NH₄⁺ Regeneration and Uptake in Mesotrophic Lakes ; Diurnal and Seasonal Variations

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Abstract

We conducted ¹⁵NH₄⁺ dilution experiments to examine temporal variations in NH₄⁺ regeneration and uptake in the pelagic environments of mesotrophic Lakes Kizaki and Biwa. In Lake Kizaki, both NH₄⁺ regeneration and uptake rates showed no apparent diurnal periodicity during summer (July and August), and the regeneration : uptake ratio was close to one over the course of the day, suggesting that regeneration and uptake were tightly coupled regardless of light conditions. Size fractionation experiments showed that bacterial NH₄⁺ regeneration was substantial throughout the day, suggesting that a microbial loop was responsible for the rapid turnover of NH₄⁺. Seasonal measurements revealed that NH₄⁺ regeneration and uptake rates were highest in summer in both lakes. Correlation analyses indicated that temperature, nutrients and chlorophyll-*a* concentrations had little effect on the uptake rates. The regeneration : uptake ratio was close to one (0.95 ± 0.31 , $n=18$) despite large variations in nutrients and biological conditions, suggesting that phytoplankton usually take up regenerated NH₄⁺ as rapidly as they can. Our data provide direct evidence that biological regeneration in the euphotic zone is the dominant process in NH₄⁺ supply to phytoplankton in pelagic environments of mesotrophic lakes.

Key word : isotope-dilution, lakes, NH₄⁺ regeneration

1. Introduction

The ¹⁵N-isotope dilution technique (BLACKBURN, 1979 ; CAPERON *et al.*, 1979) is useful for determining *in situ* rates of NH₄⁺ regeneration and uptake simultaneously. During the past decade, this technique has been widely applied to the study of nitrogen cycling in marine environments (HARRISON, 1992). These studies have suggested that uptake of NH₄⁺ is generally well balanced by regeneration on a time scale of hours (HARRISON, 1992), although exceptions have been also observed in several environments. For instance, GLIBERT (1982) found a large excess of regeneration relative to uptake during a bloom of mixotrophic dinoflagellates in Vineyard Sound. HARRISON (1978) and GLIBERT *et al.* (1991) observed that the regeneration : uptake ratio (R/U ratio) increased along with an increase in the distance from shore to offshore in coastal environments.

Uncoupling of NH₄⁺ regeneration and uptake may occur on a daily scale. In the Sargasso Sea, GLIBERT (1982) found that regeneration and uptake rates were in balance during the day, whereas regeneration far exceeded uptake at night. Similarly, in the subarctic North Pacific, WHEELER *et al.* (1989) observed that NH₄⁺ uptake was highest during daytime, while regeneration took place only at night, resulting in diurnal fluctuations in ambient NH₄⁺ concentrations. WHEELER *et al.* (1989) suggested that diurnal periodicities of production and growth within microbial food webs were responsible for diurnal variations in NH₄⁺ regeneration, although the general validity of their findings has yet to be examined.

Very little is known about seasonal and diurnal variations in the balance between NH₄⁺ regeneration and uptake in freshwater environments. Several studies have suggested that NH₄⁺ is an important nitrogen source for

freshwater phytoplankton, and that the uptake rates of NH_4^+ may vary greatly on seasonal and diurnal time scales in response to changes in light, temperature, nutrient regimes, the composition of phytoplankton communities and other factors (TAKAHASHI and SAIJO, 1981; MCCARTHY *et al.*, 1982; BERMAN *et al.*, 1984; MITAMURA and SAIJO, 1986; MIYAZAKI *et al.*, 1987). However, variation in the couplings of NH_4^+ regeneration and uptake have been poorly understood in lake ecosystems (AXLER *et al.*, 1981; DODDS *et al.*, 1991). To our knowledge, no previous study has examined the diurnal dynamics of NH_4^+ regeneration in lakes.

Recently, HAGA *et al.* (1995) demonstrated apparent seasonal variations in NH_4^+ regeneration rates in Lakes Kizaki and Biwa. The purpose of our study was to examine whether regeneration can contribute to seasonal and diurnal variations in NH_4^+ uptake activity in these lakes.

2. Materials and methods

2-1. Study sites

Experiments were carried out at the center ($36^{\circ}33'\text{N}$, $137^{\circ}50'\text{E}$) of Lake Kizaki (surface area, 1.4 km^2 ; max. depth, 29 m) and at an off-shore station ($35^{\circ}10'\text{N}$, $135^{\circ}85'\text{E}$, depth, 40 m) in the north basin of Lake Biwa (surface area, 616 km^2 ; max. depth, 104 m). These lakes are both in a mesotrophic status, although chlorophyll-*a* concentrations and primary production rates indicate that Lake Kizaki is more eutrophic than Lake Biwa (see HAGA *et al.*, 1995).

2-2. Measurement of NH_4^+ regeneration and uptake rates

Diurnal variations in NH_4^+ regeneration and uptake rates was examined in the euphotic zone (2, 4, 6, and 8 m depths) during summer stratification period (23-24 July and 24-25 August 1991) in Lake Kizaki. Samples of lake water were collected usually with a Van-Dorn water sampler at four sampling periods (11:00, 17:00, 23:00 and 05:00). A portion of sample water was immediately filtered through a GF/F

filter (precombusted at 450°C for $>4 \text{ hr}$) to analyze NH_4^+ , NO_3^- and chlorophyll-*a* concentrations at the beginning of the incubation. The filters and filtrates were frozen and stored at -20°C . Remaining sample water was contained in acid-washed clear 21-polycarbonate bottles, supplemented with $^{15}\text{NH}_4^+$ (atom% $^{15}\text{N}=99.7\%$ Shoko Tsusho Co. Ltd., final concentration of $0.05 \mu\text{M}$), and incubated *in situ* for 2.5 hours. The incubation was terminated by filtering the sample water through GF/F filters. The filters were dried over night at 55°C and used for determining the concentration of particulate nitrogen (PN) (see below). The filtrate was stored in a freezer (-20°C) for later analysis of the concentration and ^{15}N content of NH_4^+ at the end of the incubation (see below). In order to determine NH_4^+ regeneration and uptake rates by bacteria (at 2 m in August), lake water was filtered by gravity through a Nuclepore filter (pore size $1.0\text{-}\mu\text{m}$), then incubated as described above.

Seasonal variations in NH_4^+ regeneration and uptake rates were examined in Lake Kizaki (4 m in 1991 and 2 m in 1992) and Lake Biwa (2.5 m in 1992). Incubation protocols corresponded to those as described above except that incubation times were 2-24 hours depending on temperature. Duplicate or triplicate bottles were used for each measurement, except for a single incubation bottle used in Lake Kizaki in 1991.

Rates of NH_4^+ regeneration and uptake were calculated by Blackburn-Caperon equations (BLACKBURN, 1979; CAPERON *et al.*, 1979). Atom % $^{15}\text{NH}_4^+$ of initial samples was calculated from ambient NH_4^+ concentrations and the amount of supplemented tracer solution. Atom % $^{15}\text{NH}_4^+$ of incubated sample water was determined by mass spectrometry after indotymol extraction (HAGA and SAKAMOTO, 1995).

2-3. Chemical analysis

Concentration of NH_4^+ was determined by a phenol-hypochlorite reaction method (SAGI, 1966). Concentrations of NO_3^- and NO_2^- were determined by Technicon Auto Analyzer II

(OTSUKI, 1978). Chlorophyll-*a* concentration was determined after the method of MARKER *et al.* (1980). Concentration of PN was determined by a mass spectrometer (ANELVA, TE-150) equipped with combustion-and reduction furnaces (OTSUKI *et al.*, 1983).

3. Results and discussion

3-1. Diurnal variations in NH₄⁺ regeneration and uptake rates in Lake Kizaki

Diurnal variations in NH₄⁺ regeneration and uptake rates were examined during summer (23–24 July and 24–25 August 1991) in Lake Kizaki. The euphotic zone depths (Secchi depth × 2.5) were 8.8–10 m in both experiments. Figures 1 and 2 show nutrients, PN and chlorophyll-*a* concentrations at each sampling time in July and August, respectively. In July, NH₄⁺ concentrations were low ($\leq 0.2 \mu\text{M}$) at every sampling

depth throughout the day. Concentrations of NO₃⁻, PN and chlorophyll-*a* were changed little most of sampling periods. In August, NH₄⁺ concentrations were low ($\leq 0.3 \mu\text{M}$) at 2 and 4 m throughout the day, while significantly increasing from midday to evening at 6 m. NO₃⁻ concentrations varied greatly at 8 m, suggesting a sporadic event such as an upwelling may have occurred at this layer. Chlorophyll-*a* concentrations at 2 m increased from 8 $\mu\text{gchl}\cdot\text{l}^{-1}$ to 18 $\mu\text{gchl}\cdot\text{l}^{-1}$ during midday-evening but were relatively constraint for the following periods.

Figure 3 shows diurnal variations in NH₄⁺ regeneration and uptake rates in July (Fig. 3 A) and August (Fig. 3 B). We found no apparent variations in diurnal patterns for either NH₄⁺ regeneration or uptake rates in these experiments. The percentages of regeneration and uptake rates relative to corresponding values obtained at the initial sampling period (11:00)

Fig. 1. Diurnal variations in nutrients, PN and chlorophyll-*a* concentrations on 23–24 July 1992 in Lake Kizaki. Symbols represent ; ○: 2 m, ●: 4 m, ▽: 6 m, and ▼: 8 m.

Fig. 2. As in Fig. 1, but on 24–25 August 1991 in Lake Kizaki.

did not differ significantly (Student *t*-test, $P > 0.05$) from 100 throughout the day (Table 1). Regeneration and uptake rates of NH_4^+ at 8 m depth were highly variable (data not shown), and these values were omitted in this calculation because we suspect that this variation was caused by unintentional sampling of epilimnion water due to internal waves.

We found that R/U ratios were close to one (range 0.53–1.56, average 0.93 ± 0.22 ; Table 1) over the course of the day, suggesting that phytoplankton (and presumably bacteria) successively took up regenerated NH_4^+ throughout the day in Lake Kizaki. Consistent with this, ambient NH_4^+ concentrations varied little

during the sampling periods except in one case (at 6 m in August, Table 2). The minimal responses of NH_4^+ uptake to diurnal variations in light intensity in Lake Kizaki apparently contradict with previous propositions that NH_4^+ uptake activity of phytoplankton depends on light intensity in both culture (SYRETT 1962) and lake environments (BERMAN *et al.*, 1984; MIYAZAKI *et al.*, 1987). However, our results are consistent with findings by TAKAHASHI and SAIJO (1981) and MITAMURA and SAIJO (1986), respectively, who examined diurnal variations in N uptake rates in Lakes Kizaki and Biwa. TAKAHASHI and SAIJO (1981) demonstrated the NH_4^+ uptake rates at night were as high as 70 % of those during daytime. MITAMURA and SAIJO (1986) suggested that uptake rates of NH_4^+ were only moderately (20–30 %) higher during the day than at night, although those of NO_3^- during the day were substantially (4–5 fold) greater than those at night. Because NH_4^+ may account for ≥ 80 % of total nitrogen uptake in Lake Kizaki during summer (TAKAHASHI and SAIJO, 1981), continuous uptake of NH_4^+ in the dark (Table 1) would indicate that nitrogen assimilation is not tightly coupled with photosynthetic carbon assimilation by phytoplankton in this lake. MIYAZAKI *et al.* (1987) suggested that carbohydrate produced during the daytime and stored in phytoplankton cells may be converted to nitrogen-containing compounds at night, presumably leading to the assimilation of NH_4^+ to cell biomass in the dark.

Recent studies suggest that marine bacteria take up NH_4^+ in oceanic (WHEELER and KIRCHMAN, 1986) and coastal (TUPAS and KOIKE, 1991) environments. If that was also the case in our study, bacteria may contribute to NH_4^+ uptake at night. HAGA *et al.* (1995) found significant NH_4^+ uptake activity in the $<1\text{-}\mu\text{m}$ fraction in summer in Lake Kizaki, while the uptake rates were less than 50 % of the regeneration rates. Furthermore, they stated that the uptake rates in the $<1\text{-}\mu\text{m}$ fraction should be overestimated because of the contribution of phytoplankton in this size fraction and the relative high concentration of tracer (0.5

A. 23–24 July

B. 24–25 August

Fig. 3. Diurnal variations in NH_4^+ regeneration and uptake rates in July and August in Lake Kizaki. Symbols represent: ○: 2 m, ●: 4 m, ▽: 6 m, and ▼: 8 m.

Table 1. Diurnal variations in rates of NH₄⁺ regeneration, uptake, and R/U ratio in the euphotic zone of Lake Kizaki in July and August 1991. Figures represent percentages of regeneration and uptake relative to corresponding value obtained at initial sampling period (11:00). Data in the euphotic zone (2, 4, and 6 m) were pooled. Errors are standard deviation (SD, *n*=3).

Sampling periods	Regeneration (%)	Uptake (%)	R:U
23-24 July			
11:00	100	100	0.8±0.2
17:00	138± 57	100±15	1.0±0.2
23:00	187±123	113±45	1.2±0.4
05:00	126± 77	89±16	1.0±0.2
24-25 August			
11:00	100	100	0.8±0.2
17:00	110±29	88±17	1.0±0.1
23:00	73±33	66±32	0.9±0.2
05:00	68±27	63±30	0.8±0.1

Table 2. Concentrations of NH₄⁺ (μM) at each sampling period and depth in the experiments shown in Table 1. Figures in parentheses represent standard deviations (*n*=3).

	Sampling period	Depth		
		2m	4m	6m
23-24 July	11:00	0.13 (<0.01)	0.16 (<0.01)	0.18 (0.06)
	17:00	0.16 (0.06)	0.01 (0.04)	0.16 (0.10)
	23:00	0.16 (0.03)	0.11 (0.04)	0.12 (0.03)
	05:00	0.12 (0.04)	0.10 (<0.01)	0.15 (0.05)
24-25 August	11:00	0.25 (0.07)	0.24 (0.05)	0.36 (0.02)
	17:00	0.25 (0.04)	0.28 (0.05)	0.82 (0.01)
	23:00	0.25 (0.03)	0.30 (0.02)	1.03 (0.06)
	05:00	0.32 (0.06)	0.37 (0.06)	1.24 (0.05)

μM). In Lake Kizaki in August 1991, bacterial NH₄⁺ regeneration rates did not increase significantly at night (see below), and the contribution to total NH₄⁺ regeneration rates was ≤30 % (see below). Thus bacteria may not be responsible for continuous NH₄⁺ uptake during night in this lake during summer.

Tight coupling of NH₄⁺ regeneration and uptake throughout the day in Lake Kizaki are in high contrast to with previous results from oceanic marine environments (GLIBERT, 1982; WHEELER *et al.*, 1989), which indicated that R/U ratios are substantially higher at night than during the day (as much as *a*≥40 fold

difference). WHEELER *et al.* (1989) found that NH₄⁺ regeneration took place only at night in the subarctic North Pacific. They postulated that diurnal changes in activity of bacteria and heterotrophic nanoflagellates, major bacterivorous grazers, caused diurnal periodicity in NH₄⁺ regeneration in this region. HAGA *et al.* (1995) demonstrated that bacteria are the second most important components of heterotrophic communities in NH₄⁺ regeneration in Lake Kizaki during summer, accounting for 25-38 % of total NH₄⁺ regeneration during July-September 1992. To test whether bacteria exhibit diurnal variations in NH₄⁺ regeneration, we conducted

Fig. 4. Diurnal changes in NH_4^+ regeneration rates in total (○) and $<1\text{-}\mu\text{m}$ size fraction (●) at 2 m depth in Lake Kizaki. Experiments were carried out on 24–25 August 1991.

^{15}N -isotope dilution experiments using the lake water prefiltered through $1\text{-}\mu\text{m}$ -pore size Nucleopore filters (2 m depth, 24–25 August, Fig. 4). Bacteria accounted for substantial fraction (16–30 %) of total NH_4^+ regeneration in this experiment. Our measurements, based on single-bottle incubation, did not allow us to make statistical comparisons for each rate of NH_4^+ regeneration in the $<1\text{-}\mu\text{m}$ fraction. Nevertheless, the coefficient of variation (C.V., standard deviation/average $\times 100$) calculated for daily estimates of regeneration rates (17 %, $n=4$) was relatively small compared to the CV that we observed in our measurements of NH_4^+ regeneration in the $<1\text{-}\mu\text{m}$ fraction with triplicate bottles (4–80%, mean = $28 \pm 26\%$, $n=7$, HAGA *et al.*, 1995). Thus, our measurements led us to conclude that bacterial NH_4^+ regeneration did not vary significantly over the course of the day. This conclusion implies that daily scale regulation mechanisms of NH_4^+ regeneration rates in Lake Kizaki may differ from those in the subarctic North Pacific, in which bacterial NH_4^+ regeneration may be significant at night but not during the day (WHEELER *et al.*, 1989).

Less pronounced diurnal variations in bacterial NH_4^+ regeneration in Lake Kizaki (Fig. 4) could be due to the supply of nitrogen-rich, labile-dissolved organic matter that fuels bacterial production and NH_4^+ regeneration activity. Recent studies have stressed the importance of dissolved organic nitrogen production to nitrogen cycling in aquatic ecosystems (*e.g.*, BRONK

et al., 1994), although the source and dynamics of dissolved organic matter have been poorly understood (NAGATA and KIRCHMAN, 1992). Further examination emphasizing the relationships between bacterial growth and labile dissolved organic nitrogen (*e.g.*, dissolved-free and combined amino acids, SIMON and ROSENSTOCK, 1992) is needed to clarify the mechanisms of NH_4^+ regeneration in aquatic environments.

3-2. Seasonal variation in NH_4^+ regeneration and uptake rates in Lakes Kizaki and Biwa

Seasonal variations in NH_4^+ regeneration and uptake rates were examined in Lakes

Fig. 5. Seasonal variations in NH_4^+ regeneration and uptake rates and related parameters in Lake Kizaki (4 m depth in 1991 and 2 m depth in 1992). A: temperature, B: NH_4^+ (▽) and NO_3^- (▼) concentrations, C: Chlorophyll-*a* (□) and PN (■) concentrations, D: rates of NH_4^+ regeneration (◇) and uptake (◆).

Fig. 6. As in Fig. 5, but in Lake Biwa. Sampling depth was 2.5 m.

Table 3. Regression analyses among rates of NH₄⁺ regeneration, uptake, chlorophyll-specific uptake rates and relative parameters. RNH₄⁺: regeneration rate, PNH₄⁺: uptake rate, sPNH₄⁺: chlorophyll-specific uptake rate (μmol·μgchl⁻¹·h⁻¹). [NO₃⁻] and [NH₄⁺], respectively, represent concentrations. Sample numbers are *n*=18.

	RNH ₄ ⁺	PNH ₄ ⁺	sPNH ₄ ⁺
Temp.	0.49*	0.64*	0.27
Chlorophyll.	0.25	0.29	—
[NO ₃ ⁻]	-0.31	-0.39	-0.09
[NH ₄ ⁺]	-0.10	-0.23	0.25
RNH ₄ ⁺	—	0.94*	0.21

* *P* < 0.05

Kizaki (1991-1992) and Biwa (1992). During the study periods, water temperature varied in the range of 8.1-24.4°C in Lake Kizaki and 17.4-27.7°C in Lake Biwa. Thermal stratification developed in early summer and persisted during the study periods in both lakes (data not shown). The regeneration and uptake rates and related parameters in these lakes are shown in Figures 5 and 6. PN and chlorophyll-*a* concentrations in Lake Biwa (2.4-6.2 μgchl·l⁻¹ and 3.8-9.6 μM, Fig. 6 C) were generally lower than those in Lake Kizaki during summer-late autumn (6.5-23.4 μgchl·l⁻¹ and 7.8-13.3 μM, Fig. 5 C). However, NH₄⁺ and NO₃⁻ concentrations were similar in both lakes. In Lake Kizaki, NH₄⁺ concentrations continuously decreased from April (6 μM) to July (0.2 μM) and remained at low levels (≤0.3 μM) during July-September 1991. They were frequently low (≤0.3 μM) during May-December 1992 except for two days (0.6 μM on August 26 and 1.0 μM on September 12). In Lake Biwa, NH₄⁺ concentrations were less than 0.5 μM except on August 31 (1.0 μM). Concentration of NO₃⁻ was usually ≥1.0 μM (1.0-11.1 μM) in both lakes except for one period (0.3 μM in July in Lake Biwa).

Rates of NH₄⁺ regeneration (0.01-0.27 μmol·l⁻¹·h⁻¹) and uptake (<0.01-0.27 μmol·l⁻¹·h⁻¹) showed remarkable seasonality, reaching a maximum in summer in Lake Kizaki (Fig. 5 D). Those rates were highest in August and the lowest in November in Lake Biwa (Fig. 6 D). These results agree with previous studies that found the high uptake rate and short turnover time (less than 10 hr.) of NH₄⁺ during midsummer in Lakes Kizaki (TAKAHASHI and SAIJO, 1981) and Biwa (MITAMURA and SAIJO, 1986).

We tested whether temperature, nutrients and chlorophyll-*a* concentrations affected NH₄⁺ regeneration and uptake rates (Table 3). Correlation analyses indicate that NH₄⁺ uptake rates correlated positively with temperature (*P* < 0.05, *n* = 18, *r* = 0.64) but the chlorophyll-*a*-specific NH₄⁺ uptake rate (μmol·μgchl⁻¹·h⁻¹) did not (*P* > 0.1, *r* = 0.24), suggesting that temperature did not directly affect NH₄⁺ uptake activity. Concentrations of NH₄⁺, NO₃⁻ and

chlorophyll-*a* may not be important factors for regulating NH_4^+ uptake activity in Lakes Kizaki and Biwa. Rate of NH_4^+ uptake correlated well with the regeneration rates ($P < 0.01$, $r = 0.94$, Table 3) and the regeneration: uptake ratio (R/U ratio) was close to one (0.95 ± 0.31) throughout the study periods. These results suggest that NH_4^+ uptake rate may be regulated principally by the NH_4^+ regeneration rate in the euphotic zone of both lakes. Our results provide direct evidence that the high NH_4^+ requirement of phytoplankton in Lakes Kizaki and Biwa is indeed fulfilled by NH_4^+ actively regenerated in the water column (TAKAHASHI and SAIJO, 1981; MITAMURA and SAIJO, 1986). This conclusion agrees well with the results in marine (HARRISON, 1992) and oligotrophic lake (AXLER *et al.*, 1981; DODDS *et al.*, 1991) environments.

Although transport of NH_4^+ from river, sediment, and atmospheric depositions would be significant under certain circumstances, external inputs of NH_4^+ were presumably insignificant, as evidenced by the fact that NH_4^+ in the incubation bottles changed little during the incubation.

It should be noted that the ^{15}N -isotope dilution approach examines regeneration and uptake on a time scale of hours (incubation time in this study = 2–24 hr), which may not account for changes in NH_4^+ concentrations on a longer time scale. For example, our results showing a decrease in ambient NH_4^+ concentration from 6.0 to 1.0 μM between April and May in Lake Kizaki (Fig. 5 B) could result from the difference in regeneration and uptake rates of $0.005 \mu\text{mol} \cdot \text{l}^{-1} \cdot \text{h}^{-1}$, a difference too small to be detected by our experimental methods.

The close coupling of high rates of regeneration with uptake was observed under low NH_4^+ concentrations and high chlorophyll-*a* concentrations during the summer (June–October in Lake Kizaki and July–November in Lake Biwa). This suggests that ambient NH_4^+ concentrations were far below the saturation level of the uptake activity of phytoplankton during this period. Then, short turnover time of NH_4^+ (0.5–9.3 hr) during summer-autumn is another

indication that NH_4^+ regeneration rates may determine the upper-limit of NH_4^+ uptake by phytoplankton (and presumably bacteria) in this period.

It would be difficult to explain why regeneration was well balanced by uptake during the "pre-bloom" period in Lake Kizaki (April–May 1991), when ambient NH_4^+ concentrations were high (up to 6.0 μM , Fig. 3 B, D). Since the half-saturating constant for NH_4^+ uptake by phytoplankton has been generally reported to be in the range of 0.05–1.1 μM (BERMAN *et al.*, 1984), the short-term coupling of NH_4^+ regeneration and uptake at high NH_4^+ concentrations would hardly be explained by the rapid utilization of regenerated NH_4^+ by phytoplankton. In marine environments, GLIBERT (1982) reported a similar phenomenon, i.e., uptake and regeneration were approximately equal when NH_4^+ concentrations $> 1 \mu\text{M}$. Although the mechanisms of this equilibrium are unclear, we point out that the balance of NH_4^+ regeneration and uptake in high NH_4^+ concentration regimes could have potentially important implications for understanding phytoplankton succession and new production (DUGDALE and GOERING, 1967). This is because high NH_4^+ concentrations would inhibit the use of NO_3^- (McCARTHY *et al.*, 1977, 1982; TAKAHASHI and SAIJO, 1981), leading to a shift in phytoplankton community composition (EPPLEY *et al.*, 1979). Further investigations into the relationship between phytoplankton species composition and nitrogen dynamics are required to address these issues in greater detail.

4. Conclusion

Our diurnal and seasonal measurements of NH_4^+ regeneration and uptake rates in Lakes Kizaki and Biwa clearly indicate that zooplankton excretion and microbial mineralization of organic compounds should be the major supply route for NH_4^+ in the euphotic zone of mesotrophic lake environments. HAGA *et al.* (1995) previously reported that the microbial food web constructed by bacteria and bacterivorous nano- and micrograzers accounted for up to 98% of the total NH_4^+ regeneration in both

lakes. They suggested that weight-specific NH₄⁺ regeneration rates by bacteria increased substantially with increase of temperature (HAGA *et al.*, 1995). Furthermore, measurements of the bacterial utilization of dissolved amino acids have suggested that the rates of NH₄⁺ regeneration by bacteria could reach high levels during the summer stratification period in Lake Constance (ROSENSTOCK and SIMON, 1994). These findings imply that bacterial NH₄⁺ regeneration is generally accelerated during the summer stratification period, which largely influences seasonal patterns of NH₄⁺ regeneration in lakes. Close association between NH₄⁺ regeneration and uptake in Lakes Kizaki and Biwa indicate that bacteria may play a key role in nitrogen cycling within the euphotic zone of mesotrophic lake ecosystems.

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摘 要

中栄養湖に於けるアンモニアの再生と 取り込み；日周変化及び季節変化

中栄養な環境にある木崎湖と琵琶湖でアンモニアの再生速度と取り込み速度の日周変化及び季節変化を、¹⁵N-同位体希釈法を用いて調べた。

木崎湖で夏(7月及び8月)にアンモニアの再生速度と取り込み速度の日周変化を調べたところ、いずれの速度も明確な日周変動パターンを示さず、再生速度：取り込み速度比(R:U比)は一日を通して常にほぼ1になった。この結果は、木崎湖では夏の間、有光層中に再生されたアンモニアが、光の強度に関係なく速やかにプランクトン群

集によって消費されることを示している。サイズ分画法を用いて <1 μm 画分のアンモニア再生速度の日周変化を8月に測定したところ、再生速度は一日を通じてほとんど変化せず、バクテリアとその捕食者群集が速やかなアンモニアの回転の原動力となっていたと考えられた。

木崎湖と琵琶湖でアンモニアの再生速度と取り込み速度の季節変動を調べたところ、いずれの湖においても両速度が夏に最大となることが見いだされた。回帰分析の結果、水温や栄養塩濃度、クロロフィル濃度はアンモニアの取り込み速度を規定する重要な要因とはなっていなかった。水温、栄養塩やクロロフィル濃度の変動に関わらず、木崎湖と琵琶湖では常にアンモニアの取り込み速度と再生速度の比がほぼ1 (0.95 ± 0.31 , $n=18$)となり、植物プランクトンは有光層中に再生されたアンモニアを常に最大限の速度で取り込んでいることが明らかになった。

本研究の結果は、中栄養湖でも貧栄養湖や海洋と同様に、植物プランクトンに対する主要なアンモニアの供給過程が有光層中の生物群集が行うアンモニアの再生であることを示している。

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