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Horizontal differences in ecosystem metabolism of a large shallow lake

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SUMMARY

The causes of horizontal differences in metabolic activities between lake zones are still poorly understood. We carried out a two-year study of lake metabolism in two contrasting parts of a large shallow lake using the open-water technique based on high-frequency measurements of dissolved oxygen concentrations. We expected that the more sheltered and macrophyte-rich southern part of the lake receiving a high hydraulic load from the main inflow will exhibit equal or higher rate of metabolic processes compared to the open pelagic zone, and higher temporal variability, including anomalous metabolic estimates such as negative gross primary production (GPP) or community respiration (CR) due to rapid water exchange. Our results showed that anomalous metabolic estimates occurred at both stations with a similar frequency and were related rather to certain wind directions, which likely contributed to stronger water exchange between the littoral and pelagic zones. Periods of auto- and heterotrophy (daily mean NEP> or <0) had a 50:50 distribution at the Central Station while the proportions were 30:70 at the Southern Station. High areal GPP estimated in our study exceeding nearly twice the long-term average ^{14}C primary production, showed the advantages of the free-water technique in integrating the metabolism of all communities, a large part of which has remained undetected by the traditional bottle or chamber incubation techniques.

1. Introduction

First studies on lake metabolism based on changes in dissolved oxygen concentrations were carried out already 80–90 years ago (Gaarder and Gran, 1927; Winberg, 1934). In the first approaches, water was enclosed in light and dark chambers or bottles and incubated in the water body for hours until the formation of measurable gradients in dissolved oxygen content. The method enabled a simultaneous measurement of photosynthesis (gross primary production, GPP), and respiration (R), and calculating their difference, the net primary production, as both GPP and R were going on in the light bottles but only respiration in the dark bottle. Over decades, a number of modified incubation techniques including those using labelling with ^{14}C (Steeman Nielsen, 1952) have been developed and employed for measuring metabolic rates within aquatic ecosystems, however the "container effect" (Parker and Samsel, 1970) has remained one of the main disadvantages of these methods. Furthermore, the common incubation technique is routinely used to measure pelagic plankton metabolism only and in order to include also benthic production, the method must be combined with sediment chamber incubations (Kemp et al., 1997; Gazeau et al., 2005) or long glass cylinders enclosing the full water column in a chamber (Teal, 1957). Additional modifications in the experimental setup or separate measurements are required to cover the metabolism of the entire ecosystem including also macrophyte stands and nekton.

The diel changes in water column oxygen content were first used by Sargent and Austin (1949) as a basis to calculate rates of production and respiration of a coral reef and the methods became widely accepted since the 1950s in studies addressing whole-ecosystem gross primary production (GPP), community respiration (CR) and the net ecosystem production (NEP). The need for high resolution data on aquatic metabolism for detecting ecosystem-scale responses to anthropogenic or climatic perturbations on one hand, and technological development of sensors, data loggers and telecommunication systems, on the other, gave a new impetus to metabolism studies in the 2000s, especially in lakes (Cole et al., 2000; Lauster et al., 2006; Staehr and Sand-Jensen, 2007), which active role in transforming the terrestrial carbon flux to the ocean has been recently re-evaluated (Algesten et al., 2003; Huttunen et al., 2003; Sobek et al., 2006; Downing et al., 2008; Cole et al., 2007). The free water method for assessing lake metabolism using probes has obvious advantages compared to incubation techniques

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as it is free from "container effects", has a high temporal resolution, integrates the metabolic processes over the entire food web and over larger areas, and it has become easier, cheaper and more reliable (Staehr et al., 2012a). The disadvantages of the free water method are mostly related to uncertainties in the extent of spatial integration, both vertically (Coloso et al., 2008; Sadro et al., 2011) and horizontally (Lauster et al., 2006; Van de Bogert et al., 2007), and increased variability and anomalies caused by advective mixing of water masses (Sadro et al., 2011), which can be overcome by increasing the number of measurements (Staehr et al., 2010) or by improved characterisation of spatial and temporal variability in metabolism within the context of physical dynamics.

Lake Võrtsjärv has served as a long-term model lake for Estonian University of Life Sciences, Centre for Limnology. Whole ecosystem studies since the mid-1960s including 18 years of annual primary production measurements with the ^{14}C technique (Nõges et al., 2011) form a solid basis for lake metabolism studies. The two clearly distinct parts that can be delineated in the lake based on hydromorphology, wind stress, water chemistry, macrophyte vegetation, and plankton (Feldmann and Nõges, 2007; Nõges and Tuvikene, 2012), provide a unique opportunity to study the effect of these differences on metabolic variables in these contrasting parts of the lake and to test hypotheses applicable also to other large shallow lakes. We hypothesized that the smaller part characterised by high hydraulic and nutrient load from the main inflow will exhibit much higher temporal variability of metabolic processes and higher number of anomalous values (estimated negative GPP, or CR seemingly producing oxygen) caused by advective change of water masses. Our previous measurements of macrophyte and periphyton productivity (Nõges et al., 2010) suggested that the metabolism in this part of the lake, partly overgrown by macrophytes, may be equal or even exceed that of the broad pelagic area despite substantially lower phytoplankton development. Given the high variability of wind speed and direction and the very different shelter conditions between the two parts of the lake, we expected to see a stronger wind signal in the advective "noise" in daily metabolism data from the open part of the lake compared to the sheltered southern part but also a decrease in this "noise" after smoothing the data.

2. Material and methods

2.1. Site description and the sampling stations

Lake Võrtsjärv is a large, shallow, eutrophic lake in Central Estonia. At mean water level, the lake area is 270 km^2, volume 750 million m^3, mean depth 2.8 m and maximum depth 6 m. Eighteen rivers and streams collect their water from the 3104-km^2 mostly cultivated catchment where the soils have been formed on carbonate rich glacial and glacifluvial sediments covering the Mid-Devonian sandstone bedrock. The basin of the largest inflow, the Väike Emajõgi River entering the lake from the south (Fig. 1), occupies 41% of the lake's total catchment area. The mean water residence time of the lake is one year. The annual mean amplitude of the naturally fluctuating water level is 1.4 m, but the absolute range of 3.1 m exceeds the mean depth of the lake. Westerly and south-westerly winds dominate in the area, which cause almost continuous full mixing of the lake's water column. In the surroundings of Võrtsjärv the mean monthly air temperature ranges from −6.7 in January to 16.8 °C in July, the annual amount of precipitation is 590 mm and the average sum of sunshine duration is 117 h in winter (D, J, F) and 741 h in summer (J, J, A) (Haberman et al., 1998). The total solar irradiance at L. Võrtsjärv is 170 MJ m^{-2} for winter months (D, J, F) and 1693 MJ m^{-2} in summer (J, J, A) (Eerme, 2012). The monthly mean water temperature reaches its maximum of 19.8 °C in July. The ice cover lasts on average 130 days from November to April (Nõges and Nõges, 2014).

Võrtsjärv is strongly eutrophic characterised by a mean total *N* concentration of 1.4 g m^{-3}, a total *P* concentration of 50 mg m^{-3} and a mean chlorophyll-a concentration of 31 mg m^{-3}. The water is alkaline (pH 8.2 ± 0.4; HCO_3 203 ± 51 mg/L) with a high buffering capacity and seston content. During the ice-free period, the mean transparency does not exceed 1 m (Nõges and Nõges, 2012). The euphotic depth, estimated as the penetration depth of 1% of the subsurface photosynthetically active radiation (PAR), varies from 1.6 to 3.2 m mostly covering the 2.8-m water column. According to the mean daily phytoplankton ^{14}C primary production of 880 mg C m^{-2} day^{-1} from June to October and the mean annual PP of 208 ± 27 g C m^{-2} $year^{-1}$ (in 1982–2009), Võrtsjärv is located close to the nutrient-saturated production boundary determined by latitude (Nõges et al., 2011).

In order to get a picture of the possible ranges of metabolic parameters in Võrtsjärv and to have an insight to the controlling factors, we placed the two stations for measuring lake metabolism in contrasting areas of the lake. The Central Station located close to the deepest point of the lake near the eastern shore has been the main monitoring site of the lake since the 1960s. A recent study (Nõges and Tuvikene, 2012) showed that the deep Central Station was characterised by the lowest average variability in chemical, physical, and plankton parameters among 10 stations studied and was representative for more than 90% of the lake's aquatory regarding common phytoplankton and water chemistry variables. Due to strong wave action and light limitation at the bottom, the submerged macrophyte vegetation in the lake proper is sparse. The Southern Station was located in the southern part of the lake, at a distance of about 3.5 km from the river mouth of the mean inflow, at a boundary where the running water conditions are being replaced by standing water conditions. At this site the typical lake phytoplankton first appears while the fast water exchange further south prevents the establishment of the cyanobacterial community characteristic of Võrtsjärv. Still the estimated mean water residence time at this site was approximately 4.5 days which, in combination with wind currents, created a highly variable environment. The narrow southern part of the lake has a rich vegetation of both submerged (mostly *Myriophyllum spicatum* L.) and floating-leaved (*Nuphar lutea* (L.) Sm.) macrophytes offering habitat for other groups of biota but supposedly not limiting water exchange.

2.2. Field measurements

To characterise lake metabolism, we measured the dynamics of dissolved oxygen (DO) and water temperature (T_w) at the two stations at 1 m depth. At both stations T_w was additionally measured at two depths: 0.5 m from the surface and 0.5 m from the bottom to check for accidental stratification events. The maximum depth in spring reached 1.5 m at the Southern Station and 4 m at the Central Station. At the Central Station, measurements lasted from 30 April to 8 December in 2011 and from 7 June to 30 November in 2012. At the Southern Station, the probe was deployed from 30 April to 8 November in 2011 and from 7 June to 30 October in 2012. No measurements were done under the ice and a couple of data gaps at the Southern Station in 2012 (1.07–10.07 and 7.09–21.09) occurred due to technical reasons. A comparable period from both stations and both years covered the months from June to October.

In addition to DO and T_w needed for metabolism calculations, chlorophyll fluorescence (Chl) and the concentration of total dissolved solids (TDS) were continuously measured at 1 m depth. We used two identical YSI 6600 V2-4 multi-parameter probes at the stations equipped with self-cleaned YSI ROX optical oxygen sensors (model 6150), temperature-conductivity sensors and