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EUTROPHICATION IN LAKES

The bacterioplankton of Lake Taihu, China: abundance, biomass, and production

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Abstract Abundance, biomass and production of pelagic bacteria were examined over one year at monthly sampling intervals across a trophic profile in Meiliang Bay, Lake Taihu. With the lowest density in the open lake, the bacterial abundance showed a clear trend in relation to trophic status. The carbon content per cell was higher in autumn and winter, and the opposite was true for bacterial biomass. Bacterial ^{3}[H]-*TdR* and ^{14}[C]-Leu incorporation rates, cell production, turnover times and carbon production varied during the annual cycle at different sites. The ratio of bacterial production to primary production was high, independently of the method used, indicates that the microbial food web in Lake Taihu is an important component of the total food web of the lake and dominated by external inputs.

Keywords Eutrophication · Trophic status · Bacterial biomass · Bacterial production · Lake Taihu

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Eutrophication of shallow lakes with special reference to Lake Taihu, China

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Introduction

Bacteria play a pivotal role in aquatic ecosystems. They use dissolved organic matter (DOM), which is mineralized and transformed into biomass, forming the base of the microbial food web (Azam et al., 1983). Measurement of bacterial cell numbers and biomass is, thus, a central aspect in the study of plankton.

By using fluorescent dyes and epifluorescence microscopy for direct counting (Hobbie et al., 1977; Porter & Feig, 1980; reviewed by Raymond, 1994), combined with automated image analysis (Psenner, 1991a, b) or electron microscopy (Krambeck et al., 1981) for measuring bacterial size distribution and cell volumes, reliable estimates of bacterial biomass can be made. Using the incorporation of radio-labeled precursors into DNA (Thymidine) and proteins (Leucine) (Fuhrman & Azam, 1980, 1982; Kirchman et al., 1985, 1986), as well as other approaches, e.g., the frequency of dividing cells (Davis & Sieburth,

1984), realistic estimates of in situ bacterioplankton production can be achieved.

Eutrophication and contaminant enrichment can directly and indirectly affect structure and functioning of microbial food webs, because any changes in trophic state of a water body would affect the relative significance of microorganisms and alter the entire pelagic food web (Weisse, 1991; Sommaruga, 1995). Bacterial abundance (Bird & Kalff, 1984) and production (Cole et al., 1988) correlate with phytoplankton biomass and primary production. Therefore, bacterial biomass and production will be enhanced with increased nutrient loading and primary production (Weisse, 1991). Also, the abundance and biomass of other microbial food web components (such as autotrophic picoplankton, small eukaryotic algae, heterotrophic nanoflagellates, ciliates and metazoan microplankton) will increase, which will decrease the relative importance of the microbial food web to carbon flux (Weisse, 1991).

In this paper, we reported a study on selected microbial parameters along a trophic gradient in Lake Taihu, a large shallow lake in eastern China. The major aim of these studies was to evaluate the relationships between the bacterioplankton abundance, cell volume and biomass, production and the trophic state of lake. We tested the hypothesis that bacteria and lake eutrophication are tightly coupled and bacterial growth in lakes largely occurs at the expense of allochthonous carbon sources other than phytoplankton production.

Materials and methods

Sampling sites

Lake Taihu is the third largest fresh water lake in China and is influenced by intensive blooms of blue-green alga during summer. In Meiliang Bay, at the northern end of Lake Taihu at the inflow of the main tributary, a north-south profile across the bay and a transverse profile from west to east were chosen (Fig. 1). These five stations represented different trophic levels, including a highly contaminated area at the river mouth (#0) and several sites in Meiliang Bay with nutrient levels decreasing with distance from the river mouth (3#, #5, and site #2 in front of the Taihu Station). The site with the lowest influence from nutrient inputs by the river is the open area (#8) in the center of the lake.

Sampling

Samples were taken with a 5 l Patalas–Schindler sampler. A 50 ml sub-sample was transferred into a glass bottle (75 ml) containing 2.5 ml of prefiltered (pore size, 0.2 μm) formaldehyde (final concentration 2%). The glass bottles were washed with acid, rinsed with particle-free distilled water and autoclaved one day before use. After return to the laboratory, samples were stored in a refrigerator at 4°C until slides for enumeration and image analysis were prepared.

Bacterial abundance

For bacteria abundance, a well-mixed sub-sample was diluted with particle-free distilled water (1:40) and stained with 4′, 6′-diamidino-2-phenylindole (DAPI, Sigma) at a final concentration of 2 μg ml^{-1} for 7 min (modified from Porter & Feig, 1980; Raymond et al., 1994; Posch et al., 2001). After staining, samples were filtered onto black polycarbonate filters (0.2 μm pore size, 25 mm diameter, Poretics^{TM}) and embedded in nonfluorescent immersion oil (Cargille type A, Cargille Laboratories, Inc., USA). On each slide, at least 400 bacteria were counted at 1600× with a Zeiss Axiovert 135 M epifluorescence microscope equipped with a HBO 50 W mercury lamp and a filter set for UV excitation (BP 365, FT 395, LP397 nm, Zeiss filter set 01) (Zeiss, Germany).

Bacterial biomass

Bacterial biomass is the product of cell abundance and carbon content per cell. Measurement of cell sizes and carbon contents is described elsewhere. Briefly, cell length and width were measured microscopically using a DAPI concentration of 1 μg ml^{-1} and a sensitive camera coupled to an image analysis system. Carbon

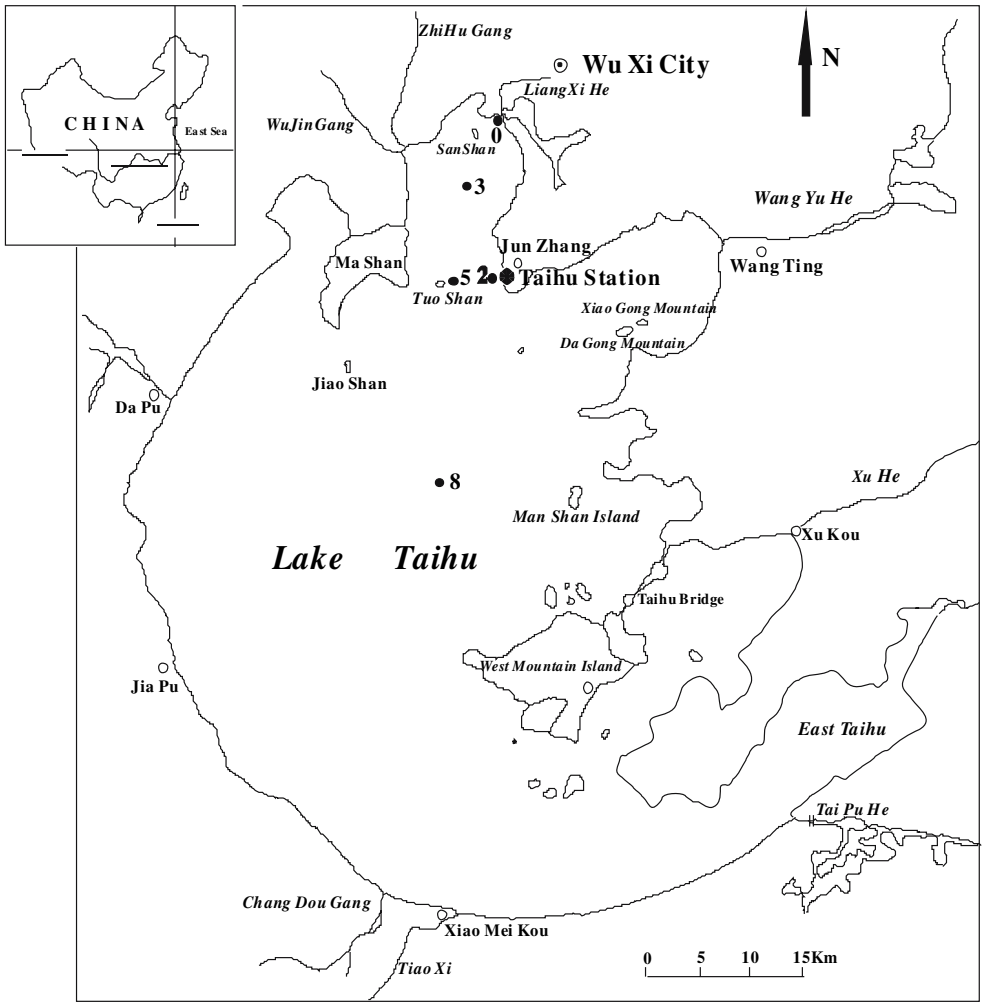

Fig. 1 The location of the sampling sites in Lake Taihu

content was inferred by an empirical formula established under comparable staining procedures (Loferer-Krößbacher et al., 1998; Posch et al., 2001).

Metabolically active bacteria

A 500 ml sub-sample was transferred into a glass bottle prepared as above. After return to the laboratory, 1 ml of 2-(*p*-iodophenyl)-3-(*p*-nitrophenyl)-5-phenyl tetrazolium chloride (INT) stock solution (2 mg ml^{-1}) was added to 10 ml of sample in 20 ml polyethylene vials (INT final conc. ca. 0.02%). All samples were incubated at in situ temperature in a water bath for 1 h without any substrate addition. After incubation, samples were fixed with pre-filtered (pore size, 0.2 μm) formaldehyde (final concentration 2%). Samples were stored in a refrigerator at 4°C at least 1 h and no longer than 24 h before preparation (modified from Zimmermann et al., 1978; Dufour & Colon, 1992; Thom et al., 1993). Other procedures were the same as for bacterial abundance estimations. A blue filter and halogen lamp were used for INT measurements.

Bacterial production (BP)

A dual-label incubation method was used to measure incorporation of thymidine (*TdR*) and leucine (Leu) by adding [^{3}H]-*TdR* and [^{14}C]-Leu to a single sample and collecting cold-TCA-insoluble

material (modified from Chin-Leo & Kirchman, 1988; Kirchman & Hoch, 1988). For each sample, triplicates of 10 ml each and one control (already containing 0.5 ml of 0.2 μm pre-filtered formalin at a final concentration of 2%) were used. In each sub-sample, 100 nM (final concentration) of [^{14}C]-Leu (specific activity, 308 mCi mmol^{-1}, Amersham Life Science, England.) was added, and samples were incubated for 40 min in a water bath at in situ temperature. After 40 min, 10 nM (final concentration) of [^{3}H]-*TdR* (specific activity, 81 Ci mmol^{-1}, Amersham Life Science, England.) was added, and samples were incubated for an additional 20 min. The incubation was stopped by adding 0.5 ml formalin at a final concentration of 2%. After incubation, samples were filtered through cellulose nitrate filters (Sartorius^{TM}, 0.2 μm pore size, 25 mm diameter). Then, 5 ml of ice-cold 5% TCA were added for 5 min to extract macromolecular fractions. The filter was rinsed 3 times with 5 ml of ice-cold 5% TCA. Radioactivity incorporated into cellular material was assayed by a Beckman liquid scintillation counter (LS-8000IC).

According to the literature (Simon & Azam 1989, Wetzel & Likens 2000), the following formulas and conversion factors were used to calculate bacterial [^{3}H]-*TdR* and [^{14}C]-Leu incorporation, cell production and carbon production.

$$[^{3}\mathrm{H}] - TdR.\text{incorporation [n mol } TdR\ \mathrm{l}^{-1}\ \mathrm{h}^{-1}] = \frac{U \times 4.5 \times 10^{-13}}{S \times T \times V}$$

where 4.5×10^{-13} = the number of curies per dpm; U = dpm of the filter; S = Specific activity of the *TdR* [Ci mmol^{-1}]; T = Incubation time [h]; V = Volume of filtered sample [l].

Cell production [cells l^{-1} h^{-1}] = 2×10^{18} cells mol^{-1} *TdR*

Carbon production [μg C l^{-1} h^{-1}] = TI × CP × CC

where TI = *TdR* incorporation [moles*TdR* l^{-1} h^{-1}]; CP = Cell production [cells mol^{-1}]; CC = Cellular carbon content [μg C cell^{-1}].

$$[^{14}\mathrm{C}] \text{ - Leu. incorporation [n mol Leu } \mathrm{l}^{-1}\ \mathrm{h}^{-1}] = \frac{U \times 4.5 \times 10^{-13}}{S \times T \times V}$$

where 4.5×10^{-13} = the number of curies per dpm; U = dpm of the filter; S = Specific activity of the Leu [Ci mmol^{-1}]; T = Incubation time [h]; V = Volume of filtered sample [l].

Cell production [cells l^{-1} h^{-1}] = 0.07×10^{18} cells mol^{-1} Leu.

BCP [μg C l^{-1} h^{-1}] = mol. Leu (inc.) × (7.3/100)$^{-1}$ × 131.2 × ID × (C/protein)

where: 131.2 = molecular weight of leucine

(7.3/100)$^{-1}$ = mole% of leucine in protein, hence 0.073

C/protein = ratio of cellular carbon to protein, best estimate = 0.86

ID = Isotope dilution; here ID = 2

Results

Some physical and chemical parameters in different parts of Lake Taihu during May 1998 to May 1999 are presented in Electronic Supplementary material. Due to the shallowness of the lake and strong winds, the water column remained mixed. However, nutrient concentrations, Chl *a* concentration, and other physical and chemical parameters varied among the sampling sites and showed a clear trophic gradient from the river mouth (hypertrophy), Meliang Bay (eutrophy) to the open lake (meso/eutrophy).

Bacterial abundance

The distribution patterns of bacterial abundance varied significantly along the trophic gradient of this lake (One-way ANOVA, $P = 0.005$). At the hypertrophic river mouth, the highest bacterial abundance was determined. With the mean value of 15.4×10^{9} l^{-1}, the bacterial abundance was ca. 55% higher than the mean in eutrophic Meiliang Bay and almost twice as high as the meso/eutrophic open lake (Fig. 2).

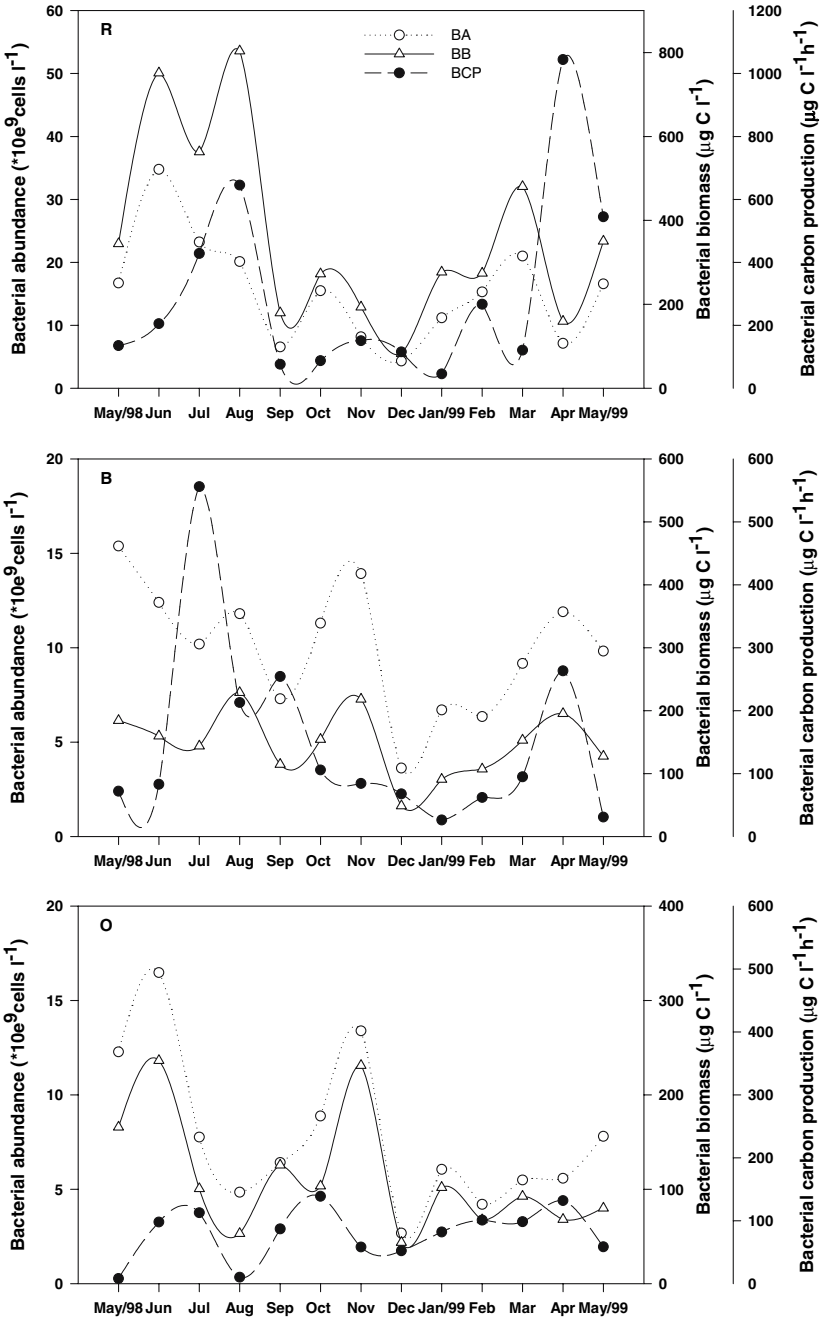

Fig. 2 Seasonal distribution of bacterial abundance, biomass and carbon production at 3 different sites of Lake Taihu from May 1998 to May 1999. R ... river mouth; B ... Meiliang Bay; O ... open lake

Bacterial biomass

The bacterial biomass also markedly increased along the trophic gradient of Lake Taihu (Fig. 2). At the hypertrophic river mouth, the mean bacterial biomass was 364 ± 225 μg C l^{-1}, i.e. ca. 1.5 times and 2.2 times higher than that at eutrophic Meiliang Bay and the open lake, respectively.

The difference between the highest and lowest value was ca. tenfold at the river mouth, while only ca. fivefold were recorded both in the Meiliang Bay and the open lake. No significant differences for seasonality were found in different trophic area of this lake (One-way ANOVA, $P > 0.05$).

Active bacteria

A highly significant positive correlation was found between the number of active bacteria and the total bacterial abundance in all parts of this lake, although this relationship varied among the habitats (Fig. 3.). In the hypertrophic river mouth, the mean ratio of active bacteria versus total bacterial abundance (34%) was slightly higher than that in the eutrophic Meiliang Bay (29%) and the meso/eutrophic open lake (28%). Variation of the percentage of active cells between the different trophic sites was smaller than the variation in abundance and biomass.

Bacterial production

The bacterial [^{3}H]-*TdR* incorporation rate also increased along the trophic gradient, and showed a significantly different over time (One-way ANOVA, $P < 0.0001$, $n = 65$) and space (One-way ANOVA, $P = 0.04$, $n = 65$), although the distribution patterns were similar in all of the sites. At the river mouth, with the maximum value of 14603 pmol l^{-1} h^{-1}, the annual mean value of [^{3}H]-*TdR* incorporation rate was ca. 1.2 times than Meiliang Bay and 2.2 times higher than the open lake, respectively (Table 1).

While the turnover times estimated from cell production were extremely fast and highly variable among the sampling sites (Fig. 3). At the hypertrophic river mouth, the mean turnover times was only ca. 87% less than the open lake, although the cell production was ca. 3 times higher (Fig. 3). Differences of turnover times within the temporal (One-way ANOVA, $P > 0.05$, $n = 65$) and spatial (One-way ANOVA, $P > 0.05$, $n = 65$) distribution were not significant.

Bacterial carbon production at different sites showed a similar distribution pattern as bacterial [^{3}H]-*TdR* incorporation rate, particularly at the river mouth and in Meiliang Bay (Fig. 2). With a mean of 141.8 ± 52.8 μg C l^{-1} h^{-1} at the river mouth, bacterial carbon production was ca. 2.4 and 4.5 times higher than means at Meiliang Bay and the open lake, respectively.

Temporal distribution of bacterial incorporation rates at different sites were similar for both [^{14}C]-Leu and [^{3}H]-*TdR*, even though the value for [^{14}C]-Leu was much higher (Figs. 3 and 4). No significant differences were found between bacterial cell production based on either method (Paired *t*-test, $P > 0.05$). However, turnover times estimated from [^{3}H]-*TdR* and [^{14}C]-Leu at the river mouth (One-way ANOVA, $P = 0.002$, $n = 39$) and Meiliang Bay (One-way ANOVA, $P = 0.001$, $n = 39$) were significantly different, although cell production based on both methods was not significantly different. In the open lake, no significant difference was found (One-way ANOVA, $P > 0.05$, $n = 39$).

While a clear positive correlation between [^{3}H]-*TdR* and [^{14}C]-Leu measurement was found, bacterial carbon production measured by [^{14}C]-Leu was ca. 2 times higher than that of [^{3}H]-*TdR* (Fig. 4). Since both methods are based on measuring some aspect of macromolecular synthesis (DNA for *TdR*, Protein for Leu), it is possible to convert these incorporation rates to rates of macromolecular synthesis and, in turn, to biomass production. But this conversion depends on detailed information about several cellular components, thus bacterial cell size and biomass were measured at the same time (Figs. 3 and 5).

Discussion

Factors affecting bacterial abundance and activity

Bacterioplankton assemblages often are dominated by inactive or dormant cells, and only a small fraction of bacterial cells appear to be metabolically active in aquatic systems (Stevenson, 1978; Mason et al., 1986). However, the fraction of active cells varies in time and space (Zimmerman et al., 1978; Quinn, 1984). Over a broad range of aquatic systems, the total number

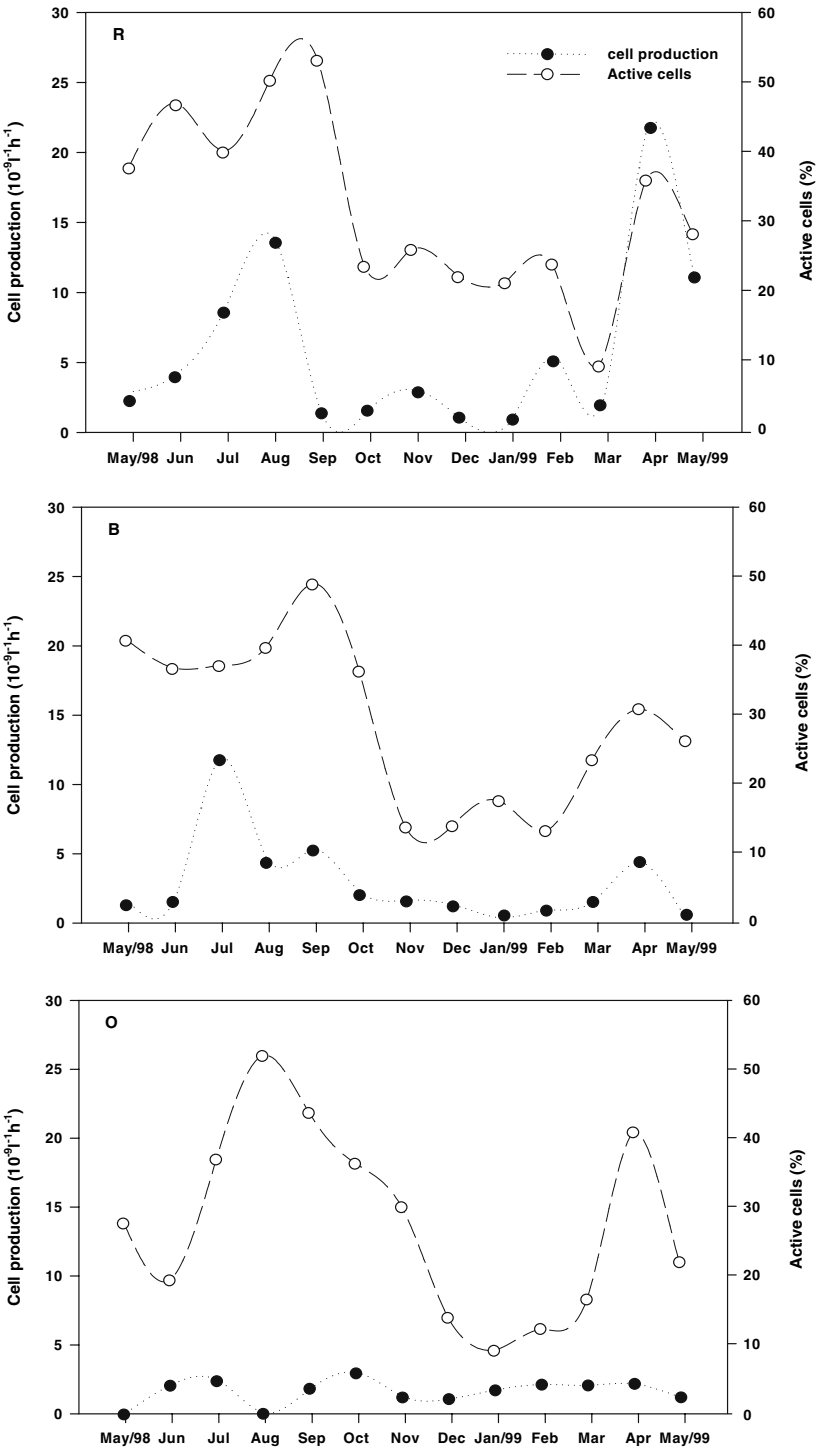

Fig. 3 Seasonal distribution of cell production rates and percentage of active cells at 3 different sites of Lake Taihu from May 1998 to May 1999. R ... river mouth; B ...Meiliang Bay; O ... open lake

Table 1 Leucine and Thymidine incorporation rates (pmol l^{-1} h^{-1}) at different sites of Lake Taihu

		TdR	Leu	*TdR*/Lue
R	Mean ± S.E	2878.8 ± 1069.0	92.2 ± 25.3	31.2
	Range	343.3–14603.2	14.0–323.9	24.5–45.1
B	Mean ± S.E	1338.8 ± 409.3	45.6 ± 12.6	29.4
	Range	195.2–4755.8	8.1–172.4	24.1–27.6
O	Mean ± S.E	886.5 ± 150.0	24.7 ± 3.5	35.9
	Range	68.1–2124.1	2.5–43.0	27.2–49.4

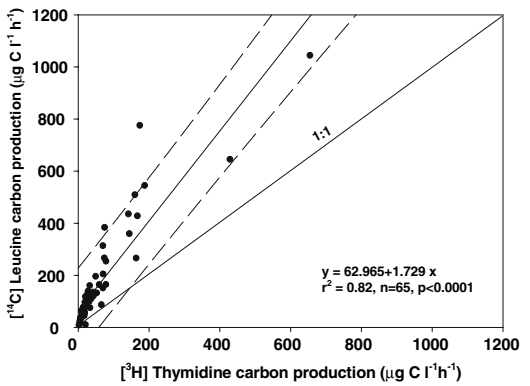

Fig. 4 Correlation of bacterial carbon production measured by [^{3}H] *TdR* and [^{14}C] leu in Lake Taihu from 1998 to 1999. $r^2 = 0.82$, $n = 65$, $p < 0.0001$. The dashed line shows the 95% confidence limits

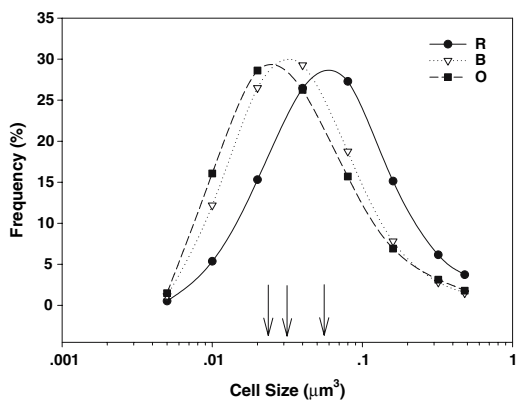

Fig. 5 The distribution of bacterial cell size at 3 different sites of Lake Taihu. R ... river mouth; B ... Meiliang Bay; O ... open lake

of bacteria varied by three orders of magnitude, active bacteria varied by four orders of magnitude, and the proportion of active cells increased systematically along gradients of enrichment from ultra-oligotrophic open ocean areas (<5%) to highly productive estuaries (>50%) (Del Giorgio & Scarborough, 1995).

With lowest bacterial abundance in the open lake, bacterial density showed a clear trend in relation to trophic status in Lake Taihu (Fig. 2), corresponding to the overall trend of abundance increase with system enrichment (Weisse, 1991). Bacterial abundance in the highly contaminated river mouth, however, was only slightly higher and not significantly different from those observed in eutrophic Meiliang Bay. Similar results were obtained by Azam et al. (1983) and Bird & Kalff (1984), who also found that fluctuations of bacterial biomass are small across trophic gradients. The low rate of increase in total bacterial density may imply that total bacterial biomass tends to be more uniform among systems, and their relative contribution to community biomass declines with increasing system productivity (Fuhrman et al., 1989). This indicates that structural and functional characteristics of the 'microbial loop' may be operating differently in stressed versus unstressed ecosystems (Munawar & Weisse, 1989).

With a mean ratio of ca. 34%, 29% and 28% in the river mouth, Meiliang Bay and open lake, respectively, the ratio of metabolically active bacteria to total bacterial abundance does not always correspond to these environmental gradients, although a significant positive correlation between total bacterial abundance and active bacteria existed in all parts of Lake Taihu (Fig. 3). However, data on total and active bacteria from the literature for aquatic systems show that our data are in the range of pelagic systems in general (Del Giorgio & Scarborough, 1995). The estimated average proportion of active cells in this work was similar to the mean for published data on lake bacteria (23%) (Del Giorgio & Scarborough, 1995), although some papers show that this ratio can reach 100% in a hypertrophic lake (Sommaruga, 1995). In most aquatic systems, there is a pool of rapidly growing cells embedded in a larger matrix of inactive bacteria, and the relative size of the active and inactive pools varies systematically along gradients of enrichment (Del Giorgio & Scarborough, 1995). This large variance among systems may also reveal that there are differential control

mechanisms for active and inactive bacteria in different ecosystems.

Although Billen (1990) suggested that the lack of simultaneous changes in phytoplankton and bacterioplankton abundance on a seasonal scale is caused, in many cases, by the delayed response of bacteria to phytoplankton development, it is reasonable that the number of active cells is more variable among systems than the total number of bacteria, and that only metabolically active bacterioplankton are responsible for growth, nutrient uptake and transformation of organic carbon substrates (Del Giorgio & Scarborough, 1995). Moreover, this variation may be masked by a rather large and constant pool of inactive bacteria. Thus, the function of bacterioplankton, based on the total number of bacteria, may have to be revised to accommodate large variations in the proportion of metabolically active cells (Del Giorgio & Scarborough, 1995). However, like other planktonic components, bacterioplankton density and production are correlated positively to system productivity, such as nutrient concentration, dissolved organic carbon, chlorophyll *a*, and primary production (Cole et al., 1988).

Leucine and Thymidine incorporation

Although there are still technical problems, incorporation of [^{3}H] thymidine (*TdR*) into DNA and [^{14}C] leucine (Leu) into protein are considered the most reliable methods (Fuhrman & Azam, 1980; Chin-Leo & Kirchman, 1988). However, accurate estimates of bacterial production depend on use of an appropriate conversion factor (Chin-Leo & Kirchman, 1988), which may vary (even by more than a factor of 100) over short time and space scales (Kirchman et al., 1986; Chin-Leo & Kirchman, 1988; Smits & Riemann, 1988). In this case, observed variation in thymidine incorporation could be due to changes in conversion factors rather than bacterial production (Kirchman & Hoch, 1988). So, it is necessary to ensure that observed changes in *TdR* incorporation are due to real changes in bacterial production, not in the conversion factor or some artifact (Chin-Leo & Kirchman, 1988).

When both *TdR* and Leu incorporation are measured in a single incubation by the dual-label approach, agreement between independent measurements made simultaneously should separate real changes from artifacts more effectively than a single-label approach (Fig. 4). Thus, we are confident that observed variations reflect real changes in the metabolism of bacterial assemblages (Kirchman et al., 1986). In addition, incorporation rates determined from dual-label incubations differed only slightly from those obtained from single-label incubations (Chin-Leo & Kirchman, 1988). The dual-label procedure, however, can reduce the time and material needed to perform simultaneous measurements of *TdR* and Leu incorporation, while minimizing errors.

Physico-chemical parameters directly or indirectly affecting bacterial production vary over time and relatively short distances (Kirchman & Hoch, 1988), which may cause methodological problems, especially in attempting to measure bacterial production. For this reason, the dual-label approach was used to measure *TdR* and Leu incorporation. In spite of problems inherent to each method, *TdR* and Leu incorporation rates covaried and gave the same qualitative picture of bacterial production in different parts of Lake Taihu (Table 1, Fig. 4). Although bacterial carbon production data lay within the broad range of the literature, bacterial carbon production measured by Leu was ca. 2 to 3 times higher than by *TdR*. This may indicate that conversion factors in Lake Taihu vary by a factor of two or so and differences may be due to methodology. Servais (1992) suggested that bacterial production measured by *TdR* seems to be systematically underestimated compared with those measured by Leu.

Bacterial production and its coupling with primary production

Bacterial production can be used to estimate average growth rate of bacterial assemblages and as an indicator of bacterial response to fluctuations in environmental conditions (Chin-Leo & Kirchman, 1988). Bacterial abundance and production are correlated positively with phytoplankton biomass and primary production in a broad range of freshwater and marine systems, and

bacterial production varied from 2% to >80% of primary production (Bird & Kalff, 1984; Cole et al., 1988). However, bacterial abundance and production do not increase proportionally with chlorophyll concentration as well as primary production (Robarts et al., 1994), although a positive empirical relationship was found between bacterial abundance and chlorophyll concentration in fresh and marine waters (Bird & Kalff, 1984).

Lake Taihu data show that bacterioplankton production was higher at the river mouth than in the open lake (Table 1, Fig. 3). Bacterial production (both measured by *TdR* and Leu) and phytoplankton biomass at the river mouth and in Meiliang Bay were correlated positively, but not in the open lake. The bacterial production to primary production ratio varied among the sampling sites (One-way ANOVA, $P = 0.023$, $n = 65$) and increased along the trophic gradient with a mean value ca. 2 and 4 times higher than in Meiliang Bay and the open lake, respectively. At the same time, no significant correlation between primary production and bacterial secondary production based on [^{3}H]-*TdR* and [^{14}C]-Leu measurement was found in any part of Lake Taihu.

The mean ratio of bacterioplankton production to primary production (Table 2) presented a similar picture to that in humic-rich reservoirs, where bacterioplankton production was usually ca. 2 to 4 times higher than primary production (Balogh & Vörös, 1997). These authors found that lakes receiving large amounts of humic compounds contain larger standing stocks of pelagic bacteria than less humic lakes, suggesting a large non-phytoplankton carbon source. Our results support the hypothesis that bacterial growth in lakes largely occurs at the expense of allochthonous carbon sources rather than phytoplankton production, especially at the river mouth and in Meiliang Bay, where organic matter is entering from the river. Moreover, the ratio of bacterioplankton to primary production decreases with trophic status (Table 2), which is in agreement with other results (Cole et al., 1988), who associated increasing eutrophication and bacterioplankton production, and a decreasing ratio of bacterioplankton biomass and production to Chl *a*. They suggested that the relative importance of bacterioplankton in lake ecosystems seem to decrease markedly with trophic status of the studied ecosystems (Cole et al. 1988).

Conclusions

With the highest value in the hypertrophic river mouth, the abundance, biomass and production of pelagic bacteria markedly increased along the trophic gradient of Lake Taihu (the open lake, Meiliang Bay, and the river mouth). A positive correlation between bacterial production (measured by *TdR* and Leu) and phytoplankton biomass was found in the river mouth and Meiliang Bay, but not in the open lake. The bacterial to primary production ratio increased with trophic status. No significant correlation between primary production and bacterial secondary production was found in any part of Lake Taihu. Our results support the hypothesis that bacteria and lake eutrophication are tightly

Table 2 Comparison of primary production and bacterial secondary production (μg C l^{-1} h^{-1}) at different sites of Lake Taihu from May 1998 to May 1999

		PP	*TdR*	Leu	*TdR*/PP	Leu/PP
R	Mean ± S.E	79.1 ± 8.1	141.8 ± 52.8	297.1 ± 81.5	1.8 ± 0.5	4.0 ± 1.0
	Range	37.0–138.4	17.0–654.5	45.1–1044.1	0.2–5.9	0.5–11.6
B	Mean ± S.E	76.0 ± 9.4	41.2 ± 7.9	147.1 ± 25.6	0.8 ± 0.2	3.1 ± 0.7
	Range	19.8–309.1	4.2–173.8	16.2–775.3	0.1–4.7	0.2–19.7
O	Mean ± S.E	76.1 ± 9.3	25.8 ± 4.7	79.8 ± 11.4	0.5 ± 0.1	1.5 ± 0.4
	Range	18.9–135.6	1.8–65.3	8.2–138.7	0.01–1.6	0.1–5.3

* The primary production (PP) was calculated from Chl *a* concentration by using the empirical formula: PP = –0.63 + 0.197 × Chl *a*, ($r = 0.90$) (Huang et al., 2001), where PP (mg O_2 m^{-2} d^{-1}), Chl *a* (mg m^{-3}), by using the factor of 2.67 to convert the O_2 unit to C unit (Sorokin, 1999)

coupled and bacterial growth in lakes largely occurs at the expense of allochthonous carbon sources other than phytoplankton production (Balogh & Vörös, 1997), especially at the river mouth and in Meiliang Bay. Moreover, the ratio of bacterioplankton to primary production decreases with trophic status (Table 2)

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