Korean J. Limnol. 42 (1) : 48~57 (2009)

Photosynthetic Activity of Epiphytic Algae in Embayment Reed Zone in a Lagoon Connected with Lake Biwa

Osamu Mitamura*, Junji Tachibana[1], Noriko Ishida[2], Yasushi Seike[3] and Jun-Kil Choi[4]

(Limnological Laboratory, School of Environmental Science, University of Shiga Prefecture, Hikone 522-0057, Japan

[1]Department of Science, Osaka Prefectural Education Center, Sumiyoshi-ku, Osaka 558-0011, Japan

[2]Faculty of Literature, Nagoya Women's University, Tenpaku-ku, Nagoya 468-8507, Japan

[3]Department of Material Science, Faculty of Science and Engineering, Shimane University, Matsue 690-8504, Japan

[4]Department of Biological Science, Sangji University, Wonju 220-702, Korea)

Primary production of epiphytic and planktonic algae in a shallow reed zone of a lagoon Nishinoko was investigated. Concentrations of nutrients varied widely horizontally and locally in the lagoon. It seems that the reed zone has a heterogeneous environment. The photosynthetic rates of epiphytic and planktonic algae were 7 to 14 mg C surface stem m^{-2} hr^{-1} and 12 to 46 mg C m^{-3} hr^{-1}, respectively. The areal primary production of epiphytic algae was estimated as 4 to 13 mg C m^{-2} hr^{-1} from the stem density of *Phragmites* and the water depth at each station. The production of phytoplankton, on the other hand, was 5 to 56 mg C m^{-2} hr^{-1}. The contribution of epiphytic algae to total primary production averaged 53%, although the assimilation number was much lower than that of phytoplankton. The present results indicate that the epiphytic algae are one of the significant primary producers in the reed zone.

Key words : epiphytic algae, photosynthesis, reed zone, lagoon, Lake Biwa

INTRODUCTION

In shallow near-shore areas, a dense biomass of *Phragmites* and epiphytic algae on submerged parts of its stems are observed. Epiphytic algae contribute to the primary production and biogeochemical cycle in the reed zone. In a lagoon Nishinoko connected with Lake Biwa, *Phragmites communis* covers an area of 1.1 km^2, and comprises almost of macrophytes. In the reed zone, *Phragmites* has a large substratum for epiphytic algal colonization throughout the year. In the littoral zone of lagoons, the standing crop of these epiphytic algae is generally higher than that of phytoplankton. Accordingly, the reed zone is an important area for the study of biogeochemical dynamics in a freshwater ecosystem.

The contribution of the epiphytic algae to primary production is related to the available surface area of reed stems as the periphytic substratum. The photosynthetic rate of periphyton has been investigated in freshwater lakes (Duthie and Jones, 1990; Maltais and Vincent, 1997; Nozaki, 2001; Ishida *et al*., 2006) and rivers (Aizaki, 1980; Hill and Boston, 1991). The measurement of epiphytic primary production on reed stems has been studied by several workers (e.g., Cat-

*Corresponding author: Tel: +81-749-28-8261, Fax: +81-749-28-8247, E-mail: mitamura@ses.usp.ac.jp

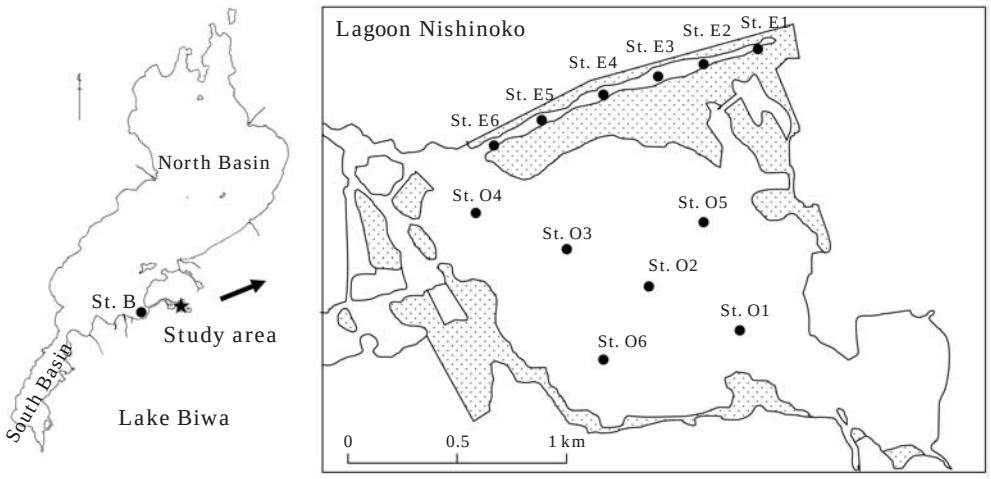

Fig. 1. Investigation stations in the embayment and open water areas in a lagoon Nishinoko connected with Lake Biwa. Dotted areas indicate the reed zones.

taneo and Kalff, 1980; Allen and Ocevski, 1981; Rjber *et al*., 1984; Müller, 1995, 1996; Liboriussen and Jeppesen, 2003). Assimilation number, light-saturated chlorophyll *a* specific photosynthetic rate, seems to be effective parameter for comparison among the algal photosynthesis in different environments, as denoted by Harrison and Platt (1978), although the values might fluctuate by their environmental parameters such as water temperature (Eppley, 1972; Harrison and Platt, 1980), irradiance (Müller, 1995, 1996), nutrient limitation (Eppley, 1972; Harrison and Platt, 1980), and algal species and its size (Mandelli *et al*., 1970; Glooschenko *et al*., 1974; Malone, 1977).

The aim of this study has been to provide information on the photosynthetic activities of epiphytic and planktonic algae and the contribution of epiphytic algae to the primary production in a shallow embayment area of a lagoon Nishinoko connected with the north basin of Lake Biwa.

STUDY AREA AND METHODS

1. Study site and sampling procedure

A lagoon Nishinoko (35° 26′N, 136° 07′E) is the largest lagoon around Lake Biwa, covering an area of 2.8 km^2 with a maximum depth of 4 m (Fig. 1). The present investigations were conducted out at typically large-scale reed zone. The field observations were conducted on calm days at the narrow embayment stations (Sts. E1～E6), where the *Phragmites* zone extended from land to water, in October, 1997. The distance between stations in embayment area was put in short space because the environmental conditions varied widely at respective stations. St. E1 locates inmost area but St. E6 is the gateway area of the embayment, connected with open area of the lagoon. A eutrophic embayment water area covers an area of 0.082 km^2, having the reed zone of 0.065 km^2 with density of 200 stem m^{-2}. The water depth of submerged portion of the stems was 0.3～0.5 m, and the bottom sediments were composed of mud. The Sts. O1～O6 in an open water area in Nishinoko and St. B in a littoral area of Lake Biwa were also placed as a reference.

The *Phragmites* generally remains for three years. The old submerged stems accounted for approximately half of the total reed stems during the investigation period. The standing crop of epiphytic algae on old reed stems was generally greater than that on new reed stems, a similar tendency to the results by Rjber *et al*. (1984). Accordingly, the reed stems employed in this investigation were chosen proportionally in the ratio of new to old numbers. At each station, both new and old stems of *Phragmites* were cut above the rhizomes and returned to the laboratory. The substrate section used was a length of approximately 5 cm. Low chlorophyll *a* (Chl. *a*) amounts on the reed stems were observed near the water surface and just above the sediment. Müller (1995) denoted a similar vertical variation in the epiphytic algal Chl. *a* on *Phragmites*. Therefore, random sections of the stem were used for the experi-

ments.

2. Determination of photosynthetic rate by epiphytic algae

It is difficult to operate for the estimation of accurate photosynthetic rate by attached algal community on the biotic substrate under natural aquatic environments. In general, two procedures have been examined, such as rubbing the attached algal community from artificial substrates after incubation for photosynthesis measurement (Allen, 1971; Tanimizu *et al*., 1981) and scrapping from the biotic substrates before incubation (Hickman and Klarer, 1973; Hooper and Robinson, 1976; Mitamura and Tachibana, 1999). In a preliminary examination before the present experiments, the submerged parts of reed stems were cut into several sections and placed in incubation bottles for a determination of the photosynthetic rate of epiphytic algae. The results provided higher photosynthetic rates, caused likely by the enriching effects of nutrients exuded from the cut sections. Therefore, in the present study the latter procedure, stripping from the reed stems, was employed for the determination of photosynthetic rate of epiphytic algae on *Phragmites* stems. The epiphytic substances were gently removed from the surface of reed stems using a paintbrush with filtered lagoon water through a glass fiber filter (Whatman GF/F). The stripped epiphyton was subdivided for photosynthesis measurement and chemical analyses.

It is a complicated procedure to manage the water movement for a determination of the photosynthetic rate. Mitamura and Tachibana (1999) indicated that there were no appreciable difference between the photosynthetic rates in the samples of low epiphytic algal concentrations (less than 50 mg chl. *a* m^{-3}) and the rates under water movement using no stripped epiphytic algae. The influence of the removal of epiphytic algae from the substrate before incubation was reduced by this dilution technique. In the present study, therefore, the dilute samples were used to determine the photosynthesis of epiphytic algae. The damage to epiphytic algae caused by stripping them off the substrate may occur. But in the present investigations, the damage was minor for the photosynthetic rate and assimilation number.

The photosynthetic rate of epiphytic algae on the surface of reed stems was determined in the laboratory incubator by the radiocarbon method (Steemann Nielsen, 1952). An appropriate amount of epiphytic algae was suspended in filtered lagoon water taken from the reed zone through a glass fiber filter (Whatman GF/F). Water samples containing epiphytic algae were poured into two series of clear glass bottles and inoculated with ^{14}C bicarbonate solution to a final concentration of 185 kBq L^{-1}. The transparent (light) and dark bottles were incubated under 400 μ Einst m^{-2} sec^{-1} using daylight-type fluorescent lamps in a water tank at a water temperature similar to that of the sampling station. After four hours of incubation, biological activity was terminated by adding formaldehyde solution. Sample water in each glass bottle was then filtered through a membrane filter (Millipore HA type). The filter was put in a scintillation vial with 10 mL of scintillation fluid (BRAY, 1960). The radioactivity was then measured with a liquid scintillation spectrometer (Aloka LSC-651). The photosynthetic rates of phytoplankton in water of the reed zone and the open area in Nishinoko were measured in the same way as in the photosynthetic measurement of epiphytic algae. The value under saturated level of irradiance in the present investigation seemed to indicate the maximum photosynthetic rate. The concentration of total carbon dioxide in the sample water was determined with an infra-red carbon dioxide analyzer (Beckman 864), as described by Satake *et al*. (1972).

3. Chemical analyses

No appreciable vertical changes in the chemical parameters were observed in advance of the present investigations. The water samples were collected with a plastic pail from surface layer at respective station, and then used for the measurement of general physicochemical parameters (water temperature, pH, electric conductivity and dissolved oxygen), nitrogenous, phosphorus and silicious nutrients, and particulate carbon and Chl. *a*. Phytoplankton samples were collected with a plastic pail from surface layer. After collection, the phytoplankton were immediately preserved by adding concentrated formaldehyde solution (approximately 0.2% solution as final concentration), and stored in a refrigerator to await microscopic counting and identification of species.

The standing crop of epiphytic algae on the reed stems and planktonic algae were estimated in

Table 1. Concentrations of nitrogenous (TNN : sum of ammonia, nitrite, nitrate and urea nitrogen), phosphorus (DIP : phosphate phosphorus) and silicious (DSi : silicate silicon) nutrients at Sts. E1～E6 (embayment water area) and Sts. O1～O6 (open water area) in a lagoon Nishinoko, and at St. B in a littoral area of Lake Biwa. Data shows an average value with standard deviation.

	Embayment area (Sts. E1～E6)	Open area (Sts. O1～O6)	Lake Biwa (St. B)
TNN ($\mu g\ N\ L^{-1}$)	83±17	860±127	134
Ammonia ($\mu g\ N\ L^{-1}$)	26±6	65±47	16
Nitrite ($\mu g\ N\ L^{-1}$)	4±1	13±3	10
Nitrate ($\mu g\ N\ L^{-1}$)	35±8	751±93	102
Urea ($\mu g\ N\ L^{-1}$)	17±5	23±6	7
DIP ($\mu g\ N\ L^{-1}$)	21±2	36±7	16
DSi ($mg\ N\ L^{-1}$)	4.5±0.7	6.4±0.3	1.7

terms of Chl. *a*. Chl. *a* concentration was measured, using 90% acetone as the extraction solvent according to the method of SCOR/Unesco (1966). Epiphytic or particulate carbon (EC or PC) was determined with a CHN Corder (Yanaco MT-5 type).

To determine the concentration of nutrients, dissolved organic matter and particulate matter, the collected water samples were immediately filtered through glass fiber filters (Whatman GF/F) treated by ignition at 420°C. The filters and filtrates were then stored at −20°C in a deep freezer until chemical analyses in the laboratory. The sample for the determination of silicate was filtered through a paper filter (Toyo No. 5C) and stored in a refrigerator.

Water temperature was taken with a thermistor-thermometer (Tohodentan type ET-5). The pH was measured with a pH meter (Yokogawa PH-82). Electric conductivity with a conductivity meter (Yokogawa model SC-51), and was equated to the value at 25°C. Dissolve oxygen was estimated by a Winkler technique according to Golterman *et al.* (1978). Ammonia was determined by the method described by Sagi (1966), nitrite after Bendschneider and Robinson (1952), nitrate after Wood *et al.* (1967), urea after Newell *et al.* (1967), phosphate (DIP) after Murphy and Riley (1962), and silicate (DSi) was analyzed according to Mullin and Riley (1955).

RESULTS AND DISCUSSION

1. General physicochemical features

Transparency (Secchi disk depth) ranged from 0.8 to 1.1 m in the embayment water area but high values of 1.3 to 1.8 m in the open areas in Nishinoko lagoon. Water temperature ranged from 19.6 to 20.8°C and 19.5 to 19.9°C, pH value 6.4 to 7.6 and 6.7 to 7.2, respectively. The water samples were almost saturated with dissolved oxygen at all stations, namely 82 to 107%. Conductivity was different in each observation stations, taking 7.9 to 14.9 $mS\ m^{-1}$. Low values were recorded at stations in the narrow embayment section. These values in the lagoon Nishinoko were high compared with those obtained at St. B in Lake Biwa.

2. Distributions of biogeochemical constituents

Total dissolved nitrogenous nutrients (TNN : sum of ammonia, nitrite, nitrate and urea nitrogen) ranged 83±17 $\mu g\ N\ L^{-1}$ as an average value with standard deviation at Sts. E1～E6 in the embayment water area and 860±127 $\mu g\ N\ L^{-1}$ at Sts. O1～O6 in the open area (Table 1). Low values were obtained in the embayment area. The predominant component of nitrogenous nutrients was nitrate. Information on the distribution of urea in lagoons is extremely limited. The urea concentrations in the lagoon Nishinoko were higher or comparable with those in Lake Biwa, reported by Mitamura and Saijo (1981). Urea is one of the important compounds which serve as a nitrogen source for phytoplankton in natural waters (Eppley *et al.*, 1971; McCarthy *et al.*, 1982; Mitamura and Saijo, 1986). In the narrow embayment area of Nishinoko the contribution of urea nitrogen in TNN was found to be very high (16 to 24%), although an appreciable contribution (2.3 to 3.2%) was observed even in the open area. The present results indicate that the urea in water of reed zone is also one of the essential nitrogenous com-

pounds for epiphytic algal growth. Considerable changes in horizontal distribution, especially in the case of ammonia, were found. Concentrations of phosphate were generally limited, with the values of 21 ± 2 μg P L^{-1} in the embayment area and 39 ± 11 μg P L^{-1} in the open area. The molar ratio of TNN : DIP was calculated as 8 to 11 at the embayment stations and 44 to 62 at the open stations. Forsberg and Ryding (1980) reported that DIN : DIP ratio of 5 or less (by weight) indicated nitrogen limitation, and a ratio of 12 or greater meant phosphorus limitation. The present results seemed to indicate that the phosphorus was generally the limiting parameter for the growth of algae in the open area of Nishinoko. High concentrations of silicate were observed, and were influenced by the river water from its watershed. The silicate concentrations seem to be sufficient as a silica source for epiphytic and planktonic algae, even if the algae are mainly composed of diatoms. In the present investigations, these nutrients in the reed zone showed an irregular pattern in its distribution. In contrast, the concentrations of these nitrogenous, phosphorus, and silicious nutrients in a littoral St. B in Lake Biwa showed lower values than those at stations, especially in the open area, in a lagoon Nishinoko.

Cell density of phytoplankton in the embayment water area ranged from 1×10^6 to 2×10^7 cell m^{-3}.

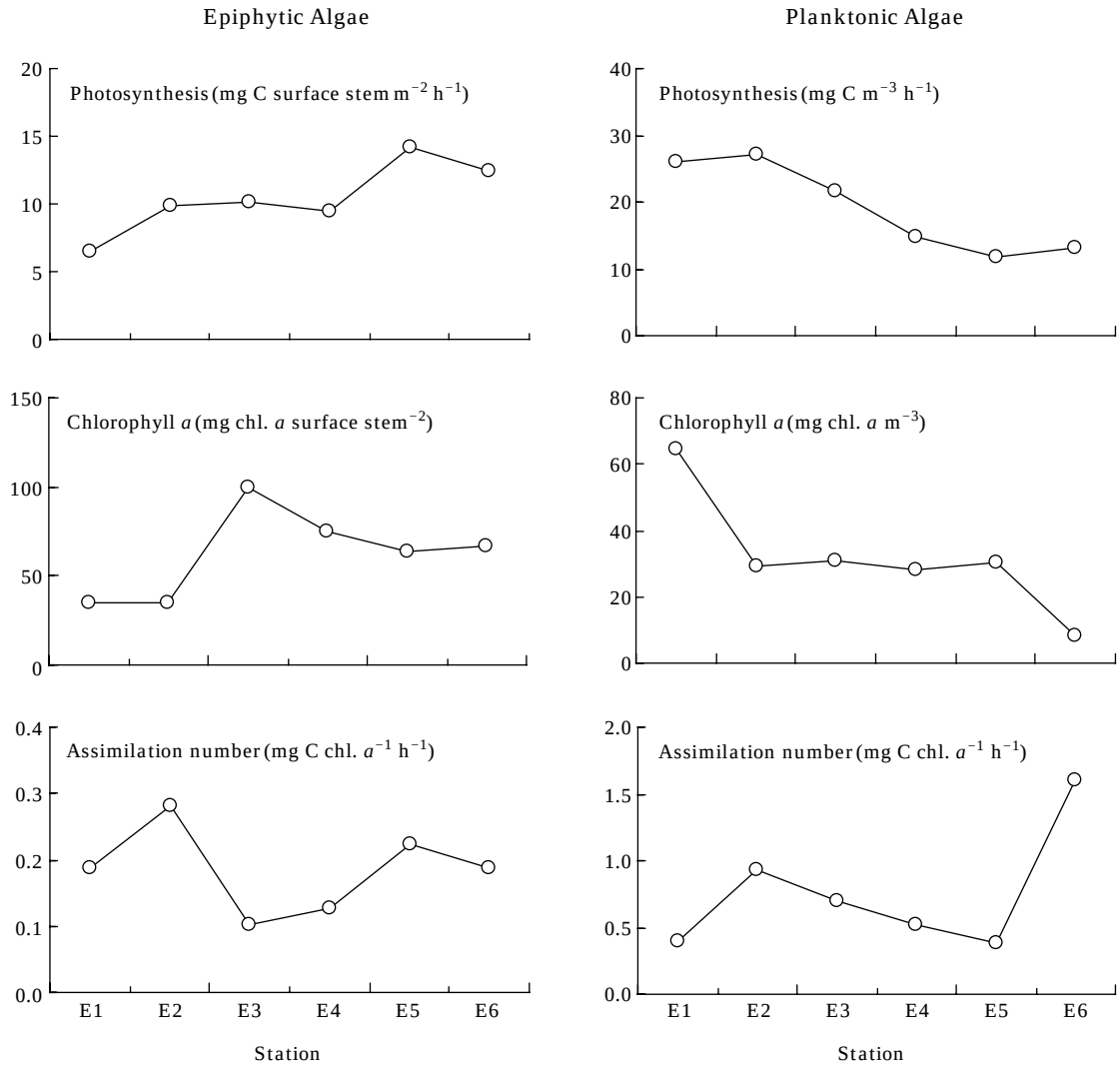

Fig. 2. Distributions of photosynthetic rate, chlorophyll *a* amount and assimilation number of epiphytic and planktonic algae at Sts. E1～E6 in the embayment water area in a lagoon Nishinoko.

Table 2. Epiphytic and planktonic carbon (g C surface stem m^{-2} or g C m^{-3}), chlorophyll *a* (mg chl. *a* surface stem m^{-2} or mg chl. *a* m^{-3}) and its ratio (mg C mg chl. a^{-1}), and photosynthetic rate (mg C surface stem m^{-2} hr^{-1} or mg C m^{-3} hr^{-1}) and assimilation number (mg C mg chl. a^{-1} hr^{-1}) at Sts. E1～E6 (embayment water area), Sts. O1～O6 (open water area) and St. B (Lake Biwa). Data show an average value with standard deviation or an average with range in parenthesis.

	Embayment area		Open area	Lake Biwa
	Epiphytic	Planktonic	Planktonic	Planktonic
Carbon	5.47±1.93	2.87±0.80	1.18±0.23	1.52
Chlorophyll *a*	63±25	32±18	7.2±0.8	8.4
C/Chl. *a*	90 (75～122)	108 (60～193)	164 (130～207)	182
Photosynthetic rate	10.4±2.6	19.0±6.8	23.5±9.8	30.3
Assimilation number	0.18 (0.10～0.28)	0.76 (0.38～1.61)	3.24 (2.29～5.29)	3.60

In the open area and Lake Biwa the biomass was 4×10^6 to 2×10^7 cell m^{-3} and 9×10^5 cell m^{-3}, respectively. Low biomass was observed at the stations in the embayment water area. Predominant species among the phytoplankton was Euglenophyceae *Euglena* spp. at the embayment stations, but a Chlorophyceae *Staurastrum dorsidentiferum* var. *ornatum* at stations in the open area and in Lake Biwa. The epiphytic algae on *Phragmites* stem, on the other hand, were mainly composed of several species in Bacillariophyceae. The distribution patterns in the cell density of phytoplankton in respective water areas (embayment, open and Lake Biwa) had not a resemblance to those in amounts of phytoplankton, as described below. This seems to be caused that the size of phytoplankton cells was differed among the areas, having different species composition. The patterns in phytoplankton biomass also showed no relation to the levels in concentrations of nutrients, suggesting that the concentrations were sufficient in their algal growth, especially in open area.

3. Photosynthetic rate of epiphytic algae on reed stem

Chlorophyll *a* amount of epiphytic algae at the embayment Sts. E1～E6 was 63±25 (average value with SD) mg chl. *a* surface stem m^{-2} and was fluctuated widely among stations. The amount of phytoplankton, on the other hand, was 32 ±18 mg chl. *a* m^{-3} at the embayment six stations and 7.2±0.8 mg chl. *a* m^{-3} at the open Sts. O1～O6, respectively (Fig. 2 and Table 2). High Chl. *a* amount in the embayment area seemed to be consisted of an appreciable amount of epiphytic algae stripped from the surface of reed stems, as well as high cell density of phytoplankton. The ratios of epiphytic carbon to Chl. *a* were calculated as 75 to 122 (averaged 90) mg C mg chl. a^{-1}. The particulate carbon to Chl. *a* ratios, on the other hand, was 60 to 193 (averaged 108) mg C mg chl. a^{-1} at the embayment stations and 130 to 207 (averaged 164) mg C mg chl. a^{-1} at the open stations. The low ratios obtained in the narrow embayment area suggest that the epiphytic and planktonic algae had been kept high ability of photosynthesis.

As shown in Fig. 2 and Table 2, the photosynthetic rate of epiphytic algae was 7.6 to 14.2 (10.4 ±2.6) mg C surface stem m^{-2} hr^{-1} at the embayment Sts. E1～E6. High values were obtained at Sts. E5 and E6 and low value at inmost St. E1. The photosynthetic rates of epiphytic algae varied widely among stations. The photosynthetic rate of phytoplankton, on the other hand, ranged from 11.7 to 27.1 (19.0±6.8) mg C m^{-3} hr^{-1} at the embayment stations, 14.9 to 40.7 (23.5±9.8) mg C m^{-3} hr^{-1} at the open stations and 30.3 mg C m^{-3} hr^{-1} at a littoral St. B in Lake Biwa, respectively. The rates in the embayment area showed lower values than in the open area. The photosynthetic rate of phytoplankton corresponded to a large degree with their standing crop. However, the rate of epiphytic algae may be influenced by other parameters. Suzuki *et al.* (1993) reported that the net photosynthetic rate of epiphytic algae on *Phragmites* stem was approximately 50 mg C surface stem m^{-2} d^{-1} in a reed zone located in the south basin of Lake Biwa. Hooper and Robinson (1976) also found that the photosynthesis of epiphytic algae on reed stems was 5 to 90 mg C surface stem m^{-2} d^{-1} in a marsh pond. The present values were comparable or lower than those reported by them.

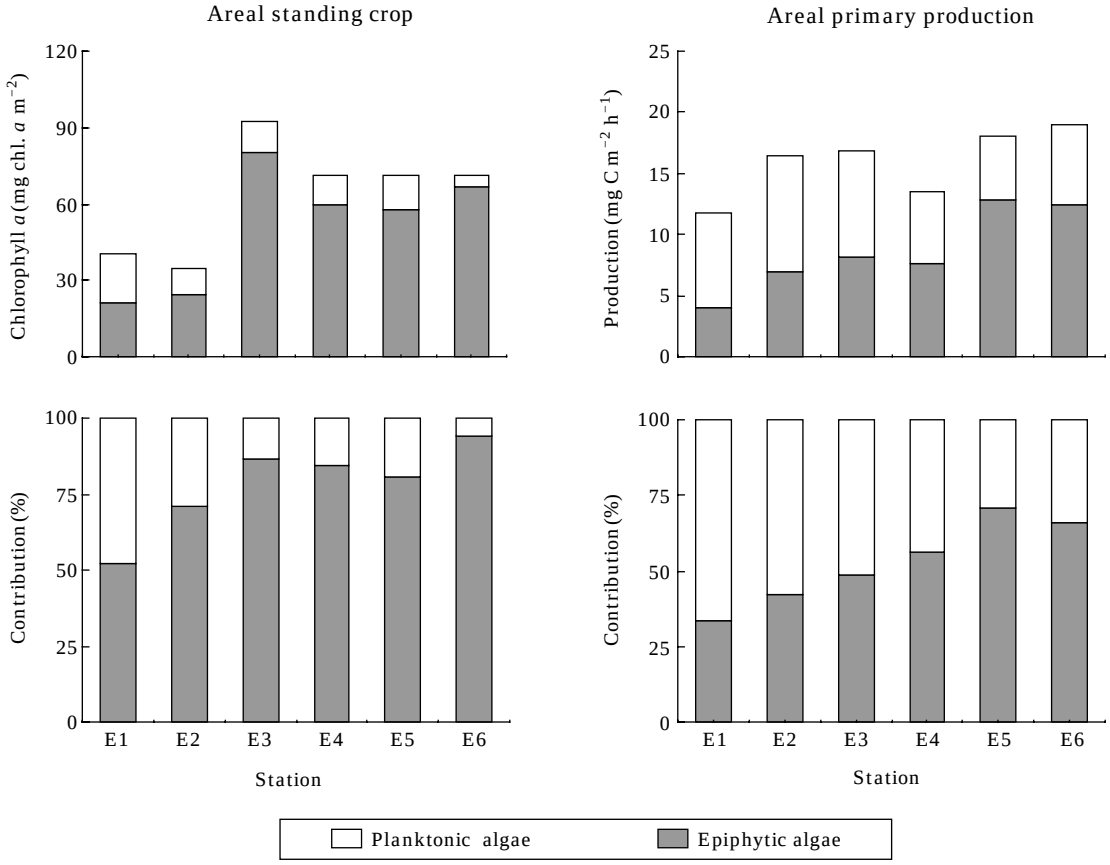

Fig. 3. Areal standing crop and primary production of epiphytic and planktonic algae, and the epiphytic contribution to total standing crop and production at Sts. E1～E6 in the embayment water area in a lagoon Nishinoko. Shaded and open columns indicate epiphytic and planktonic algae, respectively.

4. Photosynthetic activity of epiphytic algae

Assimilation number of epiphytic algae, photosynthetic capacity of the cell under respective water temperature and nutrients concentration in the field, was calculated as 0.10 to 0.28 (averaged 0.18) mg C mg chl. a^{-1} hr^{-1} (Fig. 2 and Table 2). On the other hand, the assimilation number of planktonic algae was considerably high, with 0.38 to 1.61 (averaged 0.76) mg C mg chl. a^{-1} hr^{-1} at the embayment stations and 2.3 to 5.3 (averaged 3.2) mg C mg chl. a^{-1} hr^{-1} at the open stations. At a littoral St. B high value was also obtained, namely averaged 3.6 mg C mg chl. a^{-1} hr^{-1}, similar values to the pelagic phytoplankton obtained in autumn season in the north basin of Lake Biwa reported by Mitamura *et al.* (1999) and in the south basin by Nakanishi *et al.* (1988). The photosynthetic activities of phytoplankton in the narrow embayment area were lower than those in the open area. It seemed to be caused that the assimilation numbers of phytoplankton in the dense *Phragmites* zone were limited by low photosynthetic active radiation (PAR), due to the shading effect from the aerial leafy stalks of *Phragmites*, as suggested by Müller (1995), and/or the portion of planktonic algae in the embayment area was consisted of the originated epiphytic algae with low photosynthetic activity. Müller (1995) reported that the assimilation number of epiphytic algae averaged 0.29 mg C chl. a^{-1} hr^{-1} in a eutrophic lake. Similar values for epiphytic algae on reed stems were obtained by Meulemans (1988). The present values resembled those of the epiphytic algae by previous investigators (Meulemans, 1988; Müller, 1995) and those of epilithic algae on the gravel and rock at the upper littoral area in the north basin of Lake Biwa by Nozaki (2001) and Ishida *et al.* (2006). However, the present photosynthetic activity of epiphytic algae on

Phragmites stem showed much lower values than those of epilithic and periphytic community obtained by Duthie and Jones (1990) and Maltais and Vincent (1997). The assimilation numbers of epiphytic algae on *Phragmites* stem and their range might be influenced by the thickness of the periphytic layer affecting light intensity, the chemical and biological conditions within the periphytic layers, grazing by zoobenthos, and the species composition of epiphytic algae and its activity, as described above.

5. Contribution of epiphytic algae to areal primary production

Areal standing crop and primary production of epiphytic algae on reed stems and planktonic algae in the narrow embayment water area was calculated from both the stem density of *Phragmites* and the water depth at respective station (Fig. 3). The areal total standing crop was estimated as 35 to 93 (64±22, an average with SD) mg chl. *a* m^{-2}, namely 21 to 80 (52±24) mg chl. *a* m^{-2} in epiphytic fraction and 4 to 19 (12±5) mg chl. *a* m^{-2} in planktonic fraction. The areal amount of epiphytic algae in the reed zone was 52 to 94% (averaged 78%) of the total algal standing crop (sum of epiphytic and planktonic algae) in the submerged parts of reed zone.

The areal primary production by epiphytic algae was estimated as 4.0 to 12.8 (8.7±3.4) mg C m^{-2} hr^{-1}. The areal rate by planktonic algae, on the other hand, was 5.2 to 9.5 (7.3±1.7) mg C m^{-2} hr^{-1}. The contribution of epiphytic algae to the total primary production was 34 to 71% (averaged 53%), although the assimilation numbers were much lower than those of planktonic algae. High contributions in epiphytic algal production were found in a clear lake (Liboriussen and Jeppesen, 2003). Allen and Ocevski (1981) measured the primary production of the epiphytic algae on *Phragmites* in the littoral area of Lake Ohrid and found appreciably high contribution compared with the planktonic algae. A similar tendency was also reported by Cattaneo and Kalff (1980) for the epiphytic algae on macrophytes in Lake Memphremagog.

The reed zone in a lagoon Nishinoko had a high stem density of *Phragmites*. High contribution was due to a high standing crop of the epiphytic algae. Miura *et al.* (1978) reported that the primary production of epiphytic algae on reed stems was 70 to 140 mg C m^{-2} d^{-1}, and that it contributed 90% of total primary production in a eutrophic reed zone in the south basin of Lake Biwa. Rjber *et al.* (1984) also found high primary production of epiphytic algae on *Phragmites* in a eutrophic Danish lake. The present values were low compared with their results.

In conclusion, the present investigations suggest that the epiphytic algal assemblage is one of the principal primary producers and that it plays a significant role in the biogeochemical cycle in a lagoon Nishinoko connected with the north basin of Lake Biwa. To elucidate the accurate primary production in the lagoon, further investigations of several variables, such as the epiphytic-planktonic algal interaction, the influences of physical, chemical and biological parameters, and the physiological metabolism, would be required.

ACKNOWLEDGEMENTS

The authors wish to thank the laboratory members of School of Environmental Sciences, University of Shiga Prefecture, and Division of Natural Sciences, Osaka Kyoiku University, for their generous assistance in the chemical analyses and in the filed investigations.

LITERATURE CITED

Aizaki, M. 1980. Changes in standing crop and photosynthetic rate attendant on the film development of periphyton in a shallow eutrophic river. *Jpn. J. Limnol.* **41**: 225-234.

Allen, H.L. 1971. Primary production, chemoorganotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. *Ecol. Monogr.* **61**: 97-127.

Allen, H.L. and B.T. Ocevski. 1981. Comparative primary productivity of algal epiphytes on three species of macrophyte in the littoral zone of Lake Ohrid, Yugoslavia. *Ecography* **4**: 155-160.

Bendschneider, K. and R.J. Robinson. 1952. A new spectrophotometric method for the determination of nitrite in sea water. *J. Mar. Res.* **11**: 87-96.

Bray, G.A. 1960. A simple efficient liquid scintillator for counting aqueous solutions in a liquid scintillation counter. *Anal. Biochem.* **1**: 279-285.

Cattaneo, A. and J. Kalff. 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnol. Oceanogr.* **25**: 280-289.

Duthie, H.C. and D.K. Jones. 1990. Epilithic algal pro-

ductivity on the submerged Niagara Escarpment, Georgian Bay, Canada. *Verh. Internat. Verein. Limnol.* **24**: 411-415.

Eppley, R.W. 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.* **70**: 1063-1085.

Eppley, R.W., F.A. Carlucci, O. Holm-Hansen, D. Kiefer, J.J. McCarthy, E. Venrick and P.M. Williams. 1971. Phytoplankton growth and composition in shipboard cultures supplied with nitrate, ammonium, or urea as the nitrogen source. *Limnol. Oceanogr.* **16**: 741-751.

Forsberg, C. and S.O. Ryding. 1980. Eutrophication parameters and trophic state indices in 30 Swedish wast-receiving lakes. *Arch. Hydrobiol.* **89**: 189-207.

Glooschenko, W.A., J.E. Moor, M. Munawar and R.A. Vollenweider. 1974. Primary production in Lake Ontario and Erie: a comparative study. *J. Fish. Res. Bd. Canada* **31**: 253-263.

Golterman, H.L., R.S. Climo and M.A.M. Ohstad. 1978. Methods for physical and chemical analysis of fresh waters. International Biological Programe. Handbooks No. 8, Blackwell Scientific Publications, Oxford, 213pp.

Harrison, W.G. and T. Platt. 1980. Variations in assimilation number of coastal marine phytoplankton: Effect of environmental covariates. *J. Plankton Res.* **2**: 249-260.

Hickman, M. and D.M. Klarer. 1973. Methods for measuring the primary productivity and standing crops of an epiphytic algal community attached to *Scirpus validus* Vahl. *Int. Revue ges. Hydrobiol.* **58**: 893-901.

Hill, W.R. and H.L. Boston. 1991. Community development alters photosynthesis-irradiance relations in stream periphyton. *Limnol. Oceanogr.* **36**: 1375-1389.

Hooper, N.M. and G.G.C. Robinson. 1976. Primary production of epiphytic algae in a marsh pond. *Can. J. Bot.* **54**: 2810-2815.

Ishida, N., O. Mitamura and M. Nakayama. 2006. Seasonal variation in biomass and photosynthetic activity of epilitic algae on a rock at the upper littoral area in the north basin of Lake Biwa, Japan. *Limnology* **7**: 175-183.

Liboriussen, L. and E. Jeppesen. 2003. Temporal dynamics in epipelic, pelagic and epiphytic algal production in a clear and a turbid shallow lake. *Freshwat. Biol.* **48**: 418-431.

Malone, T.C. 1977. Light-saturated photosynthesis by phytoplankton size fraction in the New York Bight, U.S.A. *Mar. Biol.* **42**: 281-292.

Maltais, M.J. and W.F. Vincent. 1997. Periphyton community structure and dynamics in a subarctic lake. *Can. J. Bot.* **75**: 1556-1569.

Mandelli, E.F., P.R. Burkholder, T.E. Doheny and R. Brody. 1970. Studies of primary productivity in coastal waters in southern Long Island, New York. *Mar. Biol.* **7**: 191-202.

McCarthy, J.J., D. Wynne and T. Berman. 1982. The uptake of dissolved nitrogenous nutrients by Lake Kinneret (Israel) microplankton. *Limnol. Oceanogr.* ***27***: 673-680.

Meulemans, J.T. 1988. Seasonal changes in biomass and production of periphyton growing upon reed in Lake Maarsseveen I. *Arch. Hydrobiol.* **112**: 21-42.

Mitamura, O., H. Maeda and M. Kawashima. 1999. Seasonal change in photosynthetic activity of photoautotrophic picoplankton in Lake Biwa. *Jpn. J. Limnol.* **60**: 453-467.

Mitamura, O. and Y. Saijo. 1981. Studies on the seasonal changes of dissolved organic carbon, nitrogen, phosphorus and urea concentration in Lake Biwa. *Arch. Hydrobiol.* **91**: 1-14.

Mitamura, O. and Y. Saijo. 1986. Urea metabolism and its significance in the nitrogen cycle in the euphotic layer of Lake Biwa. I. In situ measurement of nitrogen assimilation and urea decomposition. *Arch. Hydrobiol.* **107**: 23-51.

Mitamura, O. and J. Tachibana. 1999. Primary productivity of epiphytic and planktonic algae and biogeochemical characteristics at reed zone of Lake Biwa. *Jpn. J. Limnol.* **60**: 265-280.

Miura, T., T. Tanimizu, Y. Iwasa and A. Kawakita. 1978. Macroinvertebrates as an important supplier of nitrogenous nutrients in a dense macrophyte zone in Lake Biwa. *Verh. Internat. Verein. Limnol.* **20**: 1116-1121.

Müller, U. 1995. Vertical zonation and production rates of epiphytic algae on *Phragmites australis*. *Freshwater Biology* **34**: 69-80.

Müller, U. 1996. Production rates of epiphytic algae in a eutrophic lake. *Hydrobiologia* **330**: 37-45.

Mullin, J.B. and J.P. Riley. 1955. The colorimetric determination of silicate with special reference to sea and natural waters. *Anal. Chim. Acta* **12**: 162-176.

Murphy, J. and J.P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* **27**: 31-36.

Nakanishi, M., T. Narita, N. Suzuki and O. Mitamura. 1988. Assimilation number and primary productivity of phytoplankton in the south basin of Lake Biwa. *Jpn. J. Limnol.* **49**: 175-184.

Newell, B.S., B. Morgan and J. Cundy. 1967. The determination of urea in seawater. *J. Mar. Res.* **25**: 201-202.

Nozaki, K. 2001. Abrupt change in primary productivity in a littoral zone of Lake Biwa with the development of a filamentous green-algal community. *Freshwat. Biol.* **46**: 587-602.

Rjber, H.H., J.P. Sørensen and H.H. Schierup. 1984. Primary productivity and biomass of epiphytes on Phragmites australis in a eutrophic Danish lake. *Ecography* **7**: 202-210.

Sagi, T. 1966. Determination of ammonia in sea water

by the indophenol method and its application to the coastal and off-shore waters. *Oceanogr. Mag.* **18**: 43-51.

Satake, K., Y. Saijo and H. Tominaga. 1972. Determination of small quantities of carbon dioxide in natural waters. *Jpn. J. Limnol.* **33**: 16-20.

SCOR/Unesco Working Group 17. 1966. Determination of photosynthetic pigments in sea water. UNESCO 69pp.

Steemann Nielsen, E. 1952. Use of radio active carbon (^{14}C) for measuring organic production in the sea. *J. Cons. int. Explor. Mer.* **18**: 117-140.

Suzuki, N., M. Kawashima, S. Endoh, Y. Itakura and Y. Kimura. 1993. Study on the reed community at Lake Biwa -Physical, chemical and ecological characteristics in the reed community-. *Mem. Fac. Edu., Shiga Univ., Ser. Nat. Sci.* **43**: 19-41.

Tanimizu, K., T. Miura and M. Higashi. 1981. Effect of water movement on the photosynthetic rate of an algal community attached to reed stems. *Verh. Internat. Verein. Limnol.* **21**: 584-589.

Wood, E.D., F.A.J. Armstrong and F.A. Richards. 1967. Determination of nitrate in sea water by cadmium-copper reduction to nitrite. *J. Mar. Biol. Ass. U.K.* **47**: 23-31.

(Manuscript received 16 December 2008,
Revision accepted 30 January 2009)