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Does different *versus* equal daytime and night-time respiration matter for quantification of lake metabolism using diel dissolved oxygen cycles?

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Abstract – Diel dissolved oxygen (DO) measurements can be used to estimate water metabolism of aquatic systems, in particular, lakes, lagoons and streams in terms of gross primary production (GPP), ecosystem respiration (R_{eco}) and net ecosystem production (NEP). One of the main assumptions in the calculation of lake metabolism is that R_{eco} is the same for daytime ($R_{daytime}$) and nighttime (R_{darkhr}). This study aimed at testing the equal $R_{daytime}$ and R_{darkhr} assumption to estimate GPP, R_{eco} and NEP in a littoral zone of a temperate shallow lake (Lake Yeniçağa) in northwestern Turkey with and without the assumption. Based on the equal R_{darkhr} and $R_{daytime}$ assumption, values calculated for GPP and $R_{daytime}$ were different than those based on the different R_{darkhr} and $R_{daytime}$ assumption ($P < 0.001$). GPP was lower by 7.5% in July, 49.6% in September and 14.9% in October, while R_{eco} was lower by 5.9% in July and 55.8% in September. GPP was higher by 8.9% in August and 55% in November, while R_{eco} was higher by 7.8% in August and 23.9% in November.

Key words: Aquatic ecosystems / diel dissolved oxygen / ecosystem respiration / lake metabolism / shallow lake

Introduction

Diel dissolved oxygen (DO) measurements can be used to estimate water metabolism of aquatic systems, in particular, lakes, lagoons and streams in terms of gross primary production (GPP), ecosystem respiration (R_{eco}) and net ecosystem production (NEP) (Seeley, 1969; Wang *et al*., 2003; Vallino *et al*., 2005; Staehr and Sand-Jensen, 2007; Van de Bogert *et al*., 2007; Ciavatta *et al*., 2008; Hanson *et al*., 2008; Staehr *et al*., 2010). Quantification and monitoring of diel DO cycles assume that changes in DO indicate an ecosystem state of a water body as a result of photosynthetic production, respiratory consumption, and exchange of oxygen between air and water. Methods to measure diel DO have advantages such as provision of GPP, R_{eco} and NEP, ease of their aggregation to temporal scales of interest, prevention of bottle and/or container effects, ease of data collection and measurement of whole-ecosystem metabolism (Van de Bogert *et al*., 2007; Staehr *et al*., 2010). Diel DO measurements have difficulties with issues such as the quantification of air–water flux and spatial/temporal heterogeneity. Van de Bogert *et al*. (2010) developed a spatial model to better understand the underlying heterogeneity and to determine the relative contributions of benthic-littoral *versus* pelagic processes. In addition, one of the main assumptions in the calculation of lake metabolism is that R_{eco} is the same for daytime and night-time. Based on this assumption, GPP, R_{eco}, and NEP in various aquatic ecosystems were estimated in the related literature (Odum, 1956; Hanson *et al*., 2003; Lauster *et al*., 2006; Staeher and Sand-Jensen, 2007; Staeher *et al*., 2010). However, Wang *et al*. (2003) and Holtgrieve *et al*. (2010) accounted for R_{eco} as a function of water temperature (T_w).

The objective of this study was to test the effect of the equal daytime ($R_{daytime}$) and nighttime (R_{darkhr}) assumption on GPP, R_{eco} and NEP estimates in a littoral zone of a temperate shallow lake (Lake Yeniçağa) in northwestern Turkey with and without the assumption.

Material and methods

Study site

Lake Yeniçağa (Bolu) is located in northwestern Black Sea region of Turkey under the influence of a temperate climate regime with a warm summer season and a cool and

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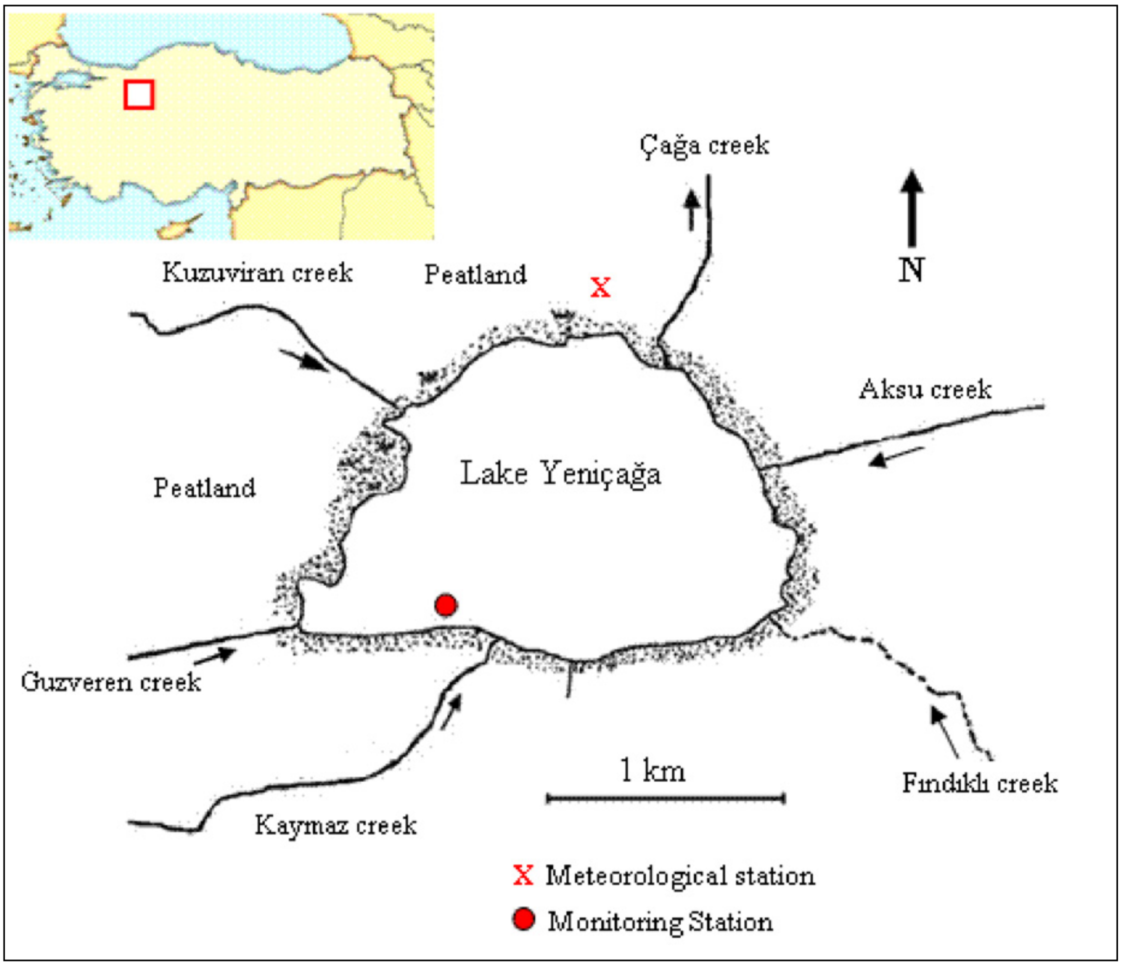

Fig. 1. Location of Lake Yeniçağa (Bolu).

rainy winter season (Fig. 1). Long-term mean annual temperature and precipitation were 10.2 °C and 538 mm, respectively (Dengiz *et al*., 2009). Water temperature in the lake varied between 25 °C in July and August and 6 °C in December of 2010. Lake Yeniçağa is a polymictic shallow non-stratifying lake with a 1.8-km^2 surface area and a 3-m average depth which seasonally fluctuates. The entire water column mixes more or less continuously. Altitude of the lake is approximately 990 m above sea level. A thick reed belt surrounds the lake. There is peatland on the west and northwest of the lake. The peatland is wetted intermittently depending on water level. Phytoplankton community of the lake was dominated by cyanobacteria and green algae. *Anabaena* sp. and *Merismopedia glauca* (Ehrenberg) Kützing, 1845 were the most dominant cyanobacteria species. *Oocystis parva*, *Scenedesmus* sp. and *Eudorina unicocca* predominated Chlorophyta. Zooplankton community of the lake was dominated by Copepods, Cladocerans, Rotifers and Naupli. The most frequently encountered Rotifers species were *Keratella quadrata*, *Filinia longgiseta*, *Brachionus urceolaris* and *Asplanchna priodonta* (Saygı, 2005). Cladoceran community was dominated especially by large-bodied species including *Daphnia* spp. Copepod community was dominated by *Acanthodiaptomus denticornis*, *Eucyclops serrulatus*, *Macrocyclops albidus* and *Metacyclops gracilis* (Saygı, 2005).

In situ measurements

Dissolved oxygen (DO, mg.L^{-1}), electrical conductivity (EC, mS.cm^{-1}), T_w and pH were measured using CS511-L Sensorex DO Probe, CS547A Conductivity/Temperature Probe and CSIM11 pH Probe (Campbell Scientific, Inc., Logan, UT, USA), respectively. The probes deployment was in the littoral zone. The probes were placed close to shore at a distance from shore where the water depth was approximately 1 m. Time interval of the measurements at a water depth of 0.6 m was 15 min, and data were recorded hourly as the mean of 15-min measurements. Every 15 days, the probes were cleaned and calibrated according to their manual instructions. The reference temperature for the measurement of EC is 25 °C. Fouling was minimized locating the probes in a dark box.

The solar radiation (SR, W.m^{-2}), wind speed (WS, m.s^{-1}) and air temperature (T_a, °C) were measured using T107 Weather Stations (Campbell Scientific Inc., Logan, UT, USA). The water quality data were recorded from

Table 1. Equations to estimate lake metabolism (modified from Staehr *et al.*, 2010).

Parameter	Equation
Day fraction	Day fraction = light hours/24 h
	Daytime is assumed if net SR is greater than 40 W.m^{-2} in any hours (see Table 3)
$NEP_{daytime}$	NEP_{hr} (mg O_2.m^{-3}.h^{-1}) = $\Delta O_2 – F/Z_{mix}$
	$NEP_{daytime}$ (mg O_2.m^{-3}.daylight period^{-1}) = mean NEP_{hr} during daylight × day fraction × 24
R	R_{darkhr} (mg O_2.m^{-3}.h^{-1}) = − mean nighttime NEP_{hr}
	R_{night} (mg O_2.m^{-3}.d^{-1}) = total R_{darkhr}
	$R_{daytime}$ (mg O_2.m^{-3}.h^{-1}): estimated depending on T_w, EC and pH (see text)
	R_{day} (mg O_2.m^{-3}.d^{-1}) = total $R_{daytime}$
	R_{eco} (mg O_2.m^{-3}.d^{-1}) = $R_{night} + R_{day}$
GPP	GPP (mg O_2.m^{-3}.d^{-1}) = $NEP_{daytime} + R_{daytime}$
NEP	NEP (mg O_2.m^{-3}.d^{-1}) = GPP − R_{day} − R_{night}

$NEP_{daytime}$, daytime net ecosystem production; NEP_{hr}, hourly net ecosystem production; R_{darkhr}, mean nighttime ecosystem respiration; R_{night}, total nighttime ecosystem respiration; $R_{daytime}$, daytime ecosystem respiration; R_{day}, total daytime ecosystem respiration; R_{eco}, total ecosystem respiration.

July 1 to November 30 in 2010. The meteorological data were recorded as of July 12 until to November 30. Meteorological station was installed about 1 km north of Lake Yeniçağa at an elevation of 988 m above sea level (Fig. 1).

Quantification of lake metabolism

The zero-dimensional DO mass balance model was used to estimate the lake metabolism in this study and includes four processes as follows (Staehr *et al.*, 2010):

$$\Delta O_2/\Delta t = GPP - R_{eco} \pm F/Z_{mix} \pm A \qquad (1)$$

where $\Delta O_2/\Delta t$ is the change in DO concentration over time (mg O_2.m^{-3}.h^{-1}), GPP is gross primary production (mg O_2.m^{-3}.h^{-1}), R_{eco} is ecosystem respiration (mg O_2.m^{-3}.h^{-1}), F/Z_{mix} is the oxygen exchange with the atmosphere (mg O_2.m^{-3}.h^{-1}), Z_{mix} is mixed layer depth (m), and A includes all the other processes that change DO concentration (mg O_2.m^{-3}.h^{-1}) such as horizontal and vertical advection within the lake. F/Z_{mix} was considered negative (−) and positive (+) for downward and upward fluxes for DO, respectively.

The oxygen exchange with the atmosphere (F) was computed as follows (Staehr *et al.*, 2010):

$$F\left(\mathrm{mgO_2.m^{-3}.h^{-1}}\right) = k(O_{2measurment} - O_{2sat})/Z_{mix} \qquad (2)$$

where O_{2sat} (mg.L^{-1}) is oxygen saturation as a function of both T_w and the equation of Weiss (1970) which was corrected for altitude according to the United States Geological Survey (USGS) Water Quality Technical Memoranda 81.11 and 81.15 (USGS, 1981). The coefficient k (m.h^{-1}) was estimated using the Schmidt number (Sc) and gas piston velocity corresponding to a Schmidt number of 600 (k_{600}). The T_w-dependent Schmidt number was calculated hourly using the equation of Wanninkhof (1992). k_{600} (m.h^{-1}) depends on wind speed at 10 m height and was calculated hourly using the equation of Cole and Caraco (1998). Wind speed at 10 m height was calculated according to Smith (1985) using wind speed at the 3-m height. Physical gas flux was divided by the mixing depth, Z_{mix} (m), to express the value in volumetric units. Lake Yeniçağa is a shallow lake that is not subject to the thermal stratification. Z_{mix} was used in the calculations assuming that it equals to depth of 1 m. A was not accounted for in this study. The other equations used to calculate metabolism are given in Table 1.

Non-linear regression models were fitted to changes in DO and F for each month separately, and the resultant non-linear regression models were used to estimate GPP, R_{eco} and NEP. The rate of change in DO ($\Delta O_2/\Delta t$) was calculated using the first derivative of sinusoidal equations developed for DO. In the calculation of R_{eco}, photosynthesis was considered not to take place (GPP = 0) during nighttime. When equation (1) was rearranged according to GPP = 0, R_{darkhr} equals $-NEP_{hr}$. To test the equal daytime and nighttime respiration assumption (*e.g.*, Odum, 1956; Hanson *et al.*, 2003; Lauster *et al.*, 2006; Staeher and Sand-Jensen, 2007; Staeher *et al.*, 2010), R_{darkhr} was expressed as a function of T_w and pH, and the resultant multiple non-linear regression models were used to estimate $R_{daytime}$ for each month separately. Results were presented comparatively based on the calculations with and without the equal $R_{daytime}$ and R_{darkhr} assumption.

Statistical analyses

Statistical analyses were performed using SigmaPlot 11.0 and Minitab 15.1. Best-fit multiple non-linear regression models of DO, F and R_{darkhr} were chosen using adjusted coefficient of determination (R^2_{adj}), standard error (SE), variance inflation factors (VIF) and Mallows' C_p of the best subsets procedure. Paired-t test was used to test mean difference between R_{eco} values and between GPP values with and without the equal $R_{daytime}$ and R_{darkhr} assumption.

Results

Water quality and environmental factors

Descriptive statistics for the period of July 1–November 30 (2010) indicated that hourly diel DO had

Table 2. Descriptive statistics of water quality data.

Month	Descriptive statistics	n	EC (mS.cm^{-1})	T_w (°C)	pH	DO (mg.L^{-1})
July	Mean ± SD	744	0.56 ± 0.03	24.63 ± 1.70	8.28 ± 0.21	8.27 ± 2.23
	Max		0.62	29.83	8.78	16.95
	Min		0.46	20.75	7.66	0.85
	CV		5.82	6.93	2.62	27.00
August*	Mean ± SD	744	0.50 ± 0.06	24.99 ± 3.49	8.33 ± 0.49	6.82 ± 3.83
	Max		0.70	32.48	9.79	17.80
	Min		0.40	14.62	7.56	0.5
	CV		11.03	13.97	5.99	56.13
September*	Mean ± SD	720	–	16.88 ± 3.20	8.69 ± 0.32	9.50 ± 1.44
	Max			26.48	9.75	19.86
	Min			9.01	7.84	7.23
	CV			18.95	3.79	15.24
October*	Mean ± SD	744	–	10.55 ± 2.78	8.26 ± 0.16	7.48 ± 2.91
	Max			19.22	9.14	11.35
	Min			2.23	7.80	1.35
	CV			26.38	2.05	38.91
November	Mean ± SD	720	0.36 ± 0.008	10.33 ± 0.77	8.50 ± 0.25	6.36 ± 2.11
	Max		0.39	13.33	9.15	12.92
	Min		0.34	9.01	8.15	2.63
	CV		2.46	7.47	2.95	33.24

SD, standard deviation; CV, coefficient of variation; EC, electrical conductivity; T_w, water temperature; DO, dissolved oxygen. *EC values could not be measured as of August 21 until the end of October due to malfunctioning of the device.

the largest temporal variability in August (CV = 56.13) and varied between 0.5 and 17.80 mg.L^{-1} (Table 2). DO concentration in September reached a maximum of 19.86 mg.L^{-1}. There was also a strong seasonal variation in T_w in parallel to changes in air temperature, with T_w on average ranging from 24.9 ± 3.4 °C in August to 10.3 ± 0.7 °C in November. The lake water EC was low and within the range of freshwaters. pH was above 8 for the most of the study period and reached a maximum of 9.79 in August and a minimum of 7.56 in August.

Maximum and minimum air temperatures were 34.1 °C in August and −4.9 °C in November, respectively. Maximum and minimum wind speed values were 8.05 and 0.001 m.s^{-1} in November, respectively. Mean wind speed was 2.09 ± 1.47 m.s^{-1} in July, and 1.66 ± 1.18 m.s^{-1} in November. Mean SR during the study period varied between 88 ± 147 and 270 ± 320 W.m^{-2}, with a maximum value of 944 W.m^{-2} in July (Table 3).

Lake metabolism

Multiple non-linear regression models of DO and F built to estimate rates of GPP and R_{eco} in the littoral zone of Lake Yeniçağa are presented in Tables 4 and 5. When a sinusoidal function was fitted to monthly DO data as a function of local hours, R^2_{adj} values ranged from 76% (SE = 0.1642) in October to 93% (SE = 0.3600) in July. When a Gaussian function was fitted to monthly F data, R^2_{adj} values ranged from 90% in November to 96.6% in September.

As was stated before, R_{darkhr} was expressed as a function of T_w and pH, and the resultant multiple non-linear regression model was used to estimate $R_{daytime}$ for each month. The multiple non-linear regression model built for R_{darkhr} is as follows:

$$R_{darkhr} = -0.642 + 0.000001\,T_w^4 - 0.000917.77\ \mathrm{pH}^3 \left(R^2_{adj} = 74.0\%;\ \mathrm{SE} = 0.141;\ n = 57;\ \mathrm{VIF} < 10;\ P < 0.001\right). \tag{3}$$

Our results based on the different $R_{daytime}$ and R_{darkhr} assumption showed that GPP ranged from 12.47 mg O_2.m^{-3}.d^{-1} in August to 0.75 mg O_2.m^{-3}.d^{-1} in November (Table 6). Ecosystem respiration (R_{eco}) was estimated at 14.31 g O_2.m^{-3}.d^{-1} in August and 2.57 mg O_2.m^{-3}.d^{-1} in September. NEP$_{daytime}$ varied between 4.63 mg O_2.m^{-3}.daylight period^{-1} and −0.27 mg O_2.m^{-3}.daylight period^{-1}, while NEP varied between 0.32 mg O_2.m^{-3}.d^{-1} and −2.52 mg O_2.m^{-3}.d^{-1}.

Based on the equal R_{darkhr} and $R_{daytime}$ assumption, values calculated for GPP and R_{day} (Table 6) were different than those in Table 6. GPP was lower by 7.5% in July, 49.6% in September and 14.9% in October, while R_{eco} was lower by 5.9% in July and 55.8% in September (Table 6). On the other hand, GPP was higher by 8.9% in August and 55% in November, while R_{eco} was higher by 7.8% in August and 23.9% in November.

As expected, during July and August when SR and T_w were high (see Table 3), GPP, R_{eco} and NEP$_{daytime}$ were higher than during the rest of the study period. During the daytime, benthic-littoral zone exhibited net autotrophic activity (GPP:$R_{day} > 1$, NEP$_{daytime} > 0$) in July, August and September. For the diel period (day + night), benthic-littoral zone was dominated by net heterotrophic activity (GPP:$R_{eco} < 1$, NEP < 0) in all months except for September.

Table 3. Descriptive statistics of meteorological data.

Month	Descriptive statistics	n	T_a (°C)	WS ($m.s^{-1}$)	SR ($W.m^{-2}$)	Day time (h)
July	Mean ± SD	463	20.08 ± 5.66	2.09 ± 1.47	245.0 ± 294.2	14
	Max		33.64	6.69	944.0	
	Min		7.40	0.37	0.0	
	CV		28.19	70.55	120.8	
August	Mean ± SD	744	20.54 ± 6.66	2.05 ± 1.47	270.0 ± 320.0	14
	Max		34.16	6.66	905.0	
	Min		7.24	0.20	0.0	
	CV		32.43	71.65	118.2	
September	Mean ± SD	720	15.81 ± 5.51	2.05 ± 1.27	186.0 ± 256.9	12
	Max		29.20	5.52	854.0	
	Min		3.52	0.29	0.0	
	CV		34.86	62.13	138.03	
October	Mean ± SD	744	8.76 ± 4.79	1.66 ± 1.05	88.2 ± 147.4	11
	Max		20.33	7.52	722.7	
	Min		−3.03	0.11	0.0	
	CV		57.74	63.35	166.98	
November	Mean ± SD	720	8.61 ± 6.82	1.66 ± 1.18	104.0 ± 163.5	11
	Max		23.61	8.05	582.3	
	Min		−4.93	0.001	0.0	
	CV		79.16	71.15	157.15	

SD, standard deviation; CV, coefficient of variation; WS, wind speed; T_a, air temperature; SR, solar radiation.

Table 4. Non-linear regression models of diel DO dynamics on a monthly basis (July–November) as a function of local hour.

Month	Equation	Parameter value	R^2_{adj} (%)	SE	P
July	$y_0 + a*\sin(2*\pi*hour/b + c)$	$a = 1.9504$; $b = 20.9853$; $c = 3.0742$; $y_0 = 8.3329$	93.17	0.3600	<0.0001
August	$y_0 + a*\sin(2*\pi*hour/b + c)$	$a = 2.9918$; $b = 21.7499$; $c = 3.0444$; $y_0 = 6.8494$	92.17	0.5983	<0.0001
September	$y_0 + a*\sin(2*\pi*hour/b + c)$	$a = 0.2596$; $b = 18.9457$; $c = 1.6185$; $y_0 = 9.4703$	80.86	0.0888	<0.0001
October	$y_0 + a*\sin(2*\pi*hour/b + c)$	$a = 0.4280$; $b = 19.5683$; $c = 3.1695$; $y_0 = 7.5222$	76.01	0.1642	<0.0001
November	$y_0 + a*\sin(2*\pi*hour/b + c)$	$a = 1.1416$; $b = 19.7463$; $c = 3.1131$; $y_0 = 6.4552$	78.93	0.4007	<0.0001

Table 5. Non-linear regression models of F dynamics on a monthly basis (July–November) as a function of local hour.

Month	Equation	Parameter value	R^2_{adj} (%)	SE	P
July	$y_0 + a*\exp(-0.5*((hour–x_0)/b)\hat{}2)$	$a = -0.1025$; $b = 3.0825$; $x_0 = 15.9174$; $y_0 = 0.0068$	94.61	0.0088	<0.0001
August	$y_0 + a*\exp(-0.5*((hour–x_0)/b)\hat{}2)$	$a = -0.1269$; $b = 3.1446$; $x_0 = 16.5630$; $y_0 = 0.0385$	92.17	0.0134	<0.0001
September	$y_0 + a*\exp(-0.5*((hour–x_0)/b)\hat{}2)$	$a = -0.0487$; $b = 2.6803$; $x_0 = 15.9386$; $y_0 = -0.0105$	96.61	0.0032	<0.0001
October	$y_0 + a*\exp(-0.5*((hour–x_0)/b)\hat{}2)$	$a = -0.0195$; $b = 2.4049$; $x_0 = 14.3399$; $y_0 = 0.0539$	90.56	0.0022	<0.0001
November	$y_0 + a*\exp(-0.5*((hour–x_0)/b)\hat{}2)$	$a = -0.0503$; $b = 1.7093$; $x_0 = 15.5149$; $y_0 = 0.0816$	96.00	0.0032	<0.0001

Table 6. Estimation of lake metabolism based on the assumptions that R_{darkhr} does not equal $R_{daytime}$ *versus* that R_{darkhr} equals $R_{daytime}$.

Month	NEP (mg $O_2.m^{-3}.d^{-1}$)	$NEP_{daytime}$ (mg $O_2.m^{-3}$.daylight period^{-1})	GPP (mg $O_2.m^{-3}.d^{-1}$)	R_{eco} (mg $O_2.m^{-3}.d^{-1}$)	R_{day} (mg $O_2.m^{-3}.d^{-1}$)	R_{night} (mg $O_2.m^{-3}.d^{-1}$)
Estimation of lake metabolism based on the assumption that R_{darkhr} does not equal $R_{daytime}$						
July	−2.52	2.07	9.18	11.69	7.10	4.59
August	−1.83	4.63	12.47	14.31	7.84	6.47
September	0.32	0.89	2.89	2.57	2.00	0.57
October	−1.65	−0.07	1.49	3.14	1.56	1.58
November	−2.21	−0.27	0.75	2.96	1.02	1.94
Estimation of lake metabolism based on the assumption that R_{darkhr} equals $R_{daytime}$						
July	−2.52	2.07	8.49	11.01	6.42	4.59
August	−1.83	4.63	13.69	15.52	9.05	6.47
September	0.32	0.89	1.46	1.13	0.57	0.57
October	−1.65	−0.07	1.27	2.92	1.34	1.58
November	−2.21	−0.27	1.67	3.89	1.94	1.94

NEP, net ecosystem production; $NEP_{daytime}$, daytime net ecosystem production; GPP, gross primary production; R_{eco}, ecosystem respiration; R_{day}, total daytime ecosystem respiration; R_{night}, total nighttime ecosystem respiration.

Discussion

The term R_{eco} was defined differently in lake metabolism-related studies in the literature so as to include different processes. For example, Odum (1956) defined R_{eco} as an uptake of oxygen from the water as a result of respiration of benthic organisms, planktonic organisms and sometimes chemical oxidation and excluded oxidation of organic matter from R_{eco}. Thomann and Mueller (1987) stated that R_{eco} generally included microbial respiration for the carbonaceous biochemical oxygen demand (CBOD) and nitrogenous biochemical oxygen demand (NBOD); however, considered R_{eco} to equal planktonic respiration only. Staehr *et al.* (2010) also defined R_{eco} as oxygen consumption by all organisms in the ecosystem during the entire diel cycle and excluded the processes of photochemical oxidation and abiotic consumption of oxygen from the definition of R_{eco}. Holtgrieve *et al.* (2010) defined R_{eco} so as to include all oxygen-consuming reactions including heterotrophic respiration, and chemical oxidation and photo-oxidation. Similarly, Van De Bogert *et al.* (2007) defined R_{eco} so as to represent the sum of the processes affecting DO concentration. Wang *et al.* (2003) and Ciavatta *et al.* (2008) defined R_{eco} as the general system respiration and did not specify processes involved in R_{eco}. As can be seen from the related literature, all or some of the processes that decrease DO concentration have been aggregated under the term R_{eco}. To compare lake metabolism-related studies across lakes of different character, what processes R_{eco} involves needs to be clarified. It is also very difficult to discriminate among contributions of each of the processes considered in R_{eco} such as autotrophic respiration, and heterotrophic respiration including oxidation of CBOD and NBOD using diel DO techniques. In this study, all the biological processes utilizing DO were incorporated in the calculation of R_{eco}.

The inclusion or exclusion of the equal daytime and nighttime respiration assumption for the calculation of lake metabolism led to significant differences between GPP and R_{eco} estimates ($P < 0.001$). With the assumption that R_{darkhr} equals $R_{daytime}$, lower $R_{daytime}$, and thus, GPP values were obtained as Staehr *et al.* (2010) reported. Results in this study are also consistent with findings of Markager and Sand-Jensen (1989) that showed that there was systematic decrease in nighttime R_{darkhr} in ponds where dense phytoplankton communities occur. The R_{eco} values estimated as a function of T_w, pH and EC in this study alleviated the issue of overestimation of R_{eco} values based on the equal R_{darkhr} and $R_{daytime}$ assumption.

Benthic-littoral zone of Lake Yeniçağa exhibited net autotrophic activity during the summer daytime which was consistent with diel DO and pH cycles. However, when diel (both day and night) cycles were taken into account, Lake Yeniçağa was dominated by net heterotrophic activity during all the months except for September. This may be attributed to increased inputs of dissolved organic matter to the lake, which may boost R_{eco} and decrease NEP due to greater light attenuation in the water column, and resuspension mechanism that causes transfer to the water column of organic matter deposited in the lake sediments, particularly, in shallow lakes, thus reducing light penetration.

Negative GPP and R_{eco} values were also found in the calculations based on hourly DO data. The same issue was encountered using weekly and monthly mean values of DO. Noisy diel DO curves may result in negative GPP values, and similarly, adjective transport of DO may cause negative R_{eco} values (Staehr *et al.*, 2010). Staehr *et al.* (2010) suggested use of smoothing techniques and frequent measurements to overcome this issue. In this study, the issue was solved building non-linear regression models of DO and F for each month. Negative GPP and R_{eco} values encountered in this study may be related to the exclusion of the term A and the processes that A represents. In the future, spatial variations in DO, and thus, in lake metabolism need to be taken into account using diel techniques.

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