Note

Decomposition Activity and Nutrient Regeneration Rates in the Hypolimnion of the North Basin of Lake Biwa

Toshihiro Miyajima

Abstract

In the course of a recent survey on nutrient dynamics in the north basin of Lake Biwa, an abundant accumulation of nitrate was observed in the hypolimnion during the stagnation period, and the regeneration rate of nitrogen in the hypolimnion was estimated to be 40.5 mmol·m⁻²·mon⁻¹. However, it was calculated on the basis of oxygen consumption that the C:N ratio of organic matter mineralized within the hypolimnion should have been 19-21, which suggested a low regeneration efficiency of nitrogen relative to carbon. Dissolved phosphate was found to be accumulated in small concentrations near the bottom, but the regeneration rate of phosphate was very low (0.22 mmol·m⁻²·mon⁻¹), and the activity of hypolimnetic biota seemed to contribute hardly at all to phosphorus recycling in this basin. Possible factors determining the regeneration efficiency of nutrients are discussed in relation to the physiological properties of the hypolimnetic microbial metabolism.

Key words: regeneration efficiency, nitrogen, phosphorus, selective mineralization

1. Introduction

The north basin of Lake Biwa is known as a phosphorus-limited, mesotrophic lake in which an aerobic condition prevails in the whole water column throughout the year. Vernal heating of the surface lake water causes the development of the thermocline at a depth of 10-20 m in this basin, and a deep hypolimnion larger in volume than the epilimnion is enclosed and isolated below the thermocline over the major part of the year (from March/April to December/January). A significant fraction of both the photosynthetic products produced in the epilimnion and the fluvially imported organic material is thought to fall into the hypolimnion ("tropholytic zone"), and to decompose there during the stagnation period. Thus, the recycling of its decomposition products, that is, inorganic nutrients from the hypolimnion to the epilimnion ("trophogenic zone"), is one of the most important factors governing both the productivity and the material transfer in this basin.

Generally speaking, the internal recycling of nutrients such as ammonia and phosphate in the aerobic hypolimnion is relatively minor compared with eutrophicated environments where seasonal bottom anoxia occurs. In particular, previous researchers (Kawashima et al., 1976; Tezuka, 1984; Mitamura et al., 1987) have observed that the concentration of phosphate was always very low throughout the water column of the north basin of Lake Biwa, and suggested that virtually no phosphorus was recycled in the hypolimnion during the stagnation period. The lack of phosphorus recycling from the hypolimnion or the bottom mud has been recognized to play a part in the evolution of phosphorus-limited conditions which are common to many lacustrine environments (Schindler, 1977; Tezuka, 1986).
Nevertheless, the activity of hypolimnetic decomposition and its contribution to nutrient regeneration in this basin has seldom been studied and discussed quantitatively to date (an exception is the recent study of MAEDA et al., (1987), who estimated the decomposition rate of settling organic particles by sediment trap experiments). In the present study, the author estimated the regeneration rates of nutrients in the hypolimnion of this basin during the stagnation period, and discusses possible factors governing the regeneration efficiencies of nitrogen and phosphorus. Some problems for future solution derived from the discussion are suggested.

2. Material and methods

The vertical distributions of particulate organic carbon (POC) and nitrogen (PON) and particulate phosphorus (PP), as well as those of inorganic nutrients such as PO$_4^{3-}$, NH$_4^+$, NO$_2^-$ and NO$_3^-$ were surveyed monthly from May 1988 to April 1989, in the course of the regular limnological survey of Lake Biwa conducted by the Center for Ecological Research (formerly the Otsu Hydrobiological Station), Kyoto University. Data on water temperature (obtained with a thermistor thermometer) and dissolved oxygen (measured by the Winkler method) were kindly provided by T. UEDA, the technical chief of the regular limnological survey.

The sampling site was Station Ie-1 (depth, 73 m; see MORI et al., 1967), located in the north basin of Lake Biwa. Water samples for the determinations of particulate matter and inorganic nutrients were obtained with a Van-Dorn sampler (3 litres in volume). The vertical sampling interval was 10 m (see Fig. 1). After being transported to the laboratory, a portion (1-2 litres) of each water sample was filtered through a preignited, acid-washed glass fibre filter (Whatman, type GF/F). The filters were dried and then subjected to determinations of POC and PON. The filtrates were used for measurements of dissolved inorganic nutrients and total dissolved phosphorus (TDP). A portion of the residual unfiltered sample was used for a determination of total phosphorus (TP).

Concentrations of particulate phosphorus (PP) were calculated as TP minus TDP.

POC and PON were determined by use of a CHN analyzer (Yanaco, model MT-3). Measurements of PO$_4^{3-}$, NH$_4^+$, NO$_2^-$ and NO$_3^-$ were made according to the following methods: molybdenum blue, salicylate-hypochlorite (BOWER and HOLM-HANSEN, 1980), Bendschneider-Robinson, and sodium salicylate (SCHEINER, 1974), respectively. TP and TDP were measured after peroxodisulphate digestion.

3. Results

Typical vertical distributions of physical, chemical, and biological factors in the stagnation period are illustrated in Figure 1. An accumulation of nitrate and a small but significant accumulation of phosphate were observed in the hypolimnion. The concentration of nitrite was always negligibly small (<0.3 $\mu$M) compared with nitrate and ammonia.

Figure 2 shows the seasonal changes in the concentrations of oxygen, nitrate, and phosphate in the 70 m layer. The concentration of nitrate increased linearly throughout the stagnation period, whereas that of phosphate remained constant from July to January.

The vertical and seasonal distributions of the C : N and C : P ratios of the suspended material are shown semiquantitatively in Figure 3. The C : N ratio (atomic ratio) of the particulate material in the epilimnion ranged 6-10 throughout the year, which was slightly lower than that in the layers below the thermocline (ranging 6-13). The C : P ratio, on the contrary, tended to decrease from the epilimnion to the hypolimnion. Previously, based on sediment-trap experiments, MAEDA et al., (1987) found that the particulate material sinking across the thermocline had higher C : N and lower C : P ratios than the whole standing stock of material suspended in the epilimnion in the north basin of Lake Biwa. In the hypolimnion, both the C : N and C : P ratios showed a tendency to decrease with increasing depth (Fig. 3).

Figure 4 shows the seasonal changes in the contents of particulate organic carbon and
Hypolimnetic Metabolism in Lake Biwa

Fig. 1. Vertical profiles of twelve physical, chemical, and biological parameters at Station Ie-1, on 10 August 1988. Bacteria counted by AODC method; chlorophyll $a$ and pheopigment measured fluorometrically.

Fig. 2. Seasonal changes in concentrations of oxygen, nitrate, and phosphate within bottom lake water (70 m layer) from May 1988 to April 1989. Regression lines (broken) and correlation coefficients ($r$) shown for the stagnation period.

The consumption rate of oxygen as well as the regeneration rates of nitrate and phosphate in the hypolimnion during the stable thermal stratification period were estimated from the monthly increment or decrement in the standing stock of oxygen, nitrate, and phosphate (Table 1). In estimations for the segment of water column between 20 and 70 m (the upper half of Table 1), the standing stocks of these species were calculated by integrating the vertical concentration profiles (using the trapezoid approximation) over the segment, and the contributions from the eddy-diffusional fluxes across the thermocline were corrected by heat dissipation estimation (Hutchinson, 1941) on the calculation of the monthly variations of standing stocks. The amount of carbon that should been mineralized into carbon dioxide within the hypolimnion was calculated assuming that aerobic mineralization in the hypolimnion followed the stoichiometric equation:

\[
(\text{CH}_2\text{O})_x(\text{NH}_3)_y(\text{H}_3\text{PO}_4)_z + (x+2y)\text{O}_2 = x\ \text{CO}_2 + y\ \text{HNO}_3 + (x+y)\text{H}_2\text{O} + z\ \text{H}_3\text{PO}_4
\]  

As seen in this equation, the organic carbon decomposed by the hypolimnetic biota was assumed to have an electron donating capacity (on average) equivalent to the carbohydrates. Nutrient regeneration rates for the 70 m layer...
Fig. 3. Isopleths for vertical and seasonal distributions of POC : PON ratio (A) and POC : PP ratio (B) from May 1988 to April 1989. Values represented as atomic ratios. Putative lower boundary of surface circulated layer also depicted as broken line.
Fig. 4. Seasonal changes in standing stocks of POC, PON, and PP within entire water column.

Table 1. Hypolimnetic consumption rates of oxygen and regeneration rates of nitrate, phosphate, and carbon dioxide, estimated for segment of water column between 20 and 70 m (upper half), and 70 m layer alone (lower half). See text for estimation procedure.

<table>
<thead>
<tr>
<th>Depth (period)</th>
<th>Species</th>
<th>Monthly incrementa</th>
<th>Stoichiometryb</th>
</tr>
</thead>
<tbody>
<tr>
<td>20 m–70 m</td>
<td>$O_2$</td>
<td>$-935 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{mon}^{-1}$</td>
<td>23 (4200)</td>
</tr>
<tr>
<td>(June–October)</td>
<td>$\text{NO}_3^-$</td>
<td>40.5</td>
<td>1 (180)</td>
</tr>
<tr>
<td></td>
<td>$\text{PO}_4^{3-}$</td>
<td>0.22</td>
<td>- (1)</td>
</tr>
<tr>
<td></td>
<td>$\text{CO}_2$</td>
<td>854</td>
<td>21 (3800)</td>
</tr>
<tr>
<td>70 m</td>
<td>$O_2$</td>
<td>$-18.7 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{mon}^{-1}$</td>
<td>20 (1000)</td>
</tr>
<tr>
<td>(May–January)</td>
<td>$\text{NO}_3^-$</td>
<td>0.90</td>
<td>1 (50)</td>
</tr>
<tr>
<td></td>
<td>$\text{PO}_4^{3-}$</td>
<td>0.019</td>
<td>- (1)</td>
</tr>
<tr>
<td></td>
<td>$\text{CO}_2$</td>
<td>16.9</td>
<td>19 (950)</td>
</tr>
</tbody>
</table>

aPositive and negative values indicate regeneration and consumption rates, respectively.
bNumbers outside and inside parentheses are ratios of consumption or regeneration rates of relevant species to regeneration rates of nitrate and phosphate, respectively.

were separately estimated (the lower half of Table 1). In this case, the oxygen consumption and the nitrate regeneration rates were estimated directly from Figure 2, and the contributions from the eddy-diffusional fluxes were not taken into account. Note that the ratio of the $\text{CO}_2$ production rate to the phosphate regeneration rate in the 70 m layer is calculated to be one-fourth that of the ratio in the entire hypolimnion (20–70 m).

4. Discussion

In the whole water column of the north basin of the Lake Biwa, the aerobic condition prevails throughout the stagnation period, and thus the metabolic activity of the hypolimnetic biota is dominated by aerophilic microbial decomposers. These decomposers are nourished with both dissolved and particulate organic material that is either produced autochthonously in the euphotic zone, or is somehow
introduced as allochthonous material. Regardless of its origin, the organic material, insofar as it is subject to the aerobic metabolism, is mineralized ultimately into carbon dioxide, nitrate and so forth at the expense of oxygen. The activity of the hypolimnetic biota in this basin should thus be reflected primarily in the oxygen consumption rate during the stagnation period. The production of nitrate in the series of aerophilic metabolism involves nitrification which is usually attributed to chemolithotrophic nitrifying bacteria. However, nitrification can be also regarded as one of the heterotrophic processes in the sense that the reducing power of the substrates for this process (NH$_4^+$ and NO$_2^-$) originates in the photosynthesis of plants. Therefore, we can conceptually include even the nitrifiers and other chemolithotrophs in the category of decomposers (Rich and WETZEL, 1978).

According to Eq. (1), the mineralization rate of organic carbon during aerobic decomposition in the hypolimnion can be estimated if both the consumption rate of oxygen and the regeneration rate of nitrate are known (Table 1). We can then compare the calculated mineralization rate of carbon in the hypolimnion with the primary production in this basin. According to NAKANISHI et al. (in press), the daily gross primary production in the euphotic zone of the north basin of Lake Biwa ranged 910–2,670 mg C•m$^{-2}$•d$^{-1}$, of which 23–38% was consumed by the respiration of phytoplankton itself, and 4–11% was excreted by phytoplankton as extracellular dissolved organic carbon. The mineralization rate of organic carbon within the hypolimnion estimated in this study (854 mmol•m$^{-2}$•mon$^{-1}$, see Table 1) is equivalent to 13–37% of the gross primary production, and 18–71% of the net primary production reported by NAKANISHI et al (in press). The hypolimnetic mineralization rate cannot be related immediately to primary production because the hypolimnetic decomposers may not utilize merely the products of autochthonous primary production, but also allochthonous organic material such as the debris of submerged vascular plants and fluvially introduced organic matter of terrestrial origin. Yet, since the magnitude of hypolimnetic metabolism was not so small compared with that of the primary production, it is expected that the activity of hypolimnetic decomposers might exert a significant influence on the primary productivity of this basin through regeneration of inorganic nutrients such as nitrate and phosphate.

The active regeneration of nitrate in the hypolimnion of the north basin of Lake Biwa has been previously supported by some authors on the basis that an abundant accumulation of nitrate was always observed in the hypolimnion during the stagnation period (KAWASHIMA et al., 1976; TEZUKA 1984; MITAMURA et al., 1987). A similar hypolimnetic accumulation of nitrate was observed again in this study (Fig. 1), with the concentrations of accumulated nitrate not differing significantly from the ones in the reports mentioned above. Nevertheless, the ratio of mineralized carbon to nitrogen calculated on the basis of Eq. (1) (Table 1) was proved to range 19–21, which was almost twice as high as the C : N ratio of the particulate organic material suspended in the hypolimnion (Fig. 3). Thus, it appears likely that the overall regeneration efficiency of organic nitrogen within the hypolimnion might not be as high as that of organic carbon.

Indeed, the hypolimnetic metabolism does not utilize only the particulate organic material but the dissolved one. According to TEZUKA et al. (unpublished data), the concentration of dissolved organic carbon was 6–9 times as high as that of particulate organic carbon in the hypolimnion of this basin, and was 1.1–1.8 times as high in the epilimnion as in the hypolimnion. Thus, it may be supposed that both the standing stock of dissolved organic material in the hypolimnion, as well as the diffusional supply of it from the epilimnion to the hypolimnion should have affected the hypolimnetic metabolism to some extent. However, since neither the C : N ratio nor the availability for microbial decomposers of the dissolved organic material has been determined yet, no further discussion is possible of the extent to which the high C : N ratio calculated for the mineralized organic
material (Table 1) should be attributed to the effect of dissolved organic material.

Alternative, or at least subsidiary, explanations for the above mentioned anomaly of the C:N ratios include selective mineralization of organic carbon in preference to organic nitrogen in the course of microbial decomposition of detrital material. This view has already been espoused based on the vertical change in the POC : PON ratio in the hypolimnion of this basin (Tezuoka, 1985). It has been also supported by laboratory experiments which revealed that bacteria could grow without releasing inorganic nitrogenous compounds if they were fed with substrate of a high C : N ratio (Tezuoka, 1990). However, to hypothesize that all the organic carbon and nitrogen introduced into the aquatic and sedimentary detrital food web is eventually mineralized into carbon dioxide and nitrate, the observed disproportionality in the C : N ratio can not be attributed solely to selective mineralization by bacterial decomposers. Therefore, it seems necessary, in explaining such a phenomenon by selective mineralization alone, to take account of the sequestration of some part of nitrogen from the detrital food web by some means either before or after mineralization. Likely mechanisms for such a process include: 1) sedimentation of a part of the particulate organic material, followed by immobilization of nitrogen within the sediment in preference to carbon, or 2) transformation of formerly regenerated nitrate into molecular nitrogen by denitrifiers. The latter process, had it occurred, should have resulted in an apparent but unreal low regeneration efficiency of nitrogen in the course of the calculation performed in Table 1.

In contrast to the gross accumulation of nitrate, phosphate barely accumulated within the hypolimnion during the stagnation period (Fig. 1). The calculated C : P ratios for organic material mineralized during the stagnation period (Table 1) were extremely high compared with the C : P ratio of suspended material (Fig. 3). These results suggested that phosphorus incorporated in the particulate organic material was hardly regenerated as dissolved phosphate in the water column. Similarly to the case of nitrogen, the selective retention of phosphorus in the course of bacterial decomposition of phosphorus-limited substrate (C : P > 60) has been demonstrated experimentally by Tezuoka (1990). Since the C : N ratio of suspended material always exceeded 60 (Fig. 3), the observed low regeneration efficiency of phosphate can be explained rationally by selective retention. One of the necessary consequences of the selective retention of phosphorus within suspended material is the concentration of phosphorus relative to carbon in the suspensoid. With this in mind, the observed increase in the content of particulate phosphorus in the whole water column during the holomixis period (Fig. 4) can be explained as a result of the vertical circulation of lake water inhibiting the deposition of phosphorus-concentrated particles which would otherwise be deposited in the sediment during the stagnation period.

It is evident as well, however, that a small but by no means negligible concentration of phosphate accumulated near the bottom mud during the stagnation period (Figs. 1 and 2). Such a phenomenon had been reported previously by Mitamura et al. (1987), but not by Kawashima et al. (1976) and Tezuoka (1984). Thus, such an accumulation of phosphate may be a consequence of recent eutrophication of this basin. The author inclines to the view that the accumulation of phosphate must have been brought about mainly by reductive dissolution of sedimentary ferric hydroxide-phosphate complexes caused by the prevalence of a reductive condition over the sediment during the stagnation period. The reason being that, 1) phosphate accumulation was confined within the vicinity of the water/mud interface (Fig. 1), and 2) the concentration of phosphate did not increase after July (Fig. 2). But it is also possible that microbiological decomposition of particulate organic material near the bottom may have regenerated phosphate, since the particulate material in the deepmost layer of the water column had a relatively low C : P ratio (Fig. 3). In particular, the regeneration efficiency of
phosphorus should be more or less enhanced when the bacterial population is consumed by phagotrophic organisms such as microflagellates (MIYAJIMA, in press), rather than when bacteria are the sole decomposers, as was the case in the experiments of TEZUKA (1990).

As seen in the above discussion, the regeneration rates of inorganic nutrients in the hypolimnion is not always proportional to the relative contents of the elements in the organic material that is supplied to the hypolimnion. Such a disproportionality is thought to be due, at least partially, to the physiological properties of hypolimnetic detrital food webs, such as the selective incorporation of limited elements or the phagotrophic activities. Thus, further basic and detailed information on the physiology and community structure of the hypolimnetic detrital food web is now needed to describe the mechanism of nutrient recycling and to predict its responses to eutrophication.

In particular, several essential aspects remain to be studied before attempting to depict the whole picture of hypolimnetic metabolism in Lake Biwa.

1) To appreciate the role of hypolimnetic metabolism in reference to the metabolism of the entire lake, contributions of both autochthonous and allochthonous inputs of organic material to the decomposing activity (e.g. oxygen consumption rate) in the hypolimnion must be distinctly elucidated.

2) To determine the exact regeneration efficiency of nitrogen, the origin, flux, C : N ratio, and availability for microbial decomposers of the dissolved organic material must be studied.

3) For the same purpose, quantitative information on the behavior of nitrogen after mineralization (i.e. nitrification and denitrification) is also needed.

4) To understand and predict the behavior of phosphorus, it seems necessary to study the role of the sediment/lake water interactions from both a chemical and biological point of view.

The last point is of special importance in relation to the management of the productivity and water quality in Lake Biwa, since this lake is phosphorus-limited, and any changes in the recycling efficiency of phosphorus may exert a profound effect on the lake's primary productivity.

Acknowledgements

The author is grateful to A. KAWABATA and O. KAWAI for technical assistance in the field. Some data of physical parameters used in this report were kindly given by T. UEDA. Critical comments on the manuscript by Prof. Y. TEZUKA, Kyoto University, are also acknowledged.

References


MAEDA, H., O. MITAMURA, T. KODAMA, M. EGUCHI,


(著者：宮島利宏，京都大学生態学研究センター，〒520-01 大津市下坂本4-1-23；Toshihiro Miyajima, Center for Ecological Research, Kyoto University, Shimosakamoto, Otsu 520-01.)

Received: 15 April 1991
Accepted: 13 September 1991