Seasonal Abundance, Grazing Impacts on Bacteria, and Vertical Distribution of Heterotrophic Microflagellates in the South Basin of Lake Biwa*

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Abstract

Seasonal abundance of heterotrophic microflagellates and bacteria was investigated at an offshore station (water depth, *ca.* 4 m) in the south basin of Lake Biwa (eutrophic water basin) during May to October 1984. Cell abundance of flagellates and bacteria ranged from 1.7×10^3 to 9.7×10^3 cells·ml⁻¹ and 2.5×10^6 to 1.5×10^7 cells·ml⁻¹, respectively. The instantaneous grazing rate (*g*) of flagellates on bacteria was estimated from the total cell volume of flagellates and the volume specific clearance rate of flagellates reported in the literature. The *g* values ranged from 0.003 to 0.020 h⁻¹. The instantaneous growth rate (*μ*) of bacteria estimated from the frequency of dividing cells method ranged from 0.009 to 0.034 h⁻¹. From the values of *g* and *μ*, it was estimated that 13-130% of bacterial daily production was consumed by flagellates. Vertical distribution of flagellates at the dredged area (water depth, *ca.* 12 m) of the same water basin revealed that flagellates reached maximum abundance in a subsurface layer (6 m-depth) during the stratification. The significance of flagellates as bacterial consumers and some characteristics of their occurrence in the eutrophic water body are discussed.

Key words : grazing impact, heterotrophic microflagellates, Lake Biwa, planktonic bacteria

1. Introduction

It has been suggested that heterotrophic microflagellates are significant consumers of planktonic bacteria in seas (FENCHEL, 1982c ; SIEBURTH and DAVIS, 1982 ; SHERR *et al.*, 1984), estuaries (WRIGHT and COFFIN, 1984) and lakes (GÜDE, 1986 ; SCAVIA and LAIRD, 1987 ; NAGATA, 1988). However, little is known about the abundance, grazing impacts on bacteria, and distribution of flagellates in eutrophic lakes (RIEMANN, 1985).

From the enclosure experiments conducted in eutrophic Slottssø, Denmark, RIEMANN (1985) found that the abundance of flagellates is markedly influenced by the population density of macrozooplankters (>140 μm) in the enclosures. He observed that the cell densities of flagellates in the enclosures that included dense macrozooplankters were only 1 to 7% of those found in the other enclosures with few macrozooplankters. He also

calculated the grazing rate of flagellates, and suggested the significant grazing impacts on bacteria in the enclosures with many flagellates. In Lake Oglethorpe, SANDERS and PORTER (1986) assessed grazing rate of protozoans on bacteria by the antibiotics method. They estimated that protozoans consume 60-80% of epilimnetic bacterial standing crop per day. PEDRÓS-ALÍO and BROCK (1982), on the other hand, assumed that grazing by flagellates is negligible for the consideration of the loss factor of epilimnetic bacteria in eutrophic Lake Mendota.

In the present study, seasonal abundance of heterotrophic microflagellates was examined at a sampling station located in a eutrophic, shallow water basin of Lake Biwa (the south basin), and grazing impacts of flagellates on bacteria were assessed. Vertical distribution of flagellates at the dredged area of the same basin was also investigated. Some characteristics of the occurrence of

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flagellates in this basin are compared with the results previously obtained in the north basin of Lake Biwa, a mesotrophic, deep water body (NAGATA, 1987, 1988).

2. Study site

The south basin of Lake Biwa (Fig. 1) is a eutrophic shallow water basin (surface area, 57 km², mean water depth, 3.5 m). Recent trophic state (TEZUKA, 1984) and bacterial level (NAGATA, 1984) of this lake have been described. One sampling station (St. Nb5, depth *ca.* 4 m) for the seasonal investigation was located in the center of this basin, while the other sampling station (St. D, water depth *ca.* 12 m) for the examination of vertical distribution was located in the dredged area (500 m×500 m). Details of the location, morphometry and water quality of this area have been described by TERASHIMA and UEDA (1982).

3. Materials and methods

Surface water samples were collected at St. Nb5 between 14 May and 24 October 1984. At St. D,

Fig. 1. Two sampling stations in Lake Biwa (Nb5 and D).

samples were collected vertically by a 3-liter Van Dorn water sampler on 9 August, 18 September, and 12 October 1984. Samples for bacteria were fixed with 2% formalin (final conc.), but with 1% glutaraldehyde (final conc.) for flagellates. The samples were kept cool until they were processed (up to 3 weeks). Bacteria were enumerated by the acridine orange direct count method (HOBBIE *et al.*, 1977 ; NAGATA, 1984), while heterotrophic microflagellates were enumerated by epifluorescence microscopy using fluorescein isothiocyanate (SHERR and SHERR, 1983 ; NAGATA, 1986b). Two filters were used for each sample, and the range of the duplicates was 2-41% (mean 13) of the mean value for bacteria and 0-48% (mean 15) for flagellates. Details of the procedures for counting bacteria and flagellates have been described elsewhere (NAGATA, 1988). Bacteria and flagellates were sized with an ocular micrometer ($\times 1,250$). For each sample, 20 cells were measured for bacteria 1, and 43-123 cells (mean 79) for flagellates. Cell volume was estimated assuming the shape of bacteria to be spherical or cylindrical with hemispherical ends, and that of flagellates to be spherical or ellipsoidal. Carbon biomass was estimated using a conversion factor of 100 fg C $\cdot \mu\text{m}^{-3}$ for bacteria (NAGATA, 1986a), and 71 fg C $\cdot \mu\text{m}^{-3}$ for flagellates (FENCHEL and FINLAY, 1983). The frequency of dividing cells (FDC) of bacteria was determined according to HAGSTRÖM *et al.* (1979).

Grazing impact of flagellates on bacteria was assessed by comparing the instantaneous growth rate of bacteria with the instantaneous grazing rate of flagellates on bacteria. The instantaneous grazing rate was calculated from total cell volume (cell abundance multiplied by mean cell volume) of flagellates. The assumptions of this method are that flagellates can, in an hour, clear bacteria from a volume of water that is 10^5 times their own cell volume at 20°C (FENCHEL, 1982b) and that Q_{10} of the clearance rate is 2 (FENCHEL, 1987). The instantaneous growth rate of bacteria was estimated by the FDC method (HAGSTRÖM *et al.*, 1979). The FDC-growth rate calibration equation derived for the north basin of Lake Biwa (NAGATA, 1987) was used for the calculation.

Chlorophyll *a* concentration was measured spectrofluorometrically (STRICKLAND and PARSONS, 1972). Dissolved oxygen concentration was measured by the Winkler method.

4. Results

At St. Nb5, cell abundance of heterotrophic flagellates ranged from 1.7×10^3 to 9.7×10^3 cells·ml⁻¹ (Fig. 2). Although no quantitative estimation was undertaken, the flagellates were commonly unattached forms. More than 70% of flagellates were 2 to 4 μ m in terms of equivalent spherical diameter (Fig. 3). Mean cell volume for each sample ranged from 9 to 35 μ m³ (mean 21) (data not shown). From the cell abundance and the mean cell volume, the biomass of flagellates was estimated to be 2.4–13 μ g C·l⁻¹ (Fig. 2).

The range of bacterial abundance was from 2.5×10^6 to 1.5×10^7 cells·ml⁻¹ (Fig. 2). Contribution of attached bacteria in cell number ranged from 0 (not detected) to 21% (mean 6.6) (data not shown). Mean cell volume of bacteria calculated for the whole samples was 0.095 μ m³ (n=300, SD=0.080). Using this mean volume, the bacterial biomass was

Fig. 2. Seasonal variations of water temperature (WT), chlorophyll *a* concentration (CHL), bacterial abundance (B), abundance of heterotrophic microflagellates (F), and carbon biomass of heterotrophic microflagellates (FB) at Station Nb5 (surface water).

Fig. 3. Size frequency distribution of heterotrophic microflagellates. Samples were collected at Station Nb5 during 14 May to 24 October 1984. Total number of sized cell was 1580.

estimated to be 25–150 μ g C·l⁻¹, and the biomass of flagellates corresponded to 2–26% (mean 10) of the bacterial biomass.

To assess the factors that possibly control the variables for flagellates (*i.e.*, cell abundance, mean cell volume and biomass), simple linear correlations (r) between the variables for flagellates and those for environments (*i.e.*, bacterial abundance, water temperature and chlorophyll *a* concentration) were calculated. But no significant ($P < 0.05$) correlation was found between these variables except in two cases, *i.e.*, between the abundance of flagellates and water temperature ($r = -0.62$), and between the abundance of flagellates and chlorophyll *a* concentration ($r = 0.49$).

The instantaneous grazing rate of flagellates ranged from 0.006 to 0.017 hr⁻¹, and the instantaneous growth rate of bacteria ranged from 0.010 to 0.034 hr⁻¹ (Table 1). It can be suggested that grazing impacts of flagellates on bacteria were significant, because the grazing rate corresponded to 13–130% of the growth rate (Table 1).

On 9 August and 18 September, the water column at St. D was thermally stratified and oxygen depleted below 8 m (August) and 10 m (September) (Fig. 4). In these circumstances, highest density of flagellates was found at 6 m, and bacteria was more abundant in the upper 6-m layer than in the lower layer. Vertical variation in abundance was more pronounced for flagellates than for bacteria. Mean cell volume of flagellates

Table 1. Instantaneous growth rate (μ) of bacteria and instantaneous grazing rate (g) of heterotrophic microflagellates in the south basin of Lake Biwa (Station Nb5 ; samples were obtained in 1984).

	Bacterial abundance (10^6 cells $\cdot$ ml $^{-1}$)	Frequency of dividing cells (FDC ; %)	$\mu^{(1)}$ (hr $^{-1}$)	$g^{(2)}$ (hr $^{-1}$)	g/μ (%)
14 May	2.5	2.9	0.013	0.006	46
11 June	4.8	4.8	0.024	0.020	83
25 June	5.7	3.3	0.015	0.018	120
2 July	4.7	4.8	0.024	0.003	13
9 July	6.8	5.8	0.034	0.016	47
16 July	7.1	4.3	0.021	0.017	81
24 July	8.6	3.1	0.014	0.017	121
30 July	9.1	5.6	0.032	0.009	28
6 August	15	2.7	0.012	0.014	117
13 August	11	2.2	0.010	0.007	70
20 August	8.8	2.6	0.012	0.012	100
28 September	8.7	2.8	0.013	0.009	69
8 October	13	2.3	0.011	0.008	73
17 October	7.6	4.2	0.020	0.007	35
24 October	6.3	1.9	0.009	0.012	133

(1) μ was estimated from FDC using the calibration equation ; $\ln \mu = 0.33\text{FDC} - 5.3$ (NAGATA, 1987).

(2) g was estimated from biomass of flagellates assuming that a flagellate clears a water 10^5 times its own cell volume at 20 C (FENCHEL, 1982b) and Q_{10} is 2 (FENCHEL, 1987).

and bacteria was large in the anoxic layer (Fig. 4). On 12 October, the circulation of the water body was manifest from profiles of water temperature and dissolved oxygen. On this date, flagellates distributed evenly, while bacteria and chlorophyll a showed maxima in a near bottom layer (11.5 m).

5. Discussion

Abundance of flagellates reached 10^4 cells $\cdot$ ml $^{-1}$, and that of bacteria reached 10^7 cells $\cdot$ ml $^{-1}$ in the south basin of Lake Biwa (Figs. 2, 4). These levels are higher than those in the north basin (Table 2). The higher primary production rate, allochthonous organic input, and resuspension of bottom mud in the south basin may well be related to the higher abundance of heterotrophic microbes. However, factors that determine the seasonal dynamics of flagellates and bacteria could not be decided in the present study. Although the correlation analysis indicated that flagellates tend to be more abundant when the water temperature is low and the chlorophyll a is high, the mechanism underlying these correlations is open to further research.

In Lake Biwa, the cell size of bacteria and

flagellates is almost the same in the both basins. The mean cell volume [μm^3] of flagellates and bacteria for the south basin was 21 and 0.095, respectively, while those for the north basin (epilimnion) was 19 and 0.101, respectively. [The data for the north basin are from NAGATA (1988).] A similarity in the mode of heterotrophic microbe existence was also noted between the two basins, *i.e.* unattached forms of flagellates and bacteria are most common not only in the north basin (NAGATA, 1988) but also in the south basin (see above). This suggests that the prevailing mode of flagellate-bacterial trophic linkage is one between unattached bacteria and flagellates in Lake Biwa. However, in order to ascertain this hypothesis, further measurements of the activity of attached vs. unattached microbes (NAGATA, 1987) is needed for the samples of the south basin.

In the present study, the grazing rate of flagellates on bacteria was calculated from the total cell volume of flagellates. The volume specific clearance rate reported in the literature (FENCHEL, 1982b) was used for this calculation. FENCHEL (1982b) estimated clearance rates on bacteria by six strains of flagellates (size, 20–200 μm^3), and

Fig. 4. Vertical distributions of water temperature (WT), dissolved oxygen concentration (DO), chlorophyll *a* concentration (CHL), bacterial abundance (B), abundance of heterotrophic microflagellates (F), mean cell volume of heterotrophic microflagellates (FV), and mean cell volume of bacteria (BV). Samples were collected at Station D on 9 August 1984 (top panel), 18 September 1984 (middle panel), and 12 October 1984 (bottom panel).

found that they can clear a water 10^5 times (range, $5 \times 10^4 - 1 \times 10^6$) their own cell volumes per hour at 20°C, except for *Actinomonas mirabilis*, which can filter 10^6 times its cell volume. Since the higher clearance rate of *A. mirabilis* was ascribed to its ability to filter water with a coarse-meshed (1-3.5 µm) sieving apparatus (FENCHEL, 1982a), and it was suggested that this species adapted to collect particles larger than natural bacteria (ca. 0.5-1 µm) (FENCHEL, 1982b), such a high value would not

be suitable for the calculation of the grazing rate on natural planktonic bacteria. SHERR, *et al.* (1983) also measured the clearance rate on bacteria of *Monas* sp., and found that volume specific clearance rate of this species was similar to FENCHEL's values except for *A. mirabilis*. From the above information, it was assumed that a flagellate cell of Lake Biwa clears water 10^5 times its own cell volume per hour at 20°C and Q_{10} is 2 (FENCHEL, 1987) in estimating the grazing rate of flagellates. By this method, the grazing rate (number of bacteria·flagellate⁻¹·hr⁻¹) will be overestimated, if bacterial biomass exceeds the level at which the grazing rate reaches the maximum grazing rate (FENCHEL, 1980). However, the grazing rates calculated in this study (instantaneous grazing rate multiplied by bacterial density) were usually below the maximum grazing rate reported for some strains of small flagellates (27 bacteria·hr⁻¹ for *Monosiga* sp. [size, 20 µm³], and 54 bacteria·hr⁻¹ for *Pleuromonas jaculans* [size, 90 µm³]; FENCHEL, 1982b). Therefore, it was considered that the grazing rate of flagellates may not be overestimated. In the north basin of Lake Biwa, NAGATA (1988) found that grazing rates estimated by this method are consistent with those derived from bacterial growth in fractionated samples, suggesting the reliability of the method.

From the comparison of the grazing rate of flagellates and growth rate of bacteria (Table 1), it was suggested that a significant fraction (13-130%) of bacterial production is consumed by flagellates. These data indicate that flagellates are significant consumers of planktonic bacteria not only in meso- and oligotrophic environments (SIEBURTH and DAVIS, 1982; FENCHEL, 1982c; SHERR *et al.*, 1984; GÜDE, 1986; SCAVIA and LAIRD, 1987; NAGATA, 1988), but also in shallow eutrophic lake environments. For the consideration of the loss factor of bacteria in eutrophic environments, the grazing of flagellates should be examined. Moreover, the necessity of research on the role of the "microbial loop" (AZAM *et al.*, 1983) in the energy transfer and matter cycling within eutrophic lake environments should be stressed. However, the possibility that there are bacterivores other than heterotrophic flagellates in the investigated area must be also noted. Crustaceans (NAGATA, 1985; NAGATA and OKAMOTO, 1988), rotifers (BOGDAN *et al.*, 1980), ciliates (SHERR and SHERR, 1987), and mixotrophic flagellates (KIMURA and

Table 2. Comparison of the abundance of heterotrophic microflagellates and bacteria between the north basin and the south basin of Lake Biwa ⁽¹⁾.

	Flagellates (10^3 cells $\cdot$ ml $^{-1}$)		Bacteria (10^6 cells $\cdot$ ml $^{-1}$)	
	Min-Max	Mean (C.V.) ⁽²⁾	Min-Max	Mean (C.V.) ⁽²⁾
South basin (St. Nb5)	1.7-9.7	4.4(50)	2.5-15	8.0(41)
North basin (St. Ie)	1.0-3.9	1.9(42)	1.6-6.2	3.9(28)

(1) Surface water samples were collected during 14 May to 24 October 1984. For flagellates, 20 pairs of data (each pair of the samples was obtained on the same date) were compared, while for bacteria, 15 pairs of data were compared. Data for the north basin (St. Ie) are from NAGATA (1988).

(2) C.V., coefficient of variation (%).

ISHIDA, 1985) may also utilize bacterial resources.

Finally we discuss vertical distribution of heterotrophic microbes at St. D. In the anoxic layer, flagellates and bacteria were larger in size than in the oxic layer (Fig. 4), suggesting that morphologically distinct microbes exist in the anoxic layer (PEDRÓS-ALÍO and BROCK, 1982). An outstanding trend of the vertical distribution pattern of flagellates was the maxima of abundance at a depth of 6 m on 9 August and 18 September. This depth was the oxic-anoxic boundary layer (August), or the bottom of the oxic layer (September). SOROKIN (1965) has proposed that, in stratified water column with the anoxic hypolimnion, the supply of reduced compounds from the anoxic layer enhances chemosynthetic activity of bacteria at the oxic-anoxic interface, and that the density of protozoans is highest in this layer. More recently, maxima of bacterial cell density, heterotrophic activity (incorporation rate of leucine) of bacteria, and cell density of bacterivorous protozoans (scuticociliates) were found in the oxic-anoxic boundary of the stratified Lake Oglethorpe (PACE, 1982; McDONOUGH *et al.*, 1986). Although the maximum of bacterial density in the oxic-anoxic boundary layer was not found at St. D in Lake Biwa (Fig. 4), it was considered that bacterial activity would be the highest in this layer, because higher flagellate activity may enhance bacterial activity (SIEBURTH and DAVIS, 1982), and the subsurface maxima of the flagellates were found in the present study (Fig. 4). However, movement of water and grazing activity of larger suspension feeders may also affect the vertical distribution pattern of heterotrophic microbes in a complex manner. Therefore, in order to assess the validity of the above hypothesis, research on the vertical distribution of the activity of flagellates and bacteria is needed.

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摘 要

琵琶湖南湖における従属栄養性小型鞭毛虫の
季節的消長、細菌に対する摂食影響、および垂直分布

1984年の5月から10月までの間、富栄養水域である琵琶湖南湖湖心部の定点(水深約4 m)において、従属栄養性小型鞭毛虫と細菌の細胞数の季節変動を調査した。鞭毛虫と細菌の細胞数は、それぞれ、 1.7×10^3 – 9.7×10^3 cells $\cdot$ ml $^{-1}$ 、および 2.5×10^6 – 1.5×10^7 cells $\cdot$ ml $^{-1}$ の範囲で変動した。細菌に対する鞭毛虫の瞬間摂食速度を鞭毛虫の現存量から推定したところ、 0.003 – 0.020 hr $^{-1}$ の範囲の値を示し、一方、分裂細胞頻度から推定した細菌の瞬間増殖速度は 0.009 – 0.034 hr $^{-1}$ の範囲の値を示した。これらのデータから、1日当たりの細菌生産量の13–130%は鞭毛虫によって消費されているものと推定された。次に、しゅんせつ跡地(水深約12 m)において鞭毛虫の垂直分布を調べたところ、成層期には細胞数の垂表水層極大が見られた。細菌消費者としての鞭毛虫の重要性や富栄養水体における鞭毛虫出現の特徴について考察を加えた。

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