BACTERIOPLANKTON DYNAMICS AND ECOLOGICAL ROLE IN ESTUARINE, COASTAL AND SHELF WATERS OF FRENCH GUIANA.

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Abstract

Bacterioplankton dynamics (abundance and productivity) was assessed in estuarine, coastal and shelf waters of French Guiana, submitted to important local and remote (Amazon) continental inputs. Cruises were carried out at different seasonal periods (wet and dry season), from 2001 to 2004 in local estuaries, in coastal waters (0-20m depth), and also in the continental shelf during a NBC retroflexion period in October 2003, as part of the ELISA and CHICO projects (IRD), in the framework of the French PNEC Guyane program. Bacterial dynamics were compared to phytoplankton dynamics in order to estimate the ecological role of heterotrophic bacteria in these particular highly productive tropical coastal systems.
This study enabled a first assessment of the high spatio-temporal variability of the microplankton distribution over the Guianese shelf, which has necessary consequences on the whole trophic web dynamics, including fishing resources.

Key Words : Bacterioplankton – Heterotrophic Bacterial Production – Phytoplankton dynamics – Blooms - Tropical Coastal Systems – Amazon influence

Introduction

Microbial communities define the magnitude and pathways of organic matter, nutrient and energy dynamics in aquatic systems. Although microbial metabolism and productivity are at present being described marine ecosystems, only scarce information on microbial dynamics is available in a wide range of neritic and oceanic regions, especially in tropical systems. Such information is important to fully understand topics such as biogeochemical processes and gradients that can have local and global consequences.
Bacterioplankton dynamics was studied in estuarine, littoral and shelf waters of French Guiana, from 2000 to 2003, in the framework of the French National Program of Coastal Environnement (PNEC) and the IRD projects ELISA. We followed the magnitude and the temporal and spatial variability of bacterial abundance and production, and we compared them to that of chlorophyll *a* and phytoplankton as well as to the biogeochemical characteristics of water masses encountered. The influence of the Amazon waters over the F. Guiana shelf was investigated during a cruise (CHICO-1) in October 2003, corresponding to the retroflexion period of the North Brazil Current (NBC).
Phytoplankton and bacterioplankton stocks and productivities were studied in order to assess the relative importance of both compartments over this wide shelf area. In this coastal environment, the large amounts of allochtonous matter and dissolved nutrients driven from both the local or remote (Amazon) sources constitute enhancing factors for microbial activity, depending mainly on hydrodynamical processes.

Material & Methods

Sampling strategy

ELISA cruises

The Kaw river estuarine and nearby littoral and coastal waters were sampled at different periods in July and November 2000 (Artigas & Guiral, 2002) and in April and June 2001.
From 2002 to 2004, coastal waters were sampled at different seasons (wet and dry seasons) in central F. Guiana, with transects from Approuague, Kaw and Mahury estuaries to the inner shelf (20m depth, ELISA cruises, Fig. 1). The objective of these cruises were to assess the role of local river inputs *vs* Amazon water (outer limit of the area)

- 7 cruises from August 2002 to June 2004.
- 3 transects from 0 to 20 m depth (6 stations): physics, chemistry, micro-plankton associated dynamics.
- 3 rivers (and associated estuaries) sampled (Mahury, Kaw and Approuague).

CHICO cruises

The influence of the Amazon waters over the F. Guiana shelf was investigated during a cruise (CHICO-1) in October 2003, corresponding to the retroflexion period of the North Brazil Current (NBC).
The cruise was divided into two legs:
- Leg 1 (3-7 October 2003) in the S.W. part or the shelf (transects R1, R2, R3, Fig. 1).
- Leg 2 (8-15 October 2003) covering the entire F. Guiana continental shelf, from R1 to R6 transects, Fig. 1).

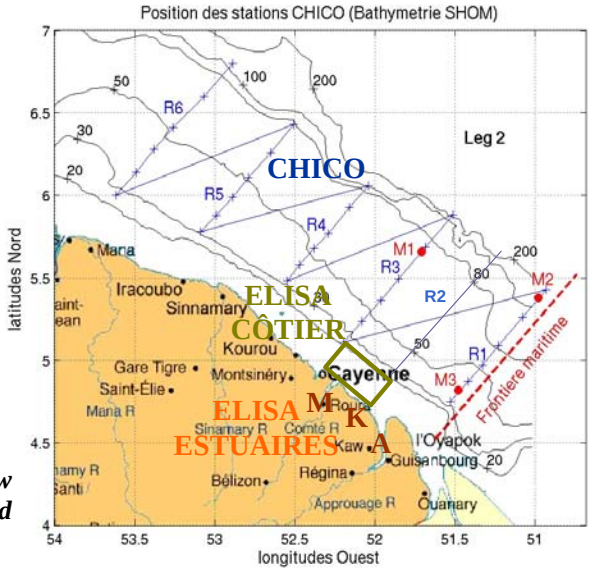

Fig. 1: Sampling areas of estuarine (Mahury – M, Kaw – K & Approuague – A), coastal ("ELISA Côtier") and shelf waters (CHICO) –F rench Guiana (2001-2004)

Sample collection and chemical measurements

Surface waters were collected and stored in 1L polycarbonate bottles, at ambient temperature (protected from overheating and from light). Measurements of temperature, conductivity, chlorinity and pH, were performed *in situ* and/or back in the laboratory. Aliquots were filtered onto GF/F and GF/C Whatman® filters in order to estimate the suspended particulate latter charge (SPM), chlorophyll *a* and phaeopigments (see below), C, N and P (CHN Analyzer, and Technicon analyzer). Dissolved concentrations of inorganic and organic N- and P- nutrients were measured on filtrates (coulorimetric method, Technicon Analyzer).

Chlorophyll a *and phytoplankton biomass*

Concentrations of chlorophyll *a* and phaeopigments (expressed as chlorophyll *a* equivalents) were estimated by extractive fluorometry (Yentsch & Menzel, 1963): filters were ground and extracted in 90% acetone overnight, and then centrifugated at 3000 g during 15 minutes at 4°C. Phytoplankton biomass was estimated from chlorophyll *a* concentrations, by assuming a mean conversion factor currently used in coastal waters: 50 µg C chl a^{-1} (Redalje, 1983). Samples were also taken for estimating phytoplankton abundance and diversity.

Bacterioplankton abundance and biomass

Water samples, collected in sterile 40ml flasks, were preserved with buffered formalin at a final concentration of 2 % and stored refigerated in the dark until analysis. At CHICO-1 cruise, seawater samples were also preserved with 2% paraformaldehyde, frozen onboard and stored in liquid nitrogen, for flow cytometry analysis (Thyssen et al., 2005). Bacterial

abundance was estimated by epifluorescence, using the 4-6-diamidino-2-phenyl-indole (DAPI, Porter & Feig, 1980) method, at 4 µg.ml^{-1} final concentration (Artigas, 1998). Subsamples were gently filtered onto 0.2µm Black-coulored polycarbonate filters (Isopore - Millipore®) and analyzed at a wavelength of 365 nm on a Leitz DMRB microscope (LEICA) equiped with a 100W mercury lamp, at a magnification of x 1,250. Subsamples carrying important suspended matter, were pre-treated by an addition of 150 µl of Tween, sonicated at 35khz for 5 min, and centrifugated at 3000 g during 10 min at 4°C (Chelvadonné & Godfroy, 1997; Hubas et al., 2007). The abundance of free bacteria was estimated in untreated diluted samples and/or in subsamples pre-filtered through a 3µm filter. FCM analysis was performed in a Cytoron Absolute (Ortho Diagnostic systems), after staining bacterial nucleic acids with SybrGreen (Molecular Probes®) and incubated 15 minutes. Bacterial biomass was estimated by assuming a conversion factor of 20 fgC cell^{-1} (Posch *et al.*, 2001).

Bacterial and Primary Production

Total bacterial production was estimated from rates of ^{3}H-Thymidine incorporation into bacterial DNA (Fuhrman and Azam, 1982). Water samples (3 replicates and 2 formalin-killed blank) were incubated in the dark at *in situ* surface temperature for 1 to 1.5 h using 40 to 20 nM ^{3}H-Thymidine as a final saturation concentration, and converted into cell and C production (Artigas et al., 2000). Primary Productivity was estimated by dark/light O2 incubations made at *in situ* temperature and O2 net production converted into C net production by the factor estimated by Iriarte et al. (1996).

Results & Discussion

ELISA estuarine cruises

The Kaw estuary and littoral zone were sampled at two different periods, after an intermediate rain stop in April 2001 and in the mid of the wet season in July 2001. We observed high levels of chlorophyll *a* both in estuarine and littoral stations (as it was found during dry season by Artigas & Guiral, 2002) whereas these levels were lower in June 2001. On the other hand, bacterial abundance was not correlated with chlorophyll *a* in estuarine or coastal waters (as it was the casein Artigas & Guiral, 2002). Low values were recorded in coastal waters that showed quite constant levels of abundance. Bacterial production was high in estuarine waters in April 2001 but dropped to relatively low levels in coastal waters. During the wet season we measured higher values than in April in coastal waters

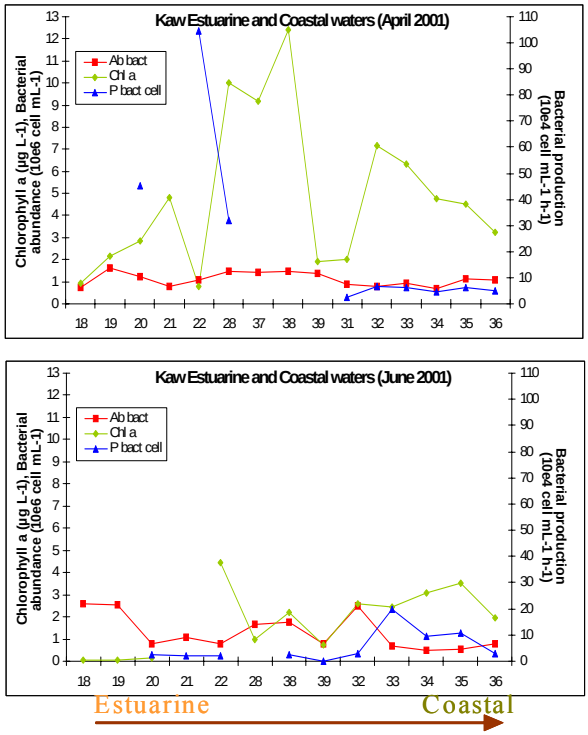

Fig. 2: Chlorophyll a, Bacterial abundance and Bacterial production in estuarine (18-28) littoral (38-32) and coastal waters (33-36) off Kaw River (2001)

ELISA coastal cruises

During the cruises carried out in littoral, coastal and inner-shelf waters (ELISA cruises), we observed different periods of high or low phytoplankton levels corresponding to different seasonal periods (wet, dry, and intermediate seasons). Among these periods, maximum chlorophyll *a* concentrations were often associated to littoral turbid waters, especially in dry

and/or intermediate periods (as it was found for 2001 estuarine and littoral cruises) when turbidity decreases. Chlorophyll concentrations decreased drastically from coastal to inner-shelf stations (Fig. 2). Chlorophyll concentrations were sometimes also high at inner shelf waters, in June 2004 (wet period) an intermediate period of March 2003 (Tab. 1 & Fig. 2).

Table 1 : ELISA cruises from 2002 to 2004, showing the seasonal conditions, hydrodynamics of oeanic currents and relative magnitude of phytoplankton outbursts detected both by important chlorophyll a values and phytoplankton abundance.

Cruises	Date	Climatology	Phytoplankton outburst	localisation of max phyto abundance	retroflexion
ELISA 1	august 2002	begining of dry season			yes
ELISA 2	**november 2002**	**dry season**	**++**	**littoral**	**yes**
ELISA 3	march 2003	stop rain - wet season	++	littoral and innershelf	no
ELISA 4	june 2003	wet season	+	--	no
ELISA 5	**july 2003**	begining of dry season	**++**	**littoral**	**yes**
ELISA 6	september 2003 (time of CHICO 1)	dry season	+	--	yes
ELISA 7	**june 2004**	**wet season**	**++**	**littoral & innershelf**	**no**

Bacterial abundance did not show any clear trend from littoral to coastal and inner-shelf waters, excepted a slight accumulation in coastal intermediate stations of some of the three transects in March, July and September 2003. However, when considering the percentage of attached cells, we found a clear decreasing gradient corresponding mainly to cells attached to the important amounts of suspended matter measured in littoral waters (re suspension of mud banks and fluid mud). However, when considering the amount of bacterial cells per g of suspended solids (data not shown) we found an important concentration of bacterial cells mostly at intermediate and inner shelf waters, but not linked to periods with high amount of phytoplankton in these waters.

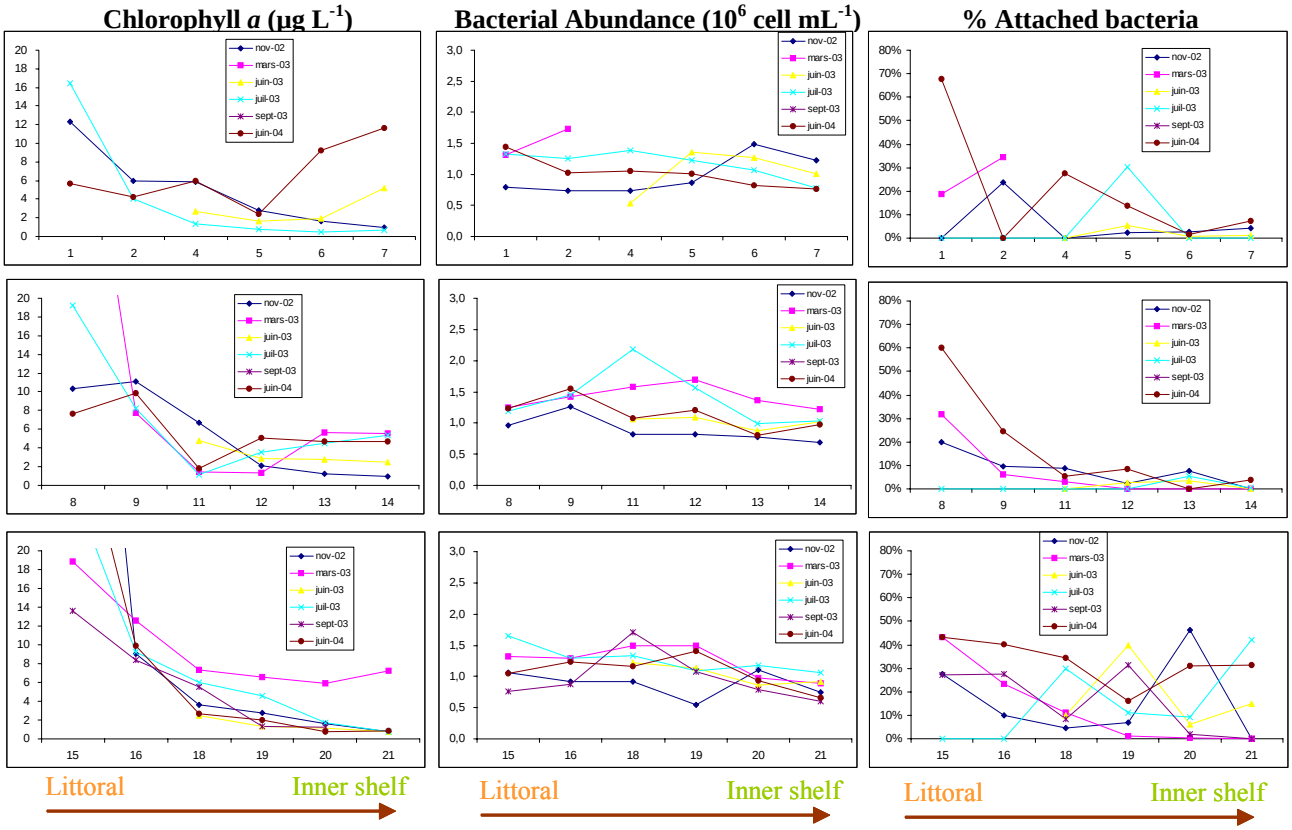

Fig. 3: Chlorophyll a (left), Bacterial abundance (center) and Bacterial production (right) in littoral and coastal surface waters off Cayenne (top), Kaw River (middle) and Approuague rivers (bottom) – ELISA cruises (2002-2004)

Bacterial production showed a decreasing gradient from littoral to inner-shelf stations (Fig. 4), more or less underlined depending on the period and transect considered. The highest bacterial production levels were recorded in littoral waters in November 2002 and in March and July 2003 in the Cayenne and Kaw transects, whereas in June 2004 higher levels corresponded to littoral waters of Kaw and Approuague transects. High levels of bacterial production were also recorded offshore at inner-shelf stations essentially in March 2003 and June 2004. Therefore, we clearly found a spatial distribution pattern of bacterial heterotrophic production affected both by the amounts of continental material (littoral waters) and phytoplankton outbursts (littoral and inner shelf waters), but not necessary linked to the bacterial abundance, what could mean that bacterial communities would be regulated by grazing pressure (Billen et al., 1990). Bacterial production was also apparently linked to primary production (data not shown) during the March 2003 cruise and in general matched the distribution of dissolved organic matter (DON, data not shown).

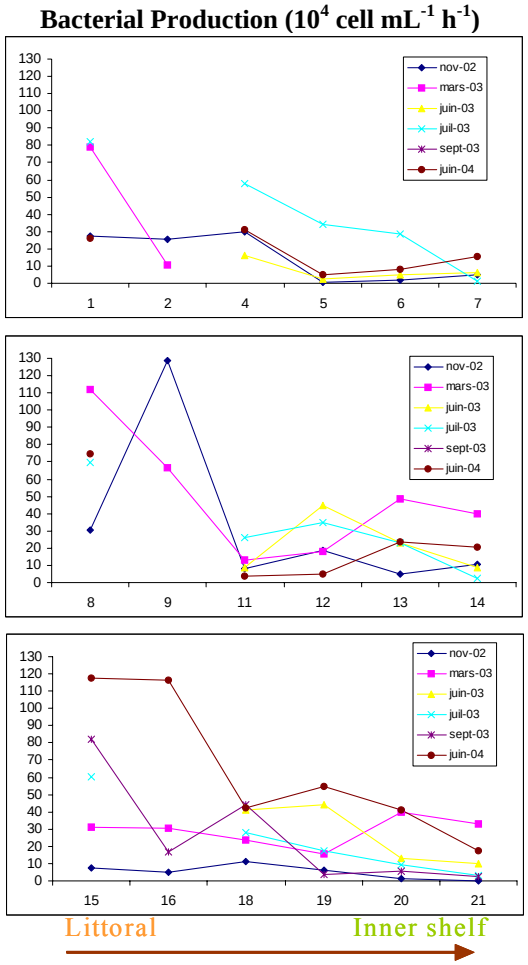

Fig. 4: Bacterial production (10^4cell mL^{-1}·h^{-1}) in littoral and coastal surface waters off Cayenne (top), Kaw river (middle) and Approuague river (bottom) – ELISA cruises (2002-2004)

CHICO - 1 cruise

During the first leg (3-7 October 2003) of the CHICO-1 cruise, a phytoplankton bloom was detected on the SE mid-shelf stations (Fig. 5), corresponding to a phytoplankton bloom of Diatoms but also to a concentration of nano and pico-Eukarya , and of *Prochlorochoccus* (data not shown). Primary Production levels were high at these mid shelf stations (Artigas et al., 2005).

Bacterioplankton abundance was also high near the area of phytoplankton maximum, but also accumulated at the shelf margin in oceanic waters. However, the highest proportion of high nucleic acid bacteria (Fig. 5) together with the highest levels of bacterial production (not shown) corresponded mainly to the area of highest chlorophyll and phytoplankton concentration.

At Leg -2, just one week later, the shelf was depleted of nutrients (data not shown) and of chlorophyll *a*, and phytoplankton levels were also very low, excepted in a small SW inner shelf area, in front of the Oyapok river. Bacterial abundance was also high in this area, but high abundance spread from the S to a great portion of the shelf. This accumulation of bacterial cells did not match sharply with the highest % of HNA cells that were found in inner-shelf stations, but in general inner and mid-shelf showed more than 50% of HNA cells. Bacterial production was not measured during this second part of the cruise.

Duringthe CHICO-1 cruise, we found an apparent coupling and uncoupling of bacterial dynamics with phytoplankton dynamics, high levels of bacterial abundance remaining in the period after the end of the bloom or after these waters were exported towards the Atlantic Ocean waters within an Amazon ring (Baklouti et al., 2007).

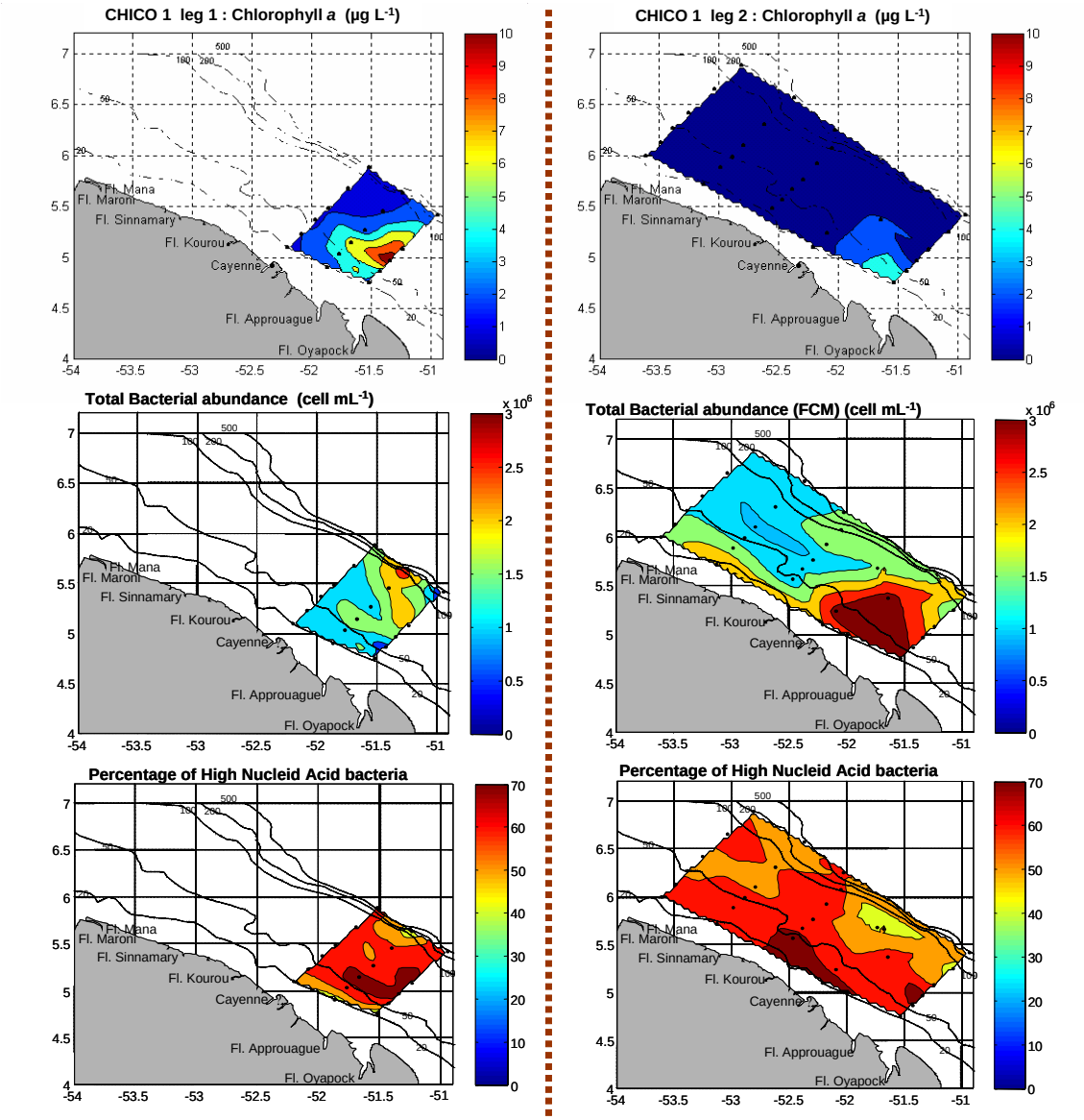

Fig. 5: Chlorophyll a (top), Bacterial total abundance (middle) and percentage of high nucleic acid bacteria (HNA, bottom) in F. Guiana surface shelf waters during (left – Leg1) and after a phytoplankton bloom (right – Leg2) – CHICO - 1 cruise (October 2003)

Bacterial compared dynamics in estuarine, littoral, coastal and shelf waters

Bacterioplankton abundance, that was quite stable especially in littoral and coastal waters, was not correlated with any of the hydrochemical parameters by considering the entire set of data, but apparently fitted the distribution of phytoplankton in shelf waters during the retroflexion period. Therefore, as in other estuarine and coastal systems, bacterial communities of estuarine, littoral and coastal waters of F. Guiana would probably be regulated by "top-down" processes, as it is the case in other tropical and temperate estuarine systems (Alongi, 1998). Estimated bacterial biomass ranged from 14.5 to more than 50 µg C L^{-1} in estuarine and coastal waters, the highest values being recorded during the CHICO-1 cruise during the second Leg. Attached bacteria represented on average from around 10 % of

total cells (dry season, in coastal and shelf waters) up to 23% in coastal waters during the wet season and to 47,1% in estuarine and littoral waters during the wet season (Table 2).
When compared to phytoplankton biomass, bacterial biomass represented from an average of 13%-16% (estuarine and coastal bloom situations of April 2001, November 2002, March 2003 and of June 2004) up to 22%-28% during the CHICO-1 bloom situation (and the July 2003 cruise) to more than 100% during the wet season in estuarine-littoral waters in June 2001 and the second part of the CHICO-1 cruise (after the bloom). Bacterial production levels were high and ranged between 0.1 up to 6.3 µgC L^{-1} h^{-1} in shelf waters (during the bloom period), and up to more than 20 µgC L^{-1} h^{-1} in littoral and coastal waters at bloom periods (November 2002, March 2003 and June 2004 and April 2001 in estuarine waters). In these littoral highly turbid systems, continuous mixing of water masses with rather different characteristics occurs, and allochtonous continental materials, river-borne phytoplankton, phytobenthos and macrophyta detritus would be predominant, even during the phytopankton blooming periods, when the organic fraction would be dominated by the autochtonous biomass produced. High heterotrophical bacterial productivities has been reported in the maximum turbidity zones of estuaries, in a great proportion attributed to attached bacteria (Goosen *et al*., 1999). Although much of the particulate material delivered to the coastal ocean and driven from the Amazon river would be refractory and intially resistant to microbial degradation (Hedges *et al*., 1994), the reminerilization of both terrestrial and marine driven organic carbon in these nearshore and estuarine waters would be more efficient in mobile mud systems (Aller *et al*., 1996), and would be of similar importance in resuspended mud deposits that were characterized in the littoral sampling area. Moreover, the bacterial diversity in these coastal mud deposits along the French Guiana coastal area would be high (Madrid *et al*., 2001), suggesting an important amount of metabolic pathways or potentialities of these attached bacterial community.

Table 2 : Average cruise values and Standard Deviation (S.D.) of the % of Attached bacteria, Bacterial productivity (Bacterial production/Bacterial biomass), Bacterial biomass/Phytoplankton biomass, (Bact b/Phyto b), Bacterial production/Primary Production (Bact Prod/PP) and Phytoplankton Productivity (PP/Phyto b) for the entire period of ELISA and CHICO-1 cruises (2001-2004).

Cruises - Periods (2001-2004)	% Att bacteria (%)	S.D.	Bact productivity (BP/Bact b, h-1)	S.D.	Bact b/Phyto b (%)	S.D.	Bact Prod/PP (%)	S.D.	Phyto productivity (PP/Phyto b, h-1)	S.D.
Estuarine-Littoral April 2001	24,2%	27,0%	0,21	0,31	16,0%	13,9%				
Estuarine Littoral June 2001	47,1%	21,3%	0,08	0,10	352,7%	713,4%				
ELISA 2 - Nov 2002 (dry season)	9,8%	12,3%	0,19	0,25	15,8%	15,2%				
ELISA 3 - March 2003 (intermediate)	12,4%	15,1%	0,31	0,23	12,9%	15,4%	16,7%	8,8%	0,13	0,07
ELISA 4- June 2003 (wet season)	*7,0%*	*11,3%*	*0,19*	*0,14*	*21,8%*	*12,6%*	*6,9%*	*5,3%*	*0,12*	*0,10*
ELISA 5- July 2003 (dry season)	10,7%	14,9%	0,24	0,19	27,6%	28,8%	9,5%	12,7%	0,63	0,38
ELISA 6 - September 2003 (dry season)	16,1%	14,2%	0,28	0,41	18,1%	13,7%	29,8%	40,1%	0,16	0,10
ELISA 7- June 2004 (wet season)	23,1%	20,5%	0,35	0,31	13,5%	12,5%	15,8%	15,2%	0,31	0,28
CHICO 1 Leg 1- bloom situation	10,0%	10,0%	0,04	0,04	26,6%	20,1%	5,5%	9,9%	0,13	0,14
CHICO Leg 2 - non bloom situation					177,2%	135,1%			0,19	0,25

**ELISA 4 – June 2003 (only inner shelf stations were sampled)*

Bacterial productivity (Table 2) ranged from an average of 0.04 h^{-1} in shelf waters during the mid-shelf bloom, typically found in coastal temperate waters when phytoplankton blooms occur (Artigas et al., 2000; Lamy et al., 2006) up to 0.20 h^{-1} (April 2001 estuarine waters, November 2002 littoral and coastal waters and June 2003 inner shelf waters) and to more than 0.30 h^{-1} during both bloom situations in coastal waters (March 2003 and June 2004), meaning that bacterial abundance will be renewed in about 3 hours. When comparing it to Primary Production, bacterial production averaged from less than 10 % in March 2003 (coastal) and

October 2003 (shelf) up to 16% in June 2004 (coastal bloom) and 30 % in September 2003. That means that, by considering a bacterial growth efficiency of 30%, from of 1/3 to almost 100% of equivalent C photosyntheticaly produced would be channelled though bacterioplankton.

Conclusions

In tropical coastal systems submitted to important local or remote continental inputs, the concurrence of different dissolved organic sources and particulate origins and composition, makes the dynamics of the heterotrophic bacterioplankton being influenced by a multitude of factors of diversified magnitudes and effects. Therefore, bacterioplankton communities appeared to be controlled both by grazing (bacterial abundance) and by substrate supply (bacterial hetrotrophic production based on both autochtonous phytoplankton derived matter and allochtonous inputs). Bacterial dynamics appeared to follow phytoplankton distribution, especially when phytoplankton underwent relatively short-term outbursts away from the maximum turbidity zone. Their ecological role is to fuel the "microbial loop" both in shelf than in coastal and estuarine waters, where benthic-pelagic coupling is enhanced. The high productivity values recorded are probably related to important mineralization processes that would be linked to the important amounts of phytoplankton and fresh-derived organic matter that characterize these areas.

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