

Benthic Boundary Layer macrofauna from the upper continental slope and the Cap Ferret canyon (Bay of Biscay)

Benthic Boundary Layer
Hyperbenthic sledge
Continental slope
Canyon
Bay of Biscay

Couche d'eau adjacente au fond
Traîneau hyperbenthique
Talus continental
Canyon
Golfe de Gascogne

Jean-Claude DAUVIN ^a, Jean-Claude SORBE ^b and Jean-Claude LORGERE ^c

^a Muséum National d'Histoire Naturelle, Laboratoire de Biologie des Invertébrés Marins et Malacologie, CNRS-URA 699, 57, rue Cuvier, 75231 Paris Cedex 05, France.

^b Laboratoire d'Océanographie Biologique, Université de Bordeaux I, 2, rue Jolyet, 33120 Arcachon, France.

^c Station Biologique de Roscoff, CNRS-UPR 4601 et Université Paris VI, B.P. 74, 29680 Roscoff, France.

Received 20/07/94, in revised form 3/01/95, accepted 6/01/95.

ABSTRACT

A new version of a hyperbenthic sledge with four superposed nets was used from 346 m to 3070 m depth in the southern part of the Bay of Biscay. This gear collects the near-bottom swimming macrofauna. The dominant zoological groups are asellot isopods and gammaridean amphipods. Two types of animal density gradient are observed: a vertically decreasing gradient from the lower to the upper level of the sledge at each station; and a depth-related decreasing gradient from the upper continental slope to the lowest stations in the Cap Ferret Canyon. Three different assemblages can be distinguished: between 346 m and 523 m on muddy sand; between 600 m and 1100 m on mud; and in Cap Ferret Canyon between 3040 m and 3070 m on mud. These results are compared with similar data on deep hyperbenthic communities from other areas of the northeastern Atlantic.

RÉSUMÉ

La macrofaune de la couche d'eau adjacente au fond du talus continental et du Canyon du Cap-Ferret (Golfe de Gascogne).

Une nouvelle version de traîneau hyperbenthique avec quatre filets superposés a été utilisée entre 346 et 3070 m de profondeur dans la partie méridionale du Golfe de Gascogne. Cet engin échantillonne toute la macrofaune nageuse vivant juste au-dessus du fond. Les principaux groupes zoologiques échantillonnés sont les Isopodes Asellotes et les Amphipodes Gammaridés. La répartition de la faune montre deux types de gradients verticaux : une décroissance de la densité des organismes du filet inférieur du traîneau au filet supérieur montrant une concentration des organismes à proximité de l'interface eau-sédiment, et une décroissance de la densité des organismes depuis les stations du talus continental les plus

riches aux stations du Canyon du Cap Ferret les plus pauvres. Trois grands types d'assemblages faunistiques ont été distingués : celui des fonds de sables vaseux entre 346 m et 523 m de profondeur, celui des vases du bathyal supérieur entre 600 m et 1000 m de profondeur, et celui des vases profondes du Canyon du Cap Ferret entre 3040 m et 3070 m de profondeur. Ces résultats sont comparés avec des données semblables acquises sur les communautés hyperbenthiques profondes du nord-est Atlantique.

Oceanologica Acta, 1995, 18, 1, 113-122.

INTRODUCTION

The hyperbenthic fauna, often designated as the suprabenthos, includes bottom plankton, demersal zooplankton and benthopelagic plankton, as well as all bottom – dependent animals that migrate on a regular daily or seasonal basis (Brunel *et al.*, 1978). Although some hyperbenthic communities from the infralittoral and circalittoral depths have now been studied (see Hesthagen, 1970; Brunel *et al.*, 1978; Sorbe, 1984; Sainte-Marie and Brunel, 1985; Chevrier *et al.*, 1991; Wildish *et al.*, 1992), the deeper ones from the bathyal zone remain unknown. Deep suprabenthic fauna could be an important element in the food chain in the deep sea, as these fauna may ingest organic matter within the Benthic Boundary Layer (BBL). This was the hypothesis proposed by J.-C. Sorbe in a study under the French "ECOMARGE" programme, which evaluated the impact of sedimenting particulate matter in the deep sea. Sampling at these depths required a sledge that could quantitatively collect the hyperbenthic fauna in the water layer adjacent to the sea floor. Over some fluid sediments, however it is difficult to sample only the swimming fauna due to the sledge biting into the bottom, disturbing the surface and producing a resuspension of sediment, epi- and infauna (Hessler, pers. comm.). Accordingly, the fauna collected by the sledge, particularly in the lower net, corresponds to the benthic boundary layer (BBL) macrofauna (Wildish *et al.*, 1992): *i.e.* zooplankton, invertebrate larvae and drifting epifauna and infauna, as well as hyperbenthic fauna *sensu* Brunel *et al.* (1978). Wishner (1980) used an opening-closing net attached to the Deep Tow instrument of the Scripps Institution to collect zooplankton of the BBL. Horizontal transects with the Deep Tow system were made from 10 to 100 m above the bottom at depths from about 1000 to 3200 m in the Pacific Ocean. Later, benthopelagic zooplankton was collected in the BBL at 1 to 50 m above the bottom using a multiple opening-closing net system attached to the Alvin submersible (Gowing and Wishner, 1986; Wishner and Gowing, 1987). Nevertheless, with these zooplankton samplers, the water column just above the sediment was not sampled. The sledge used in the present work is able to collect the BBL fauna in the first metre above the sea bottom.

In this note, we give the composition of the benthic boundary layer macrofauna, as sampled with a new hyperbenthic sledge from the southern part of the Bay of Biscay at depths between 346 m and 3070 m.

THE SLEDGE

The principle of the BBL sledge (Fig. 1) is based on the GIROQ version of the MACER sledge (Brunel *et al.*, 1978) as modified by Wildish *et al.* (1992). The modifications comprise the addition of two boxes and two nets to permit sampling of the benthic boundary layer macrofauna at four levels; the lower box theoretically samples the fauna 10 cm above the bottom (Dauvin and Lorgeré, 1989). The frame is made of 30-mm stainless steel and constructed in two parts that can be dismantled. Its total length is 4.2 m, width 1.14 m and height 1.51 m; in the air, its weight is about 300 kg. The anterior part of the sledge (AP), 2.03 m in length, holds four superposed boxes (B1, B2, B3 and B4), an opening-closing mechanism (OCM) and two lateral fins (LF) that stabilize the sledge during descending and rising motions. Four standard plankton nets with 0.5 mm mesh (no 0) are hooked behind the boxes. The sledge slides over the seabed on two lateral skates; a stainless steel sheet between the skates prevents sinking into the mud. The posterior part (PP) of the sledge, dismantled and light, assures the protection and the support of the nets and the collectors. The sledge was redesigned and built by Quemener Manufacturing (Saint-Pol de Léon, Finistère, France).

The width of each box is 0.60 m and the height 0.30 m; the surface area of opening is 0.18 m². The corresponding nets sample at four levels above the sea-bed: 0.10 to 0.40 m (net 1); 0.45 to 0.75 m (net 2); 0.80 to 1.10 m (net 3); and 1.15 to 1.45 m (net 4); each has a "TSK" flow-meter fixed in the middle of the box by three stainless steel bands. A window (W) on the side of each box allows reading of the number of revolutions of its propeller.

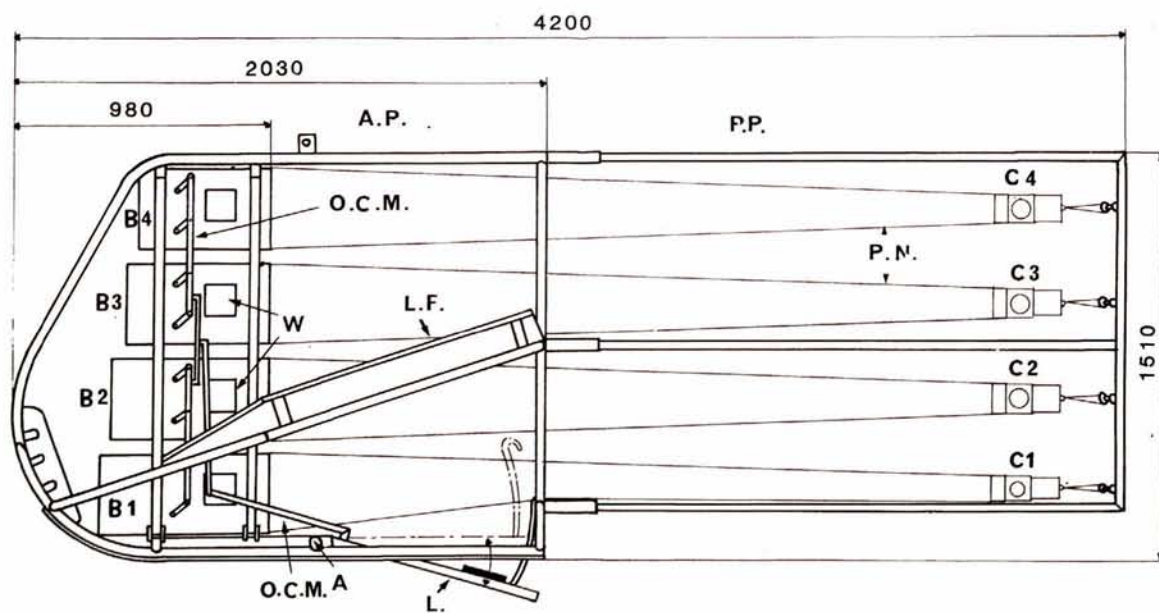
The opening-closing mechanism is similar that described by Brunel *et al.* (1978). Two shutters open (horizontal position) or close (vertical position) the door of the boxes by means of a lead-weighted lever (L) located under the sledge. The lever pivots on an axle (A) welded to each side of the sledge. The door is open when the sledge comes into contact with the sea bed and closes automatically whenever the sledge leaves the bottom to avoid contaminating BBL samples.

STUDY AREA AND SAMPLING

The fifteen surveyed stations were located off Arcachon Bay on the continental slope at depths between 346 m and



(a)



(b)

Figure 1

New version of the Macer-GIROQ hyperbenthic sledge. a) Photograph of the sledge. b) Lateral schematic view : A.P. : anterior part; B1 : box 1; B2 : box 2; B3 : box 3; B4 : box 4; O.C.M. : opening-closing mechanism; L.F. : lateral fins; L. lever; A. : axle; W. : window; P.P. posterior part; P.N. : plankton net; C1 : collector 1; C2 : collector 2; C3 : collector 3; C4 : collector 4 (lengths in mm).

Nouvelle version du traîneau hyperbenthique Macer-GIROQ. a) Photographie du traîneau. b) Vue latérale schématique : A.P. : partie antérieure ; B1 : boîte 1 ; B2 : boîte 2 ; B3 : boîte 3 ; B4 : boîte 4 ; O.C.M. : mécanisme d'ouverture-fermeture ; L.F. : stabilisateurs latéraux ; L : levier ; A. : axe ; W. : fenêtre ; P.P. partie postérieure ; P.N. : filet à plancton ; C1 : collecteur 1 ; C2 : collecteur 2 ; C3 : collecteur 3 ; C4 : collecteur 4 (longueurs en mm).

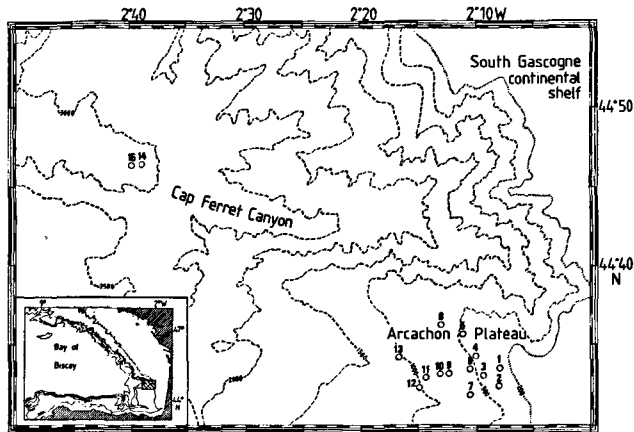


Figure 2

Station location map for Arcachon Plateau and Cap Ferret Canyon.

Carte de localisation des stations du talus continental et du canyon du Cap Ferret.

1099 m (Arcachon Plateau) and in Cap Ferret Canyon at 3040 and 3070 m (Fig. 2; Tab. 1). The upper slope stations (1 to 4) were on muddy sands, and the deeper ones (5 to 15) were muddy (Elizalde *et al.*, 1993a). In these muds, the sledge may bite into the upper fluid sediment (5 to 10 cm, Elizalde *et al.*, 1993a), simultaneously sampling endo- and epi-benthic animals. This phenomenon may also lead to the resuspension of the animals into the near-bottom water layer (Hessler, pers. comm.). So, on deep sea sediments, the fauna collected by a sledge may be a mixture of true hyperbenthos and an unknown fraction of the endo- and epibenthos.

The sledge was towed at about 1.5 to 2 knots. A pinger, used at both canyon stations, was fixed on the towline 50 m ahead of the sledge and kept in position at 40 m above the sea bottom, permitting knowledge of sledge contact with the sea bed. The stations were sampled during three cruises in 1989: in April and May (samples 1 to 4, 6, 7, 9 to 13) and in July (samples 5, 8, 14 and 15). All samples were collected by day except samples 6 and 13, which were collected at night.

The volume of filtered water in m^3 was calculated using the following formula: $V = N_t \cdot p \cdot S$, with N_t = number of rotor revolutions, p = rotor constant (0.152) given by the Tsurumi-Seiki Co., Ltd, Japan, and S = net opening area ($0.18 m^2$). The mean filtered water volume for the four levels varied from $51.5 m^3$ to $389.3 m^3$ (Tab. 1). Four mean filtered volumes ranged between 50 and $100 m^3$, six between 100 and $150 m^3$, two between 150 and $200 m^3$, and two between 200 and $300 m^3$; one was greater than $350 m^3$ (Tab. 1); the mean filtered volume was $150.6 m^3$. The sampled area in m^2 at each station was calculated using the formula: $S = N_t \cdot p \cdot W$, where W = width of sampling box, 0.6 m (Tab. 1). The sampled surface varied between 171 and $1298 m^2$ with three samples under $300 m^2$, seven samples between 300 and $500 m^2$, and three samples greater than $700 m^2$.

Sediment was found in variable quantities in the lower net, indicating digging into the seabed and/or the presence of particles resuspended by the towing cable just ahead of the

sledge, and consequently contamination by benthic epi- and infauna. The volume of sediment obtained was dependent on the nature of the bottom: on muddy sand on the upper part of the slope (300 m-500 m), the quantity of collected sediment was insignificant: 0 to $5 cm^3$; on the mud (600 m-3070 m), the volume of sediment was higher and reached $600 cm^3$ in some samples.

Live fauna was fixed on board with 10 % neutral formalin and sorted under a dissecting microscope; animals were preserved in 70 % alcohol. The collected fauna was then sorted into various taxa. Species were identified and counted, excluding zooplanktonic and non-crustacean components (copepods, ostracods, polychaetes, molluscs, echinoderms). The density of species was calculated and expressed as number of individuals per $100 m^3$ or as number of individuals per $100 m^2$, in order to compare our data with previously published data on deep Atlantic communities.

RESULTS

Altogether 38,460 individuals were collected at the 15 stations (15 hauls and 57 samples), with a mean of 2564 individuals per station. The number of individuals collected varied between 470 in station 14 and 8242 at station 5 (Tab. 2). The density varied from $1.89 ind. m^{-2}$ at station 4 to $15.88 ind. m^{-2}$ at station 5. The two richest stations (8 and 9) were sampled during the summer. On the muddy sand stations (1 to 4), the density values ranged between 4.73 to $9.46 ind. m^{-2}$ with a mean density of $6.68 \pm 2.03 ind. m^{-2}$ ($x \pm s.d.$: standard deviation). On the muddy slope stations, excluding summer stations, the density varied between 1.89 to $5.97 ind. m^{-2}$ with a mean density of $3.20 \pm 1.40 ind. m^{-2}$ ($x \pm s.d.$). The relationship between density and depth at the stations from the continental slope, excluding stations 5 and 8, was: $N. ind. m^{-2} = -0.0063 depth + 8.7654$ ($n = 11$; $r = -0.6981$). The mean density for the two summer stations 5 and 8 reached $14.87 \pm 1.43 ind. m^{-2}$. The mean density for the two canyon stations 14 and 15 was lower: $2.13 \pm 0.34 ind. m^{-2}$ ($x \pm s.d.$). These results show a depth-related decreasing density gradient and suggest a seasonal variation of the density of the slope macrofauna.

Isopoda accounted for some 50 % of the collected fauna; Amphipoda, 22.8 %; Mysidacea, 12.8 %; Cumacea, 6.3 %; and Euphausiacea, 5.1 %. The other groups accounted for 0.03 to 1.1 % of the total specimens.

The density of Mysidacea fluctuated between 0.28 and $2.83 ind. m^{-2}$ on the Arcachon Plateau and was very low in the Cap Ferret Canyon. The density of Amphipoda fluctuated between 0.53 and $1.48 ind. m^{-2}$ except for stations 5, 8 and 9 where it reached 2.68, 3.70 and $2.63 ind. m^{-2}$ respectively. The density of Cumacea was low in the upper part of the Arcachon Plateau (346 m-523 m): 0.03 to $0.10 ind. m^{-2}$, and then fluctuated between 0.19 and $0.56 ind. m^{-2}$ for the deeper stations. The density of Isopoda was higher than $2.0 ind. m^{-2}$ in the upper part of the Arcachon Plateau and lower than $2.0 ind. m^{-2}$ between 600 m and 1100 m from the Arcachon Plateau and in the Cap Ferret Canyon,

Table 1

Main characteristics of the sampling data for the hyperbenthic hauls carried out on the Arcachon plateau and the Cap Ferret Canyon. - no data; * no sample.

Principales caractéristiques des différents traits de traîneaux sur les stations du talus continental et du canyon du Cap Ferret. - pas de données, * pas d'échantillon biologique.

Station	Position and depth in m at the beginning and the end of the tow	Day/ Night	Volume of filtered water in m ³				Mean filtered volume in m ³ ± SD	Sampled area in m ²
			Net 1	Net 2	Net 3	Net 4		
1	44°33,30'N - 2°08,30'W	346 D	150	154	153	158	153.8 ± 3.3	512
	44°33,20'N - 2°08,30'W	347						
2	44°32,58'N - 2°08,17'W	390 D	50	49	55	52	51.5 ± 2.6	171
	44°32,55'N - 2°08,12'W	383						
3	44°33,11'N - 2°09,85'W	425 D	110	111	112	128	115.3 ± 8.5	384
	44°33,02'N - 2°09,98'W	437						
4	44°34,38'N - 2°10,18'W	485 D	138	117	144		133.0 ± 14.2	443
	44°34,29'N - 2°10,07'W	484						
5	44°35,57'N - 2°11,21'W	523 D	162	155	156	151	156.0 ± 4.5	519
	44°35,64'N - 2°10,66'W	522						
6	44°33,40'N - 2°10,70'W	608 N	240	243	254	232	242.3 ± 9.1	807
	44°33,40'N - 2°10,70'W	611						
7	44°31,90'N - 2°10,80'W	660 D	251	279	287	298	278.8 ± 20.1	928
	44°31,70'N - 2°10,80'W	714						
8	44°36,21'N - 2°12,84'W	714 D	105	111	115	119	112.5 ± 6.0	375
	44°36,52'N - 2°12,95'W	708						
9	44°33,22'N - 2°12,48'W	740 D	92	109	112	131*	111.0 ± 16.0	370
	44°33,11'N - 2°12,59'W	754						
10	44°33,10'N - 2°13,13'W	791 D	63	101	104	126*	98.5 ± 26.1	328
	44°33,02'N - 2°13,09'W	790						
11	44°32,89'N - 2°14,24'W	923 D	72	80	82	101*	83.8 ± 12.3	279
	44°32,79'N - 2°14,32'W	924						
12	44°32,30'N - 2°15,10'W	1024 D	120	139	153	161	143.8 ± 18.0	477
	44°32,00'N - 2°15,10'W	1043						
13	44°34,19'N - 2°16,18'W	1097 N	98	118	116	127	114.8 ± 12.1	382
	44°34,10'N - 2°16,50'W	1099						
14	44°46,24'N - 2°38,57'W	3040 D	71	71	67	90	74.8 ± 10.3	249
	44°46,33'N - 2°38,70'W	3042						
15	44°46,27'N - 2°39,49'W	3058 D	492	354	377	334	389.3 ± 70.7	1298
	44°46,29'N - 2°39,77'W	3070						

except at station 8 where the Asellota *Munnopsurus atlanticus* Bonnier, 1896 had a density of 6.3 ind. m⁻², accounting for 81 % of the Isopoda and 45 % of the collected fauna. Tanaidacea densities were low, but show an increasing trend with depth. The density Euphausiacea fluctuated between 0.04 and 1.0 ind. m⁻² on the Arcachon Plateau and was very low in the Cap Ferret Canyon. The density of Decapoda was higher than 0.10 ind. m⁻² in the upper part of the Arcachon Plateau and lower than 0.10 ind. m⁻² at

greater depths except at station 8; its density was very low in the Cap Ferret Canyon.

Table 3 shows the vertical distribution of the fauna above the bottom for samples 8 (714-708 m), 12 (1024-1043 m) and 15 (3058-3070 m). In each sample, we observed a drastic reduction of the collected fauna between net 1 and net 2; this trend was most pronounced at station 8. We also observed a slight decrease in abundance between net 2 and the upper nets 3 and 4, suggesting that the hyperbenthic

Table 2

Abundance (No. ind.) and density ($N.m^{-2}$) of the fauna collected by the four nets of the sledge (April, May and July 1989). Stations 1 to 13 : Arcachon Plateau; stations 14 and 15 : Cap Ferret Canyon.

Abondance (No. ind.) et densité ($N. m^{-2}$) de la faune échantillonnée dans les quatre filets du traîneau (avril, mai et juillet 1989). Stations 1 à 13 : talus continental, stations 14 et 15 : canyon du Cap Ferret.

Station		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	TOTAL
Pycnogonida	No. ind	0	0	0	0	0	0	0	2	0	0	0	0	0	22	111	135
	$N. m^{-2}$	0	0	0	0	0	0	0	0.005	0	0	0	0	0	0.09	0.09	
Nebaliacea	No. ind	0	0	0	0	1	0	0	0	1	0	0	0	7	2	0	11
	$N. m^{-2}$	0	0	0	0	0.002	0	0	0	0.003	0	0	0	0.02	0.01	0	
Mysidacea	No. ind	282	72	399	416	1471	457	386	526	245	92	174	275	111	5	24	4935
	$N. m^{-2}$	0.55	0.42	1.04	0.94	2.83	0.57	0.42	1.4	0.66	0.28	0.62	0.58	0.29	0.02	0.02	
Amphipoda	No. ind	313	109	569	246	1389	895	500	1389	973	319	405	417	403	131	726	8784
	$N. m^{-2}$	0.61	0.64	1.48	0.56	2.68	1.11	0.54	3.7	2.63	0.97	1.45	0.87	1.05	0.53	0.56	
Cumacea	No. ind	32	5	39	13	282	265	255	209	187	105	115	240	204	48	437	2436
	$N. m^{-2}$	0.06	0.03	0.1	0.03	0.54	0.33	0.27	0.56	0.51	0.32	0.41	0.5	0.53	0.19	0.34	
Isopoda	No. ind	2348	402	2422	1766	5027	1301	401	2931	719	160	112	70	68	222	1573	19522
	$N. m^{-2}$	4.59	2.35	6.31	3.99	9.69	1.61	0.43	7.82	1.94	0.49	0.4	0.15	0.18	0.89	1.21	
Tanaidacea	No. ind	0	0	0	1	4	1	0	5	1	3	1	60	16	16	89	197
	$N. m^{-2}$	0	0	0	0.002	0.008	0.001	0	0.01	0.003	0.009	0.004	0.13	0.04	0.06	0.07	
Euphausiacea	No. ind	434	171	151	55	19	247	173	91	51	58	66	241	87	22	107	1973
	$N. m^{-2}$	0.85	1	0.39	0.12	1.04	0.31	0.19	0.24	0.14	0.18	0.24	0.51	0.23	0.09	0.08	
Decapoda	No. ind	53	50	51	47	43	36	33	43	26	9	10	4	13	2	5	425
	$N. m^{-2}$	0.1	0.29	0.13	0.11	0.08	0.04	0.04	0.11	0.07	0.03	0.04	0.01	0.03	0.01	0.004	
Pisces	No. ind	2	0	2	0	6	3	5	2	7	4	1	8	1	0	1	42
	$N. m^{-2}$	0.004	0	0.005	0	0.01	0.004	0.005	0.005	0.02	0.01	0.004	0.02	0.003	0	0.001	
TOTAL	N. ind.	3464	809	3633	2544	8242	3205	1753	5198	2210	750	884	1315	910	470	3073	38460
	$N. m^{-2}$	6.77	4.73	9.46	5.74	15.88	3.97	1.89	13.86	5.97	2.29	3.17	2.76	2.38	1.89	2.37	

fauna was concentrated just above the sea floor. Three main groups could be identified in relation to their swimming activity: those with low swimming activity: Cumacea and Tanaidacea; those with moderate swimming activity: Amphipoda, Isopoda and Mysidacea; and the rest with high swimming activity: Euphausiacea.

The analysis of the BBL macrofauna at a specific level is now available for stations 3, 8 and 12 (respectively stations A, B, and C from Elizalde *et al.*, 1993b). Table 4 shows density values for some selected species in the four near-bottom water layers (sledge samples), and in the 5-10 cm oxidized uppermost layer of the sediment (benthic samples collected with a Smith McIntyre grab on muddy sand at 400 m, and with a Flusha box corer on mud at 700 m, Elizalde *et al.*, 1993a). Most of these species selected from the sledge samples are not represented in the benthic samples, probably due to patchiness and the small area investigated by the grab and the box corer (respectively 0.1 and 0.065 m^{-2} per sample; seven replicates at each station) and to the poor sampling performance of these gears for motile species. The Mysidacea *Paramblyops rostrata*, the Amphipoda *Halice abyssii*, *Andaniexis mimonectes*, *Rhachotropis distincta* and the Isopoda *Munnopsurus atlanticus* are exclusively sampled in the near-bottom water layers and apparently absent in the sediment. The Amphipoda *Cheirocratus intermedius*, *Harpinia laevis*, and the Tanaidacea *Typhlotanais* sp. are found in the bottom

samples and in the lowermost level of the sledge. The Amphipoda *Harpinia excavata*, the Mysidacea *Parapseudomma calloplura*, the Cumacea *Campylapsis sulcata*, and the Tanaidacea *Ilyarachna longicornis* are present only in the lowermost level of the sledge. So, some of the species are surprisingly absent in benthic samples, whilst others are well represented in the sediment as expected and are also present in the lower net of the sledge. Two possible interpretations are: contamination of the lower net by digging of the sledge into the sediment, especially on muddy bottoms; and escape reaction by epi- or infauna into the near-bottom layer due to sledge disturbance.

DISCUSSION

The BBL sledge acts as a zooplankton net working in the benthic boundary layer; it concentrates the fauna adjacent to the sea floor. The quantity of material collected with this type of sampler will permit further dynamic studies on deep-sea communities and dominant species.

These results furnish the first data for the benthic boundary layer macrofauna of the upper part of the continental slope (300-1100 m) and the bathyal zone in the southern part of the Bay of Biscay. Three different faunal assemblages

Table 3

Density (N. ind. 100 m⁻³) of the major taxa collected in the four near-bottom water layers sampled by the sledge. Stations 8 and 12 : Arcachon Plateau; station 15 : Cap Ferret Canyon.

Densité (N. ind. 100 m⁻³) des principaux taxa échantillonnés près du fond par le traîneau. Stations 8 et 12 : talus continental, station 15 : canyon du Cap Ferret.

Sample	Water layer (m)	0.10-0.40	0.45-0.75	0.80-1.10	1.15-1.45
8	Pycnogonida	1.9	0.0	0.0	0.0
	Mysidacea	457.1	19.8	11.3	9.2
	Amphipoda	1162.9	98.2	32.2	18.5
	Cumacea	191.4	4.5	1.7	0.8
	Isopoda	2607.6	115.3	33.9	21.8
	Tanaidacea	4.8	5.0	0.0	0.0
	Euphausiacea	1.9	21.6	23.5	31.9
	Decapoda	34.3	4.5	1.7	0.0
	Pisces	1.0	0.9	0.0	0.0
	TOTAL	4462.9	264.8	104.3	82.2
12	Mysidacea	30.8	28.1	73.9	53.4
	Amphipoda	293.3	24.5	13.1	6.8
	Cumacea	190.0	2.9	2.6	2.5
	Isopoda	55.8	2.2	0.0	0.0
	Tanaidacea	49.2	0.7	0.0	0.0
	Euphausiacea	4.2	54.0	50.3	52.2
	Decapoda	0.0	0.0	0.7	1.9
	Pisces	1.7	3.6	0.0	0.6
	TOTAL	625.0	116.0	140.6	117.4
	15	Pycnogonida	21.5	1.1	0.0
Mysidacea		2.0	1.4	1.9	0.6
Amphipoda		76.0	70.7	19.6	8.4
Cumacea		84.8	4.5	0.3	0.9
Isopoda		275.2	45.8	11.6	3.9
Tanaidacea		16.5	1.1	0.5	0.6
Euphausiacea		0.0	12.7	11.6	5.4
Decapoda		0.4	0.3	0.3	0.3
Pisces		0.0	0.3	0.0	0.0
TOTAL		476.4	137.9	45.8	20.4

could be distinguished. In the upper part of the Arcachon Plateau between -346 and -523 m, on muddy sand influenced by the Atlantic water mass (temperature: about 11°C; salinity: 35.52 PSU), the fauna is characterized by high densities with dominance of Asellota Isopoda. At intermediate depths, between 600 and 1100 m, on mud in Mediterranean outflow water with high salinity (observed values at 1000 m depth in Cap Ferret Canyon: 9.6 °C and 35.76 PSU), amphipods are dominant, except at station 8; there is also a significant density of Cumacea. Furthermore, the intermediate Mediterranean water is identified northwards and influences the bathymetric zonation of the bathyal benthic fauna of the Rockall Trough (Gage, 1986). In the Cap Ferret Canyon stations (near-bottom temperature and salinity: 2.6°C and 34.92 PSU), the fauna is dominated by Isopoda; there are low abundances of Mysidacea, Euphausiacea and Decapoda, and significant amounts of Pycnogonida and Tanaidacea.

Only few comparisons can be made with other deep Atlantic studies (Dahl *et al.*, 1976; Laubier and Sibuet, 1979). Due to the disparity in the sampling method, only the data obtained with an the epibenthic sledge are retained for comparisons (Tab. 5). The hyperbenthic sledge gave higher values than the epibenthic sledge for Mysidacea, Amphipoda, and Isopoda, and lower values for Tanaidacea. Estimations of the density of Pycnogonida and Cumacea were variable from station to station and from gear to gear.

Tanaidacea and Cumacea collected by the sledge have a low swimming activity, as shown by their vertical distribution pattern (mainly abundant in the sediment and in the near-bottom water layer; Tables 3 and 4). Elizalde *et al.* (1993b) identified three tanaid species at station 12: *Sphyrapus malleolus*, *Apseudes spinosus* and *Typhlotanais* sp.; 98.4 % of the collected individuals were found in net 1. At the same station, 22 cumacean species were recorded, and for the two dominant ones (*Epileucon pusillus* and *Makrokyllindrus longipes*), 98 % of the specimens were sampled in net 1. Most tanaid species have a typically benthic behaviour (Holdich and Jones, 1983); they live in constructed tubes on the surface of the substratum or burrow into the uppermost layer of the sediment (Gardiner, 1975; Bird and Holdich, 1984, 1989). Nevertheless, some species are known to be well adapted for a natatory lifestyle (Bird and Holdich, 1989) and "swimming males" have been captured as high as 100 m above the abyssal substratum (Kudinova-Pasternak, 1970). Cumacea are typically benthic species which can perform vertical migrations in the water column at night (Jones, 1976; Kaartvedt, 1986). Neritic species may migrate up to the most superficial layer of the ocean (Macquart-Moulin, 1991) whereas in the deep-sea forms the amplitude of such vertical migrations is restricted to the benthic boundary layer (Kaartvedt, 1989; Elizalde, 1994).

The swimming activity of the benthic Amphipoda increases at night and a variety of nocturnal migration patterns may be found in the near-bottom water layer (Sainte-Marie and Brunel, 1985). From our results, some species must be considered as endobenthic or with low swimming activity, *e.g.* *Harpinia* spp. (Elizalde *et al.*, 1993b); inversely, *Rhachotropis* spp. and *Halice abyssis* are typically hyperbenthic species with a strong swimming behaviour. Generally, bathyal Amphipoda do not swim beyond 15-20 m above the bottom (Kaartvedt, 1989; Elizalde, 1994); in the deeper abyssal plain, the small scavenging amphipods (demersal guild) have their greatest abundance within 1 m of the sediment (Ingram and Hessler, 1983).

Most of the collected Isopoda species are mainly concentrated in the lower net; some of them, such as *Ischnomesus* sp. and *Haplomesus* sp. (Elizalde *et al.*, 1993b) are considered as endobenthic components (Harrison, 1989; Hessler and Strömberg, 1989). *Ilyarachna longicornis* is known to burrow backwards into the sediment as observed by Hessler and Strömberg (1989). Surprisingly, in the southern part of the Bay of Biscay, it is not sampled by benthic gears (Tab. 4); although the greatest densities are recorded in the near-bottom water layer sampled by the sledge, the presence of some individuals in samples from nets 2 and 3 (Elizalde *et al.*, 1993b) reflects the swimming ability of this species which belongs to the temporary hyperbenthic fauna. While not collected at all by benthic samplers

Table 4

Comparative densities (N. ind. 100 m⁻²) for some selected Peracarida on muddy sand (- 400 m depth) and mud (- 700 m depth) from the upper part of the southern Bay of Biscay continental slope. Sampling undertaken with benthic gears (SMI / Smith McIntyre grab; KF: Flusha box corer; see Elizalde et al., 1993a and Elizalde et al., 1993b) and the hyperbenthic sledge.

Mys : Mysidacea, Amp : Amphipoda, Cum : Cumacea, Iso : Isopoda, Tan : Tanaidacea.

Comparaison des densités (N. ind. 100 m⁻²) de quelques Péracarides échantillonnés sur les sables vaseux (400 m de profondeur) et sur les vases (700 m de profondeur) de la partie supérieure du talus continental. Échantillonnage benthique (SMI / benne Smith McIntyre ; KF : carrolier Flusha ; voir Elizalde et al., 1993a et Elizalde et al., 1993b) et échantillonnage au traîneau.

Mys : Mysidacea, Amp : Amphipoda, Cum : Cumacea, Iso : Isopoda, Tan : Tanaidacea.

Muddy sand					
Gear	SMI	Sledge			
Level		Net 1	Net 2	Net 3	Net 4
Taxa					
<i>Parapseudomma calloplura</i> (Mys)	0.0	16.6	2.9	0.3	0.0
<i>Paramblyops rostrata</i> (Mys)	0.0	48.4	6.3	0.5	0.3
<i>Cheirocratus intermedius</i> (Amp)	571.4	4.4	0.0	0.0	0.0
<i>Halice abyssii</i> (Amp)	0.0	14.6	1.0	0.0	0.0
<i>Harpinia laevis</i> (Amp)	142.9	1.0	0.0	0.0	0.0
<i>Rhachotropis</i> spA. (Amp)	142.9	14.3	1.0	0.8	0.0
<i>Campylaspis sulcata</i> (Cum)	0.0	4.2	0.0	0.0	0.0
<i>Ilyarachna longicornis</i> (Iso)	0.0	30.7	0.0	0.0	0.0
<i>Munnopsurus atlanticus</i> (Iso)	0.0	475.8	75.8	8.3	1.6
Mud					
Gear	KF	Sledge			
Level		Net 1	Net 2	Net 3	Net 4
Taxa					
<i>Parapseudomma calloplura</i> (Mys)	0.0	16.3	0.0	0.0	0.0
<i>Paramblyops rostrata</i> (Mys)	0.0	22.1	0.0	0.3	0.0
<i>Andaniexis mimonectes</i> (Amp)	0.0	93.8	4.8	0.3	1.1
<i>Halice abyssii</i> (Amp)	0.0	13.6	2.4	0.8	0.3
<i>Harpinia excavata</i> (Amp)	0.0	1.6	0.0	0.0	0.0
<i>Rhachotropis distincta</i> (Amp)	0.0	168.5	5.9	1.3	0.8
<i>Campylaspis squamifera</i> (Cum)	0.0	19.7	0.3	0.0	0.0
<i>Ilyarachna longicornis</i> (Iso)	0.0	23.7	1.6	0.5	0.0
<i>Munnopsurus atlanticus</i> (Iso)	0.0	588.3	28.0	8.0	6.1
<i>Typhlotanais</i> sp. (Tan)	219.8	0.8	0.0	0.0	0.0

(Tab. 4; Elizalde et al., 1993b), *Munnopsurus atlanticus* is actually a dominant Isopoda species on the upper part of the continental slope in the south Gascogne area as revealed by sledge sampling (Elizalde and Sorbe, 1993); its presence in the four water layers sampled by the sledge (Elizalde et al., 1993b) shows that it can swim at least up to 1.15-1.45 m above the bottom (not recorded in 30 mab planktonic samples, Elizalde, 1994); as for *Ilyarachna longicornis*, this swimming ability is powered by use of paddle-like pereopods V-VII (Hessler and Strömberg, 1989).

Mysidacea are typically hyperbenthic species and their swimming ability is demonstrated by diel vertical migrations observed in many species (Mauchline, 1980; Fossa, 1985, 1986; Kaartved, 1985). As a rule, deep-sea mysids are not collected by benthic samplers (Tab. 4), confirming that burrowing behaviour is not common among species living deeper than about 200 m (Fossa, 1986); in sledge samples, they are mainly concentrated in the near-bottom water layer (Elizalde et al., 1993b) but some *Boreomysis* species can swim higher up in the water column as pointed out by Fossa (1985, 1986), Kaartvedt (1985, 1989) and Elizalde et al. (1991).

Although a contamination of hyperbenthic samples by benthic species has to be suspected, mainly in the lower net, it appears that some species have an actual hyperbenthic behaviour. A good example is given by the Isopoda *Munnopsurus atlanticus*. This species is very abundant above the sea floor with decreasing density from the lower to the upper level, and has never been collected with benthic samplers in the same area (Elizalde and Sorbe, 1993). Conversely, most of the Tanaidacea are infaunal and they are abundant in the stations sampled with a box-corer and grab at continental slope stations (Tab. 4) and at both deep ECOFER stations 14 and 15 (Gerino and Stora, unpublished data). The low abundance of Tanaidacea in the sledge samples indicates that the biting of the sledge is probably limited, and that it preferentially samples the fauna just above the sediment. The complete identification of the fauna can provide new information on the lifestyle and classification of the species as endobenthic, epibenthic, and hyperbenthic species as previously proposed by Harrison (1989) and Hessler and Strömberg (1989) for the deep-sea aselott isopods and by Sainte-Marie and Brunel (1985) for circalittoral amphipods.

Table 5

Density ($N. ind. m^{-2}$) of Pycnogonida and Peracarida in some stations at about 3000 m in the northeastern Atlantic. BIOGAS: Bay of Biscay (Laubier and Sibuet, 1979); NORBI: Norwegian Sea (Dahl et al., 1976) and ECOFER: Bay of Biscay (this study).

Densité ($N. ind. m^{-2}$) des Pycnogonides et des Pécaricides de quelques stations échantillonnées par 3000 m de profondeur en Atlantique nord-est. BIOGAS : Golfe de Gascogne (Laubier et Sibuet, 1979) ; NORBI : mer de Norvège (Dahl et al., 1976) et ECOFER : Golfe de Gascogne (cette étude).

Cruise	BIOGAS		NORBI		ECOFER	
	Epibenthic sledge		Hyperbenthic sledge			
Station	2	2	5	10	14	15
Depth (m)	3000	3016	2957	2941	3040	3065
Pycnogonida	0.005	0.044	0.397	0.067	0.088	0.086
Mysidacea	0.000	0.000	<0.001	0.000	0.020	0.018
Amphipoda	0.230	0.068	0.350	0.106	0.526	0.559
Cumacea	0.300	0.000	0.000	0.000	0.193	0.337
Isopoda	0.250	0.515	0.723	0.380	0.892	1.212
Tanaidacea	0.080	0.293	0.611	0.329	0.064	0.069

Acknowledgements

This study was a part of the "ECOMARGE" programme of CNRS-INSU. The authors thank the crews of R.V. Côte

d'Aquitaine and R.V. Le Noroît for their valuable assistance in fieldwork, Dr R.R. Hessler for helpful comments on an earlier version of the manuscript, and E. O'Ceidigh for help for English proofreading.

REFERENCES

- Brunel P., M. Besner, D. Messier, L. Poirier, D. Granger, M. Weinstein (1978). Le traîneau Macer-GIROQ: appareil amélioré pour l'échantillonnage de la petite faune nageuse au voisinage du fond. *Inter. Rev. Gesam. Hydrob.* **63**, 815-829.
- Bird G.J., D.M. Holdich (1984). New Deep-sea Leptognathiid Tanaids (Crustacea, Tanaidacea) from the North-East Atlantic. *Zool. Scripta* **13**, 285-315.
- Bird G.J., D.M. Holdich (1989). Recolonisation of artificial sediments in the deep Bay of Biscay by Tanaidaceans (Crustacea: Peracarida), with a description of a new species of *Pseudotanaidais*. *J. mar. biol. Ass. U.K.* **69**, 307-317.
- Chevrier A., P. Brunel, D. Wildish (1991). Structure of a hyperbenthic shelf sub-community of gammaridean Amphipoda in the bay of Fundy compared with similar sub-communities in the Gulf of St Lawrence. *Hydrobiologia* **223**, 81-104.
- Dahl E., L. Laubier, M. Sibuet, J.-O. Strömberg (1976). Some quantitative results on benthic communities of the deep Norwegian Sea. *Astarte* **9**, 61-79.
- Dauvin J.-C., J.-C. Lorgeré (1989). Modifications du traîneau Macer-GIROQ pour l'amélioration de l'échantillonnage quantitatif étagé de la faune suprabenthique. *J. Rech. Océanogr.* **14**, 65-67.
- Elizalde M., J.-C. Dauvin, J.-C. Sorbe (1991). Les Mysidacés suprabenthiques de la marge sud du Canyon du Cap-Ferret (Golfe de Gascogne) : répartition bathymétrique et activité natatoire. *Ann. Inst. Océanog.* **67**, 129-144.
- Elizalde M., J.-C. Sorbe (1993). Postmarsupial development of *Munnopsurus atlanticus* (Bonnier, 1896), a dominant asellote isopod from the upper continental slope of the Bay of Biscay. *Crustaceana* **65**, 159-175.
- Elizalde M., O. Weber, J.-C. Sorbe (1993a). Influence des caractères sédimentologiques sur la distribution des Crustacés benthiques de la pente atlantique (golfe de Gascogne ; marge sud du canyon du Cap-Ferret). *Actes du III^e Colloque d'"Océanographie du Golfe de Gascogne"* 269-273.
- Elizalde M., J.-C. Sorbe, J.-C. Dauvin (1993b). Las comunidades suprabentónicas batiales del golfo de Vizcaya (margen sur del cañon de cap Ferret): composición faunística y estructura. *Publ. esp. Inst. Espanol Oceanogr.* **11**, 247-258.
- Elizalde M. (1994). Les communautés suprabenthiques bathyales de la marge sud du canyon du Cap-Ferret (Golfe de Gascogne). *Thèse de Doctorat de l'Université de Bordeaux I*, 242 p.
- Fossa J.H. (1985). Near-bottom vertical zonation during daytime of deep-living hyperbenthic Mysids (Crustacea : Mysidacea). *Sarsia* **70**, 297-307.
- Fossa J.H. (1986). Aquarium observations on vertical zonation and bottom relationships of some deep-living hyperbenthic Mysids (Crustacea: Mysidacea). *Ophelia* **25**, 107-117.
- Gage J.D. (1986). The benthic fauna of the Rockall Trough: regional distribution and bathymetric zonation. *Proc. Roy. Soc. Edinburgh* **88B**, 159-174.
- Gardiner L.F. (1975). The systematics, postmarsupial development, and ecology of the deep-sea family Neotanaimidae (Crustacea: Tanaidacea). *Smithson. Contr. Zool.* **170**, 1-265.
- Gowing M.M., K.F. Wishner (1986). Trophic relationships of the deep-sea copepods from the benthic boundary layer of the Santa Catalina Basin, California. *Deep-Sea Research* **33**, 939-961.
- Harrison K. (1989). Are deep-sea asellote isopods infaunal or epifaunal? *Crustaceana* **56**, 317-319.
- Hessler R.R., J.-O. Strömberg (1989). Behavior of Janiroidean Isopods (Asellota), with special reference to deep-sea genera. *Sarsia* **74**, 145-159.
- Hesthagen I.H. (1970). On the near-bottom plankton and benthic invertebrate fauna of the Josephine Seamount and the Great Meteor Seamount. *"Meteor" Forschungsergebnisse* **8**, 61-70.

Holdich D.M., N.S. Jones (1983). Tanaids. *Synop. Brit. Fauna* **27**, 1-98.

Ingram C.L., R.R. Hessler (1983). Distribution and behavior of scavenging amphipods from the central North Pacific. *Deep-Sea Res.* **30**, 683-706.

Jones N.S. (1976). British cumaceans. *Synop. Brit. Fauna* **7**, 1-63.

Kaartvedt S. (1985). Diel changes in small-scale vertical distribution of hyperbenthic Mysids. *Sarsia* **70**, 287-295.

Kaartvedt S. (1986). Diel activity patterns in deep-living cumaceans and amphipods. *Mar. Ecol. Progr. Ser.* **30**, 243-249.

Kaartvedt S. (1989). Nocturnal swimming of Gammaridean Amphipod and Cumacean Crustacea in Masfjorden, Norway. *Sarsia* **74**, 187-193.

Kudinova-Pasternak R.K. (1970). Tanaidacea of the Kurile-Kamchatka Trench. *Trudy Inst. Okeanol. Akad. Nauk SSSR.* **86**, 341-380.

Laubier L., M. Sibuet (1979). Ecology of the benthic communities of the deep North East Atlantic. *Ambio, spec. rep.* **6**, 37-42.

Macquart-Moulin C. (1991). La phase pélagique nocturne des Cumacés. *J. Plankt. Res.* **13**, 313-337.

Mauchline J. (1980). The biology of Mysids and Euphausiids. *Adv. Mar. Biol.* **18**, 1-681.

Sainte-Marie B., P. Brunel (1985). Hyperbenthic gradients of swimming activity by cold-water gammaridean amphipod Crustacea over a muddy shelf in the Gulf of Saint-Lawrence. *Mar. Ecol. Progr. Ser.* **23**, 57-69.

Sorbe J.-C. (1984). Contribution à la connaissance des peuplements suprabenthiques néritiques sud-Gascogne. *Thèse Doctorat d'Etat, Université de Bordeaux I*, 265 pp.+ annexes, 36 p.

Wishner K.F. (1980). Aspects of the community ecology of deep-sea benthopelagic plankton with special attention to Gymnopleid Copepods. *Mar. Biol.* **60**, 179-187.

Wishner K.F., M.M. Gowing (1987). *In situ* filtering and ingestion rates of the deep-sea boundary-layer zooplankton in the Santa Catalina Basin. *Mar. Biol.* **94**, 357-366.

Wildish D., A.J. Wilson, B. Frost (1992). Benthic Boundary Layer macrofauna of Browns Bank, Northwest Atlantic, as potential prey of juvenile benthic Fish. *Can. J. Fish Aquat. Sci.* **49**, 91-98.
