Ecosystem Metabolism and Oxygen Deficit in Lake Maninjau: Insight from High-Frequency Measurement

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Abstract

High-frequency measurement provides a sophisticated insight in capturing environmental patterns. Compared to traditional discrete measurement, high-frequency sensors allow a better understanding of any processes particularly those with temporal scale characteristics. Lake metabolism is one of the exemplars getting advantage of such better resolution measurement. The dynamics of dissolved oxygen concentration (DO) observed in an hourly manner, even in minutes, may explain the balance of photosynthetic activity as expressed by gross primary production (GPP), respiration (R), and atmospheric exchange. Using a coupled thermistor-chain and oxygen sensor, we computed lake metabolism of the eutrophic Lake Maninjau. Characterized by high phytoplankton productivity fueled by the abundance of nutrient availability, DO concentration in Lake Maninjau is likely to be supersaturated. On the other hand, floating cage aquaculture operated in the lake may have a consequence in increasing water column heterotrophy, that is oxygen demanding community. Through a simple mathematical model, we revealed that water column respiration in Lake Maninjau is higher than gross primary production (R > GPP) with an average of 12.1 mg O$_2$ L$^{-1}$ day$^{-1}$ and 9.0 mg O$_2$ L$^{-1}$ day$^{-1}$, respectively. Our findings highlight that as heterotrophy in eutrophic lakes may relatively be high, oxygen depletion in the water column may occur in any instance, especially in lakes where dense floating cage aquaculture is in place.

Keywords: lake metabolism, dissolved oxygen, high-frequency monitoring, heterotrophy

Abstrak

Metabolisme Ekosistem dan Defisit Oksigen di Danau Maninjau: Kajian dari Pengamatan dengan Sensor Beresolusi Tinggi. Dalam menangkap fenomena alam dibutuhkan pengamatan dengan sensor yang mampu merekam pada resolusi waktu tinggi. Dibandingkan dengan pengamatan tradisional, yaitu pengamatan musiman, penggunaan sensor mampu memberikan informasi lebih detail tentang proses yang terjadi pada skala temporal apa...
Dinamika oksigen terlarut (DO) dapat dimonitor dalam resolusi jam, bahkan menit, sehingga proses yang berperan dalam kesetimbangan oksigen baik itu produktivitas primer bruto (GPP), respirasi (R), maupun pertukaran oksigen antara air dan udara dapat diestimasi. Dengan menggunakan rangkaian termistor dan sensor oksigen kami mengkaji metabolisme Danau Maninjau. Sebagai danau eutrofik dengan produktivitas fitoplankton tinggi, seharusnya Danau Maninjau memiliki DO yang tinggi. Di samping itu, keberadaan keramba jaring apung dapat memberikan dampak pada heterotrofi yang tinggi, yaitu komunitas yang bergantung pada ketersediaan oksigen. Penghitungan matematika sederhana dalam metabolisme danau pada penelitian ini menunjukkan bahwa respirasi lebih tinggi daripada produktivitas primer bruto (R > GPP), yaitu 12,1 mg O₂ L⁻¹ hari⁻¹ dan 9,0 mg O₂ L⁻¹ hari⁻¹. Hasil kajian ini menggarisbawahi bahwa kemungkinan heterotrofi pada danau-danau eutrofik cukup tinggi. Untuk itu, defisiensi oksigen di badan air danau eutrofik dapat terjadi kapan saja, terutama pada danau-danau dengan keramba jaring apung yang padat.

Kata kunci: metabolisme danau, oksigen terlarut, monitoring resolusi tinggi, heterotrofi

Introduction

Nowadays, to better understand environmental processes, scientists are generating insights into variables previously not monitored by traditional discrete sampling (Hamilton et al., 2015). High-resolution temporal data in an hourly manner, even in minutes, allows an improved interpretation of natural processes that cycle in diel or longer temporal scales (Rose et al., 2016). The development of high-frequency in situ observatories in an aquatic environment with a variety of sensors assists limnologists in measuring both abiotic (e.g. temperature, light, dissolved oxygen, and pH) and biotic (e.g. chlorophyll fluorescence and phycocyanin) characteristics in which such evolution enlightens inland water science (Benson et al., 2010).

High-frequency measurement of free-water dissolved oxygen (DO) is now commonly used in estimating ecosystem metabolism (Dugan et al., 2016; Solomon et al., 2013; Staehr et al., 2012). This term is used to determine rates of gross primary production (GPP) by autotrophs and respiration (R) of both autotrophs and heterotrophs as major metabolic pathways in aquatics by which organic matter is produced and destructed (Staehr et al., 2012). Ecosystem metabolism is also applied as one of the metrics in determining lake trophic state and plankton biomass structure (del Giorgio et al., 1999).

In this paper, we present estimates of ecosystem metabolism of Lake Maninjau arrayed from a continuous monitoring buoy. Using a simple mathematical model fed by a unique data set we reconstructed DO dynamics in Lake Maninjau by applying the estimated ecosystem metabolism and lake-atmospheric interaction. We hypothesized that the respiration rate in Lake Maninjau exceeds primary production (R > GPP). As a eutrophic lake, characterized by high chlorophyll-a concentration fueled by the abundance of nutrients, both total phosphorous (TP) and total nitrogen (TN) (Sulastri et al., 2019), the epilimnetic layer of Lake Maninjau should have been supersaturated with DO. Massive fish killings in floating cages, however, have been reported quite frequently. Lake Maninjau has been crowded by in-lake aquaculture for years, hence, there is a consequence of high demand of oxygen for the system. Despite the hydrodynamic force in moving the anoxic bottom water upward to the surface (Santoso et al., 2018; Fukushima et al., 2017), oxygen demand by heterotrophs for respiration (including inorganic material oxidation and organic
matter decomposition) may also be substantial in reducing DO availability in the epilimnion.

**Materials and Methods**

Lake Maninjau, located in West Sumatra, Indonesia, is a deep eutrophic system in the tropics with a surface area of 99.5 km², a volume of 10.1 km³, a mean depth of 105 m, and a maximum depth of 165 m (Figure 1). Chlorophyll-a concentrations varied from 4.0 to 35.3 µg L⁻¹ with TP and TN ranged 22–300 µg L⁻¹ and 415–1,486 µg L⁻¹, respectively (Sulastri et al., 2019). Lake Maninjau is one of the lakes in the country with a dense in-lake aquaculture. In 2013, 12,090 tons of fish were harvested from 16,210 floating cage units operated in the lake (Syandri et al., 2014).

In 2014, Research Centre for Limnology LIPI was deploying a high-frequency monitoring buoy on Lake Maninjau in which the location is indicated by a dark triangle. (Figure 1), initially installed to serve lake manager as a caution tool in perceiving possible anoxic epilimnion. This buoy was equipped with a set of Dallas DS18B20 thermistor chain placed at 2 m intervals from 0.5 m to 62 m depth and an optical DO sensor (Ponsel OPTOD®) at 0.5 m below the water surface. A HOBO U30 weather station was also installed by the lake at the Research Station of LIPI.

A set of time series data generated by monitoring instruments (recorded in every 5 to 10 minutes interval) was employed for modeling surface water DO. We assumed that changes in DO in hourly interval was due to ecosystem metabolism (GPP and R) and diffusive exchange with the atmosphere (Flux) involving errors of the estimates (Ɛ). Thus,

\[
DO_{[t+1]} = DO_{[t]} + GPP_{[t]} - R_{[t]} \pm Flux_{[t]} + \epsilon_{[t]} \quad (1)
\]

The oxygen diffusion can be directed toward the lake (positive) or lost to the atmosphere (negative). We followed Hanson et al. (2008) in computing GPP and R, where

![Figure 1. Lake Maninjau in West Sumatra and its bathymetry](image-url)
\[ \text{GPP} = P_{\text{max}} \left( 1 - e^{-\frac{IP \times I}{P_{\text{max}}}} \right) \]  
\[ R = R_0 \times IR \]

Briefly, GPP can be calculated as a function of photosynthetic active radiation (PAR, \( I \)), primary productivity per unit of PAR (IP), and maximum primary productivity (\( P_{\text{max}} \)), while R is a function of nighttime respiration (\( R_0 \)) and respiration per unit of PAR (IR). An optimization routine L-BFGS-B: R (Core Team, 2019) was used to derive \( P_{\text{max}}, IP, IR, \) and \( R_0 \) over a list of range values following Hanson et al. (2008) (Table 1) by minimizing the negative log-likelihood of the errors (\( \epsilon \)). PAR was derived from the measured incoming shortwave radiation (Britton & Dodd, 1976).

Diffusive exchange, Flux, was calculated as

\[ \text{Flux} = \frac{k_{DO} \times (DO - DO_{\text{sat}})}{Z_{\text{mix}}} \]  

where \( DO_{\text{sat}} \) is the saturation concentration of oxygen at a given temperature and atmospheric pressure (Benson & Krause, 1984); \( Z_{\text{mix}} \) is the mixed layer depth calculated as the shallowest depth at which the rate of water density change exceeded 0.075 kg m\(^{-3}\) m\(^{-1}\) (Coloso et al., 2011). The gas exchange coefficient for oxygen, \( k_{DO} \), was calculated as

\[ k_{DO} = k \times \left( \frac{\text{ScO}_2}{600} \right)^{-n} \]  

where \( k \) is the gas transfer coefficient, \( \text{ScO}_2 \) is the Schmidt number for oxygen at a given temperature and water density (Wanninkhof, 1992) and \( n \) is a dimensionless coefficient to represent shear at the water surface (Crusius & Wanninkhof, 2003). \( k \) was estimated using a surface renewal model based on wind speed and buoyancy flux (MacIntyre et al., 2010). All computation and analyses were performed using the R statistical package Version 3.5.3 (Core Team, 2019).

Table 1. Free parameters used for dissolved oxygen simulation

| Parameters | Units | Range    |
|------------|-------|----------|
| \( P_{\text{max}} \) = maximum primary productivity | mg O\(_2\) L\(^{-1}\) d\(^{-1}\) | 0.1–50.0 |
| \( IP \) = primary productivity per unit of PAR | mg O\(_2\) L\(^{-1}\) d\(^{-1}\) * (mmol l m\(^{-2}\) s\(^{-1}\))\(^{-1}\) | 0.0–1.0 |
| \( IR \) = respiration per unit of PAR | mg O\(_2\) L\(^{-1}\) d\(^{-1}\) * (mmol l m\(^{-2}\) s\(^{-1}\))\(^{-1}\) | 0.0–0.1 |
| \( R_0 \) = nighttime respiration | mg O\(_2\) L\(^{-1}\) d\(^{-1}\) | 0.0–10.0 |

Results

Observations over 3 months of monitoring (15 Apr 2017 to 23 Jul 2017) showed DO concentration ranged 0.4–19.7 mg L\(^{-1}\). There were great concentration swings from undersaturated to supersaturated on a daily basis (Figure 2a). More than 50% of the concentration was below saturation. Bootstrapped data into hourly bin showed the diel pattern of DO dynamics in Lake Maninjau (Figure 2b). The supersaturated DO was likely to evolve from around 10 am to 5 pm, the rest lay below saturation.

Our DO model fits nicely with the observed data (Figure 3a). With \( R^2 = 0.955 \) and RMSE = 0.954 mg L\(^{-1}\), our simulation, therefore, shows that DO dynamics in Lake Maninjau can be explained by ecosystem metabolism, although associated errors (\( \epsilon \)) are embedded. The model is able to simulate the diel DO concentration in the lake (Figure 3b). During the day, as GPP is
fueled by incoming solar radiation, DO increases. GPP rate in producing DO is reduced as solar radiation faded. R is responsible in consuming DO, especially during the night when GPP is switched off (Figure 4a). We found that R is dominant over the period of our simulation (Figure 4b). While GPP is averaged at 9.0 mg O\textsubscript{2} L\textsuperscript{-1} day\textsuperscript{-1}, R is calculated at 12.1 mg O\textsubscript{2} L\textsuperscript{-1} day\textsuperscript{-1}. These findings strengthen our hypothesis that the respiration rate in Lake Maninjau exceeds primary production (R > GPP).

Figure 2. a. The observed dissolved oxygen (DO) collected from high-frequency monitoring buoy at Lake Maninjau; b. The diel pattern of DO dynamics drawn from the hourly binned data. Red line indicates saturation concentration. Black line indicates median, dark grey is 95% confidence interval, and light grey is the quartile of the bootstrapped data.

Figure 3. a. The modeled DO after error $\epsilon$ [equation (1)] subtraction vs. the observed data; b. The snapshot (19–21 Jun 2017) of DO diel pattern. Open circle and black line indicate the observed and the modeled DO (embedded with $\epsilon$), respectively. The horizontal dashed line indicates saturation concentration. The incoming solar radiation as PAR is shown by the red line.
Figure 4.  a. A diel snapshot (19–21 Jun 2017) of GPP and R computed by the model. dDO is the rate of hourly change in DO concentration; b. The ratio between GPP and R over the observation period. Diagonal line represents 1:1 ratio where GPP and R are in balance.

Discussion

High-frequency measurement enables a better understanding of the dynamic nature of dissolved oxygen, which had not previously been documented using traditional discrete sampling, particularly in Lake Maninjau. Monthly and weekly, even daily, oxygen observations might be able to capture trends of seasonal concentration and give the general idea of the ongoing condition of the lake (Fukushima et al., 2017). However, these techniques could not provide a better picture of the process involved in concentration dynamics (Lukman et al., 2014). Not only depicting the phenomenon at a finer scale, together with modeling techniques, high-frequency data also allows better analysis of the governing process of the phenomenon.

Of the three months of monitoring, we revealed that dissolved oxygen in surface water of Lake Maninjau is more likely to be undersaturated (Figure 2a and 1b). As explained by the model, the low DO is caused by the metabolic imbalance between GPP and R. Given that R exceeded GPP for 89% of the 100 estimates of ecosystem metabolism (Figure 4b), heterotrophy is more prevalent than net autotrophy (Hagerthey et al., 2010). While respiration of stored allochthonous organic matter and benthic respiration have been reported as the dominant contributor for ecosystem respiration (Hoellein et al., 2013), our results may contradict those findings. We suspect that water column heterotroph in Lake Maninjau is an important element in governing the respiration. As autotrophic respiration is associated with a photosynthetic activity, with a ratio between 0.8 and 1.0 (Solomon et al., 2013), heterotrophic and baseline respiration (del Giorgio & Williams, 2005) would be the driving force of the high respiration rate in Lake Maninjau. While heterotrophic respiration depends on the availability of labile organic matter, both autochthonous and allochthonous, baseline respiration is supported by allochthonous organic matter inputs and recalcitrant autochthonous organic matter (Solomon et al., 2013). We did not distinguish our respiration model outputs into those metrics. However, knowing that most streams feed Lake Maninjau periodically...
(Apip, personal communication), respiration due to allochthonous inputs could be considerably low. On the other hand, autochthonous inputs are suspected to be high as floating cage aquaculture in the lake massively operating (Syandri et al., 2014). The intensive pellet feeding in fish farming, as well as feces as a byproduct of fish growth in the cage, supplied a considerable amount of organic matter to the lake (Gondwe et al., 2012; Hakanson, 2005). Hence, inputs from aquaculture activities could fuel heterotrophic respiration. Although organic matter concentrations in Lake Maninjau have been reported (Lukman et al., 2014), the magnitude of heterotrophic respiration in metabolizing organic substrate is still lacking. Further investigation of this subject is therefore necessary.

As heterotrophy in Lake Maninjau is dominant over autotrophy (Figure 4b), hypoxic (DO < 2 mg L\(^{-1}\)) epilimnion is likely to occur (Figure 2a and b). Oxygen depletion in the water column may therefore occur in any instance. Despite the importance of the weather-induced physical process that enables the transport of anoxic (DO < 0.2 mg L\(^{-1}\)) hypolimnion water to move upward (Santoso et al., 2018; Fukushima et al., 2017), heterotrophic metabolism oxygen demand in Lake Maninjau depletes surface DO at a rate of 12.1 mg O\(_2\) L\(^{-1}\) d\(^{-1}\). In fact, primary productivity in the lake only produces DO of 9.0 mg O\(_2\) L\(^{-1}\) day\(^{-1}\). Therefore, at this stage, Lake Maninjau has a deficit in oxygen availability. When heterotrophs breathe the available DO and the GPP is turned off during darkness, midnight until dawn is the critical time for hypoxia to occur (Figure 2b and 2b). This is in agreement with reports from local fish growers where massive fish killings usually occurred just before dawn.

This study revealed the imbalance of the ecosystem metabolism of Lake Maninjau where respiration is higher than productivity. While this does not indicate the total annual metabolic rate of the lake, our estimates may however correspond to the highest primary productivity as it represents the dry season (April to July) rate. Therefore, respiration during the rainy season (November to February) may be higher than our current estimates due to the lower sunshine period and higher rainfall rates. Strong wind events and low insolation are common during this period in which it may allow desertification and diffuse anoxic deep water to the surface (Santoso et al., 2018). Whole-lake metabolic estimates, however, are yet to be calculated. The spatial variation in metabolism across the lake is the challenge of estimation. More deployed sensors can considerably provide more confidence in daily lake-wide estimates (Van de Bogert et al., 2012). Alternatively, high-frequency data coupled with the hydrodynamic-ecological model may advance the estimate. The later approach will extend the analysis to the full advection-diffusion reaction that includes water parcel transports (Antenucci et al., 2013).

**Conclusion**

This study demonstrated the interest of high-frequency monitoring to better analyze the occurrence of natural phenomena, in particular the dynamics of dissolved oxygen in surface water. Using a simple mathematical model, this study revealed that water column respiration is greater than gross primary production (R > GPP), which highlights the dominance of heterotrophs over autotrophs. The results indicate that the high rate of respiration is likely to be generated by the abundance of organic matter from in-lake fish farming. A better understanding of the metabolism of organic matter is therefore necessary. In addition, coupled with the hydrodynamic-ecological model, high-frequency monitoring would advance estimates of the whole-lake metabolism.
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