

On the structure of the neritic suprabenthic communities from the Portuguese continental margin

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ABSTRACT: This work presents the investigations made on the neritic suprabenthic communities of the Portuguese margin (continental shelf and upper slope) exposed to seasonal upwelling. These communities were sampled during the AVEIRO-94 cruise at 5 sites located along an E-W bathymetric transect from 21 to 299 m depth using a suprabenthic sled with superposed nets. In the 0 to 100 cm water layer, the total densities ranged from 700.2 to 13591.7 ind. 100m⁻². During daytime, the motile fauna was mainly concentrated within the 0 to 50 cm water layer (76.2 to 97.2% of the total abundance). The night-time sample at the shallower site showed a more even distribution of the fauna in the near-bottom water layers (nocturnal migratory behaviour of some motile species). The Shannon diversity (H') values ranged from 1.84 to 3.54 for the shelf sites and increased at the upper slope site (4.15). Mysids and amphipods were generally dominant except for at the middle part of the shelf where the latter was replaced by euphausiids. The suprabenthic fauna off Aveiro was compared with similar data from the same bathymetric sampling levels off Arcachon (Bay of Biscay). Multivariate analysis showed that differences in faunal composition between the 2 geographic areas were smaller than depth-related variations within geographic areas. The results were discussed in relation to other suprabenthic communities from the northeastern Atlantic.

KEY WORDS: Suprabenthos · Portuguese continental margin · Community structure

INTRODUCTION

In recent years knowledge on the suprabenthic communities of the NE Atlantic has increased. Diel activity patterns (Kaartvedt 1985, 1986, Macquart-Moulin 1985, Zouhiri & Dauvin 1996) and bathymetric distribution (Fosså & Brattegard 1990, Elizalde et al. 1991) of a number of species have been described. Several infralittoral and circalittoral areas have been studied from the North Sea (Buhl-Jensen & Fosså 1991, Hamerlynck & Mees 1991) to the English Channel (Dauvin et al. 1994, Wang & Dauvin 1994, Zouhiri & Dauvin 1996) and the Bay of Biscay (Sorbe 1982, 1984, 1989, Cornet et al. 1983). Deeper communities from the

bathyal zone have also been studied in the latter area (Elizalde et al. 1993). However southern European (Iberian margin) suprabenthos remains unknown. Few systematic works have been carried out on the continental shelf off Portugal. Monteiro Marques (1979) and Sousa Reis et al. (1982) conducted biocoenotic studies off the southern and southwestern coast. Marques & Bellan-Santini (1985, 1991, 1993) studied the biodiversity and distributional ecology of amphipod crustaceans based on several benthic surveys carried out systematically along the coast.

The suprabenthos, i.e. the faunal assemblage (mainly small crustaceans) living in the immediate vicinity of the bottom (Beyer 1958, Brunel et al. 1978), is known to be an important source of food for demersal fishes (Sorbe 1981, 1984, Astthorsson 1985). On the west Iberian margin the neritic environment is domi-

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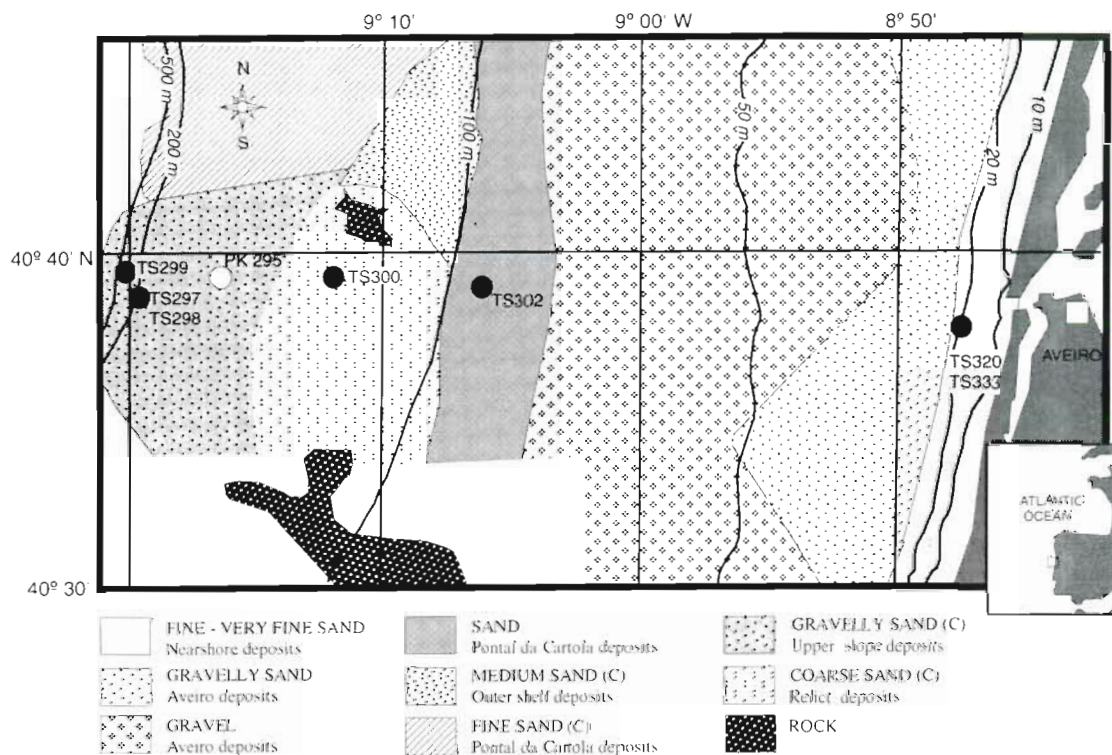


Fig. 1. Map of the study area on the NW Portuguese continental margin off Aveiro and location of the stations sampled during AVEIRO-94 cruise. Sedimentary deposits from Abrantes et al. (1994). (●) Suprabenthic stations. (○) Hyponeuston station. C: carbonate-rich sediments

nated by the occurrence of coastal upwelling in summer and early autumn (Wooster et al. 1976, Fiúza et al. 1982). Under such peculiar hydrographic conditions suprabenthic organisms are probably a major link in the food web of this area where coastal fisheries remain an important economic activity.

The suprabenthic communities of the NW Portuguese continental margin (21 to 299 m depth) were sampled during the cruise AVEIRO-94 that took place in the summer of 1994. This study is only a small part of a wider research programme designed to enhance the basic knowledge of this area including zooplankton, benthos, suprabenthos, sedimentology and geophysics (see also Cunha et al. 1997). The results are compared with similar data from the same bathymetric levels in the Bay of Biscay (Sorbe 1982, 1984, 1989, Cornet et al. 1983) and discussed in relation to other NE Atlantic suprabenthic communities.

Our objectives for the present work were: (1) to investigate the density, diversity and bathymetric distribution of the suprabenthos along a transect on the NW Portuguese continental margin off Aveiro; (2) to compare the suprabenthic fauna from 2 different areas in the NE Atlantic, one exposed to coastal upwelling (Aveiro) and another one where coastal upwelling does not occur (Arcachon, Bay of Biscay).

STUDY AREA

Fig. 1 shows the study area on the Portuguese continental shelf and the location of the sampling sites.

On the west Iberian margin the hydrodynamic conditions are dominated by the occurrence of coastal upwelling in summer and early autumn (Wooster et al. 1976, Fiúza et al. 1982). The prevailing northerly winds during summer produce a flow from the north and away from the shore, inducing coastal upwelling. The general pattern comprises a surface equatorward flow and a poleward undercurrent (Silva 1992). In addition to local wind forcing, upwelling patterns off Portugal are also determined by the coastal morphology and the shelf and upper slope features (Fiúza 1982). In the northern coastal margin, characterised by a much wider shelf and a steeper slope, bottom friction tends to be more important. In this area the surface equatorward jet appears at a coastal position and, as the wind persists, it extends vertically to the bottom and consistently moves offshore, its outermost position being dependent on the duration of the event (Silva 1992). In the winter, southerly or westerly winds produce a poleward surface flow along the coast and the upwelling ceases (Frouin et al. 1990, Haynes & Barton 1990).

The available information concerning near-bottom currents on the NW Portuguese shelf is scarce. The direction of near-bottom currents is probably related to the above mentioned hydrological conditions in neritic waters.

On the Portuguese margin off Aveiro the surficial sediments are dominated by sand with a low content of gravel and mud. On the inner and middle shelf, the sand is mainly terrigenous. In the calmer hydrodynamic environment of the outer shelf and upper slope the sediment is enriched by biogenic particles (foraminifera and mollusc shells). The biogenic content is related to a decrease in the supply of terrigenous particles and probably induced by upwelling conditions. Gravel occurs mainly in 2 bands parallel to the coast line: a wide inner shelf terrigenous band between 30 and 90 m depth and a more restricted one, biogenic, on the outer shelf. Mud (silt and clay) content is low, increasing seawards. This trend is related to the higher near-bottom energy levels on the inner shelf. The observed clay fraction deficiency may be due to the changes occurring in the bottom currents that allow deposition of silt but inhibit generalised deposition of clay. It is possible that important quantities of the finest sediments come from northern areas where the energy available to resuspension in storm conditions is higher than in the study area. Due to the currents these sediments are subsequently redistributed southwards. The dynamic perturbation induced by the rocky outcrop of Pontal da Cartola may lead to the low mud fraction arriving to the study area (Abrantes et al. 1994). Table 1 shows the main sediment characteristics in the area where the suprabenthos was sampled.

The values of the near-bottom water temperature off Aveiro in the vicinity of the sampling sites are pre-

sented in Table 1. These values range from 12.5°C on the outer shelf to 14.0°C near the shore (STD unpublished data measured in July-August during cruise AVEIRO-94).

MATERIAL AND METHODS

Sampling. The suprabenthic communities were sampled at 5 sites (7 TS stations) on an E-W bathymetric transect with a slightly modified version of the suprabenthic sled described by Sorbe (1983). This sled is equipped with an opening-closing system activated by the contact with the seafloor. The superposed nets (0.5 mm mesh size) allow quantitative sampling of the motile fauna in 2 water layers (0 to 50 and 50 to 100 cm) above the seafloor. The volume (V in m^3) of filtered water was estimated with the values given by a TSK flowmeter placed in the opening of the right upper net using the following formula: $V = N_i p S$ (N_i : number of rotor revolutions; p : rotor constant = 0.159 m; S : net opening area = 0.36 m^2). The area (A in m^2) sampled by the sled can also be estimated from the flowmeter measurements using the following formula: $A = N_i p l$ (width of the net, l : 0.71 m). The sled is towed at ca 1.5 knots over the seafloor during each haul.

Seven suprabenthic samples were collected during the cruise AVEIRO-94 (July-August 1994) at 5 sites along a bathymetric transect (Table 2): TS320 and TS333 (21 m) on inner shelf fine sand deposits, TS302 (91 m) on Pontal da Cartola fine sand deposits with less than 5% silt and clay content, TS300 (125 m) on coarse sand relict deposits, TS298 and TS297 (185 to 188 m) on outer shelf gravelly sand deposits and TS299 (299 m) on upper slope gravelly sand deposits. Sampling was carried out during the day except for the haul TS333 taken at night. The hyponeuston (0 to 70 cm) was also sampled during the night with a FAO

Table 1 Near-bottom water temperature (STD probe) and surficial sediment characteristics (Reineck box corer KR) near the sampled suprabenthic sites. Mz: granulometric mean; Md: granulometric median; OM: organic matter content

Stn:	KR 004	KR 254	KR 268	KR 273
Date (1994)	21 July	29 July	29 July	29 July
Position N	40° 37.64'	40° 38.56'	40° 38.55'	40° 38.51'
W	8° 48.93'	9° 06.39'	9° 13.18'	9° 18.34'
Depth (m)	23	91	133	164
Temperature (°C)	13.4	12.7	12.6	12.5
Gravel (%)	0.0	0.0	0.0	0.0
Coarse sand (%)	1.0	1.0	86.5	26.0
Medium sand (%)	8.0	6.0	11.0	30.0
Fine sand (%)	89.0	92.0	2.5	40.0
Silt and clay (%)	2.0	1.0	0.0	4.0
Mz (mm)	0.113	0.177	0.956	0.279
Md (mm)	0.105	0.177	1.091	0.289
OM (%)	1.14	1.35	4.21	3.06

Table 2. Main characteristics of the sampling stations located along a bathymetric transect on the continental shelf and upper slope off Aveiro. Time, position and depth are given for the beginning of the haul

Stn	Date (1994)	Time (h)	Position		Depth (m)
			N	W	
TS297	30 Jul	09:12	40° 37.84'	9° 19.88'	188
TS298	30 Jul	10:20	40° 37.97'	9° 19.79'	185
TS299	30 Jul	11:13	40° 39.05'	9° 20.36'	299
TS300	30 Jul	12:56	40° 38.70'	9° 11.98'	125
TS302	30 Jul	14:02	40° 38.43'	9° 06.54'	91
TS320	1 Aug	16:08	40° 37.76'	8° 48.34'	21
TS333	1 Aug	22:55	40° 37.74'	8° 48.29'	21

net (0.5 mm mesh size; 1 m diameter) at 1 site on the outer shelf (PK295, 148 m water depth).

The collected fauna was fixed on board with 10% neutral formalin and then sorted into various taxa under a dissecting microscope. Species were identified and counted, excluding polychaetes, molluscs, echinoderms and zooplanktonic components (copepods, ostracods). The density of species was estimated and expressed as number of individuals per 100 m³ (ind. 100m⁻³) for the 0 to 50 and 50 to 100 cm water layers and as number of individuals per 100 m² (ind. 100m⁻²) for the 0 to 100 cm water layer.

Numerical methods. The Shannon index H' (\log_2) and evenness J' (in Scherrer 1984) were estimated for each sampling station.

Aveiro data were compared with similar south Gascony data (Sorbe 1984, 1989, unpubl. data) collected at 5 sites off Arcachon (RETRODE cruises during July 1981 and July 1985) with the same suprabenthic gear. The comparative analysis of data was performed using the statistical package PRIMER (Carr et al. 1993). The abundance data were first organised into a samples/species matrix. UPGMA classification and non-metric MDS (multi-dimensional scaling) ordination (Kruskal & Wish 1978) were performed using the Bray-Curtis similarity measure (Bray & Curtis 1957) after fourth root transformation of the data. For the species classification the data were standardised and the taxa with less than 1% of the total abundance in each of all the samples were discarded. An analysis of similarities by randomisation/permutation tests (ANOSIM) was performed on the MDS results (Clarke 1993). Two important factors were considered in this comparison: the geographic location and the bathymetric level of the stations. It might be anticipated that the community will change naturally from one geographic area to another and it is important to separate this effect from any changes associated with depth itself. A 2-way crossed layout was used to assess the significance of the geographic and bathymetric differences in the community structure. This means that the tests for differences between geographic groups are averaged across all bathymetric groups and vice versa (Clarke 1993). The *a priori* groups of stations considered were Aveiro and Arcachon for geographic differences, and inner shelf (21 to 31 m depth), outer shelf (91 to 188 m) and upper slope (299 to 311 m) for bathymetric differences. Using the 2-way crossed layout the effect of depth can be compared against a background of changing community structure in a wide spatial (geographic) scale.

Finally, k-dominance curves (Lambhead et al. 1983) were drawn for each sample to illustrate differences in community structure between bathymetric levels and geographic areas.

RESULTS

A total of 173 taxa were collected in the bathymetric range covered by this study. Amphipods, mysids, cumaceans and decapods were the best represented groups (42, 15, 14 and 13% of the total number of species, respectively). Several species are new records for the Portuguese coast (Cunha et al. 1997). The mysid *Hypererythrops* sp. and the cumaceans *Procampylaspis* sp. and *Cumella* sp. are probably new species.

Species richness, density and diversity

The number of species increased from 23 at the shallowest site (daytime haul at 21 m) to a maximum of 74 at the deepest site (Table 3). This trend was due to the increasing number of mysid, amphipod and decapod species from the inner shelf site to the outer shelf sites. At the upper slope site (299 m) cumaceans and isopods reached their highest number of species. Amphipod species were numerous at all stations (38 to 57% of the total number of species) followed by mysids and decapods at the outer shelf stations and by cumaceans at the inner shelf and upper slope stations.

Density values (Table 3) ranged from 700 ind. 100m⁻² on the inner shelf (TS320) to 13592 ind. 100m⁻² on the middle shelf (TS300). Mysids were the most abundant group (281 to 10702 ind. 100m⁻²) especially on the inner and middle shelf. The maximum density of euphausiids and fishes was observed at the same bathymetric levels (2125 and 62 ind. 100m⁻², respectively, at TS302). Amphipod densities were quite constant, ranging from 144 to 175 ind. 100m⁻² at the shallowest sites and from 400 to 672 ind. 100m⁻² at the deepest sites. Decapods were more abundant (105 to 359 ind. 100m⁻²) on the shelf and isopods reached the higher abundance (53 ind. 100m⁻²) at the deepest site (299 m). There was not a defined bathymetric trend in the abundance of cumaceans (14 to 61 ind. 100m⁻²). The density of the other groups (pycnogonids, leptostraceans and tanaids) was very low (less than 5 ind. 100m⁻²) in all stations sampled.

Table 4 shows the relative contribution of each group to the total abundance in each station and illustrates the dominance of mysids in the suprabenthos collected during daytime. They are only outnumbered by euphausiids at 91 m depth and by amphipods at the upper slope site.

The most abundant species collected off Aveiro were the mysids *Leptomysis gracilis* and *Anchialina agilis* and the euphausiid *Nyctiphanes couchi* (densities up to 9401, 1054 and 2125 ind. 100m⁻², respectively). Table 5 shows the percent contribution of the dominant species at each station. The cumulative percent-

Table 3. Specific richness, density, diversity and evenness of the shelf and upper slope suprabenthic communities off Aveiro. D: daytime haul; N: night-time haul; S: number of species

Stn	Depth (m)	Water layer (cm)	Specific richness (S)	Density		Diversity (Shannon H')	Evenness (J')
				Dv (ind. 100m ⁻³)	Ds (ind. 100m ⁻²)		
TS333 N	21	0-50	27	1287.0		3.12	0.66
		50-100	26	650.7		3.51	0.75
		0-100	31		982.3	3.35	0.68
TS320 D	21	0-50	21	1167.6		2.43	0.55
		50-100	16	213.1		3.33	0.83
		0-100	23		700.2	2.81	0.62
TS302 D	91	0-50	37	6786.6		2.25	0.43
		50-100	20	2125.4		1.26	0.29
		0-100	40		4518.0	2.12	0.40
TS300 D	125	0-50	60	24857.0		1.67	0.28
		50-100	26	2020.5		2.20	0.47
		0-100	63		13591.7	1.82	0.30
TS298 D	185	0-50	56	2715.7		3.33	0.57
		50-100	7	78.0		0.74	0.26
		0-100	56		1414.2	3.36	0.58
TS297 D	188	0-50	67	3113.5		3.32	0.55
		50-100	20	68.5		2.95	0.68
		0-100	67		1613.3	3.36	0.55
TS299 D	299	0-50	74	1523.6		4.09	0.66
		50-100	12	283.1		2.14	0.60
		0-100	74		916.1	4.15	0.67

Table 4. Abundance (%) of the main taxonomic groups within the shelf and upper slope suprabenthic communities off Aveiro. PYC: Pycnogonida; LEP: Leptostraca; MYS: Mysidacea; AMP: Amphipoda; CUM: Cumacea; ISO: Isopoda; TAN: Tanaidacea; EUP: Euphausiacea; DEC: Decapoda; PIS: Pisces. -: 0.0. D: daytime haul; N: night-time haul

Stn (depth)	Water layer (cm)	PYC	LEP	MYS	AMP	CUM	ISO	TAN	EUP	DEC	PIS
TS333 N (21 m)	0-50	--	--	15.6	74.8	6.3	-	-	-	3.3	-
	50-100	-	-	11.8	63.8	17.7	0.2	-	-	6.3	0.2
	0-100	-	-	14.3	71.1	10.1	0.1	-	-	4.3	0.1
TS320 D (21 m)	0-50	-	-	80.1	14.4	2.9	-	-	-	1.1	1.5
	50-100	-	--	20.2	54.8	23.9	-	-	-	1.1	-
	0-100	-	--	70.9	20.6	6.2	-	-	-	1.0	1.3
TS302 D (91 m)	0-50	-	--	53.5	4.4	0.7	0.1	-	38.1	2.5	0.7
	50-100	-	-	16.7	2.2	0.2	0.1	-	75.5	1.8	3.5
	0-100	-	-	44.7	3.9	0.6	0.1	-	47.0	2.3	1.4
TS300 D (125 m)	0-50	0.1	0.1	82.2	4.8	0.4	0.1	0.1	9.5	2.6	0.1
	50-100	-	-	35.8	5.6	0.4	0.1	-	55.7	2.4	-
	0-100	0.1	0.1	78.7	4.9	0.4	0.1	-	13.0	2.6	0.1
TS298 D (185 m)	0-50	-	0.1	44.1	38.5	2.4	0.4	-	4.3	10.1	0.1
	50-100	-	-	2.6	8.6	-	-	-	88.8	-	-
	0-100	-	0.1	43.0	37.6	2.4	0.4	-	6.6	9.8	0.1
TS297 D (188 m)	0-50	-	0.1	50.6	33.7	0.8	0.2	-	1.5	13.0	0.1
	50-100	-	-	18.8	35.3	2.9	-	-	42.4	0.6	-
	0-100	-	0.1	49.9	33.8	0.9	0.2	-	2.3	12.7	0.1
TS299 D (299 m)	0-50	-	-	36.3	42.3	6.7	4.5	-	3.8	6.4	-
	50-100	-	-	0.6	51.2	0.6	0.3	-	24.8	22.5	-
	0-100	-	-	30.7	43.6	5.8	3.9	-	7.1	8.9	-

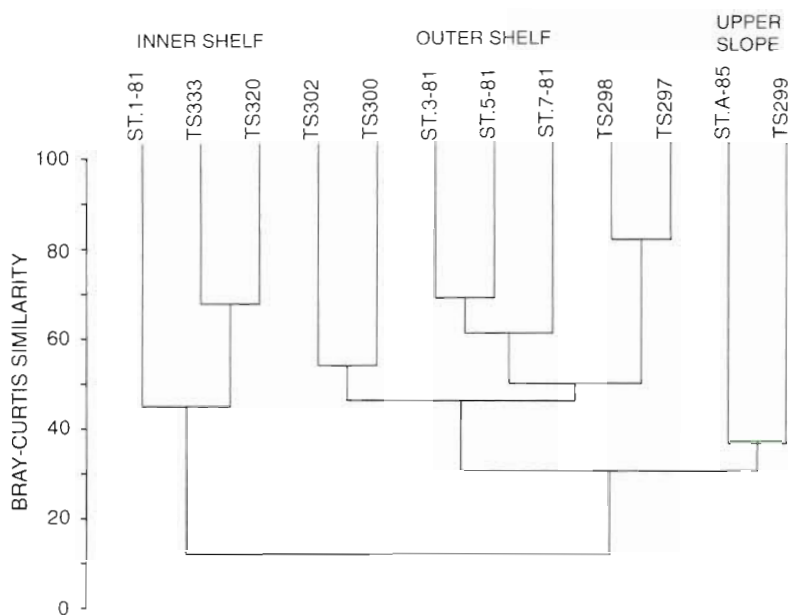


Fig. 2. Cluster analysis on the data from the suprabenthic communities off Aveiro (TS samples) and off Arcachon (ST samples). Three sample groups are distinguished in relation to depth. Arcachon data from Sorbe (1984, 1989, unpubl. data)

the outer shelf and finally *Hemimysis abyssicola* on the upper slope. *Rhachotropis integricauda* was the most abundant amphipod with density values ranging from 180 to 338 ind. 100m⁻² on the outer shelf and upper slope.

The highest diversity value (4.15) was observed at the upper slope station (Table 3) as a result of a higher number of species and a more even distribution of their abundance. Despite the high species richness (63) and due to the strong dominance of *Leptomysis gracilis* (69.2% of the total abundance), the lowest diversity and evenness values ($H' = 1.82$, $J' = 0.30$) were observed on the middle shelf (TS300).

Faunal assemblages

The dendrogram (Fig. 2) shows the classification of the Aveiro and Arcachon stations into 3 groups related to depth: inner shelf, outer shelf and upper slope.

age of the 5 dominant species of the total abundance was high, specially at the middle shelf stations. *Nycetiphanes couchi* is always ranked amongst the 5 dominant species except for at the 21 m depth site (TS333 and TS320). Mysids have an outstanding role in the community structure occupying the leading ranks in almost all stations: *Mesopodopsis slabberi* and *Gastrosaccus* spp. at the shallower site (daytime haul), *Anchialina agilis* and *Leptomysis gracilis* on the middle shelf, *Mysideis parva* and *Erythropros neapolitana* on

The similarity between communities of the same bathymetric level from different geographical areas is higher (33.2 to 54.4%) than the similarity between communities of the same area but from different bathymetric levels (1.5 to 39.5%).

Fig. 3 shows the dendrogram based on the similarities between species. The 87 species considered for this analysis (see 'Material and methods') were classified into 5 groups. These groups can be associated with the bathymetric levels and geographic areas where the

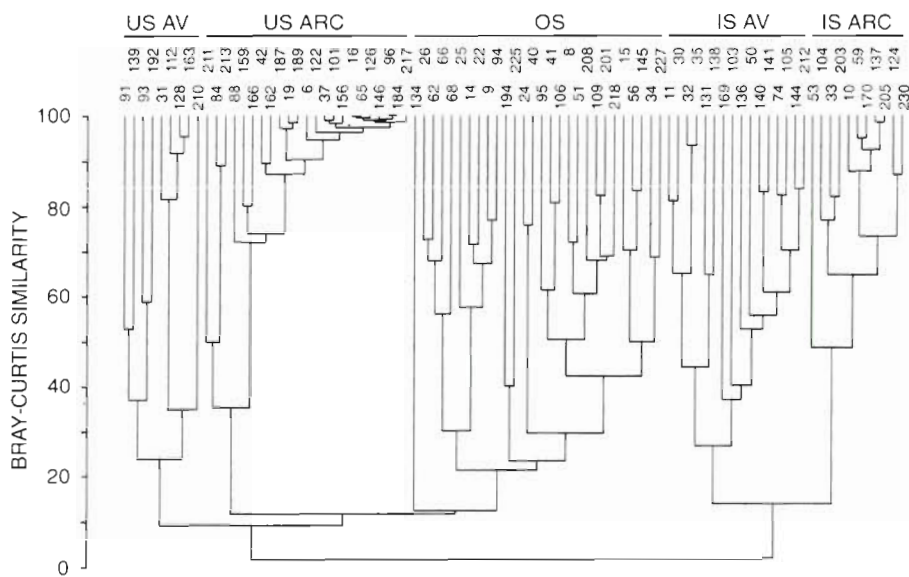


Fig. 3. Cluster analysis showing the classification of 87 species from the suprabenthic communities off Aveiro and off Arcachon. The species groups can be related to different bathymetric levels. Species codes listed in Table 9. Arcachon data from Sorbe (1984, 1989, unpubl. data). US AV: upper slope, Aveiro; US ARC: upper slope, Arcachon; OS: outer shelf; IS AV: inner shelf, Aveiro; IS ARC: inner shelf, Arcachon

species concerned have their greatest abundance or only occurrence: upper slope off Aveiro, upper slope off Arcachon, outer shelf, inner shelf off Aveiro and inner shelf off Arcachon.

Table 5. Abundance (%) of the 5 dominant suprabenthic species at the stations sampled on the continental shelf and upper slope off Aveiro (0 to 100 cm water layer). D: daytime haul; N: night-time haul. MYS: Mysidacea; AMP: Amphipoda; EUP: Euphausiacea; DEC: Decapoda

		%
TS333 N (21 m)		
AMP	<i>Periocolodes longimanus</i>	22.8
AMP	<i>Argissa hamatipes</i>	17.5
AMP	<i>Orchomenella nana</i>	14.7
AMP	<i>Megaluropus agilis</i>	10.3
MYS	<i>Schistomysis kervillei</i>	6.4
Total		71.7
TS320 D (21 m)		
MYS	<i>Mesopodopsis slabberi</i>	36.9
MYS	<i>Gastrosaccus</i> spp. (juv.)	22.2
AMP	<i>Argissa hamatipes</i>	7.2
MYS	<i>Schistomysis kervillei</i>	6.0
AMP	<i>Pariambus typicus</i>	4.6
Total		76.9
TS302 D (91 m)		
EUP	<i>Nyctiphanes couchi</i>	47.0
MYS	<i>Anchialina agilis</i>	23.3
MYS	<i>Leptomysis gracilis</i>	19.1
DEC	<i>Philocheras bispinosus</i>	1.9
MYS	<i>Erythroops elegans</i>	1.6
Total		92.9
TS300 D (125 m)		
MYS	<i>Leptomysis gracilis</i>	69.2
EUP	<i>Nyctiphanes couchi</i>	13.0
MYS	<i>Anchialina agilis</i>	7.2
DEC	<i>Philocheras bispinosus</i>	2.0
MYS	<i>Erythroops elegans</i>	1.2
Total		92.6
TS298 D (185 m)		
MYS	<i>Mysideis parva</i>	24.0
AMP	<i>Rhachotropis integricauda</i>	23.9
MYS	<i>Erythroops neapolitana</i>	14.7
DEC	<i>Philocheras bispinosus</i>	9.4
EUP	<i>Nyctiphanes couchi</i>	6.7
Total		78.7
TS297 D (188 m)		
MYS	<i>Mysideis parva</i>	26.8
AMP	<i>Rhachotropis integricauda</i>	19.8
MYS	<i>Erythroops neapolitana</i>	17.3
DEC	<i>Philocheras bispinosus</i>	11.4
EUP	<i>Nyctiphanes couchi</i>	2.9
Total		78.2
TS299 D (299 m)		
MYS	<i>Hemimysis abyssicola</i>	20.7
AMP	<i>Rhachotropis integricauda</i>	19.7
AMP	<i>Scopelocheirus hopei</i>	10.0
EUP	<i>Nyctiphanes couchi</i>	6.0
MYS	<i>Parapseudomma calloplura</i>	5.8
Total		62.2

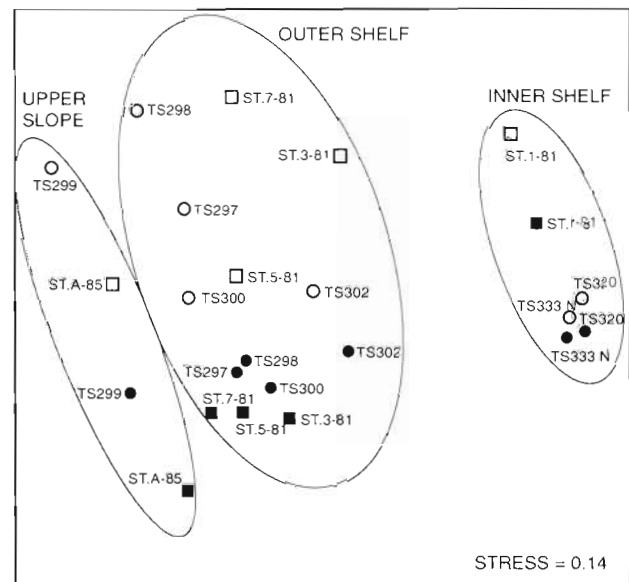


Fig. 4. MDS (multi-dimensional scaling) plot of the suprabenthic stations off Aveiro and off Arcachon. Stress: <0.05 = excellent representation; <0.1 = good; <0.2 = still useful; >0.2 = difficult to interpret. Arcachon data from Sorbe (1984, 1989, unpubl. data). (□, ■) Arcachon stations, (○, ●) Aveiro stations (full symbols: 0 to 50 cm water layer; open symbols: 50 to 100 cm water layer). N: night-time haul

Fig. 4 and Table 6 show the results of the MDS and ANOSIM for all stations from Aveiro and Arcachon (the water layers in each haul were considered separately). The communities from different bathymetric levels occupy defined positions in the plot but the separation of the stations by geographic areas is not clear. Nevertheless, the ANOSIM tests show that the differences in the community structure are significant when geographic areas as well as bathymetric levels are compared.

Table 6. Results of the ANOSIM global and pairwise tests. The statistic estimated for each permutation used is considered significant when its value is greater than or equal to the sample statistic. IS: inner shelf; OS: outer shelf; US: upper slope

	Sample statistic	Permutations used	Significant statistics	Significance level (%)
Global tests				
Geographic	0.209	10000	382	3.8*
Bathymetric	0.780	10000	0	0.0***
Pairwise tests				
(IS, OS)	0.861	10000	2	0.0***
(IS, US)	1.000	45 ^a	1	2.2*
(OS, US)	0.492	1260 ^a	13	1.0**

^aAll possible permutations were used

Near-bottom vertical distribution and diel changes

All suprabenthic communities off Aveiro showed a decrease in the number of species and density from the lower to the higher water layer sampled by the sled (Table 3, daytime hauls). On average 89% of the individuals were collected in the immediate vicinity of the seafloor (0 to 50 cm water layer). This trend was more evident on the middle and outer shelf where the density in the lower water layer was more than 10-fold the upper one. From the major taxonomic groups only euphausiids (mainly represented by *Nyctiphanes couchi*) consistently showed an equitable distribution in the 2 water layers. On average 64% of the euphausiids were collected in the lower water layer. At the inner shelf site (daytime TS station), amphipods and cumaceans also showed similar densities in the 2 water layers but this pattern was not observed at the other stations except for a few species. Only the amphipods *Scopelocheirus hopei*, *Trischizostoma nicaense* and *Pontocrates arenarius*, the cumacean *Bodotria pulchella* and the decapods *Pasiphaea sivado* (juv.) and *Galathea* sp. (juv.) were collected in higher numbers in the upper net.

In the MDS plot (Fig. 4), the distance between water layers from the same station reflects the near-bottom vertical distribution of the fauna. This distance is smaller at the shallower stations, specially off Aveiro. At the stations where the suprabenthos is more concentrated in the immediate vicinity of the seafloor (higher density and number of species), the distance between water layers in the MDS plot is larger. The different dispersion of the points referring to the upper and to the lower layers illustrates the difference in the structure of the faunal assemblage of the 2 water layers. The larger dispersion of the upper layer points may be interpreted as a result of the impoverished faunal assemblage with lower number of species and density values. The higher specific richness and abundance of the lower water layer allow a better characterisation of the faunal assemblage which is illustrated in the MDS plot by the closeness of the points and the marked delineation of the groups.

The night-time haul (station TS333) at the shallower site illustrated the increase of species richness, density and diversity due to the nocturnal arrival of some species into the 0 to 100 cm water layer (Table 3). The higher number of species and density in the upper water layer during the night due to the increase of the swimming activity of the suprabenthos results in a more equitable distribution in the sampled water column. The daytime structure (station TS320) is dominated by mysids (70.9% of the total density in the 0 to 100 cm water layer) followed by amphipods (20.6%). During the night, the total abundance of mysids

Table 7 Density (ind. 100m⁻³) of some species collected on the outer shelf in the near-bottom environment (TS300) and in the hyponeuston (PK295). MYS: Mysidacea; AMP: Amphipoda; ISO: Isopoda; EUP: Euphausiacea; DEC: Decapoda. -: 0.0. D: daytime sample; N: night-time sample

Water layer (cm):	TS300, D		PK295, N
	0–50	50–100	0–70
MYS <i>Siriella norvegica</i>	–	–	1.0
MYS <i>Anchialina agilis</i>	1625.0	304.5	448.6
MYS <i>Haplostylus lobatus</i>	2.3	2.3	56.5
MYS <i>Leptomysis gracilis</i>	18293.2	295.5	8.8
AMP <i>Ichnopus spinicornis</i>	–	–	0.5
ISO <i>Eurydice truncata</i>	–	–	17.0
ISO <i>Idotea metallica</i>	–	–	0.5
EUP <i>Nyctiphanes couchi</i>	2370.5	1122.7	491.5
DEC <i>Processa caniculata</i>	2.3	–	–
DEC <i>Processa</i> sp. (juv.)	–	–	1.5
DEC <i>Callinassa</i> sp. (juv.)	–	4.5	1.0

decreases but amphipods, cumaceans and decapods increase their densities expressively (Table 4). Amphipods replace mysids in the first ranks of dominance (71.1% of amphipods against 14.3% of mysids).

At the species level, Table 5 shows the replacement of the daytime dominant mysids *Mesopodopsis slabberi* and *Gastrosaccus* spp. by the amphipods *Perioculodes longimanus*, *Orchomenella nana* and *Megaluropus agilis*. The amphipod *Argissa hamatipes* and the mysid *Schistomysis kervillei* are dominant species in both day and night structures. The percent contribution of the 5 dominant species clearly shows a more even distribution of species abundances in the night-time structure that, together with the increase in the number of species, leads to a higher diversity value (Tables 3 & 5).

The hyponeuston night-time sample taken on the outer shelf (Table 7) showed that *Nyctiphanes couchi*, *Anchialina agilis*, *Haplostylus lobatus* and *Leptomysis gracilis* found in the vicinity of the seafloor during the day are able to swim up into the water column and concentrate near the surface during the night.

DISCUSSION

The suprabenthic communities have been studied for the last decade in several areas of the NE Atlantic Ocean. In these studies a variety of sleds have been used to sample the near-bottom motile fauna at different depth ranges. Most studies deal with coastal areas and the available data is scarcer for deeper communities. There are some taxonomic groups like mysids or amphipods that are preferentially studied. Other groups, like cumaceans or isopods, are often neglected.

This discussion must be considered taking into account the variety of the available data and the different levels of possible comparisons.

From the 146 taxa collected off Aveiro and identified to the species level, 119 (81.5%) were cited in suprabenthic studies concerning northern Atlantic regions (Table 8). The highest number of common records (104) was found for the Bay of Biscay where the available data covers a depth range from 0 to 1100 m (Sorbe 1982, 1984, 1989, Elizalde et al. 1991, 1993, Dauvin & Sorbe 1995, Dauvin et al. 1995, Sorbe & Weber 1995). In all other regions the number of common records is much lower: 43 for the English Channel (depth range: 8 to 75 m; Dauvin et al. 1994, Wang & Dauvin 1994, Zouhiri & Dauvin 1996), 21 for the Dutch Delta (0 to 15 m; Hamerlynck & Mees 1991, Cattrijsse et al. 1993, Mees et al. 1993), 40 for the Gullmarfjord (33 to 116 m; Buhl-Jensen & Fosså 1991), 35 for western Norway (0 to 380 m; Buhl-Jensen 1986, Fosså & Brattegard 1990, Brattegard & Fosså 1991) and 5 for the Northeast Water Polynya in Greenland (45 to 517 m; Brandt et al. 1996).

All mysid and euphausiid species, about 80% of the amphipod, cumacean and decapod species and 45% of isopod species collected off Aveiro had been recorded in the suprabenthos of northern Atlantic regions.

Some species not cited for the NE Atlantic are known from southern areas: *Abludomelita aculeata* was previously considered as Mediterranean endemic; *Pardia punctata* is known from the coast of Senegal and Mediterranean sea (cf. Ruffo 1982, 1989).

Species richness, density and diversity

On the continental margin off Aveiro the number of suprabenthic species increased from the shallower to the deeper sampling sites. The same trend and similar values of specific richness were observed for the communities off Arcachon (Sorbe 1984, 1989, unpubl. data): 25 to 70 species were found from the inner shelf site (31 m depth) to the upper slope (311 m). At the outer shelf stations the number of species ranged from 59 to 68. Higher species richness values (97 to 116 species per sampling station) have been recorded for deeper bathyal communities (Elizalde et al. 1993, Sorbe & Weber 1995).

As in Aveiro communities, amphipods are commonly the best represented group by species number in the NE Atlantic suprabenthos. Mysids and decapods are also well represented in coastal communities (Buhl-Jensen & Fosså 1991, Hamerlynck & Mees 1991, Dauvin et al. 1994) whilst in deeper bathyal areas isopods and cumaceans have higher species numbers (Elizalde et al. 1993, Brandt 1995).

The density of the suprabenthos off Aveiro is high, specially on the outer shelf, where 24857 ind. 100m⁻³ are recorded in the 0 to 50 cm water layer (TS300). Dauvin et al. (1994) gathered density values (Macer-GIROQ sled) of North Atlantic suprabenthic communities from several sources. The higher densities mentioned were 2726 to 4462 ind. 100m⁻³ (10 to 40 cm water layer) in the bathyal communities of the Bay of Biscay (Elizalde et al. 1993). Dauvin et al. (1994) also mention that the highest densities were generally recorded on fine sediment in regions with an important input of organic matter to the bottom environment as for the muddy sediment from the continental shelf of the Bay of Biscay (Sorbe 1984) or in the Gullmarfjord (Buhl-Jensen & Fosså 1991). In the Aveiro communities the high densities cannot be associated with the same sediment characteristics since fine particles and organic matter contents are very low. On the other hand the seasonal upwelling events and its effects on the primary production regime could be related to the observed density values of suprabenthos on the continental shelf off Aveiro. The extremely high densities of some of the sampling stations are mainly due to the occurrence of swarms of species known to have a very good swimming ability like the mysids *Leptomysis gracilis*, *Anchialina agilis* and the euphausiid *Nyctiphanes couchi*. Mysids are known to migrate actively to areas of high primary productivity (Wooldridge 1989) and several authors (Clutter 1967, Fosså 1985, Hargreaves 1985) suggest that increased food availability may be an important factor acting on the swimming activity and causing increased abundance of these suprabenthic organisms. Besides the behavioural and environmental factors, the life cycle features of suprabenthic species may determine density fluctuations that induce temporal changes in the community structure (Boysen 1975, Buhl-Jensen & Fosså 1991, Hamerlynck & Mees 1991, Dauvin et al. 1994).

Fig. 5 shows the percent contribution of the main groups to the total density for Aveiro and Arcachon communities. In both areas there is a high dominance of mysids at the outer shelf stations. The increased abundance of isopods and cumaceans at the upper slope site, both in Aveiro and Arcachon, leads to a more even contribution of the main taxonomic groups. Overall, in the Arcachon communities the distribution of abundance is more equitable, mainly due to higher contributions of decapods, cumaceans and isopods. Despite this difference most species are common to Aveiro and Arcachon and some of them are dominant in the same bathymetric level at both geographic areas: *Schistomysis kervillei* and *Argissa hamatipes* at the inner shelf site, *Anchialina agilis*, *Leptomysis gracilis*, *Erythrope neapolitana*, *Nyctiphanes couchi* and *Philocheras bispinosus* at the outer shelf stations and

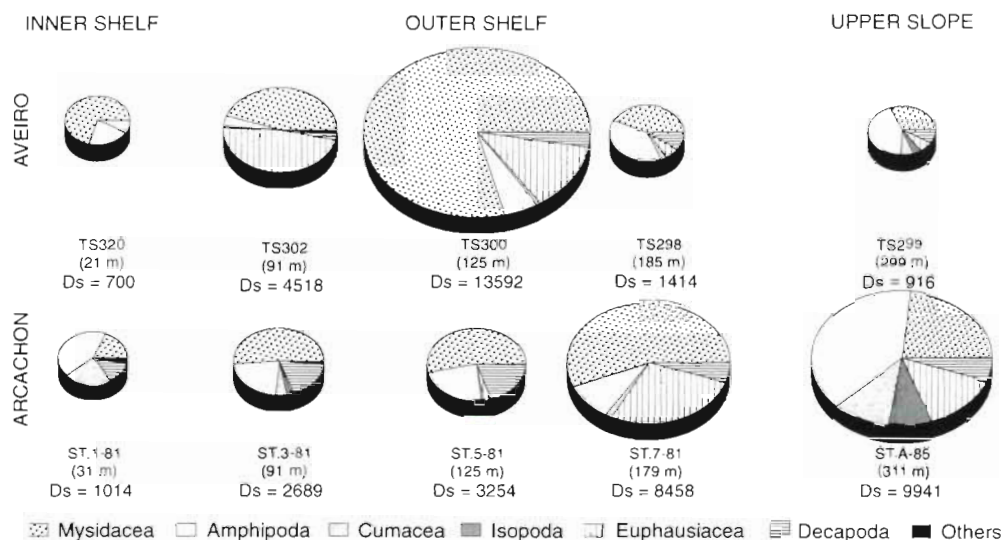


Fig. 5. Abundance of the main taxonomic groups in the suprabenthic communities off Aveiro and off Arcachon. Data from the 0 to 100 cm water layer sampled by the sled. Arcachon data from Sorbe (1984, 1989, unpubl. data). Ds: density (ind. 100m⁻²)

Parapseudomma calloplura and *N. couchi* at the upper slope site (see also Table 5).

Mysids, amphipods and decapods are usually the most abundant groups in coastal communities (Buhl-Jensen & Fosså 1991, Hamerlynck & Mees 1991) whereas isopods and cumaceans are often dominant in deeper bathyal areas (Elizalde et al. 1993, Sorbe & Weber 1995). In the Northeast Water Polynya region (Brandt et al. 1996), characterised by very fine sediments, cumaceans and isopods occur more frequently on softer, finer sediment and in slightly deeper waters, whereas amphipods dominate at shallower sites and in coarser sediment. In the western English Channel (Dauvin et al. 1994) amphipods dominate the coarse sand community. However, in the fine sand community of the eastern English Channel (Wang & Dauvin 1994) amphipods are not abundant and cumaceans are the most abundant group. Dauvin et al. (1994) suggest that higher numbers of species and individuals of cumaceans are probably associated with higher percentages of fine particles in the sediment in shallow waters.

The diversity and evenness values observed in the suprabenthic communities off Aveiro are in the range of the values observed in other communities (Sorbe 1984, 1989, Brattegard & Fosså 1991, Dauvin et al. 1994). In Arcachon communities and for the same bathymetric levels, these values ($H' = 3.4$ to 4.8 , $J' = 0.56$ to 0.79) are higher than in the Aveiro community. In the coarse sand community of the English Channel, H' varied between 1.50 and 3.79 and J' between 0.27 and 0.73 and at the Norwegian Trough, the diversity H' ranged from 0.66 to 2.57. In deeper communities (400 to 1100 m) of the Bay of Biscay, diversity reached

values higher than 5 (Elizalde et al. 1993, Sorbe & Weber 1995).

Faunal assemblages

Table 9 shows the depth range of the species grouped by cluster analysis and associated with the different bathymetric levels off Aveiro and off Arcachon. On the whole, there is an accordance with the data from other sources. This table illustrates that, despite the wide geographic distribution of most of the species collected off Aveiro, their bathymetric distribution is often restricted to a certain depth range. When the Aveiro and Arcachon communities were compared it was clear that the similarity between communities of the same bathymetric level from the 2 geographical areas was always higher than the similarity between communities of the same area but from different bathymetric levels. The multivariate analysis of the faunal data consistently revealed significant differences in the suprabenthic communities related to a depth gradient and the associated environmental factors. However, the differences between the 2 geographical areas were not so clearly defined.

Despite the high number of common species and the likeness in the faunal assemblages, there are important differences between the 2 geographical areas. Some of these differences were pointed out and discussed above. The importance of the upwelling in increasing the density of mysids or the influence of sediment type on the density of cumaceans are examples of the relation between environmental factors and community structure.

Table 8. Number of species of the main taxonomic groups collected off Aveiro that have been recorded in the suprabenthos of other areas in the NE Atlantic (total number of species recorded off Aveiro in brackets). Data were gathered from Sorbe (1982, 1984, 1989), Elizalde et al. (1991, 1993), Dauvin & Sorbe (1995), Dauvin et al. (1995), Sorbe & Weber (1995) (Bay of Biscay); Dauvin et al. (1994), Wang & Dauvin (1994), Zouhiri & Dauvin (1996) (English Channel); Hamerlynck & Mees (1991), Cattrijsse et al. (1993), Mees et al. (1993) (Dutch Delta); Buhl-Jensen & Fosså (1991) (Gullmarfjord); Buhl-Jensen (1986), Fosså & Brattegard (1990), Brattegard & Fosså (1991) (western Norway); Brandt et al. (1996) (Greenland). PYC: Pycnogonida; LEP: Leptostraca; MYS: Mysidacea; AMP: Amphipoda; CUM: Cumacea; ISO: Isopoda; TAN: Tanaidacea; EUP: Euphausiacea; DEC: Decapoda

Area	Depth (m)	PYC (1)	LEP (2)	MYS (25)	AMP (66)	CUM (22)	ISO (11)	TAN (1)	EUP (4)	DEC (14)	Total (146)
Bay of Biscay	0–1100	1	1	22	46	15	4	1	4	10	104
English Channel	8–75	–	–	11	23	5	1	–	1	2	43
Dutch Delta	0–15	–	–	5	11	3	–	–	1	1	21
Gullmarfjord	33–116	–	–	9	28	–	–	–	–	3	40
Western Norway	0–380	–	–	12	19	–	–	–	–	4	35
Greenland	45–517	–	–	–	5	–	–	–	–	–	5
All areas		1	1	25	54	17	5	1	4	11	119

The grain size, patchy distribution and low mud content of the sediments in the Portuguese margin off Aveiro may be interpreted as the outcome of a complex hydrodynamic environment. The fine particles enrichment trend with increasing depth indicates calmer conditions in the outer shelf and upper slope. Nevertheless, the prevalence of coarse sediments reveals the existence of a high energy environment probably with strong bottom currents. On the other hand, the occurrence of upwelling changes the current regime seasonally.

These rather perturbed conditions can be considered as natural causes of stress or instability that certainly influence the community structure of the suprabenthos off Aveiro. The overwhelming dominance of a single species at the inner and middle shelf opposed to a more even distribution of abundance at the outer shelf and upper slope is probably associated with the existing hydrodynamic conditions and physical constraints of the sediment type. In Arcachon communities where a more stable environment occurs, the diversity and evenness values are higher and the dominance of the most abundant species is always lower than 28%.

Lamshead et al. (1983) have shown the usefulness of dominance curves in the comparison of faunal assemblages. The information yielded by these curves overcomes the difficulty in interpreting diversity and evenness values. Their ability to detect changes in the community structure patterns caused by natural or unnatural causes is also suggested.

The relative position of the dominance curves (Fig. 6) shows that Aveiro communities always exhibit higher dominance than Arcachon communities. Dominance is the reverse of equitability and has an inverse relationship with diversity (Lamshead et al. 1983). Higher dominance is the result of the increased proportional

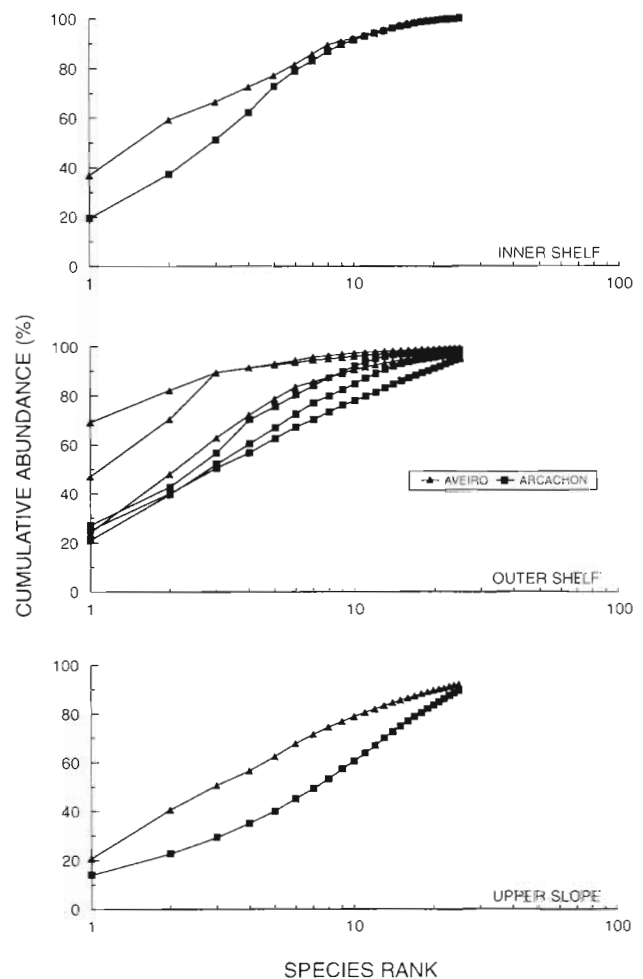


Fig. 6. K-dominance curves for the suprabenthic communities off Aveiro and off Arcachon. Data from the 0 to 100 cm water layer sampled by the sled. Arcachon data from Sorbe (1984, 1989, unpubl. data)

Table 9. Observed depth range (m) of the species contributing more than 1% to the total abundance of TS (Aveiro) and ST (Arcachon) samples. Species are grouped following the cluster analysis (species codes in brackets). Known distribution data of species in the NE Atlantic were gathered from Brattegard & Fosså (1991), Buhl-Jensen & Fosså (1991), Dauvin & Sorbe (1995), Dauvin et al. (1995), Elizalde & Sorbe (1993), Elizalde & Sorbe (1993), Fosså & Brattegard (1990), Hamerlynck & Mees (1991), Lagardère & Nouvel (1980), Marques & Bellan-Santini (1993), Sorbe (1984, 1989), Sorbe & Weber (1995), Wang & Dauvin (1994), Zouhir & Dauvin (1996)

Group	TS samples (Aveiro)	Depth range (m) ST samples (Arcachon)	Known distribution	Group	TS samples (Aveiro)	Depth range (m) ST samples (Arcachon)	Known distribution
Upper slope; Aveiro				Outer shell (continued)			
(91) <i>Scopelocheirus hopei</i>	125–299	31–311	31–717	(24) <i>Leptomysis gracilis</i>	91–188	91–179	30–400
(139) <i>Iphinoe serrata</i>	125–299	91–311		(40) <i>Ampelisca spooneri</i>	91–188	179	22–383
(93) <i>Trischizostoma nicaeense</i>	91–299	311	40–923	(95) <i>Meiphipidippella macra</i>	91–299	91–311	8–323
(192) <i>Meganicydianes norvegica</i>	125–299	311	125–1043	(41) <i>Ampelisca</i> sp.	21–188		
(31) <i>Hemimysis abyssicola</i>	125–299		125–410	(106) <i>Westwoodilla caecula</i>	125–299	91–311	19–1043
(112) <i>Epimeria parasitica</i>	125–299		125–1043	(8) <i>Anchialina agilis</i>	91–188	91–179	8–188
(128) <i>Syrhoë affinis</i>	299		299–717	(51) <i>Apherusa bispinosa</i>	91–188	91–179	39–346
(163) <i>Campylaspis verrucosa</i>	299		299–425	(208) <i>Pandalina brevirostris</i>	91–299	91–179	75–299
(210) <i>Pasiphaea sivado</i> (juv.)	188–299		188–669	(109) <i>Synchelidium</i> sp.	91–299	91–179	
Upper slope; Arcachon				(201) <i>Philocheirus bispinosus</i>	91–299	91–179	31–315
(211) <i>Processa canaliculata</i>	125–299	125–311	91–437	(218) <i>Paguridae</i> ind. (juv.)	31–179		
(84) <i>Hippomedon deniculatus</i>		125–311	75–1098	(15) <i>Erythrops elegans</i>	91–125	91	0–125
(213) <i>Processa novelli holthuisi</i>	188–299	91–311	75–395	(56) <i>Siphonocetes striatus</i>	125–188	91	91–188
(88) <i>Orchomenella nana</i>	21–299	31–311	0–1098	(145) <i>Diastylodes biplicata</i>	91–299	91–125	91–299
(159) <i>Campylaspis glabra</i>	185–299	91–311	91–717	(34) <i>Schistomysis ornata</i>	188	91–179	30–188
(166) <i>Nannastarcus</i> sp. ?		125–311		(227) <i>Gobiidae</i> ind. (juv.)	21–125	91–125	
(42) <i>Amphilochoides boeckii</i>	185	91–311	91–395	Inner shell; Aveiro			
(162) <i>Campylaspis sulcata</i>	299	125–311	125–437	(11) <i>Gastrosaccus</i> spp. (juv.)	21–125		
(187) <i>Ilyarachna longicornis</i>	299	311	179–1043	(30) <i>Acanthomysis longicornis</i>	21	31	0–91
(19) <i>Parapseudomma calloplura</i>	299	311	299–1100	(32) <i>Mesopodopsis slabberti</i>	21		0–42
(189) <i>Munnopsurus atlanticus</i>	299	311	299–717	(35) <i>Schistomysis spiritus</i>	21		0–116
(6) <i>Boreomysis megalops</i>	299	179–311	100–1099	(131) <i>Pariambus typicus</i>	21–91	31–91	0–91
(122) <i>Stegoccephaloides christianseni</i>	185	311	40–747	(138) <i>Bodotria pulchella</i>	21		
(37) <i>Mysidella typica</i>	188–299	311	100–600	(169) <i>Pseudocuma longicornis</i>	21–91	31–311	0–91
(101) <i>Monoculodes packardii</i>	299	311	40–1043	(103) <i>Penoculodes longimanus</i>	21–188		8–791
(156) <i>Mesolamprops mediterranea</i>	299	311		(136) <i>Bodotria arenosa</i>	21–185		
(16) <i>Hypererythroptus serrventer</i>	299	311	311–1099	(50) <i>Argissa hamatipes</i>	21	31–311	8–1098
(65) <i>Rhachitropis grimaldi</i>		311	311–1043	(140) <i>Iphinoë trispinosa</i>	21		21–75
(126) <i>Bruzelia typica</i>		311	311–714	(141) <i>Diastylis bradyi</i>	21	31	0–31
(146) <i>Diastylodes serrata</i>		91–311	91–714	(74) <i>Megaluroptus agilis</i>	21	31	0–125
(96) <i>Bathymedon longimanus</i>		311	42–1098	(105) <i>Pontocrates arenarius</i>	21	31	0–91
(184) <i>Disconectes latirostris</i>		311	311–717	(144) <i>Diastylis</i> sp. (juv.)	21	31	
(217) <i>Munida</i> spp. (juv.)		91–311		(212) <i>Processa modica</i>	21		0–31
Outer shell				Inner shell; Arcachon			
(134) <i>Parathemisto</i> sp.		31–311	91–717	(53) <i>Apherusa ovalipes</i>		31–125	0–346
(26) <i>Mysidella parva</i>	91–299	91–311	75–1098	(104) <i>Pontocrates allamannus</i>	21	31	0–113
(62) <i>Eusirus longipes</i>	125–299	91–311	125–346	(33) <i>Schistomysis kervillei</i>	21	31	0–31
(66) <i>Rhachitropis integricauda</i>	125–299	179–311		(203) <i>Philocheirus trispinosus</i>	21	31	0–31
(68) <i>Abiodomella aculeata</i>	125–299			(10) <i>Gastrosaccus spinifer</i>	21	31	0–107
(25) <i>Leptomysis megalops</i>	91–188	125–179	91–188	(59) <i>Atylus swammerdami</i>	21	31	0–107
(14) <i>Erythroptus neapolitana</i>	185–299	125–311	125–523	(170) <i>Pseudocuma similis</i>		31	
(22) <i>Parerythroptus paucispinosa</i>	125–188	91–179	75–311	(137) <i>Bodotria armoricana</i>		31	
(9) <i>Haplostylus lobatus</i>	125–188	91–311	12–1098	(205) <i>Cragon crangon</i>		31	0–116
(94) <i>Trypanites longipes</i>	91–299	91–311	0–714	(124) <i>Stenothoe valida</i>		31	0–91
(194) <i>Nyctiphanes couchi</i>	91–188	91–311		(230) <i>Bothidae</i> ind.		31–125	
(225) <i>Pisces</i> ind. (juv.)							

abundance of some species that, behaving in an opportunistic way, are somehow better equipped to face natural or unnatural constraints. The remarkable densities reached by *Nyctiphanes couchi* or *Leptomysis gracilis* on the Portuguese continental shelf can be considered as examples of such a behaviour.

Near-bottom vertical distribution and diel changes

The vertical distribution of the motile fauna in the Aveiro communities showed the same general pattern observed in other geographical areas including the Bay of Biscay: decrease of species richness and density from the water-sediment interface (Sorbe 1984, 1989). The impoverished faunal assemblage leads to a higher variability among samples from the upper water layer sampled by the sled that is revealed by a wider dispersion of the points in the MDS plot (see Warwick & Clarke 1993).

In the suprabenthic communities off Aveiro most individuals concentrate in the immediate vicinity of the bottom during the day. The nocturnal increase in the abundance of amphipods and cumaceans in the 2 near-bottom water layers at the shallowest site illustrates the emergence behaviour and increased swimming activity of these organisms during the night. On the other hand, the high catches of mysids and euphausiids in the hyponeuston during the night confirm the nocturnal upwards migration of such suprabenthic species. These observations are based on only 1 sample of nocturnal suprabenthos and 1 sample of nocturnal hyponeuston, nevertheless they are validated by similar observations of other authors.

Swimming activity and diel changes in the vertical distribution of suprabenthic species have been studied and described by several authors (Russell 1925, Champalbert & Macquart-Moulin 1970, Hesthagen 1973, Macquart-Moulin 1984, 1991, 1992, Fosså 1985, Kaartvedt 1985, 1986, 1989, Macquart-Moulin & Patrìti 1993, Macquart-Moulin & Ribera Maycas 1995, Dauvin & Zouhiri 1996). Species-specific behavioural patterns together with other factors such as light, currents or food availability determine the swimming activity and thus the vertical distribution of suprabenthic animals (Fosså 1985, 1986, Elizalde et al. 1991, Vallet et al. 1995).

On the whole these studies also documented that swimming activity increases during the night. Amphipods and cumaceans usually emerge from the sediment but do not commonly swim high up into the water column (Kaartvedt 1986, 1989). However some amphipod species are frequently collected in pelagic or hyponeustonic catches (Macquart-Moulin 1984). For instance, the lysianassid *Ichnopus spinicornis* collected

in the nocturnal hyponeuston of Portuguese waters was also mentioned as belonging to the 'planktonic group' by Macquart-Moulin (1984). As in this study, the cirrolanid isopod *Eurydice truncata* was frequently collected during the night in hyponeustonic waters with a maximal density as high as 195 ind. 100m⁻³ (Champalbert & Macquart-Moulin 1970, Macquart-Moulin 1992, Macquart-Moulin & Patrìti 1993).

In contrast to amphipods and cumaceans, most of the suprabenthic mysids migrate upwards during the night and some of them are collected near the surface in high densities (Kaartvedt 1985). For instance, *Siriella norvegica*, *Leptomysis gracilis*, *Haplostylus lobatus* and *Anchialina agilis* were also observed nocturnally in the hyponeuston of neritic waters with densities as high as 375 and 277 ind. 100m⁻³ for the latter 2 species respectively (Champalbert & Macquart-Moulin 1970, Macquart-Moulin & Patrìti 1993, Macquart-Moulin & Ribera Maycas 1995).

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Appendix 1. Density of the suprabenthic species collected with a sled in the 0–50, 50–100 and 0–100 cm near-bottom water layers at 7 stations on the continental shelf and upper slope off Aveiro (NW Portugal). Dv: ind. 100m⁻³; Ds: ind. 100m⁻²; 0.0. Juv.: juveniles; F: females; M: males; * damaged specimens

Taxon	TS333		TS320		TS302		TS300		TS298		TS297		TS299		
	Haul Depth (m)	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	0–50 50–100 0–100	
Pycnogonida															
<i>Anoplodactylus petiolatus</i>							2.3								
Leptostraca															
<i>Nebalia cf. clausi</i>									0.7		0.4				
<i>Sarsinebalia typhlops</i>							4.5								
Mysidacea															
<i>Lophogaster typicus</i>									1.3		3.0	0.4	1.7	11.2	
<i>Boreomysis megalops</i>														9.3	
<i>Anchialina agilis</i>					1934.4	144.8	1054.0	1625.0	304.5	975.9					0.6
<i>Haplostylus lobatus</i>								2.3	2.3	2.3	0.8				0.4
<i>Gastrosaccus spumifer</i>	0.8	3.4	2.1												
<i>Gastrosaccus</i> spp. (juv.)	68.9	41.2	55.8	295.9	11.3	155.9	15.9	2.3	9.2						
<i>Dactylepterythrops dimorpha</i>															
<i>Erythroptus neapolitana</i>										410.3	0.7	208.2	544.1	6.0	278.9
<i>Erythroptus elegans</i>					139.3	5.5	73.4	297.7	25.0	163.2					10.3
<i>Hyperythroptus</i> sp.								6.8	4.5	5.7					4.7
<i>Peramblyrops rufirata</i>															9.3
<i>Papapseudomina calloplura</i>															104.7
<i>Parerythroptus paucispinosa</i>															0.9
<i>Pseudomima affinis</i>								20.5	2.3	11.5			52.7	0.8	27.1
<i>Leptomysis gracilis</i>															3.7
<i>Leptomysis megalops</i>					1500.0	199.5	861.5	18293.2	295.5	9401.1					0.8
<i>Mysideis parva</i>					2.7	1.4	31.8	2.3	17.2	58.7			29.7	91.1	0.4
<i>Mysidopsis angusta</i>					13.7	2.7	8.3	131.8	4.5	69.0			1.3	340.2	5.3
<i>Mysidopsis didelphys</i>					16.4		8.3			1.3	0.7		3.4		1.7
<i>Mysidopsis gibbosa</i>													3.0		8.2
<i>Acanthomysis longicornis</i>	0.8		0.4												
<i>Hammimysis abyssicola</i>	22.7	4.2	16.2	60.1	1.1	31.1									
<i>Mesopodopsis slabberi</i>	3.4	2.5	3.0	481.9	28.3	238.9		6.8	79.5	43.7					
<i>Schistomysis kerwilli</i>	98.3	23.2	62.6	80.5	2.3	42.0									
<i>Schistomysis ornata</i>															
<i>Schistomysis spiritus</i>				17.0		8.6									
<i>Schistomysis</i> spp. (juv.)					16.4		8.3								
<i>Mysidella typica</i>															
Amphipoda															
<i>Iphimedia ubi-ubi</i>					32.8		16.6								
<i>Ampelisca spooneri</i>					2.7		1.4	15.9		8.0			1.3		1.3
<i>Anipelsca</i> spp.	1.7		0.9				75.0		2.0	37.9			1.0	0.4	0.2
<i>Amphilocheoides boeckii</i>									20.4	10.4			10.4	29.0	14.7
<i>Anphilochus neapolitanus</i>	3.4	1.7	2.6	2.3		1.2			0.7				0.3	5.6	2.9
<i>Paramphilocheoides odontonyx</i>					41.0		20.8								
<i>Citana abyssicola</i>															
<i>Aora gracilis</i>															
<i>Lembois</i> sp.															
<i>Argisshii hamatipes</i>	188.2	150.4	171.6	60.1	39.7	50.6	1.4	18.2		9.2			1.7		1.3
<i>Apherusa bispinosa</i>					106.6	16.4	62.3	229.5	22.7	127.6			1.3	5.6	2.9

Appendix 1 (continued)

Taxon	TS333		TS320		TS302		TS300		TS298		TS297		TS299	
	Dv	Ds	Dv	Ds	Dv	Ds	Dv	Ds	Dv	Ds	Dv	Ds	Dv	Ds
<i>Apherusa clevei</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Corophium insidiosum</i>	-	0.8	-	-	-	-	-	-	-	0.7	-	-	-	-
<i>Corophium sextonae</i>	-	-	-	1.1	-	-	-	-	-	-	-	-	-	-
<i>Siphonocetes striatus</i>	-	-	-	-	-	-	70.5	35.6	-	9.9	15.8	-	8.0	-
<i>Unciola crenatipalma</i>	-	-	-	-	5.5	2.8	-	-	-	-	0.8	-	0.4	-
<i>Atylus falcatius</i>	-	-	-	1.1	-	-	-	-	-	-	-	-	-	-
<i>Atylus swammerdami</i>	0.8	2.5	1.7	-	-	-	-	-	-	-	-	-	-	-
<i>Atylus vedlomensis</i>	-	-	-	-	-	-	113.6	57.5	11.2	3.4	3.4	-	1.7	7.5
<i>Lepechinella manco</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	3.8
<i>Eusirus longipes</i>	-	-	-	-	-	-	2.3	1.1	13.9	7.0	33.5	1.1	17.6	0.9
<i>Rhachotropis integricauda</i>	-	-	-	-	-	-	2.3	1.1	663.6	4.0	620.9	7.9	318.8	8.4
<i>Rhachotropis rostrata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	354.2
<i>Abudomelita aculeata</i>	-	-	-	-	-	-	2.3	1.1	40.9	-	75.3	-	38.2	0.9
<i>Abudomelita obusata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	15.0
<i>Abudomelita obusata</i>	0.8	-	0.4	1.1	5.5	2.8	-	-	-	-	-	-	-	7.6
<i>Cheirocratus intermedius</i> (M)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cheirocratus</i> sp. (F)	-	-	-	-	-	-	6.8	3.4	3.3	1.7	4.1	0.4	2.3	-
<i>Maera othonis</i>	-	-	-	-	-	-	6.8	3.4	-	-	0.4	-	0.2	0.9
<i>Megaluropius agilis</i>	106.7	92.4	100.9	31.7	26.1	29.3	-	-	-	-	-	-	-	-
<i>Gammaropsis sophiae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	2.8
<i>Gammaropsis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bathyporeia gracilis</i>	6.7	3.4	5.1	-	1.1	0.6	-	-	-	-	-	-	-	-
<i>Ischyrocerus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leucothoe liljeborgi</i>	-	-	-	-	2.7	2.7	2.8	-	1.3	-	-	-	-	-
<i>Leucothoe spincarpa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Idunella longirostris</i>	2.5	-	1.3	-	-	-	4.5	2.3	-	-	-	-	-	-
<i>Hippomedon cf. massiliensis</i>	4.2	-	2.1	-	-	-	-	-	-	-	-	-	-	-
<i>Ichneopus spinicornis</i>	-	-	-	-	-	-	-	-	0.7	-	-	-	-	-
<i>Lysianassa plumosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9
<i>Orchomenella nana</i>	224.4	61.3	144.8	4.5	7.9	6.3	25.0	12.6	24.4	12.4	85.1	-	43.1	4.7
<i>Pardia cf. punctata</i>	-	-	-	-	-	-	-	-	1.3	0.7	8.7	-	4.4	2.4
<i>Scopelocheirus hopei</i>	-	-	-	-	-	-	86.4	56.8	0.7	0.3	1.5	6.0	3.8	72.9
<i>Trischizostoma nicaeense</i>	-	-	-	-	-	-	2.7	4.5	3.4	-	-	-	-	107.5
<i>Meiphipippella macra</i>	-	-	-	-	46.4	10.9	29.1	41.4	10.6	5.3	5.3	-	2.7	35.5
<i>Bathymedon monoculodiformis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	2.8
<i>Haliceon aequicornis</i>	-	-	-	-	-	-	2.3	1.1	11.2	5.7	9.0	0.4	4.8	1.9
<i>Monoculodes acutipes</i>	-	-	-	-	-	-	13.6	2.3	8.0	-	1.1	-	0.6	3.7
<i>Monoculodes gibbosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	4.7
<i>Monoculodes packardii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9
<i>Oediceropsis brevicornis</i>	-	-	-	-	-	-	-	-	-	25.7	36.5	2.3	19.7	-
<i>Peroculodes longimanus</i>	368.9	73.9	224.4	9.1	5.7	7.5	27.3	13.8	50.8	-	-	-	-	-
<i>Pontocrates altamannus</i>	8.4	8.4	8.5	1.1	2.3	1.7	-	-	-	-	-	-	-	-
<i>Pontocrates arenarius</i>	20.2	15.1	17.9	4.5	12.5	8.6	-	-	-	-	-	-	-	-
<i>Westwoodilla caecula</i>	-	-	-	-	-	-	268.2	11.4	141.4	1.3	69.3	3.8	37.0	68.2
<i>Westwoodilla rectrostris</i>	-	-	-	-	-	-	111.4	56.3	0.7	0.3	-	-	-	-
<i>Synchelidium</i> spp.	-	-	-	-	-	-	38.6	6.8	23.0	16.0	30.9	-	15.7	2.8
<i>Epimeria cornigera</i>	-	-	-	-	-	-	-	-	-	-	1.1	0.4	0.8	-

Appendix 1 (continued)

Taxon	Haul	TS333	TS320	TS302	TS300	TS298	TS297	TS299	
	Depth (m)	21	21	91	125	185	188	299	
	Water layers (cm)	0–50	0–50	0–50	0–50	0–50	0–50	0–50	
	Volume (m ³)	59.5	44.1	18.3	22	75.8	132.8	53.5	
	Area (m ²)	117.4	86.9	36.1	43.5	149.6	261.9	105.6	
	Dv	Ds	Dv	Ds	Dv	Ds	Dv	Ds	
Amphipoda (continued)									
<i>Epimeria parasitica</i>	-	-	-	-	2.3	-	-	25.2	-
<i>Halicydes anomalus</i>	-	-	-	-	-	-	1.1	-	-
<i>Harpinia pectinata</i>	-	-	-	-	2.3	-	-	-	-
<i>Harpinia</i> sp.	-	-	-	-	2.3	-	-	-	-
<i>Stenopleustes malmgreni</i>	-	-	5.5	2.7	4.2	-	0.4	-	-
<i>Andanexis mimonecetes</i>	-	-	-	-	-	-	-	1.9	0.9
<i>Stegocephaloides auratus</i>	-	-	-	-	-	2.0	-	14.0	7.1
<i>Stegocephaloides christianseni</i>	-	-	-	-	-	-	1.9	-	-
<i>Stenothoe marina</i>	-	-	5.5	2.7	4.2	-	0.4	-	-
<i>Stenothoe rubrovittata</i>	-	-	-	-	-	0.7	-	-	-
<i>Pseudotiron bouvieri</i>	-	-	-	-	-	-	-	3.7	1.9
<i>Syrrohoe affinis</i>	0.8	0.9	-	-	-	-	-	15.9	8.0
<i>Syrrohoites pusilla</i>	-	-	-	-	-	-	-	3.7	1.9
<i>Parrambus typicus</i>	25.2	4.2	42.0	21.5	32.2	-	-	2.8	1.4
<i>Phitsica marina</i>	-	-	-	2.7	1.4	1.3	-	-	-
<i>Parathemisio</i> sp.	-	-	-	-	-	0.7	0.7	-	-
<i>Gammaridea</i> ind.	-	-	-	-	2.3	-	0.4	0.9	0.5
Cumacea									
<i>Bodotria arenosa</i>	13.4	21.8	17.9	5.7	11.3	8.6	-	-	-
<i>Bodotria pulchella</i>	21.8	6.7	14.5	21.5	30.6	26.5	-	-	-
<i>Iphinoe serrata</i>	-	-	-	-	29.5	2.3	16.1	-	18.5
<i>Iphinoe trispinosa</i>	16.8	42.0	29.8	-	-	-	-	-	-
<i>Diastylis bradyi</i>	4.2	19.3	11.9	-	-	-	-	-	-
<i>Diastylis laevis</i>	-	-	-	1.1	0.6	-	-	-	-
<i>Diastylis</i> sp. (juv.)	16.8	12.6	14.9	3.4	2.3	2.9	-	-	-
<i>Diastylis</i> sp.	-	-	-	5.5	2.8	19.8	10.0	6.8	0.9
<i>Ekleptostylis walkeri</i>	-	-	-	-	2.3	1.1	-	0.4	-
<i>Leptostylis macrura</i>	-	-	-	-	-	-	-	6.5	3.3
<i>Leptostylis</i> sp.	-	-	-	-	6.8	3.4	-	-	-
<i>Macrokylindrus longicaudatus</i>	-	-	-	-	2.3	1.1	-	-	-
<i>Macrokylindrus longipes</i>	-	-	-	-	-	-	-	3.7	0.9
<i>Macrokylindrus cf. stebbingsi</i>	-	-	-	-	-	-	-	1.9	0.9
<i>Macrokylindrus</i> sp.	-	-	-	-	-	0.7	-	-	-
<i>Mesolimnopsis mediterranea</i>	-	-	-	-	-	-	-	7.5	3.8
<i>Fiadorella truncatula</i>	-	-	-	-	2.3	1.1	-	-	-
<i>Campylaspis glabra</i>	-	-	-	-	-	2.0	0.4	6.5	3.3
<i>Campylaspis horridoides</i>	-	-	-	-	-	-	-	0.9	0.5
<i>Campylaspis macrophthalma</i>	-	-	-	-	-	-	-	9.3	4.7
<i>Campylaspis sulcata</i>	-	-	-	-	-	-	-	0.9	0.5
<i>Campylaspis verrucosa</i>	-	-	-	-	-	-	-	18.7	9.9
<i>Cumella pygmaea</i>	-	-	-	-	6.8	2.3	4.6	9.8	0.4
<i>Cumella</i> sp.	-	-	-	-	-	4.0	0.8	0.9	0.5
<i>Procampylaspis armata</i>	-	-	-	-	-	-	-	4.7	2.4
<i>Procampylaspis</i> sp.	-	-	-	-	-	-	-	2.8	1.4
<i>Pseudocuma longicornis</i>	8.4	12.6	10.6	2.3	3.4	2.9	35.5	2.7	19.4
Isopoda									
<i>Gnathia</i> sp.	-	-	-	-	11.4	2.3	6.9	5.6	1.9
<i>Aegia cf. ventriosaj</i>	-	-	-	-	-	-	-	0.9	0.5
<i>Eurydice spinigera</i>	-	0.8	0.4	-	-	-	-	-	-

Appendix 1 (continued)

Taxon	TS333		TS320		TS302		TS300		TS298		TS297		TS299								
	Dv	Ds	Dv	Ds	Dv	Ds	Dv	Ds	Dv	Ds	Dv	Ds	Dv	Ds							
Isopoda (continued)																					
<i>Asiaticia</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Sphaeroma</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Eugerdia filipes</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Munna</i> cf. <i>limicola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Paramunna typica</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Disconectes</i> cf. <i>furcatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Disconectes phalangium</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Ilyarachna</i> cf. <i>argentina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Ilyarachna longicornis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Pseudarachna hirsuta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Munnopsurus atlanticus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
Tanaidacea																					
<i>Apselodes spinosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
Euphausiacea																					
<i>Meganyciophanes norvegica</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Nyctiphanes couchi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Thysanoessa longicaudata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Stylocheiron longicorne</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
Decapoda																					
<i>Solenocera membranacea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Lucifer typicus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Philoceras echinulatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Philoceras bispinosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Philoceras sculptus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Philoceras trispinosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Pontophilus spinosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Hyppolite leptometrae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Hyppolittidae</i> (juv.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Pandalina brevis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Pasiphaea sivado</i> (juv.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Processa canaliculata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Processa modica</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Processa novaei holthuisi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Callinassa</i> sp. (juv.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Upogebia</i> sp. (juv.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Galathea</i> sp. (juv.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Munida</i> sp. (juv.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Paguridae</i> (juv.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Ebalia</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Eurynome aspera</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
Majidae ind.	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
Portunidae (juv.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
Pisces																					
Juveniles ind.	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Callionymus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
Gobiidae ind.	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
<i>Microchirus variegatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
Total	1287.0	650.7	982.3	1167.6	213.1	700.2	6786.6	2125.4	4518.6	24857.0	2020.5	13591.7	2715.7	78.0	1414.2	3113.5	68.5	1613.3	1523.6	283.1	916.1

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