RESEARCH PAPER

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Transport and accumulation of bloom-forming cyanobacteria in a large, mid-latitude lake: the gyre-*Microcystis* hypothesis

Abstract Toxic cyanobacterial blooms have occurred in the near-shore waters of the North Basin of Lake Biwa, Japan, since 1994, and have been attributed to deterioration of water quality in the enriched littoral zone of the lake. From 1997 onwards, the bloom-forming cyanobacteria have been observed with increasing frequency in the deep offshore waters of the North Basin. In the present study, we examined the mechanisms responsible for these bloom populations in the main body of the lake. Specifically, we addressed the hypothesis that buoyant, nutrient-replete colonies of cyanobacteria are generated inshore, are advected offshore by large-scale horizontal transport processes, and subsequently accumulate in the downwelling center of large surface gyres that characterize the overall circulation pattern in the epilimnion of the North Basin. Diel variations of *Microcystis* biomass at the center and the edge of the Lake Biwa gyre were monitored at 6-h intervals on August 23–24, 2000, and the horizontal distribution of buoyant *Microcystis* was determined on October 6. The hydrodynamic structure of the first gyre was determined over the preceding 2 days by an on-board Acoustic Doppler Current Profiler (ADCP). The gyre was characterized by a counterclockwise horizontal current that could potentially advect material large distances offshore, a downwelling current near the center of the gyre, and an upwelling current at the edge of the gyre, caused by the radial pressure gradients. The biomass of *Microcystis* near the water surface was greater at the center than at the edge of the gyre, and the biomass at 5 m depth at the edge of the gyre was greater than that at the water surface or at the thermocline near the edge of the gyre. The results are consistent with the gyre-*Microcystis* hypothesis, and show the potential for accumulation of large concentrations of cyanobacteria in deep offshore lake environments that are normally considered unsuitable for cyanobacterial blooms.

Key words Bloom-forming cyanobacteria · Gyres · Hydrodynamic processes · Physical-biotic coupling · Toxic algae

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Introduction

Phytoplankton patchiness and blooms have been related to physical processes operating over a great variety of scales, ranging from small-scale turbulence (Jimenez 1997; Jou 1997), Langmuir circulation (George and Edwards 1973; Harris and Lott 1973) and wind-driven currents (Verhagen 1994; George and Edwards 1976; Ishikawa et al. 1999), to large-scale processes such as the Gulf Stream (Wiebe et al. 1976; Hitchcock et al. 1994, 1998) and oceanic upwelling (Chavez and Barber 1987; Chavez et al. 1991). Although advection and turbulent mixing processes must greatly influence phytoplankton distribution (Okubo 1978), relatively few studies have examined the mechanisms controlling phytoplankton patchiness in large lakes (Powell et al. 1975). This lack of information is due not only to the difficulty of measuring the great variety of dynamic responses in phytoplankton species assemblages (Reynolds 1989), but also to the difficulty of obtaining spatially broad coverage of hydrodynamic processes in large lakes.

Surface advection is likely to exert a strong effect on the spatial and temporal structure of phytoplankton communities in large lakes. A characteristic feature that is often found in such mid-latitude ecosystems during the period

of stratification is the existence of one or more persistent gyres that result from the geostrophic balance between the horizontal pressure gradients and the Coriolis force (Endoh et al. 1995). These gyres give rise to horizontal advection at scales ranging from kilometers to tens of kilometers, depending on the size of the lake (Endoh 1995; Kumagai et al. 1998). Information about the structure of these features is becoming increasingly available from the use of acoustic Doppler current profilers (ADCP) to map the velocity field.

Lake Biwa, Japan, is located at latitude 34°58′–35°31′ N and longitude 135°52′–136°17′ E (Fig. 1). It has a surface area of 670 km^2, with a deep northern main basin (maximum depth, 104 m; mean depth, 43 m) and a shallow southern sub-basin (mean depth, 3.5 m). It is a monomictic lake that is stratified from May to October and vertically well mixed in winter. Three gyres, initially documented by the Kobe Marine Observatory in the summer of 1925 (Suda et al. 1926), form during stratification in the North Basin. In order from north to south, the gyres are called the first gyre (counterclockwise circulation), the second gyre (clockwise circulation), and the third gyre (counterclockwise circulation). Okamoto and Morikawa (1961) found that the counterclockwise gyres were geostrophically balanced to the first order. Since then, several methods of measuring the gyres have been applied, and some of their physical characteristics have been clarified (e.g., Endoh 1986; Endoh et al.

1995). Recently, the use of ADCP technology has allowed us to determine the spatial and seasonal structure of these gyres within relatively short time intervals of a few days (Kumagai et al. 1998). Current research on the lake is focused on the development of a three-dimensional numerical simulation model of water currents, that can be coupled with an ecological process model.

Over the past several decades, the water quality of Lake Biwa has deteriorated because of high nutrient loading from the surrounding catchments. Even in the North Basin, which is considered a mesotrophic system (Tezuka 1992), there have been toxic summer blooms of cyanobacteria at some inshore harbors since 1994 (Yoshida et al. 1996) and offshore since 1997. Bloom-forming cyanobacteria can now be observed in late summer throughout the epilimnion of Lake Biwa (Kumagai et al. 1999). These blooms have created great public concern, and intensive monitoring of cyanobacteria has been necessary for social reasons because Lake Biwa supplies drinking water to nearly 14 million people in the Shiga, Kyoto, Osaka, Nara, and Hyogo districts. The dominant bloom-forming taxa are highly buoyant colonies of the genus *Microcystis.* They are unlikely to be germinated and recruited from bottom offshore sediments, and it has been suggested that these cyanobacterial populations are mostly transported from the enriched littoral areas of the lake (Ishikawa et al., submitted for publication).

In the present study, we addressed the "gyre-*Microcystis* hypothesis" that buoyant *Microcystis* colonies are generated inshore, are advected offshore, and then accumulate near the center of the first gyre by hydrodynamic processes in Lake Biwa, as seen in Fig. 2. We evaluated this hypothesis by making detailed current measurements by ADCP and by mapping the vertical and horizontal distribution of chlorophyll *a* and of the bloom-forming cyanobacteria.
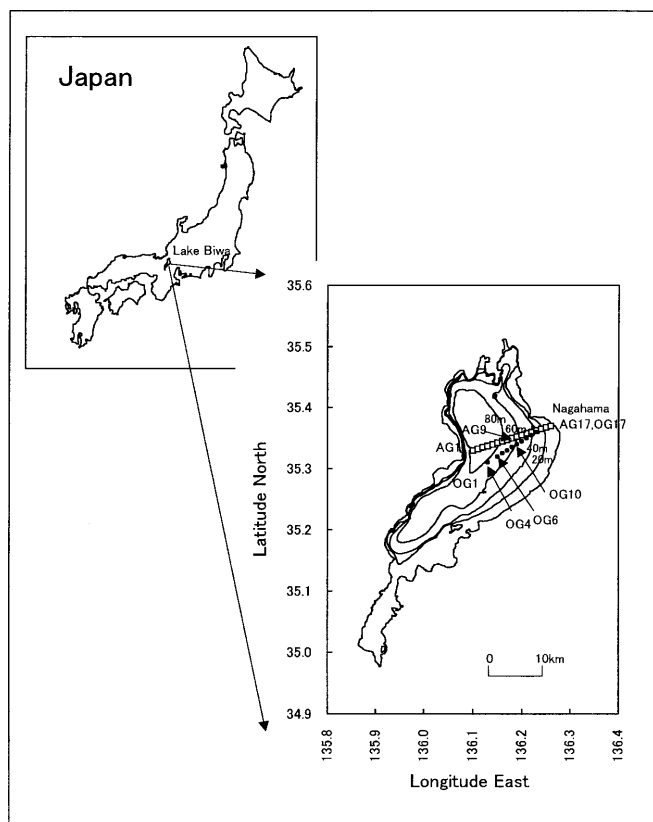
Methods

Measurement of gyre currents by ADCP

Current measurements were made with a 300-kHz, broadband ADCP (RD Instruments) installed on the bottom of R/V Hakken of the Lake Biwa Research Institute. This instrument is able to measure the water current at 2.00-m intervals between 6.88 m from the surface to 6.88 m above the lake bottom with an accuracy of 0.05 m s^{-1}. The output data were averaged over 15 s. This means that for a surface velocity of R/V Hakken of 8 knots, the horizontal data interval is 60 m. The ADCP measurement takes almost 2 days to cover the assigned area in the North Basin of Lake Biwa. Previous ADCP measurements have shown that the gyre structure does not change significantly, even if the results from 2 days are combined (Kumagai et al. 1998). Water currents were interpolated with the vertical profiles of ADCP data on a 500 m × 500 m grid mesh by a hyperbolic function method to compare them with the results calculated by a numerical simulation model.

Fig. 1. Map of Lake Biwa, showing the sampling sites

Fig. 2. Schematic view of the "gyre hypothesis," which postulates that high concentrations of buoyant cyanobacteria are generated inshore, advected offshore by the first gyre, and then accumulate in the central downwelling region of the gyre
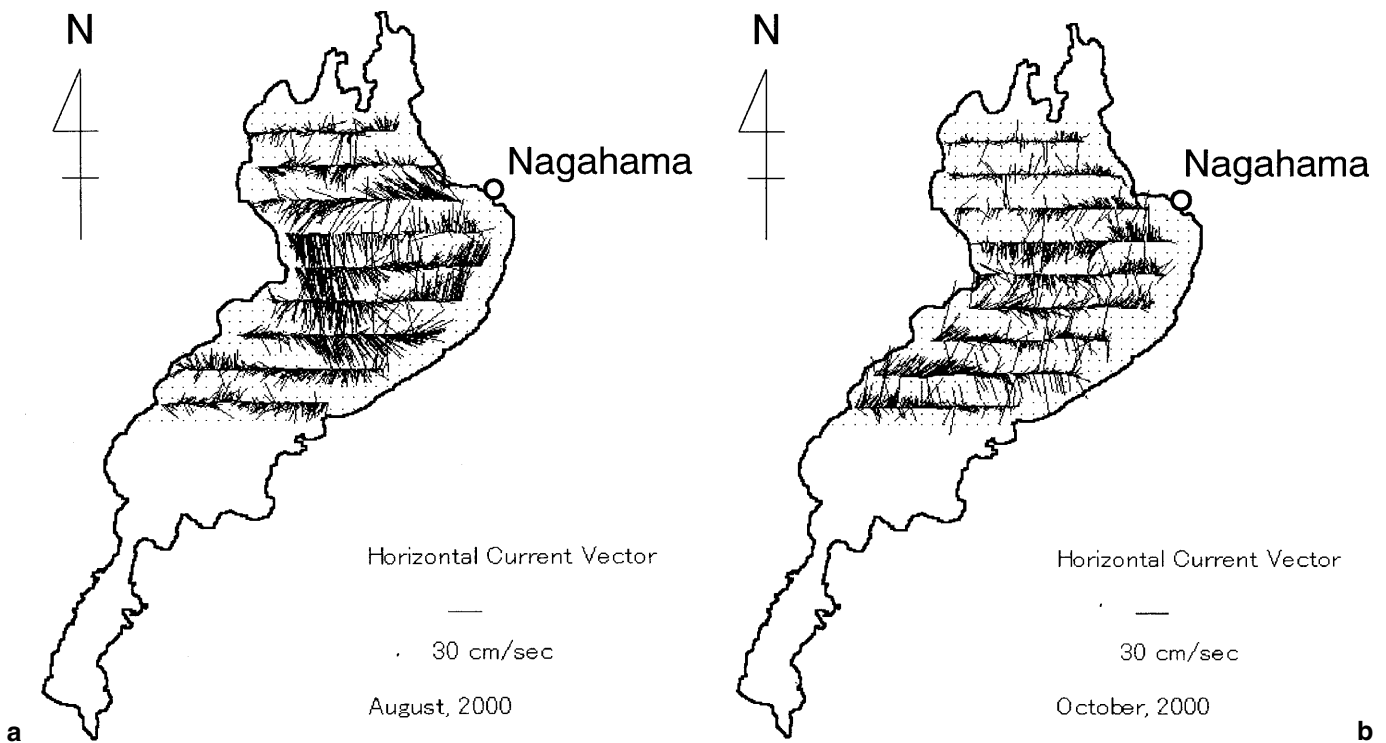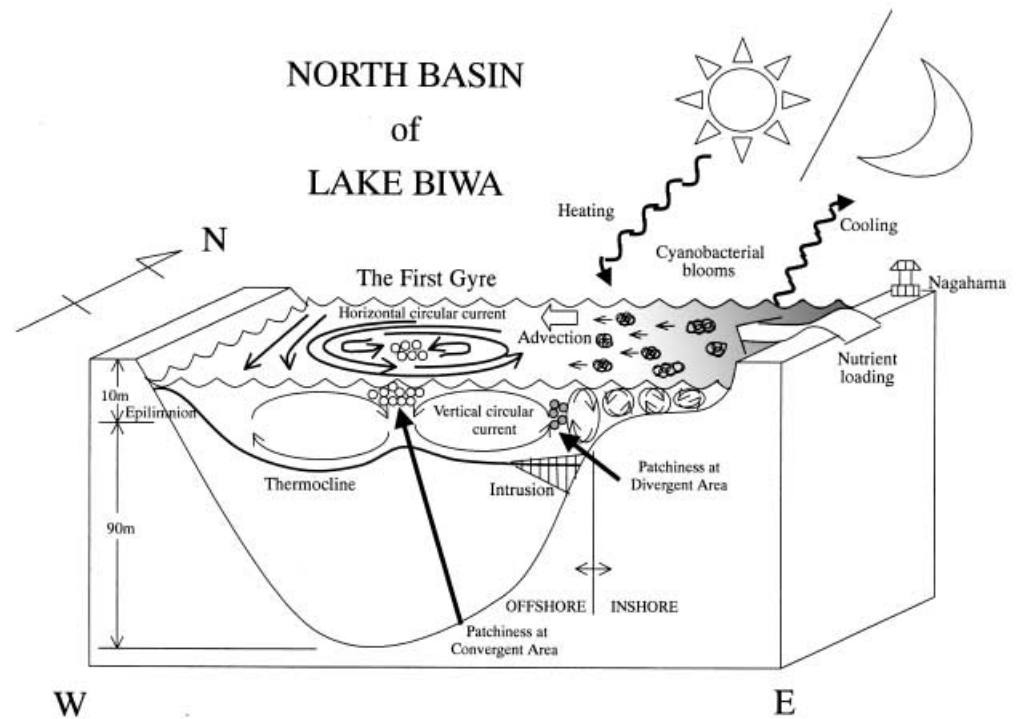
Fig. 3. Water currents at 6.6 m depth in Lake Biwa as measured by Acoustic Doppler Current Profiler, August 21–22, 2000 (**a**), and October 4–5, 2000 (**b**)

Vertical profiles of water temperature and chlorophyll a concentration

A calibrated fluorometer (Chlorotech, ACL200-PDK, Alec Electronics) was used to measure water temperature and chlorophyll *a* fluorescence from the water surface to 20 m

depth between 10 h on August 23, 2000, and 10 h on August 24 at 6-h intervals. At 10 h on August 23, we measured water temperature and fluorescence at 17 stations from AG1 to AG17 fixed along a transect from Nagahama and the center of the first gyre (Figs. 2 and 3a). The locations of these stations were determined on the basis of ADCP transects

performed within 2 days prior to this experiment. The vertical profiles were measured at two stations (AG1 and AG17) at 16h on August 23, at three stations (AG9, AG12, and AG17) at 22h on August 23 and 4h on August 24, and at five stations (AG1, AG5, AG9, AG12, and AG17) at 10h on August 24.

Phytoplankton sampling and counting

Fifteen-liter water samples were taken from the surface with a sampling bucket at three stations (AG9, AG12, and AG17) from 10h on August 23 to 10h on August 24, 2000, at 6-h intervals. In addition, the 17 stations (OG1 to OG17) at 10h on October 6, 2000, were fixed on the line crossing the center of the first gyre measured by ADCP on October 4–5 (Figs. 1 and 3b). OG10 was on the center of the gyre, and OG 17 was the same station as AG17 in Nagahama Harbor. The phytoplankton samples were collected across the gyre (OG6 to OG14) and at the inshore harbor (OG17) in the same way as on August 23 in order to compare the distribution of bloom-forming cyanobacteria. Twelve-liter water samples were collected at 5m depth and also at the thermocline (8m at AG9 and 10m at AG12) using a Van Dorn water sampler at the same time that water temperature and chlorophyll *a* were measured on August 23–24. Cyanobacterial colonies and other phytoplankton were collected with a 20-μm mesh net and were fixed with Lugol's iodine solution to a final concentration of 1%.

In these samples, the dominant phytoplankton species was *Coelastrum polycordum* (Chlorophyceae), and the dominant bloom-forming cyanobacterium was *Microcystis* spp. Either 40 fields of view or a minimum of 400 colonies of *C. polycordum* and *Microcystis* were counted by using a Sedgwick-Rafter counting chamber and a binocular microscope.

The meteorological conditions during phytoplankton sampling on August 23–24 and October 6 were measured at the Hikone AMeDAS station, about 10km southeast of the center of the first gyre. These data were provided by the Japan Meteorological Agency.

Nutrient analysis

In order to determine the nutrient distribution across the first gyre, water samples for nutrient analysis were taken at five stations (AG1, AG5, AG9, AG12, and AG17) at 10h on August 23, 2000. Our previous measurements in the summer of 1999 showed that the temporal change over 24h of nutrient concentrations was small relative to spatial variations in the epilimnion (Ishikawa et al., unpublished). The samples were taken from the surface at 0m with a sampling bucket, and from 5m and the thermocline (12m at AG1, 9m at AG5, 8m at AG9, and 10m at AG12; the same depths at which samples were taken for counting phytoplankton) using a Van Dorn water sampler. At the shallowest station, AG17, samples were collected only at the surface and at 2.2m depth at the same observation time. At 10h on October 6, surface samples for nutrient analysis were collected at OG4, OG10, OG13, and OG17. The samples were analyzed for ammonium (NH_4-N) by the method described in Sagi (1966), for nitrate (NO_3-N) with an Auto Analyzer (AACS-II, BRAN + LUEBBE), and for soluble reactive phosphorus (SRP) by the molybdenum mixed-reagent method (Murphy and Riley 1962) after filtration through glass fiber filters (Whatman GF/F).

Results

Meteorological condition

The air temperatures, precipitation, wind speeds, and wind directions at the observation times are summarized in Table 1. The air temperatures during the 24-h sampling period on August 23–24 fluctuated significantly above and below the surface water temperatures at each observation time. A maximum of 32.3°C was observed at 16h and a minimum of 23.2°C at 4h. On October 6 in the early autumn, the air temperature at 10h was cooler than in August in the middle of summer. The total amounts of solar radiation observed on August 23 and 24 and on October 6 were 6.1, 6.1, and 3.3kW m^{-2}, respectively (from monthly reports of the Hikone Meteorological Station 2000) and there was no recorded precipitation. The wind direction changed considerably. During the daytime on August 23–24, the winds blew from NNW to WNW; however, at 4h the wind direction changed almost to the opposite direction, SE. The wind speed varied between 2 and 5m s^{-1} on August 23–24 and was 1m s^{-1} at 10h on October 6.

ADCP mapping of the first gyre

Horizontal current vectors measured by ADCP during the daytime on August 21–22 and October 4–5 showed the first

Table 1. Meteorological conditions at the observation times

Date	Time	Air temperature (°C)	Precipitation (mm h^{-1})	Wind direction	Wind speed (m s^{-1})
August 23, 2000	10h 00	31.1	0	NNW	2
	16h 00	32.3	0	NNW	5
	22h 00	27.0	0	WNW	4
August 24, 2000	04h 00	23.2	0	SE	2
	10h 00	29.1	0	WNW	2
October 6, 2000	10h 00	21.3	0	W	1

gyre, as seen in Fig. 3a and b, respectively. The center of the first gyre was at 35°21.12′ N, 136°10.86′ E, and the diameter of the gyre was about 15 km on August 21–22. Later, although it was not so clear as the gyre in August, the center was at 35°11.39′ N, 136°20.10′ E, and the diameter was about 12 km on October 4–5. The first gyre moved toward the SE from August to October and appeared to be reduced in size (Kumagai et al. 1998).

Although the vertical velocities were too small to be measured by on-board ADCP, we could estimate the order and direction of vertical currents by combining the vertical velocities measured by ADCP and the mass conservation from horizontal current velocities. Those values might have some reflection errors due to settling of particles (approximately $10^{-5}\,\mathrm{m\,s^{-1}}$), but the results obtained seem to be consistent with the calculated results of numerical simulation models (Oonishi 1975; Endoh 1978).

The calculations were done as follows:

1. The horizontal scale (L) of upward currents at 7 m depth was estimated with the ADCP data from 136°5.3′ E to 136°14.3′ E along the line of 35°21.12′ N crossing the center of the first gyre in the case of the August experiment.
2. The flux (F) due to horizontal currents between the water surface and 20 m depth was estimated from the ADCP data along the same line.
3. The mean vertical velocity was calculated by F/L to be $0.000588\,\mathrm{m\,s^{-1}}$.
4. Each value of vertical velocity along the line of 35°21.12′ N was calibrated with the mean vertical velocity obtained above, and the results, including horizontal mean velocities of the first gyre, are depicted in Table 2.

The vertically averaged horizontal current velocities were between 0.08 and 0.16 m s^{-1} in the epilimnion near the edge of the first gyre and were reduced to zero near the center. The corresponding vertical velocities were between 0.0003 and 0.0007 m s^{-1} near the edge and between −0.0001 and −0.0005 m s^{-1} near the center of the first gyre, where vertically upward shows positive. From the trajectory analy-

sis, it was found that the water in the edge could reach to the center after almost 40 to 50 h.

Temperature

The water temperature contour distribution between depths of 0 and 20 m on the cross-section of the first gyre at 10 h on August 23, 2000, is given in Fig. 4. The water temperatures in this surface layer ranged between 16° and 29°C. The water temperature in the layer between 0 and 3 m in shallow areas was higher by approximately 2°C, and the temperature at the center of the gyre was lower by approximately 2°C than that of the offshore epilimnion. These observations indicate the presence of a heated shallow region and a downwelling flow near the cold central region. As seen in Fig. 4, the cool water from the surface to 3 m depth at the center of the first gyre looks unstable, but it can be explained by the cooling at the water surface and
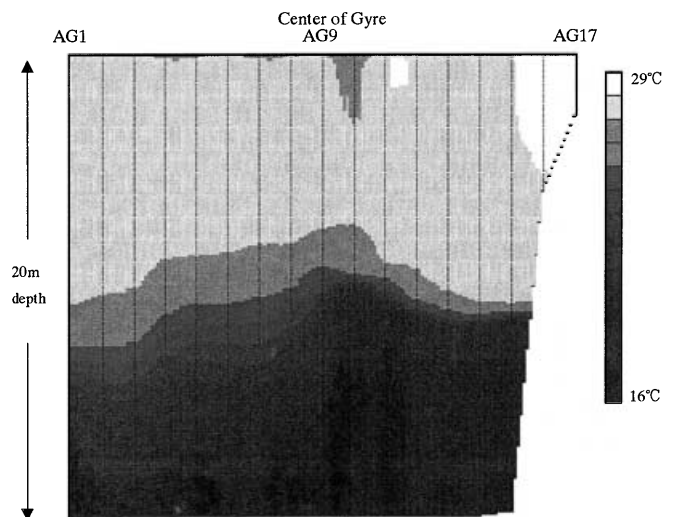

**Fig. 4.** Vertical water temperature contours at 10 h 00 on August 23, 2000

Table 2. Mean velocities of horizontal and vertical currents (m s^{-1}) in the first gyre measured by on-board ADCP

Location	Horizontal current		Vertical current		n
	Mean	SD	Mean	SD	
136°06.0′	0.157	0.015	0.000441	0.000240	38
136°06.6′	0.166	0.008	0.000653	0.000079	38
136°07.2′	0.145	0.021	0.000371	0.000335	38
136°07.8′	0.111	0.017	−0.000232	0.000346	38
136°08.4′	0.088	0.009	−0.000543	0.000136	38
136°09.0′	0.075	0.006	−0.000382	0.000185	38
136°09.6′	0.066	0.006	−0.000081	0.000174	38
136°10.2′	0.047	0.018	−0.000021	0.000123	38
136°10.8′	0.007	0.028	−0.000339	0.000265	38
136°11.4′	−0.037	0.020	−0.000524	0.000158	38
136°12.0′	−0.063	0.010	−0.000396	0.000149	38
136°12.6′	−0.078	0.010	−0.000242	0.000137	38
136°13.2′	−0.087	0.004	−0.000180	0.000041	38
136°13.8′	−0.059	0.033	0.000103	0.000329	38

accumulation of the cooler water at the center due to the convergence of the gyre. Actually, the air temperature until 10h during August was cooler than the surface water temperature (Water Resources Development Public Corporation, Lake Biwa Branch, unpublished).
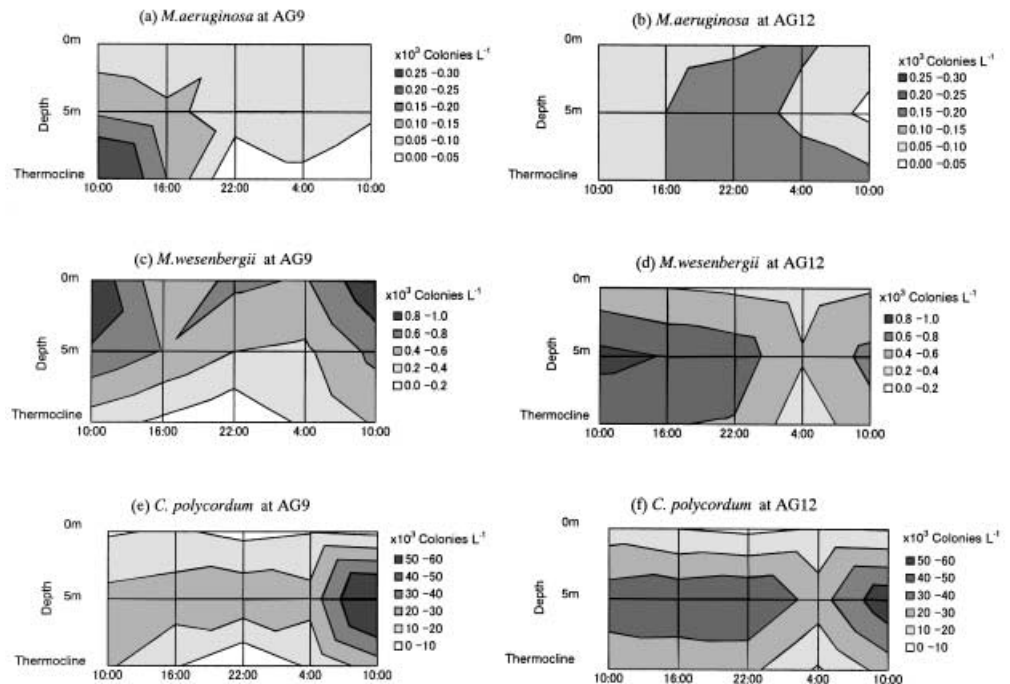
Chlorophyll *a* concentration

The concentration of chlorophyll *a* ranged from 0 to 13 mg m^{-3} in the surface layer (between 0 and 20m depths) at 10h in the August 23 samples (Fig. 5). Water masses with high concentrations of chlorophyll *a* were observed in an inshore area near AG17, in a thin layer between 0 and 1m
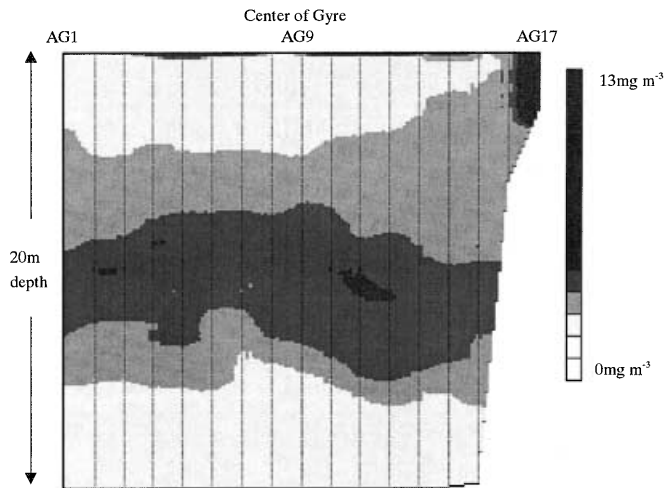
Fig. 5. Vertical chlorophyll *a* concentration contours at 10h 00 on August 23, 2000
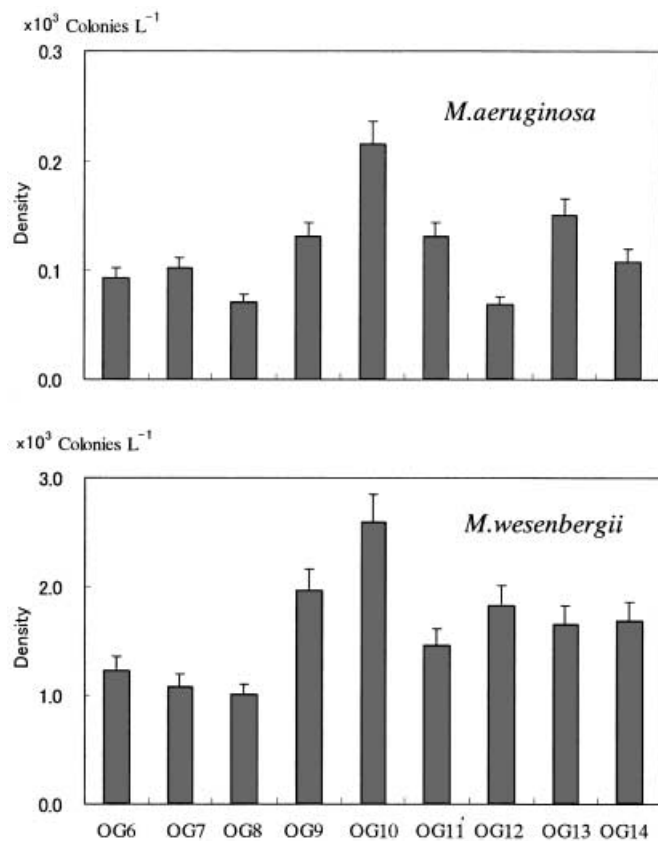
depth below offshore water surface sporadically, and in the thermocline. We could not see any sinking of phytoplankton near the center of the gyre like water temperature distributions (Figs. 4 and 5), and it might be caused by the difference between passive water temperature and active phytoplankton.

Dominant phytoplankton biomass and its distribution

The dominant phytoplankton species on August 23–24 at the time of sampling was the colonial chlorophyte *Coelastrum polycordum*. The two most common *Microcystis* species found in the North Basin, *M. wesenbergii* and *M. aeruginosa*, were both observed at relatively low concentrations during the period of sampling. The averaged density of *M. aeruginosa* from seven samples (0m, 5m, and the thermocline of AG9 and AG12 and at 0m of AG17) decreased from 120 colonies l^{-1} at 10h on August 23 to 70 colonies l^{-1} at 10h on August 24. The averaged density of *M. wesenbergii* with the seven samples at 10h on August 23 was 610 colonies l^{-1}, decreased to 320 colonies l^{-1} at 4h, and then recovered to 540 colonies l^{-1} at 10h on August 24. The similarly averaged density of *C. polycordum* at 10h was 1830 colonies l^{-1}, decreased to 1290 colonies l^{-1} at 4h, and increased again to 2480 colonies l^{-1} at 10h on August 24.

Temporal changes in the vertical distribution of *M. aeruginosa*, *M. wesenbergii*, and *C. polycordum* at two different stations at the center (AG9) and edge (AG12) of the first gyre are presented in Fig. 6. At AG9, *M. aeruginosa* had the highest density in the thermocline at 10h on August 23 but was not recorded at that depth at 22h on August 23 and at 4h and 10h on August 24 (Fig. 6a). At AG12, *M.*

Fig. 6. Diel variations of *Microcystis* and *Coelastrum* biomass at the three depths at the center and the edge of the first gyre. **a**, **b** *Microcystis aeruginosa*; **c**, **d** *Microcystis wesenbergii*; **e**, **f** *Coelastrum polycordum*; sampling times, 10h 00 August 23, 16h 00, 22h 00, 4h 00 August 24, 10h 00 August 24; sampling depths, 0m, 5m, and the thermocline; the values of 5m and thermocline at 16h 00 were interpolated from the neighboring values

Fig. 7. Buoyant *Microcystis* biomass at stations across the first gyre on October 6, 2000

aeruginosa had higher concentrations during the night and did not have surface accumulations (Fig. 6b). There were diel changes in the total density of *M. wesenbergii* at the three depths, with higher values during the day than during the night (Fig. 6c and d). At AG9, the densities of *M. wesenbergii* at 0 m were higher than at 5 m and at the thermocline (Fig. 6c). On the other hand, at AG12, the densities of *M. wesenbergii* at 5 m were higher than at other depths (Fig. 6d). The highest peaks of *C. polycordum* at AG9 and AG12 were observed at 5 m at both stations.

At 10 h on October 6, 2000, the mean density of *M. aeruginosa* in three samples (0 m at OG9, OG12, and OG17) was 120 colonies l^{-1}, slightly higher than that observed at the same time on August 23 and 24 (77 and 93 colonies l^{-1}, respectively). The mean density of *M. wesenbergii* in three samples (the same samples as *M. aeruginosa*) was 1450 colonies l^{-1}, which was also higher than that in the August samples at 10 h (410 and 380 colonies l^{-1}, respectively). The biomass of *Microcystis* increased between August and October. The horizontal distribution of *Microcystis* at 0 m across the gyre at 10 h on October 6 is shown in Fig. 7. The density of *M. aeruginosa* at OG17 was the second highest among the 10 horizontal stations. In contrast, *M. wesenbergii* concentrations at OG17 were the lowest among the 10 stations. The highest concentrations for both species were observed at the center of the gyre near OG9 and OG10.
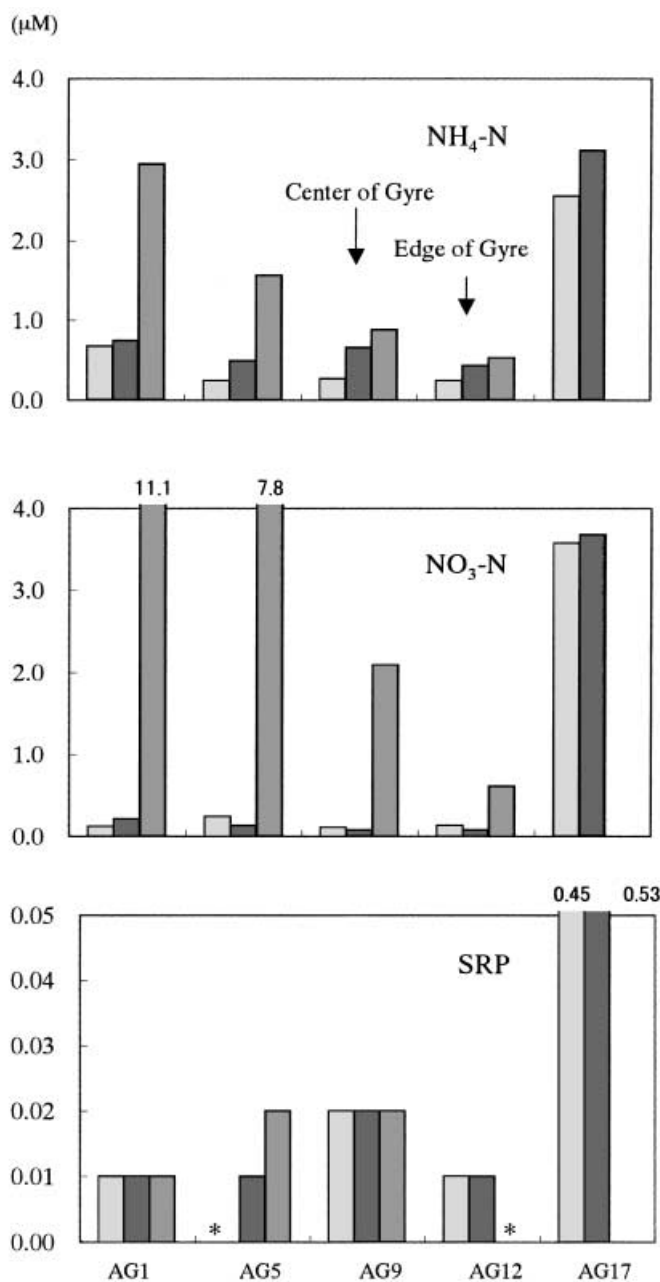
Fig. 8. Nutrient concentrations at 10 h 00 on August 23, 2000. *Left bar*, 0 m depth; *middle bar*, 5 m depth; *right bar*, on the thermocline; * below detection

Nutrient status

Ammonium (NH$_4$-N), nitrate (NO$_3$-N), and soluble reactive phosphorus (SRP) concentrations at 0 m, 5 m, and the thermocline for AG1, AG5, AG9, and AG12 and at 0 m and 2.5 m depths for AG17 are shown in Fig. 8; the concentrations at 0 m for OG4, OG10, OG13, and OG17 are given in Fig. 9. At offshore stations AG1, AG5, AG9, and AG12, the NH$_4$-N, NO$_3$-N, and SRP concentrations at the epilimnion tended to be much lower than those at inshore AG17. The NH$_4$-N concentrations at 0 m and 5 m depths for AG1, AG5, AG9, and AG12 were low (less than 1.0 μM).
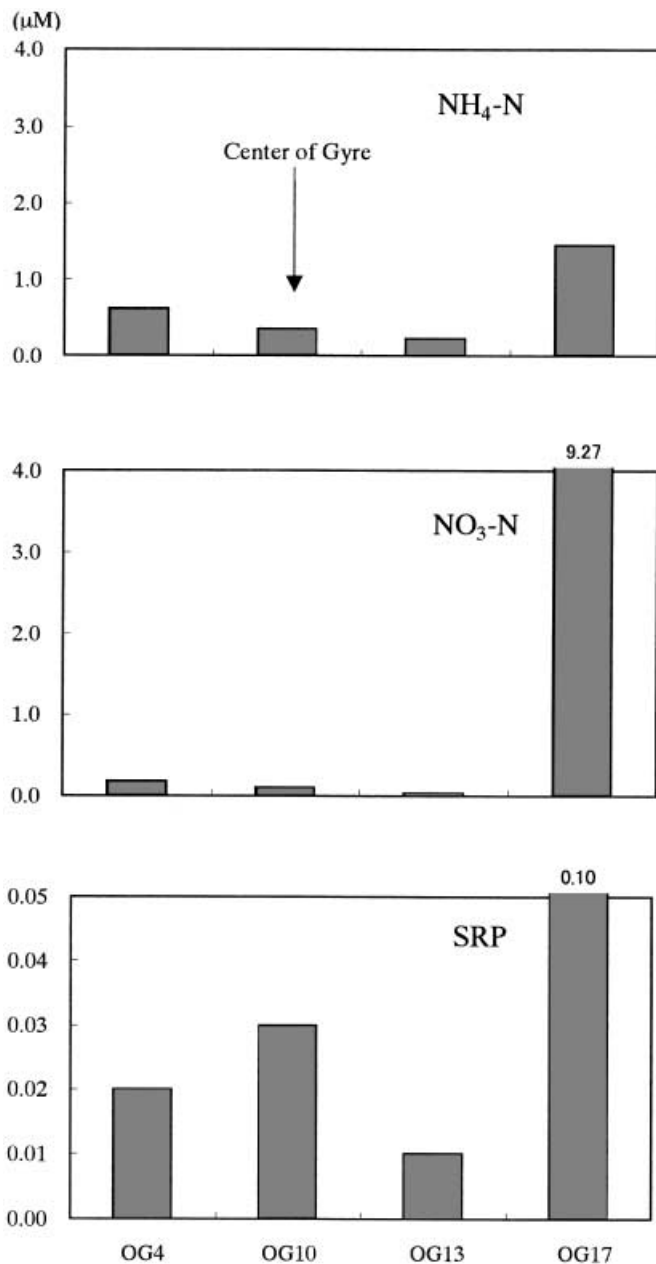
Fig. 9. Surface nutrient concentrations of NH₄-N, NO₃-N, and SRP at 10 h 00 on October 6, 2000

The NH₄-N concentrations at the thermocline were higher than at the surface, and the concentrations of AG1 and AG5 were higher than those of AG9 and AG12. Hence the differences among the three depths at AG12 were smaller than those at AG1 or AG5. The NO₃-N concentrations at 0 m and 5 m depths for AG1, AG5, AG9, and AG12 were low (less than 0.25 μM), and there were no consistent differences among the NO₃-N concentrations at 0 m and 5 m depths. The NO₃-N concentrations at the thermocline were much higher than at 0 m and 5 m depths, and those on the western side of the gyre (AG1 and AG5) were slightly higher than those at AG9 and AG12. On the contrary, there was little difference among SRP concentrations

at the three depths for AG1, AG5, AG9, and AG12, although the concentrations at the thermocline for AG5 and at the three depths for AG9 were slightly higher than those in the other offshore samples collected at the three depths.

At three offshore stations (OG4, OG10, and OG13) on October 6, the concentrations of NH₄-N, NO₃-N, and SRP at 0 m tended to be much lower than those at inshore OG17 as well as that on August 23, and the offshore concentrations were as low as that on August 23 (Fig. 9). NH₄-N and NO₃-N on the west side of the gyre (OG4) were higher than at the center and on the east side of the gyre (OG13). SRP was slightly higher at the center of the gyre (OG10), as on August 23.

Discussion

Our field observations of the distribution of buoyant cyanobacteria in Lake Biwa showed that *Microcystis* colonies accumulated near the center of the first gyre at 10 h in summer and early autumn (Figs. 6b and 7). It seems unlikely that this accumulation was due to the growth of *Microcystis* offshore, since the nutrient concentrations were consistently low in both August and October (Figs. 8 and 9; Shiga Prefectural Government 2000). Furthermore, over several days, the growth rate of *Microcystis*, which was estimated by both a frequency of dividing cells (FDC) experiment (Nakahara 1999) and a bottle incubation (Ishikawa et al., in press), was too low to form visible patchiness at the center of the gyre.

Microcystis wesenbergii showed diel changes in biomass and had the highest concentrations in the surface layer at the center of the gyre and at 5 m depth at the edge of the gyre (Fig. 6c and d). Because the estimated downwelling velocity according to ADCP near the center of the first gyre (-0.0001 to $-0.0005\,\mathrm{m\,s^{-1}}$) was much less than the maximum migration velocity of *Microcystis* ($0.003\,\mathrm{m\,s^{-1}}$), the vertical circulation does not seem to interfere with the vertical movement of *Microcystis*.

On the other hand, the nonbuoyant phytoplankton species *Coelastrum polychordum* has a distribution that contrasted markedly with that of the *Microcystis* colonies, with no changes in density at the center or the edge of the first gyre (Fig. 6e and f). The descending velocity of *C. polychordum* estimated by Stokes' law was about $-0.0005\,\mathrm{m\,s^{-1}}$, and this was almost compatible with the ADCP estimated upwelling velocity of 0.0004 to $0.0008\,\mathrm{m\,s^{-1}}$.

Stommel (1949) and Smayda (1970) discussed the accumulation mechanisms within Langmuir circulations, and showed how negatively buoyant particles will be selectively concentrated in the upwelling region, positively buoyant particles will accumulate above the downwelling region, and neutrally buoyant particles will be distributed randomly. Buoyant *Microcystis* can modify their ballast of photosynthetic products and thereby change their buoyancy (e.g., Kromkamp and Mur 1984; Takamura and Yasuno

1984; Thomas and Walsby 1985; Ibelings et al. 1991; Oliver 1994). In this way, *Microcystis* colonies could follow any one of the three distribution patterns surmised from the Langmuir circulation.

Langmuir circulation is characterized by vertical water movements at wind speeds in excess of $3–5\,\mathrm{m\,s^{-1}}$ and the presence of wind waves (e.g., Langmuir 1938; Faller 1971). In contrast, the first gyre has a large-scale vertical circulation current in the epilimnion, as shown by Endoh (1978) using a diagnostic model. Although these two types of circulation differ in scale and dynamics, the mechanisms of accumulation of buoyant organisms are likely to be similar in both, because they are governed by the same vertical flow characteristics. Thus, gyral currents would lead to an accumulation of positively buoyant colonies of *M. wesenbergii* at the surface in areas of converging currents; this is consistent with the observations at 10h (Fig. 6c). Conversely, where colonies lose their buoyancy, they would be more likely to accumulate in the metalimnion in areas of divergence; this is consistent with the observations in Fig. 6d. The horizontal distribution of *M. aeruginosa* on October 6 is also consistent with the gyre-*Microcystis* hypothesis. However, in the August sampling, this species did not accumulate in the center of the gyre, but instead decreased offshore (Fig. 6a). At least two factions might account for this difference from the other trends. First, *M. aeruginosa* tends to be strongly affected by wind (Ishikawa et al. 1999), and the wind speed during the survey on August 23–24 was higher than that on October 6 (Table 1). The strong winds on this date may have prevented the offshore transport of colonies and given rise to more general dispersion and dilution of colonies in the North Basin. Second, this species may have had insufficient nutrient supplies to sustain its populations offshore. Nutrient concentrations were low in the North Basin, and stored reserves may have been exhausted at this time, giving rise to a loss of buoyancy and sinking. Ishikawa et al. (in press) collected colonies of *M. aeruginosa* from the inshore water and incubated them in the offshore water of the North Basin. They found that the colonies could survive for 2 or 3 days using nutrients stored in their bodies, dividing only once or twice during these days. Generally speaking, nutrient-limited colonies decrease their synthesis of new gas vesicles, and as a result they lose their buoyancy (Oliver and Ganf 2000).

It is of interest that the density of *Microcystis* was maximal at 10h and not at 4h when *Microcystis* accumulated near the gyre center in August 23–24 and October 6. Many studies on the vertical migration of *Microcystis* have shown that colonies migrate up the water column in the early morning after respiratory consumption of their photosynthetic products during the night (Reynolds 1987; Ibelings et al. 1991; Takamura and Yasuno 1984; Walsby and McAllster 1987; Kim and Chu 2000). Thus, the *Microcystis* colonies observed at 0m at 10h were probably the result of the early morning accumulation of buoyant colonies.

Nakahara (2000, 2001) obtained detailed measurements of the horizontal pattern of *Microcystis* distribution in the North Basin of Lake Biwa. These data sets show high concentrations of biomass in the summers of 1999 and 2000 near positions that would coincide near the center of the first gyre. However horizontal distribution patterns in September 1998 (Watanabe 1999) and September 2000 (unpublished data) on an east–west transect line starting at Nagahama did not show offshore accumulation of *Microcystis*. There are two possible reasons for this difference in the results. One is that the observation lines were not exactly across the center of the first gyre, since there were no concurrent velocity measurements. Second, the observations did not encompass 24h of sampling, and patches influenced by diel migration may have been missed. In the present study, we therefore combined our spatial survey of *Microcystis* distribution with 24-h sampling and ADCP measurements.

The gyre-*Microcystis* hypothesis describes a combination of physical and biotic processes whereby buoyant particles such as bloom-forming cyanobacteria are transported from inshore to offshore and accumulate in the surface waters at the downwelling center of the gyre (Fig. 2). The spatial extent of the accumulated patch will be dictated by the balance of processes such as advection, growth, and losses induced by diffusion, grazing, and decomposition. In Lake Biwa, because the stable gyre and the bloom-forming buoyant *Microcystis* appear at almost the same time of the year, the gyre-*Microcystis* combined model can be used as a good natural indicator to understand the offshore-inshore and physico-biological coupling processes.

In conclusion, our field data from the North Basin of Lake Biwa are consistent with, but are not definite proof of, the gyre-*Microcystis* hypothesis. The future direction of this study will encompass both modeling and high-resolution analysis of population community-structure approaches in order to assess the extent of growth and physical accumulation individually. Our observations imply that the offshore populations of *Microcystis* are the result of a balance between advection within the gyre from inshore source regions, accumulation in the central downwelling region of the gyre, and various physical and biological loss processes. The existence and size of the North Basin *Microcystis* patch could be considered an integrated index of lake ecosystem health. Given that these species are toxic (Watanabe 1999) and are a major source of public concern, more detailed studies are required to understand the exact mechanisms governing the production of *Microcystis* spp. blooms and, most importantly, the future options for control of these noxious species.

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