# Response of biota to sedimentary organic matter quality of the West Gironde mud patch, Bay of Biscay (France)

Benthos
Electron-transport-System (ETS)
Meiofauna
POC quality
Organic matter

Benthos
Systèmes transporteurs d'électrons (ETS)
Méiofaune
Qualité du COP
Matière organique

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ABSTRACT

Relationships between benthos and sedimentary organic matter quality were analyzed in the West Gironde Mud Patch (WGMP), on the shelf of the Bay of Biscay, off the Gironde estuary, as part of the multidisciplinary national programme Ecomarge, a JGOFS-France contribution. At three stations located on an east-west transect and at different periods from 1985 to 1988, the following parameters of the sediment were analyzed: POC (particulate organic carbon); $\Sigma$ (sum of easily extractable macromolecules thought to be the most degradable part of particulate organic matter); pigments as indices of organic matter quality; ETS (electron-transport-system) activities and meiofauna densities as indices of benthic responses. Sediments from the WGMP have an overall low organic carbon content (0.8 %) ; the labile organic fraction ($\Sigma$) does not exceed 10 % of the total sedimentary POM (particulate organic matter). Nevertheless, the supply of freshly-formed matter was marked both by pigment and $\Sigma$ increases, especially westwards.

ETS activity was significantly linked to POC, $\Sigma$ and chlorophyll *a*. The ETS: POC ratio was lower than in neighbouring coastal areas (*i. e.* the Gironde estuary and Arcachon Bay) but ETS: $\Sigma$ was of the same magnitude in the three zones, reaching values close to ETS: $\Sigma$ ratios found in live bacteria. It was concluded that $\Sigma$ could mainly be composed of biomass itself; the detrital part of $\Sigma$, thought to be rapidly incorporated into living material, would not accumulate.

The distribution of meiofauna abundances did not follow the same gradients as pigments, ETS and $\Sigma$, and presumably depended on environmental factors other than those analyzed here.

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RÉSUMÉ

Réponse de la biota à la qualité de la matière organique sédimentaire de la vasière Ouest-Gironde, golfe de Gascogne (France)

Les relations entre le benthos et la qualité de la matière organique sédimentaire ont été analysées sur la vasière Ouest-Gironde (VOG), située sur le plateau continental du golfe de Gascogne, au large de l'estuaire de la Gironde, dans le cadre du programme national de recherche Écomarge, contribution de JGOFS-France. En trois stations situées sur un transect Est-Ouest et à différentes périodes de 1985 à 1988, les paramètres suivants du sédiment ont été analysés : COP (carbone organique particulaire) ; Σ (somme des macromolécules facilement extractibles supposées être la part la plus dégradable de la matière organique particulaire) ; pigments en tant qu'indices de qualité de la matière organique ; activités ETS (Electron Transport System) et densités de méiofaune en tant qu'indices de la réponse benthique.

Les sédiments de la VOG ont une teneur en carbone organique globalement faible (0,8 %) ; la fraction organique labile (Σ) n'excède pas 10 % de la matière organique sédimentaire totale. Néanmoins, l'apport de matériel frais est marqué par des pics de pigments et de Σ, notamment vers l'ouest. L'activité ETS est liée de façon significative aux paramètres COP et chlorophylle *a*. Le rapport ETS/COP est plus bas que dans la zone côtière environnante (c'est-à-dire l'estuaire de la Gironde et le bassin d'Arcachon), mais ETS/Σ est du même ordre de grandeur dans les trois zones, atteignant des valeurs proches de celles trouvées dans la matière bactérienne vivante. Il est conclu que Σ proviendrait principalement de la biomasse elle-même ; la part détritique de Σ étant rapidement incorporée dans le matériel vivant ne s'accumulerait pas.

La distribution de l'abondance de la méiofaune ne présente pas les mêmes gradients que les pigments, ETS et Σ et dépend probablement d'autres facteurs environnementaux que ceux analysés ici.

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## INTRODUCTION

Particulate organic matter which reaches the sediment has different fates depending on its capacity for oxidation and on the prevailing environmental conditions (Henrichs and Reeburgh, 1987 ; Canfield, 1989). Deposited organic particles (when they do not return to the general cycle in the water column as the result hydrodynamic events or through the food webs of epibenthic organisms) can be either consumed by the benthos or buried in the sediment. In the former case, they undergo rather fast transformations, being mineralized and/or incorporated into the benthic biomass; while in the latter their changes may be extremely slow. The transformation of organic molecules in the upper layers of sediment (early diagenesis) which depends on benthic biological activities, plays the main role in recycling carbon and nutrients. Knowledge of carbon quality, *i. e.* its availability for the benthos, is thus the key to understanding the importance of sediment in aquatic ecosystems (Rice and Rhods, 1989). Contrary to what might be expected, clear positive correlations between degradability of sedimentary carbon and benthic responses are not easy to prove because of: a) the difficulty in defining and measuring the degradable (available) part of organic matter; and b) the choice of criteria for benthic response.

Carbon degradability can be studied in several ways: by considering the nutritional value of particles in laboratory experiments (Cammen, 1980; Williams, 1981; Rice *et al.*, 1986); by studying relations between the biochemical composition of organic matter and benthos distribution (Laane *et al.*, 1987); by following decomposition rates of organic matter in microcosms (Henrichs and Doyle, 1986; Lin, 1988); or by evaluating the amount of degradable matter through the carbon gradients below the sediment surface (Reimers and Suess, 1983; Emerson *et al.*, 1985; Silverberg *et al.*, 1985; Wilson *et al.*, 1985). Numerous analytical methods have been applied to suspended particles and sediments in order to quantify the degradable fraction, which may be the acid-labile fraction (Gadel, 1980; Tenore, 1981) or the easily extractable macromolecular fraction, i.e. proteins, carbohydrates, lipids, *etc.* (Widdows *et al.*, 1979; Héral and Deslous-Paoli, 1983; Khripounoff and Rowe, 1985; Laane *et al.*, 1987; Mayer *et al.*, 1988; Mayer, 1989). We considered the analysis of macromolecular content (biopolymers) to be the most suitable method to assess the easily degradable part of sedimentary organic matter (Berner, 1980).

Concerning the benthic response, extensive research shows major decreases of benthic biomass and activities from coastal areas to deep-sea zones, related to decrease in organic matter supply (Sorokin, 1978; Smith, 1978; Dinet and Khripounoff, 1980; Jorgensen, 1983; Jahnke and Jackson, 1987). One of the reasons for these results is probably the large decrease in carbon richness from coastal to abyssal regions. We also found good correlations between benthic biomass and sedimentary carbon content in strongly marked gradient areas of tidal flats (Relexans *et al.*,1992).

Among the tools for quantifying total benthic metabolic activities, measurement of Electron-Transport-System (ETS) activity has often been used as an index of overall metabolism (Packard, 1971). The method first applied to plankton was later used for sediment (Wieser and Zech, 1976; Olanczuck-Neyman and Vosjan, 1977; Jones and Simon, 1979; Pamatmat *et al.*, 1981; Christensen, 1983;

Pfannkuche *et al.*, 1983; Broberg, 1985; de Wilde *et al.*, 1986). As ETS activity is measured in conditions of $V_{max}$ (with excess of electron donors NADH, NADPH and of electron acceptor, INT) it represents the respiratory potential of the benthic communities and its value by far exceeds the actual metabolism rates (Houri-Davignon *et al.*, 1989). Therefore, ETS may be considered as an index of biomass (Packard *et al.*, 1983; Brugeaille *et al.*, 1987; Brugeaille, 1988; Relexans *et al.*, 1988).

Investigation of the relationships between particulate carbon quality and the biological response, which is the goal of the present study, is included in the French national programme Ecomarge, a part of the French contribution to JGOFS. ETS activity is mainly linked to microorganisms (which have, in principle, fast turnover rates of biomass): consequently, such activity should be sensitive to the shifts in carbon quality. In the same way, meiofauna with high P:B ratios should be a good indicator of the food supply. Therefore, ETS activity and meiofauna analysis were chosen in the present study to characterize the benthic response, while biomacromolecular content (proteins, soluble carbohydrates, total lipids and pigments) was used to identify carbon quality. The study was carried out in a mud patch of the Bay of Biscay, off the Gironde estuary, which is an intermediate deposition area for the particles circulating from the continent to the slope and the deep-sea areas.

## MATERIAL AND METHODS

### Study area

The West Gironde Mud Patch (WGMP) is a well defined clay-silt sedimentary zone surrounded by sandy gravel formations. It is 420 km$^{-2}$ wide, from 30 m to 75 m deep and oriented NE-SW, and is situated 25 km off the mouth of the Gironde estuary (Fig. 1). It traps about 50 % of the suspended matter originating from the estuary and a deposition rate of 30 cm to 40 cm.century$^{-1}$ has been calculated

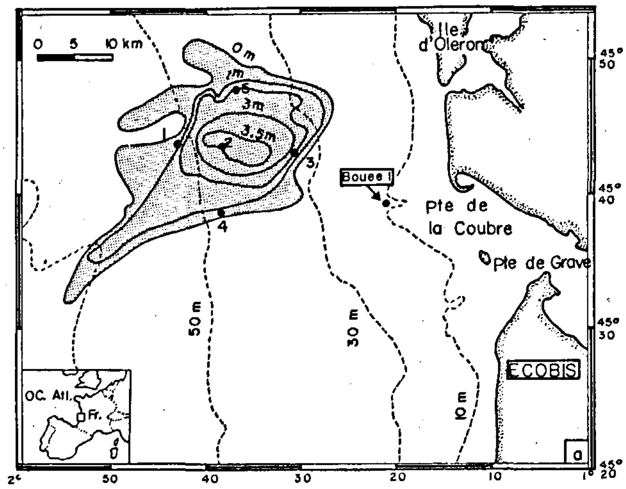


Figure 1

*Map of sampling stations and isopatches of mud deposit (Ecobis campaigns).*

(Lesueur *et al.*, 1989). According to Jouanneau *et al.* (1989), the westward oceanic side is characterized by constant fine sedimentation while, in the inner part, there are seasonal sedimentary deposits originating from the Gironde (transient sedimentation).

### Sampling and analysis

The sampling area was surveyed at three stations on an east-west transect (Fig. 1): a western (1), central (2) and eastern (3) station at three different depths (60, 45 and 30 m), during ten campaigns at different times of year, from May 1985 to November 1988 (Tab. 1).

Sediments, sampled with a Reineck box corer, were analyzed for POC, protein, carbohydrate and lipid content, ETS activity and meiofauna; pigment analysis was added to the six 1988 campaigns. All these analyses were routinely made on the 0-1 cm section of a single box core; at some sampling dates (March, June and September 1988) cores

Table 1

*Contents of POC, Σ (sum of proteins, carbohydrates and lipids) Σ:POM (Particulate Organic Matter calculated as POC x 2) and pigments in the first centimetre of sediment.*

| STATIONS | EAST | | | | | CENTRE | | | | | WEST | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CRUISES | POC mg/g$^{-1}$ | Σ mg.g$^{-1}$ | Σ/POM % | Pigm. μg.g$^{-1}$ | Chl *a* μg.g$^{-1}$ | POC mg.g$^{-1}$ | Σ mg.g$^{-1}$ | Σ/POM % | Pigm. μg.g$^{-1}$ | Chl *a* μg.g$^{-1}$ | POC mg.g$^{-1}$ | Σ mg.g$^{-1}$ | Σ/POM % | Pigm. μg.g$^{-1}$ | Chl *a* μg.g$^{-1}$ |
| **May 1985** | 9.0 | | | | | 8.0 | | | | | 9.3 | | | | |
| **April 1987** | 4.7 | 0.970 | 10.3 | | | 8.2 | 1.305 | 8.0 | | | | | | | |
| **June** | 3.9 | 0.900 | 11.5 | | | 7.4 | 1.455 | 9.8 | | | 9.5 | 1.345 | 7.1 | | |
| **September** | 3.2 | 0.840 | 13.1 | | | 7.0 | 1.190 | 8.5 | 10.99 | 0.33 | 7.8 | 1.230 | 7.9 | | |
| **March 1988** | 5.1 | 1.440 | 14.1 | 9.48 | 0.47 | 6.3 | 1.445 | 11.5 | 9.27 | 0.56 | 8.3 | 1.900 | 11.4 | 12.56 | 1.13 |
| **May** | 5.2 | 1.140 | 11.0 | 9.30 | 1.30 | 8.5 | 1.525 | 9.0 | 15.39 | 1.69 | 12.2 | 1.935 | 7.9 | 19.11 | 2.87 |
| **June** | 10.1 | 1.655 | 8.2 | 13.15 | 1.18 | 11.6 | 1.920 | 8.3 | 20.38 | 2.85 | 10.0 | 1.810 | 9.1 | 16.86 | 1.69 |
| **July** | 5.7 | 1.185 | 10.4 | 13.07 | 1.57 | 8.0 | 1.250 | 7.8 | 12.39 | 1.12 | 10.8 | 1.655 | 7.7 | 14.37 | 1.29 |
| **September** | 6.6 | 1.245 | 9.4 | 10.91 | 0.76 | 6.9 | 1.380 | 10.0 | 10.40 | 0.73 | 9.1 | 1.950 | 10.7 | 17.32 | 1.91 |
| **November** | 12.9 | 1.625 | 6.3 | 15.85 | 0.79 | 8.3 | 1.325 | 8.0 | 11.66 | 0.33 | 9.6 | 1.565 | 8.1 | 11.63 | 0.58 |
| **MEAN** | 6.6 | 1.220 | 10.5 | | 1.01 | 8.0 | 1.420 | 9.0 | | 1.09 | 9.6 | 1.675 | 8.7 | | 1.58 |
| **± 95 % CI** | ± 2.2 | ± 0.230 | ± 1.8 | | ± 0.4 | ± 1.0 | ± 0.165 | ± 0.9 | | ± 0.8 | ± 0.9 | ± 0.230 | ± 1.3 | | ± 0.80 |

were sliced at different levels (0-1 cm, 1-5 cm, 5-10 cm, > 10 cm) to estimate stratification. In addition, during the six 1988 cruises, carbon content was also measured in the 0-1 mm surface layer.

The analysis of POC content and quality was made on homogenized sediment previously dried in an oven at 50°C. POC was oxidized with $H_2SO_4$-$Cr_2O_7K_2$ and the excess oxidant titrated with Mohr's salt, according to Strickland and Parsons' (1972) method; glucose was used as reference. Protein was analyzed in a NaOH extract (0.1 N, 2 hrs, 50°C: Daumas *et al.*, 1974) according to Bradford's protocol (1976) improved by Setchell's (1981); ovalbumine was the reference. Carbohydrates were measured on aqueous extracts (10 min. at 100°C) based on the procedure of Dubois *et al.* (1956) improved by Montreuil and Spik (1963) with glucose as reference. Lipid content was determined in methanol-chloroform extracts (Bligh and Dyer, 1959), weighing the dry residue after complete evaporation of the solvent.

Pigments from freeze-dried sediment samples were measured by fluorometry on acetone 90 % extracts before and after acidification (Lorenzen, 1967).

ETS activity was measured in samples stored in liquid nitrogen, with Owens and King's protocol (1975) using a Sonimasse sonifier (Christensen and Packard, 1977; 1979; Relexans and Etcheber, 1985) as a homogenizer. Three or four successive extractions were needed to give an almost-complete extraction of respiratory enzymes. The trial was routinely conducted at 20°C and from 4-25°C to calculate Ea (Apparent Activation Energy) using the Arrhenius equation. The results are expressed in µl oxygen-equivalent.$h^{-1}$, at 20°C. In samples collected in 1988, chemical reduction of INT was measured in supernatants left 2-4 days at 0-4°C in the dark, in order to destroy enzymatic activity, without modifying the chemical characteristics of the reductor substances in supernatants. Results presented here express total ETS activity (chemical and biochemical). When measured, chemical ETS activity did not exceed 20 % of the total and did not vary between samples. Hence, trends described in the following paragraghs are not corrected.

Three replicate cores (2.8 cm diameter, x 10-12 cm) were taken from the Reineck box for meiofauna extraction. Samples were preserved in 5 % formalin and stained with Rose-Bengal. In the laboratory, they were washed through a 1-mm mesh and collected on a 63 µm sieve. The fauna was then extracted from the remaining sediment by flotation in Ludox HS 40 (de Jonge and Bouwman, 1977).

All data means are given with a 95 % confidence interval. As the hypothesis of a normal distribution was not confirmed for most of the parameters, we used the non-parametric Kruskall-Wallis one-way analysis of variance rather than the parametric ANOVA analysis to test the differences between sites. Spearman's rank correlation coefficients were used for the same reason.

RESULTS

## Surface POC content and quality

Results are shown in Table 1 for the uppermost centimetre, *i. e.* in the layer expected to be the most responsive to the shifts in environmental conditions.

In short, POC content, varying from 0.32 to 1.29 % of dry sediment, was low: the mean value, 0.80 % ± 0.09, was much lower than the POC content of the high turbidity zone from the Gironde estuary (1.5 %; Etcheber, 1986). Organic carbon content of sediments increased significantly from 6.6 mg $g^{-1}$ to 9.6 mg $g^{-1}$ from the eastern station to the western one (Kruskall-Wallis analysis of variance: $H = 8.37, P = 0.015$). No clear seasonal variation was observed except at the western station, where the highest content was noted during the summer campaign (Tab. 1).

The sum $\Sigma$ (proteins + carbohydrates + lipids), assumed to be the most labile fraction of the sedimentary organic matter, also showed a significant increase from east to west with mean concentrations of 1.22, 1.42 and 1.68 mg $g^{-1}$ at the eastern, central and western stations respectively ($H = 8.27, P = 0.016$). The ratio $\Sigma$:POM (particulate organic matter # 2 * POC) rarely exceeded 10 %, with an average value of 9.4 % ± 0.8. No clear seasonal variation of this parameter was apparent. Even if a slight decrease of the importance of the labile organic fraction was observed in the 0-1 cm layer from the eastern station to the western one, this trend remained non-significant ($H = 4.75, P = 0.114$).

Pigments measured in sediment were mainly phaeopigments (chlorophyll *a* was always less than 15 % of the total pigment content); they are thought to originate from the water column (from marine and/or estuarine plankton) rather than from the phytobenthos. Whatever its origin, the presence of chlorophyll *a* is an indication of freshly-photosynthesized matter. Annual averages of total pigments and

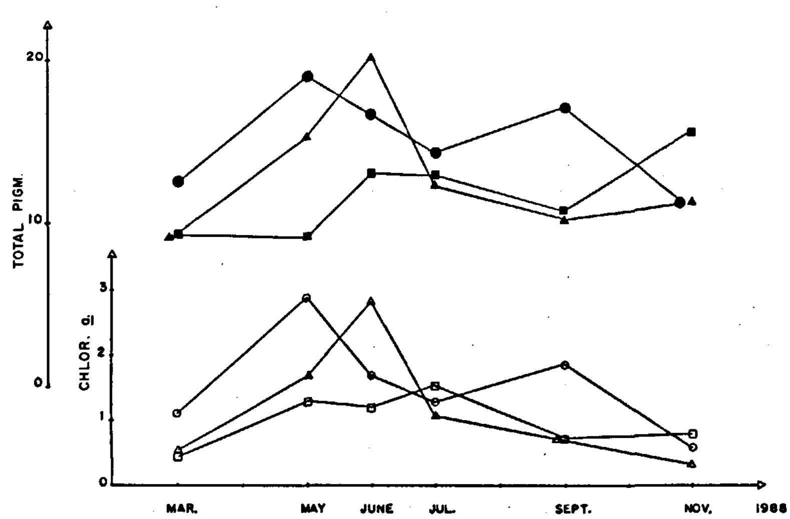


Figure 2

*Concentrations of total pigments and chlorophyll* a *(µg.$g^{-1}$ of dry sediment) in the upper first centimetre of sediment during 1988. Squares (Ů): eastern stations; triangles (Δ): centre; circles (o): western stations.*

chlorophyll *a* content showed a slight non-significant gradient (H = 3.44, p = 0.179 and H = 2.83, p = 0.242 respectively) increasing from east to west. Both total pigments and chlorophyll *a* exhibit "seasonal" variations (based on 1988 data only) with the highest values during the summer campaigns (Fig. 2, Tab. 1).

### Surface ETS activity measurements

At each station, large variations were found depending on the different campaigns (Fig. 2): ETS activity might differ from two to four times in the eastern, central and western areas respectively. A clear increase was observed from east to west (H = 9.28, p = 0.0096) by comparing the averages in the three areas. The differences were especially notable during summer periods (Fig. 3): seasonal variations of ETS activity were clearly exhibited in the western station but were not as distinct in the central one and non-apparent in the eastern one.

Apparent Activation Energy (Ea) was calculated from incubation experiments at various temperatures. We found an average value of 7.200 (± 720) cal.mole$^{-1}$; for each area the values were 6.916 (± 1.343; n = 6), 7.312 (± 1.853; n = 6) and 7.368 (± 1.564; n = 6) cal.mole$^{-1}$ respectively, from the eastern to the western side.

The EST:POC and ETS:Σ ratios for September 1987 at the eastern station strongly differed from the general pattern distribution for all the other values; we considered this ETS value as questionable and excluded it from the calculations (Tab. 2). With this restriction, ETS:POC (Fig. 3) and ETS:Σ generally showed the highest values from May to September; moreover, the ratios were slightly higher in the western area than in the other ones.

### Meiofauna abundance

Meiofaunal abundances, from counts made on the entire core, are seen in Table 3. Meiobenthic organisms live in a three-dimensional environment and the fluctuations of surface abundance are to a great extent the result of the active and passive movements of the meiofauna, both vertically and horizontally (Arlt, 1988). The total sediment content (0-10-12 cm) is, therefore, considered as representative of meiofaunal density under a definite surface area.

Meiofauna displayed great temporal variations (Fig. 4). However, the geographical distribution of the abundances mostly showed a decreasing gradient from the eastern station (1,728 ind/10 cm$^2$) to the western station (1,288 ind/10 cm$^2$), the difference not being statistically significant (H = 0.492, p = 0.782). This distribution differs completely from the patterns previously seen for POC, Σ, ETS activity and pigments.

The highest abundances were recorded in June-July, but also in November 1988 (Fig. 4). Strong variations may be observed at the same periods of different years (compare May 1985 and May 1988, June 1987 and June 1988, September 1987 and September 1988); these could not be explained by temperature variations. Throughout the year, the strongest variations were observed in the richest sta-

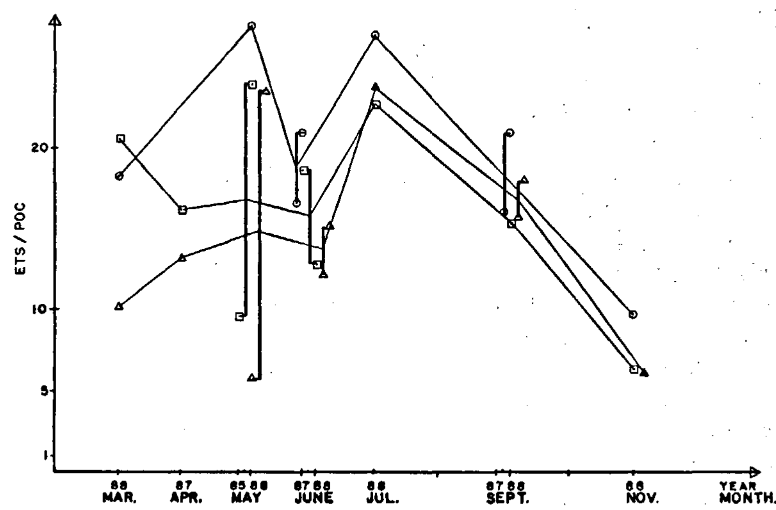


Figure 3

*Seasonal variations of ETS activity (µl02 h$^{-1}$) per mg POC in the first centimetre of sediment. Same legend as Figure 2.*

Table 2

*ETS activity (µl$O_2$.g$^{-1}$ at 20° C), ETS:POC and ETS:Σ ratios in the first centimetre of sediment. * questionable values excluded from calculations.*

| Stations | East | | | Centre | | | West | | |
|---|---|---|---|---|---|---|---|---|---|
| Cruises | ETS activity | ETS/POC | ETS/Σ | ETS activity | ETS/POC | ETS/Σ | ETS activity | ETS/POC | ETS/Σ |
| **May 1985** | 86 | 9.6 | | 46.0 | 5.75 | | | | |
| **April 1987** | 76 | 16.2 | 78.0 | 108.0 | 13.2 | 83.0 | | | |
| **June** | 73 | 18.7 | 81.0 | 113.0 | 15.3 | 78.0 | 214.0 | 22.5 | 159.0 |
| **September** | 150* | 46.9* | 179.0* | 126.0 | 18.0 | 106.0 | 164.0 | 21.0 | 133.0 |
| **March 1988** | 105 | 20.6 | 73.0 | 65.0 | 10.3 | 45.0 | 152.0 | 18.3 | 80.0 |
| **May** | 125 | 24.0 | 110.0 | 202.0 | 23.8 | 132.0 | 325.0 | 26.5 | 168.0 |
| **June** | 130 | 12.9 | 79.0 | 142.0 | 12.2 | 74.0 | 165.0 | 16.5 | 91.0 |
| **July** | 130 | 22.8 | 110.0 | 190.0 | 23.75 | 152.0 | 293.0 | 27.1 | 177.0 |
| **September** | 102 | 15.5 | 82.0 | 108.0 | 15.65 | 78.0 | 145.0 | 15.9 | 74.0 |
| **November** | 83 | 6.4 | 51.0 | 51.0 | 6.15 | 38.0 | 95.0 | 9.9 | 61.0 |
| **Mean** | 101 | 16.3 | 83.0 | 115.1 | 14.40 | 87.3 | 194.1 | 19.7 | 117.9 |
| **95 % CI** | ± 18 | ± 4.5 | ± 16.2 | ± 38.0 | ± 4.75 | ± 28.7 | ± 65.6 | ± 5.2 | ± 39.0 |

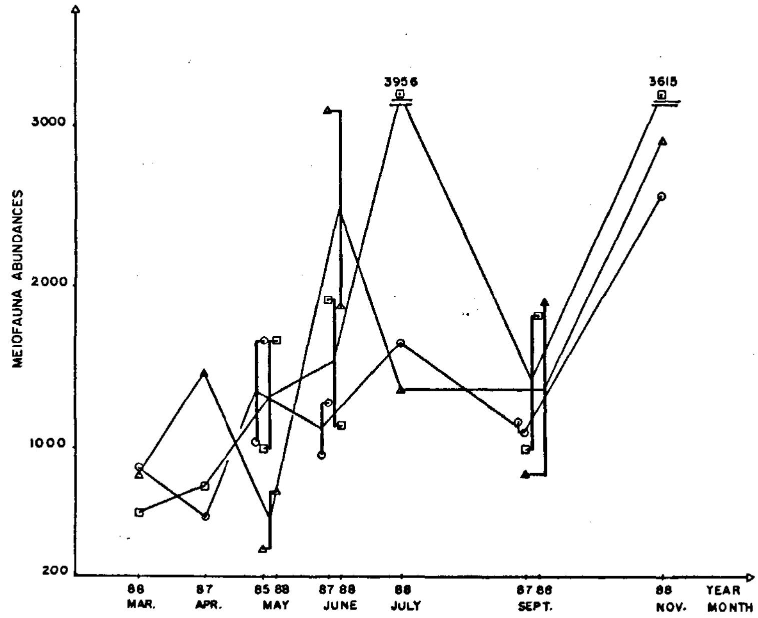


Figure 4

*Seasonal variations of meiofauna abundances in total sediment (number of individuals per 10 cm²). Same legend as Figure 2.*

tions (variation coefficients: 68.6 and 60.0 % for the eastern and central stations respectively), while the poorest station (west) seems to be relatively more stable (variation coefficient: 43.3 %).

In all the samples, nematodes were the dominant phylum, representing more than 80 % of the total density. They were followed in abundance by copepods. Other taxa comprised kinorhynchs, oligochaetes and a number of temporary meiofaunal organisms such as polychaetes and bivalves. The difference in the proportion of the dominant groups was not significant between the sampling stations.

### Vertical gradients below the sediment surface

All parameters were measured at four depths below the surface during three campaigns (Tab. 4). There was no clear gradient for POC nor for Σ:POM within the sediment, at least to the depth we studied (< 15 cm). Nevertheless, comparisons of POC contents in the 0-1 mm and in the 0-1 cm layers during the six 1988 campaigns (Tab. 5) indicated, in most cases, an increase of the organic fraction in the upper surface layer, especially in the eastern station.

Total pigment and chlorophyll *a* contents showed strong enrichment in the uppermost layer, while the poorest layer was the deepest. ETS activity was generally higher in the 0-1 cm than in the 4-5 cm layers; below this depth, the values tended to increase and, in most cases, the highest ETS activity was found beyond 10 cm in depth.

The vertical distribution of meiofauna was studied during the six 1988 campaigns. Examples of distribution are given in Table 4. On average, 92 to 95 % of the organisms were concentrated in the first 5 cm. Practically no individuals were found below 10 cm in depth. The uppermost centimetre contained 28.9 ± 5.9 % of the total meiofauna at the western station, 37.5 ± 13.3 % at the central station and 31.7 ± 11.6 % at the eastern station. This means that meiobenthic organisms are located slightly deeper in the sediment at the western station than at the other ones. The variation of this distribution was also lower at the outer station. Compared to the other taxa, nematodes were found deeper in the sediment, comprising 82 to 88 % of the total meiofauna in the first centimetre, and 93 to 95 % in the 1-5 cm layer.

## DISCUSSION

Quantitative and qualitative investigation of the sedimentary organic matter of the WGMP and of its relation to the benthos allowed us to enumerate certain characteristics of this environment, relating to its ecological functioning.

Table 3

*Abundance of meiofauna in the WGPM (number of individuals.10 cm⁻²). N = nematodes ; C = copepods ; O = other ; T = total. t°C = mean temperature in the superficial sediment.*

| STATIONS | | EAST | | | | CENTRE | | | | WEST | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cruises** | **T°C** | **N** | **C** | **O** | **T** | **N** | **C** | **O** | **T** | **N** | **C** | **O** | **T** |
| **May 1985** | | 886 | 42 | 78 | 1 006 | 315 | 6 | 48 | 369 | 1 444 | 82 | 116 | 1 652 |
| **April 1987** | 10.6 | 650 | 43 | 72 | 765 | 1 267 | 25 | 165 | 1 457 | 333 | 21 | 215 | 569 |
| **June** | 11.5 | 1 591 | 54 | 266 | 1 911 | 2 611 | 144 | 355 | 3 110 | 794 | 45 | 125 | 964 |
| **September** | 15.2 | 699 | 256 | 54 | 1 009 | 686 | 18 | 125 | 829 | 761 | 47 | 287 | 1 095 |
| **March 1988** | 10.0 | 379 | 6 | 12 | 397 | 794 | 2 | 34 | 830 | 784 | 48 | 49 | 881 |
| **May** | 12.7 | 1 531 | 51 | 79 | 1 661 | 661 | 21 | 45 | 727 | 954 | 22 | 63 | 1 039 |
| **June** | 13.0 | 940 | 44 | 149 | 1 133 | 1 578 | 53 | 250 | 1 881 | 1 195 | 8 | 80 | 1 283 |
| **July** | 14.5 | 3 654 | 209 | 93 | 3 956 | 1 292 | 20 | 56 | 1 368 | 1 523 | 53 | 78 | 1 654 |
| **September** | 16.5 | 1 584 | 107 | 31 | 1 822 | 1 739 | 71 | 97 | 1 907 | 1 081 | 31 | 55 | 1 167 |
| **November** | 16.0 | 3 427 | 66 | 122 | 3 615 | 2 577 | 60 | 276 | 2 913 | 2 124 | 140 | 307 | 2 571 |
| **MEAN** | | 1 544 | 88 | 96 | 1 728 | 1 352 | 42 | 145 | 1 539 | 1 099 | 50 | 138 | 1 288 |
| **± 95% C.I.** | | ± 745 | ± 53 | ± 47 | ± 774 | ± 515 | ± 27 | ± 74 | ± 604 | ± 329 | ± 25 | ± 63 | ± 365 |

Table 4

*Variations of the parameters studied deep within the sediment. Same units as in Tables 1, 2 and 3, except for meiofauna expressed as individuals.10 $cm^{-3}$.*

| STATION | DEPTH | EAST | | | | | | CENTRE | | | | | | WEST | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cruises | (cm) | POC | Σ/POM | Pigm. | Chl.a | ETS | Meio. | POC | Σ/POM | Pigm. | Chl.a | ETS | Meio. | POC | Σ/POM | Pigm. | Chl.a | ETS | Meio. |
| March 1988 | 0-1 | 5.1 | 14.1 | 9.48 | 0.47 | 105 | 60 | 6.3 | 11.5 | 9.27 | 0.56 | 65 | 173 | 8.3 | 11.4 | 12.60 | 1.13 | 152 | 272 |
| | 1-5 | 6.3 | 12.8 | 6.80 | 0.00 | 57 | 80 | 7.9 | 9.4 | 7.66 | 0.38 | 103 | 155 | 12.3 | 8.3 | 14.00 | 0.56 | 66 | 146 |
| | 5-10 | 10.8 | 8.6 | 6.62 | 0.33 | 85 | 1 | 8.0 | 7.5 | 5.90 | 0.18 | 90 | 8 | 8.6 | 11.2 | 10.20 | 0.21 | 50 | 5 |
| | > 10 | 8.4 | 9.0 | 5.60 | 0.17 | 93 | | 7.8 | 8.5 | 5.03 | 0.35 | 101 | | 9.9 | 10.3 | 9.07 | 0.36 | 64 | |
| June 1988 | 0-1 | 10.1 | 8.2 | 13.1 | 1.18 | 130 | 377 | 11.6 | 8.3 | 20.4 | 2.85 | 142 | 916 | 10.0 | 9.0 | 16.9 | 1.69 | 165 | 484 |
| | 1-5 | 6.3 | 7.0 | 7.18 | 0.72 | 114 | 164 | 6.6 | 7.4 | 9.56 | 0.77 | 142 | 219 | 9.7 | 7.8 | 12.7 | 0.64 | 196 | 145 |
| | 5-10 | 5.0 | 7.3 | 6.45 | 0.64 | 120 | 1 | 6.8 | 8.2 | 6.22 | 0.37 | 195 | 18 | 11.5 | 6.7 | 8.79 | 0.18 | 250 | 44 |
| | > 10 | 6.8 | 7.8 | 7.69 | 0.69 | 150 | | 7.0 | 7.8 | 5.08 | 0.15 | 170 | 1 | 11.1 | 7.0 | 8.76 | 0.35 | 220 | 1 |
| Sept. 1988 | 0-1 | 6.6 | 9.4 | 10.9 | 0.76 | 102 | 570 | 6.9 | 10.0 | 10.4 | 0.73 | 108 | 592 | 9.1 | 10.7 | 17.3 | 1.91 | 145 | 259 |
| | 1-5 | 3.7 | 9.8 | 4.54 | 0.00 | 52 | 306 | 9.0 | 9.7 | 7.58 | 0.38 | 113 | 270 | 12.4 | 9.5 | 16.6 | 1.00 | 144 | 213 |
| | 5-10 | 7.2 | 6.7 | 6.12 | 0.37 | 108 | 7 | | | 8.10 | 0.41 | 105 | 47 | 10.6 | 10.1 | 8.75 | 0.00 | 160 | 11 |
| | > 10 | 7.1 | 10.1 | 2.23 | 0.36 | 152 | | 8.8 | 7.3 | 5.39 | 0.38 | 90 | | 10.1 | 11.2 | 7.88 | 000 | 120 | |

Table 5

*Comparison of POC content (% dry weight) of 0-1 mm and 0-1 cm layers of sediments during 1988 campaigns.*

| STATIONS | | EAST | CENTRE | WEST |
|---|---|---|---|---|
| Cruises | Level | | POC % | |
| March 1988 | 0-1 mm | 1.48 | 0.78 | |
| | 0-1 cm | 0.51 | 0.63 | 0.83 |
| May | 0-1 mm | 0.71 | 0.90 | |
| | 0-1 cm | 0.52 | 0.85 | 1.22 |
| June | 0-1 mm | 1.05 | 1.03 | 0.96 |
| | 0-1 cm | 1.01 | 1.16 | 1.00 |
| July | 0-1 mm | 0.62 | 0.82 | 1.22 |
| | 0-1 cm | 0.57 | 0.80 | 1.08 |
| September | 0-1 mm | 0.82 | 0.86 | 0.72 |
| | 0-1 cm | 0.66 | 0.69 | 0.91 |
| November | 0-1 mm | 1.38 | 0.78 | 0.90 |
| | 0-1 cm | 1.29 | 0.83 | 0.96 |

## Weakness of seasonal variations

For all the parameters, except the meiofauna, the observed variations remain very moderate most of the time, suggesting that the WGMP is a very "monotonous" area. The case of organic carbon content is representative in this connection: the absence of clear seasonal variation and the low concentrations may be explained by a mixing with terrigeneous particles coming from the Gironde estuary, to which are added some silt, poor in organic carbon, originating on the adjacent shelf, and a minor contribution of marine particles (Jouanneau *et al.*, 1989; Lesueur *et al.*, 1989). Only the chlorophyll *a* content shows pronounced seasonal variations, with higher concentrations during the summer. This fact can be related to the planktonic blooms indentified in the study of organic carbon content of suspended matter in surface waters (Lin, 1988). Nevertheless, the slight east-west gradients observed may be related to the substantial differences in sediment composition since, from east to west, the quantity of fine particles increases and the sandy-silty fraction decreases (Jouanneau *et al.*, 1989).

It is worth adding that sampling of the first centimetre has presumably hidden some variations which would appear more clearly if a finer slice of sediment had been examined. This was shown for POC, when organic carbon content in the first millimetre revealed variations (especially at the eastern station), more pronounced than for the whole first centimetre.

Nevertheless, a fresh supply of organic matter is indicated by slight increases in Σ and chlorophyll *a* content of sediment towards the west; but this supply appears low when compared to the bulk of total sedimentary carbon. Given the deposition rate of suspended matter (about 3 to 4 $mm.year^{-1}$: Lesueur *et al.*, 1989), the fresh carbon supply in the WGMP is difficult to measure with sampling strategies of 1 cm in depth.

## Importance of the turbation processes

The term "turbation" is used here to designate both bioturbation processes (the importance of which was clearly shown by Jouanneau *et al.*, 1989) and influences of hydrodynamic conditions which are particularly important in such an environment. Turbation processes account, at least in part, for the absence of gradient in several centimetres under the surface for most of the measured parameters. In the same way, the presence of traces of chlorophyll *a* at depths of more than 10 cm in the sediment, as well as the distribution of meiofauna, confirm the importance of mixing processes.

The stratification of meiofauna was not strongly pronounced in the present study (29 to 38 % of the fauna in the uppermost centimetre). Generally, in muddy sediments, more than 50 % of the meiofauna are concentrated at this level. Values from 75 to 90 % are not infrequent in sheltered areas (Escaravage *et al.*, 1990). In muddy detrital sediments of South Carolina estuaries, Coull and Bell (1979) found that 94 % of all the fauna was located in the upper 1 cm of sediment. Vertical zonation is typically controlled by the change between aerobic and anaerobic conditions in the sediments. The lack of high concentrations of meiofauna near the sediment surface suggests (oxygen penetration was not measured) that the sediment of the WGMP must be well oxygenated: this can be related to turbation processes.

## Correlations between POC quality, ETS activity and meiofauna

Correlations between all measured parameters were calculated (Tab. 6). ETS activity is significantly linked to POC and Σ, and more strongly linked to chlorophyll *a*. In fact, all parameters (except meiofauna) show a significant positive correlation with POC, which itself shows a good positive correlation with fine particle content. The low value of the coefficients may be attributed to the narrow variation range of the parameters studied.

Table 6

*Spearman's rank correlation coefficients between the studied variables. POC, Σ, Chlorophyll* a *and ETS are from the 0-1 centimetre layer, while meiofauna abundances are from the whole core* (see *text).*

| | POC (mg/g) | Σ (mg/g) | Chlorophyll a (µg/g) | ETS ($\mu l O_2\ g^{-1}\ h^{-1}$) |
|---|---|---|---|---|
| **Meiofauna** (No. ind. 10 $cm^{-2}$) | n = 29<br>r = 0.1498<br>n. s. | n = 26<br>r = -0.0154<br>n. s. | n = 19<br>r = 0.0083<br>n. s | n = 27<br>r = -0.1236<br>n. s. |
| **ETS** ($\mu l\ O2\ g^{-1}\ h^{-1}$) | n = 27<br>r = 0.4438<br>p < 0.025 | n = 25<br>r = 0.4188<br>p < 0.025 | n = 19<br>r = 0.7351<br>p < 0.001 | |
| **Chlorophyll *a*** ($\mu g\ g^{-1}$) | n = 19<br>r = 0.4649<br>p < 0.025 | n = 19<br>r = 0.5469<br>p < 0.01 | | |
| **Σ** ($mg\ g^{-1}$) | n = 26<br>r = 0.8181<br>p < 0.001 | | | |

It has been shown that ETS activity (as biological potential) on one hand, and Σ and pigments (as indices of degradable organic matter) on the other, vary along the same low gradient, increasing westwards, from the coastal zone. Relationships between ETS activity and degradable organic matter may be discussed according to two hypotheses: a) as a constituent of living organisms, ETS is linked to the biopolymers of the biomass itself; b) biomass (and then ETS activity) is thought to be dependent on the occurrence of available matter which ensures its turnover.

The Σ considered to be degradable organic matter is presumably a part of detrital available macromolecules plus the living constituents which are directly available only after death. These two components cannot be distinguished as biomass markers (*e. g.* ATP) were not measured.

Fortunately some ETS:Σ ratio values ($\mu l\ O_2.h^{-1}$: mg) in living organisms are available in the literature (Relexans *et al.*, 1992): from 23 to 43 from meiofauna and for 65 to 310 for bacteria (Tab. 7). The mean value of ETS:Σ calculated for sediment of the WGMP from data from Table 2, is 96 ± 16, *i. e.* a value of the same magnitude as that calculated for biomass. Therefore, Σ measured here could correspond mainly to the biomass itself, which could largely account for relationships between ETS and Σ.

The distribution of meiofauna does not follow the gradient found for POC, ETS, Σ and pigments; the eastern station is generally richer than those in the centre and west. However, the difference is not significant. No correlation is found between meiofauna numbers and any of the parameters chosen for characterizing organic matter.

In general, a positive correlation between meiofauna abundance and the amount of organic matter has been demonstrated in areas of low benthic food availability, such as the deep sea (Dinet and Khripounoff, 1980; Thiel, 1983; Shirayama, 1984) and the Baltic Sea (Elmgren, 1978). On the other hand, in littoral areas, a relative independence from carbon sources has often been observed (Montagna *et al.*, 1983; Alongi, 1988; Widbom and Elmgren, 1988). In some cases,

Table 7

*Biogeochemical ratios calculated in coastal areas of the Bay of Biscay and from some living organisms. ETS is given at 20°C. a) corrected for temperature and converted to Kenner and Ahmed's methodology standard; b) according to Σ = organic matter = POC x 2; c) calculated term based on POC = ATP x 250; d) calculated term based on Σ = protein x 2*

| STUDY AREAS (mg/g) | POC/SED. (mg/g) | Σ/OM (mg/g) | ETS/POC ($\mu l\ O_2$/mg) | ETS/Σ ($\mu l\ O_2$/mg) | REFERENCES |
|---|---|---|---|---|---|
| **Arcachon Bay** | 48.7 ± 12.6<br>n = 20 | 130 ± 25<br>n = 28 | 18.6 ± 2.4<br>n = 28 | 82 ± 11<br>n = 28 | Relexans *et al.* (1992) |
| **Gironde inlet** | 12.5 ± 0.8<br>n = 36 | 112 ± 11<br>n = 36 | 26.4 ± 2.2<br>n = 36 | 120 ± 11<br>n = 36 | Bachelet (1987) |
| **West Gironde mud patch** | 8.0 ± 0.9<br>n = 29 | 94 ± 7<br>n = 28 | 16.6 ± 2.4<br>n = 25 | 96 ± 16<br>n = 25 | This study |
| **MARINE BACTERIA** | | | | | |
| ***Vibrio anguillarum*** | | | # 130 (a) | # 65 (b) | Christensen *et al.* (1980) |
| **Natural populations** | | | 230 (c) | 115 (b) | Romano *et al.* (1987) |
| **Culture of two species** | | | 620 | 310 (b) | Brugeaille (1988) |
| **MEIOFAUNA** | | | | | |
| **Nematodes** | | | | 23 (d) | Relexans (1989) |
| **Copepods** | | | | 43 (d) | Relexans (1989) |

however, when strong gradients occur, correlations between meiofauna and organic matter can be found (Castel *et al.*, 1989) but they must be considered as secondary consequences of variations in the structure of the sediment as well as direct responses to food availability. In the case of the WGMP, where gradients of sedimentary organic matter are so slight, the difference of meiofaunal abundance between the eastern and western stations is probably due to a difference in the properties of the sediment, *e. g.* the increase of silt-clay content towards the west, inducing clogging of the interstitial pores and compaction of the sediment.

The lack of correlations between ETS activity and meiofauna abundances confirms that the contribution of meiofauna to the total respiratory potential of sediment is presumably low, as shown in a few studies in coastal areas (Houri-Davignon *et al.*, 1989; Relexans, 1989; Relexans *et al.*, 1992).

## Similarity between this area and neighbouring coastal environments

The WGMP, which appears to be a "monotonous" area, becomes more interesting when compared to other areas at varying distances from the Gironde estuary. From data obtained during campaigns in the inlet of the Gironde estuary (Ecocha: Bachelet, 1987) and in the Bay of Arcachon (GIS: Relexans *et al.*, 1992) with the same methods as those presented here, the three areas can be compared (Tab. 7). POC content of sediment (only the < 63 µ fraction was considered here, to eliminate the effects due to the highly variable sandy proportions) strongly differs in the three areas, the richest being Arcachon, the poorest being the WGMP. Σ:OM (organic matter) varies in the same way but much more slightly than POC does; this means that large increases of POC are always accompanied by a certain amount of degradable molecules: in all the areas, Σ is significantly linked to POC. ETS:POC shows the same pattern as Σ:OM. ETS:Σ is nearly constant (from 82 to 120 µm $O_2.h^{-1}.mg^{-1}$) and of same magnitude as it is in living material. Therefore, in the three areas, the major part of organic matter measured according to our technique as "degradable matter" (*i. e.* Σ) is thought to consist mainly of biomass constituents. The detrital part of Σ, readily available for the benthos may be low because it is rapidly incorporated into the biomass and/or mineralized by biological processes.

## CONCLUSION

The WGMP seems to be a relatively monotonous area, formed by settlement of particles from the Gironde estuary, enriched with silts moving on the shelf. Sediments of the WGMP have a poor organic carbon content (0.8 %), of which the labile organic fraction (Σ) does not exceed 10 % of the total sedimentary organic matter. Only pigment content exhibited clear seasonal variations. Nevertheless, freshly-formed organic matter supply was marked by both pigment and Σ increases westwards (*i. e.* towards the open ocean). Vertical profiles of chlorophyll, ETS activity and meiofauna distribution are related to bioturbation processes.

ETS activity was found to be significantly linked to POC, Σ and chlorophyll *a*. When the ratios of ETS to the other parameters above were compared with the same ratios calculated in coastal areas near the WGMP, it was found that ETS:POC in the WGMP (# 16.6 µl $O_2$ $h^{-1}.mg^{-1}$) was the lowest (#26.4 and #18.6 in the Gironde inlet and in the Bay of Arcachon, respectively), while ETS:Σ was quite similar (from 82 to 120) in the three areas. As the latter ratio is not far from the one which can be evaluated in living organisms (in spite of the lack of data in this type of research field), it is suggested that in these areas, Σ may mainly represent biomass itself; the detrital part of the macromolecular content seems to be quickly incorporated into the living material and does not appear to accumulate.

In this study, meiofauna distribution does not seem to be linked to either POC, Σ or pigments; its distribution probably depends on other criteria than those analyzed here. ETS activity seems to be essentially linked to microbenthic and bacterial compartments and can be considered in various environments as an indirect index of sedimentary carbon quality.

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