

## Bathyal cumacean assemblages from the southern margin of the Cap Ferret Canyon (SE Bay of Biscay)

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**Summary:** The structure of the cumacean assemblages from the southern margin of the Cap Ferret Canyon was studied at 13 stations ranging from 346 to 1099 m depth with a modified Macer-GIROQ suprabenthic sledge (four superimposed nets; 0.5 mm mesh size). A total of 1885 specimens were collected and classified into 5 families and 42 species. The total abundances fluctuated between 2.8 ind./100 m<sup>2</sup> (station TS04; 484-485 m) and 55.8 ind./100 m<sup>2</sup> (station TS08; 714-708 m). The highest values of species richness and diversity were recorded at station TS13 (1097-1099 m): S=25 species; H' (log<sub>2</sub>)=4.05. The near-bottom vertical distribution of the cumacean fauna showed the same pattern at all stations: at least 60% of the individuals were sampled by the lower net of the sledge and a drastic abundance decrease occurred between the two lowermost water layers sampled by the sledge. The multivariate analysis carried out on abundance data discriminated three main groups of stations distributed across depth (TS09 excluded): group Ia (346-485 m) characterized by the dominance of Nannastacidae (57.2%) at family level and *Campylaspis sulcata*, *Leptostylis macrura* at species level; group Ib (522-714 m) characterized by the dominance of Nannastacidae (66.1%) at family level and *Campylaspis squamifera*, *C. laevigata* and *Leptostylis macrura* at species level; and group II (790-1099 m) characterized by the dominance of Diastylidae (40.3%) at family level and *Makrokyldrus (Adiastylis) josephinae*, *Leucon (Epileucon) pusillus* and *Diastylodes serratus* at species level. According to this analysis, the main faunal change occurs between group I and II between 714 and 790 m, in relation to changes in the texture of surficial sediments. Although bathyal cumacean assemblages appear to be less abundant than those studied on continental shelves, they are significantly more diverse. However, such results could be in part related to the use of different sampling methods.

**Keywords:** Cumacea; assemblages; suprabenthos; bathyal; Bay of Biscay; NE Atlantic Ocean.

### Comunidades batiales de cumáceos en el margen sur del cañón de Cap Ferret (SE del golfo de Vizcaya)

**Resumen:** Se ha estudiado la estructura de las comunidades de cumáceos del margen sur del cañón de Cap Ferret en 13 estaciones, distribuidas desde los 346 hasta los 1099 m de profundidad con un patín suprabentónico Macer-GIROQ modificado (cuatro redes superpuestas; 0.5 mm de malla). En total, se recolectaron 1885 especímenes que fueron clasificados en cinco familias y 42 especies. La densidad total varió entre 2.8 ind./100 m<sup>2</sup> (estación TS04; 484-485 m) y 55.8 ind./100 m<sup>2</sup> (estación TS08; 714-708 m). Los valores máximos de riqueza específica y diversidad se obtuvieron en la estación TS13 (1097-1099 m): S=25 especies; H' (log<sub>2</sub>)=4.05. La distribución vertical cercana al fondo de la fauna de cumáceos mostró el mismo patrón en las diferentes estaciones: al menos el 60% de los individuos fue muestreado en la red inferior del patín y se observó un descenso drástico de la abundancia entre las dos capas de agua inferiores muestreadas por el patín. El análisis multivariante llevado a cabo con los datos de densidad discrimina tres grupos principales de estaciones (excluida TS09) distribuidos según la profundidad: el grupo Ia (346-485 m) caracterizado por la dominancia de los Nannastacidae (57.2%) a nivel de familia, y por *Campylaspis sulcata* y *Leptostylis macrura* a nivel de especie; el grupo Ib (522-714 m) caracterizado también por la dominancia de los Nannastacidae (66.1%) a nivel de familia, pero por *Campylaspis squamifera*, *C. laevigata* y *Leptostylis macrura* a nivel de especie; el grupo II (790-1099 m) caracterizado por la dominancia de los Diastylidae (40.3%) a nivel de familia, y por *Makrokyldrus (Adiastylis) josephinae*, *Leucon (Epileucon) pusillus* y *Diastylodes serratus* a nivel de especie. De acuerdo con este análisis, el principal cambio faunístico ocurre entre los grupos I y II entre 714 y 790 m, relacionado con cambios en la textura de los sedimentos superficiales. Aunque las comunidades de cumáceos batiales parecen ser menos densas que las estudiadas en la plataforma continental, son significativamente más diversas. No obstante, estos resultados podrían estar en parte relacionados con el uso de métodos de muestreo diferentes.

**Palabras clave:** Cumacea; comunidades; suprabentos; batial; golfo de Bizcaya; océano Atlántico NE.

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## INTRODUCTION

Cumaceans (more than 1750 known species; see Watling and Gerken 2019) are small peracarid crustaceans widely distributed from intertidal to hadal bottoms (Jones 1969) and showing the highest diversity in bathyal environments (Jones and Sanders 1972, Reyss 1973, Gage and Tyler 1992), a bathymetric distributional pattern also recognized for most benthic taxa (Rex et al. 1997, Rex and Etter 2010). Furthermore, they represent one of the main faunal components of marine suprabenthic assemblages (Mees and Jones 1997) because they live close to the sediment-water interface, burrowing in the top layer substratum or swimming in the near-bottom water (see Foxon 1936, Forsman 1938, Dixon 1944).

The deep cumacean fauna of the NE Atlantic Ocean (including the Bay of Biscay) is probably one of the best known in the world thanks to the taxonomical works of Bonnier (1896), Fage (1929), Reyss (1974a, b, 1978), Jones (1974, 1984, 1985) and Bishop (1981a, b) but also to the pioneering study of Lagardère (1977) on their bathymetric distribution in the southern part of the Bay of Biscay. However, quantitative information on the structure of the corresponding taxocenoses remains very scarce in this area. To fill this gap, a new research programme was initiated in 1984 on the structure of bathyal suprabenthic communities from the southern margin of the Cap Ferret Canyon (SE Bay of Biscay, off Arcachon Bay). During the ESSAIS and ECOFER cruises carried out in 1989, a new set of stations located along a bathymetric gradient was sampled with a suprabenthic sledge. The abundant material collected with this gear was studied at the highest taxonomical level (Dauvin et al. 1995) as well as at the lowest one for all the suprabenthic fauna collected at three stations (Elizalde et al. 1993a, Elizalde 1994) and for mysids (Elizalde et al. 1991) and amphipods (Dauvin and Sorbe 1995) according to the species identification progress. According to Dauvin et al. (1995), cumaceans are the fourth most abundant group in this material (5.6% of the total collected fauna), after isopods (50.8%), amphipods (22.7%) and mysids (14.1%), and their percentage contribution increases with depth in the study area (0.5%-22.4% of the whole fauna collected at each sampling station). The present work is a new contribution to the knowledge of bathyal suprabenthic assemblages from the Cap Ferret area aimed at describing patterns of bathymetric as well as the near-bottom vertical distribution of cumacean species, estimating abundance of individuals and characterizing inter-specific associations.

## MATERIALS AND METHODS

### Study area

The study area is located on bathyal soft bottoms from the southern margin of the Cap Ferret Canyon. In that area, surficial sediments were sampled during previous surveys with box corers for granulometric

analyses and estimation of their organic content (see data in Elizalde et al. 1991, 1993b, Elizalde 1994). Etcheber et al. (1999) synthesized the whole available sedimentological information accumulated in the Cap Ferret region (canyon and its lateral margins). On the southern margin of the canyon, the bathymetric distribution of the sediment fractions is clearly related to the general morphology of the area, showing a narrow sandy lobe extending down to 800 m depth, to the north of the study area. This feature is probably related to the impact of alongslope bottom currents limiting the local deposition of fine particles (see Durrieu de Madron et al. 1999). In the study area, the mean grain size decreases with depth, from 160  $\mu\text{m}$  at the shelf break to a value stabilized around 10  $\mu\text{m}$  from about 600 m down to 3000 m. Conversely, the carbon organic content of sediments (measured in the 1 cm top layer of cores, expressed as % of sediment dry weight) increases with depth, between 0.23% at the shelf break and 1.36% at around 1000 m depth. The dominant fractions (>50%) allow two sedimentary zones to be distinguished according to depth: an upper muddy sand zone characterized by a decreasing dominance of fine sands with depth and a lower mud zone characterized by a dominance of fine silts and clay, and by stabilized values of the mean grain size according to depth. Following the definition given by Stanley et al. (1983), the mud-line is therefore located at about 600 m depth in the study area, a limit representing the erosion-deposition boundary beneath which the organic content of surficial sediments increases in response to the deposition of silty and/or clayey particles (Etcheber et al. 1999).

According to Durrieu de Madron et al. (1999), two superimposed water masses were detected during the ECOFER experiments in the upper part of the Cap Ferret region, inferred from CTD profiles within the Cap Ferret Canyon: (1) a low-salinity water mass extending between 200 and 600 m in the water column, referred to as Eastern North Atlantic Water and characterized by a salinity minimum of 35.51 and a temperature of 10.8°C at 500 m water depth; and (2) a high saline core of Mediterranean Overflow Water detected between 700 and 1300 m water depth, characterized a salinity maximum of 35.76, a temperature of 9.8°C and an oxygen minimum of 3.6 ml L<sup>-1</sup> at about 1000 m water depth. Furthermore, an intermediate nepheloid layer centred at a depth of around 500 m and horizontally detached from the seafloor was detected at the head and on the flanks of the canyon during all five ECOFER experiments (1989-1991). It is supposed that both Eastern North Atlantic Water and Mediterranean Overflow Water impinge on the slope in the study area (canyon southern margin) and therefore impact the structure of the underlying bathyal benthic communities.

### Sampling

During the ESSAIS I, ESSAIS II and ECOFER I surveys carried out between April and July 1989, 13 stations ranging from 346 to 1099 m depth (Fig. 1; Table 1) were sampled with a modified Macer-GIROQ

suprabenthic sledge (full description in Dauvin et al. 1995). This gear is equipped with four superimposed nets (0.5 mm mesh size) that simultaneously sample four water layers above the seafloor (N1, 10-40 cm; N2, 45-75 cm; N3, 80-110 cm; N4, 115-145 cm) and with an opening-closing system of these nets acting by contact with the seafloor. Each net is fixed on a rectangular metallic box (height, 30 cm; width, 60 cm) equipped with a TSK flowmeter that estimates the haul length and the bottom area swept by the sledge during each haul (calculated from the mean value of the available flowmeter measurements; see Table 1). Based on these estimates, the standardized abundances of species are expressed in individuals/100 m<sup>2</sup> (cumulative values from the four sledge nets N1-N4). The sledge was towed over the seafloor at a speed of 1-2 knots. All samplings were carried out during daytime (between 8 and 18 h), except TS06 and TS13, which were carried out at night before midnight (see Table 1). The collected material was fixed on board with a solution of 10% neutral formalin in sea water until sorting into major taxonomical groups at the laboratory. All groups (including cumaceans) were then transferred to and preserved in 70% ethanol until species identification.

### Data analyses

Following Brunel (1972) and Sainte-Marie and Brunel (1985), an index K of swimming activity above the bottom was computed for each species, expressed as follows:

$$\begin{aligned} K1 &= \sum N1 / \sum Nt \\ K2 &= \sum N2 / \sum Nt \\ K3 &= \sum N3 / \sum Nt \\ K4 &= \sum N4 / \sum Nt \end{aligned}$$

where  $\sum N1$ ,  $\sum N2$ ,  $\sum N3$  and  $\sum N4$  are the abundances (number of individuals) in the 10-40, 45-75, 80-110 and 115-145 cm water layers above the bottom, respectively; and  $\sum Nt$  is the total number of individuals in the four water layers sampled by the sledge (cumulative values from all available water layers and stations, excluding TS09). This K index can vary

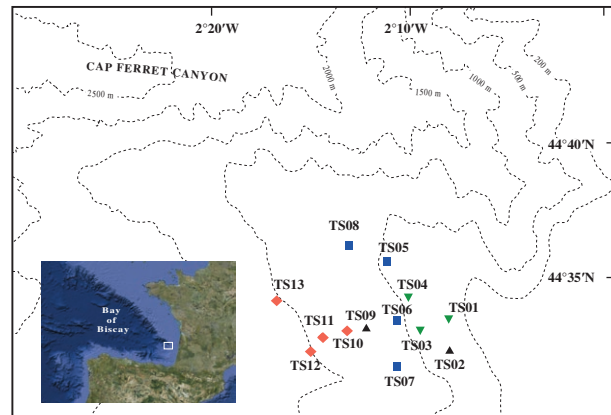


Fig. 1. – Geographical location of the 13 slope stations sampled with a suprabenthic sledge on the southern margin of the Cap Ferret Canyon (ESSAIS and ECOFER oceanographic cruises). Station symbols: green triangles, assemblage Ia; blue squares, assemblage Ib; red diamonds, assemblage II; black triangles, stations outside the groups or not analysed (see text).

from 0 (when a given species is absent at the level considered) to 1 (when all the specimens are sampled in the same water layer).

Abundance data (Dt, ind./100 m<sup>2</sup>) were analysed using the Plymouth Routine in Multivariate Ecological Research (PRIMER v 5.0) software package (Clarke and Gorley 2001). Univariate diversity indices (Shannon-Wiener diversity  $H'$  using  $\log_2$ , Pielou evenness  $J'$ ) were calculated from species abundances with the DIVERSE routine. A matrix of similarity between samples was constructed by means of the Bray-Curtis measure applied to square-root transformed species abundances in order to down-weight the contribution of abundant species. From this matrix, the 12 suprabenthic samples (sample TS09 excluded – damaged material) were classified by cluster analysis based on the complete linkage sorting algorithm. A graphical ordination was carried out on the same matrix using non-metric multidimensional scaling. Finally, the SIMPER routine was used to identify species that most contributed to within-group similarity and between-group dissimilarity.

Mean values of data sets were statistically compared using t tests according to Dagnelie (1975).

Table 1. – Haul characteristics and geographical position of stations sampled with a suprabenthic sledge on the southern margin of the Cap Ferret Canyon during the ESSAIS and ECOFER cruises. Estimated bottom area swept by the sledge during each haul (calculated from TSK flowmeter measurements). <sup>a</sup>: time and position of the boat at the beginning of the haul on the bottom; <sup>b</sup>: depth (below the boat) at the beginning and at the end of the haul on the bottom.

Cruise	Haul code	Date (d/m/y)	Time <sup>a</sup> (h:m)	Position <sup>a</sup>		Depth <sup>b</sup> (m)	Area (m <sup>2</sup> )
				N	W		
ESSAIS I	TS01	21/4/89	15:50	44°33.30'	2°08.30'	346-347	512
ESSAIS II	TS02	18/5/89	08:11	44°32.58'	2°08.17'	390-383	171
ESSAIS II	TS03	18/5/89	17:59	44°33.11'	2°09.85'	425-437	384
ESSAIS II	TS04	18/5/89	10:43	44°34.38'	2°10.18'	485-484	443
ECOFER I	TS05	01/7/89	13:20	44°35.57'	2°11.21'	523-522	519
ESSAIS I	TS06	21/4/89	22:27	44°33.40'	2°10.70'	608-611	807
ESSAIS I	TS07	21/4/89	17:19	44°31.90'	2°10.80'	660-714	928
ECOFER I	TS08	01/7/89	15:59	44°36.21'	2°12.84'	714-708	375
ESSAIS II	TS09	18/5/89	16:31	44°33.22'	2°12.48'	740-754	370
ESSAIS II	TS10	18/5/89	13:36	44°33.10'	2°13.13'	791-790	328
ESSAIS II	TS11	18/5/89	15:00	44°32.89'	2°14.24'	923-924	279
ESSAIS I	TS12	22/4/89	8:33	44°32.30'	2°15.10'	1024-1043	477
ESSAIS II	TS13	17/5/89	23:10	44°34.19'	2°16.18'	1097-1099	382

Table 2. – Abundance of cumacean species sampled with a suprabenthic sledge at 13 stations on the southern margin of the Cap Ferret Canyon and relative abundance (%) of corresponding cumacean families. TS09 station not studied at family/species level due to bad conservation of material. Dt, cumulative abundance (ind./100 m<sup>2</sup>) in the 3 or 4 near-bottom water layers sampled by the sledge; –, 0; \*, damaged specimen.

Haul code	TS01		TS02		TS03		TS04		TS05		TS06		TS07		TS08		TS09		TS10		TS11		TS12		TS13			
	346-347	512	390-383	171	425-437	384	485-484	443	523-522	519	608-611	807	660-714	928	714-708	375	740-754	370	791-790	328	923-924	279	1024-1043	477	1097-1099	382	Dt	%
Family BODOTRIIDAE																												
<i>Bathycuma brevisotstre</i>																												
<i>Cyclaspis longicaudata</i>																												
<i>Cyclaspoides sarsi</i>																												
<i>Iphinoe serrata</i>			0.6																									
Family DIASTYLIDAE																												
<i>Diastylis cornuta</i>			47.6		22.8		64.3		30.5		22.5		17.5		13.4													
<i>Diastylis tumida</i>									0.2				0.1															
<i>Diastylis biplicatus</i>									0.6		2.7		0.5															
<i>Diastylisoides serratus</i>		1.0			0.5		0.2		5.0		0.9		0.5		4.3													
<i>Leptostylis longimana</i>																												
<i>Leptostylis macrura</i>		2.0			1.8		1.6		9.6		3.1		2.4		2.4													
<i>Leptostylis</i> sp.A											0.2																	
<i>Leptostylis</i> sp.B																												
<i>Makrokylindrus</i> (A.) <i>anomalous</i>																												
<i>Makrokylindrus</i> (A.) <i>joosephinae</i>			0.6								0.1		1.1		0.8													
<i>Makrokylindrus</i> (A.) <i>longicaudatus</i>																												
<i>Makrokylindrus</i> (A.) <i>longipes</i>																												
<i>Makrokylindrus</i> sp.*																												
<i>Vemakylindrus hastatus</i>			0.6		4.9		7.1		15.2		4.5		0.1		6.3													
Family LAMPROPIDAE																												
<i>Hemilamprops normani</i>																												
<i>Mesolamprops denticulatus</i>		0.4			0.5		0.2		7.1		1.4		1.0		2.7													
<i>Platysympus typicus</i>									0.6				0.2		0.8													
<i>Platylphlops orbicularis</i>																												
Family LEUCONIDAE																												
<i>Eudorella</i> cf. <i>parvula</i>																												
<i>Ithyleucon sorbei</i>																												
<i>Leucon</i> (C.) <i>tener</i>																												
<i>Leucon</i> (E.) <i>ensis</i>																												
<i>Leucon</i> (E.) <i>pusillus</i>																												
<i>Leucon</i> (L.) <i>affinis</i>																												
<i>Leucon</i> (L.) sp.*																												
<i>Leucon</i> (M.) <i>siphonatus</i>																												
Family NANNASTACIDAE																												
<i>Campylaspis glabra</i>		46.0		40.0	72.3		28.6		49.3		66.0		77.2		76.5													
<i>Campylaspis laevigata</i>		0.4			1.0		0.2		3.5		3.0		2.0		2.9													
<i>Campylaspis nitens</i>							0.2		3.5		3.8		3.8		7.5													
<i>Campylaspis rostrata</i>													0.2		0.3													
<i>Campylaspis squamifera</i>					0.5		0.2		11.9		12.4		12.3		20.0													
<i>Campylaspis sulcata</i>		2.5		0.6	4.2				2.3																			
<i>Cumella</i> (C.) <i>divisa</i>																												
<i>Cumellopsis puritani</i>																												
<i>Nannastacus atlanticus</i>																												
<i>Procampylaspis armata</i>																												
<i>Procampylaspis omnidion</i>																												
<i>Schizocuma spinoculatum</i>																												
<i>Syloptocuma gracillimum</i>					1.6		0.2		3.5		1.1		0.8		1.6													
Cumacea unidentified*																												
	6.3	100	3.0	100	10.1	100	2.8	100	50.5	100	31.5	100	26.8	100	55.8	100	50.3	100	30.8	100	40.5	100	48.0	100	49.9	100	4.5	9.0



Table 3. – Species richness (S), total abundance (Dt, ind./100 m<sup>2</sup>), Shannon-Wiener diversity index (H', log<sub>2</sub>) and Pielou evenness (J') of the cumacean fauna sampled with a suprabenthic sledge at 13 stations on the southern margin of the Cap Ferret Canyon (values from nets N1-N4). –, no data.

Haul code	S	Dt	H'	J'
TS01	5	6.3	1.98	0.85
TS02	5	3.0	2.32	1.00
TS03	7	10.1	2.37	0.84
TS04	7	2.8	2.09	0.75
TS05	13	50.5	3.05	0.83
TS06	16	31.5	2.88	0.72
TS07	17	26.8	2.76	0.67
TS08	13	55.8	2.86	0.77
TS09	–	50.3	–	–
TS10	19	30.8	3.53	0.83
TS11	22	40.5	3.93	0.88
TS12	22	48.0	3.60	0.81
TS13	25	49.9	4.05	0.87

RESULTS

A total of 1885 cumacean specimens were collected. Of these, 87.7% were identified and classified into 5 families (Nannastacidae, 47.5%; Diastylidae, 30.1%; Leuconidae, 12.7%; Lampropidae, 6.9%; Bodotriidae, 2.8%) and 42 species (Table 2; Supplementary Material Table S1). The number of species (species richness) per station ranged from 5 at stations TS01 and TS02 to 25 at station TS13 (Table 3). The total abundances fluctuated between a minimum of 2.8 ind./100 m<sup>2</sup> at station TS04 and a maximum of 55.8 ind./100 m<sup>2</sup> at station TS08. The diversity indexes H' ranged between 1.98 (TS01) and 4.05 (TS13). All these three structural indices are significantly correlated with depth (species richness r=0.960, p<0.001; abundances r=0.732, p<0.01; diversity r=0.927, p<0.001). Even at station TS07 where the nannastacid *Campylaspis squamifera* was highly dominant (45.9% of the individuals), the evenness values, J', were relatively high (≥0.67) but were correlated neither with depth (r=0.078, p>0.05) nor with H' values (r=0.093, p>0.05).

At family level, samples from the 0-145 cm water layer were numerically dominated by Nannastacidae or Diastylidae in the shallower part of the study area

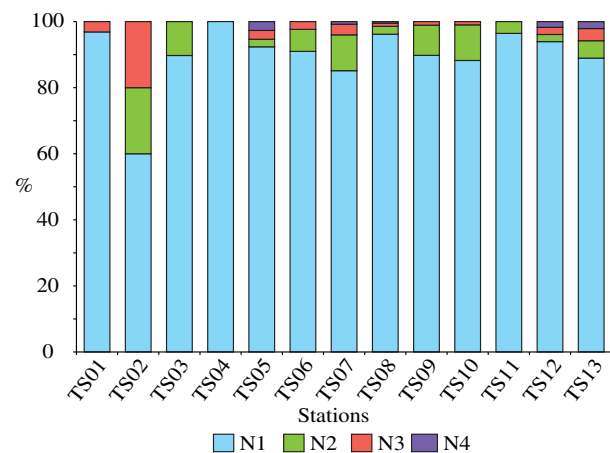


Fig. 2. – Percentage contribution of nets N1-N4 samples to the whole suprabenthic cumacean fauna sampled by the sledge at each of the 13 slope stations from the southern margin of the Cap Ferret Canyon.

(although with low abundances between 346 and 485 m), and the Nannastacidae were progressively replaced by Leuconidae below 700 m depth. At species level (Table 2), the highest abundances in the 0-145 cm water layer were recorded for the Nannastacidae *Campylaspis squamifera* (20.0 ind./100 m<sup>2</sup>, TS08), the Leuconidae *Leucon (Epileucon) pusillus* (11.1 ind./100 m<sup>2</sup>, TS12) and the Nannastacidae *Procampylaspis armata* (10.4 ind./100 m<sup>2</sup>, TS08). The Diastylidae *Diastylodes serratus* showed the widest bathymetric distribution in the study area, being captured between 346 and 1099 m depth (present at 11 stations).

As shown in Figure 2, the near-bottom vertical distribution of the cumacean fauna showed the same pattern at every station: at least 60.0% of the individuals were sampled by the lower net of the sledge, whereas only 0% to 2.7% of them were captured at the uppermost level, demonstrating that these small peracarids

Table 4. – Index (K) of swimming activity (see text) calculated for cumacean species sampled by a sledge in the 10-40, 45-85, 90-110 and 115-145 cm near-bottom water layers during the ESSAIS and ECOFER surveys. ΣNt, total number of specimens (cumulative values from all available water layers and stations, excluding TS09).

Taxa	ΣNt	K1	K2	K3	K4
Family BODOTRIIDAE					
<i>Bathycuma brevirostre</i>	11	1.00	0.00	0.00	0.00
<i>Cyclaspis longicaudata</i>	26	0.88	0.12	0.00	0.00
<i>Cyclaspoides sarsi</i>	8	1.00	0.00	0.00	0.00
<i>Iphinoe serrata</i>	1	0.00	0.00	1.00	0.00
Family DIASTYLIDAE					
<i>Diastylis cornuta</i>	2	0.50	0.00	0.00	0.50
<i>Diastylis tumida</i>	6	1.00	0.00	0.00	0.00
<i>Diastylodes biplicatus</i>	33	0.94	0.06	0.00	0.00
<i>Diastylodes serratus</i>	128	0.72	0.13	0.08	0.07
<i>Leptostylis longimana</i>	6	1.00	0.00	0.00	0.00
<i>Leptostylis macrura</i>	133	0.97	0.02	0.01	0.00
<i>Leptostylis sp.A</i>	3	1.00	0.00	0.00	0.00
<i>Leptostylis sp.B</i>	1	1.00	0.00	0.00	0.00
<i>Makrokylindrus (A.) anomalus</i>	1	1.00	0.00	0.00	0.00
<i>Makrokylindrus (A.) josephinae</i>	123	0.93	0.04	0.03	0.00
<i>Makrokylindrus (A.) longicaudatus</i>	8	0.88	0.13	0.00	0.00
<i>Makrokylindrus (A.) longipes</i>	7	1.00	0.00	0.00	0.00
<i>Vemakylindrus hastatus</i>	39	1.00	0.00	0.00	0.00
Family LAMPROPIDAE					
<i>Hemilamprops normani</i>	28	0.93	0.04	0.00	0.04
<i>Mesolamprops denticulatus</i>	72	0.82	0.08	0.07	0.03
<i>Platysympus typicus</i>	12	1.00	0.00	0.00	0.00
<i>Platytyphlops orbicularis</i>	4	1.00	0.00	0.00	0.00
Family LEUCONIDAE					
<i>Eudorella cf. parvula</i>	26	0.96	0.00	0.04	0.00
<i>Ithyleucon sorbei</i>	18	0.94	0.06	0.00	0.00
<i>Leucon (C.) tener</i>	9	1.00	0.00	0.00	0.00
<i>Leucon (E.) ensis</i>	11	1.00	0.00	0.00	0.00
<i>Leucon (E.) pusillus</i>	87	0.98	0.01	0.01	0.00
<i>Leucon (L.) affinis</i>	19	0.89	0.05	0.05	0.00
<i>Leucon (L.) sp.</i>	11	1.00	0.00	0.00	0.00
<i>Leucon (M.) siphonatus</i>	31	0.87	0.06	0.06	0.00
Family NANNASTACIDAE					
<i>Campylaspis glabra</i>	84	0.9	0.06	0.01	0.02
<i>Campylaspis laevigata</i>	123	0.95	0.04	0.01	0.00
<i>Campylaspis nitens</i>	8	1.00	0.00	0.00	0.00
<i>Campylaspis rostrata</i>	2	1.00	0.00	0.00	0.00
<i>Campylaspis squamifera</i>	368	0.91	0.07	0.01	0.00
<i>Campylaspis sulcata</i>	42	0.98	0.02	0.00	0.00
<i>Cumella (C.) divisa</i>	1	1.00	0.00	0.00	0.00
<i>Cumellopsis puritani</i>	9	1.00	0.00	0.00	0.00
<i>Nannastacus atlanticus</i>	2	1.00	0.00	0.00	0.00
<i>Procampylaspis armata</i>	85	0.95	0.02	0.01	0.01
<i>Procampylaspis omnidion</i>	4	1.00	0.00	0.00	0.00
<i>Schizocuma spinoculatum</i>	11	1.00	0.00	0.00	0.00
<i>Styloptocuma gracillimum</i>	50	0.98	0.00	0.02	0.00
Global	1653	0.92	0.05	0.02	0.01

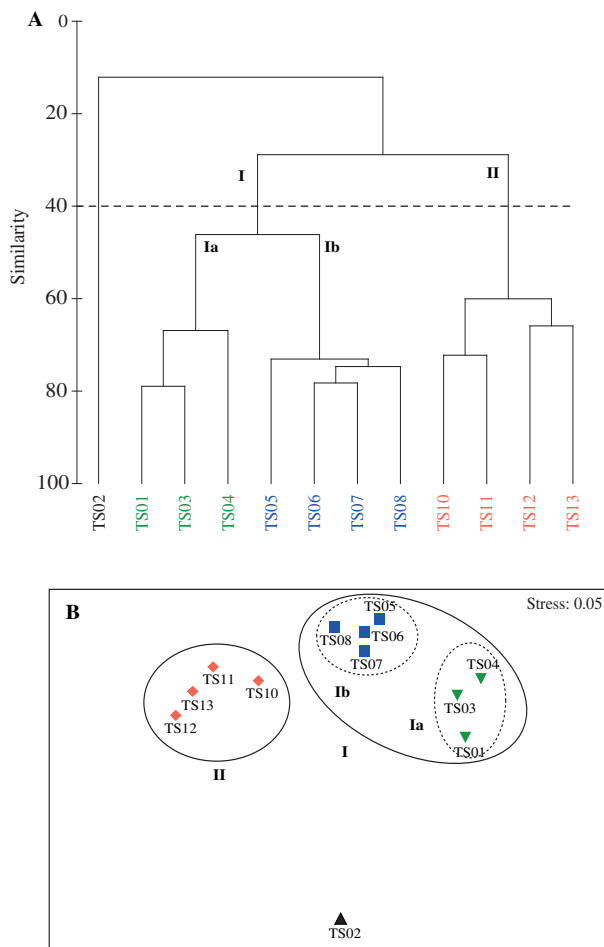


Fig. 3. – Hierarchical cluster analysis (A) and non-metric multidimensional scaling (B) of the 12 slope stations (TS09 excluded; see text) based on square-root transformed abundances and Bray-Curtis similarity measure.

are concentrated close to the seafloor during both daytime and night-time (see the case of the night-time samples TS06 and TS13). Furthermore, both families and species showed a drastic abundance decrease between the N1 and N2 lowermost waters layers and species richness showed the same vertical decreasing trend (see Table 4 and S1). Twenty-one species were exclusively sampled in the 10-40 cm water layer and therefore had a K1 index of 1: *Bathycuma brevirostre*, *Cyclaspoides sarsi*, *Diastylis tumida*, *Leptostylis longimana*, *Leptostylis* sp.A, *Leptostylis* sp.B, *Makrokyllindrus* (*Adiastylis*) *anomalus*, *M. (A.) longipes*, *Vemakylindrus hastatus*, *Platysympus typicus*, *Platytyphlops orbicularis*, *Leucon* (*Crymoleucon*) *tener*, *Leucon* (*Epileucon*) *ensis* and *Leucon* (*Leucon*) sp., *Campylaspis nitens*, *C. rostrata*, *Cumella* (*Cumella*) *divisa*, *Cumellopsis puritani*, *Nannastacus atlanticus*, *Procampylaspis omnidion* and *Schizocuma spinoculatum*. The other species showed high K1 values (range: 0.50-0.98) in the lowermost level and lower K2-K4 decreasing values (range: 0.33-0) in the upper ones. Only six species were also sampled in the 115-145 cm water layer, with a generally very low K4 index, probably attesting their higher swimming abilities than the preceding ones: *Diastylis cornuta*, *Diastylodes serratus*; *Hemilamprops normani*, *Mesolamprops denticulatus*; *Campylaspis glabra* and *Procampylaspis armata*. *Iphinoe serrata*, a shelf-origin bodotriid, was sporadically sampled in the 80-110 cm water layer of station TS02 (only one specimen caught).

As presented in Figure 3, the cluster analysis carried out on abundance data reveals the existence of three main groups of stations distributed over depth (station TS02 being outside the groups), and the multidimensional scaling ordination shows similar results to those of the dendrogram, with an excellent stress

Table 5. – Average dissimilarity between the 3 main station groups discriminated by the multivariate analysis of the 12 sampling stations (station TS02 discarded) and contribution of cumacean species to total dissimilarity. A cut-off at a cumulative dissimilarity of 85% was applied. Av. diss., average dissimilarity.

Groups Ia vs Ib Av. diss.: 63.9	%	Groups Ia vs II Av. diss.: 86.85	%	Groups Ib vs II Av. diss.: 70.09	%
<i>Campylaspis squamifera</i>	20.73	<i>Makrokyllindrus</i> ( <i>A.</i> ) <i>josephinae</i>	9.90	<i>Campylaspis squamifera</i>	8.85
<i>Campylaspis laevigata</i>	12.10	<i>Leucon</i> ( <i>E.</i> ) <i>pusillus</i>	7.95	<i>Leucon</i> ( <i>E.</i> ) <i>pusillus</i>	6.81
<i>Procampylaspis armata</i>	7.46	<i>Procampylaspis armata</i>	5.90	<i>Makrokyllindrus</i> ( <i>A.</i> ) <i>josephinae</i>	6.63
<i>Campylaspis sulcata</i>	6.59	<i>Hemilamprops normani</i>	5.15	<i>Leptostylis macrura</i>	5.09
<i>Campylaspis glabra</i>	6.14	<i>Vemakylindrus hastatus</i>	5.00	<i>Mesolamprops denticulatus</i>	4.98
<i>Mesolamprops denticulatus</i>	6.10	<i>Cyclaspis longicaudata</i>	4.86	<i>Campylaspis laevigata</i>	4.40
<i>Diastylodes biplicatus</i>	5.09	<i>Diastylodes serratus</i>	4.70	<i>Hemilamprops normani</i>	4.38
<i>Leucon</i> ( <i>L.</i> ) <i>affinis</i>	5.03	<i>Leucon</i> ( <i>M.</i> ) <i>siphonatus</i>	4.32	<i>Cyclaspis longicaudata</i>	4.15
<i>Styloptocuma gracillimum</i>	4.93	<i>Campylaspis sulcata</i>	4.30	<i>Campylaspis glabra</i>	3.92
<i>Diastylodes serratus</i>	4.81	<i>Leptostylis macrura</i>	3.63	<i>Vemakylindrus hastatus</i>	3.78
<i>Leptostylis macrura</i>	3.86	<i>Eudorella</i> cf. <i>parvula</i>	3.03	<i>Procampylaspis armata</i>	3.52
<i>Makrokyllindrus</i> ( <i>A.</i> ) <i>josephinae</i>	3.60	<i>Campylaspis squamifera</i>	2.60	<i>Leucon</i> ( <i>L.</i> ) <i>affinis</i>	2.55
		<i>Bathycuma brevirostre</i>	2.53	<i>Styloptocuma gracillimum</i>	2.55
		<i>Leucon</i> ( <i>C.</i> ) <i>tener</i>	2.53	<i>Diastylodes serratus</i>	2.52
		<i>Ithyleucon sorbei</i>	2.46	<i>Eudorella</i> cf. <i>parvula</i>	2.47
		<i>Campylaspis laevigata</i>	2.29	<i>Leucon</i> ( <i>M.</i> ) <i>siphonatus</i>	2.44
		<i>Leucon</i> ( <i>L.</i> ) sp.	2.28	<i>Bathycuma brevirostre</i>	2.20
		<i>Mesolamprops denticulatus</i>	2.17	<i>Ithyleucon sorbei</i>	2.16
		<i>Platytyphlops orbicularis</i>	2.00	<i>Leucon</i> ( <i>C.</i> ) <i>tener</i>	2.15
		<i>Diastylis tumida</i>	1.94	<i>Diastylodes biplicatus</i>	1.98
		<i>Leucon</i> ( <i>E.</i> ) <i>ensis</i>	1.86	<i>Leucon</i> ( <i>L.</i> ) sp.	1.98
		<i>Styloptocuma gracillimum</i>	1.75	<i>Platytyphlops orbicularis</i>	1.70
		<i>Campylaspis glabra</i>	1.66	<i>Leucon</i> ( <i>E.</i> ) <i>ensis</i>	1.63
		<i>Diastylodes biplicatus</i>	1.35	<i>Diastylis tumida</i>	1.61
				<i>Platysympus typicus</i>	1.30

Table 6. – Biotic characteristics of the cumacean assemblages Ia, Ib and II discriminated by the multivariate analysis of abundance data (based on cumulative values from nets N1-N4). Species ranked according to their average contribution to within-group similarity (%Sim); their respective contribution (%D) to mean total abundance of each assemblage is also included. A cut-off at a cumulative similarity of 80% was applied; sd, standard deviation.

Assemblages		Ia	Ib	II
Haul codes TS		1, 3, 4	5, 6, 7, 8	10, 11, 12, 13
Depth range (m)		346-485	522-714	790-1099
Species richness (S)	range	5-7	13-17	19-25
	cumulative	13	22	35
Abundance (ind./100 m <sup>2</sup> )	mean ±sd	6.3 ± 1.2	14.8 ± 2.1	22.0 ± 2.4
	range	2.8-10.1	26.8-55.8	30.8-49.9
Diversity (H', log <sub>2</sub> )	mean ±sd	6.4 ± 3.7	41.2 ± 14.2	42.3 ± 8.7
	range	1.98-2.37	2.76-3.05	3.53-4.05
Evenness (J')	Mean ±sd	2.15 ± 0.20	2.89 ± 0.12	3.78 ± 0.25
	range	0.75-0.85	0.67-0.83	0.81-0.88
Main species (%Sim / %D)	mean ±sd	0.81 ± 0.06	0.75 ± 0.07	0.85 ± 0.03
		<i>Leptostylis macrura</i> (36.4 / 28.1)	<i>Campylaspis squamifera</i> (24.7 / 34.4)	<i>Makrokyllindrus (A.) josephinae</i> (15.8 / 17.2)
	<i>Diastylodes serratus</i> (14.7 / 8.9)	<i>Campylaspis laevigata</i> (13.6 / 11.3)	<i>Leucon pusillus</i> (10.9 / 12.6)	
	<i>Campylaspis glabra</i> (14.1 / 8.3)	<i>Leptostylis macrura</i> (11.2 / 10.6)	<i>Diastylodes serratus</i> (10.8 / 10.2)	
	<i>Mesolamprops denticulatus</i> (14.1 / 5.7)	<i>Campylaspis glabra</i> (11.0 / 6.9)	<i>Procampylaspis armata</i> (7.8 / 6.3)	
	<i>Campylaspis sulcata</i> (12.7 / 34.9)	<i>Mesolamprops denticulatus</i> (8.2 / 7.4)	<i>Hemilamprops normani</i> (7.5 / 4.8)	
		<i>Styloptocuma gracillimum</i> (7.1 / 4.3)	<i>Cyclaspis longicaudata</i> (7.0 / 4.4)	
		<i>Diastylodes serratus</i> (7.0 / 6.5)	<i>Leucon (M.) siphonatus</i> (6.5 / 3.4)	
			<i>Vemakylindrus hastatus</i> (6.3 / 5.4)	
			<i>Platytyphlops orbicularis</i> (3.1 / 0.7)	
			<i>Campylaspis squamifera</i> (2.8 / 2.5)	
			<i>Leucon (C.) tener</i> (2.5 / 1.6)	

value of 0.05. As shown in Table 5, the average dissimilarity between these groups was  $\geq 63.9$ , with the highest value recorded between groups Ia and II. Two nannastacids mainly contributed to the total dissimilarity between groups Ia and Ib: *Campylaspis squamifera* (20.73%) and *C. laevigata* (12.10%). Dissimilarity between other paired groups was due to a higher number of contributing species, with *Makrokyllindrus (Adiastylis) josephinae* (9.90%) and *Campylaspis squamifera* (8.85%) as the top species for paired groups Ia-II and Ib-II, respectively.

Group Ia (3 stations between 346 and 485 m depth; average within-group similarity 63.8) is characterized by the numerical dominance of Nannastacidae (57.2%), the absence of Bodotriidae and Leuconidae and a low total abundance of  $6.4 \pm 3.7$  ind./100 m<sup>2</sup> (mean±SD). *Leptostylis macrura*, *Diastylodes serratus*, *Campylaspis glabra*, *Mesolamprops denticulatus* and *Campylaspis sulcata* accounted for 92.0% of the average within-group similarity (Table 6). *Campylaspis sulcata* was the most abundant species of this assemblage, with a mean value of  $2.2 \pm 2.1$  ind./100 m<sup>2</sup> (mean±SD) and a contribution of 34.9% to total group abundance, followed by *Leptostylis macrura* (28.1%), *Styloptocuma gracillimum* (9.4%), *Diastylodes serratus* (8.9%) and *Campylaspis glabra* (8.3%).

Group Ib (4 stations between 522 and 714 m depth; average within-group similarity 71.3) was also characterized by the dominance of Nannastacidae (66.1%) and the absence of Bodotriidae but marked by the appear-

ance of Leuconidae and a higher total abundance than the preceding one ( $41.2 \pm 14.2$  ind./100 m<sup>2</sup>, mean±SD). *Campylaspis squamifera*, *C. laevigata*, *Leptostylis macrura*, *Campylaspis glabra*, *Mesolamprops denticulatus*, *Styloptocuma gracillimum* and *Diastylodes serratus* accounted for 82.8% of the average within-group similarity (Table 6). *Campylaspis squamifera* was the most abundant species of this assemblage, with a mean value of  $14.2 \pm 3.9$  ind./100 m<sup>2</sup> (mean±SD) and a contribution of 34.4% to total group abundance, followed by *C. laevigata* (11.3%), *Leptostylis macrura* (10.6%), *Mesolamprops denticulatus* (7.4%) and *Procampylaspis armata* (7.0%). Three species, *Diastylis cornuta*, *Leucon (Leucon) affinis* and *Cumellopsis puritani*, were found exclusively in this assemblage.

Group II (4 stations between 790 and 1099 m depth; average within-group similarity 61.3) was characterized by the dominance of Diastylidae (40.3%), the appearance of Bodotriidae and a total abundance of  $42.3 \pm 8.7$  ind./100 m<sup>2</sup> (mean±SD). This group showed the highest mean values of species richness, total abundance and diversity indices (Table 6). *Makrokyllindrus (Adiastylis) josephinae*, *Leucon (Epileucon) pusillus*, *Diastylodes serratus*, *Procampylaspis armata*, *Hemilamprops normani*, *Cyclaspis longicaudata*, *Leucon (Macrauloleucon) siphonatus*, *Vemakylindrus hastatus*, *Platytyphlops orbicularis*, *Campylaspis squamifera* and *Leucon (Crymoleucon) tener* accounted for 81.0% of the average within-group similarity (Table 6). *Makrokyllindrus (A.) josephinae* was the



most abundant species of this assemblage, with a mean value of  $7.3 \pm 1.5$  ind./100 m<sup>2</sup> (mean $\pm$ SD) and a contribution of 17.2% to total group abundance, followed by *Leucon* (*Epileucon*) *pusillus* (12.6%), *Diastylodes serratus* (10.2%), *Procampylaspis armata* (6.3%) and *Vemakylindrus hastatus* (5.4%). 18 species were found exclusively in this assemblage, demonstrating an evident renewal of the cumacean fauna at this bathymetric level: *Bathycuma brevirostre*, *Cyclaspis longicaudata*, *Cyclaspoides sarsi*, *Leptostylis longimana*, *Leptostylis* sp.B, *Makrokyllindrus* (*Adiastylis*) *anomalus*, *M. (A.) longicaudatus*, *M. (A.) longipes*, *Hemilamprops normani*, *Platytyphlops orbicularis*, *Ithyleucon sorbei*, *Leucon* (*Crymoleucon*) *tener*, *Leucon* (*Epileucon*) *ensis*, *L. (E.) pusillus*, *Campylaspis rostrata*, *Cumella* (*Cumella*) *divisa*, *Procampylaspis omnidion* and *Schizocuma spinoculatum*.

## DISCUSSION

Lagardère (1977) carried out a pioneering study on the bathyal cumacean fauna of the southeastern Bay of Biscay (composition and bathymetric distribution of species in the depth range 200-1400 m). According to modern nomenclature (see Băcescu 1992, Corbera and Sorbe 1999), we suggest the following equivalence between species (Lagardère's taxa in brackets): *Vemakylindrus hastatus* (= *Diastylis* cf. *hastata*), *Eudorella* cf. *parvula* (= *E. truncatula*), *Cumella* (*Cumella*) *divisa* (= *Cumella* sp.), *Nannastacus atlanticus* (= *Nannastacus* sp.) and *Styloptocuma gracillimum* (= *Cumella gracillimana*). Within the restricted depth range 200-1000 m (comparable to the present study), Lagardère listed 37 species belonging to Nannastacidae, Diastylidae, Leuconidae, Bodotriidae and Lampropidae (decreasing order of species richness), slightly lower than the value obtained herein (43 species). *Eudorella hirsuta* (Sars, 1869) is probably a misidentification (= *Eudorella* cf. *parvula*?), as is *Campylaspis horrida* Sars, 1869 recorded on the upper slope of Arctic waters according to Jones (1984). Although not recorded during the present survey, *Hemilamprops roseus* (Norman, 1863) and *Campylaspis macrophthalma* Sars, 1878 were sampled on the outer shelf adjacent to our study area (Sorbe 1984); *Vaunthompsonia cristata* Bate, 1858, *Campylaspis verrucosa* Sars, 1866 and *Campylaspis vitrea* Calman, 1906 were sampled in the Capbreton canyon area (Frutos and Sorbe 2014, 2017); and *Hemilamprops cristatus* (Sars, 1870) and *Leucon* (*Epileucon*) *longirostris* Sars, 1871 were mentioned from bathyal bottoms of the Bay of Biscay (Jones 1985, Frutos and Sorbe 2014). Therefore, except probable misidentified species, all cumaceans mentioned by Lagardère (1977) were found again in more recent studies on the bathyal benthic cumacean fauna of the SE Bay of Biscay. Furthermore, a new genus and species, *Ithyleucon sorbei*, were described from the material collected during the present study (Corbera 2012), and two apparently undescribed species of the genus *Leptostylis* remain to be studied.

Previously reported from the NE Atlantic between Norway and British Islands but also from the Azores and the Gulf of Cadiz, *Diastylis tumida* (740-924 m)

is mentioned for the first time in the Bay of Biscay (present study). Originally described from bathyal bottoms of the Gulf of Lion, *Mesolamprops denticulatus* Ledoyer, 1983 was more recently discovered in the NE Atlantic Ocean as far as the Faeroe–Shetland Channel at 259-753 m (Shalla and Bishop 2007) as well as in the southern Bay of Biscay (Frutos and Sorbe 2014, Capbreton Canyon; Sorbe and Elizalde 2014, southern margin of the Cap Ferret Canyon).

Up to now, the structure of deep cumacean assemblages has been poorly investigated. In the southern Bay of Biscay, recent studies on bathyal suprabenthic assemblages (Frutos and Sorbe 2014, 2017, Sorbe and Elizalde 2014) showed that they constitute one of the main components of the near-bottom motile fauna (suprabenthic ecophase), in addition to amphipods, isopods and mysids. However, another part of these assemblages is known to inhabit surficial sediments constituting the endobenthic ecophase of these populations (Fage 1951, Jones 1976, Băcescu and Petrescu 1999). These burrowing individuals are inadequately sampled by suprabenthic sledges, mainly designed to sample the near-bottom motile fauna (epi-/suprabenthic ecophase). Therefore, more realistic estimations of benthic cumacean abundances should ideally combine sampling with sledges and grabs/box cores. To our knowledge, such a methodology has never been implemented in the study of these benthic communities. Table 7 shows some structural data on diverse shelf and slope cumacean assemblages, sampled with either suprabenthic sledges or grabs. The abundance data (maximum recorded values for each study) given by suprabenthic sampling are in the same order of magnitude for shelf (range: 1.2-6.5 ind. m<sup>-2</sup>) and slope assemblages (range: 0.3-5.4 ind. m<sup>-2</sup>), and the corresponding mean values are statistically equal ( $t_{\text{obs}}=1.256$ ; d.f.=10;  $p>0.05$ ). In shelf assemblages, these suprabenthic abundances are generally much lower than values obtained with grab sampling (range: 153-24000 ind. m<sup>-2</sup>) and far from the worldwide maximum value mentioned by Hawkinson (1992) in the case of the coastal Diastylidae *Diastylopsis dawsoni* Smith, 1880 from Agate Bay, California (up to 119881 ind. m<sup>-2</sup>; Ekman grab).

According to the structural data presented in Table 7, species richness (maximum values) is generally higher in slope assemblages (range: 7-25 species per station) than in shelf ones (range: 4-15 species per station). Such a trend is also verified when considering the St mean values for slope ( $29.2 \pm 13.0$  species per station; mean $\pm$ SD) and shelf ( $10.9 \pm 6.6$  species per station) assemblages of the studied areas ( $t_{\text{obs}}=3.733$ ; d.f.=15;  $p<0.001$ ). Furthermore, within the slope assemblages studied herein, the cumulative species richness increases with depth: 13, 22 and 35 species for assemblages Ia, Ib and II, respectively. Although without statistical significance, the diversity values,  $H'$ , are also higher in slope assemblages (range: 3.41-4.05) than in the shelf ones (range: 1.24-3.21), corroborating previous observations on bathyal cumacean assemblages (Jones and Sanders 1972, Reyss 1973) as well as on all bathyal suprabenthic assemblages (Frutos and Sorbe 2014, 2017, Sorbe and Elizalde 2014).



Table 7. – Comparison of structural data reported for shelf and slope cumacean assemblages from various geographical areas. Smax/Dmax, maximum value of species richness/abundance recorded at a sampling station in the study area. St, total species richness recorded in the whole study area. H', maximum value of the Shannon-Wiener diversity index recorded at a sampling station of the study area. –, no data. <sup>a</sup> unpublished data; <sup>b</sup> calculated from rough data mentioned in reference; <sup>c,d</sup> daytime, night-time samplings; <sup>e</sup> recalculated from original data in ind./100 m<sup>3</sup> (conversion factor: 0.515 10<sup>-2</sup>).

Bathymetrical and geographical areas	Sampling gear	Depth range (m)	Smax	St	Dmax (ind. m <sup>-2</sup> )	H' (log <sub>2</sub> )	References
<b>Shelf areas</b>							
Hendaye beach (NE Atlantic)	sledge	0-0.2	-	5	-	-	San Vicente and Sorbe 2001
Creixell beach (NW Mediterranean)	sledge	0.5-3.5	-	6	-	-	San Vicente and Sorbe 1999
Galician ria (NE Atlantic)	grab	0-28.2	4	4	153.6	-	Cacabelos et al. 2010
Catalan Sea (NW Mediterranean)	grab	15	10	1	333.0	-	Corbera et al. 2013
Persian Gulf	grab	15-30	4 <sup>a</sup>	8	260.0 <sup>a</sup>	1.24 <sup>a</sup>	Martin et al. 2010
Levantine Sea (E Mediterranean)	grab	1.9-63	8	18	24000.0	2.04	Corbera and Galil 2016
Catalan Sea (NW Mediterranean)	grab	5-70	8	22	612.0	2.58 <sup>b</sup>	Corbera and Cardell 1995
Aquitanian shelf (NE Atlantic)	sledge	31 <sup>c</sup>	5	7	2.4 <sup>c</sup>	1.69	Sorbe 1984
«	«	91 <sup>c</sup>	9	14	3.2 <sup>c</sup>	2.46	«
«	«	91 <sup>d</sup>	10	14	6.5 <sup>c</sup>	2.49	«
«	«	126 <sup>c</sup>	12	15	1.2 <sup>c</sup>	3.21	«
«	«	179 <sup>c</sup>	15	17	4.3 <sup>c</sup>	2.93	«
<b>Slope areas</b>							
Cap Ferret slope (NE Atlantic)	sledge	386-420	7	9	0.3	-	Sorbe and Elizalde 2014
Capbreton Canyon (NE Atlantic)	sledge	151-797	12	25	3.0	-	Frutos and Sorbe 2017
Kostarrenkala (NE Atlantic)	sledge	175-1000	24	38	5.4	-	Frutos and Sorbe 2014
Cap Ferret slope (NE Atlantic)	sledge	346-1099	25	42	0.6	4.05	this study
Catalan Sea (NW Mediterranean)	sledge	389-1859	19	32	2.5	3.41 <sup>b</sup>	Cartes and Sorbe 1997
Cap Ferret Canyon (NE Atlantic)	sledge	2410-2425	-	-	1.7	-	Sorbe 1999
Cap Ferret Canyon (NE Atlantic)	sledge	3058-3070	-	-	0.3	-	«

According to our multivariate analysis (see Fig. 3), two main faunal changes occur in the cumacean fauna collected on the upper bathyal of the southern Bay of Biscay. The first one is observed between 485 and 522 m, and the second one (more clearly marked) between 714 and 790 m. In the upper part of the study area, the substratum consists of muddy fine sands (*ca.* 400 m depth, median grain size [Mz]=73.9 µm; particles <63 µm [pelites]=38.2%; organic carbon content [C<sub>org</sub>]=0.37% of sediment dry weight; see Etcheber et al 1999 and Elizalde 1994). The edge of the adjacent shelf is characterized by comparable bottoms (*ca.* 179 m depth: Mz=100.0 µm; pelites=20.0%; see Sorbe 1984). This similarity in the texture of surficial sediments favours the extension of some shelf species down to the upper bathyal (for instance the Bodotriidae *Iphinoe serrata* and the Nannastacidae *Nannastacus atlanticus*). Separating the cumacean assemblages Ia and Ib, the upper ecotone at about 500 m depth is related to the apparition of muddy sediments (characterized by a pelitic fraction ≥50%; see Elizalde 1994) that are more fluid than the shallower sandy bottoms. This structural change on the sedimentary coverage has a probable effect on the functioning of the suprabenthic sledge. Primarily designed to slide on compact sandy bottoms thanks to its lateral skates (see Dauvin et al. 1995), this device probably skims the uppermost sediment layer on fluid muddy bottoms and thus samples surficial infaunal components in addition to the suprabenthic ones. This phenomenon is attested by a significant increase in cumacean mean abundances below 500 m depths: 42.7±10.6 ind./100 m<sup>2</sup> (mean±SD) versus 5.6±3.4 ind./100 m<sup>2</sup> at shallower depths (*t*<sub>obs</sub>=48.4; d.f.=11; *p*<0.001). It should be noted that no Leuconidae were observed within the assemblage Ia (346-485 m), although *Leucon* (*Macrauloleucon*) *siphonatus* curiously showed a disjoint bathymetric distribution, being present on both muddy sand bottoms of the outer

shelf (91-179 m; Sorbe 1984) and deeper muddy slope bottoms (608-1099 m; this study).

These new observations corroborate the eurybathic (100-4380 m; Fage 1951) and eurytopic distribution of this strange cumacean with an unusually long branchial siphon (longer than the carapace in some adults; Fage 1951). This morphological peculiarity is probably an adaptive character allowing this species to colonize very diverse benthic habitats. The lower ecotone is imprecisely located between 714 and 791 m depth (due to absence of detailed data for the cumacean fauna of haul TS09). It constitutes the upper limit of the cumacean assemblage II installed on muddy bottoms characterized by a higher organic carbon content of surficial sediments (C<sub>org</sub> from 0.84% at 720 m to 1.36% at 995 m) and a pelitic fraction ≥84% (see Etcheber et al. 1999). At *ca.* 1099 m (the lower limit of the present study area), the surficial sediments show the following features: Mz=12.3 µm; pelites=92.6%, mainly constituted by particles <15 µm (clay=58.0%); C<sub>org</sub>=1.30% (see Elizalde 1994). This assemblage probably extends on deeper bathyal bottoms because it is composed of many bathyal/abyssal species (not found at shallower depths in the present study), such as *Bathycuma brevivostre* (350-1700 m), *Cyclaspis longicaudata* (189-3350 m) and *Cyclaspoides sarsi* (698-1099 m); *Makrokyllindrus* (*Adiastylis*) *anomalous* (950-1550 m), *M. (A.) longicaudatus* (650-1287 m) and *M. (A.) longipes* (15-1227 m); *Hemilamprops normani* (220-3000 m) and *Platytyphlops orbicularis* (423-1739 m); *Leucon* (*Crymoleucon*) *tener* (790-1445 m), *Leucon* (*Epileucon*) *ensis* (790-2006 m) and *L. (E.) pusillus* (610-1780 m); and *Campylaspis rostrata* (220-2338 m), *Cumella* (*Cumella*) *divisa* (610-2864 m), *Procampylaspis omnidion* (860-4749 m) and *Schizocuma spinoculatum* (1097-2900 m) (distributional data according to Sars 1899, Hansen 1920, Fage 1951, Bishop 1981b, Jones 1984, Gerken 2018).

In addition to these surficial sedimentary characters that certainly play a major role in the bathymetric distribution and local abundance of cumaceans, the bathyal bottoms investigated during the present study are impacted by the benthic impingement of two superimposed water bodies: the Eastern North Atlantic Water between 200 and 600 m and Mediterranean Overflow Water between 700 and 1300 m (Durieu de Madron et al. 1999). Inferred from CTD profiles carried out in the water column inside the Cap Ferret Canyon (Durieu de Madron et al. 1999) as well as on its southern margin (unpublished data collected during various oceanographic cruises in all seasons except winter), hydrographic conditions in the near-bottom bathyal environment can be supposedly described as follows in order to assess their possible role in the distribution and structuration of the cumacean assemblages detected across the upper slope. Assemblage Ia (346–485 m) is bathed by the Eastern North Atlantic Water, corresponding to near-bottom waters with a salinity range of 35.52 to 5.74, a temperature range of 10.5 to 11.3°C and an oxygen concentration range of 4.16 to 4.48 ml L<sup>-1</sup>. Assemblage Ib (522–754 m) is also bathed by the same water body, corresponding to near-bottom waters with a salinity range of 35.54 to 35.85, a temperature range of 10.1 to 10.7°C and an oxygen concentration range of 3.76 to 4.16 ml L<sup>-1</sup>. Assemblage II (790–1099 m) is under the influence of the Mediterranean Overflow Water, corresponding to near-bottom waters with a salinity range of 35.69 to 35.77, a temperature range of 9.1 to 10.1°C and an oxygen concentration range of 3.65 to 3.69 ml L<sup>-1</sup>. Whatever the bathymetric level in the upper bathyal, near-bottom temperatures show weak fluctuations during the annual cycle ( $\leq 1^\circ\text{C}$ ; inferred from seasonal CTD profiles). This environmental variable is probably not the triggering factor of reproductive mechanisms in these cumaceans, as is the case with some peracarid and decapod populations from adjacent shelf waters (Sorbe 1984, San Vicente and Sorbe 2013). Furthermore, even in the case of the Mediterranean waters (minimum O<sub>2</sub> concentration: 3.60 ml L<sup>-1</sup>), the near-bottom waters are far from dysoxia as defined by Levin (2003) for oceanic waters ( $\leq 1.0$  ml L<sup>-1</sup>), with O<sub>2</sub> saturation values  $\geq 57.24\%$ . As pointed out by Diaz and Rosenberg (1995), the actual O<sub>2</sub> values are probably lower at the water-sediment interface, but the alongslope bottom currents known to periodically occur in the study area (Sorbe and Weber 1995, Durieu de Madron et al. 1999) promote the renewal of their near-bottom waters and probably prevent the occurrence of dysoxic bottom events. Finally, it should be noted that the actual impact of these hydrographic variables on the biology and behaviour of benthic peracaridans is far from being well understood.

Although little is known about the diet of cumaceans (see Jones 1976, Băcescu and Petrescu 1999, Błażewicz-Paszkowycz and Ligowski 2002), the distribution of some species could be related to food availability in the bottom environment. The nannastacid species belonging to genera *Campylaspis* and *Procampylaspis* are thought to be predators on foraminifers and small crustaceans, based on the

structure of their mouthparts modified as piercing organs and on the analysis of their gut contents (Jones 1976, Błażewicz-Paszkowycz and Ligowski 2002). In the southern Bay of Biscay, the noteworthy numerical dominance of *Campylaspis* species between 425 and 714 m (see Table S1) is concomitant with the abundance of some benthic agglutinated foraminifers at the same bathymetric level, as reported by Elizalde et al. (1999). Elizalde et al. (1999) showed that the agglutinated foraminifer *Pseudoclavulina mexicana* (Cushman, 1922) is preyed upon by the isopod *Munnopsurus atlanticus* (Bonnier, 1896), crushed by the robust mandibles of this species. Such a trophic link with benthic agglutinated foraminifers remains to be demonstrated in the case of the nannastacid species from the southern Bay of Biscay. The other cumaceans taxa herein mentioned are generally classified as detritivores (see Błażewicz-Paszkowycz and Ligowski 2002 for Antarctic species). The development of their bathyal populations is dependent on periodical inputs of nutritive particles originating from the euphotic zone (overlying pelagial waters and/or adjacent shelf areas).

The present results on the bathyal cumacean fauna can be compared with previous published analyses carried out on the other peracarids from the same collection data (346–1099 m), such as the Mysidacea (Elizalde et al. 1991; obsolete denomination, grouping current orders Lophogastrida and Mysida) and the Amphipoda (Dauvin and Sorbe 1995). In each of these bathyal taxocœnoses, three assemblages have been detected related to depth (assemblages A, B and C for convenience of presentation). The ecotone separating the uppermost assemblages A and B is located around 500 m depth for the three taxocœnoses. As demonstrated herein for cumaceans, these faunal changes are mainly related to a modification of the sedimentary cover (correlated to peculiar hydrodynamic conditions at the shelf break/upper slope), from muddy sands in the upper levels to muddy bottoms below 500 m depth. The upper assemblages A are partly composed of shelf species extending their bathymetric distribution to the muddy sand bottoms of the upper slope (for instance, the amphipods *Amphilochooides boeckii* G.O. Sars, 1892, *Rhachotropis integricauda* Carausu, 1948, *Iphimedia obesa* Rathke, 1843, *Hippomedon denticulatus* (Spence Bate, 1857), *Westwoodilla caecula* (Spence Bate, 1857), *Apherusa bispinosa* (Spence Bate, 1857) and *A. ovalipes* Norman and Scott, 1906; and the mysids *Leptomysis gracilis* (G.O. Sars, 1864) and *Mysideis parva* Zimmer, 1915). The bathymetric location of the lower ecotone separating assemblages B and C is variable according to taxocœnoses, probably reflecting different sensibility of taxa /species to near-bottom environmental changes. For cumaceans and amphipods, this ecotone is located between 714 and 754 m (Dauvin and Sorbe 1995; this study), suggesting that some amphipods are also affected by the increase in organic carbon in muddy surficial sediments, as mentioned above for cumaceans. For mysids, this lower ecotone is significantly located deeper on the slope (between 924 and 1024 m), probably related to the oxygen minimum

zone (OMZ; O<sub>2</sub> concentration minimum =3.6 ml L<sup>-1</sup>) detected between 908 and 942 m on CTD profiles carried out in the study area (see Durieu de Madron et al. 1999). According to available distributional data (Nouvel and Lagardère 1976, Lagardère and Nouvel 1980, Elizalde et al. 1991), this OMZ actually constitutes the lower bathymetric limit of some upper bathyal mysids such as *Amblyops spiniferus* Nouvel and Lagardère, 1976, *Pseudomma kruppi* W. Tattersall, 1909 and *Mysidella biscayensis* Lagardère and Nouvel, 1980, as well as the upper limit of the deeper bathyal mysid *Dactylamblyops thaumatops* W. Tattersall, 1907 (the numerically dominant species of the deep mysid assemblage). Surprisingly, this OMZ has apparently no impact on the depth distribution of cumacean assemblages but a slight effect on amphipod assemblages, as suggested by the correspondence analysis of data (see Dauvin and Sorbe 1995). Vaquer-Sunyer and Duarte (2008) showed that hypoxia thresholds vary greatly across marine benthic organisms, crustaceans being the most sensitive, but without detailed information on peracarids. Due to their known higher swimming activity (see Mauchline 1980, Elizalde et al. 1991), mysids probably have higher oxygen requirements than most amphipods and cumaceans.

## CONCLUSIONS

In the upper bathyal of the SE Bay of Biscay, cumaceans constitute an important fraction of the suprabenthic fauna, although they are characterized by a lower diversity and abundance than amphipods (a major group in many near-bottom deep assemblages, as pointed out by Frutos et al. 2017). Within the study area, a minimum of 42 cumacean species were censused (some of them putatively new to science), belonging to 5 families (mainly Nannastacidae and Diastylidae). As for other major taxocenoses, three across-slope cumacean assemblages were detected, mainly structured by depth and surficial sediments (granulometric composition and organic content). This study is a contribution to a better knowledge of the small near-bottom peracarid fauna of the NE Atlantic slope (a major food resource for demersal fishes; see Sorbe 1981), a deep marine area increasingly impacted by many anthropogenic activities (Levin and Dayton 2009).

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article and at the following link:  
<http://scimar.icm.csic.es/scimar/supplm/sm05031esm.pdf>

Table S1. – Vertical distribution of cumacean individuals in the near-bottom water layers (N1, 10-40 cm; N2, 45-75 cm; N3, 80-110 cm; N4, 115-145 cm above the seafloor) sampled by a suprabenthic sledge at 13 stations on the southern margin of the Cap Ferret Canyon. TS09 samples only partially studied due to bad conservation of material. –, 0; \*, damaged specimens.

## **Bathyal cumacean assemblages from the southern margin of the Cap Ferret Canyon (SE Bay of Biscay)**

Jordi Corbera, Jean Claude Sorbe

Supplementary material



Table S1 (cont.). – Vertical distribution of cumacean individuals in the near-bottom water layers (N1, 10–40 cm; N2, 45–75 cm; N3, 80–110 cm; N4, 115–145 cm above the sea floor) sampled by the suprabenthic sledge at 13 stations on the southern margin of the Cap Ferret Canyon. TS09 samples only partially studied due to bad conservation of material. –, 0; \*, damaged specimens.

Haul code	TS08				TS09				TS10				TS11				TS12				TS13			
	714–708		740–754		791–790		923–924		1024–1043		1097–1099		1024–1043		923–924		791–790		1097–1099		1024–1043		923–924	
	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4
<b>Family BODOTRIIDAE</b>																								
<i>Bathycuma brevisotre</i> (Norman, 1879)																								
<i>Cyclaspis longicaudata</i> Sars, 1865																								
<i>Cyclaspoides sarsi</i> Bonnier, 1896																								
<i>Iphinoe serrata</i> Norman, 1867																								
Family DIASTYLIDAE																								
<i>Diasylis cornuta</i> (Boeck, 1864)																								
<i>Diasylis tumida</i> (Lilleborg, 1855)																								
<i>Diasylodes biplicatus</i> (GO Sars, 1865)																								
<i>Diasylodes serratus</i> (GO Sars, 1865)																								
<i>Leptostylis longimana</i> (GO Sars, 1865)																								
<i>Leptostylis macrura</i> (GO Sars, 1870)																								
<i>Leptostylis</i> sp.A																								
<i>Leptostylis</i> sp.B																								
<i>Makrokylinidrus</i> ( <i>Adiasylis</i> ) <i>anomalous</i> (Bonnier, 1896)																								
<i>Makrokylinidrus</i> ( <i>Adiasylis</i> ) <i>josephinae</i> (GO Sars, 1871)																								
<i>Makrokylinidrus</i> ( <i>Adiasylis</i> ) <i>longicaudatus</i> (Bonnier, 1896)																								
<i>Makrokylinidrus</i> ( <i>Adiasylis</i> ) <i>longipes</i> (GO Sars, 1871)																								
<i>Makrokylinidrus</i> sp.*																								
<i>Vemakylindrus hastatus</i> (Hansen, 1920)																								
Family LAMPROPIDAE																								
<i>Hemilamprops normani</i> Bonnier, 1896																								
<i>Mesolamprops denticulatus</i> Ledoyer, 1983																								
<i>Platytympus typicus</i> (GO Sars, 1870)																								
<i>Platytyphlops orbicularis</i> (Calman, 1905)																								
Family LEUCONIDAE																								
<i>Eudorella</i> cf. <i>parvula</i> Hansen, 1920																								
<i>Ithyleucon sorbei</i> Corbera, 2012																								
<i>Leucon</i> ( <i>Crymoleucon</i> ) <i>tener</i> Hansen, 1920																								
<i>Leucon</i> ( <i>Epileucon</i> ) <i>ensis</i> (Bishop, 1981)																								
<i>Leucon</i> ( <i>Epileucon</i> ) <i>pusillus</i> (Bishop, 1981)																								
<i>Leucon</i> ( <i>Leucon</i> ) <i>affinis</i> Fage, 1951																								
<i>Leucon</i> ( <i>Leucon</i> ) sp.*																								
<i>Leucon</i> ( <i>Macrauloucon</i> ) <i>siphonatus</i> Calman, 1905																								
Family NANNASTACIDAE																								
<i>Campylaspis glabra</i> GO Sars, 1878																								
<i>Campylaspis laevigata</i> Jones, 1974																								
<i>Campylaspis nitens</i> Bonnier, 1896																								
<i>Campylaspis rostrata</i> Calman, 1905																								
<i>Campylaspis squamifera</i> Fage, 1929																								
<i>Campylaspis sulcata</i> GO Sars, 1870																								
<i>Cumella</i> ( <i>Cumella</i> ) <i>divisa</i> Jones, 1984																								
<i>Cumellopsis puritani</i> Calman, 1906																								
<i>Nannastacus atlanticus</i> Bacescu and Muradian, 1972																								
<i>Procampylaspis armata</i> Bonnier, 1896																								
<i>Procampylaspis omnidion</i> Jones, 1984																								
<i>Schizocuma spinoculatum</i> (Jones, 1984)																								
<i>Syloptocuma gracillimum</i> (Calman, 1905)																								
Cumacea unidentified *																								
Number of individuals 201 5 2 1 167 17 2 90 11 1 108 4 0 217 5 5 4 169 10 7 4																								
Number of species 13 3 2 1 5 5 1 19 6 1 22 1 0 22 5 3 2 25 1 4 1																								