediment resuspension (unless they are dominated by submerged macrophytes that can reduce resuspension). Sediment resuspension also reduces light availability in the water column (Scheffer 2004). Nixdorf and Deneke (1997) studied shallow eutrophic lakes of different depth and morphometry in the northern part of Germany. ‘Very shallow’ lakes studied by the authors had much higher pelagic respiration compared to other shallow lakes.

In the present study we compared gross planktonic community production (GPP) and total planktonic respiration (TCR) in a coastal lake which we consider to be one of a ‘very shallow’ type, in order:

• to assess the effect of selected site factors (temperature, light)
• to assess the production to respira-
tion ratio in the pelagic zone in a course of a year, and
• to recognize whether intensive poly-
mixis that causes resuspension of
organic matter from the bottom de-
posits might contribute to the overall
production or respiration in the pe-
lagic zone.

Lake Gardno is one of the largest lakes
in Poland and is also one of the two largest
coastal lakes at the Polish coast of the Bal-
tic Sea. It is located in the northern Poland
(Pomerania) at the Baltic Sea coast (54°39´ N,
17°07´E) separated from the sea water by
a sandy bar. The lake is shallow (1.2–1.3 m
depth) and large (area 25 km\(^2\)) and the lake
volume amounts to 31 × 10\(^6\) m\(^3\) (Balicki
1981, Cyberski and Jędrasik 2003). The
lake is polymictic due to low depth and large
surface exposed to winds blowing over the
Baltic Sea. A few percent of the lake area is
covered by standing macrophytes like
\textit{Typha}
forming a belt along its shoreline. Some parts
of the bottom are also covered by submerged
macrophytes (\textit{e.g.} from genus \textit{Potamogeton}
and \textit{Myriophyllum}) (Kraska 2003).

Research carried out in the 1980s and at
present indicates that Gardno Lake is eutro-
phic with high nutrient concentration (aver-
geage values: total nitrogen 4 mg L\(^{-1}\); total phos-
phorus 0.4 mg L\(^{-1}\), Trojanowski 2003) and
high chlorophyll \(a\) content throughout the
whole vegetation season with average value of
87 μg Chl L\(^{-1}\). It receives most of the fresh wa-
ter inflow from the River Łupawa (the aver-
age flow of \(ca\) 8.2 m\(^3\) s\(^{-1}\)). The average annual
fresh water residence time amounts to about
41 days. The outflow of the lake is directly
connected with the sea through the
\(ca\) 2 km long channel; thus, the lake is partly brackish.
Because the Baltic Sea is tideless, sea water in-
trusions occur on irregular basis. Cyberski
and Jędrasik (2003) estimated the total sea
water inflow at about 0.57 m\(^3\) s\(^{-1}\).

Gross phytoplankton primary produc-
tion (GPP) and total planktonic community
respiration (TCR) were measured with use
of the oxygen light-and-dark bottle method,
with \textit{in situ} incubation lasting 24 h. Measure-
ments were performed twice a month in 2006
and once a month in 2007, from April 2006 to
November 2007 and one last measurement on
February 2008 (altogether 24 measurements).
The measurement point was located off-
shore to represent the most open and well
mixed area of the lake as determined by Ficek
and Wielgat-Rychert (2009). \textit{In situ} mea-
surements were carried out down to 1.2 m.
The water column was very homogeneous as
indicated by chlorophyll profiles (Ficek and
Wielgat-Rychert 2009), therefore water
for all incubations was sampled at one depth
only – just below the surface.

In 2006, transparent and dark bottles
were incubated at depths 0.0, 0.3, 0.6, and
1.2 m in triplicates. Starting from April 2007,
bottles were incubated at 10-cm depth inter-
vals down to 0.6 m depth and 20-cm intervals
down to 1.2 m depth and transparent bottles
were incubated in duplicates. Similarly, after
initial TCR measurements, number of TCR
bottles was reduced because no difference
along vertical profile was found (standard de-
vation (SD) is presented in Fig. 3 where inte-
grated TCR values are shown).

Before incubations, water was siphoned
\textit{via} a gas-tight tube into \(ca\) 120-ml glass Wink-
ker’s bottles. Oxygen was measured with a
standard Winkler technique and the mea-
surements started in the field where manga-
nous sulfate and sodium hydroxide-potassi-
um iodite mixture were added to the bottles
to stop biological processes.

Depth-integrated GPP and TCR were cal-
culated assuming a linear interpolation between
successive measurements down to the depth of
1.2 m. Production and consumption of oxygen
were transformed into carbon units (mg C m\(^{-2}\)
d\(^{-1}\)) with use of photosynthetic quotient, PQ = 1.2,
and conservative respiration quotient, RQ
= 1.0, the most typical values used for lakes sug-

Together with GPP and TCR measure-
ments, temperature, Secchi depth visibil-
ity, nutrient concentrations, total suspended
matter content (TSM), and conductivity were
measured in the surface layer. Chlorophyll
concentrations were measured according to
a standard spectrophotometric method with
acetone extraction without correction for
phaeopigments (Jeffrey and Humphrey
1975). In order to measure total suspended
matter, known volume of water was filtered
through pre-weighed Whatman GF/F filters
and weight again after drying the filters at
105°C to a constant weight.
Water temperature ranged from 2°C to 24.5°C (Fig. 1). Daily irradiance was measured at meteorological stations located ca 20 km in the southeastern direction. Mean daily wind speed during incubation days amounted to 2.8 m s\(^{-1}\) ranging from 1.9 to 4.4. The extreme blast of winds reached up to 24 m s\(^{-1}\). Extremely strong winds were measured on July 31, September 6, 2006, and November 12, 2007. Lake Gardno receives inflows of the sea water from the Baltic. During measurements, mean salinity (at incubation location) amounted to 0.64‰ (ranging from 0.14–1.6‰) (A. Jarosiewicz, personal communication). Secchi depth visibility was measured in the morning, at the onset of incubation. The average value amounted to 0.5 m (ranging from 0.15–1.1 m), and the average for the vegetation period (May-September) was 0.4 m.

Chlorophyll content was high during the whole year, also quite often in wintertime (Fig. 2). There was no regular seasonal pattern in chlorophyll content during vegetation season as is often the case in shallow lakes (Schefver 2004) where e.g. a clear-water phase is not always observed, especially in lakes with high chlorophyll content. The deepest dip in chlorophyll content during vegetation season was measured in June 2006 (30 μg Chl L\(^{-1}\)) however it is not clear if it can be attributed to the clear-water phase or to the low wind conditions (preceding this mea-
measurement date) that enhanced sedimentation of phytoplankton from the water column to the bottom (this chlorophyll minimum coincided with TSM minimum). Low chlorophyll values (as low as 10 μg Chl L⁻¹) were noted also in winter. Extremely high chlorophyll values were noted on the occasions directly after periods of very strong winds: in September 2006 (303 μg Chl L⁻¹) and November 2007 (200 μg Chl L⁻¹). The average value for the vegetation season amounted to 87 μg Chl L⁻¹. It should be noted that chlorophyll values measured here were not corrected for phaeopigments.

Total suspended matter (TSM) content in water (Fig. 2) changed according to a similar pattern as chlorophyll content; without a clear seasonal trend, from 7.6 mg L⁻¹ to 133 mg L⁻¹. Chlorophyll content correlated to the TSM content ($R^2 = 0.57$, $P = 0.0002$) as algae constituted a relatively constant part of the TSM.

More than two-thirds of the depth-integrated GPP took place in the upper 60 cm, however, distribution of the GPP along its vertical profile was linked to the amount of light available in the water column. Form May to October the surface production was hampered by photoinhibition except periods when suspended matter content in water was very high after periods of strong winds, e.g. on September 6, 2006. Compensation depth (depth where NPP net primary production = 0, i.e. where GPP minus TCR = 0) was close to 1 m during most of the vegetation period (Fig. 2). In colder parts of a year, euphotic zone usually reached below the average lake depth. Directly after periods of strong winds, as seen from chlorophyll and total suspended matter concentrations (Fig. 2), net primary production was restricted to a narrow surface layer; with minimum depth of the euphotic zone of 0.3 m.

During two-year measurement period (years 2006 and 2007), annual GPP amounted to 402 and 471 g C m⁻², and TCR amounted to 192 and 223 g C m⁻² respectively. High GPP and TCR were measured throughout the whole vegetation season in pelagic zone of Lake Gardno (Fig. 3). GPP values revealed short term variations as opposed to TCR that seemed to decrease and increase more steadily following changes in water temperature (Figs. 1, 3). Production in Lake Gardno was high during the whole vegetation season, both is spring and in summer – typically for shallow, polymictic lakes in a temperate zone (Wetzel 2001). Daily GPP values ranged from 92 mg C m⁻² d⁻¹ to 3627 mg C m⁻² d⁻¹. Daily TCR values ranged from 73 mg C m⁻² d⁻¹ to 1680 mg C m⁻² d⁻¹. In winter (December to February) GPP amounted to 19 g C m⁻² (about 4% of the annual value) and TCR values amounted to 7 g C m⁻² that is about 3% of the annual value.

We identified two factors regulating TCR process in Lake Gardno: temperature and suspended matter content (Fig. 4). Two regression relationships were calculated to relate TCR to temperature: one was based on depth integrated TCR values (mg C m⁻² d⁻¹) and the

Fig. 3. Seasonal variation of depth-integrated total community respiration (TCR) and gross primary production (GPP) values (mg C m⁻² d⁻¹) in Lake Gardno.
second one – TCR per unit of TSM (mg C m⁻² d⁻¹)/(g TSM m⁻²). Both models explained about 60% of the TCR variability (TCR = 139 × EXP (0.1 × TEMP), R² = 0.66, P < 0.0001 and TCR = 4.5 × EXP (0.076 × TEMP), R² = 0.61, P < 0.0001, respectively). Value of Q₁₀ calculated from both equations equaled 2.8 and 2.15, respectively, in the 2–24.5°C temperature range. Suspended matter content in water was another factor of similar importance influencing TCR rate (explained about 54% of the TCR variability). In Lake Gardno, areal TCR values depended on the amount of TSM in the water column (TCR = 19.5 × TSM + 14.2, R² = 0.54, P = 0.0006) as shown in Fig. 4.

We found two factors regulating GPP process in Lake Gardno: light and temperature. Unlike TCR, GPP did not correlate with TSM content. GPP correlated with daily PAR dose (kJ m⁻² d⁻¹) (GPP = 0.15 × PAR + 674, R² = 0.56, P < 0.0001). As mentioned above, the changing light climate in water resulted in marked GPP fluctuations between measurement days observed in vegetation season e.g. in 2006 when measurements were conducted more often. Relation of maximum volumetric values of GPP per unit of chlorophyll to temperature was expressed by the following equation: GPP = 0.85 × EXP (0.06 × TEMP) (R² = 0.60, P < 0.0001). Value of Q₁₀ calculated from this equation amounted to 2.23 in the 2–24.5°C temperature range.

Measurements of gross primary production in pelagic zone and total pelagic community respiration indicated that, on annual
basis, Lake Gardno pelagic system is net autotrophic that is, production exceeds respiration. Respiration was decoupled from production of organic matter. GPP to TCR ratio amounted to 2.1 on yearly basis (assuming $PQ = 1.2$ and $RQ = 1$). During period of vegetation, TCR in the water column constituted, on average, about 40% of GPP (Fig. 5). Likely, part of the organic matter produced in the water column is transferred to the bottom sediments where it is decomposed. Preliminary study on sediment respiration (six measurements) conducted in the coastal zone of Lake Gardno indicated that sediment respiration constituted from about 50% to 100% of the pelagic respiration (Rycher t and Wielgat-Rycher t 2008), with the exception of winter when this portion was lower. Respiration in the central part of a lake, where sediment has more accumulative character, might be even higher. Thus, only a small part of the material produced in the pelagic zone is probably exported to the sea with lake outflow.

Lake Gardno is shallow, exposed to winds from the Baltic Sea and does not have a stratified water column (Ficek and Wielgat-Rychert 2009). The lake suspended matter content (TSM) content does not correlate with temperature (that is, factors other than seasonal changes of plankton biomass contribute to the overall matter content in water); e.g. TSM noted in November 2007 was over 5 times higher than the lowest value noted during vegetation season, that is, in June 2006 (see Fig. 2). Therefore, we attribute changes in the pelagic TSM content to the wind induced resuspension, which increases matter content in water (measured here as TSM content) and influences pelagic respiration processes (TCR). The susceptibility of lake sediment to resuspension depends on sediment type, on the shape and the depth of a lake. Lake Gardno is particularly susceptible to resuspension due to its pan-like shape. Scheffer (2004) gives a formula that allows calculation of a wavelength in a lake in relation to the wind fetch and the lake depth. Using this formula, the minimum wind speed needed for the waves to reach the bottom of Lake Gardno (and thus start resuspension within the whole lake area) is 2.6 m s$^{-1}$ if we consider the maximum length of the lake (6.9 km) as the maximum wind fetch. During the whole two-year period of our study, that is, between January 2006 and February 2008, mean daily wind speed equal to or exceeding 2.9 m s$^{-1}$ was noted for about 53% days (mean daily wind speed amounted to 3.7 m s$^{-1}$). Other authors give similar values, e.g. according to meteorological data from the 1965–76 period quoted by Cyberski and Jędrasik (2003), the annual average wind speed amounted to 4.1 m s$^{-1}$ at coastal meteo-station about 19 km west from measurement point in Lake Gardno. Moreover, it is probably, not only the average daily wind speed that is important for sediment resuspension. Blasts of wind, even those lasting relatively shortly, and thus unimportant for the average daily wind speed values, may also induce resuspension and increase TSM content in water.

ACKNOWLEDGEMENTS: We would like to thank Institute of Geography, Pomeranian University in Słupsk for access to their data on wind measurements.

REFERENCES


Jeffrey S.W., Humphrey G.F. 1975 – New spectrophotometric equation for determining chlorophyll a, b, c1 and c2 – Biochem. Physiol. Pfl. 167: 194–204.


Received after revision January 2010