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Diel fluctuations of bacterial abundance and productivity in a shallow eutrophic tropical lagoon

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With 4 figures and 2 tables in the text

Abstract

Abundance and productivity (^3H thymidine incorporation) of free-living and attached bacteria from surface waters were studied from hourly samples during typical hydrological conditions (rainy and flood seasons) in three different bays of the Ebrié Lagoon (Côte d'Ivoire). Several additional biological variables (particulate organic carbon, phytoplankton biomass, zooplankton density) were also recorded in order to establish possible relations with bacterial parameters.

Three diel experiments were performed in a floating mesocosm (1.5 m^3) in order to obtain information on nutrient sources and to follow the sedimentation process. Simultaneously, samples were also collected outside the mesocosm in order to know the eventual modifications of environmental conditions in the lagoon. Diel changes in abundance of total bacteria were very slight; fluctuations in abundance of attached bacteria were significantly correlated with the particulate organic carbon level. Contrary to bacterial abundance, obvious diel cycles of tritiated thymidine incorporation rates were noted both inside and outside the mesocosm, especially due to free-living bacteria with maximum nocturnal values. Two distinct bacterial communities were present in these planktonic tropical systems, regulated by particle abundance for attached cells and by dissolved nutrients for free-living bacteria. No coupling was observed between phytoplankton and bacterioplankton parameters, suggesting that exudates are not crucial to bacterial growth. Significant correlations were noted between zooplanktonic abundance and free-living bacterial productivity. Finally, night time stimulation of bacterial production might be interpreted as a consequence of nocturnal upward migration of zooplankton in these shallow waters.

Introduction

Numerous studies have been based on diel variations of bacterial characteristics because micro-organisms react quickly to changes in their environment. These short term variations of bacterioplankton parameters are now clearly established in different latitudes (MEYER-REIL et al. 1979, FUHRMAN et al. 1985, BOUVY & DELILLE 1988) and may result from two phenomena: nutrient

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availability (bottom-up factors) and predation pressure (top-down factors). Several investigations have shown that tight couplings exist between bacteria and phytoplankton (AZAM et al. 1983) and/or between bacteria and zooplankton (EPPLEY et al. 1981). Organic substrates issued from phytoplankton via exudation or cell lysis may be used directly for bacterial growth. PEDUZZI & HERNDL (1992) recently concluded that zooplankton activity may be a key factor for bacterial growth by providing organic substrates via sloppy-feeding, excretion and fecal pellets. But the existence of other processes such as viral infection (PROCTOR & FUHRMAN 1990), sedimentation and grazing by microzooplankton (RIEMANN 1985) and/or nanoplanktonic heterotrophs (GÜDE 1989) may be responsible for the diel variations of bacterial production. These different fates of bacterial communities seem to depend on the bacterial cell distribution. Indeed, it is well known that in contrast to free-living bacteria, attached bacteria can use particles as a substrate for growth. Although many studies have dealt with distinction between attached and free-living bacteria, only a few investigations have dealt with the diel variations of their metabolic activity.

The purpose of this study was to determine the diel fluctuations in bacterioplankton abundance and productivity (total and free-living bacteria) and some related parameters (particulate organic carbon, phytoplankton and zooplankton) in order to obtain information on the respective importance of the different sources of nutrients. Investigations were carried out at 3 sites of the shallow eutrophic Ebrié Lagoon (Côte d'Ivoire). Due to hydrodynamic movements (tide, current, wind induced waves) in Ebrié Lagoon (GUIRAL 1992, ARFI et al. 1993) and in order to study the same water mass and to follow the sedimentation processes, a floating enclosure was used over a 24-hr period. From data collected simultaneously inside and outside this mesocosm, the importance of the two bacterial communities in organic matter cycling is also discussed.

Materials and methods

The diel surveys were performed in 3 bays of the Ebrié Lagoon, each of them characterized by different haline conditions: mesohaline for Abou-Abou, euryhaline for Biétri and oligohaline for Mopoyem. The floating enclosure, made with a polyethylene bag (1.5 m^3) mounted on an inox frame, was filled by pumping subsurface lagoon water at night (10 p.m.) in order to include the zooplanktonic communities (TORRÉTON 1991). Sampling started at 6 a.m. the next day by collecting water with a 2 l Niskin bottle every 2 hours for 24 h. Nine diel studies were conducted in the mesocosm during the 3 hydrological seasons (dry, rainy and flood season). Of those 9 studies, samples were simultaneously collected inside and outside the mesocosm only during 3 surveys (Abou-Abou during the rainy season; Biétri and Mopoyem during the flood season) which are described in the present paper.

Samples for determination of bacterioplankton abundance were divided in two fractions (total and < 3 μm after gentle filtration on Nuclepore membranes). The fraction inferior to 3 μm was considered as free-living cells (TORRÉTON 1991). After fixation with buffered formalin (2 % final concentration) and staining with DAPI (PORTER & FEIG 1980), bacterial cells were enumerated by epifluorescence microscopy. Abundance of attached bacteria was obtained by calculating the difference between the total and free-living cells.

Bacterial production was determined from the rate of tritiated thymidine incorporation into macromolecules (FUHRMAN & AZAM 1980, TORRÉTON & BOUVY 1991). After incubation, two fractions were isolated (total and < 3 μm, see above). Thymidine incorporation rates of attached bacteria were obtained by calculating the difference between total and free-living cells activity.

Standard methods were used for other biological parameters. Particulate organic carbon (POC) was determined by filtering water on precombusted glass fiber filters (Whatman GF/F) and analyzed in a Leco CHN analyzer after decarbonatation. Chlorophyll-a concentration was measured by fluorometry on methanol extracts of phytoplankton retained on Whatman GF/F filters. Zooplankton abundance was estimated by pumping subsurface water from outside the mesocosm using an immersed pump (7 m^3/h) during 1 min. Animals were collected on a 60 μm mesh-size net and then fixed and preserved in buffered 5 % formalin; dominant zooplankton taxa were enumerated using a stereomicroscope.

Non parametric tests (Spearman rank correlation) were performed between the different parameters studied. Correlation coefficients were only reported if the p value was inferior or equal to 5 %.

Results and discussion

Characteristics of the three sites in the Ebrié Lagoon

From daily average values of studied parameters obtained inside and outside the mesocosm, the mean characteristics of the three sites are reported in Table 1. Biétri Bay is located in the urban zone of Abidjan and is characterized by high pollution levels from agro-industrial and domestic sewage (ARFI et al. 1981); this bay is considered as a very eutrophic system. Abou-Abou Bay is a brackish, non polluted area (CARMOUZE & CAUMETTE 1985) whereas Mopoyem Bay is an oligohaline non polluted system (PAGANO & SAINT-JEAN 1988).

All values were higher in Biétri Bay than in Abou-Abou and Mopoyem Bays and daily average values for all parameters were similar between mesocosm water and lagoon water (Table 1). Daily means of total bacterial abundance were close to 10×10^9/l in Mopoyem and Abou-Abou Bays and 20×10^9/l in Biétri Bay. Attached bacteria were always less numerous than free-living bacteria in the three sites (Table 1). The higher percentages of fixation were systematically observed at the flood season (Mopoyem and Biétri Bays) characterized by more turbid water and high POC concentrations. This contribution of attached bacteria to the total bacterial abundance has been the subject of a great number of investigations and this ratio is variable depending

Table 1. Daily average values for major parameters in the three bays.

Units		Total bacterial abundance 10^9 cells/l	% attached bacteria	Total thymidine incorporation nmol $l^{-1} h^{-1}$	Specific incorporation rate 10^{-20} $cell^{-1} h^{-1}$	Chlorophyll µg/l	POC µg/l
Mopoyem (flood season)	inside	10.1	31	0.44	4.3	25	2192
	outside	13.5	23	0.56	4.1	23	–
Abou-Abou (rainy season)	inside	11.6	7	0.87	7.5	23	887
	outside	11.6	7	0.82	7.1	27	–
Biétri (flood season)	inside	19.2	39	1.23	6.4	112	6896
	outside	23.8	35	1.70	7.0	124	–

on the characteristics of the aquatic system. In most mesotrophic to eutrophic aquatic ecosystems, the proportions of attached bacteria vary about 30 % (e.g. PEDROS-ALIO & BROCK 1983).

Although the hydrological conditions were different between the three sites, labelled DNA represented a constant proportion of cold TCA precipitate (average 19.2 %; TORRÉTON & BOUVY 1991). Thus, comparisons of daily means of tritiated thymidine incorporation rates were possible; lower values were found in samples from Abou-Abou and Mopoyem Bays. Contributions of attached bacteria to total incorporation rate followed the same trend as abundance, with a percentage of 6 %, 22 % and 29 % in Abou-Abou, Mopoyem and Biétri Bays, respectively.

Free-living and attached bacteria showed similar specific incorporation rates during the rainy season (7×10^{-20} mol $cell^{-1} h^{-1}$ in Abou-Abou Bay). However, specific activity was significantly lower ($p < 0.01$) for attached bacteria during the flood season (3 and 5×10^{-20} mol $cell^{-1} h^{-1}$ in Mopoyem and Biétri Bays, respectively). Generally, the specific activity of attached bacteria is greater than that of free-living cells (SIMON 1985), although some authors found no differences in specific activity of attached and free-living bacteria (DUCKLOW & KIRCHMAN 1983). It appears that in a eutrophic environment, such as the Ebrié Lagoon characterized by high concentrations of dissolved nutrients (CARMOUZE & CAUMETTE 1985), free-living bacteria can have the same contribution to the cycling of organic matter as attached bacteria. In contrast, LETARTE et al. (1992) concluded from a study of 8 Canadian lakes that large bacteria characterized by a shorter doubling time than those of small bacteria play a dominant role in organic matter transfer. But incorporation of diverse substrates should be tested to conclude the actual activity of bacterial communities.

Daily average values of chlorophyll-a concentrations in the mesocosm averaged to 23, 25 and 112 µg/l in Abou-Abou, Mopoyem and Biétri Bays, respectively (Table 1) and were close to concentrations noted outside the mesocosm. These values are characteristic of eutrophic pelagic environments (Du-

FOUR 1982). Inside the enclosure, shading by the buoys resulted in a 20% decrease of phytoplanktonic production and may explain the possible decrease of chlorophyll concentrations at the end of the diel cycle (TORRÉTON 1991). POC concentrations averaged to 887, 2192 and 6896 μg/l in Abou-Abou, Mopoyem and Biétri Bays, respectively (Table 1), and these data confirm the eutrophic status of the lagoon.

Diel fluctuations of bacterioplankton

Diel changes in total numbers of bacterial cells were small during the 3 cycles (Figs. 1, 2 and 3). Coefficients of variation averaged 11.6% and 9.3% inside and outside the mesocosm, respectively. These values were similar to the reproducibility of the abundance estimation (unpublished data). Total thymidine incorporation rates showed more important fluctuations (coefficients of variation of 22% and 21% inside and outside the mesocosm). The tritiated thymidine method (TORRÉTON & BOUVY 1991) used to precipitate and hydrolyse macromolecules showed an average standard deviation between triplicates of 6%. Thus the obvious diel fluctuations of tritiated thymidine incorporation rate were very significant. No positive correlation was found in the three bays between total bacterial abundance and total thymidine incorporation rates (Table 2). These results have also been noted by several authors (SIMON & TILZER 1987) which explained that a correlation depended on the percentage of fast and slow growing bacteria in the pelagic zone.

Large differences between attached and free-living bacteria were revealed from a comparison between production and abundance (Figs. 1, 2 and 3). Significant correlations were noted between total and free-living bacterial production in the three bays both in the mesocosm and the lagoon (Table 2). This fact confirms the importance of free-living bacteria as mineralizing agent of organic matter. However no correlation was observed between tritiated thymidine incorporation rates and abundance of free-living bacteria in contrast to significant correlations between these two parameters for attached bacteria in the three bays. Despite the stable bacterial numbers, these two distinct communities have different nutrient sources for their growth rates. This observation corroborates the results of IRIBERRI et al. (1990) and UNANUE et al. (1992) in different pelagic systems.

Factors controlling attached bacteria

Abundance of attached bacteria, outside the mesocosm, did not show obvious diel variations and fluctuated more irregularly than those observed for free-living bacteria. Hydrodynamic perturbations observed in Ebrié Lagoon are mainly related to the wind-induced water movements. Under certain favorable conditions (fetch, wind velocity, bathymetry and bed roughness), the

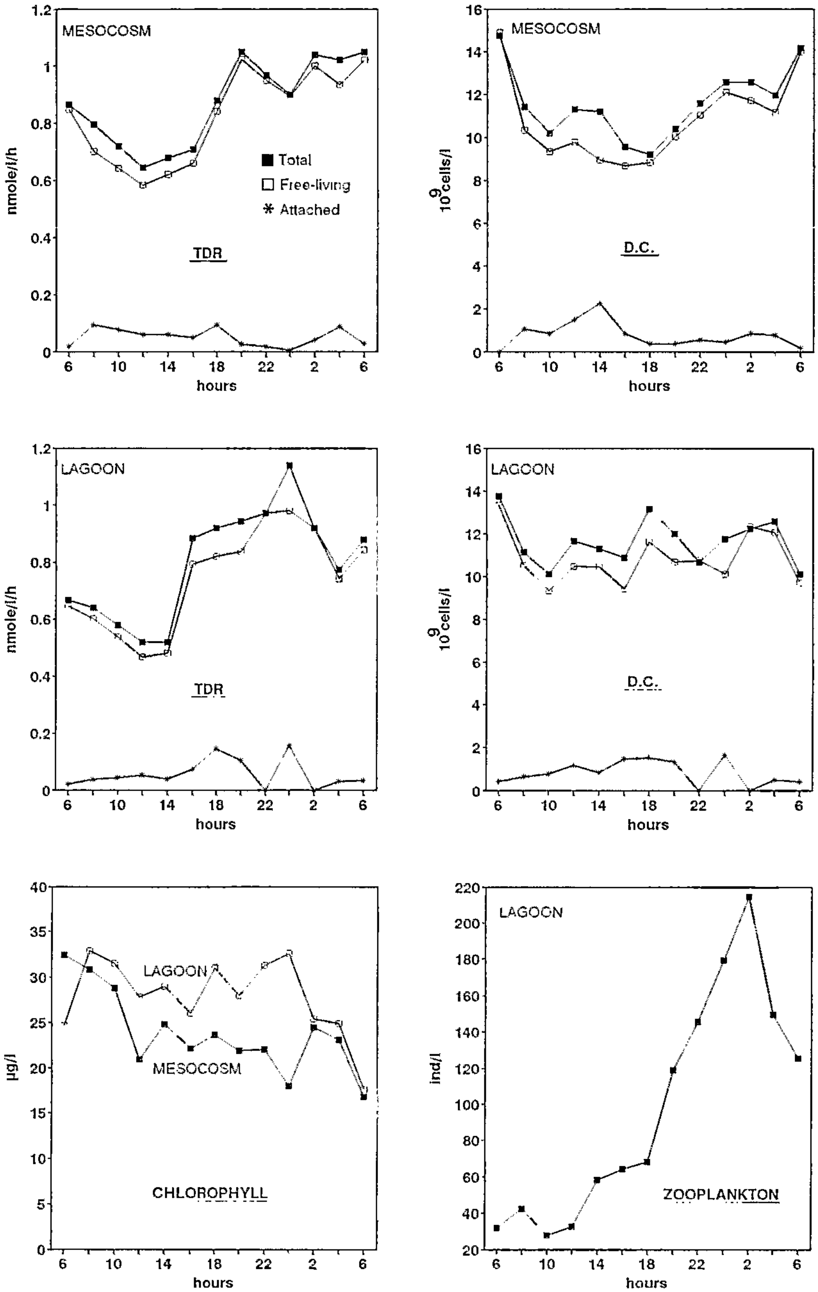

Fig. 1. Diel fluctuations of studied variables in Abou-Abou Bay: D.C.: direct counts of bacterial cells (expressed in 10^9 cells/l), TDR: thymidine incorporation rate (expressed in nmole $l^{-1} h^{-1}$).

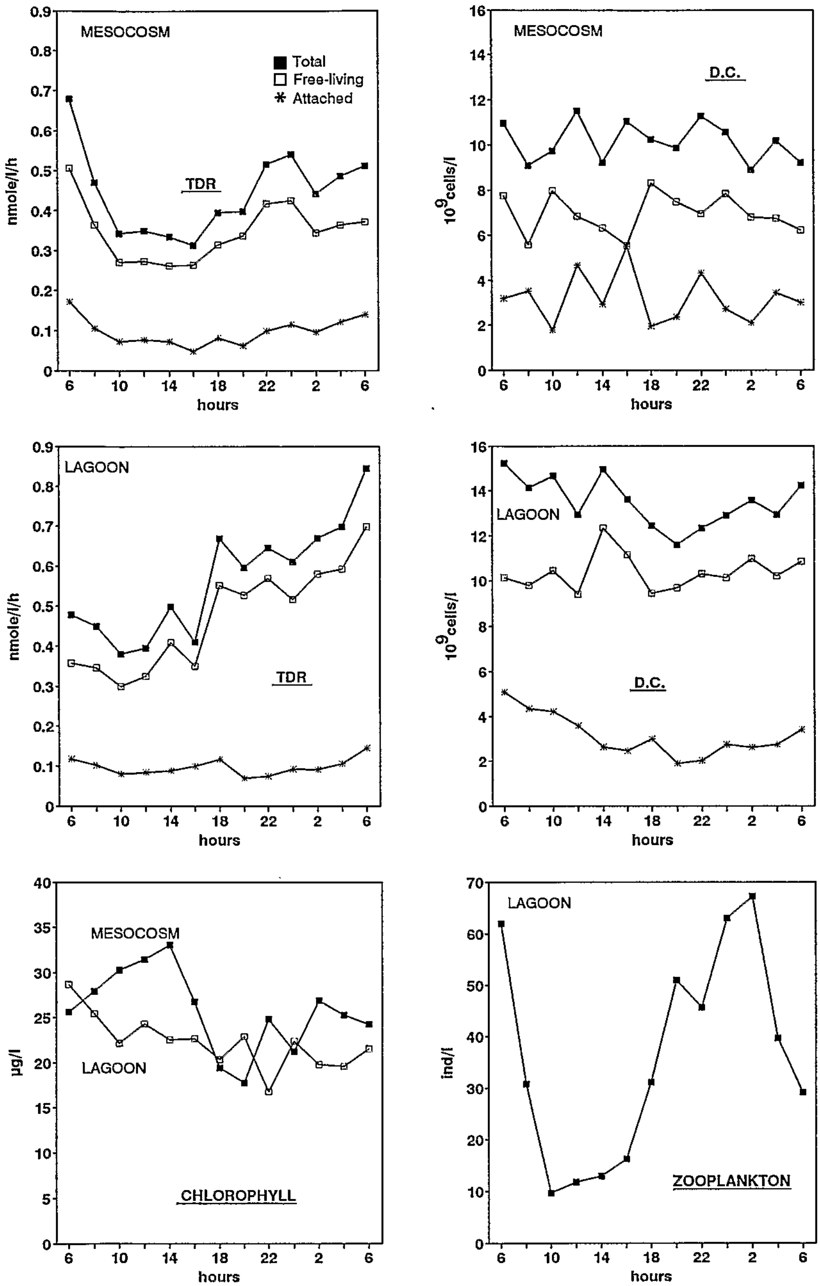

Fig. 2. Diel fluctuations of studied variables in Mopoyem Bay: D.C.: direct counts of bacterial cells; TDR: thymidine incorporation rate.

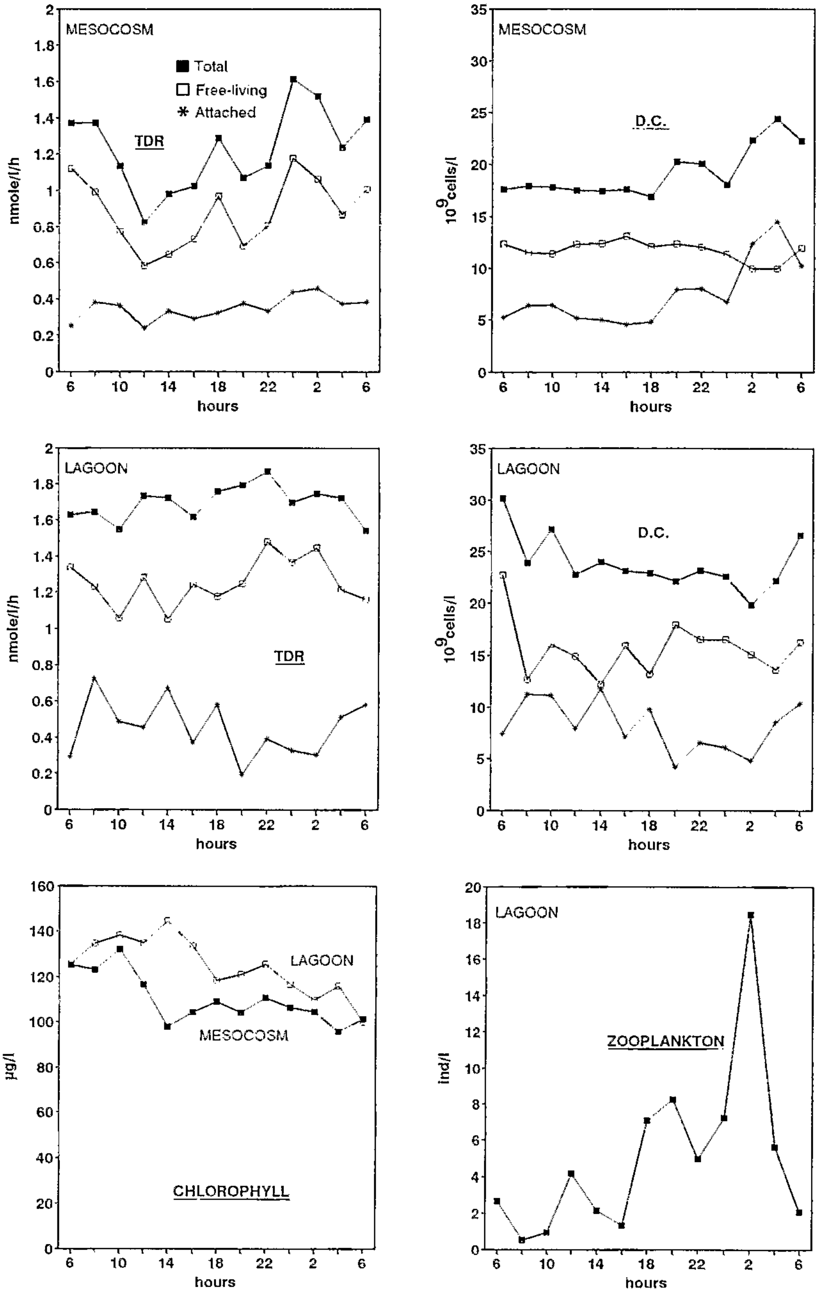

Fig. 3. Diel fluctuations of studied variables in Biétri Bay: D.C.: direct counts of bacterial cells; TDR: thymidine incorporation rate.

Table 2. Matrix correlation of Spearman's rank coefficients between the studied variables in the three bay. *, **, ***: significance at 0.05, 0.01, 0.001, respectively.

	Tdr free living	Tdr attached	DC total	DC free living	DC attached	Chlo	Zoopk
Tdr total	0.98 (***)	–	–	–	–	−0.63 (*)	0.60 (*)
Tdr free living	–	–	–	–	–	−0.62 (*)	0.59 (*)
Tdr attached	–	–	–	–	0.55 (*)	–	–
DC total	–	–	–	–	0.60 (*)	–	–
DC free living	–	Mopoyem	–	–	–	–	–
DC attached	–	–	–	–	–	–	–
Chlo	–	–	–	–	–	–	–
Tdr total	0.97 (***)	– –	–	–	–	–	0.67 (*)
Tdr free living	–	–	–	–	–	–	0.73 (**)
Tdr attached	–	–	–	–	0.98 (***)	–	–
DC total	–	–	–	0.80 (***)	–	–	–
DC free living	–	Abou-Abou	–	–	–	–	–
DC attached	–	–	–	–	–	–	–
Chlo	–	–	–	–	–	–	–
Tdr total	0.58 (*)	–	−0.60 (*)	–	–	–	0.71 (**)
Tdr free living	–	−0.71 (**)	–	–	−0.82 (**)	–	0.58 (*)
Tdr attached	–	–	–	−0.77 (**)	0.90 (***)	–	−0.57 (*)
DC total	–	–	–	–	0.64 (*)	–	−0.79 (**)
DC free living	–	Biétri	–	–	−0.65 (*)	–	–
DC attached	–	–	–	–	–	–	−0.73 (**)
Chlo	–	–	–	–	–	–	−0.59 (*)

Abbreviations: Tdr (thymidine incorporation rate); DC (direct counts); Chlo (chlorophyll biomass), Zoopk (zooplanktonic density).

dominant Austral Trade winds can create waves inducing sediment resuspension in the bays of Ebrié Lagoon (Arfi et al. 1993). Many studies have demonstrated that wave-induced turbulence controls productivity in shallow ecosystems (Wainright 1987). In our study, wind influence was considerably reduced inside the enclosure and could explain some of the differences observed inside and outside the mesocosm. The correlation between the abundance of attached bacteria and the POC (Fig. 4; for the 9 experiments; Torréton 1991) may support this explanation as generally reported in estuaries (Bell & Albright 1981) that attached bacterial activity depends on particles (nature, concentration). With sediment traps placed outside and inside the mesocosm, rates of sedimented materials were estimated; sedimentation process is responsible for the daily exportation of 55 % of the attached bacterial biomass in the study area (see Torréton 1991).

Factors controlling free-living bacteria

Appreciable diurnal changes were observed in tritiated thymidine incorporation rates of free-living bacteria both inside and outside the mesocosm, with maximum values during the night. This nocturnal increase did not correspond

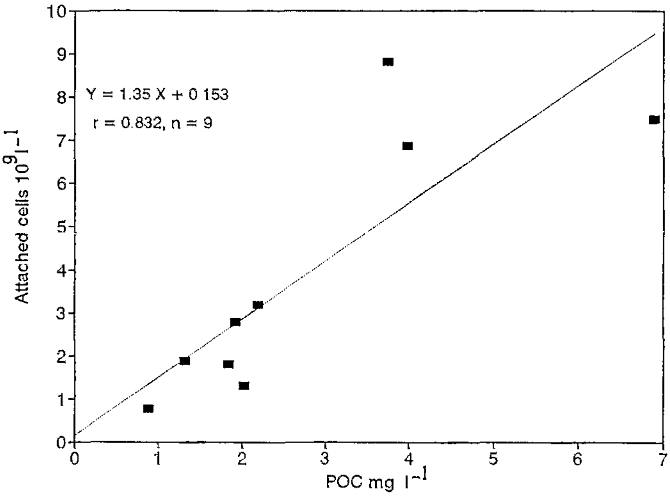

Fig. 4. Linear regression of daily averages between abundance of attached bacteria and POC in the three bays during three seasons (9 cycles).

to an increase of phytoplankton biomass (Figs. 1, 2 and 3). The diel variations of tritiated thymidine incorporation rates of free-living bacteria showed no significant positive correlation with changes of chlorophyll concentration in the three bays (Table 2). The same pattern was observed for bacterial and phytoplanktonic productivity (values ranged from 1.3 to 6.2 gC $m^{-2} j^{-1}$ according to the bay; Torréton 1991); in addition, on an areal basis for the water column, bacterial productions were high compared to primary productions and averaged 29 %, 48 % and 75 % of planktonic primary production (Biétri, Mopoyem and Abou-Abou Bays, respectively; mean value of 58 % for the Ebrié Lagoon, Torréton 1991). Direct measurements of phytoplankton excretion in these areas have shown that it represented only 10–15 % of the total autotrophic production (Pagès & Lemasson 1981). If the main substrates of bacterial communities are derived from phytoplankton, a variation in phytoplanktonic production may induce a variation in the bacterial growth rate. Generally, close relationships between occurrence and activity of algae and bacteria may be partly due to the release of dissolved organic carbon via phytoplankton exudation (Larsson & Hagström 1982). Since no direct coupling was noted between phytoplanktonic production and bacterial growth in the ecosystem studied, this suggests that phytoplanktonic extracellular release is not very crucial to bacterial activity.

However, the nocturnal increases in tritiated thymidine incorporation rates of free-living bacteria were simultaneously observed with the increase of zooplankton abundance (Figs. 1, 2 and 3). Significant positive correlations were observed between the tritiated thymidine incorporation rates of total and free-living bacteria and zooplanktonic abundance in the three sites outside the mesocosm (Table 2). The zooplankton communities were largely dominated by the copepod *Acartia clausi,* which represented 52 to 100 % of the total abundance. Furthermore, this copepod is the main migrant species showing obvious nycthemeral variations with a peak at subsurface at night between 8 p.m. and 2 a.m. (Figs. 1, 2 and 3), which corresponds to the well-known nocturnal vertical migration of this species (Pagano & Saint-Jean 1988). Two phenomena linked to zooplankton occurrence may explain this bacterial increase of tritiated thymidine incorporation rates during the night:

- Grazing pressure of zooplankton may be exerted on bacterial grazers (like protozoan, not enumerated in this present study); recent works have demonstrated that the predatory activity of protozoan was exerted particularly on large bacterial cells (Chrzanowski & Simek 1990). However no significant change in bacterial volume was noticed between day and night to support this hypothesis (data not shown). Mean cell volumes were similar at all sites with an average of 0.10 μm^3 in Abou-Abou and Mopoyem Bays and 0.12 μm^3 in Biétri Bay (Torréton 1991). Furthermore, the precision of cell volume determination in this study was close to 20 % and thus it was difficult, here, to establish interpretations on possible modifications of biovolume by grazers.
- Zooplankton communities release nutrients either by sloppy feeding (destruction of algal cells during ingestion), excretion or fecal pellet egestion (Lampert 1978). The chlorophyll-a concentrations followed a sinusoidal pattern, with the highest concentration during the day, and the lowest at night (Figs. 1, 2 and 3). However, sedimentation rates showed that sinking was very important in the Ebrié Lagoon (Torréton 1991) and this process may explain the decrease of chlorophyll concentrations during the night. Negative correlations were observed between chlorophyll concentrations and zooplanktonic abundance in the three bays with significant correlation in Biétri Bay (Table 2). The nocturnal minimum of chlorophyll-a may also be considered as an indication of zooplankton grazing. Lampert & Taylor (1985) clearly demonstrated the influence of zooplankton migration on the distribution of nutrients in an eutrophic lake. Zooplankton grazing may increase the dissolved free amino acid pool potentially available for bacterial utilization, thus stimulating bacterial activity (Riemann et al. 1986). Moreover, the most abundant species of zooplankton (*Acartia clausi*) in the Ebrié Lagoon feeds near the bottom during the day with a maximum gut fluorescence observed at 4 p.m. (Pagano & Saint-Jean 1988). These authors estimated a 2-hour transit time for this species. This would suggest a maximum egestion of fecal pellets at 6 p.m., coinciding to the beginning of upward migration of zooplankton. This phenomenon associated with the nocturnal grazing of zooplankton in upper layers may explain the increase

of tritiated thymidine incorporation rates of free-living bacteria. Recent work, based on a model, has established that fecal pellets may release all their dissolved organic compounds into the surrounding water (JUMARS et al. 1989). From laboratory experiments, PEDUZZI & HERNDL (1992) clearly demonstrated that zooplankton activity may play a major role in providing dissolved organic substrates for bacterial growth. Thus in this study, night-time increase of bacterial incorporation rates in the surface waters might be related to the nocturnal upward migration of zooplankton.

Conclusion

In this paper, we have demonstrated that only diel studies allow an understanding of the development of planktonic communities. Two bacterial communities can be distinguished in Ebrié Lagoon, regulated by the concentration of particulate matter for attached bacteria and by the availability of dissolved nutrients for free-living bacteria. In this eutrophic tropical lagoon, dissolved photosynthetic exudates did not explain the maximum bacterial activity of free-living bacteria noted at night. This night time stimulation of bacteria might be linked to the nocturnal activity of zooplankton (egestion of fecal pellets and sloppy feeding). Finally one major problem is the lack of knowledge of the mechanism and sources for the production of bacterial substrates. At a lagoon scale, bacterial production represented a mean percentage of 58 % of the primary production, and this ratio suggests that heterotrophic bacterial communities (especially free-living bacteria) play a key role in the decomposition of organic matter and in the dynamics of this shallow tropical system. Future studies should be able to demonstrate the importance of zooplankton in trophic coupling in Ebrié Lagoon, knowing that heterotrophic protozoan are consumed by zooplankton that also graze directly on bacteria.

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