

The distribution of meiofauna and its contribution to detritic pathways in tidal flats (Arcachon Bay, France)

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SUMMARY: In Arcachon Bay, the intertidal area is mainly occupied by sandbanks, oyster parks and seagrass beds. The aim of this study was to estimate the meiofaunal contribution to the trophic systems of these biotopes. Seven stations from the inlet to the inside of the bay have been studied seasonally during the year 1986. Meiofaunal stratification presents different patterns according to the facies but 75 % to 90 % of the total abundance is restricted to the top cm in all the stations. The meiofauna, strongly dominated by Nematodes (> 75 %), shows a noticeable temporal stability through the year: meiofaunal communities of low density and diversity dominated by omnivorous-predatory Nematodes characterize the open sea sandy stations with low detritus content; on the contrary, the sheltered seagrass and oyster park stations with high organic carbon content have communities of high density and diversity, dominated by deposit and epistrate feeders. From a comparison of the meiofaunal and microphytobenthic biomasses and associated productions, meiofauna is suspected to consume an important part of the yearly benthic primary production: 60 % in sandbanks, 42 % in oyster parks and 76 % in seagrass beds. When the needs of macrofauna are taken into account, it seems unlikely that the primary production can sustain the benthic secondary production, particularly in seagrass bed and oyster park sediments. In these areas, the high content of detrital organic carbon (130 g C m⁻²) constitutes a substitute food source for meiofauna as well as for macrofauna.

Key words: meiofauna, detritic pathways, tidal flats, soft-bottom benthos.

INTRODUCTION

Most of the biological activity in sheltered estuarine areas is located in the sediments of intertidal flats. For several areas, as for instance mudflats of British estuaries (WARWICK *et al.*, 1979; BAIRD & MILNE, 1981), the tidal flats of the Wadden Sea (KUIPERS *et al.*, 1981), the importance of the meiofauna in terms of metabolic activity has been stressed. Notwithstanding a small biomass as compared to macrofauna, meiofauna plays an important role in the benthic ecosystem due to a high metabolic rate per unit of weight (GERLACH, 1971; LASSERRE *et al.*, 1976).

In Arcachon Bay, 70 % of the intertidal area is occupied by seagrass beds: *Zostera noltii* (Horn.) and oyster parks: *Crassostrea gigas* (Thunberg). These biological structures are determining factors in the

benthic ecosystem; seagrass detritus and oyster deposits, trapped within the sediment, are important sources of organic matter and energy which contribute powerfully to the benthic resources (HARRISSON & MANN, 1975; SORNIN *et al.*, 1983).

The aim of the present study was to determine the role of meiobenthos in these ecosystems since few investigations involving seagrass or oysters and their associated parameters have focused on meiofauna. For this purpose, we used a similar approach as described by WITTE & ZIJLSTRA (1984). These authors conclude to the low contribution of meiofauna to the benthic food web in a tidal flat of the Wadden Sea. An estimation of the meiobenthic biomass and food requirements is given and compared with the resources: particulate organic carbon, autochthonous primary production and pelagic imports.

STUDY AREA, MATERIAL AND METHODS

The Bay of Arcachon (44°40' N, 1°10' W) forms a triangular embayment on the South-West french Atlantic coast (Fig. 1). Channels and intertidal areas cover 155 km² but only 40 km² of the bay are subtidal. In the intertidal areas, seagrass beds and oyster parks occupy respectively 8000 and 1200 ha. The bay and the ocean are connected by a narrow channel. The oceanic water entering at each tide is diluted by fresh water input mainly from the eastern part of the bay. Temperature and salinity variations are directly proportional to the distance 'upstream' from the inlet. The tidal range is quite great in the Arcachon Bay, ranging from 3.90 m at spring tide to 2.00 m at neap tide. In the intertidal zone, hydrodynamic processes create a sediment gradient: pure sands are found at the entrance of the bay while silt and clay dominate in the sheltered mudflats of the inner part.

Seven stations were sampled seasonally during the year 1986 (12 February, 23 April, 21 July and 13 September). These stations belong to 3 sites located in different parts of the bay (Fig. 1). Near the inlet, the Cap Ferret site provides 2 stations: 1 unvegetated sandbank (CFs) and 1 oyster park (CFo). The 5 other stations are located in the Ile aux oiseaux, situated in

the central part of the bay. On the East coast of the island, 3 stations are studied: 1 unvegetated sandbank (EIs), 1 oyster park (EIo) and 1 *Zostera* bed (EIz). Two stations are situated on the more sheltered North coast: 1 oyster park (NIo) and 1 seagrass bed (NIz). Schematically, at Cap Ferret, the more oceanic site, the ranges of temperature (9.3-21.5 °C) and salinity (24.6-33.5) are narrower than in the Ile aux Oiseaux (8.6-22.7 °C and 24.1-33.7 respectively). Waters of the Cap Ferret are warmer and more saline in summer, colder and less saline in winter.

Sampling was carried out at low tide; for meiofauna and microphytobenthos, four cores were taken with tubes of 2.8 cm internal diameter. Sampling was restricted to the top 10 cm and the cores sliced at regular levels for an estimation of meiofaunal stratification. Samples were preserved in 5 % formalin, stained with Rose-Bengal, sieved over a 2 mm mesh and collected on a 63 µm sieve. The fauna was extracted from the sediment by flotation in LUDOX HS 40. In samples from the East coast of the Ile aux oiseaux, the Nematodes were identified to the genus level and the trophic groups determined according to WIESER (1953).

Meiofaunal biomasses were obtained by weighing 10 to 100 individuals representative of the major taxa on a Mettler ME 22 microbalance (sensitivity: 0.1 µg). Before weighing, the animals were rinsed in distilled water and dried at 60 °C for 24 h.

Microphytobenthic biomass was estimated from chlorophyll pigments contained in the top cm of the sample, measured by spectrophotometry after acetone extraction of wet sediment (PARSONS *et al.*, 1984).

The particulate organic carbon (POC) content of the sediment was estimated by using the method described in PARSONS *et al.* (1984). The silt content was determined as the percentage of sedimentary fraction smaller than 63 µm.

RESULTS

POC and microphytobenthic biomass

POC and silt content, strongly linked (Table I), increase from stations with high hydrodynamical conditions (EIs and CFs) to the more sheltered stations (NIo and NIz). At Cap Ferret, trophic activity of oysters enhances the sedimentation of fine particles; this explains the great difference observed between the two adjacent stations CFs and CFo. Such a phenomenon also acts in the Ile aux oiseaux between EIs and EIo. The sedimentation induced by seagrass beds is equally illustrated by high values of silt content and POC concentrations which are very similar to the percentages observed in the oyster parks.

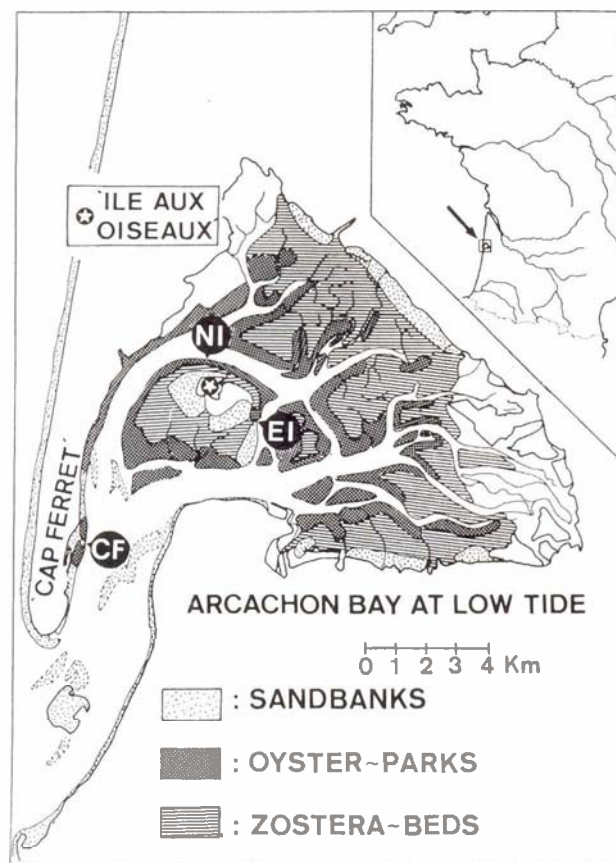


FIG. 1. — Localisation of the sampling sites; CF, Cap Ferret; EI, East Island; NI, North Island.

TABLE I. — Annual averages of edaphic parameters (± 1 s.d.) and concentrations of benthic chlorophyll pigments. B, Estimates of the microphytobenthic biomass (C/Chl. a ± 40)

<i>S'</i>	<i>Silt</i> (% d.w.)	<i>POC</i> (% d.w.)	<i>Chl.a</i> ($\mu\text{g cm}^{-2}$)	<i>Phaeo</i> ($\mu\text{g cm}^{-2}$)	(B) (g C m^{-2})
CFs	2.85 ± 0.54	0.42 ± 0.11	9.65 ± 2.69	7.69 ± 2.38	1.31 - 7.72
CFO	16.14 ± 3.40	1.04 ± 0.25	23.66 ± 4.02	35.82 ± 10.29	3.41 - 18.93
EIs	4.60 ± 1.60	0.70 ± 0.44	9.37 ± 1.88	2.55 ± 0.76	1.27 - 7.50
EIo	34.70 ± 1.42	2.43 ± 0.51	12.95 ± 1.47	25.36 ± 2.26	1.76 - 10.36
Elz	40.55 ± 4.00	2.90 ± 0.58	11.59 ± 3.37	14.32 ± 5.10	1.58 - 9.27
NIo	50.90 ± 2.50	3.31 ± 0.21	17.35 ± 2.45	30.22 ± 3.01	2.36 - 14.00
Nlz	51.60 ± 2.17	3.85 ± 0.50	11.96 ± 2.13	22.36 ± 3.00	1.63 - 9.57

Temporal variations of chlorophyll pigment concentrations show no reliable trend, therefore these values are averaged over the year for each station and presented in Table I. The sandy stations are characterized by both low chlorophyll pigments concentrations and high Chl. *a*/Phaeopigments ratios; this is caused by the hydrodynamism which prevents the accumulation of dead algal cells and detritus, i.e. the principal sources of phaeopigments. The high chlorophyll pigments concentrations in oyster parks result from the trophic activities of the oysters which provide an important flux of biodeposits to the benthos. The microphytobenthic biomass is slightly lower in seagrass sediments.

In Table I, the carbon values are calculated by multiplying the Chl. *a* concentrations by a standard C/Chl. *a* ratio of 40 (MONTAGNA, 1984; BODIN *et al.*, 1985). However, DE JONGE (1980) indicates that the use of a such constant ratio may involve errors varying from 34 to 50 % (overestimation and underestimation respectively); the estimated values of biomass are corrected with these percentages. These biomasses, expressed as g C m^{-2} , are within the same order of magnitude as those for other intertidal areas: 2.04 to 9.04 g C m^{-2} in Balgzand, Wadden Sea (CADÉE & HEGEMAN, 1977); 0.7 to 2.2 g C m^{-2} in Bay of Douarnenez, Brittany (BODIN *et al.*, 1985).

Meiofaunal distribution and variation

The meiofauna consists mainly of Nematodes which represent > 75 % of the total abundance averaged over all the samples. They are followed in abundance by Copepods, Turbellarians and Annelids. Other taxa (e.g. Ostracods, Hydrozoans) were

scarcely observed and always in low numbers, and so will not be further discussed.

An example of the vertical distribution of meiofauna is illustrated in figure 2. About 75 to 90 % of the meiofaunal abundance is restricted to the top cm of the sediment in all the stations. However, the colonization of the deeper layers expressed as the proportion of individuals living below the top cm does not present a uniform pattern among the stations. This proportion is the highest in EIs (sandbank), then in Cap Ferret (CFs), despite a higher density in the first cm, the deeper layers present similar abundances as EIs. The reduction of meiofaunal density between the top cm and the deeper layers is higher in CFO (Cap Ferret oyster park) than in the oyster parks of the Ile aux oiseaux (EIo and NIo). This will be discussed further in relation to the farming patterns used in Arcachon Bay. In seagrass sediments, the meiofauna presents a penetration beneath the top cm similar to that observed in the oyster parks of the Ile aux oiseaux.

As these samples were taken during the same period of the tidal cycle, the possibility of a meiofaunal migration related to the sea level was not investigated. However, it is likely that most of the meiofauna is concentrated in the first 10 cm of sediment whatever the period of the tidal cycle.

In all groups large numerical variations are observed in the course of the season and/or between stations (Fig. 3). Nematodes and Annelids are always more abundant in oyster parks and seagrass beds than in sandbanks. This pattern is the same for Copepods and Turbellarians except in July when they reach their highest density in the sandbanks. Season-

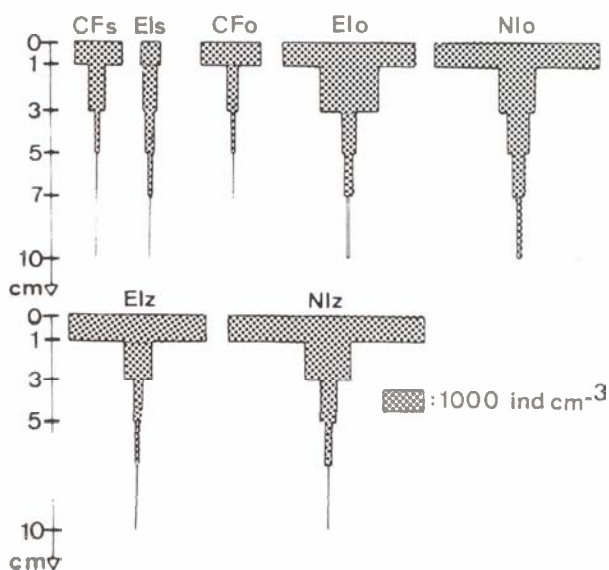


FIG. 2. — Vertical distribution of meiofaunal abundances (in February): sampling area, 10 cm^2 .

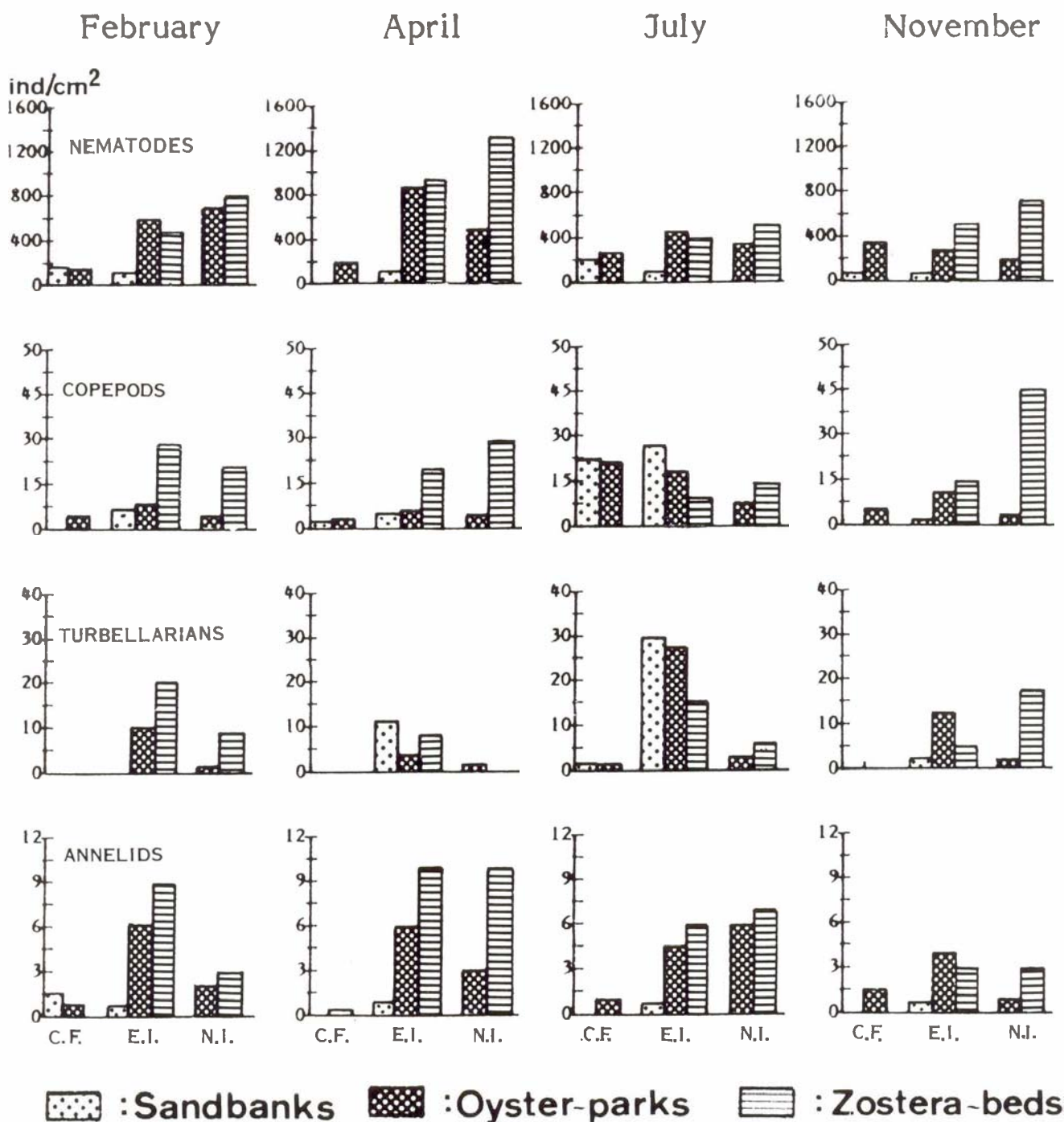


FIG. 3. — Densities of the major meiofaunal taxa in the seven stations at the four sampling dates.
CF, Cap Ferret; EI, East Island; NI, North Island.

nal and spatial variations in abundance of the major taxa are tested with a two-way analysis of variance. The analysis shows for the major taxa that consistent differences between stations are responsible for a large part of the variance observed (Table II). No significant differences can be shown between sampling periods.

A multiple regression analysis demonstrates that about 60 % of the spatial variation in Nematodes is

explained by the silt content ($r = 0.77$, $p < 0.001$). Annelids abundance is explained for about 43 % by the silt content ($r = 0.65$, $p < 0.001$). For Copepods and Turbellarians the correlation with environmental parameters is more tenuous. Nematodes representing at least 75 % of meiofauna, it is probably correct to assume that meiofaunal abundance, insensitive to seasonal influence (ANOVA, $p > 0.05$), is heavily controlled by the silt content.

Taxonomic analysis

Taxonomic analysis of the Nematodes was made for three stations: EIs, EIo and EIz, which are representative of the three facies studied: sandbanks, oyster parks and seagrass beds.

Both specific richness and diversity, H' , clearly increase with the silt content (Table III) from 35 species and $H' = 2.23$ in EIs to 63 species and $H' = 3.98$ in EIz.

Table III shows the differential distribution of the families among the stations from sandy area (EIs) to muddy areas (EIo and EIz). In EIs four families have been found which represent each more than 5 %; among them, the Thoracostomopsidae are the more abundant with 73 %. In EIz and EIo, we found seven families over 5 % which represent in EIz, 74 %, in EIo, 86 %. In these stations the Linhomoeidae and Comesomatidae are the dominant families.

With regard to the trophic groups distribution (Table III), according to WIESER (1960), and TIETJEN (1977) the predominance of deposit feeders (1A + 1B) is observed in muddy sediments. In Arca-chon Bay this group represents 53 % in EIz, 65 % in EIo and only 7.4 % in EIs. This latter station is well characterized by the high percentage of an omnivore-

TABLE II. — Analysis of variance for abundance estimates of the major meiofaunal taxa, considering the seven sampled stations and the four sampling sets.

Nematodes			
Between stations	F = 18.30	d.f. = 6	p < 0.01
Between sampling periods	F = 1.60	d.f. = 3	p > 0.05 n.s.
Copepods			
Between stations	F = 4.10	d.f. = 6	p < 0.05
Between sampling periods	F = 2.50	d.f. = 3	p > 0.05 n.s.
Turbellarians			
Between stations	F = 9.30	d.f. = 6	p < 0.01
Between sampling periods	F = 1.30	d.f. = 3	p > 0.05 n.s.
Annelids			
Between stations	F = 10.80	d.f. = 6	p < 0.01
Between sampling periods	F = 0.50	d.f. = 3	p > 0.05 n.s.

predator group (2B) which reaches 80 %. WARWICK (1971) describes a similar proportion of omnivores-predator (50 %) but in coarse sandflats and not in fine sand (our case). Moreover, it is the epistrate feeders (2A) which usually dominate in the sandy stations (WIESER, 1960; WARD, 19873). These results suggest a differential distribution of the trophic groups in accordance with the local resources: the deposit feeders are more represented in stations with a high detrital content (EIo, EIz).

TABLE III. — Distribution of the major helminthoidal families over the three stations of the East Island, number of genus representing each family, proportion of the major trophic groups, mean number of species per station and diversity level (H'). 1A, selective deposit feeders; 2A, epistrate feeders; 1B, non selective deposit feeders; 2B, omnivores-predators.

Families	EIs		EIo		EIz	
	%	No.g.	%	No.g.	%	No.g.
Thoracostomopsidae	73.0	2	0	0	0	0
Trefusiidae	0.35	1	0	0	0	0
Aegiolaimidae	0.2	1	0	0	0	0
Oncholaimidae	10.3	2	4.7	2	5.3	2
Monoposthiidae	2.9	1	0.5	2	3.6	1
Cyatholaimidae	0.6	1	2.0	2	1.8	2
Oxystominidae	0.45	2	0.9	4	2.3	4
Sphaerolaimidae	0.1	1	2.0	1	2.1	1
Axonolaimidae	1.8	2	0.35	1	4.0	2
Xyalidae	1.0	2	8.3	2	4.7	3
Microilaimidae	0.4	1	4.6	1	9.1	1
Chromadoridae	6.1	7	12.7	7	10.0	8
Desmodoridae	5.2	4	17.3	2	18.8	2
Linhomoeidae	0.5	1	18.6	2	20.6	3
Comesomatidae	0.1	1	19.9	2	5.4	2
Monhysteridae	0	0	0.45	1	0	0
Encheliidae	0	0	0.25	1	0.1	1
Rhabdodemaniidae	0	0	0.1	1	0.1	1
Anaplostomatidae	0	0	0.1	1	2.6	1
Demoscolecidae	0	0	0	0	0.2	1
Leptolaimidae	0	0	0	0	0.4	2
Anticomidae	0	0	0	0	0.5	1
Tripyloididae	0	0	0	0	1.8	2
TROPHIC GROUPS (%)	1A	3.9	33		28	
	2A	12.2	28		38	
	1B	3.5	32		25	
	2B	80.5	8		9	
No. of species		35	48		63	
Diversity		2.23	3.42		3.98	

TABLE IV. — Individual dry weight and yearly averaged biomass of the major meiofaunal taxa.

	CFs	ElS	CFo	Elo	Nlo	Elz	Nlz
Nematodes, individual d.w. (μg)	1.02	1.20	0.63	0.63	0.53	0.43	0.66
total d.w. (g m^{-2})	1.253	0.818	1.471	3.454	2.192	2.358	5.294
Copepods, individual d.w. (μg)	0.88	0.51	1.05	4.40	1.66	1.80	1.12
total d.w. (g m^{-2})	0.006	0.005	0.009	0.049	0.008	0.030	0.030
Turbellarians, individual d.w. (μg)				0.80			
total d.w. (g m^{-2})	0.002	0.089	0	0.111	0.005	0.102	0.064
Annelids, individual d.w. (μg)				5.00			
total d.w. (g m^{-2})	0.050	0.045	0.040	0.265	0.145	0.320	0.285
Other taxa, individual d.w. (μg)				3.00			
total d.w. (g m^{-2})	0.018	0.075	0.144	0.036	0.066	0.168	0.336
Meiofauna, total d.w. (g m^{-2})	1.329	1.032	1.664	3.915	2.416	2.978	6.009

Meiofaunal biomass (Table IV)

Nematodes and Copepods were weighed from samples taken in all the stations, in July when the abundances were rather high in the three sites. The individuals being small in summer (direct observation), the biomass computed over the year could have been underestimated. Annelids and Turbellarians were collected from the samples in which they were the most abundant. For the other taxa, mean biomasses are derived from published data (LASSERRE *et al.*, 1976).

For Nematodes, the individual dry weight ranges from 0.43 to 1.20 μg . These values are rather high compared with the estimates of 0.17 μg given by WARWICK *et al.* (1979) or 0.28 μg mentioned in WITTE & ZIJLSTRA (1984). However they are less than the mean dry weight of 1.5 μg proposed by LASSERRE *et al.* (1976) for the Nematodes in the salt marshes of Arcachon Bay.

For Harpacticoids, the estimates vary between 0.51 and 1.80 μg /individual with an exceptional high value of 4.4 μg in station Elo due to the predominance of a large species, *Canuella* sp., whose individual weight is 9 μg . The individual weight is 0.8 μg for Turbellarians. According to WITTE & ZIJLSTRA (1984), the mean dry weight per individual can be taken as 2 μg for Harpacticoids and Turbellarians. LASSERRE *et al.* (1976) obtain values of 1.5 and 3 μg respectively.

Finally, for Annelids (Polychaetes and Oligochaetes) we found a mean dry weight of 5 μg per individual. This value is high compared with the figure provided by WITTE & ZIJLSTRA (1984) of 1.55 μg but is consistent with the one given by LASSERRE *et al.* (1976). However, even if our estimates for Annelids is too high, the contribution of this group to the total meiofauna biomass remains low.

The product of individual weights by the yearly averaged abundances provides an estimate of the mean biomass represented by each taxon through the

year in the different stations (Table IV). As from the abundances, the Nematodes represent the greatest part of the meiofaunal biomass: 79 % in ElS and Elz, 88 % in CFo, Elo and Nlz; 90 % in Nlo and 94 % in CFs. For the Copepods, the highest biomass is observed in Elo and corresponds to the dominance of the large harpacticoid *Canuella* sp.; the lowest biomass in ElS and CFs is the consequence of the reduction of both the density and the individual dry weight which results from the predominance of interstitial Harpacticoids in the sandbanks. The highest meiofaunal biomass is reached in Nlz (6 g d.w.m^{-2}), and the lowest one in ElS (1.03 g d.w.m^{-2}).

DISCUSSION

Determination of the meiofaunal distribution

According to the present study, it seems that the density of the major taxa is mainly controlled by a spatial variable rather than by a temporal one. This agrees with WITTE & ZIJLSTRA (1984) who come to the same conclusion. This result does not mean the total independence of meiofauna to the seasonality but only, in our case, among very different stations the prevalence of a spatial determinism. This fact is well illustrated by the correlation between the majority of the taxa and the silt content. According to IVES-TER (1980) and CASTEL (1986), percent silt clay and organic content in the sediment are the most important variables in determining species distribution. Moreover these two parameters are highly correlated ($r = 0.87$, $p < 0.01$) and characterize both *Zostera* beds and oyster parks.

Our results suggest the impact of oyster parks and *Zostera* beds on the meiofaunal penetration within the sediment. The oyster parks studied here present the two farming patterns used in Arcachon Bay. In Cap Ferret, plastic bags filled with oysters are disposed on frames. These farming structures by

reducing the hydrodynamical conditions induce a massive accumulation of organic rich biodeposits which agglomerate in a compact and hardly oxygenated sediment. This, together with a poor water content, is not favourable to meiofauna. The other oyster parks situated in the Ile aux Oiseaux, are exploited on a different mode: oysters are farmed directly on the sediment without any artificial structures. The sediment, exposed to currents and waves, undergoes regular resuspension which avoids the compaction of the biodeposits and maintains oxygenated conditions. Moreover the oyster shells provide as many refuges for meiofauna and create discontinuity surfaces which join the superficial sediments to the deeper levels, facilitating the vertical movements of meiofauna.

The stratification observed for *Zostera* beds is very similar to that in oyster parks and points out the similarity of the effect induced by these facies: seagrass blades play the role of a mechanical strainer which traps fine particles (HICKS, 1986) as do oysters through biodeposition (the silt content in *Zostera* beds and oyster parks is very similar). Furthermore, the network of roots has certainly a similar effect on the meiofaunal stratification as the shells in an oyster park.

The taxonomic study performed on the Nematodes reveals some divergences with literature: a negative effect of increasing silt content on species richness and diversity is described in Liverpool Bay, specific richness of 66 and 24 are observed in stations with silt content respectively equal to 1 and 25 % (WARD, 1973). In Long Island Sound, the diversity decreases from 2.63 to 1.56 when the silt content goes up from 11 to 75 % (TIETJEN, 1977). This difference is probably due to particularities of oyster parks and seagrass bed sediments compared to the commonly studied mudflats in terms of microhabitat. According to HICKS (1986) accumulations of coarse particles and debris actively promote habitat heterogeneity for meiofauna as do oyster shells and *Zostera* roots. The two most abundant families in the muddy stations (Comesomatidae and Linhomoeidae) are commonly cited in the literature as muddy adapted families (WIESER, 1960; WARD, 1973; TIETJEN (1977). According to TIETJEN (1977), the Tripylidae are characteristic of muddy sediments, but they represent less than 2 % in EIz. On the other hand, the Desmodoridae, commonly described as typical sandy nematodes, are well represented in the muddy stations (EIo and EIz). TIETJEN (1980) in the New York Bight, observes that the Desmodoridae become very abundant when the silt content decreases; in our case, it is the Thoracostomopsidae which dominates in low silt content stations.

The differences between our observations and the published data certainly result from particularities of

oyster parks and seagrass beds. Moreover, most of these published data concern subtidal communities whereas our study deals with tidal flats.

There is a differential distribution of the trophic groups among the stations: deposit feeders dominate in the stations of high organic content and microphytobenthic biomass (EIo, EIz); whereas in the poorer station (EIs) they are replaced by the omnivores-predators. This distribution of the trophic groups points out a connection between the benthic resources and the potential consumers.

Quantification of the energy flow through the benthos

Primary production has been shown to be correlated with chlorophyll *a* by different authors (LEACH, 1970; CADÉE & HEGEMAN, 1977). According to BODIN *et al.*, (1984), a production ($\text{g C m}^{-2} \text{ yr}^{-1}$)/chlorophyll *a* ($\mu\text{g g}^{-1}$) ratio of 5 seems to give a good approximation of yearly primary production. The values of production obtained by this way (Table V) are rough estimates providing a scale of the production levels among the stations. Our values ranging from 26 to $162 \text{ g C m}^{-2} \text{ yr}^{-1}$ are in the same order of magnitude than those directly measured in similar areas: 31 in Ythan estuary (LEACH, 1970); 58 to 170 in Dutch Wadden Sea (CADÉE & HEGEMAN, 1974); 29 to 188 in the Balgzand, Wadden Sea (CADÉE & HEGEMAN, 1977); 143 g C m^{-2} in the Lynher estuary (WARWICK *et al.*, 1979); 36 to 81 in the Ems Dollard estuary (B.O.E.D.E., 1985).

According to GERLACH (1978), the meiofaunal biomass expressed in g dry weight are convertible in g C by dividing by two (Table V). From this biomass in term of carbon content, it is possible to estimate an annual production using a P/B ratio. GERLACH (1978) proposes a general P/B ratio of 10 yr^{-1} for the whole meiofauna. According to WARWICK *et al.* (1979), the different taxa have to be distinguished as follows: P/B = 8.4 for Nematodes, 18 for Harpacticoids, and 5 for Annelids and Turbellarians. Estimates of P/B for meiofauna can also be calculated

TABLE V. — Microphytobenthic production vs meiofaunal production and food demand.

	Microphytobenthos	Meiobenthos	
	Production ($\text{g C m}^{-2} \text{ yr}^{-1}$)	Food demand ($\text{g C m}^{-2} \text{ yr}^{-1}$)	Production ($\text{g C m}^{-2} \text{ yr}^{-1}$)
CFs	26.1 - 44.15	21.68	6.50
EIs	25.70 - 33.95	17.04	5.11
CFo	87.15 - 109.35	27.12	8.14
EIo	57.30 - 87.90	64.84	19.45
NIo	121.25 - 162.05	39.39	11.82
EIz	40.55 - 85.65	42.57	13.00
NIz	95.05 - 141.15	98.00	29.40

from individual oxygen uptake measurements. These values are converted in $\text{kcal g}^{-1} \text{yr}^{-1}$, assuming that $1 \text{ mg O}_2 \text{ respired} = 3.34 \text{ calories}$ (PARSONS *et al.*, 1984), in order to calculate the production (P) associated to this respiration (R). This is achieved through an equation given by SCHWINGHAMER *et al.*, (1986):

$$\log_{10}(R) = 0.367 + 0.993 \log_{10}(P);$$

(P and R in $\text{kcal g}^{-1} \text{yr}^{-1}$).

LASSERRE *et al.* (1976) give values of individual oxygen uptake for the major meiofaunal taxa living in Arcachon Bay. From this are estimated the P/B for each taxon: 9.75 for Nematodes, 21 for Copepods, 11.3 for Turbellarians, 9.7 for Annelids and 9.12 for the other taxa. When compared with those proposed by WARWICK *et al.* (1979), these P/B are about the same for Nematodes and Copepods but differ from a factor of 2 for the other taxa. However, since the animals were issued from the same geographical area, and concerning same sized individuals as our study, the values given by LASSERRE *et al.* (1976) are maintained for the further calculation of production (Table V).

Considering a net production efficiency of 32.5 % (WARWICK *et al.*, 1979), a rough estimate of the annual meiofaunal requirements can be drawn from the annual production (Table V). The meiofaunal food requirements are, except in CFo and NIo, of the same magnitude as the low estimate of primary benthic production. In CFo and NIo, the oyster biodeposition by enhanced sedimentation of phytoplankton allows the benthic algal biomass to exceed the meiofaunal food requirements. Moreover, the estimates of the macrofaunal densities performed during the same survey (AUBY & LABOURG, pers. comm.), allow an assessment of the global benthic food consumption. According to its biomass, a P/B of 1 and a conversion efficiency of 30 %, macrofauna is suspected to consume $30 \text{ g C m}^{-2} \text{yr}^{-1}$ in EIs, $70 \text{ g C m}^{-2} \text{yr}^{-1}$ in NIo and CFo, $120 \text{ g C m}^{-2} \text{yr}^{-1}$ in CFs EIo and EIZ, and $160 \text{ g C m}^{-2} \text{yr}^{-1}$ in NIZ. When summing these values with those obtained for meiofauna, it seems unlikely that the primary organic carbon can sustain the benthic secondary production. In oyster parks and *Zostera* beds, a large part of the benthic food demand is certainly met by the detritic pathway. This assertion is supported by the predominance, in these facies, of deposit feeders.

These results are in accordance with those obtained by KUIPERS *et al.* (1981) who define 'the small food web' (bacteria, microfauna and meiofauna) consuming 70 to 80 % of all organic material available at each step of the food chain; in our case the benthic organic material consists principally of detrital parti-

cles. Inversely, WITTE & ZIJLSTRA (1984) conclude to the low contribution of meiofauna to the benthic food web. But in their case, meiofaunal biomass was very low, 0.45 g C m^{-2} , compared with the average of 1.4 g C m^{-2} observed in the present study. In the intertidal mudflats of Arcachon Bay the biogenic structures created by oysters and seagrass strongly control the functioning of the benthic ecosystem and allow the meiobenthos to play an important role in the detritic pathway.

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