Meiobenthos of the Bay of Saint-Brieuc (North Brittany, France). I: Quantitative distribution in subtidal and intertidal zones

Meiobenthos
Quantitative distribution
French coast of English Channel
Intertidal and subtidal zones
Organic matter

Méiobenthos
Répartition quantitative
Côte française de la Manche
Zones intertidale et subtidale
Matière organique

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ABSTRACT

In the eutrophicated Bay of Saint-Brieuc (western English Channel, France), density and biomass of the multicellular meiofauna were estimated in different intertidal and subtidal biotopes, in winter and late spring. Mean annual biomass varies from 0.5 to 2.3 $g.m^{-2}$ in the intertidal zone, and from 0.5 to 1.1 $g.m^{-2}$ in the subtidal zone. Vertical distribution (0-5 *versus* 5-10 cm) of taxa was considered in the intertidal zone. Results are discussed and compared to literature data: figures were similar to those of comparable biotopes, and there was no detectable effect of eutrophication on meiofauna density and vertical distribution in this area. The "seasonal stability" of nematodes was in contrast with a clear annual cycle in harpacticoid copepods. Biomass values for microphytobenthos and macrobenthos on the same sites are also given. Abiotic and biotic factors of the quantitative distribution are discussed, the stability of the biotope (depth) and the sediment grain size being apparently the most important.

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RÉSUMÉ

Le méiobenthos de la baie de Saint-Brieuc (Bretagne Nord, France). I : Répartition quantitative dans les zones intertidale et subtidale

La densité et la biomasse de la méiofaune pluricellulaire de la baie de Saint-Brieuc (Manche Ouest, France) ont été estimées dans différents biotopes intertidaux et subtidaux soumis à eutrophisation, en hiver et à la fin du printemps. Les biomasses moyennes annuelles varient de 0,5 à 2,3 $g.m^{-2}$ dans la zone intertidale, et de 0,5 à 1.1 $g.m^{-2}$ dans la zone subtidale. La distribution verticale des taxons a été étudiée dans les couches 0-5 et 5-10 cm de la zone intertidale. Les résultats sont discutés et comparés aux données de la littérature : les valeurs sont similaires à celles relevées dans des biotopes comparables et, dans cette région, l'eutrophisation n'a apparemment pas d'effet sur les densités et la distribution verticale de la méiofaune. La «stabilité saisonnière» des nématodes s'oppose au cycle annuel marqué des copépodes harpacticoïdes. Les biomasses du microphytobenthos et de la macrofaune relevées aux mêmes stations sont également indiquées. Les facteurs biotiques et abiotiques de la distribution quantitative sont discutés, l'importance de la stabilité du biotope et de la granulométrie étant une fois de plus mise en évidence.

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INTRODUCTION

The Bay of Saint-Brieuc (North Brittany, France) was chosen as a suitable site to specify the role of benthic processes in the response of a coastal ecosystem to increasing nutrient and organic matter inputs originating from a watershed, *i. e.* to some "eutrophication" ["Euphorbe" oceanographic programme managed by the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) from 1987 to 1991]. The primary aim of the project was to determine the structure of the benthic food web (from bacteria to macroconsumers) in order to define the "structural base" in which energy and matter fluxes should be quantified. The first step was the identification and biomass estimation of benthic assemblages in this area, the meiofauna being considered as an important compartment owing to its rapid turnover, as well as potential food for macrofauna (Hicks and Coull, 1983; Gee, 1989) and potential consumer of bacteria, microphytobenthos, detritus, etc. (Wieser, 1953; Giere, 1975; Hicks and Coull, *op. cit.*).

Meiofaunal standing stocks were evaluated in both the intertidal and subtidal zones and compared to published data in order to determine the impact of eutrophication and to situate the state of the Bay of Saint-Brieuc in relation to the pollution pattern described by Pearson and Rosenberg (1978).

Densities of the major meiofauna taxa were estimated at the supposed winter minimum and late spring maximum, and biomass values were calculated from individual mean dry weights given in the literature. Figures were compared with similar estimates of microphytobenthos and macrofauna biomass (given by Bodin *et al.*, 1989 and Gros and Hamon, 1988 respectively).

MATERIAL AND METHODS

Study sites

The Bay of St. Brieuc is a euhaline (*sensu* Muus, 1967) tidal bay on the northern coast of Brittany (France), widely open to the western English Channel (Fig. 1). Hydrodynamic conditions within the bay are relatively simple: water exchange is slow, driven by tidal mixing and wind, with little or no gravitational circulation generated by streamflow. A crude approximation of the water mass average residence time is about three weeks (Gros *et al.*, 1990). The most striking feature is the tidal amplitude, with a mean of about 8 m, but reaching a maximum of 13 m during spring tides. Tidal and wind mixing promotes longitudinal and vertical homogeneity of the water column; stra-

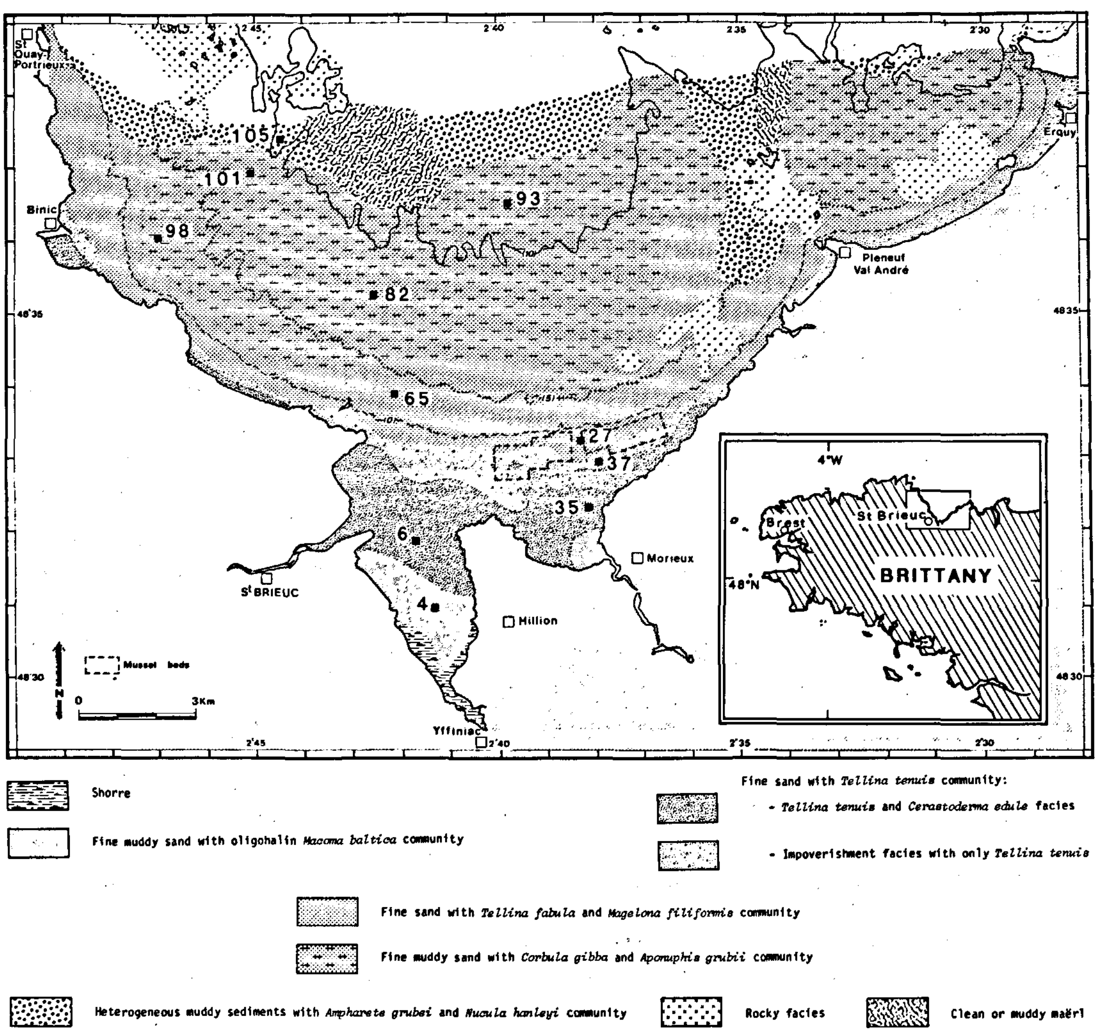

Figure 1

Biosedimentary structure of the Bay of Saint-Brieuc, with location of the study stations (modified from Gros et al.*, 1988 and Thouzeau and Hamon, 1992).*

Carte biosédimentaire de la baie de Saint-Brieuc et emplacement des stations (d'après Gros *et al.*, 1988 et Thouzeau and Hamon, 1992).

Table 1

Abiotic factors. Between brackets, values measured in March 1988.

Facteurs abiotiques. Entre parenthèses, valeurs mesurées en mars 1988.

	Intertidal zone					***Subtidal zone***					
	St. 4	**St. 6**	**St. 27**	**St. 35**	**St. 37**	**St. 65**	**St. 82**	**St. 93**	**St. 98**	**St. 101**	**St. 105**
Depth (m)	+7.4	+6.5	+2.0	+5.8	+3.8	-3.4	-8.7	-11.0	-2.6	-7.1	-9.5
Median grain size (µm)	156-162 (115)	156-162 (115)	<156 (94)	94-100 (75)	156-162 (125)	<156 (110)	<94 (105)	156-162 (180) +maërl	156-162	271 (180)	1510 +maërl
Sorting coefficient	1.16 (1.14)	1.16 (1.22)	1.16 (1.25)	1.17 (1.23)	1.16 (1.25)	1.16 (1.45)	1.17	1.16 (1.12)	1.16	2.65 (2.43)	1.52
Skewness coefficient	1-0.96	1-0.96	1-0.96	1.01-1.04	1-0.96	1-0.96	1.01-1.04	1-0.96	1-0.96	3.03	0.76
Silt/clay (%)	1.7 (1.91)	1.3 (1.81)	1.6 (2.17)	6.3 (4.03)	1.2 (1.90)	5.3 (6.12)	35.7 (30.65)	12.5 (5.97)	9.6	8.8 (3.11)	13.0
Total org. matter (% dry weight)	0.98	1.37	1.12	1.67	1.05	1.89	3.88	4.40	1.93	1.80	5.12
Water content (%)	26.1	29.8	26.6	29.1	27.1	26.0	37.7	35.9	26.9	42.2	33.1
Porosity	0.38	0.41	0.39	0.42	0.37	0.39	0.49	0.49	0.41	0.51	0.47
Depth RPD (cm)	<5	5-10	5-10	10-15	10-15						

tification, if it occurs, is rather weak and located only in the upper reaches of the bay. Moreover, the percentage of fresh water is less than 5 % (except during very high river flow), and salinities range from 30 to 35 (Thouzeau, 1991; Gros *et al.*, 1990).

The three main rivers entering the bay have a total drainage area of 941 km^2. Recently, there has been increased urban population, sewage networks and use of fertilizers in this area and a corresponding increase in environmental problems. In 1988, roughly 105 tons of dissolved inorganic nitrogen ($NO_3 + NO_4$) and 320 t of dissolved inorganic phosphorus (PO_4) were exported from the drainage basins into the bay. Input of suspended particulate matter has been estimated at 13,700 $t.y^{-1}$, some 6 % of which is represented by organic carbon. The bay has become increasingly "eutrophicated", as witnessed by excessive growth of benthic green macroalgae (*Ulva*) in summer. But this eutrophication is limited to the intertidal zone and never induces anoxic conditions. Moreover, Gros and Hamon (1988) recorded low rates of total organic matter in sediments: less than 2 % in the intertidal zone and at most 6 % in the centre of the subtidal zone, organic carbon rarely representing more than 1 %.

Sampling took place at five intertidal and six subtidal sites, numbered (Tab. 1) as in the original IFREMER report (Gros and Hamon, 1988). Depth of subtidal sites ranged from about 2 to 13 m. Stations were chosen as being representative of structural entities and macrofaunal assemblages. All the intertidal stations (4 to 37) were fine sands, the dominant substrate in the bay (Tab. 1, Fig. 1), but one of them (35) was slightly muddy (silt/clay content: 4 %). Sediment characteristics of subtidal sites were more varied: two (65 and 98) were fine muddy sand; two (93 and 101) heterogenous (fine to medium) muddy sand; one (105) heterogeneous (medium to coarse) muddy sand; and one (82) sandy muds (silt/clay content > 30 %) at the centre of the bay.

Sorting coefficients also express these conditions (Tab. 1). Depths of RPD were measured at intertidal sites (Tab. 1): they confirm that sediments were more stable but less oxygenated at the back of Yffiniac Cove (station 4). Temperatures range from about 8.5°C in March to 17.5°C in September (Thouzeau, 1991). Microphytobenthos biomass was estimated by D. Boucher (Bodin *et al.*, 1989).

Intertidal station 4 belongs to the oligohaline fine sand community (with *Macoma baltica* and *Nereis diversicolor*). Intertidal stations 6 and 35 belong to the euhaline fine sand community (facies with *Tellina tenuis* and *Cerastoderma edule*). Intertidal station 37 belongs to an impoverished facies of the latter (with only *Tellina tenuis*). Both intertidal station 27 and subtidal station 65 belong to the clean fine sand community (with *Tellina fabula* and *Magelona filiformis*). Subtidal stations 93, 98 and 101 belong to the muddy fine or heterogeneous sand community with "biogenic contamination" (with *Corbula gibba*, *Aponuphis grubii* and *Hyalinoecia bilineata*). Subtidal station 82 belongs to a more muddy facies of the latter. Finally, subtidal station 105 belongs to the heterogeneous muddy sand community [with *Ampharete grubei*, *Venus ovata* and *Tapes rhomboides* (Gros and Hamon, 1988; Thouzeau and Hamon, 1992)].

Fauna sampling and extraction

Samples were taken in March and July 1988 in the intertidal zone, and in March (April at station 105) and June 1988 in the subtidal zone (Tab. 2 and 3). In the intertidal zone, each sample consisted of four separate cores of 10 cm^2 by 10 cm depth, spaced several metres apart. In the subtidal zone, samples were taken with a modified Reineck corer; four subcores of 10 cm^2 were taken at each station, generally in four different samples. In this subtidal zone, subcores were only 5-6 cm long because of the sediment structure.

Cores were preserved in 5 % formalin, then washed with tap water and filtered through a sieve column [1 mm, 100 and 40 µm mesh size (Bodin, 1977)]. After staining with Rose Bengal, animals were sorted under a stereo-microscope (x 25) and individuals of the different meiofaunal taxa (except Foraminifera) were counted. In order to evaluate spatial heterogeneity, cores were sorted separately. Intertidal samples were subdivided into two parts (0-5 and 5-10 cm) in order to define the vertical distribution of the meiofauna. As nematodes were very numerous, samples were subdivided so as to sort only about four hundred nematodes in each core; other taxa were completely sorted. The following major taxa of the true or temporary meiofauna were counted in this study: nematodes, copepods (*i. e.* harpacticoids, cyclopoids, calanoids, with nauplii), gastrotrichs, turbellarians, rotifers, halacarids, tardigrades, ostracods and kinorhynchs, as well as amphipods, annelids, bivalves, tanaids, cumaceans and isopods.

Table 2

Mean density (No.10 cm^{-2}, four replicate samples) of meiofauna taxa in the intertidal zone (0-10 cm).

Densité moyenne (No.10 cm^{-2}, quatre réplicats) des différents groupes de la méiofaune dans la zone intertidale (0-10 cm).

Stations	4		6		27		35		37	
Months	March	July	March	July	March	July	March	July	March	July
Nematodes	2426	2414	3231	5556	723	747	1059	734	549	1199
Copepods	17	14	17	62	12	39	310	683	8	55
nauplii	13	18	3	7	5	26	4	10	10	46
Halacarids	3	+	+	+	+			1	+	
Gastrotrichs	114	10	30	278	45	8	6	1	25	69
Turbellarians	10	28	105	56	19	103	3	1	219	612
Ostracods	29	161	24	24	9	47	11	10	10	91
Rotifers	44	115	22	163	19	42	30	31	16	30
Tardigrades	7	813	+	134	2	+			17	30
Kinorhynchs										
Amphipods	+	+	+		+	2	+			+
Annelids	2	+	+	+	1	+	2	1	4	3
Bivalves		2	2	+	+	+	+			
Cumaceans				+	+	2	+	+	+	+
Tanaids				+		1	4	+	5	11
Isopods								+		+
Total / 10 cm2	2665	3576	3435	6282	837	1018	1430	1473	864	2147
± S.E.	1190	720	794	1412	218	266	200	378	225	155

Data processing

In each major taxon, animal size classes were determined; this permitted a biomass calculation with the aid of mean individual weights estimated for each size class according to literature data (Coull, 1970; McLachlan, 1977; Faubel, 1982; Widbom, 1984; Bodin *et al.*, 1985; Escaravage *et al.*, 1989). Mean individual weights used for this calculation were considered here as mean annual values. Temporary meiofauna was taken into account as missing in macrofauna values. Biomass is expressed in grammes of organic matter per square metre (ash-free dry weight = AFDW). The average yearly biomass is considered roughly as the arithmetic mean of the winter plus the spring biomass values; it can vary from a sediment type to another according to the size of dominant species.

Table 3

Mean density (No.10 cm^{-2}, four replicate samples) of meiofauna taxa in the subtidal zone (0-6 cm).

Densité moyenne (No.10 cm^{-2}, quatre réplicats) des différents groupes de la méiofaune dans la zone subtidale (0-6 cm).

Stations	65		82		93		98		101		105	
Months	March	June	March	June	March	June	March	June	March	June	April	June
Nematodes	1810	2086	928	1716	806	794	1538	1022	542	868	663	279
Copepods	11	21	57	190	40	76	27	64	110	236	74	204
nauplii	23	55	27	172	45	63	78	103	128	383	53	173
Halacarids	+	+	3	3	+	2		+	11	12	+	4
Gastrotrichs	5				3	+	3	+	25	174	1	1
Turbellarians		9	6	2	2	21	+	5	9	19		2
Ostracods	19	10	5	11	10	12	48	14	49	66	29	39
Rotifers	6	11	37	22	4	2	4	10	8	14	2	12
Tardigrades	+				2		11		6	24	1	3
Kinorhynchs			1	+	1	1	+		2	+		4
Amphipods	+	1	+	+	+	3	+	2	+	2	2	+
Annelids	13	9	18	25	12	11	19	16	7	11	14	21
Bivalves	1	2	4	2		3	2	+	+	+	1	3
Cumaceans		2				+	+	1	+		1	
Tanaids		+		+		+						
Isopods			+			+		5				
Total / 10 cm2	1890	2207	1087	2144	926	990	1732	1243	898	1810	841	745
± S.E.	204	626	310	260	614	150	581	444	215	356	538	202

The Mann-Whitney non-parametric U test was used to test for differences between spring and winter density and biomass values at the eleven sites, and between July densities in the 0-5 and 5-10 cm layers at intertidal sites.

Pearson's correlation coefficients were calculated and linear regression diagrams were plotted to estimate the relation degree between density, biomass and several environmental parameters [mainly Total Organic Matter (TOM), depth, Sorting index (So), % silt/clay]. To do so, depth real figures were replaced with their rank (depth increasing from number 1 to 11) because of the negative (subtidal) and positive (intertidal) values.

Table 4

Winter and late spring nematodes/copepods (N/C) ratios at each station.

Rapports nématodes/copépodes (N/C) d'hiver et de fin de printemps à chaque station.

Stations	N/C Winter	N/C Spring
4	142.7	172.4
6	190.1	89.6
27	60.3	19.2
35	3.4	1.1
37	68.6	21.8
65	164.5	99.3
82	16.3	9.0
93	20.2	10.4
98	57.0	16.0
101	4.9	3.7
105	9.0	1.4

RESULTS

Mean densities (number.10 cm^{-2} ± S.E.) of each major taxa, calculated from four replicated cores of each sample, are provided in Tables 2 (intertidal zone) and 3 (subtidal zone). In the intertidal zone, total densities ranged from about 1 000 ind. 10 cm^{-2} at station 27 to 1 500 ind. 10 cm^{-2} at stations 35 and 37 and more than 3 000 ind. 10 cm^{-2} at stations 4 and 6 (maximum 6 282 ind. 10 cm^{-2} at station 6 in July). In the subtidal zone, total densities ranged from about 800 ind. 10 cm^{-2} at station 105 to 2207 ind. 10 cm^{-2} at station 65 in June. Nematodes were always dominant: nematodes/copepods ratio (N/C) ranged from 1.1 to 190 and from 1.4 to 165 respectively in intertidal and subtidal zones (Tab. 4).

Calculated mean biomass values (g.m^{-2} ± S.E.) are given in Tables 5 (intertidal zone) and 6 (subtidal zone). In the intertidal zone, figures ranged from 0.4 to 1.7 g.m^{-2} in the upper five centimetres, and from 0.1 to 0.6 g.m^{-2} in the lower five centimetres (*i. e.* 0.5 to 2.3 g.m^{-2} for the 0-10 cm layer). At the subtidal sites (0-6 cm), values ranged from 0.5 to 1.1 g.m^{-2}. Considering the different subtidal harpacticoid copepod assemblages defined in another paper (Bodin and Le Guellec, 1992), shallow fine clean sand of stations 65 and 98 showed the highest mean biomass (0.94 g.m^{-2}), probably due to the presence of large size harpacticoid species (*Longipedia scotti*, *Canuella perplexa*, *Ectinosoma normani*, *Halectinosoma propinquum*, *etc.*) at this site. Then we have, in a decreasing order: very muddy sand (0.76 g.m^{-2}), medium badly sorted muddy sand (0.52 g.m^{-2}) and very heterogeneous coarse muddy sand (0.42 g.m^{-2}), the two latter being occupied by many small mesopsammic species.

Table 5

Mean biomass (g.m^{-2} AFDW) of meiofauna in the intertidal zone (0-10 cm).

Biomasses moyennes (g.m^{-2} PSSC) de la méiofaune dans la zone intertidale (0-10 cm).

Stations	4		6		27		35		37	
Months	March	July	March	July	March	July	March	July	March	July
Biomass (g/m2 AFDW)	1.61	1.69	1.79	2.76	0.40	0.57	0.99	1.29	0.46	1.26
± SE (n-1)	± 0.51	± 0.29	± 0.32	± 0.56	± 0.09	± 0.19	± 0.02	± 0.38	± 0.11	± 0.02
Mean biomass	1.65 ± 0.39		2.28 ± 0.67		0.49 ± 0.17		1.14 ± 0.30		0.86 ± 0.43	

Table 6

Mean biomass (g.m^{-2} AFDW) of meiofauna in the subtidal zone (0-6 cm).

Biomasses moyennes (g.m^{-2} PSSC) de la méiofaune dans la zone subtidale (0-6 cm).

Stations	65		82		93		98		101		105	
Months	March	June	March	June	March	June	March	June	March	June	April	June
Biomass (g/m2 AFDW)	0.91	1.22	0.69	1.20	0.47	0.62	0.87	0.76	0.37	0.73	0.54	0.42
± SE (n-1)	± 0.10	± 0.34	± 0.15	± 0.20	± 0.30	± 0.10	± 0.31	± 0.23	± 0.08	± 0.10	± 0.32	± 0.13
Mean biomass	1.07 ± 0.28		0.94 ± 0.31		0.55 ± 0.22		0.81 ± 0.26		0.55 ± 0.21		0.46 ± 0.19	

Table 7

*Pearson's correlation coefficients. Significance level: * = p < 0.05, ** = p < 0.01 (for 9 degrees of freedom, $r_{0.05}$ = 0.6021 and $r_{0.01}$ = 0.7348).*

Coefficients de correlation de Pearson. Degré de signification : * = p < 0.05, ** = p < 0.01 (pour 9 degrés de liberté, $r_{0.05}$ = 0.6021 et $r_{0.01}$ = 0.7348).

	T.O.M.	So index	% silt/clay	median grain size	depth	B winter	B spring
Density winter	-0.4260	-0.2826	-0.3514	-0.2618	-0.6629 *	+0.9716 **	
Density spring	-0.4267	-0.1342	-0.2697	-0.2866	-0.6194 *		+0.9633 **
Biomass winter	-0.3778	-0.3655	-0.2871	-0.2176	-0.7039 *		
Biomass spring	-0.4661	-0.2700	-0.2599	-0.3733	-0.6995 *		
N/C winter	-0.5169	-0.2688	-0.5000	-0.2832	-0.5839		
N/C spring	-0.4501	-0.2315	-0.4077	-0.2304	-0.5931		
mean N/C	-0.4702	-0.2411	-0.4385	-0.2550	-0.5807		
T.O.M.					+0.8456 **		
% silt/clay					+0.6299 *		
So index					+0.2783		

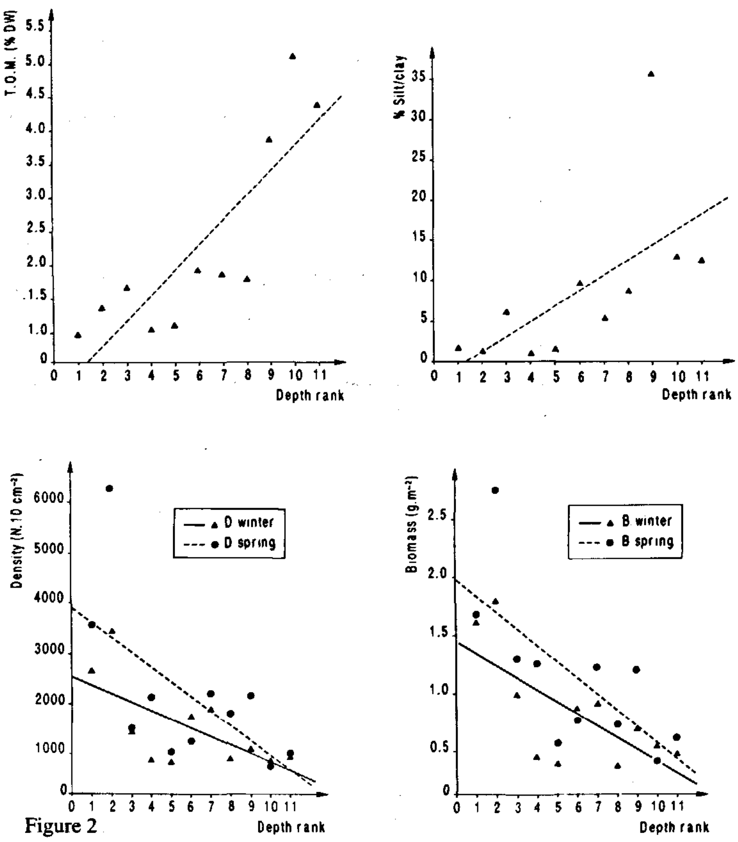

Figure 2

Significant linear regression graphs (least squares method) of T.O.M., % silt/clay, density and biomass versus *depth.*

Droites de régression linéaire significatives (méthode des moindres carrés) de la M.O.T., du pourcentage de pélites, de la densité et de la biomasse en fonction de la profondeur.

On the whole, meiofauna biomass was higher in the intertidal zone than in the subtidal zone and the same gradient for densities is enhanced: values were generally decreasing from the upper stations of the beach to the low water neap, and from the upper to the lower part of the subtidal zone. Pearson's coefficients (Tab. 7) and linear regression diagrams (Fig. 2) indicate a significantly negative correlation between density or biomass and depth ($p < 0.05$).

Comparison with microphytobenthos and macrobenthos

Biomass values of the meiofauna can be compared with those of microphytobenthos (expressed as milligrammes of organic matter per square metre) and macrofauna (expressed as grammes O.M. AFDW per square metre). Chlorophyll *a* and phaeopigment contents were measured in March (minimum) and April (maximum) both in the intertidal and subtidal sites (Bodin *et al.*, 1989). Briefly, highest values of chlorophyll *a* were recorded at stations 6 (the more sheltered) and 101 (3.07 and 1.34 $mg.m^{-2}$ respectively) and lowest values at stations 27, 37, 82 and 98 (0.04 to 0.84 $mg.m^{-2}$). Highest values of phaeopigment were recorded at stations 82 (2.82 $mg.m^{-2}$ in March) and 93 and 105 (8.78 and 8.36 $mg.m^{-2}$ in April), lowest values being recorded at stations 27 and 37 (respectively 0.57 and 0.49 $mg.m^{-2}$) as for chlorophyll *a* (Bodin *et al.*, 1989). Perhaps this is due to the intensive filtration of microphytes by nearby exploited mussel beds (4000 $t.y^{-1}$). So chlorophyll *a* and phaeopigment contents seem to be consistent with meiofauna biomass in the intertidal zone, where food could be a limiting factor for the latter, but not in the subtidal zone.

Considering macrobenthos of the sampling sites (Gros and Hamon, 1988), highest biomass mean values were recorded around intertidal stations 6 and 35 (16.1 $g.m^{-2}$), then subtidal station 82 (9.3 $g.m^{-2}$), which fit also with high biomass values of meiobenthos in those sites. But station 4 showed the smallest value of the bay (3.5 $g.m^{-2}$) where we found the second highest mean value for meiobenthos. Subtidal meiofauna mean biomass was about 4 to 13 times lower than macrofauna biomass, while in the Bay of Douarnenez (Bodin *et al.*, 1985) this ratio varied from 1.4 to 5.6.

DISCUSSION

The distribution of the different taxa among sites was relatively even. However, kinorhynchs were completely absent, and isopods rare, in the intertidal zone, while

Table 8

Mean densities (N.10 cm^{-2}) of nematodes, harpacticoid copepods, nauplii and total meiofauna in 0-5 and 5-10 cm layers of the intertidal zone.

Densités moyennes comparées (N.10 cm^{-2}) des nématodes, des harpacticoïdes, des nauplii et de la méiofaune totale dans les couches 0-5 et 5-10 cm de la zone intertidale.

Stations	4		6		27		35		37	
Months	March	July	March	July	March	July	March	July	March	July
0-5 cm										
Nematodes	1627	1962	2744	3592	517	675	676	564	342	1026
Copepods	17	14	17	60	12	39	308	675	8	54
nauplii	13	18	3	7	5	26	4	9	10	46
Total meiofauna density / 10 cm2	1699	2780	2915	3915	560	919	1014	1264	570	1906
5-10 cm										
Nematodes	799	452	487	1964	206	72	383	170	207	173
Copepods		+	+	2	+		2	8		1
nauplii	+	+	+	+		+		1	+	+
Total meiofauna density / 10 cm2	967	798	524	2368	279	100	417	210	294	242

Table 9

Results of the Mann-Whitney U (two tailed) test comparing March and June-July biomass at each station and 0-5 versus *5-10 cm intertidal densities. Significance level: ns = difference not significant, * = $p < 0.05$, ** = $p < 0.01$.*

Résultats du test U de Mann-Whitney (bilatéral) comparant les biomasses de mars et celles de juin-juillet à chaque station, ainsi que les densités de 0 à 5 et de 5 à 10 cm dans la zone intertidale. Degré de signification : ns = différence non-significative, * = p < 0.05, ** = p < 0.01.

Stations	4	6	27	35	37	65	82	93	98	101	105
Winter/Spring densities											
0-5(6) cm	ns	ns	*	ns	**	ns	**	ns	ns	**	ns
5-10 cm	ns	**	**	ns	ns						
0-10 cm	ns	**	ns	ns	**						
Winter/Spring biomass											
0-5(6) cm	ns	ns	**	*	*	ns	**	ns	ns	**	ns
5-10 cm	ns	**	**	ns	ns						
0-10 cm	ns	*	ns	ns	**						
0-5/5-10cm densities											
winter	ns	**	**	*	**						
spring	**	ns	**	**	**						

tanaids and isopods were poorly represented and copepod nauplii much more numerous in the subtidal zone.

The fact that highest quantitative figures were recorded in the upper tidal level is quite unusual but not unknown: McLachlan (1977) found the same distribution on a South African beach. At that level, fluctuations of abiotic factors (mainly temperature) are generally important, but stations 4 and 6 are also the most sheltered, and food was perhaps more rich and diverse here despite a highly significant ($p < 0.01$) positive correlation between depth and TOM (Tab. 7, Fig. 2).

Considering the taxa recorded in the 0-5 cm and 5-10 cm layers of the intertidal samples (Tab. 8), nematodes and some "true meiobenthic" taxa were still numerous between 5 and 10 cm (gastrotrichs and rotifers were even more numerous in this layer), while "temporary meiobenthos" and copepods were almost absent. The sensitivity of these latter groups to oxygen content is well known. Apart from some mesopsammic forms, most of the harpacticoid copepod species live in the upper centimetres, while many nematodes are often found below 5 cm (Fenchel and Jansson, 1966; McIntyre, 1969; McLachlan, 1978; Joint *et al.*, 1982). Authors such as McLachlan (1978) and Boucher (1980) have shown that this vertical distribution fluctuates seasonally, most of the meiobenthic groups being concentrated near the surface of the sediment (more oxygenated) in summer. But in this survey, both winter and late spring intertidal densities were almost always lower in the 5-10 cm layer (Tab. 8), meaning that oxygen content was probably not a limiting factor in this layer in summer.

Usually, the nematode/copepod (N/C) ratio is negatively correlated with median grain size (Raffaelli and Mason, 1981). Consistent with this hypothesis, the proportion of harpacticoid copepods increased in coarser sands of deep stations 101 and 105. For this reason, there is an almost significant negative correlation between N/C ratio and depth, despite the positive correlation ($p < 0.05$) between the silt/clay content and depth (Tab. 7, Fig. 2). However, this is not obvious with the median grain size; the N/C ratio was even curiously very low in fine silty sand of station 35. Thus, the N/C ratio remains ambiguous as a measure of sediment "quality" (Coull, 1985). Moreover, copepods are proportionally more numerous (except at station 4) in late spring than in winter (Tab. 4), which illustrates the clear annual cycle of this group compared with the "seasonal stability" of nematodes, especially in the English Channel (Warwick and Buchanan, 1971; Boucher, 1980; 1985).

This relative "seasonal stability" of nematodes (by far the most important group in this area) is also noticeable in that differences between supposed winter minima and late spring maxima in density or biomass were weak and significant only at stations 6, 37, 82 and 101 (Tab. 9). It is also true at stations 27 and 35 in the 0-5 cm layer, but winter biomass was higher than spring in 5-10 cm layer at station 27. There were proportionally more intertidal than subtidal

Table 10

Comparison of macro- and meiobenthic biomass (g.m^{-2} AFDW) recorded in different ecosystems, assuming that 1 gC = 12 kcal = 2 g dry weight, AFDW = 17 % wet weight and 80 % dry weight. I.O. = Indian Ocean, A.O. = Atlantic Ocean, N.S. = North Sea, E.C. = English Channel, B.S. = Baltic Sea.

Données comparées sur les biomasses (g.m^{-2} PSSC) relevées dans divers écosystèmes, sachant que 1 gC = 12 kcal = 2 g en poids sec, PSSC= 17 % du poids humide et 80 % du poids sec. I.O. = Océan Indien, A.O. = Océan Atlantique, N.S. = Mer du Nord, E.C. = Manche, B.S. = Mer Baltique.

Ecosystem	Biomass mean or range (g.m-2 AFDW) macrofauna (a)	meiofauna (b)	a/b range	Sources
Intertidal				
Danish Wadden Sea (6 m)		2.0		Smidt, 1951
Algoa Bay (I.O., S-Africa)	0.3-1.7	0.15-0.25	2-6.8	McLachlan, 1977
North Sea (Belgium)	1.2	1.0-1.3	0.9-1.2	Govaere et al., 1980
Wadden Sea (Netherland)	21.6	0.9	24	Kuipers et al., 1981
Peck's Cove (A.O., Canada)	3.0	2.3	1.3	Schwinghamer, 1983
Peck's Cove (A.O., Canada)	1.8	1.6	1.1	Schwinghamer et al., 1986
Balgzand (N.S., Netherland)	21.6	0.6	36	Witte & Zijlstra, 1984
Sylt Island (North Sea)	24	1.6	15	Reise, 1985
Arcachon-sand (A.O., France)	4.6	0.5	9.2	Renaud-Debyser & Salvat, 1963
Arcachon-muddy sand	12.6	2.2	5.7	Castel et al., 1989
False Bay sandstone beach (S-Africa)	31.7-32.1	2.2-3.0	10.7-14.4	Gibbons & Griffiths, 1986
St Brieuc Bay (E.C., France)	3.5-16.1	0.5-2.8	5.8-7	this study
Estuarian intertidal				
New England estuaries (A.O.)		3.9-7.4		Tietjen, 1969
Lynher (E. Channel, G.B.)	8.7	4.2	2.1	Warwick et al., 1979
Ythan (North Sea, G.B.)	53.4	4.1	13	Baird & Milne, 1981
Dollard (N.S., Netherland)	3.8 (1)	1.6 (2)	2.3	(1) Van Es et al., 1980
				(2) Van Es, 1982
Gironde (A.O., France)	7.0 (a)	0.6 (b)	11.7	(a) Bachelet et al., 1981
				(b) Castel et al., 1990
Subtidal				
Buzzards Bay (A.O., 18 m)		0.1-0.5		Wieser, 1960
North Sea-muds		0.6-1.3		McIntyre, 1964
Martha's Vineyard (A.O., 40-465 m)		0.2-0.9		Wigley & McIntyre, 1964
Bermuda platform (A.O., 2-13 m)		0.03-0.3		Coull, 1970
Bermuda Castle Harbor (13 m)		0.5-1.8		Coull, 1970
Kiel Bay (N.S., 6-26 m)		0.05-0.6		Scheibel, 1976
Göta River estuary (N.S., 3-50 m)	0.7-15.4	0.3-0.8	2.8-19.2	Nyholm et al., 1977
North Sea	1.7-2.2	0.6-1.9	1.1-2.8	Govaere et al., 1980
Banyuls (M.S., 14-87 m)	1.9	0.1-0.5	6.8	Guille & Soyer, 1971
Helgoland Bight (N.S., 16-49 m)	1.8-12.2	0.05-0.4	24-90	Stripp, 1969
German Bight (N.S., 35 m)		0.5-1.0		Juario, 1975
Helgoland Bight (N.S., Germ., 35 m)	7.4	0.6	12.3	Gerlach, 1978
Askö-Landsort (B.S., 9-50 m)	7.8	1.0	7.8	Ankar & Elmgren, 1976
Bothnian Bay (5-220 m)	0.15	0.3	0.5	Elmgren, 1980
Bothnian Sea (5-100 m)	10.6	1.1	9.7	Elmgren, 1980
Gullmar Fjord (Sueden, 42-120 m)	3	0.4	7.5	Evans, 1983
Fladen Ground (N.S., 150 m)	3.1	0.25	12.4	De Wilde et al., 1986
South Island (P.O., New Zld., 200 m)	6.1	0.6	10.2	Probert, 1986
Morlaix Bay (E. Channel, France)	4.6	0.4	11.5	Dauvin, 1985
Douarnenez Bay (France, 0-35 m)	3.4-12.8	0.9-2.6	1.4-5.6	Bodin et al., 1985
St. Brieuc Bay (E.C., France, 2-13 m)	9.3	0.5-1.1	8.5-19	this study
Brackish shallow subtidal				
Tvärminne (Finland, 1 m)	7.2	0.8	9	Elmgren & Ganning, 1974
Byfjord (Sueden, 0-16 m)			2.2	Rosenberg et al., 1977
Askö (Baltic Sea, 10 m)	6.2	0.8	7.7	Ankar, 1979
Narragansett Bay (A.O., USA, 7 m)		1.4-5.0		Rudnick et al., 1985
Arcachon reservoirs (0.2-1.5 m)	3.9	2.9	1.3	Castel et al., 1990
West Scotland (1-5 m)	3.0 (1)	0.9 (2)	3.3	(1) McIntyre & Eleftheriou, 1968
				(2) McIntyre & Murison, 1973

significant differences, which is consistent with a temperature determined cycle damping from the littoral towards the sublittoral zones (McIntyre and Murison, 1973). In June-July, higher densities came essentially from copepods and nauplii. The influence of seasonal fluctuations of abiotic factors (mainly temperature) on distribution and reproduction of harpacticoid copepods has often been pointed out, particularly in temperate latitudes (Swedmark, 1964; McIntyre, 1969; Coull, 1970; Hulings and Gray, 1976; Hicks and Coull, 1983).

Comparisons of inhouse-generated biological quantitative data with those derived from the literature are always difficult, especially when differences in methodology are involved (Rudnick *et al.*, 1985). For instance, the sampling operation can be done either with a corer or different types of grab, or possibly by a diver. The sampling season is also important, winter giving densities generally very different from spring or summer ones. From one author to another, the lower sieve mesh size used varies from 37 to 63 mm, sometimes more. In sorting out, temporary meiofauna and Foraminifera are either taken into account or omitted. When there is a dehydration of animals before weighing, temperature and length can also vary (50 to 110°C; 2 to 48 hours or "up to constant weight") according to authors. Also depending on the author, results are indicated in various units (µg, mg or g/10 cm^2 or m^2) of organic matter, carbon (40 or 50 % of the DW), kcalories or kjoules, as wet, dry or ash-free dry weight (80 to 90 % of the DW, less for some taxa). Biomass assessments can also vary according to literature data used to evaluate mean individual weight of the different taxa (conditions of the weighing, measurements done on portions constituted by outsized animals, *etc.*). If animal size classes are carefully determined, meiofauna biomass must vary from a type of sediment to another according to its dominant species: for instance, coarse sands are generally inhabited by small mesopsammic animals and produce low standing stocks.

Modified principally from Rudnick *et al.* (1985) and from Castel *et al.* (1990), Table 10 displays some literature data on macro- and meiobenthic biomass (converted in g.m^{-2} AFDW) in different intertidal and subtidal biotopes, despite the above-mentioned difficulties. In contrast with the "ponderal stability" of the meiofauna, compared with macrofauna, pointed out by some authors (Coull, 1970; Schwinghamer, 1983; Elmgren *et al.*, 1984; Rudnick *et al.*, 1985; Castel *et al.*, 1990), the biomass spectrum seems to be broad. On the whole, highest meiofauna biomasses correspond to estuarian intertidal areas and lowest values were generally recorded in subtidal samples.

In the Bay of St. Brieuc, intertidal zone values (mean biomass = 1.28 g.m^{-2}) were slightly higher than subtidal ones (not significant: p = 0,10). They are in the range of table 10 "intertidal" values, particularly those recorded on the North Sea coast (Govaere *et al.*, 1980; Reise, 1985), also known for its increasing eutrophication, and in Peck's Cove, Canada (Schwinghamer *et al.*, 1986). With a mean biomass of 1.65 and 2.28 g.m^{-2} respectively, stations 4 and 6 (the richest of the bay) approach Dollard estuary (1.6 g.m^{-2}). But these values, much lower than English Channel or North Sea estuarian intertidal figures (around 4 g.m^{-2}), do not reveal serious eutrophication.

Subtidal zone extreme values (mean biomass = 0.73 g.m^{-2}) also correspond to Table 10 figures, particularly those recorded in German Bight (Juario, 1975) and in northern Baltic Sea (Ankar and Elmgren, 1976; Elmgren, 1980). Similar values were also recorded in North Sea (McIntyre, 1964; Govaere *et al.*, 1980). On the other hand, values recorded in the NW Mediterranean Sea were much lower (Guille and Soyer, 1971), and higher values were recorded in Douarnenez Bay, south Brittany (Bodin *et al.*, 1985).

Given the increasing and disastrous impact of organic pollution in several areas (North Sea, Baltic Sea, Adriatic Sea, *etc.*), many authors have concentrated on the consequences for benthic organisms of natural and artificial organic matter inputs to the sediment. Recently, interest has been focused on responses of the meiofaunal components of the benthic communities (Lee *et al.*, 1974; Marcotte and Coull, 1975; Boucher, 1979; Es *et al.*, 1980; Hockin, 1983; Keller, 1984; Gee *et al.*, 1985; Moore and Pearson, 1986; Widbom and Elmgren, 1988; Austen *et al.*, 1989; Radziejewska and Drzycimski, 1990). As for macrofauna (Pearson and Rosenberg, 1978; Pearson, 1980), most of these works lead to the following pattern: a moderate load of organic matter generally induces an increase in meiofauna abundance and species richness, probably due to an enhancement of both the quantity and variety of available food resources (Gee *et al.*, 1985). Then, in the case of a higher load of organic matter, meiofauna abundance can became very high, while biomass and species richness decrease. Lastly, in conditions of excessively high inputs in sheltered areas, anoxic conditions prevail and abundance and diversity can decrease drastically until the disappearance of most species takes place (mainly harpacticoid copepods). Nevertheless, some authors have not found a positive or negative effect of such "pollution" (Widbom and Elmgren, 1988; Austen *et al.*, 1989; Radziejewska and Drzycimski, 1990).

Medium recorded densities and biomass, N/C ratios and very high harpacticoid copepod diversity (*see* Bodin and Le Guellec, 1992) prompt us to think that the Bay of Saint-Brieuc reflects the end of a "first-stage" organic pollution, around "mesotrophic" conditions described by Boucher (1979), below a putative critical level of organic matter content corresponding to a significant increase in abundance (mainly of nematodes). Of course, the exact value of this "critical level" remains to be determined. On the whole, sediment structure, hydrodynamism and depth (*i. e.* stability) seem to be the most important factors in the quantitative distribution of the meiobenthos in this bay.

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