SHORT-TERM VARIATIONS OF SESTON CHARACTERISTICS IN A SHALLOW TROPICAL LAGOON: EFFECT OF WIND-INDUCED RESUSPENSION

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KEYWORDS: resuspension; suspended particle; bacteria; phytoplankton; ciliates; tropical lagoon.

ABSTRACT
In January 1993, a 24 hour survey based on an hourly sampling was conducted in a station (1 m depth) located in the Ebrié lagoon, Côte d'Ivoire, in order to determine short-term changes in seston quality and quantity and relate them to physical conditions. Water samples were collected just below the surface and at 0.9 m depth to assess the seston distribution in the water column. Located in an estuarine environment, the study site was submitted to periodic effect of tides with low currents. Under certain conditions, sediment resuspension by wind-induced waves was observed in the shallow parts of this ecosystem. From the analysis of hydrodynamic processes (tide, wind and sedimentation rates), four basic situations were distinguished in the course of the study: a period with no wind and high sedimentation rates, a period characterized by wind-induced resuspension, followed by a period of sedimentation and finally, a period without wind during the second flood tide. The particle size spectra were similar throughout the study, the distributions being unimodal (mode of 4 µm diameter). The finer particles (<10 µm) were resuspended over the whole water column at the beginning of the resuspension period, whereas the larger particles were resuspended if the wind speed exceeded 3 m s\(^{-1}\). Phytoplankton species were found to provide information on the physical factors controlling the pelagic system: small cells, such as those of cyanobacteria (*Synechococcus* sp.), were always present over the whole tidal cycles, whereas large motile cells were predominant in the water column during the resuspension period. The seston characteristics of this part of Ebrié lagoon are mainly controlled by tidal currents, but wind-induced resuspension can modify the structure of the pelagic food web.

INTRODUCTION
Distribution of particles and nutrients in shallow coastal ecosystems are controlled by several processes such as river inflow, currents, tides and sediment resuspension. The seston components may vary in proportion, size distribution and biochemical composition as a function of hydrodynamics, and these characteristics are determinant of the food resource for pelagic filter feeders. Thus, the estimate of the carbon biomass corresponding to each of the seston components (detritus, bacteria, phytoplankton and larger organisms) can provide substantial information on the structure of ecosystems. In estuarine situations, seston characteristics can vary over a tidal cycle as a consequence of changes in current direction and intensity. Recently, FEGLEY et al. (1992) demonstrated that seston concentration can change significantly over a tidal cycle whereas its composition remained fairly constant. Seston characteristics can also be modified when sediment resuspension occurs (CARPER and BACHMAN, 1984; DEMERS et al., 1987; LUETTICH et al., 1990; KRISTENSEN et al., 1992). In shallow ecosystems, this phenomenon is considered to be a major factor controlling biological processes (FRECHETTE et al., 1988; POWELL et al., 1989; FLODERUS and PIHL, 1990; DE JONGE and VAN BEUSEKOM, 1992). Even in situations where tidal effects are intense, wind-induced waves can greatly enhance particle resus-
Located in Côte d’Ivoire (West Africa), the Ebrié lagoon is an important water body (1200 km², 132 km long, 4 km wide in average, Fig. 1) orientated East-West, perpendicular to the direction of the Austral Trade winds, predominant almost all the year long (GUIRAL, 1992; ARFI et al., 1993). The frequency of these winds blowing regularly from the South-West was estimated as 82% on an inter-annual basis (DURAND and CHANTRAINE, 1982). In this shallow tropical lagoon (4.8 m deep on average), resuspension by waves generated by the Trade winds alternates with sedimentation during low wind periods in the course of the same day (ARFI et al., 1993). The effects of resuspension on particle grading by size and sedimentation were suggested by TASTET (1974), who reported that the spatial distribution of particles coupled to the local bathymetry and fetch condition might reflect alternating phases of sinking and resuspension. PAGANO and SAINT-JEAN (1988) have described diet patterns in the chlorophyll concentration, assumed to be linked to tides (estuarine part of the lagoon) or to winds (western part). However, little is known about the biological effects of this phenomenon especially with respect to the planktonic communities, mainly because the understanding of this high frequency alternation requires a multidisciplinary approach and intensive short-term surveys. The aim of the present study, based on an hourly sampling strategy, was to describe and explain variations of seston characteristics associated with wind-induced resuspension in the course of tidal cycles. The importance of these phenomena for the functioning of the ecosystem and for the availability of potential food sources to the pelagic food web is also discussed.

**MATERIALS AND METHODS**

The study was carried out during the local dry season (a period of reduced freshwater inflow) at a station located off the north shore of the Ebrié lagoon, 40 km west of the canal of Vridi (only permanent link with the Atlantic ocean; see Fig. 1). Wind direction was recorded each hour at the station: wind velocity was measured using a cup anemometer (values integrated each minute, averaged over 5 min.). The water level was recorded every minute using a surface elevation gauge (details in ARFI et al., 1993). From a sampling station (-400 m offshore, 1 m depth), lagoon water was collected hourly, on 12 January 1993 from...
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8 h to 4 h the day after, just below the surface and at 0.9 m deep using a peristaltic pump. Conductivity was measured with a Tacussel conductimeter. Turbidity was measured as NTU on a HE9 turbidimeter. Particle size distributions were assessed using a Coulter Multisizer II equipped with a 70 μm orifice tube (Equivalent Spherical Diameter, ESD, ranging from 1.4 to 42 μm). Water for particulate organic carbon (POC) was filtered using pre-combusted Whatman GF/F filters; after acidification, the material was analyzed using a Leco CHN-analyzer. Bacterial numbers (free-living and attached cells, separated on 3 μm Nuclepore membranes) were determined by epifluorescence microscopy after staining with the fluorochrome DAPI (PORTER and FEIG, 1980). Mean bacterial volumes were estimated by measurements of cells (up to 100) using photographic slides and a digitizing tablet; carbon biomass was obtained using a conversion factor of 0.2 pg C μm⁻³ (SIMON and AZAM, 1989). Samples for determination of chlorophyll concentrations were also divided in two fractions after filtration on 3 μm Nuclepore membranes. Chlorophyll of algae <3 μm was considered as picophytoplankton, and the difference to the total chlorophyll biomass was considered as nanophytoplankton. Pigment concentrations were measured after methanol extraction using a Turner Designs fluorometer. Conversion into carbon units was done using a carbon-chlorophyll ratio calculated from previous studies. Algal cells and ciliates were identified and counted in Lugol fixed samples (Utermöhl method). Ciliate carbon biomass was obtained from biovolumes by applying a conversion factor of 0.12 pg C μm⁻³ (TURLEY et al., 1986). Sediment traps (PVC cylinders, diameter 8 cm, length 18 cm) filled with 0.45 μm filtered water and placed on the bed were deployed five times for 4 h during the study in order to quantify seston deposition. Weights of sedimented particles were obtained by filtration on GF/F filters.

RESULTS

The survey was conducted over two consecutive tidal cycles during a neap tide with a tidal amplitude close to 8 cm. The low water slack occurred from 15 to 17 h, whereas the high water slack occurred twice from 9 to 11 h and from 22 h to midnight (Fig. 2). Although conductivity was higher near the bottom (average 12.75 ± 0.73 mS cm⁻¹) than those noted near the surface (12.44 ± 0.53 mS cm⁻¹), the difference between the two means is not significant (Kruskal-Wallis non parametric test). Thus, in terms of conductivity, the water column was considered to be unstratified over the whole tidal cycle. At the sampling site, the minimum wave height (4 to 6 cm from an arbitrary zero) sufficient to induce sediment resuspension was observed between 14 and 18 h (Fig. 2), with a maximum around 17 h.

The highest sedimentation rate (6.4 g m⁻² h⁻¹) was recorded between 8 and 12 h. This period of sedimentation was followed by a period characterized by a lower quantity of sedimented material (3.2 g m⁻² h⁻¹ between 12 and 16 h). Thereafter, the sedimentation rate increased again to 5.0 g m⁻² h⁻¹ between 16 and 20 h. The two following periods (20-24 h and 0-4 h) were once again characterized by low sedimentation rates (3.9 g m⁻² h⁻¹ and 2.2 g m⁻² h⁻¹, respectively).

On the basis of the tides, wind and sedimentation rates, four different hydrodynamic situations were distinguished. First: a flat water period with intense sedimentation (8-14 h). Second: a slack low water period characterized by wind-induced waves and resuspension (14-18 h). Third: a period of weak and irregular winds, in which wave heights decreased rapidly and sedimentation predominated (18-22 h). Fourth: a period also featuring weak and irregular winds at the onset of the flood tide, characterized by very low sedimentation rates (22-4 h).
Large variations in the total particle volume were noted both at the surface and near the bottom (Fig. 3), although the size distribution of particles remained similar throughout the study period, with a single mode centered around 4 μm. During the first period, marked differences in the total volume were observed between the two levels, reflecting the high sedimentation rate (Table 1). From 15-18 h, the difference in total particle volume between the two levels was considerably lower, so the water column was homogeneous. When the wave height increased, resuspension initially affected the finest particles (ESD <3.2 μm) only, these being redistributed through the water column. The larger particles were still sinking at this stage (Fig. 4). The resuspension threshold for these large particles was reached at 17 h when the wind speed exceeded 3 m s⁻¹. At this stage, particles of ESD >3.2 μm were distributed over the whole water column. In spite of the subsequent decrease in wind speed, the abundance of large particles near the surface increased in number until 19 h and near the bottom until 20 h. Thereafter, a sharp decrease in number as well as in total volume followed until the end of the survey (Figs. 3 and 4). No difference in the particle abundance was observed between the two levels from 21 h onwards, confirming that the tidal cycle was characterized by an essentially homogeneous water column. In the surface layer, turbidity and total POC followed the same trend as the variations in total particle abundance (Table 1). Among the POC, five components were distinguished (organic detritus, bacteria, picophytoplankton, nanophytoplankton and ciliates), their average contributions being expressed in terms of carbon biomass (Table 2). Cumulatively, the living organic components represented on average 26% and 29% of the POC in the surface and the bottom levels, respectively.

The organic detritus represented the largest part of the POC (Fig. 5). A marked increase was observed at the two levels from 15 h. It reached a maximum at around 18 h, whereafter the concentrations decreased. Near the surface, a second peak was observed between 21 h and 1 h.

The bacterial biomass remained fairly constant throughout the survey (Fig. 5), with average values close to 3% and 4% of the POC at the surface and the bottom levels, respectively. Free-living bacteria represented 78% of the total bacterial number, whereas attached bacteria represented at the most 34% of the bacterial biomass during the wind-induced resuspension event.

Two peaks of algal biomass were observed at the two levels: the first one was linked to the resuspension event (maximum at 17-18 h), the second one was observed during the lateral water movement associated with the second tide. Picophytoplankton (essentially represented by Synechococcus sp., spherical cells of 2 μm diameter often associated by pairs) and nanophytoplankton (dominated by large motile cells like Cryptomonas sp. and Gymnodinium sp.) contributed equally to the first peak, whereas Synechococcus sp. dominated the phytoplanktonic community during the second tidal event. Other euryhaline and opportunistic species were also observed, such as diatoms (Melosira numuloides. Cyclotella spp.,

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Table 1. Average values of particle volume, particulate organic carbon (POC) and turbidity (Turb) for four periods during the study.

<table>
<thead>
<tr>
<th>Period</th>
<th>Level</th>
<th>Particles</th>
<th>POC</th>
<th>Turb</th>
</tr>
</thead>
<tbody>
<tr>
<td>h</td>
<td>µm³·m⁻¹</td>
<td>mg C·l⁻¹</td>
<td>NTU</td>
<td></td>
</tr>
<tr>
<td>8-14</td>
<td>Surface</td>
<td>10.6 x 10⁶</td>
<td>1.66</td>
<td>7.2</td>
</tr>
<tr>
<td></td>
<td>Bottom</td>
<td>14.6 x 10⁶</td>
<td>2.03</td>
<td>9.1</td>
</tr>
<tr>
<td>15-18</td>
<td>Surface</td>
<td>13.2 x 10⁶</td>
<td>2.37</td>
<td>8.7</td>
</tr>
<tr>
<td></td>
<td>Bottom</td>
<td>13.3 x 10⁶</td>
<td>2.44</td>
<td>9.1</td>
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<td>19-21</td>
<td>Surface</td>
<td>11.9 x 10⁶</td>
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<td>8.0</td>
</tr>
<tr>
<td></td>
<td>Bottom</td>
<td>14.7 x 10⁶</td>
<td>2.04</td>
<td>8.8</td>
</tr>
<tr>
<td>22-4</td>
<td>Surface</td>
<td>12.3 x 10⁶</td>
<td>2.21</td>
<td>8.4</td>
</tr>
<tr>
<td></td>
<td>Bottom</td>
<td>12.2 x 10⁶</td>
<td>2.09</td>
<td>8.4</td>
</tr>
</tbody>
</table>
Fig. 4. Hourly variations of abundance of four particle size classes: 1.6-3.2 μm ESD (a), 3.2-6.4 μm ESD (b), 6.4-12.8 μm ESD (c) and 12.8-25.6 μm ESD (d) at surface and bottom. Results expressed as percentage of total particle abundance.
DISCUSSION

In the Ebrie lagoon, lateral water movements are mainly related to tidal currents (Guiral, 1992). Due to the low average wind velocity (annual mean: 2 m s⁻¹), currents induced by winds are only observed in the superficial water layer. Tides and winds are characterized by the same kind of periodicity (diurnal and semi-diurnal events), but they are not always in phase. Both phenomena contribute to the spatial heterogeneity and to the physical instability of the water body, which are among the characteristics of the Ebrie lagoon (Guiral, 1992). At the sampling station, the tidal amplitude is rapidly attenuated and the currents are low, although still perceptible (less than 3 cm s⁻¹, Arefi et al., 1993). Without wind effect (after 21 h during the second tide), neither vertical conductivity and turbidity gradients nor difference in particles abundance and size distribution were observed between the two levels, indicating the existence of an homogeneous water column. This observation has been also reported by Begley et al. (1992) in a coastal lagoon in New Jersey which demonstrated that variations of seston characteristics are progressive at time of lateral water movement over a tidal cycle. Thus the seston characteristics in this part of Ebrie lagoon are mainly controlled by tides.

In our sampling site, conditions of fetch, depth, wind speed, wave height and bed roughness are sufficient to create resuspension (Arefi et al., 1993). In a general context of low water movements, the daily alternation between periods of resuspension and periods of sedimentation can induce large modifications to the particle concentrations. Sudden resuspension brings particles from the sediment into the water column. When the wind-induced turbulence reaches the water-sediment interface, the finer particles are the first to be affected by resuspension. When the wind speed increases, also larger

| Table 2: Average concentration (mg C l⁻¹ with standard deviation in parentheses) and contribution (%) of five components to the total POC over all observations (n = 21). |
|---------------------------------|----------------|----------------|----------------|
|                                | SURFACE        | BOTTOM         |                |
|                                | Mean (SD)      | Mean (SD)      |                |
|                                | %              | %              |                |
| POC                            | 2.04 (0.34)    | 2.13 (0.25)    | 100.0          |
| Bacteria                       | 0.06 (0.02)    | 0.08 (0.01)    | 3.8            |
| Picoplankton                   | 0.25 (0.09)    | 0.30 (0.06)    | 12.2           |
| Nanoplankton                   | 0.15 (0.09)    | 0.24 (0.11)    | 7.3            |
| Ciliates                        | 0.06 (0.02)    | 0.09 (0.04)    | 3.9            |
| Detritus                       | 1.50 (0.23)    | 1.52 (0.21)    | 71.4           |

Ciliates contribution to the POC was low (average close to 4%). Table 2) and their variations followed the same pattern as those of the algal biomass. The ciliate community was dominated by small organisms (around 30 µm), mostly oligotrichs (Strombidium sp. and Halteria sp. represented 70% of the total abundance) and tintinnids (Tintinnopsis sp.). No significant variations in abundance between these species were noted over the study.
particles become dispersed through the whole water column. During such wind events, the phytoplankton biomass showed a threefold increase. The proportions of attached bacteria represented toplankton biomass showed a threefold increase. the wind event. By the periodical input of nutrients and particles from the sediment in the water column, this phenomenon can be an important mechanism controlling bacterial and algal dynamics in shallow aquatic environments (WAINRIGHT, 1990).

In accordance with the estuarine situation at the study site and the origin of the water, periodic hydrodynamic processes associated with the tides are the major obvious factor controlling the quantitative and qualitative changes in seston. The water renewal induced by the tides was characterized by picoalgae (*Synechococcus* sp.) and ciliate oligotrichs which can take their food in the size range of picoplankton (WEISE, 1988). The pelagic ecosystem thus seemed to develop the microbial loop as the major food-chain. In contrast, at times of wind-induced resuspension, large algal cells were resuspended and distributed over the whole water column as long as the hydrodynamic process was intense. The temporary dominance of larger organisms in the pelagic system can therefore create a direct link to the secondary production in the classical grazer food-chain, as already suggested by KIEßROE and NIELSEN (1990). The filter feeding organisms observed in our study site (essentially rotifers and copepods, PAGANO and SAINT JEAN, 1988) are highly efficient in removing large particles. In this area of the Ebrié lagoon, previous studies have demonstrated the upward nocturnal migration of the predominant species *Acartia clausi* (e.g. TORRETON et al., 1994), a phenomenon beginning at 18 h and coinciding with the maximum egestion of fecal pellets (PAGANO and SAINT JEAN, 1988). During the present study, these organisms showed maximum gut contents at the end of the resuspension period (unpublished data). Thus, in these shallow areas of the Ebrié lagoon, wind-induced hydrodynamic processes may influence the feeding behavior of zooplankton and can temporarily become the major factor determining the structure of the pelagic food web.

REFERENCES


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