

Size, composition and distribution of particles related to wind-induced resuspension in a shallow tropical lagoon

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Abstract. The size, composition and distribution of particles in the water column were surveyed in a shallow area (1 m depth) of a tropical lagoon (Côte d'Ivoire) during a sequence of wind-induced resuspension. Water samples were collected hourly near the surface during one tidal cycle. Three characteristic periods were distinguished: a calm period with low wind speed (average 1.2 m s^{-1}), a windy period with wind speed $>3 \text{ m s}^{-1}$ (range between 4 and 6 m s^{-1}) inducing sediment resuspension and a relaxation period during the decrease of wind velocity. From the analysis of several parameters (particle size and volume, bacteria, pico- and nanophytoplankton, ciliates and detritus), sediment resuspension caused a regular injection of particles from the bed. The finest particles ($1.5\text{--}6 \mu\text{m}$: chlorophytes such as *Chlorella* spp., picocyanobacteria such as *Synechococcus*) were the first to be affected by wind-induced turbulence, whereas large particles ($6\text{--}12 \mu\text{m}$: diatoms, cyanobacteria such as *Lyngbia* spp.) were dispersed into the water column at the highest wind speed. The fate of the different seston components differed according to their size. Therefore, wind-induced resuspension could greatly influence the food web organization through the quantity, quality and size of edible particles available at a given time.

Introduction

The movement and distribution of particles in shallow ecosystems are controlled by several processes, such as currents and wind-induced resuspension. In estuarine or coastal situations, seston characteristics can vary over a tidal cycle as a consequence of changes in current direction and intensity (Roman and Tenore, 1978; Fegley *et al.*, 1992), but also under wind influence (Demers *et al.*, 1987; Weir and McManus, 1987; Powell *et al.*, 1989). In shallow lakes or reservoirs, waves can induce sediment resuspension and seston is then modified in quality as well as in quantity (Carper and Bachmann, 1984; Luettich *et al.*, 1990; Carrick *et al.*, 1993). Resuspension can influence plankton ecology through hydrological modifications, variations of nutrient concentration or light attenuation (Maccina and Soballe, 1990; Hellström, 1991; Lind and Lind, 1991; Galvez and Niell, 1992; Kristensen *et al.*, 1992). The size distribution and biochemical composition of particles can thus vary according to the recent history of the water. These characteristics are important for pelagic filter feeders because resuspension is determinant in the direct functioning of the plankton food web (Floderus and Pihl, 1990; Kiørboe and Nielsen, 1990; Abreu *et al.*, 1992; De Jonge and Van Beusekom, 1992). Therefore, an assessment of the carbon biomass corresponding to the sestonic components (detritus, bacteria, phytoplankton and larger organisms) in calm and windy conditions can provide substantial information on the organization of pelagic ecosystems in shallow environments.

Wind-induced resuspension can be related to storms (Brydsten, 1992; Ritzrau



and Graf, 1992) or to thermal winds, like those occurring daily from noon in African lakes (Ganf, 1974; Talling, 1992) or the Austral Trade winds in coastal lagoons of West Africa (Tastet, 1974; Arfi *et al.*, 1994). In the shallow Ebrié lagoon (Côte d'Ivoire; 5°N, 5°W), these weak and regular winds are blowing from the southwest (Durand and Chantraine, 1982). They are characterized by a marked diel pattern of velocity and can induce resuspension in favorable conditions of fetch, depth, wind speed, wave height and bed roughness: Arfi *et al.* (1993) and Bouvy *et al.* (1994) have demonstrated that in areas sampled on the northern shore of the lagoon, Austral Trade winds with speeds $>3 \text{ m s}^{-1}$ allow sediment resuspension. This threshold was calculated using the half-wavelength method, from a relationship linking wave characteristics and wind speed in shallow environments (Carper and Bachmann, 1984). Schematically, the day can be roughly divided into two halves, midnight–midday (low winds, flat water and particle sedimentation) and midday–midnight (moderate winds, waves and particle resuspension), since the wind speed threshold is usually passed around noon. Although this process was suspected to have wide consequences on zooplankton (Pagano and Saint-Jean, 1988), little is known about the characteristics of resuspended particles and the biological effects of these vertical transfers on planktonic communities. The aim of the present work is to study the hourly variations of (i) particle size distribution and (ii) seston composition (bacteria, algae, ciliates and detritus) in relation to resuspension in an area permanently influenced by Trade winds. The importance of this phenomenon on the functioning of the pelagic ecosystem (effects on algal productivity, fate of resuspended particles as food for grazers) is also discussed.

Method

Sampling strategy, environmental parameters

The study was carried out during the dry season (in order to avoid riverine or rain inputs) at a station located 400 m offshore on the north bank of Ebrié lagoon (Figure 1). Situated 40 km west of Vridi canal (the only permanent outlet of the lagoon into the Atlantic ocean), the sampling station is characterized by reduced tidal hydrodynamics. Owing to the low depth (1 m), this site is permanently non-stratified. The survey was conducted on 31 March 1993 between 10:00 and 24:00 h over a single tidal cycle during a neap tide. Wind direction was recorded each hour, and wind velocity was measured using a cup anemometer (values integrated each minute, averaged over 10 min). Total irradiance was integrated hourly using a Li Cor 200SB pyranometer. Light attenuation coefficients (k) were estimated from vertical profiles using a Li Cor 193SB spherical quantum sensor (4π). Water level was recorded every minute using a surface height gauge (details in Arfi *et al.*, 1993).

Water samples were collected hourly using a peristaltic pump at a depth of 0.1 m. Conductivity and temperature were measured using a Tacussel conductimeter and a HI8751 thermometer, respectively. All other parameters (see below) were obtained from samples filtered on a $63 \mu\text{m}$ nylon mesh in order to discard zooplanktonic organisms and very large particles possibly pumped.

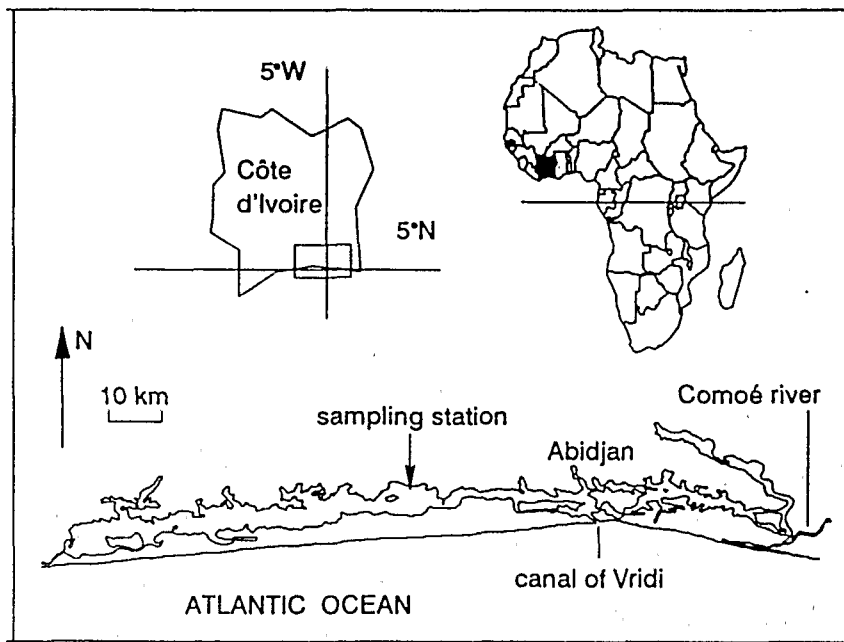


Fig. 1. Map of Ebré lagoon and location of the sampling station.

Ammonia and orthophosphate concentrations were measured on Whatman GF/F filtered water using the methods reported by Aminot and Chaussépied (1983). Size distributions, particle numbers and volumes were determined using a Coulter Multisizer II equipped with a $70\ \mu\text{m}$ orifice tube [equivalent spherical diameter (ESD) ranging from 1.5 to $42\ \mu\text{m}$]. Once the counter had been calibrated with uniform latex particles of known size (here $14\ \mu\text{m}$), 4–6 counts were averaged for each sample after blank subtraction. Owing to the tube selectivity, only the volumes calculated from ESD in the range of 1.5 – $24\ \mu\text{m}$ were considered as correctly estimated. Particle volumes were summed in classes (1.5 – 3 , 3 – 6 , 6 – 12 and 12 – $24\ \mu\text{m}$) corresponding to the size of the main algal species observed during the study. Particulate organic carbon (POC) was analyzed using a Leco CHN analyzer after filtration on pre-combusted Whatman GF/F filters and acidification.

Biological parameters

Bacterial numbers (free-living and attached cells, separated on $3\ \mu\text{m}$ Nuclepore membranes) were determined by epifluorescence microscopy after staining with DAPI (Porter and Feig, 1980). Mean bacterial volumes were estimated by measurements of cells (up to 100) using photographic slides and a digitizing device coupled with a computer; carbon biomass was obtained using a conversion factor of $0.2\ \text{pg C}\ \mu\text{m}^{-3}$ (Simon and Azam, 1989). Samples for the determination of chlorophyll concentrations were also divided into two fractions

after filtration on 3 μm Nuclepore membranes. Pigment concentrations were measured after methanol extraction using a Turner Designs fluorometer. Algae $<3 \mu\text{m}$ were considered as picophytoplankton, and the difference with the total biomass was considered as nanophytoplankton. Conversion to carbon units was achieved using a carbon:chlorophyll ratio of 35:1 (picophytoplankton) and 55:1 (nanophytoplankton), using factors calculated from previous assays. Algal cells and ciliates were identified and counted on Lugol-fixed samples (Utermöhl method). Ciliate carbon biomass was obtained from volume by applying a conversion factor of $0.12 \text{ pg C } \mu\text{m}^{-3}$ (Turley *et al.*, 1986).

Data processing

Statistical treatments (average comparisons) were based on non-parametric procedures like the Kruskal–Wallis test for intergroup differences. In the case of null hypothesis rejection, the difference between sample sets was tested using the Tukey HSD test.

Results

Wind speed and direction

From wind data recorded a few hours before the study (Figure 2a), north winds dominated until 9:00 h. This period, characterized by winds inducing no resuspension at the station, was followed by a short period of irregular wind. From 9:00 h, winds rotated west, and then southwest. During the Austral Trade winds event (10:00–24:00 h), three characteristic sequences were distinguished, separated by transitional periods (Figure 2b).

(i) The first one (10:00–12:00 h), characterized by low wind speed (average velocity 1.2 m s^{-1} , 60% of the observations $<1 \text{ m s}^{-1}$) and flat water, was defined as the 'calm period'.

(ii) Resuspension at the station was possible from noon, with a wind speed $>3 \text{ m s}^{-1}$. The highest wind speeds were observed between 15:00 and 18:00 h (mean speed 4.8 m s^{-1} , range $4\text{--}6 \text{ m s}^{-1}$); this sequence of intense Austral Trade winds was defined as the 'windy period'.

(iii) After this peak, the wind velocity decreased progressively and, just after 20:00 h, the speed was $<3.5 \text{ m s}^{-1}$. The third characteristic period (22:00–24:00 h) showed decreasing wind speed (average velocity 2.4 m s^{-1} , 83% of the observations $<3 \text{ m s}^{-1}$) and rapidly lowering waves. This period was defined as the 'relaxation period'. At the end of the survey, the wind speed was close to 1 m s^{-1} .

Hydrological context

During the survey, the tidal range was 12 cm; the two slack high waters occurred around 11:00 and 24:00 h, respectively, while the slack low water occurred around 16:00 h. Conductivity (average and SD: 20.9 and 1.5 mS cm^{-1}) and temperature (average and SD: 31.1 and 0.7°C) were characterized by low variations.

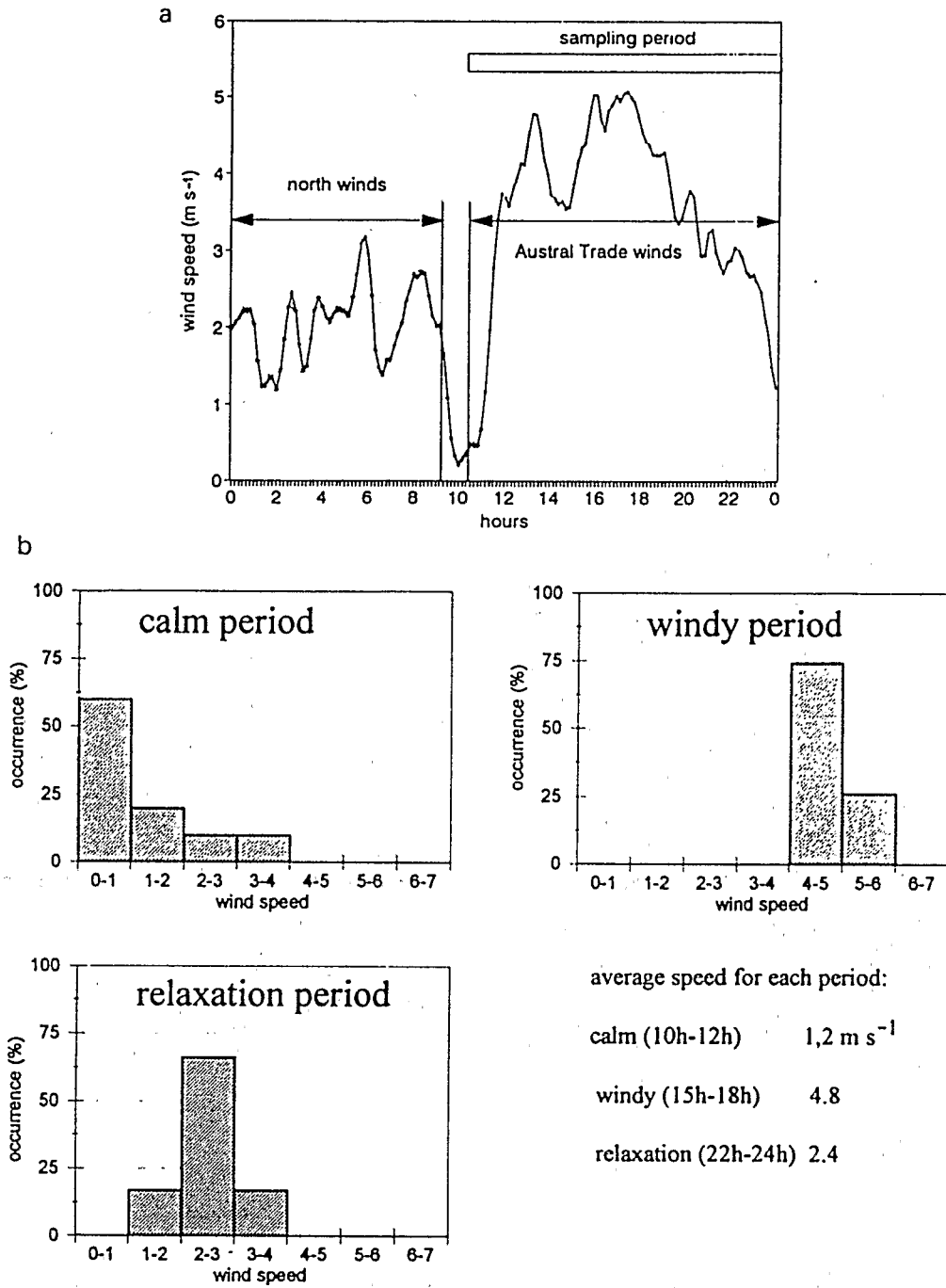


Fig. 2. (a) Wind speed time series recorded during the study (10 min time lag) and (b) wind speed frequency histograms for the sequences described.

Table I. Mean values for the different parameters studied. The intergroup difference was accepted or rejected (Kruskal-Wallis non-parametric test) and the null hypothesis of mean equality between two successive groups was rejected ('diff.', $P < 0.05$) or not rejected ('not diff.', $P > 0.05$) using the Tukey test. na, data not available (night hours)

Parameter	Calm period (10:00–12:00 h)	Windy period (15:00–18:00 h)	Relaxation period (22:00–24:00 h)
k (m^{-1})	3.32	3.77	na
NH_4-N ($\mu M l^{-1}$)	10.27	4.45	diff.
PO_4-P ($\mu M l^{-1}$)	0.73	0.05	not diff.
Mineral seston ($mg l^{-1}$)	29.7	31.5	not diff.
Organic seston ($mg l^{-1}$)	11.7	17.4	diff.
Particle volume ($mm^3 l^{-1}$)			
1.5–24 μm	12.3	25.0	diff.
1.5–3 μm class	2.2	3.7	not diff.
3–6 μm class	6.8	13.4	not diff.
6–12 μm class	2.1	5.7	diff.
12–24 μm class	1.0	2.3	diff.
POC ($mg l^{-1}$)	1.88	3.28	diff.
Bacteria as C	0.03	0.08	not diff.
Picoplankton as C	0.38	0.52	not diff.
Nanoplankton as C	0.49	1.06	diff.
Ciliates as C	0.07	0.08	not diff.
Detritus as C	0.91	1.54	not diff.
Algal volume ($mm^3 l^{-1}$)	5.36	14.67	diff.
<i>Chlorella</i> volume	2.45	6.72	not diff.
<i>Lyngbia</i> volume	0.63	3.15	diff.
<i>Gymnodinium</i> volume	0.60	1.47	not diff.
			diff.
			3.17

The study was conducted during a sunny day (total irradiance $5.98 \text{ kW m}^{-2} \text{ day}^{-1}$). Light attenuation coefficients (k) were $>3 \text{ m}^{-1}$ during the diurnal hours, reflecting the permanent water turbidity (2–3% of the incident radiation near the bed). Average values were significantly different (Table I) for calm (3.3 m^{-1}) and windy periods (3.8 m^{-1}), and the increase in the light attenuation was observed when the wind speed exceeded 3 m s^{-1} .

In contrast to the other parameter patterns, ammonia concentrations were significantly higher during the calm and the relaxation periods than during the windy period (Table I). For the whole study, average values of $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ were $8.4 \mu\text{M l}^{-1}$ (SD $3.8 \mu\text{M l}^{-1}$) and $0.6 \mu\text{M l}^{-1}$ (SD $0.1 \mu\text{M l}^{-1}$), respectively.

Seston characteristics and granulometry

Mineral particles represented the major part of the seston during the study (average 68%), and no difference was detected in the mean mineral weights between the three periods. This feature was not observed for the organic particles, which showed the highest values during the windy period (Table I). For these parameters, temporal variations were progressive, both during the phases of increasing and decreasing concentrations (Figure 3).

The particle spectra were characterized by the same distribution at an hourly scale, centered around an ESD of $4 \mu\text{m}$ (Figure 4). The particle volume increased with the wind speed as soon as the velocity was $>3 \text{ m s}^{-1}$, and was maximum between 16:00 and 17:00 h (wind speed $\sim 5 \text{ m s}^{-1}$). Then, the volume decreased until 22:00 h, and at the end of the survey values were similar to those observed in the morning. During the study, the amplitude corresponded to a 3-

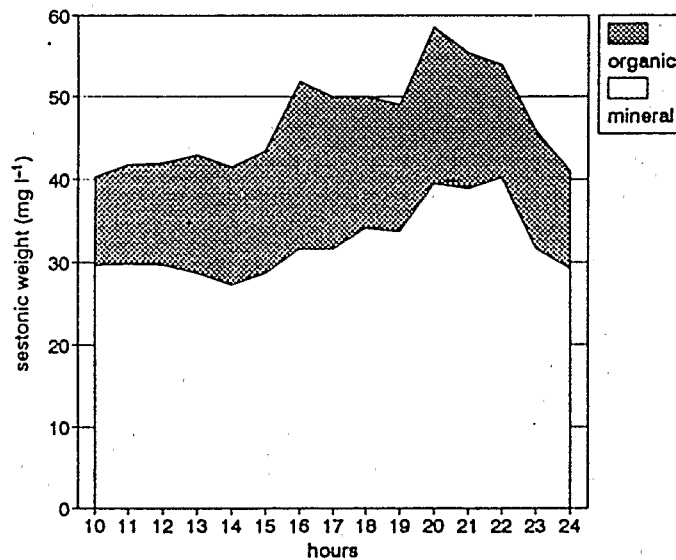


Fig. 3. Hourly variations of sestonic weight (mineral and organic).

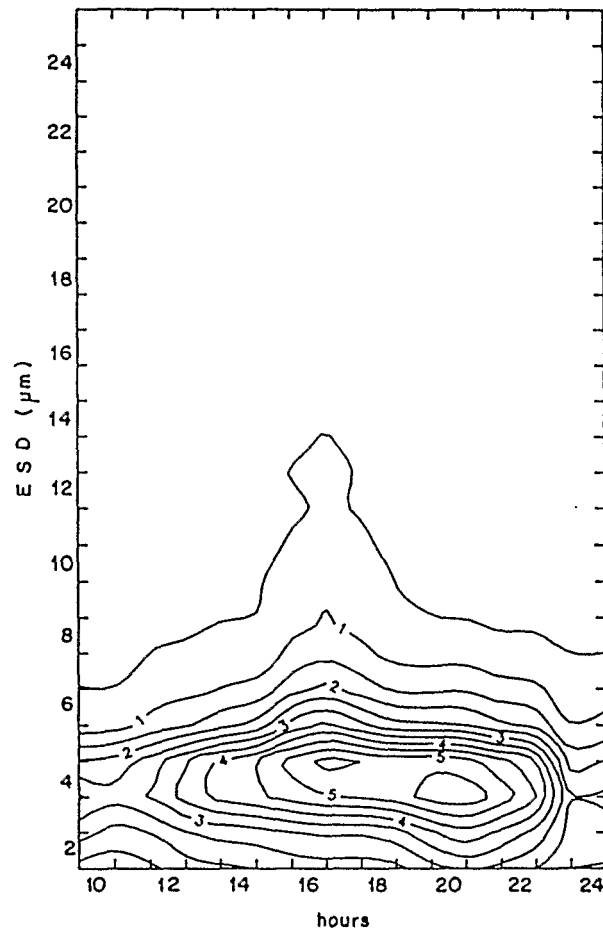


Fig. 4. Two-dimensional representation of particle volume ($\text{mm}^3 \text{ml}^{-1}$ or p.p.m.) through time (h) and particle ESD (μm).

fold increase in the particle volume near the surface. However, the four size classes showed different patterns of hourly variation (Figure 5).

(i) Abundance and volume of particles included in the 1.5–3 and 3–6 μm size classes increased progressively from 11:00 to 20:00 h, both with a 3-fold variation; this step was followed by a decrease in the particle volume at the end of the survey.

(ii) For the 6–12 μm size class, the particle volume increase was progressive until 15:00 h, and the value doubled suddenly between 15:00 and 16:00 h (wind speed $\sim 5 \text{ m s}^{-1}$). After this peak, the particle volume decreased slowly until 24:00 h.

(iii) On the contrary, the particle volume of the 12–24 μm size class showed no obvious variation from 10:00 to 15:00 h, but a 3-fold increase occurred suddenly between 16:00 and 17:00 h. After this peak, values decreased immediately and, until the end of the study, the particle volumes were similar to those observed before the windy period.

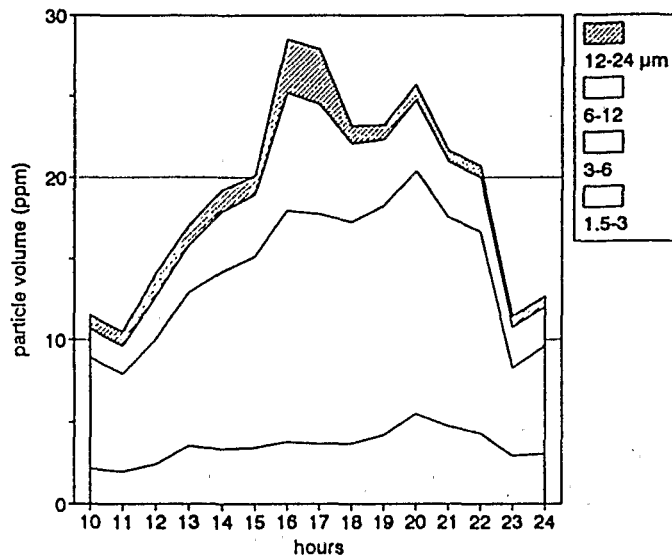


Fig. 5. Hourly variations of particle volumes for four particle size classes (1.5–3, 3–6, 6–12 and 12–24 μm ESD).

Statistically, the cumulated particle volumes corresponding to the three characteristic periods were significantly different (Table 1). For all four size classes, average volumes were significantly different during the calm period from those noted during the windy period. For particles included in the 1.5–3 and 3–6 μm size classes, the averages corresponding to the windy and the relaxation periods were not different, and the particles remained dispersed throughout the water column. On the contrary, in the 6–12 and 12–24 μm classes, the mean volumes estimated for the windy and the relaxation periods were different, due to rapid sedimentation of these large particles at decreasing wind speed.

POC characterization

POC differed significantly between the three periods. Five components were distinguished, including bacteria, picophytoplankton, nanophytoplankton, ciliates and organic detritus (Figure 6). Cumulated, the sum of the living organic material represented $\sim 53\%$ of the POC.

The bacterial biomass was low during the study, with an average of 0.07 mg C l^{-1} (2% of the POC). During the resuspension event, the bacterial number and biovolume showed a 2-fold increase. During the calm period, the biovolume distribution was unimodal, centered around a median of $0.025 \mu\text{m}^3$ ($n = 88$). During the windy period, the median increased to $0.040 \mu\text{m}^3$ ($n = 76$), while the distribution broadened (Figure 7).

The chlorophyll biomass of picophytoplankton averaged 0.48 mg C l^{-1} (18% of the POC) and differed significantly during the periods (Table 1). The biomass increased progressively during the resuspension event. Mean biomasses of the windy and the relaxation periods did not differ, indicating the persistence of the

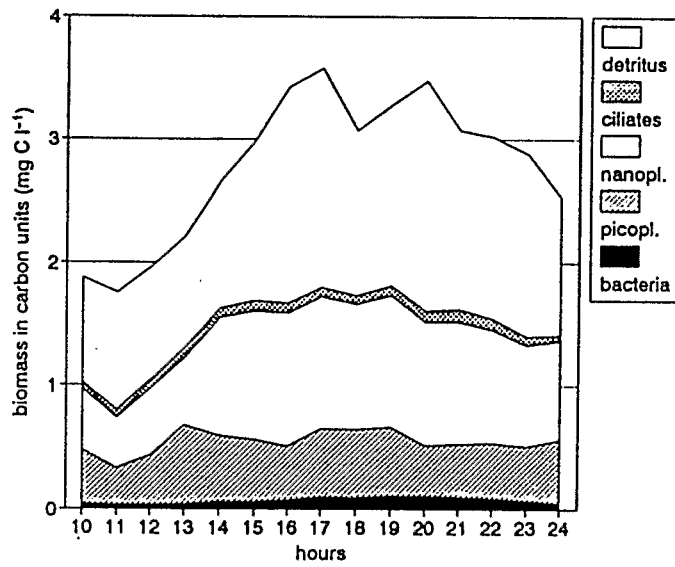


Fig. 6. Hourly variations of amounts and distributions for the five components of the POC biomass (bacteria, picophytoplankton, nanophytoplankton, ciliates and organic detritus).

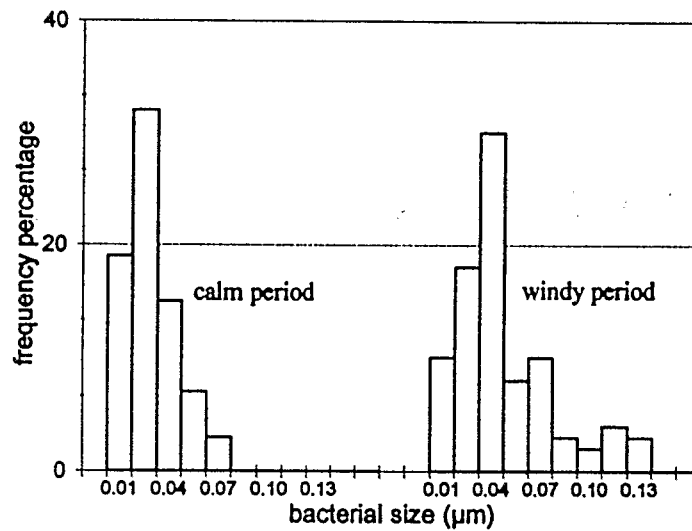


Fig. 7. Frequency histogram of bacterial volumes during the calm and windy periods.

small particles in the water column during the wind speed decrease. The chlorophyll biomass of nanophytoplankton averaged 0.85 mg C l^{-1} (30% of the POC), but differed significantly over the periods (values doubled during the windy period).

Ciliates were dominated by relatively small organisms ($30 \mu\text{m}$), like oligotrichs, representing $\sim 70\%$ of the total biomass (mostly *Strombidium* sp. and

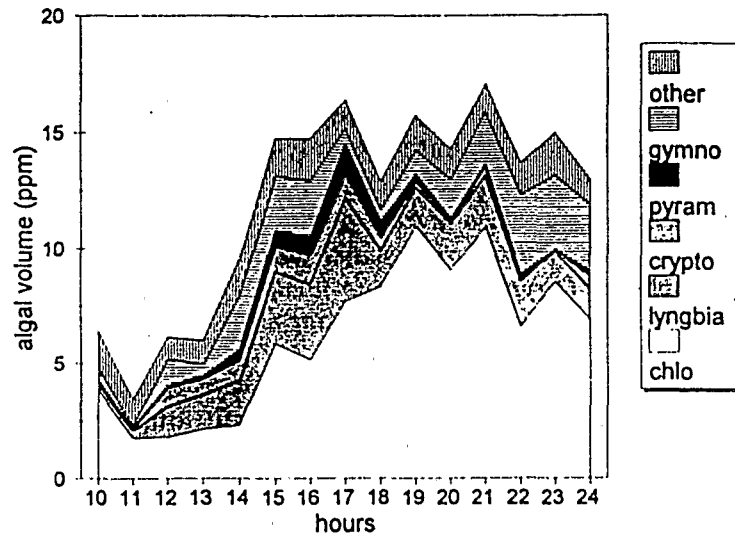


Fig. 8. Hourly variations of the main algal species abundance expressed as a volume ($\text{mm}^3 \text{ml}^{-1}$ or p.p.m.). chlo: *Chlorella* sp.; lyngbia: *Lyngbia* sp.; crypto: *Cryptomonas* spp.; gymno: *Gymnodinium* sp.; other: complement to the total volume.

Halteria sp.) and tintinnids (*Favella* sp., *Tintinnopsis* spp.). The average biomass was 0.07 mg C l^{-1} (3% of the POC). Oligotrich biomass varied, but peaked at 20:00 h (0.07 mg C l^{-1}). The biomass attributed to tintinnids was fairly constant throughout the survey. The means of the total ciliate biomass were not significantly different over the three periods (Table I).

Organic detritus represented the largest part of the POC (on average 1.31 mg C l^{-1} , 47% of the POC). The detritus fraction increased rapidly with wind speed, peaked twice during the windy period, and then decreased slowly until the end of the study. The average values corresponding to the relaxation and the windy periods were not significantly different (Table I).

Algal species

Expressed in numbers, two algal species dominated the phytoplanktonic community (*Chlorella* sp., a nanoplanktonic chlorophyte; and *Synechococcus* sp., a picocyanobacteria), with densities ranging between 10^7 and $10^8 \text{ cells l}^{-1}$. The secondary species were other cyanobacteria (*Anabaenopsis arnoldii* and *Lyngbia* spp.), a chlorophyte (*Pyramimonas grossi*) and a diatom (*Leptocylindrus minimum*), with densities in the 10^6 – $10^7 \text{ cells l}^{-1}$ range.

With the algal biomass expressed in volume, *Chlorella* sp. largely dominated, representing 24–74% of the phytoplankton volume (on average 52%). A progressive increase was observed once the wind speed was $>3 \text{ m s}^{-1}$. The maximum values noted between 19:00 and 21:00 h were five times higher than those observed at the beginning of the survey. Afterwards, the volume slowly decreased (Figure 8). This dominant species was seconded by diatoms (mainly

Leptocylindrus minimum) and, during the calm period, by flagellated chlorophytes (*P.grossi*, *Tetrastelmis* sp.). Cyanobacteria (*Lyngbia* sp., *A.arnoldii*, *Anabaena torulosa*) appeared during the windy period, and dinoflagellates (*Gymnodinium* sp., *Gonyaulax tamarensis*, *Prorocentrum minimum*) were observed just before and just after the windy period. Most of the other species observed during the study were euryhaline and opportunistic nanoplanktonic species. Very few large species were present; most of them were diatoms (*Melosira nummuloides*, *Amphiprora paludosa*, *Pleurosigma* spp.). On some samples, cryptophytes (*Cryptomonas* spp.) and euglenophytes (*Phacus* sp., *Euglena variabilis*) were observed, representing a low part of the phytoplankton volume.

For the total algal volume, as well as for the values corresponding to the dominant chlorophyte, the averages were significantly different for the calm and the windy period, but did not differ for the windy and the relaxation periods (Table I).

Discussion

Local hydrodynamics: tides, wind-induced waves

In the Ebrié lagoon area, tides and winds are characterized by the same periodicity (diurnal and semi-diurnal events), but they are not always in phase. Wind velocity is low (annual average of 2 m s^{-1}), and wind-induced currents are only observed in the superficial water layer. Horizontal water movements are then essentially related to tidal effects, particularly intense near the canal of Vridi. Both phenomena contribute to the spatial heterogeneity and to the physical instability, which are among the main characteristics of the estuarine part of the Ebrié lagoon (Guiral, 1992). However, at the sampling station located 40 km from the canal of Vridi, the tidal amplitude is strongly reduced and, if currents are still perceptible, they are more often quite low ($<3 \text{ cm s}^{-1}$; Arfi *et al.*, 1993). In the study area, hydrodynamics are not intense, and this characteristic allows the auxiliary processes to become predominant.

In this general context of slow water dynamics, the daily alternation of calm (flat water), wind-induced resuspension and relaxation periods is the main physical factor controlling the pelagic ecosystem (Bouvy *et al.*, 1994). In shallow parts of the lagoon, sediment resuspension leads to a regular injection of particles from the bed and from the lowest part of the water column (nepheloid layer). Sudden particle inputs occur during wind events, while particle distribution toward the superficial levels (wind speed increase) and particle sedimentation (wind speed decrease) are more progressive. In a previous study, Bouvy *et al.* (1994) have demonstrated that particle sinking rates and wind speed variations followed the same pattern, with the highest sedimentation rates observed during the high wind speed.

Resuspension, turbidity and light attenuation

In many aquatic systems, turbidity is linked to allochthonous inputs and/or to

wind-induced resuspension distributing inorganic and organic particles in the water column (Lind and Lind, 1991). The Ebrié lagoon is a turbid water body (Dufour, 1984), but the first obvious consequence of particle resuspension is still light attenuation, since turbidity is periodically enhanced by resuspension events which occur mainly during the daylight period. The quantity of mineral particles did not vary obviously during the present study, whereas the biomass related to organic detritus increased during the windy period. In this shallow area, the euphotic layer corresponds to the entire water column, and the daily attenuation affects only the deepest layer (10–20 cm above the bed). As a consequence, and since the water column is not stratified, the euphotic area also corresponds to the mixing layer, and resuspended algae can reach better light conditions once redistributed near the surface. The periodicity of this process linked to a diurnal increase in wind speed makes resuspension a profitable mechanism for algae, attenuating the effect of turbidity increase, even if the increasing algal concentration in the superficial layer also contributes, in turn, to the light extinction.

Resuspension and nutrients

The impact of wind resuspension on nutrient concentrations has been investigated in several aquatic systems and close relationships between wind speed and total phosphorus concentrations have been demonstrated (Kristensen *et al.*, 1992), generally when the time interval between calm and windy periods was substantial (several days or months). Sondergaard *et al.* (1992) demonstrated experimentally that a second simulation of resuspension conducted 26 h after a first one did not result in any further release of phosphorus from the sediment. In Ebrié lagoon, the wind event occurs daily and the sequences with no resuspension are short. Therefore, this process can hardly affect the nutrient concentrations because the daily ionic equilibrium between the pelagic and benthic zone hinders nutrient release from the bed.

A direct consequence of the inoculation of sedimented algal cells into the euphotic layer under wind influence is the increase in nutrient uptake, and the temporary diurnal decrease in $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ concentrations observed during the present study. With these cells sedimenting again after the wind speed decrease, the nutrient standing stock seemed to reconstitute rapidly, and nutrient concentrations at the end of the survey were close to those measured before the wind event. This context of non-limiting nutrients was favorable to the development of small species like cyanobacteria or chlorococcal green algae (as demonstrated by Sondergaard *et al.*, 1992), once resuspended in more favorable light conditions.

Resuspension and trophic resources

When the wind-induced turbulence has reached the sediment interface, the finest particles are the first to be affected by resuspension, whereas the large particles will be distributed over the entire water column once the wind speed is at its maximum. As will be explained below, the fate of the different seston

components was therefore different according to their size, but the differential inoculation of particles (organic detritus, bacterial assemblages and algal cells) under the wind influence might temporarily have created new links between trophic levels.

The fate of bacterial biomass (number and cell size) in the pelagic environment varies mainly with nutrient availability, grazing and sedimentation (see Güde, 1989). In deep areas (5 m) of Ebrié lagoon, Torrétton *et al.* (1994) demonstrated that free-living bacteria were regulated by nutrient availability and bacterial activity observed at night might be linked to the nocturnal upward movement of zooplankton. A periodic input of bacteria from the sediment can modify the microbial community structure as well as its functioning. During the calm period, pelagic bacteria were characterized by volumes significantly lower than those observed during the windy period (Wilcoxon test, $P < 0.05$). This increase in cell sizes and the increase in bacterial numbers during the windy period were related to particle resuspension at the sediment-water interface. Numerous studies have demonstrated that benthic bacteria are characterized by larger volumes than those of pelagic cells (e.g. Rhoads *et al.*, 1984). Ritzau and Graf (1992) have shown the same phenomenon in the benthic zone of Kiel Bight (20 m depth) after resuspension by a storm event. These bacterial aggregates might represent an additional food resource for microplankton grazers because their sizes are comparable to those of small phytoplankton species. In the present study, proportions of attached bacteria represented an average of 20% of the total bacterial abundance, and this percentage increased to 34% during the wind event. A new trophic link between bacterial communities and other pelagic grazers might have been created during wind-induced resuspension, knowing that large bacteria or bacterial assemblages are preferentially grazed by ciliates (Gonzalez *et al.*, 1990).

Resuspension can also temporarily modify the composition of the phytoplanktonic community, allowing several species to be resuspended and the biomass to increase in the superficial layer. Carrick *et al.* (1993) demonstrated an inoculation of nanoplanktonic algae (mainly diatoms) from the bottom zone into the water column during high-wind events. These authors have elaborated a conceptual model describing alternations in ecosystem structure and function due to wind resuspension, but their study only dealt with the composition of the algal community and not size classes or particle volumes. In the study area of Ebrié lagoon, the redistribution of algae from the bed into the water column occurs under the influence of wind-induced waves. Diatoms constituted a minor fraction of phytoplanktonic volume under low-wind conditions, while their contribution increased 2-fold during the windy period. The same process, even more intense (3- to 5-fold increases), was observed for the dominant species (*Chlorella* sp.) and for several chlorophytes and cyanobacterial species. The size distribution of these cells, depending on the wind speed during the resuspension event (Table II), can complete the model of Carrick *et al.* (1993). The inoculation of sedimented particles may be a common and important compound of the biomass in shallow productive lagoons.

Particle size profiles remained comparable during the study, but obvious

Table II. Phytoplankton size structure according to the local wind speed threshold, allowing (speed $>3 \text{ m s}^{-1}$) or not allowing (velocity $<3 \text{ m s}^{-1}$) particle resuspension

Wind speed (m s^{-1})	Wind period	Size	Abundance and distribution
<3	Calm	Picophytoplankton Nanophytoplankton	Low biomass distributed over the water column Biomass concentrated near the bed
>3	Resuspension	Picophytoplankton Nanophytoplankton	High biomass distributed over the water column Distributed in the whole water column
<3	Relaxation	Picophytoplankton Nanophytoplankton	High biomass slowly sedimenting toward the bed Biomass rapidly sedimenting toward the bed

differences appeared in the respective abundance of the size classes. The total particulate volume increased during the windy period, and decreased during the relaxation period. Significant variations were observed for the largest particles, which were resuspended once a wind speed threshold was reached. Below this threshold, these particles sank immediately. In contrast, small particles were rapidly distributed in the water column, and remained in suspension during the relaxation period. This phenomenon can greatly influence the food resource distribution, since for a given time, the quantity (in number as well as in volume), the quality (in carbon content as well as kind of seston) and the size of edible particles available will differ according to the wind speed. Secondary consumers are therefore concerned by short-term modifications of their trophic environment. Micrograzers (like ciliates), which can take food in the size range of picoplankton (Weisse, 1988), seem to be permanently favored, since small particles (bacteria, picoalgae) are always present in the water column during windy and relaxation periods. In contrast, large algal cells and organic detritus are only resuspended and distributed in the water column during the windy period. This transient presence in the pelagic environment can introduce a gap between food availability and food demand by the zooplanktonic filter feeders living in this area (essentially rotifers and copepods). In Ebrié lagoon, the dominant copepod *Acartia clausi* showed nocturnal vertical migration (Pagano and Saint Jean, 1988) and this species could be concerned by a trophic discrepancy between feeding behavior and food availability. Thus, in these shallow areas of the lagoon, wind-induced hydrodynamics may influence the pelagic food web organization, through adaptive processes or poor trophic transfers. Resuspension occurs only in shallow areas of the northern shore of Ebrié lagoon, but lateral movements (wind or tidal currents) can distribute these resuspended particles among larger areas than those directly concerned by the vertical turbulence. Therefore, particle resuspension and its ecological consequences must be taken into account in the study of shallow water bodies, even if local winds are weak and regular.

References

- Abreu,P.C., Biddanda,B.B. and Odebrecht,C. (1992) Bacterial dynamics of the Patois lagoon estuary, Southern Brazil (32°S, 52°W): relationship with phytoplankton production and suspended material. *Estuarine Coastal Shelf Sci.*, 35, 621-635.
- Aminot,A. and Chaussepied,M. (1983) *Manuel des analyses chimiques en milieu marin*. CNEXO, Brest, 395 pp.
- Arfi,R., Guiral,D. and Bouvy,M. (1993) Wind induced resuspension in a shallow tropical lagoon. *Estuarine Coastal Shelf Sci.*, 36, 587-604.
- Arfi,R., Bouvy,M. and Guiral,D. (1994) Sedimentation modified by wind induced resuspension in a shallow tropical lagoon (Côte d'Ivoire). *Neth. J. Aquat. Ecol.*, 28, 427-431.
- Bouvy,M., Arfi,R. and Guiral,D. (1994) Short term variation of seston characteristics in a shallow tropical lagoon: effects of wind induced resuspension. *Neth. J. Aquat. Ecol.*, 28, 433-440.
- Brydsten,L. (1992) Wave induced sediment resuspension in the Öre estuary, northern Sweden. *Hydrobiologia*, 235-236, 71-83.
- Carper,G.L. and Bachmann,R.W. (1984) Wind resuspension of sediments in a prairie lake. *Can. J. Fish. Aquat. Sci.*, 41, 1763-1767.
- Carrick,H.J., Aldridge,F.J. and Schleske,C.L. (1993) Wind influence phytoplankton biomass and composition in a shallow, productive lake. *Limnol. Oceanogr.*, 38, 1179-1192.

- De Jonge, V.N. and Van Beusekom, J.E.E. (1992) Contribution of resuspended microphytobenthos to total phytoplankton in the Ems estuary and its possible role for grazers. *Neth. J. Sea Res.*, **30**, 91-105.
- Demers, S., Theriault, J.-C., Bourget, E. and Bah, A. (1987) Resuspension in the shallow sublittoral zone of a macrotidal estuarine environment: wind influence. *Limnol. Oceanogr.*, **32**, 327-339.
- Dufour, Ph. (1984) Production primaire d'une lagune tropicale (Ebrié, Côte d'Ivoire). Facteurs naturels et anthropiques. Thèse d'Etat, Université Paris VI, tome 1, 166 pp.
- Durand, J.R. and Chantraine, J.M. (1982) L'environnement climatique des lagunes ivoiriennes. *Rev. Hydrobiol. Trop.*, **15**, 85-113.
- Fegley, S.R., McDonald, B.A. and Jacobsen, T.R. (1992) Short-term variation in the quantity and quality of seston available to benthic suspension feeders. *Estuarine Coastal Shelf Sci.*, **34**, 393-412.
- Floderus, S. and Pihl, L. (1990) Resuspension in the Kattegat: impact of variation in wind climate and fishery. *Estuarine Coastal Shelf Sci.*, **31**, 487-498.
- Galvez, J.A. and Niell, F.X. (1992) Sediment resuspension in a monomictic eutrophic reservoir. *Hydrobiologia*, **235-236**, 133-141.
- Ganf, G.G. (1974) Diurnal mixing and the vertical distribution of phytoplankton in a shallow equatorial lake (Lake George, Uganda). *J. Ecol.*, **62**, 611-629.
- Gonzalez, J.M., Sherr, E.B. and Sherr, B.F. (1990) Size-selective grazing of bacteria by natural assemblages of estuarine flagellates and ciliates. *Appl. Environ. Microbiol.*, **56**, 583-589.
- Güde, H. (1989) The role of grazing on bacteria in plankton succession. In Sommer, U. (ed.), *Plankton Ecology, Succession in Plankton Communities*. Springer Verlag, pp. 337-365.
- Guiral, D. (1992) L'instabilité physique, facteur d'organisation et de structuration d'un écosystème tropical saumâtre peu profond: la lagune Ebrié. *Vie Milieu*, **42**, 73-92.
- Hellström, T. (1991) The effect of resuspension on algal production in a shallow lake. *Hydrobiologia*, **213**, 183-190.
- Kjørboe, T. and Nielsen, T.G. (1990) Effect of wind stress on vertical water column structure, phytoplankton growth and productivity of planktonic copepods. In Barnes, M. and Gibson, R.N. (eds), *Trophic Interactions in the Marine Environment. Proceedings of the 24th EMBS*. Aberdeen, pp. 28-40.
- Kristensen, P., Sondergaard, M. and Jeppesen, E. (1992) Resuspension in a shallow eutrophic lake. *Hydrobiologia*, **228**, 101-109.
- Lind, O.T. and Lind, L.D. (1991) Association of turbidity and organic carbon with bacterial abundance and cell size in a large, turbid, tropical lake. *Limnol. Oceanogr.*, **36**, 1200-1208.
- Luettich, R.A., Harleman, D.R.F. and Somlyódy, L. (1990) Dynamic behavior of suspended sediment concentrations in a shallow lake perturbed by episodic wind events. *Limnol. Oceanogr.*, **35**, 1050-1067.
- Maccina, M.J. and Soballe, D.M. (1990) Wind related limnological variation in lake Okeechobee, Florida. *Lake Reservoir Manage.*, **6**, 93-100.
- Pagano, M. and Saint-Jean, L. (1988) Importance et rôle du zooplancton dans une lagune tropicale, la lagune Ebrié (Côte d'Ivoire): peuplements, biomasse, production et bilan métabolique. Thèse de Doctorat d'Etat, Université Aix-Marseille II, 390 pp.
- Porter, K.G. and Feig, Y.S. (1980) The use of DAPI for identifying and counting aquatic microflora. *Limnol. Oceanogr.*, **25**, 943-948.
- Powell, T.M., Cloern, J.E. and Huzzey, L.M. (1989) Spatial and temporal variability in south San Francisco bay (USA). 1. Horizontal distribution of salinity, suspended sediments and phytoplankton biomass and productivity. *Estuarine Coastal Shelf Sci.*, **28**, 583-597.
- Rhoads, D.C., Boyer, L.F., Welsh, B.L. and Hamson, G.R. (1984) Seasonal dynamics of detritus in the benthic turbidity zone (BTZ); implications for bottom-rack molluscan mariculture. *Bull. Mar. Sci.*, **35**, 536-549.
- Ritzrau, W. and Graf, G. (1992) Increase of microbial biomass in the benthic turbidity zone of Kiel Bight after resuspension by a storm event. *Limnol. Oceanogr.*, **37**, 1081-1086.
- Roman, M.R. and Tenore, K.R. (1978) Tidal resuspension in Buzzards Bay, Massachusetts. *Estuarine Coastal Mar. Sci.*, **6**, 37-46.
- Simon, M. and Azam, F. (1989) Protein content and protein synthesis rates of planktonic marine bacteria. *Mar. Ecol. Prog. Ser.*, **51**, 201-213.
- Sondergaard, M., Kristensen, P. and Jeppesen, E. (1992) Phosphorus release from resuspended sediment in the shallow and wind-exposed Lake Arreso, Denmark. *Hydrobiologia*, **228**, 91-99.
- Talling, J.F. (1992) Environmental regulation in African shallow lakes and wetlands. *Rev. Hydrobiol. Trop.*, **25**, 87-144.
- Tastet, J.P. (1974) L'environnement physique du système lagunaire Ebrié. *Sér. Doc. Dép. Sci. Terre, Univ. Abidjan*, **11**, 1-28.

- Torréton, J.P., Bouvy, M. and Arfi, R. (1994) Diel fluctuations of bacterial abundance and productivity in a shallow eutrophic tropical lagoon. *Arch. Hydrobiol.*, **131**, 79-92.
- Turley, C.M., Newell, R.C. and Robins, D.B. (1986) Survival strategies of two small marine ciliates and their role in regulating bacterial community structure under experimental conditions. *Mar. Ecol. Prog. Ser.*, **33**, 59-70.
- Weir, D.J. and McManus, J. (1987) The role of wind in generating turbidity maxima in the Tay estuary. *Cont. Shelf Res.*, **7**, 1315-1318.
- Weisse, T. (1988) Dynamics of autotrophic picoplankton in lake Constance. *J. Plankton Res.*, **10**, 1179-1188.

Received on March 3, 1994; accepted on October 19, 1994