Trophic coupling between bacterial and phytoplanktonic compartments in shallow tropical reservoirs (Ivory Coast, West Africa)

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ABSTRACT: Biomass and production of bacterial and phytoplanktonic communities were measured during diurnal cycles at different stations in 3 shallow tropical reservoirs (Ivory Coast). Investigations were conducted in 1995 during 2 typical hydrological seasons (dry season in March and following rainy season in December). Bacterial production in the plankton ranged from 1.2 to 26.2 $\mu\text{g C l}^{-1} \text{ h}^{-1}$ and bacterial biomass ranged from 11 to 163 $\mu\text{g C l}^{-1}$. A slope of 0.625 ($n = 93$) for the regression of log-transformed bacterial biomass versus log-transformed production suggests that the bacteria were strongly controlled by bottom-up processes. Ratios between net primary production and bacterial production averaged 67% (range 38 to 140%), indicating that the reservoirs studied can be considered as meso-eutrophic ecosystems. Average bacterial carbon demand corresponded to 97% of the net primary production, suggesting that the biological systems studied are based on autotrophic metabolism. These relationships are the result of a close metabolic coupling between bacterioplankton and phytoplankton, with a large fraction of primary production routed through heterotrophic bacteria and the microbial loop.

KEY WORDS: Bacteria · Phytoplankton · Eutrophication · Tropical reservoirs

INTRODUCTION

As shown by many theoretical, experimental and empirical studies (see reviews by Hunter & Price 1992, Hairston & Hairston 1993), the abundance of organisms within a particular trophic level is likely to be controlled by predation and/or by resource availability. Recent developments of methods have allowed ecologists to examine factors that control diversity and abundance of individuals and species of microorganisms in nature. Bacterial dynamics is influenced by environmental factors, like temperature, in temperate regions (White et al. 1991). Grazing pressure exerted by predators and/or the availability of resources (avail-

able organic matter or nutrients) can also control bacterioplankton dynamics (Billen et al. 1990). These top-down and bottom-up controls do not exist alternately but often operate simultaneously.

Generally, predators control the fate of bacterial production and heterotrophic flagellates tend to be the major bacterivores in freshwater (Sanders et al. 1989). However, ciliates, rotifers and cladocerans may also be significant consumers of bacteria (Pace et al. 1990, Bouvy et al. 1994). Other loss factors (e.g. lysis, viruses, antibiotics) may also contribute to bacterial mortality but their contributions remain unclear (Pace 1988).

Phytoplankton can directly supply bacteria with organic carbon through exudation from healthy cells and lysis of senescent and dead cells (Lancelot & Billen 1984, Vadstein et al. 1993). Correlations between direct counts of pelagic bacteria and chlorophyll *a* con-

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centrations suggest that phytoplankton contributes to the organic carbon required to support bacterial growth (Bird & Kalff 1984, Findlay et al. 1991). Bacterial production and net primary production were also correlated with a mean ratio of about 30% (5 to 50%) across a wide range of trophic states (Bird & Kalff 1984, Cole et al. 1988). Based on a compilation of published rates of phytoplanktonic production and plankton community respiration, del Giorgio & Peters (1993) suggested that plankton respiration (and in particular bacterial respiration) exceeds primary production in oligotrophic lakes. However, while bacteria appear to satisfy much of their carbon requirement from phytoplankton, these 2 components also compete for inorganic nutrients, sometimes inducing large variations between bacterial and phytoplanktonic production (Currie 1990, Le et al. 1994).

These ecological considerations are treated in a large number of studies conducted in temperate lakes (e.g. Sanders et al. 1989, Pace et al. 1990, Wylie & Currie 1991, Vadstein et al. 1993, Pace & Cole 1994b, Gasol et al. 1995, Ochs et al. 1995). Information about tropical ecosystems, especially those located in West Africa, is still very scarce (Symoens et al. 1981, Delincé 1992, Talling 1992, Melack 1996) while the application of limnological information appears urgent to address social needs. Recently, Gopal & Wetzel (1995) recognized that limnology has received little attention in the developing countries, particularly in the tropics. To our knowledge, no study has dealt with components of the pelagic microbial loop in any West African freshwater ecosystems. Microbial food webs should be considered not only as a controlling factor for bacterial activity but also as an important regulator for planktonic succession in eutrophic systems such as tropical reservoirs. The aims of this study were to provide basic data on bacterioplankton and phytoplankton (biomass and production) and on the interrelationships between these 2 compartments in 3 reservoirs located in the north of Ivory Coast. Trophic coupling between bacterial and phytoplanktonic components was

also discussed through the following question: are bacterial communities in these tropical reservoirs mainly controlled by the availability of resources for maintenance and growth requirements?

MATERIALS AND METHODS

The study is focused on permanent artificial reservoirs located in the north of Ivory Coast (8° to 10° N, 5° to 6° W; Fig. 1). Lakes were chosen with the assumption of a link between their main usage and their trophic status. The 3 lakes selected illustrate the principal situations observed in this area:

Nambengué is a small polymictic reservoir (area 10 ha, maximum depth 2 to 3 m) in the north of this Soudano-Sahelian region. Several hundred cattle come daily to drink at the lake, with a significant enrichment of the ecosystem through their excrement.

Fig. 1. Map of Ivory Coast (West Africa) and location of the 3 reservoirs (Brobo, Tiné and Nambengué) and their respective sampling stations

Tiné, also located in the north of the area, is a medium-sized polymictic reservoir (45 ha, maximum depth 6 to 7 m), with transient stratification. Its primary use is for rice irrigation. This lake was selected because of the unique presence of the fish *Lates niloticus* that was introduced into the reservoir 20 yr ago. Because of its importance as predator, this species is known to potentially exert significant pressure on the whole pelagic food web structure (Lévêque 1995).

Brobo, in the south of the delimited region, is the largest reservoir studied (area 100 ha, maximum depth 7 to 8 m). It is a private lake, with very slight pressure from human activities exerted on the ecosystem: no hydraulic constraint for irrigation and very little utilization by livestock. This lake is characterized by a regularly stratified water column with an anoxic hypolimnion. An obvious physical aspect is the great number of dead trees in the central part of the reservoir, although the impact on pelagic productivity is not known.

The choice of sampling stations in each lake was determined according to depth. For Tiné and Nambengué, there was a deep station in the downstream part of reservoirs, not far from the dikes (denoted TD, with 2 sampling levels, -0.5 and -5 m; and ND, with 2 sampling levels, -0.5 and -2 m), and 1 or 2 shallow stations (according to the number of tributaries) in the upstream part of reservoirs with subsurface sampling (TB and TM for Tiné and NA for Nambengué). For Brobo, there was the same kind of central station in the deepest part of the reservoir (denoted BC, with 3 sampling levels: -0.5, -2.5 and -5 m), an intermediate station among dead trees (BF, with 2 sampling levels: -0.5 and -2 m) and a shallow station near the west bank (BB, subsurface sampling: -0.5 m), instead of the upstream station.

Diel surveys were performed in Brobo and Nambengué in March 1995 (dry season) and in all 3 reservoirs in December 1995 (after the rainy season). Solar radiation was integrated hourly with a LiCor 200 pyranometer and a Li1000 data logger on the shore of each reservoir. Water was sampled with a 2 l horizontal Niskin bottle at 5 h intervals for a total of up to 24 h. In total, 13 surveys starting at 19:00 h were performed during this study. Temperature and conductivity were measured using a digital thermometer and a Tacussel conductivity meter, respectively. Light attenuation coefficients (k) were calculated from vertical profiles using a LiCor 193 spherical quantum sensor (4π). Dissolved nutrients ($\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$) were analyzed according to Strickland & Parsons (1972). Chlorophyll *a* concentrations were determined by the fluorometric method on algae retained on Whatman GF/F filters and methanol extraction (Yentsch & Menzel 1963). In a previous study conducted in desalted water on Ebrié Lagoon, Ivory Coast (Arfi & Bouvy 1995), we deter-

mined a C:chl ratio of 55 for large cells from measurements of carbon and chlorophyll change over time. For the present study, we adopted the C:chl ratio of 50 proposed by Eppley et al. (1977) to calculate algal carbon biomass. Primary production was measured with the ^{14}C uptake method. Replicate 125 ml light and dark glass bottles were filled with subsurface water and $\text{NaH}^{14}\text{CO}_3$ (specific activity $3.7 \text{ MBq mmol}^{-1}$, CEA, France) was added. Bottles were incubated *in situ* for 2 or 3 h around midday at 5 or 6 levels according to the maximum depth of the reservoir. Samples were then filtered onto Whatman GF/F filters and rinsed with 2% HCl followed by a rinse with filtered water. Radioactivity was determined by liquid scintillation (Beckman, LS 5000, external standards method). Gross productivity was integrated over the depth (trapeze method) and hourly data were extrapolated to daily values using solar radiation records and the ratio (light received during incubation time)/(light received over the whole day). To estimate net algal production, a percentage of 40% of the gross algal production corresponding to respiration is generally used (Likens 1975). In a previous study conducted in aquaculture ponds close to Ebrié Lagoon, we measured respiration values ranging between 28 and 42% (unpubl. data). In the same lagoon, Torrétion (1991) used a value of 40% to assess net algal production from oxygen consumption experiments of phytoplanktonic and bacterial communities. In the 3 reservoirs studied, cyanobacteria and chlorophytes represent 70 to 90% of the phytoplankton (R. Arfi, M. Bouvy, P. Cecchi, M. Pagano & L. Saint Jean unpubl.) and in such situations, respiration can represent 30 to 36% of the gross algal production (Langdon 1993). Therefore, we assumed an algal respiration value of 40% of the gross primary production.

Samples for determination of bacterioplankton were fixed with buffered formalin (2% final concentration) and stained with DAPI fluochrome (Porter & Feig 1980). Bacterial cells were counted by epifluorescence microscopy (magnification $\times 1000$). Mean bacterial volumes were determined by measurements of up to 100 cells using photographic slides and a digitizing table. Cell volumes were computed with the formula described by Krambeck et al. (1981). Although there are uncertainties about the carbon:volume ratio for planktonic bacteria (Troussellier et al. 1997), carbon biomass was estimated assuming a conversion factor of $0.2 \text{ pg C } \mu\text{m}^{-3}$ (Simon & Azam 1989) because of the small size of bacteria measured in our study (mean biovolumes $< 0.100 \text{ } \mu\text{m}^3$). Net bacterial production was measured by (methyl- ^3H)-thymidine incorporation into cold trichloroacetic acid (TCA) precipitate (Fuhrman & Azam 1980). Linearity of the response over time and the saturation uptake by thymidine concentration were tested during preliminary evaluations. Incubation

times ranged from 15 min (Nambengué) to 30 min (Tiné and Brobo). A final concentration of 20 nM was added assuming that isotope dilution can be prevented at this concentration (see Robarts & Zohary 1993). Duplicates and a control (zero time) were incubated with (methyl- ^3H)-thymidine (47 Ci mmol $^{-1}$, Amersham) in the dark at *in situ* temperature. Incorporation of ^3H -thymidine was stopped by adding ice-cold 5% (final concentration) TCA for 5 min. Radioactivity was counted by the liquid scintillation procedure and results were expressed as nmols of incorporated thymidine per litre per hour. No previous information about thymidine incorporation rates in these ecosystems was available. A conversion factor for each ecological situation was determined empirically to convert rates of thymidine incorporation into bacterial biomass production, using the approaches outlined by Riemann et al. (1987) and Ducklow (1992). A dilution-growth experiment was conducted at each survey by comparing the increase in cell numbers with the total amount of substrate incorporated (integrative method). Duplicate bottles were incubated (in the dark at 0°C) with water samples (filtered through a 1 μm pore-size filter to remove predators) diluted at a ratio of 1:9 with filtered water (pore size 0.22 μm). Subsamples were removed at 2 to 3 h intervals for a total of 14 to 20 h, depending on the reservoir. Biovolumes and abundances of bacterial cells and ^3H -thymidine incorporation were determined at each sampling as described above. The absence of flagellates was checked at each enumeration of bacterial abundance. Exponential increase rates

were determined by the slopes of the different regressions (abundance, biomass, thymidine incorporation) versus time.

Data were analyzed using the statistical package SigmaStat (Jandel Corp.). Since the normality test failed, comparisons between data sets were performed using a Mann-Whitney nonparametric test. To obtain conversion factors for bacterial biomass production, bacterial abundance and biomass and thymidine incorporation, these data were natural log transformed to meet the normality assumptions of a least-squares regression analysis. Normality of transformed data and residual values for each regression was tested by the Kolmogorov-Smirnov test. Each error created after back transformation from logarithmic to arithmetic scale (Sprugel 1983) was corrected by a conversion factor (CF).

RESULTS

Physical and chemical characteristics of the water column

Values for the main physical and chemical features of each reservoir for the 2 seasons are presented in Table 1. Nambengué is a shallow reservoir, where the water column is mixed most of the time. Abiotic parameters showed limited variations, and this site can be defined as a warm polymictic system. It was also very turbid, with a photosynthetically active radiation (PAR)

Table 1. Averages (n = 5) and standard deviation (in parentheses) of the physical and chemical variables for the 2 surveys at 2 depths. nd: not measured

	Brobo				Nambengué				Tiné	
	March		December		March		December		December	
	0.5 m	5 m	0.5 m	5 m	0.5 m	2 m	0.5 m	2 m	0.5 m	5 m
Temperature (°C)	30.1 (0.8)	27.5 (0.3)	28.9 (0.5)	27.8 (0.3)	30.4 (1.2)	29.6 (0.6)	24.9 (0.9)	24.1 (0.3)	26.8 (0.3)	26.4 (0.2)
Conductivity ($\mu\text{S cm}^{-1}$)	69.9 (2.0)	73.3 (3.8)	nd	nd	164.4 (7.0)	163.7 (5.7)	nd	nd	nd	nd
pH	8.30 (0.25)	7.61 (0.12)	nd	nd	7.76 (0.20)	7.62 (0.12)	nd	nd	nd	nd
Solar radiation ($\text{W m}^{-2} \text{d}^{-1}$)	5823	–	4318	–	5475	–	4564	–	4989	–
Light attenuation (m^{-1})	1.3		1.2		4.5		2.4		1.4	
Depth of the 1% irradiance (m)	3.5		3.8		1.0		1.9		3.3	
$\text{NH}_4\text{-N}$ (μM)	1.82 (0.62)	21.42 (4.80)	4.22 (2.79)	3.88 (3.30)	2.85 (1.04)	40.51 (4.03)	3.03 (1.75)	3.54 (2.66)	3.85 (1.73)	5.27 (1.85)
$\text{PO}_4\text{-P}$ (μM)	0.21 (0.08)	0.23 (0.13)	0.17 (0.07)	0.13 (0.08)	0.09 (0.02)	0.04 (0.02)	0.08 (0.02)	0.08 (0.01)	0.10 (0.05)	0.09 (0.02)

attenuation coefficient of 4.5 m^{-1} in March and 2.4 m^{-1} in December. The corresponding photic zone, defined as a zone receiving at least 1% of total irradiance, was 1.0 and 1.9 m, respectively. In contrast, Brobo and Tiné were thermally stratified with an aerobic layer to a depth of 4 m. PAR attenuation coefficients in Brobo and Tiné were close to 1.3 m^{-1} for both seasons, and the corresponding photic zone was around 3.5 m. In the superficial layer, ammonia concentrations in March and December were similar, with respective means of 1.82 and $4.22 \mu\text{M}$ at Brobo and 2.85 and $3.03 \mu\text{M}$ at Nambengué. At maximum depths, values were high, particularly in March (21.42 and $40.51 \mu\text{M}$, respectively, at Brobo and Nambengué). Ammonia values at Tiné in December were similar to those reported at Brobo (Table 1). High orthophosphate con-

centrations were found at Brobo and average values were significantly different between the 2 seasons studied (Mann-Whitney test, $p < 0.001$). Phosphate concentrations were not significantly different at Tiné and Nambengué.

Bacterial and phytoplanktonic biomass

Abundance and biomass of both bacteria and phytoplankton were significantly higher during the dry season (Mann-Whitney test, $p < 0.01$), except for 1 station at Brobo (hypolimnetic zone at the central station; Table 2). The highest bacterial abundances were always found at Nambengué, with mean values ranging between 0.34×10^{10} and $1.10 \times 10^{10} \text{ cells l}^{-1}$

Table 2. Averages ($n = 5$) and coefficients of variation (% in parentheses) for bacterial (density, biovolume and biomass) and phytoplankton (chlorophyll concentration and biomass) communities at 2 seasons for each depth

		Bacteria			Phytoplankton	
		Density (cells l^{-1})	Biovolume (μm^3)	Biomass ($\mu\text{g C l}^{-1}$)	Chlorophyll conc. ($\mu\text{g l}^{-1}$)	Biomass ($\mu\text{g C l}^{-1}$)
NAMBENGUÉ						
NA (bank)						
0.5 m	March	1.0×10^{10} (21.8)	0.046 (7.3)	94.2 (22.1)	56.6 (22.0)	2828 (22.0)
	December	3.4×10^9 (4.9)	0.049 (6.1)	33.6 (9.1)	26.7 (26.3)	1337 (26.3)
ND (dike)						
0.5 m	March	1.1×10^{10} (12.4)	0.054 (18.3)	121.1 (20.4)	51.3 (19.6)	2566 (19.6)
	December	3.5×10^9 (6.2)	0.059 (14.2)	40.9 (18.2)	25.9 (22.0)	1296 (22.0)
2 m	March	9.5×10^9 (11.1)	0.055 (16.8)	104.3 (31.3)	59.1 (26.5)	2957 (26.5)
	December	5.2×10^9 (5.5)	0.045 (14.9)	29.3 (20.3)	31.8 (5.1)	1593 (5.1)
BROBO						
BB (bank)						
0.5 m	March	4.6×10^9 (26.5)	0.043 (11.1)	39.4 (22.1)	17.4 (6.9)	871 (6.9)
	December	2.4×10^9 (21.3)	0.036 (10.9)	17.1 (23.3)	6.1 (14.3)	304 (14.3)
BF (tree)						
0.5 m	March	4.0×10^9 (10.3)	0.050 (10.8)	39.8 (20.4)	17.2 (3.9)	860 (3.9)
	December	2.1×10^9 (11.5)	0.063 (11.2)	26.0 (20.1)	6.8 (16.9)	343 (16.9)
2 m	March	3.7×10^9 (15.9)	0.059 (14.9)	43.8 (26.6)	21.7 (10.5)	1084 (10.5)
	December	2.2×10^9 (6.6)	0.058 (10.4)	25.1 (20.9)	12.1 (20.3)	605 (20.3)
BC (central)						
0.5 m	March	4.3×10^9 (7.98)	0.039 (11.6)	33.9 (11.5)	18.2 (9.4)	908 (9.4)
	December	2.5×10^9 (12.1)	0.039 (14.0)	19.6 (17.2)	5.9 (12.7)	297 (12.7)
2.5 m	March	4.4×10^9 (2.3)	0.027 (19.3)	24.2 (21.4)	23.6 (8.9)	1182 (8.9)
	December	2.5×10^9 (17.1)	0.052 (13.4)	25.7 (21.3)	11.3 (27.7)	567 (27.7)
5 m	March	4.2×10^9 (10.4)	0.057 (13.7)	47.6 (18.3)	34.6 (26.6)	1730 (26.6)
	December	3.1×10^9 (19.5)	0.061 (18.2)	37.2 (24.4)	36.6 (23.7)	1829 (23.7)
TINÉ						
TD (dike)						
0.5 m	December	3.2×10^9 (2.3)	0.075 (15.1)	47.7 (17.3)	16.1 (31.4)	808 (31.4)
5 m		3.4×10^9 (11.3)	0.076 (12.1)	51.3 (13.1)	14.5 (24.9)	726 (24.9)
TB (bank)						
0.5 m	December	2.7×10^9 (8.6)	0.058 (10.2)	31.4 (14.8)	20.1 (24.5)	1005 (24.5)
TM (bank)						
0.5 m	December	2.7×10^9 (13.8)	0.043 (14.1)	22.9 (23.1)	23.9 (13.6)	1195 (13.6)

(Table 2). In this reservoir, whatever the season, no variability with depth was detected at the dike station (ND). Mean bacterial biovolume fluctuated between 0.045 and 0.059 μm^3 with the lowest values found at the bank station (NA). As observed in Nambengué, bacterial abundances were not significantly different at Brobo at different depths (Table 2). Mean bacterial biovolumes were small and showed little variation, ranging between 0.027 and 0.063 μm^3 . In the epilimnion, chlorophyll concentrations ranged between 6.8 and 21.7 $\mu\text{g l}^{-1}$, with high values found at 0.5 m in March. In the hypolimnic layer at the central station (BC) in Brobo, bacterial volumes were the highest reported for this reservoir (Table 2) and chlorophyll concentrations were close to 35 $\mu\text{g l}^{-1}$ whatever the season. At Tiné in December, bacterial abundances were similar across stations and depths (Table 2) but bacterial biovolumes and biomasses were greatest at the dike station (TD). In this reservoir, chlorophyll concentrations ranged between 14.5 and 23.9 $\mu\text{g l}^{-1}$. In Nambengué, chlorophyll concentrations were always high and ranged between 25.9 $\mu\text{g l}^{-1}$ in December and 59.1 $\mu\text{g l}^{-1}$ in March.

Bacterial and phytoplanktonic production

Empirical factors converting thymidine incorporation rates into bacterial production were estimated by dilution cultures during which bacterial abundance increased exponentially. Average growth rates of

abundance and biomass were always significant during the culture until the beginning of the plateau and accounted for 86 to 99% of the variance (see r^2 in Table 3, except 1 value). Conversion factors calculated by an integrative method may be computed if similar growth rates are detected between thymidine incorporation rates and cell or biomass production. Cell production per mole of thymidine incorporated (Tdr-cell) and biomass production per mole of thymidine incorporated (Tdr-biom) are reported in Table 3. If thymidine uptake was closely coupled with cell growth rates, the increase rates in bacterial number should be close to the increase rate in thymidine incorporation. In our study, this was the case for the bacterial communities in Nambengué (in March and December) and in Brobo (in March). Thus, the conversion factor from incorporation rate and cell number was used for each situation (0.93, 1.69 and 2.56×10^{18} cells mol^{-1} thymidine incorporated, respectively; Table 3). In the other cases (Brobo and Tiné in December), thymidine uptake was closely coupled with biomass growth rates, underlining the large variation of the mean volume of cells produced. For these situations, we used biovolume-based conversion factors (0.56 and 4.38×10^{17} μm^3 mol^{-1} thymidine incorporated, respectively, at Brobo and Tiné).

Means of thymidine incorporation rates ranged from 0.108 to 1.792 $\text{nmol l}^{-1} \text{h}^{-1}$ (Table 4) with the highest values observed in Nambengué. These values were always significantly higher in March than in December (Mann-Whitney test, $p < 0.001$), with coefficients of

Table 3. Conversion factor experiments from dilution cultures. Tdr: thymidine incorporation ($\log \text{pmol thymidine l}^{-1} \text{h}^{-1}$); cell: bacterial abundance ($\log 10^9 \text{ cells l}^{-1}$); biom: bacterial biomass ($\log 10^6 \mu\text{m}^3 \text{ l}^{-1}$). Conversion factors are expressed in 10^{18} cells mol^{-1} thymidine incorporated (Tdr-cell) and in $10^{17} \mu\text{m}^3 \text{ mol}^{-1}$ thymidine incorporated (Tdr-biom). Conversion factors used in the text are in bold

Season	Parameter	Slope	(SE)	Intercept	(SE)	r ²	Growth rate (h ⁻¹)	Conversion factor	
Nambengué									
March	Tdr	0.095	0.011	1.401	0.052	0.964	0.218		
	cell	0.088	0.013	-0.881	0.078	0.981	0.202	0.93	Tdr-cell
	biom	0.191	0.029	0.871	0.184	0.976	0.439	5.01	Tdr-biom
December	Tdr	0.037	0.006	1.481	0.051	0.908	0.085		
	cell	0.027	0.002	-0.369	0.021	0.935	0.062	1.69	Tdr-cell
	biom	0.079	0.038	1.181	0.374	0.586	0.181	2.88	Tdr-biom
Brobo									
March	Tdr	0.055	0.006	0.913	0.058	0.965	0.126		
	cell	0.041	0.016	-0.243	0.192	0.865	0.094	2.56	Tdr-cell
	biom	0.145	0.018	0.893	0.216	0.984	0.333	20.8	Tdr-biom
December	Tdr	0.099	0.021	1.331	0.157	0.883	0.227		
	cell	0.042	0.006	-0.783	0.046	0.896	0.096	19.7	Tdr-cell
	biom	0.144	0.001	0.047	0.001	0.998	0.331	0.56	Tdr-biom
Tiné									
December	Tdr	0.052	0.004	1.241	0.041	0.974	0.119		
	cell	0.091	0.091	-0.757	0.103	0.994	0.209	3.24	Tdr-cell
	biom	0.081	0.081	1.281	0.007	0.946	0.186	4.38	Tdr-biom

variation of 7.3 and 8.6 % respectively (Table 4). Whatever the season, specific incorporation rates were higher in Nambengué than in the 2 other reservoirs. The specific incorporation rates in Nambengué were significantly higher in December than in March. Using the conversion factors measured for each reservoir, bacterial production was calculated from thymidine incorporation rate. A similar pattern was observed for bacterial biomass and production, with the highest values noted at Nambengué in March ($>15 \mu\text{g C l}^{-1} \text{ h}^{-1}$). The lowest production was found at Brobo in December ($<2 \mu\text{g C l}^{-1} \text{ h}^{-1}$). Primary production at different depths ranged from $1.9 \mu\text{g C l}^{-1} \text{ h}^{-1}$ at Tiné (at 5 m depth) to $306.6 \mu\text{g C l}^{-1} \text{ h}^{-1}$ at Nambengué (at 0.5 m depth in March). The highest primary production was

always measured in March, whatever the reservoir studied. Due to rapid light extinction with depth, ^{14}C fixation decreased strongly with depth (Table 4).

DISCUSSION

A body of literature exists on tropical freshwater ecosystems, but studies are generally diffuse and fragmentary. Eutrophication processes in tropical regions were debated by Thornton (1987) with many considerations for management. In a review, Lewis (1995) discussed food chain structure related to lake latitude, with a descriptive picture of tropical lakes and a comparison to temperate lakes. Melack (1996) emphasized

Table 4. Averages ($n = 5$) and coefficient of variation (% in parentheses) for bacterial (thymidine incorporation rate, specific incorporation rate and biomass production) and phytoplanktonic (primary production) communities for 2 seasons and for each depth. nd: not determined

		Bacteria			Phytoplankton
		Incorporation rate ($\text{nmol l}^{-1} \text{ h}^{-1}$)	Specific incorpor. rate ($\text{mol cell}^{-1} \text{ h}^{-1}$)	Production ($\mu\text{g C l}^{-1} \text{ h}^{-1}$)	Primary production (gross) ($\mu\text{g C l}^{-1} \text{ h}^{-1}$)
NAMBENGUÉ					
NA (bank)					
0.5 m	March	1.781 (5.7)	1.8×10^{-19} (19.7)	15.61 (5.7)	nd
	December	0.442 (11.6)	1.2×10^{-19} (12.9)	5.41 (11.6)	nd
ND (dike)					
0.5 m	March	1.672 (8.9)	1.5×10^{-19} (17.2)	17.04 (8.9)	306.6
	December	0.408 (7.8)	1.2×10^{-19} (7.7)	6.38 (7.8)	117.0
2 m	March	1.792 (8.6)	1.9×10^{-19} (13.4)	18.24 (8.6)	15.5
	December	0.387 (13.1)	1.3×10^{-19} (15.1)	4.99 (13.1)	8.4
BROBO					
BB (bank)					
0.5 m	March	0.291 (12.2)	6.9×10^{-20} (32.7)	6.37 (12.2)	nd
	December	0.152 (12.3)	6.7×10^{-20} (23.8)	1.72 (12.3)	nd
BF (tree)					
0.5 m	March	0.178 (9.3)	4.5×10^{-20} (10.6)	4.58 (9.3)	nd
	December	0.140 (19.7)	6.9×10^{-20} (32.7)	1.58 (19.7)	nd
2 m	March	0.257 (21.2)	7.3×10^{-20} (28.6)	8.02 (21.2)	nd
	December	0.137 (7.8)	6.8×10^{-20} (21.1)	1.55 (7.8)	nd
BC (central)					
0.5 m	March	0.231 (19.8)	5.4×10^{-20} (17.2)	4.74 (19.8)	91.0
	December	0.158 (21.2)	6.4×10^{-20} (27.4)	1.78 (21.1)	33.1
2.5 m	March	0.372 (23.1)	6.5×10^{-20} (24.6)	5.07 (23.1)	47.6
	December	0.172 (19.5)	7.1×10^{-20} (23.6)	1.94 (19.5)	19.2
5 m	March	nd	nd	nd	3.0
	December	nd	nd	nd	2.1
TINÉ					
TD (dike)					
0.5 m	December	0.112 (9.8)	3.5×10^{-20} (11.5)	5.42 (9.8)	42.8
5 m		0.108 (7.3)	3.2×10^{-20} (9.1)	5.29 (7.3)	1.9
TB (bank)					
0.5 m	December	0.127 (15.8)	4.8×10^{-20} (22.1)	4.77 (15.8)	nd
TM (bank)					
0.5 m	December	0.115 (11.2)	4.4×10^{-20} (18.4)	3.19 (11.2)	nd

the recent developments of the nature and causes of variability in phytoplankton abundance and productivity in tropical countries. Many studies have been conducted on the ecology and distribution of tropical plankton (Lemoalle 1981 in some African lakes; Carmouze et al. 1983 in Lake Chad; Lewis et al. 1986 in Lake Valencia, Venezuela; Lind et al. 1992 and Chrzanowski et al. 1993 in Chapala Lake, Mexico; Haberyan et al. 1995 in some Costa Rican lakes), but very few studies have treated the bacterial and phytoplanktonic dynamics in freshwater lakes at these latitudes (e.g. Gebre-Mariam & Taylor 1990 in Lake Awassa, Ethiopian Rift Valley; Tundisi et al. 1993 in many reservoirs in Brazil).

In tropical lakes, water temperature is generally linked to light irradiance. These 2 parameters show little variation and should not play a major role in the global functioning of reservoirs (Lewis 1995). Hydraulic changes linked to local perturbations and/or seasonal climatic events may represent the main control factor in reservoirs located in northern Ivory Coast. During the high water period (August to November), flooding creates an important dilution effect. These water inputs and these rains often induce drastic restructuring. Moreover, these shallow reservoirs are periodically (sometimes at a daily scale) mixed by local wind, inducing resuspension. During calm periods, diurnal stratification of the upper water column generally occurs (P. Cecchi, D. Corbin & S. Thomas unpubl.).

Bacterial abundances in the studied sites are among the highest abundances reported for reservoirs. Kilham (1981) found a bacterial density of 10^{11} cells l^{-1} from African soda lakes, whereas Gebre-Mariam & Taylor (1990) reported a mean bacterial abundance of 6.2×10^9 cells l^{-1} for Lake Awassa. In the reservoirs studied, bacterial communities were dominated by small bacteria, which resulted in exceptionally low bacterial biomass (product of abundance and biovolume). Apparently, the size of free-living bacteria does not reflect the trophic state of the environment (Simon 1987). Selective grazing exerted by predators upon the large cells of an assemblage could result in the selection of small individuals (Chrzanowski & Simek 1990). Grazing and other loss factors, such as lysis and viruses, seem to control microbial abundance in aquatic ecosystems and may approximately equal bacterial growth (e.g. Güde 1989). Bacterial production values reported in our study, assuming a daily bacterial production of 24 times the hourly rate, can rise to $400 \mu g C l^{-1} d^{-1}$ at Nambengué in March, and are at the higher end of the range of values reported by White et al. (1991) for most eutrophic lakes ($300 \mu g C l^{-1} d^{-1}$ from a survey of 22 freshwater systems). Recently, Sommaruga (1995) in a hypertrophic lake (up to $330 \mu g C l^{-1}$ of chlorophyll *a*) found a mean bacterial production

of $587 \mu g C l^{-1} d^{-1}$ with a maximum of $1071 \mu g C l^{-1} d^{-1}$ and explained it as an increase in bacterial production with increasing trophicity. Our results also indicate increases in bacterial production along a trophic gradient from mesotrophy to eutrophy (based on chlorophyll concentrations ranging from 6.1 to $56.6 \mu g l^{-1}$) in the reservoirs we studied.

Conversion factors

The conversion factor of the thymidine uptake method has been used in many studies based on theoretical and empirical approaches. Very high variability is reported for this factor (see a review by Robarts & Zohary 1993). Clearly, the choice of conversion factors and their combination with 3H incorporation rates may have a major impact on the levels of bacterial biomass production calculated in any given study. Use of the empirical approach in this study is valid, by definition, even if 100% of thymidine is incorporated into protein. Indeed, a major problem is that thymidine incorporated into bacterial DNA is almost constant and dependent on environmental conditions. Using an enzymatic procedure in a previous study in a tropical area (Ebrié Lagoon, Ivory Coast), DNA labelling appeared to represent only 20% of the total labelled macromolecules (Torréton & Bouvy 1991). In the present study (field conditions), it was not possible to assess the percentages of the different macromolecular fractions.

Our empirical conversion factors based on cell numbers ranging between 0.93 and 2.56×10^{18} cells mol^{-1} Tdr were close to the expected 'theoretical values' (1 to 2×10^{18} cells mol^{-1} Tdr) reported by Bell (1990). In Ebrié Lagoon, Torréton et al. (1989) reported a low value of 0.73×10^{18} cells mol^{-1} Tdr despite the eutrophic context. In oligotrophic water cultures, Coveney & Wetzel (1988) reported cell-number-based factors ranging from 1.1×10^{18} to 38×10^{18} cells mol^{-1} Tdr. From data obtained in tropical Lake Chapala, Chrzanowski et al. (1993) reported conversion factors ranging between 4.7×10^{19} and 5×10^{21} cells mol^{-1} Tdr, which are among the highest values ever published. In some cases in our study (Brobo and Tiné in December), incorporation of exogenous 3H -Tdr is coupled to total production of bacterial biomass rather than to production of new cells. This discrepancy (although not observed in Nambengué in December) can be linked to changes in environmental conditions after the rainy season. Thus, the apparent mean volume of cells produced increases considerably and leads to a positive relationship between cell size and DNA content. Coveney & Wetzel (1988) empirically calculated a biovolume-based conversion factor ($15.2 \times 10^{17} \mu m^3 mol^{-1}$ Tdr) which is much larger than the factors calculated in

our study (0.56 and $4.38 \times 10^{17} \mu\text{m}^3 \text{mol}^{-1}$ thymidine incorporated in December at Brobo and Tiné, respectively). Other biovolume-based conversion factors from the literature are not available for comparison, although Coveney & Wetzel (1988) concluded that those factors seem appropriate to convert ^3H incorporation rates to bacterial biomass production. Finally, we agree with the conclusion of Chrzanowski et al. (1993) that thymidine incorporation should not be considered as a routine assay of bacterial production. The determination of an empirical conversion factor appears necessary for each ecological situation and, clearly, all systems are characterized by biochemical and environmental specificities.

For further statistical analysis, the results from the hypolimnic layer at the central station of Brobo have not been included for 2 reasons. First, with the goal of homogeneity, our comparisons deal only with data from the oxygenated zone in all reservoirs. Second, many studies have recently proved that ^3H -thymidine incorporation is not an appropriate technique for estimating secondary bacterial production in anaerobic systems (e.g. Lovell & Konopka 1985).

Bacterial biomass and production

Bacterial production (BP) is the product of bacterial growth rate and bacterial biomass (BB) and is influenced by both top-down and bottom-up regulation. Kirchman (1993) suggested that temperature also may explain the variation of the BP/BB ratio because bacterial abundance, production and growth rate are temperature dependent. In tropical regions, the small diurnal and seasonal fluctuations in temperature coupled with the high density-temperature coefficient of lake waters do not explain the variation of this ratio. From

Fig. 2. Log-log linear regression of bacterial biomass on bacterial production in March and December 1995

all our data, BB and BP were significantly correlated (Fig. 2, Table 5), with the equation $\log(\text{BB}) = 1.15 + 0.625 \log(\text{BP})$. Thus, bacterial growth rates tend to be higher in systems that are more productive. Bacterial biomass was a positive function of bacterial production, supporting the hypothesis developed by Billen et al. (1990), Ducklow (1992) and Pace & Cole (1994b) that bacterial communities are strongly controlled by resources (bottom-up factors). The slope obtained in the present study was similar to those of Billen et al.

Table 5. Regression statistics (log-log transformed) and comparisons with other studies. Variables (Y, X) are BB (bacterial biomass, $\mu\text{g C l}^{-1}$), BP (bacterial production, $\mu\text{g C l}^{-1} \text{h}^{-1}$), PhytoB (phytoplanktonic biomass, $\mu\text{g C l}^{-1}$), BA (bacterial abundance, cells l^{-1}) and PhytoA (chlorophyll concentration, $\mu\text{g l}^{-1}$). n = number of data points; regression statistics (slope and intercept) are reported with their standard errors. Conversion factors (CF) are corrected for an inherent bias of log-transformed regressions (see 'Material and methods')

Source	Y	X	n	Slope	(SE)	Intercept	(SE)	r ²	F	F-test p	CF
This study	BB	BP	96	0.625	0.042	1.15	0.03	0.706	218.4	<0.001	1.008
Billen et al. (1990)	BB	BP	288	0.7	–	1.67	–	0.828	–	–	–
Ducklow (1992)	BB	BP	210	0.43	–	1.67	–	0.803	–	–	–
Dufour & Torréton (1996)	BB	BP	68	0.48	0.01	1.68	0.03	0.921	–	–	–
This study	BB	PhytoB	93	0.596	0.057	–0.21	0.17	0.542	107.6	<0.001	1.020
Simon et al. (1992)	BB	PhytoB	104	0.219	0.031	1.39	0.07	0.34	53.1	–	1.340
This study	BA	PhytoA	93	0.583	0.046	8.83	0.06	0.631	155.8	<0.001	1.016
Cole et al. (1988)	BA	PhytoA	32	0.53	–	8.97	–	0.75	–	–	–
Bird & Kalff (1984)	BA	PhytoA	13	0.569	0.271	9.27	0.19	0.66	–	–	1.087

Fig. 3. Log-log linear regression between bacterioplankton abundance and chlorophyll *a* concentration in March and December 1995

(1990) and higher than those reported by Ducklow (1992) in oceanic regions and by Dufour & Torrton (1996) in the tropical Northeastern Atlantic Ocean (Table 5). These authors linked this difference between oligotrophic and eutrophic systems to the availability of dissolved organic matter (DOM) in the system. With low concentrations of DOM (as in oligotrophic reservoirs), bacterial growth may be restricted, as in the case of oceanic regions. Nevertheless, bacterial abundance (total direct counts) is not a measure of biological activity. The proportion of active bacteria is highly variable among aquatic systems but forms a generally small fraction of the total bacterial abundance (del Giorgio & Scarborough 1995). However, the data of del Giorgio & Scarborough (1995) still support the hypothesis of substrate limitation because the proportion of active bacterial cells in freshwater and marine plankton increases with nutrient and chlorophyll concentrations.

Relationship between bacterial and phytoplanktonic biomass

Many investigators have observed significant correlations between bacteria and chlorophyll *a* in various ecosystems (Bird & Kalff 1984, Cole et al. 1988, Duck-

low & Carlson 1992, Simon et al. 1992). All these relationships have been interpreted to be the result of a close metabolic coupling between bacterioplankton and phytoplankton. Experimental studies generally confirmed this interpretation (Pace & Cole 1994a), although in certain conditions, concentrations of dissolved inorganic nutrients may be a critical factor that drives the apparent coupling between bacteria and phytoplankton (Le et al. 1994). In our study, a correlation was also observed between bacteria and phytoplankton (Fig. 3). Regressions based on both carbon biomass and cell abundance (Table 5) exhibit similar slopes (0.596 and 0.583, respectively). These slopes were comparable to those found by Cole et al. (1988) and Bird & Kalff (1984). Simon et al. (1992) always found slopes less than 0.5. This might suggest that bacterial biovolume is an important aspect of the structure of the pelagic food web.

The ratio between bacterial and phytoplanktonic biomass is generally high (>1) in marine systems and low (<0.5) for limnetic and eutrophic systems characterized by phytoplankton biomasses greater than $250 \mu\text{g C l}^{-1}$ (Simon et al. 1992). In our study, the ratios were very low (average 0.043, range between 0.017 and 0.096, $n = 96$) and tended to decrease with increasing phytoplankton biomass, as was expected for ecosystems of varying trophic state (e.g. Simon et al. 1992).

Relationship between bacterial and primary production

All data were converted to an areal basis from the depth of the photic zone for each reservoir. Net phytoplanktonic production ranged from 239 to $850 \text{ mg C m}^{-2} \text{ d}^{-1}$ and bacterial production (BP) varied between 136 and $846 \text{ mg C m}^{-2} \text{ d}^{-1}$, representing most of the primary production (PP) values (Table 6). The BP/PP ratio was quite similar during the study with a bacterioplankton production that reached an average of 67% of the net primary production (NPP). The highest value (140%) was observed in March at Nambengu. Although the NPP at Brobo was lower in December than in March, the similarity in the BP/PP ratio between the 2 seasons implies that BP was stimulated in response to PP and to algal photosynthetic exudates. Finally, except for the data from Nambengu in March, values of bacterial production on an areal basis were high, reaching up to 49% of the NPP, although the average reported by Cole et al. (1988) only rose to 30%.

Bacterial growth efficiency (BGE; percentage of organic carbon entering the bacterial cell that remains as living carbon) is now the subject of many controver-

In Nambengué reservoir in March, bacterial respiration exceeded the NPP (see Table 6) and bacteria must have used external sources of organic matter. This small reservoir is used daily by cattle and thus receives a high organic input during the dry season (March). In this eutrophic system, the high respiration of bacterioplankton relative to NPP can be explained by the availability of another source of DOM (cattle) during the dry season, the poor light penetration (light attenuation coefficient of 4.5 m^{-1}) reducing the photic zone and

This first microbial study in this type of shallow tropical reservoir in West Africa reveals a marked control of heterotrophic bacterial communities exerted by the availability of resources (algal production). Our results corroborate the recent conclusions developed by del Giorgio et al. (1997) which suggest a tendency for net autotrophic metabolism in productive lakes and estuaries (with NPP higher than $120 \mu\text{g C l}^{-1} \text{d}^{-1}$). Except for the situation at Nambengué in March, the reservoirs studied can be considered as biological systems producing high levels of dissolved oxygen. However, this bottom-up control of bacterial biomass does not exclude regulation by predation (top-down factors). Indeed, bacterioplankton may be simultaneously controlled by heterotrophic flagellates since bacteria are

	Euphotic zone (m)	Bacterial production (mg C m ⁻² d ⁻¹) Net	Bacterial respiration ^a (mg C m ⁻² d ⁻¹)	Primary production (mg C m ⁻² d ⁻¹) Gross Net ^a	NBP/NPP (%)	
March						
Brobo	3.5	414	621	1204	722	57
Nambengué	1	846	1269	1005	603	140
December						
Brobo	3.5	136	204	399	239	57
Nambengué	2	273	409	1085	651	42
Tiné	3.5	320	480	1416	850	38
Mean		398 (285)	597 (428)	1022 (1026)	613 (615)	67 (49)

^a Assuming a phytoplanktonic respiration of 40 % from gross production and a bacterial growth efficiency (BGE) of 40 % (see 'Discussion')

^a Assuming a phytoplanktonic respiration of 40 % from gross production and a bacterial growth efficiency (BGE) of 40 % (see 'Discussion')

an important source of carbon for these predators (Pace et al. 1990). High grazing rates by heterotrophic flagellates obtained from experiments based on labelled natural bacteria were noted in March at the 2 reservoirs (M. Bouvy, R. Arfi & P. Cecchi unpubl.). The smaller bacterial biovolume obtained in our study may reflect the high grazing pressure exerted by heterotrophic protozoa. Thus, a significant amount of organic carbon produced by phytoplankton and released in dissolved form may be available for the upper trophic levels via bacteria and through the planktonic microbial loop in these tropical reservoirs.

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