Algal Community Structure in a Littoral Zone in the North Basin of Lake Biwa

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ABSTRACT

Seasonal variations in the biomass and species composition of benthic and planktonic algal communities were investigated from June 1994 to April 1996 in a littoral zone with gravel in the north basin of Lake Biwa. Seasonal fluctuations in biomass were mainly brought about by the rise and fall of a filamentous green alga (FGA) *Spirogyra* sp. in the benthic algal community, together with *Closterium aciculare*, *Staurostrum dorsidentiferum* and *Gomphosphaeria lacustris* in the planktonic algal community. Comparing the benthic with the planktonic algal biomass, the former made up over 90% of the total algal biomass. This result suggests that the benthic algal community contributes highly to primary production in the littoral zone. There were extraordinary differences in the vertical-distribution pattern and light-extinction coefficient between the FGA and sessile algae (benthic algae except FGA) forming the benthic algal community, thus dividing it into two components : FGA, and sessile algal communities. From the viewpoint of the productive structure of the algal community in the littoral zone, we propose that the community should be regarded as a three-component structure of planktonic, FGA, and sessile algal communities.

Key words : filamentous green algae (FGA), littoral zone of lake, productive structure, three-component structure of algal community

INTRODUCTION

Planktonic algae, benthic algae and macrophytes play an important role as primary producers in aquatic ecosystems. The littoral zone in lakes where more than 1% of surface light intensity reaches bottom is characterized by the development of a benthic algal community and macrophytes (MOSS, 1988). Thus, in order to understand the productive structure in the littoral zone, not only the planktonic algal community but also the benthic algal community and/or macrophytes should be investigated together. However, most algal studies of the littoral zone have been mainly focussed on the benthic algal community (CATTANEO, 1987 ; MEULEMANS, 1988 ; BURKHOLDER and WETZEL, 1989 ; JONSSON, 1992 ; MÜLLER, 1994 ; HAWES and SCHWARTZ, 1996). On the other hand, there have only been a few investigations of both

planktonic and benthic algal communities or macrophytes (NAKANISHI *et al.*, 1989 ; TAKAMURA *et al.*, 1990 ; STEINMAN *et al.*, 1997).

The development of a filamentous green algal (FGA) community dominated by *Spirogyra* sp. has been observed in the littoral zone of Lake Biwa since 1983 (WATANABE *et al.*, unpublished data). Occurrence of the FGA community has been observed also in some lakes located in the north temperate region since the 1980s. FGA propagation has been studied as a biological indicator related to changes in lake environments (LORENZ and HERDENDORF, 1982 ; PIECZYŃSKA *et al.*, 1988 ; TURNER *et al.*, 1995a). However, the ecological effects of FGA intrusion on a littoral-zone ecosystem have been little studied (TURNER *et al.*, 1995b ; NOZAKI *et al.*, 1998).

In the present study, some characteristics of the algal community structure consisting of benthic and planktonic algae are discussed on the basis of seasonal variations in biomass and species composition of both communities in a littoral zone with gravel in the north basin of Lake Biwa, especially focussing on the intrusion of the FGA.

METHODS

Study site

Lake Biwa is divided into 2 basins : the north basin is 618 km² in surface area, 45 m in mean depth (maximum : 104 m) and mesotrophic ; and the south basin is 57 km², 3.5 m (maximum : 7.6 m) and eutrophic. This study was carried out in a littoral zone located at Kita-komatsu in the western part of the north basin (Fig. 1). The survey was conducted biweekly from June 1994 to April 1996. The bottom of the littoral zone was covered with gravel (diameter, 10-20 cm). Macrophytes were not present. Three sampling stations were placed on a transect in an offshore direction (Fig. 1). The depth of each station changed generally together with changes in the water level of Lake Biwa during the investigation period : 10-170 cm (mean 50

Fig. 1. Location of study site and sampling stations.

cm) at Stn. 1, 40–200 cm (mean 100 cm) at Stn. 2 and 90–250 cm (mean 150 cm) at Stn. 3. The lowest depths were recorded from June to September 1994, due to an unusual drought (HORI *et al.*, 1996).

Algal samples

Three samples of benthic algae from stones in quadrates (25 cm × 25 cm) were collected at each station by SCUBA diving. The algae were completely removed from the stones using a steel brush. On 13 July 1995 and 29 March 1996 at Stn. 2, the thickness of the benthic algal community was measured with a ruler. Planktonic algal samples were collected at a 5 cm depth at Stn. 3. All the samples kept in an ice box were carried to the laboratory within 3 h. An aliquot of each sample was filtered on a fibre glass filter (Whatman GF/C, burned at 450 °C for 2 h) for a determination of chlorophyll *a* (LORENZEN, 1967). Benthic algal samples were preserved in a 5% concentration of neutral formalin. Planktonic algae in water samples (1 litre) were fixed with neutral formalin at a final concentration of 5%, and concentrated to 10 ml. Identifications of algae were referred to descriptions by HIROSE and YAMAGISHI (1977) and WATANABE and HOUKI (1988). Algal cells were counted under a microscope using a plankton counting chamber (Matsunami S6117, square size 1 mm × 1 mm, volume 1 ml). Since algae differ greatly in size, cell numbers do not give a true picture of the actual biomass. To evaluate the algal biomass, cell volumes of each alga were calculated by the geometrical cube method (FINDENEGG, 1969; CLARKE *et al.*, 1987). The volume can be calculated from the dimensions of the cell, assuming that its form corresponds roughly to simple geometrical solids: Sphere = $(4\pi r^3)/3$, Cone = $(\pi r^2 h)/3$, Cylinder = $\pi r^2 h$, etc. Cell volumes of complex algae are calculated by a combination of some simple geometrical solids (ex. *Ceratium*, *Staurostrum*). Cell size was measured randomly using the samples collected during the investigation period. Algal cell numbers of each sample were converted to biovolumes using the mean-cell volumes of each alga (Table 1). Relations between chlorophyll *a* (benthic algae: mg m⁻², planktonic algae: mg m⁻³) and biovolume (benthic algae: 10³ mm³ m⁻², planktonic algae: 10³ mm³ m⁻³) of algal communities were shown in Figure 2. Benthic algal chlorophyll *a* was divided into two fractions of FGA and sessile algae (benthic algae except FGA) using the relation in Figure 2, because of differences in the extinction coefficients of the respective communities as described later.

Environmental conditions

Water temperature at each station was measured with a thermometer at noon. Underwater light intensity was measured vertically at 20-cm intervals with an underwater quantameter (LI-COR, LI-1000) at Stn. 3 at noon. Light attenuation in the benthic algal community was measured as follows; benthic algal samples with several different concentrations were poured into glass petri dishes. Light transmittances of the respective samples in the glass petri dishes were measured with a quantameter (Biospherical Instru-

Table 1. Mean biovolume of each alga in this study (col. : volume of colony, 100 μm : volume of 100 μm length).

Taxon	Mean (SD) (μm^3)	n	Taxon	Mean (SD) (μm^3)	n
Bacillariophyceae			<i>Dictyosphaerium pulchellum</i>	50(10)	10
<i>Achnanthes japonica</i>	36(20)	10	<i>Elakatothrix gelatinosa</i>	30(10)	10
<i>A. lanceolata</i>	89(30)	10	<i>Eudorina elegans</i> (col.)	115000(144000)	18
<i>A. minutissima</i>	38(20)	10	<i>Gloeocystis gigas</i>	220(130)	12
<i>Asterionella formosa</i>	920(290)	24	<i>Hormidium</i> sp.	1660(230)	10
<i>Aulacoseira granulata</i>	6020(3230)	40	<i>Kirchneriella lunaris</i>	40(6)	10
<i>A. solida</i>	1020(520)	10	<i>Mougeotia</i> sp.	4430(9000)	86
<i>Ceratoneis arcus</i>	470(140)	10	<i>Oedogonium</i> sp. 1	20400(19000)	72
<i>Cocconeis placentula</i>	770(320)	15	<i>Oedogonium</i> sp. 2	244000(98000)	25
<i>Cyclotella comta</i>	110(60)	15	<i>Oocystis</i> spp. (col.)	1840(220)	10
<i>C. meneghiniana</i>	105(60)	14	<i>Pediastrum simplex</i> (col.)	12400(7000)	10
<i>Cymbella cistula</i>	6440(5600)	10	<i>P. tetras</i> (col.)	1300(580)	10
<i>C. minuta</i>	1220(730)	10	<i>Quadrigula chodatii</i>	1840(100)	10
<i>C. tumida</i>	12600(12600)	10	<i>Schroederia setigera</i>	190(100)	10
<i>Denticula kuetzingii</i>	7450(3230)	10	<i>Scenedesmus acuminatus</i>	19(6)	10
<i>Diatoma hiemale</i>	990(360)	10	<i>S. denticulatus</i>	120(10)	10
<i>D. vulgare</i>	5320(1960)	10	<i>S. ecornis</i>	50(10)	10
<i>Epithemia</i> spp.	11370(9700)	10	<i>S. quadricauda</i>	160(20)	10
<i>Fragilaria capucina</i>	470(140)	214	<i>Scenedesmus</i> sp.	10(1)	10
<i>F. construens</i>	250(240)	24	<i>Sphaerocystis schroeteri</i>	70(30)	10
<i>F. crotonensis</i>	760(260)	14	<i>Spirogyra</i> sp.	388000(181000)	210
<i>F. virescens</i>	430(130)	10	<i>Stigeoclonium lubricum</i> (100 μm)	5200(2100)	51
<i>Gomphonema olivaceum</i>	160(100)	22	<i>Staurostrum arcticon</i>	44000(21500)	10
<i>G. parvulum</i>	110(80)	10	<i>S. dorsidentiferum</i>	24300(6000)	14
<i>G. tetrastigmatum</i>	780(580)	14	<i>Xanthidium antilopaeum</i>	80500(12000)	10
<i>Melosira varians</i>	7060(940)	10	<i>Ulothrix zonata</i> (100 μm)	35000(25000)	100
<i>Navicula cryptocephala</i>	320(190)	44	Cyanophyceae		
<i>Navicula lanceolata</i>	1070(420)	34	<i>Aphanothece clathrata</i> (col.)	13000(1200)	10
<i>N. viridula</i>	1300(360)	19	<i>Chroococcus</i> sp.	3(1)	10
<i>Nitzschia acicularis</i>	200(80)	10	<i>Gomphosphaeria lacustris</i> (col.)	14100(11100)	180
<i>N. actinastroides</i>	290(100)	24	<i>Homoeothrix janthina</i> (100 μm)	2830(110)	10
<i>N. dissipata</i>	110(70)	35	<i>Lyngbya martensiana</i> (100 μm)	5430(210)	10
<i>N. paleacea</i>	260(80)	16	<i>Lyngbya</i> sp. (100 μm)	340(40)	10
<i>Pinnularia gibba</i>	8190(5490)	10	<i>Oscillatoria</i> sp. 1 (100 μm)	8500(1100)	10
<i>Rhoicosphenia curvata</i>	1630(1630)	10	<i>Oscillatoria</i> sp. 2 (100 μm)	1360(50)	10
<i>Stephanodiscus carconensis</i> (winter)	6150(4530)	44	<i>Phormidium tenue</i>	30(10)	10
<i>S. carconensis</i> (spring-autumn)	770(520)	40	<i>Phormidium</i> sp. (100 μm)	530(60)	10
<i>Synedra acus</i>	1240(320)	15	Cryptophyceae		
<i>S. rumpense</i>	470(60)	18	<i>Cryptomonas ovata</i>	8000(1250)	10
<i>S. ulna</i>	1660(950)	41	Dinophyceae		
Chlorophyceae			<i>Ceratium hirundinella</i>	53000(32300)	10
<i>Actinastrum hantzschii</i>	130(90)	10	<i>Glenodinium</i> sp.	320(170)	10
<i>Ankistrodesmus falcatus</i> var. <i>mirabilis</i>	11(7)	40	<i>Gymnodinium</i> sp.	2960(1600)	10
<i>Chlamydomonas</i> spp.	300(200)	14	<i>Peridinium</i> sp.	3160(1920)	10
<i>Cladophora glomerata</i>	698000(918000)	100	Euglenophyceae		
<i>Closterium aciculare</i>	10700(3600)	51	<i>Trachelomonas</i> spp.	13000(8000)	12
<i>C. aciculare</i> var. <i>variabile</i>	1740(510)	10			
<i>Coelastrum cambricum</i> (col.)	4320(3100)	14			
<i>Cosmarium</i> sp.	290(40)	10

Fig. 2. Relationships between biovolume and chlorophyll *a* of benthic (left) and planktonic (right) algae.

ment, QSL-100) under artificial light (Toshiba reflector lamp 500 W). The light transmittance was related to the algal community thickness expressed as chlorophyll *a* (mg m^{-2}) determined by the method of LORENZEN (1967).

The extinction coefficient in water or in a benthic algal community was given by the following formula,

$$I = I_0 \exp^{-kz}$$

I_0 : photon flux density on surface water or on the top of the benthic algal community ($\mu\text{E m}^{-2} \text{s}^{-1}$)

k : extinction coefficient in water or in the benthic algal community (m^{-1} or $\text{mg chl. } a^{-1}$)

z : depth (m) or chlorophyll *a* (mg m^{-2}).

Assuming that the chlorophyll *a* contents per unit algal cell were the same, light attenuation in the benthic algal community would be estimated using the extinction coefficient and chlorophyll *a*.

Water samples for analyses of nutrients were collected from two layers : 5 cm below the surface, and just above the bottom at each station. Filtrate through fibre glass filters (Whatman GF/C, burned at 450°C for 2 h) was used for dissolved inorganic nitrogen compounds (DIN), and those through a fibre glass filter acidified with 0.1 N HCl were used for the analysis of $\text{PO}_4^{3-}\text{-P}$. Nutrients analyzed were as follows ; $\text{NH}_4^+\text{-N}$ (SOLORZANO, 1969), $\text{NO}_2^-\text{-N}$ (BENDSCHNEIDER and ROBINSON, 1952), $\text{NO}_3^-\text{-N}$ (KALFF and BENTZEN, 1984), and $\text{PO}_4^{3-}\text{-P}$ (MURPHY and RILEY, 1962).

RESULTS

Physico-chemical variables

Water temperature at each station varied seasonally from 6.1°C on 28 February 1996 to 32.6°C on 24 August 1995 (Fig. 3a). There was no

Fig. 3. Seasonal changes in water temperature (a) (s: surface, b: bottom), light-extinction coefficient in water at Stn. 3 (b), and relative light intensity reaching the top of benthic algal community (c).

significant difference in water temperature among the stations or between the surface and bottom. The light-extinction coefficients in water varied from 0.083 m^{-1} to 1.275 m^{-1} (Fig. 3b), being not so different from those of previous reports on the pelagic zone of the north basin ($0.25\text{--}1.31 \text{ m}^{-1}$, NAKANISHI, 1976; $0.276\text{--}0.767 \text{ m}^{-1}$, NAKANISHI *et al.*, 1992), though the range was greater than that in the pelagic zone. Relative light intensities just

above the benthic algal community calculated using the extinction coefficients in water were 58–98%, 36–95% and 29–92% of the surface light intensity at Stns. 1, 2 and 3, respectively (Fig. 3c). Thus, the light seemed to be sufficient for the development of the benthic algal community at all stations (STRICKLAND, 1958).

Figure 4 shows seasonal changes in DIN ($\text{NH}_4^+\text{-N}$, $\text{NO}_2^-\text{-N}$ and $\text{NO}_3^-\text{-N}$)

Fig. 4 Seasonal changes in concentrations of DIN ($\text{NH}_4^+\text{-N}$, $\text{NO}_2^-\text{-N}$ and $\text{NO}_3^-\text{-N}$) and DIP ($\text{PO}_4^{3-}\text{-P}$) in surface (s) and bottom (b) layers at each station.

and DIP ($\text{PO}_4^{3-}\text{-P}$) concentrations of the surface and bottom layers at all stations. DIN and DIP concentrations were not very different among the stations or between the surface and bottom, varying within a range of 0–48 $\mu\text{g l}^{-1}$ in $\text{NH}_4^+\text{-N}$, 0–9 $\mu\text{g l}^{-1}$ in $\text{NO}_2^-\text{-N}$, 4–396 $\mu\text{g l}^{-1}$ in $\text{NO}_3^-\text{-N}$, and 0–24 $\mu\text{g l}^{-1}$ in $\text{PO}_4^{3-}\text{-P}$. Since concentrations of $\text{NH}_4^+\text{-N}$ and $\text{NO}_2^-\text{-N}$ were usually far lower than that of $\text{NO}_3^-\text{-N}$, the total DIN concentration changed seasonally depending on the concentration of $\text{NO}_3^-\text{-N}$ at all stations. The seasonal pattern and concentration of DIN were similar to those of the offshore surface in the north basin (TEZUKA, 1984). The varying range of $\text{PO}_4^{3-}\text{-P}$ concentration was also similar to that in the pelagic zone.

These results suggest that water temperature as well as light and nutrient conditions in the water at this study site were similar to those of previous studies in the pelagic zone.

Fig. 5. Seasonal variations in total biovolumes of benthic and planktonic algae at each station (shaded area; filamentous green algae).

Fig. 6. Seasonal variations in biovolumes of predominant species of benthic algae at each station.

Seasonal variations of algal communities

The biomass of benthic and planktonic algal communities (expressed as biovolume) varied from station to station, though seasonal patterns of biomass and species composition of both communities were not so different among stations throughout the investigation period. It was characterized that peaks in the biomass of benthic and planktonic algal communities were formed by a drastic propagation by 1 or 2 species.

The biomass of the benthic algal community varied seasonally with three peaks formed in June-July 1994, November-December 1994 and June-July 1995 except for Stn. 1 (Fig. 5). The biomass ranged from 0.13 to 300×10^3 ,

Fig. 7. Seasonal variations in biovolumes of predominant species of planktonic algae at Stn. 3.

$0.87-508 \times 10^3$ and $1.55-349 \times 10^3 \text{ mm}^3 \text{ m}^{-2}$ at Stns. 1, 2 and 3, respectively. These peaks were brought about by the propagation of large FGA such as *Spirogyra* sp. and *Cladophora glomerata*. A small peak observed in January-April 1996 at all stations was formed by the small FGA *Ulothrix zonata* and by the sessile algae *Cymbella minuta*, *Cymbella tumida*, *Diatoma vulgare* and *Fragilaria capucina* (Fig. 6).

The total biomass of the planktonic algal community was $0.03-1.6 \times 10^3$, $0.04-3.2 \times 10^3$ and $0.06-5.8 \times 10^3 \text{ mm}^3 \text{ m}^{-2}$ at Stns. 1, 2 and 3, respectively (Fig. 5). The biomass of the planktonic algal community showed five peaks in the seasonal change, *i. e.*, by the propagation of *Closterium*

aciculare in June 1994, *Staurostrum dorsidentiferum* in October-December 1994, *Gomphosphaeria lacustris* in July-August 1995, and *G. lacustris*, and *S. dorsidentiferum* in October-December 1995; and *Stephanodiscus carconensis* in March-April 1996 (Fig. 7). Dominant species in the planktonic algal community were similar to those in previous studies of the pelagic zone in the north basin (NAKANISHI, 1976; TEZUKA, 1984; TEZUKA and NAKANISHI, 1991). Thus, the planktonic algal community at this study site seemed to reflect that of the pelagic zone. In fact, abiotic factors controlling the algal growth such as water temperature, light and nutrient concentrations were not very different from those of the pelagic zone.

The seasonally changing pattern of benthic algal biomass seemed to quite similar to that of the planktonic algal pattern except for October-December 1996 when a planktonic algal peak was formed by the propagation of *G. lacustris* and *S. dorsidentiferum*. The benthic algal biomass occupied more than 90% of the total algal biomass, and the contribution of FGA to the benthic algal biomass was more than 70% (Table 2).

Table 2. Variation ranges and mean values of algal biomass at each station.

Site	Algal biovolume ($10^3 \text{ mm}^3 \text{ m}^{-2}$)				Relative abundance in total algal biovolume (%)			
	Benthic algae			Planktonic algae	Benthic algae			Planktonic algae
	Total	FGA	Sessile algae		Total	FGA	Sessile algae	
Station 1								
Range	0.13-300.0	0.08-108.4	0.05-272.6	0.03-1.57	42.7-99.9	9.1-95.6	4.3-90.6	0.1-57.3
Mean	43.2	28.0	15.2	0.49	95.8	68.8	27.0	4.2
Station 2								
Range	0.87-507.5	0.75-496.6	0.12-119.8	0.04-3.17	80.6-99.9	1.8-99.0	0.4-97.0	0.1-1.94
Mean	94.0	79.4	14.6	0.96	94.5	71.2	26.3	2.5
Station 3								
Range	1.55-348.9	0.71-344.5	0.60-58.5	0.06-5.84	54.1-99.8	3.3-98.5	1.2-92.7	0.2-45.9
Mean	71.6	62.5	9.01	1.64	91.9	63.9	28.0	8.1

Light attenuation in each algal community

Light-extinction coefficients in communities of FGA and sessile algae were $0.005 \text{ (mg chl. } a^{-1})$ and $0.029 \text{ (mg chl. } a^{-1})$, respectively (Fig. 8). The extinction coefficient of the sessile algal community was similar to that in the previous studies ($0.02 \text{ mg chl. } a^{-1}$ by TOMINAGA and ICHIMURA, 1966; $0.023 \text{ mg chl. } a^{-1}$ by NAKANISHI and YAMAMURA, 1984). The extinction coefficient of the FGA community was remarkably small compared with that of the sessile algal community. One reason for the extremely low extinction coefficient of the FGA community might be due to their relatively small content of detritus and inorganic matter closely related to light attenuation when compared with those in the sessile algal community. In fact, ignition loss was 60-70% of the total dry weight in the FGA community, but less than 10% in the sessile algal community (NOZAKI, unpublished data).

The respective attenuations by planktonic, FGA and sessile algal communities were calculated using the extinction coefficients and water depth or

Fig. 8. Relations of light transmittance to chlorophyll *a* of sessile (open circle, $k=0.029$ mg chl. a^{-1}) and filamentous green alga *Spirogyra* sp. (solid circle, $k=0.005$ mg chl. a^{-1}) communities.

chlorophyll *a*. Chlorophyll *a* of the benthic algal community was roughly divided into two fractions of FGA and sessile algae using the relation in Figure 2. Light attenuation in each algal community varied seasonally over ranges of 2–40, 5–64 and 8–71% for planktonic algae, 0.1–55, 0.5–77 and 0.6–65% for the FGA, and 0.3–73, 0.2–71 and 0.8–58% for sessile algae, at Stns. 1, 2 and 3, respectively (Fig. 9). More than 99% of the surface-light intensity was attenuated by planktonic and FGA communities (Fig. 9) whenever the FGA biomass exceeded $500 \times 10^3 \text{ mm}^3 \text{ m}^{-2}$ in biovolume, corresponding to the 800 mg m^{-2} in chlorophyll *a* (Figs. 2 and 5). This fact suggests that an increase in FGA strongly depresses the growth of sessile algae by the shading.

DISCUSSION

Contribution of benthic and planktonic algae as primary producers

The relative contribution of the benthic algal community to primary production in the littoral zone varies depending on the trophic status of lakes. HANSSON (1988) reported that the contribution of the benthic algal community increases in oligotrophic lakes because of the sparsity of planktonic algal biomass, whereas it decreases in eutrophic lakes due to an increase in planktonic algal biomass. The biomass of benthic algae exceeded 90% of the total algal biomass at all stations. This suggests that the benthic algal community contributes significantly to primary production in the littoral zone (Table 2). Furthermore, FGA in the benthic algal community,

Fig. 9. Light attenuation by each algal community (Pa : planktonic algae, FGA : filamentous green algae, Sa : sessile algae) at each station.

especially *Spirogyra* sp. with its extraordinarily high biomass, seemed to be the major primary producer (Figs. 5 and 6). TAKAMURA *et al.* (1990) reported that the photosynthesis of benthic algae was light-limited by shading from the planktonic algal community during the period when chlorophyll *a* was $100\text{--}400\text{ mg m}^{-3}$ by a bloom of *Microcystis* in a littoral zone of hypertrophic Lake Kasumigaura. HANSSON (1992) also suggested that benthic algal growth was depressed by shading from the planktonic algal community in the littoral zone (depth, 0–75 cm) of Swedish lake, when the

extinction coefficient exceeded 1.5 m^{-1} . In this study, the maximum chlorophyll *a* and the extinction coefficient in the water were 6 mg m^{-3} and 1.275 m^{-1} , respectively (Figs. 2 and 3c). In comparison with the maximum chlorophyll *a* and light-extinction coefficient obtained from data of the references, the growth of the benthic algal community at this study site seemed not to be limited by shading from the planktonic algal community.

Effects of intrusion of FGA on the algal community structure

In the north basin of Lake Biwa, the benthic algal community in the littoral zone consisted only of sessile algae in 1963, and the maximum chlorophyll *a* was 100 mg m^{-2} in February (SAIJO *et al.*, 1966). In the present study, the seasonal fluctuation in biomass of the benthic algal community was affected intensely by the rise and fall of *Spirogyra*. Consequently, the maximum biomass was estimated to be $500 \times 10^3 \text{ mm}^3 \text{ m}^{-2}$ in biovolume and 800 mg m^{-2} in chlorophyll *a* (Fig. 5, cf. Fig. 2). The intrusion of FGA such as *Spirogyra* contributed to an increase in the biomass of the benthic algal community and altered the seasonal biomass pattern in the littoral zone.

Figure 10 shows the vertical profiles of algal-community structure and light attenuation at Stn. 2 on 13 July 1995 when the FGA flourished, and on 29 March 1996 when the benthic algal community consisted only of sessile algae. There were clear differences in the vertical distribution of the biomass and the relative light intensity between the two observations. On 13 July 1995, relative light intensity was attenuated to 70% of the surface intensity above the FGA community, and decreased to 0.32% above the sessile algal community through shading from the FGA community. Further,

Fig. 10. Comparisons among vertical profiles of algal community structure (Pa : planktonic algae, FGA : filamentous green algae, Sa : sessile algae) and light attenuation at Stn. 2 on 13 July 1995 and on 29 March 1996.

relative light intensity beneath the sessile algal community fell to 0.1%. On 29 March 1996, relative light intensity decreased to 68% above the sessile algal community and 11% beneath the sessile algal community. These results suggest that the development of the FGA community in the littoral zone of the lake changed the productive structure of the algal community. Development of the FGA community creates a diversiform structure in the littoral zone of a lake, and may prepare a new habitat for algae attaching to the FGA (LOWE, 1996), whereas the shade created may act negatively on the growth of sessile algae attaching to stones (cf. Fig. 9).

It is well known that a benthic algal community is stronger in its self-shading effect than a planktonic algal community, because the benthic algal cells are densely accumulated in a narrow space (AIZAKI, 1980 ; BOSTON and HILL, 1991 ; HILL and BOSTON, 1991 ; MÜLLER, 1995). In our study, the light-extinction coefficient in the FGA community was extraordinarily low ($0.005 \text{ mg chl. } a^{-1}$) as compared with that of the sessile algal community ($0.029 \text{ mg chl. } a^{-1}$). Consequently, the FGA community seemed to be less self-shading than the sessile algal community. Assuming that the light intensity at the compensation point was 1% of the surface irradiance, the potential chlorophyll *a* in the productive layer of the benthic algal community alone was estimated as approximately 850 mg m^{-2} of FGA, and as 150 mg m^{-2} of sessile algae alone at Stn. 2 on 13 July 1995 (Fig. 8). After ARUGA (1973), chlorophyll *a* in the productive layer of a planktonic algal community was below 100 mg m^{-2} in the sea and oligotrophic lakes and 100 – 1000 mg m^{-2} in meso- and eutrophic lakes, whereas it reached 200 – 250 mg m^{-2} in a sessile algal community in a river (TOMINAGA and ICHIMURA, 1966 ; AIZAKI, 1980 ; NAKANISHI and YAMAMURA, 1984) and 900 mg m^{-2} in a pure culture of *Scenedesmus* (ARUGA, 1966). The potential chlorophyll *a* in the productive layer of an FGA community is equivalent to the maximum value in eutrophic lakes and in a pure culture. It is expected that the development of an FGA community contributes to enhance the productivity in the littoral zone of lakes by increasing in the algal biomass.

An algal community in the littoral zone of lakes has been considered as having a two-component structure consisting of planktonic and benthic algal communities. In our case, FGA such as *Spirogyra* sp. have been included in the benthic algae. However, there were extraordinary differences in the light-extinction coefficient and the vertical-distribution pattern of biomass between the FGA and sessile algal communities (Figs. 8 and 10). Thus, in the littoral zone where an FGA community develops, the benthic algal community should be divided into two components, *i. e.*, FGA and sessile algal communities (Fig. 11). The effect of FGA intrusions into freshwater ecosystems has been mainly described as creating a new habitat for benthic animals (POWER, 1990a, b). In this study, from the viewpoint of the productive structure of an algal community in the littoral zone, we propose that such a community should be regarded as a three-component structure of planktonic, FGA and sessile algal communities.

Fig. 11. A schematic picture of algal community structures in the euphotic zone of pelagic and littoral zones (Pa : planktonic algae, Ba : benthic algae, FGA : filamentous green algae, Sa : sessile algae).

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琵琶湖北湖沿岸の礫帯における藻類の群落構造

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摘 要

琵琶湖北湖沿岸の礫帯において、底生藻および浮遊藻群落の現存量と種組成の季節変動を1994年6月から1996年4月にかけて調べた。現存量の大きな季節変動は、底生藻群落では糸状緑藻 *Spirogyra* sp., 浮遊藻群落では *Closterium aciculare*, *Staurastrum dorsidentiferum*, *Gomphosphaeria lacustris* の消長に起因していた。底生藻および浮遊藻群落の現存量の極大は、ともにわずか1~2種の優占的な増殖に由来していた。全藻類量に占める底生藻群落の割合は、全ての調査地点で平均90%以上であった。従って、本調査地では底生藻が基礎生産者として卓越していると評価された。湖沼沿岸帯における藻類群落の基礎生産構造は、一般的に浮遊藻および底生藻群落から成る2層構造と見なされてきた。*Spirogyra* の様な糸状緑藻も底生藻の1構成員とされてきたが、基質への付着器を持たない *Spirogyra* は、石面上で固着生活する底生藻群落（固着藻群落）を覆うように繁茂し、また群落内の光の消散係数は両群落で著しく異なっていた。従って、湖沼沿岸帯の藻類群落の基礎生産構造は、浮遊藻、糸状緑藻および固着藻群落から成る3層構造として捉えるべきであると結論付けた。