The winter hyperbenthos of the Ria Formosa - a lagoon in southern Portugal - and adjacent waters

Koen LOCK & Jan MEES
Marine Biology Section, Zoology Institute,
University of Ghent, Ledeganckstraat 35, 9000 Gent, Belgium,
Fax: (32)9 264 53 44 - e-mail: koen.lock@rug.ac.be

Abstract: The hyperbenthic fauna of the Ria Formosa, a tidal lagoon in southern Portugal, was sampled with a hand-pushed sledge during the winter of 1997. The hyperbenthic community in the lagoon differed from that of the adjacent sandy beaches of the Atlantic Ocean, as well as from that of the main river discharging into the lagoon. Calculations of density, biomass and diversity revealed higher values for the community of the lagoon. The salinity of the Ria Formosa doesn't differ from the open sea but there is a difference in exposition: the beach along the Atlantic Ocean is more exposed to currents than the beaches inside the lagoon and that is probably the main reason why a different community is found in the open sea. A different community was also found in the upstream part of the river which is correlated with the reduced salinity due to freshwater input.

Résumé : *L'hyperbenthos hivernal de la Ria Formosa - une lagune du sud Portugal - et des eaux adjacentes.* La faune de cette lagune a été échantillonnée à l'aide d'un traîneau manuel pendant l'hiver 1997. La communauté hyperbenthique de la lagune diffère de celle de la plage sableuse adjacente, sur l'Atlantique, et de celles de la principale rivière qui se déverse dans la lagune. Les calculs de densité, biomasse et diversité ont révélé des valeurs plus élevées pour la communauté de la lagune. La salinité des eaux de la Ria Formosa ne diffère pas de celle de l'océan, mais il y a une différence d'exposition : la plage le long de l'Atlantique est plus exposée aux courants que les plages de la lagune, ce qui est probablement la raison majeure de la différence dans les communautés. Une communauté différente existe aussi dans la partie supérieure de la rivière, ceci en relation avec une salinité réduite.

Keywords : hyperbenthos; Ria Formosa; Mysidacea; sandy beaches; multivariate analyses.

Introduction

Information about intertidal or very shallow subtidal hyperbenthic communities is very scarce (Mees & Jones, 1997). Colman & Segrove (1955) studied the hyperbenthos of intertidal areas in Robinhood's Bay (U.K.) and found that Amphipoda, Mysidacea and Decapoda were the dominant taxa, while Cumacea, Copepoda, Pycnogonida, Polychaeta and Gastropoda were less common. The hyperbenthos of sandy beaches (often referred to as surf plankton or tidal plankton) in South Africa (Wooldridge, 1983, 1989; Schlacher & Wooldridge, 1995), France (San Vicente & Sorbe, 1993), Spain (Munilla & Corrales, 1995) and Japan (Takahashi & Kawagushi, 1995) was always dominated by mysids as was the hyperbenthic fauna utilizing tidal marsh

creeks in the Westerschelde estuary (Cattrijsse et al., 1994). The hyperbenthos of estuaries and shallow coastal areas (< 15 m depth) of the North Atlantic has received quite some attention in recent years. Information is now available on the species composition, density and biomass of the hyperbenthos of the Westerschelde, Oosterschelde, Eems and Gironde (Mees & Hamerlynck, 1992; Mees et al., 1993, 1995). Shallow coastal waters have mainly been sampled in the southern bight of the North Sea: the English Channel (Wang & Dauvin, 1994) and the Voordelta (Hamerlynck & Mees, 1991; Mees & Hamerlynck, 1992).

In the present paper the hyperbenthos of the Ria Formosa lagoon is compared with that of adjacent Atlantic beaches and that of the main river discharging into the lagoon. Community parameters like species richness, abundance, biomass and diversity are presented.

Materials and methods

I. Study area and sampling

The study was performed in the Ria Formosa, a tidal lagoon extending for about 55 km along the south coast of the Algarve in Portugal. It consists of a system of creeks and tidal flats, bordered with salt marshes. A seaward belt of dunes protects tidal flats of up to 3 km width. The tidal elevation is 1.3 m and 2.8 m at mean neap and spring tide, respectively; the minimum and maximum areas covered by water during spring tides are 14.1 and 63.1 km^2 (Ãguas, 1986). A strongly branched system of creeks and channels is connected to the ocean by only a few outlets. There is still a rather intensive exchange of 50-75% of the water mass during each tide (Ãguas, 1986). The lagoon does not receive any significant fresh water input: the salinity of the lagoon's water ranges from 35.5 to 36.9 PSU all year round (Falcão et al., 1985). The only sources of fresh water are the Rio Gilão and some small, temporary rivers (Calvário, 1995). The water temperature varies from a minimum of 12°C in winter to a maximum of 28°C in summer (Sprung, 1994).

During the winter 1997, eight stations were sampled in the Ria Formosa, one in the Atlantic Ocean and four in the main river flowing into the lagoon (table 1, figure 1). Due to dredging activities for the maintenance of shipping lanes to the main harbours, there is a strong erosion of the seaward beaches and dunes which results in a steep slope and strong wave action. It was therefore impossible to take quantitative samples on the seaward side of the Ria Formosa, except for the eastern end of the lagoon where no dredging takes place.

Samples were collected with a 50 cm wide, hand-pushed sledge which sampled the lowest 20 cm of the water column. The net had a length of 90 cm and a mesh size of 1x1 mm. The total area of the net's mouth was 0.1 m². In order to compare catches from different localities, all

Table 1. List of the sampling sites and dates.
N.L. : North Latitude.
W.L. : West Longitude.
Tableau 1 : Sites d'échantillonnages : localités et dates.
N.L. : Latitude Nord.
W.L. : Longitude Ouest.

Code	Name station	District	N.L.	W.L.	Sampling date
L1	Praia de Faro	Faro	37°00'	8°00'	30/01/1997
L2	Esteiro do Ramalhete	Faro	37°00'	7°57'	30/01/1997
L3	Esteiro da Mortina	Olhão	37°01'	7°51'	31/01/1997
L4	Praia dos Cavacos	Olhão	37°02'	7°48'	31/01/1997
L5	Arroteiade Baixo	Olhão	37°04'	7°44'	01/02/1997
L6	Santa Luzia	Tavira	37°06'	7°40'	01/02/1997
L7	Canal de Tavira	Tavira	37°07'	7°30'	02/02/1997
L8	Vila Nova de Cacela	Tavira	37°09'	7°32'	03/02/1997
R1	Rio Gilão	Tavira	37°07'	7°30'	02/02/1997
R2	Tavira	Tavira	37°07'	7°31'	02/02/1997
R3	Rio Séqua	Tavira	37°07'	7°31'	02/02/1997
R4	Asseca	Tavira	37°08'	7°31'	02/02/1997
O1	Atlantic Ocean	Tavira	37°09'	7°32'	03/02/1997

samples were taken during daytime from 1 hour before to 1 hour after low water. On each occasion, the sledge was pushed over a distance of 25 m. Sampling depth ranged from 50 to 100 cm. Three replicates were successively taken per station. The samples were immediately rinsed over a 1 mm sieve and preserved in an alcohol solution, 70% final concentration. Rose Bengal was added to facilitate sorting.

II. Processing of samples and data analysis

In the laboratory all animals were sorted out, identified, if possible to species level, and counted. Amphipods of the genera *Corophium, Microdeutopus* and *Siphonoecetes* could not always be identified at the species level. Similarly, the pelagic eggs of fish, the ectoparasitic Cymothoinae and the praniza's of Gnathiidae were recorded as such and were not specifically identified. Most species could be identified with keys provided by Hayward & Ryland, 1995. Different developmental stages of decapods were treated as separate ecological species. All individuals per species were measured (standard length: distance from the base of the rostral tip to the end of the last abdominal segment for crustaceans; from the tip of the nose to the base of the caudal fin for fishes) and their biomass was derived from length - ash-free dry weight regressions. All density and biomass data are presented as numbers of individuals (N) and mg ash-free dry weigth (AFDW) per 37.5 m² (i.e. the surface area covered by the three pooled replicates). These values correspond to a volume of 7.5 m³ water filtered through the net.

Diversity was calculated as Hill's diversity numbers (Hill, 1973). This set of indices incorporates the most
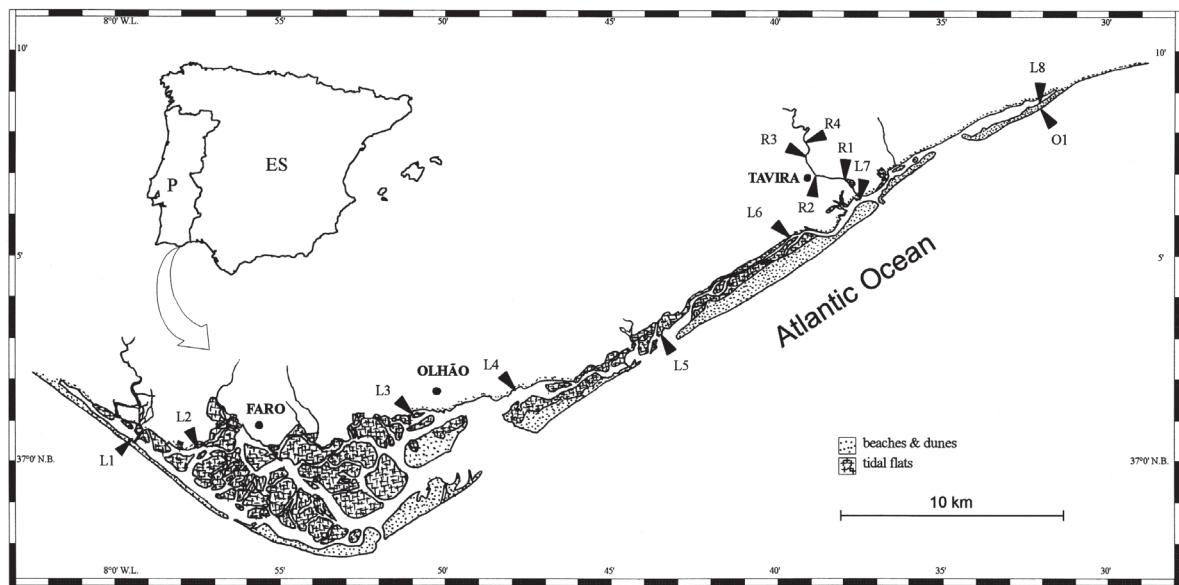
Figure 1. Study area with location of the sampling sites. For details see table 1.
Figure 1. Localité étudiée et sites d'échantillonage. Pour des détails sur ces sites, voir le tableau 1.

widely used diversity measures in a continuum of indices of the orders -∞ to +∞. The indices differ in their tendency to include or to ignore the relatively rarer species: the impact of dominance increases and the influence of species richness decreases with an increasing order of the diversity number. Of particular interest are:

$N_0 = S$ with S = the number of species
$N_1 = e^H$ with H = Shannon-Wiener index
$H = -\sum p_i \ln(p_i)$ (p_i = the relative abundance of the ith dominant species)
$N_2 = SI^{-1}$ with SI = Simpson's dominance index
$SI = \sum p_i^2$
$N_\infty = p_1^{-1}$ with p_1 = the relative abundance of the most abundant species.

The sampling sites were classified into clusters according to species composition using the classification program TWINSPAN (Two-Way INdicator SPecies ANalysis) (Hill, 1979). TWINSPAN also yields indicator species characterizing the various communities. The cutlevels used in the analysis were 0, 0.2, 0.8, 2.8, 40 and 100 mg AFDW per trawl for the biomass data and 0, 1, 2, 4, 9 and 20 animals per trawl for the density data. To check the stability of the TWINSPAN results and to reveal the degree of similarity between and within the detected clusters of samples, a group-average sorting cluster analysis with Bray-Curtis similarities (Bray & Curtis, 1957) was performed on the log-transformed density and biomass data and the Correspondence Analysis (CA) option from the program package CANOCO (Ter Braak, 1988) was applied on the

same data. To compare densities, biomasses and diversities between the different communities, a Kruskal-Wallis ANOVA and post-hoc multiple comparisons were used (Conover, 1980).

Results

I. Exploration of the data matrix

A total of 50 taxa was recorded (table 2). Mysidacea were the dominant taxon (8 species, 73% of the total number of individuals caught). Decapoda (9 species, 9.1%), Amphipoda (16 species, 7.6%), Pisces (3 species, 7.1%) and Isopoda (7 species, 1.4%) were subdominant. Cumacea (1 species), Opisthobranchia (2 species), Tanaidacea (2 species), Diptera (1 species) and Thaliacea (1 species) were rare and made up less than 1% of the hyperbenthic fauna. *Lepidochitona cinereus* (Linnaeus, 1767) (Polyplacophora) and *Amphipholis squamata* (Delle Chiaje, 1828) (Ophiuroidea) were recorded from the lagoon but were excluded from the data matrix as they are considered truly epibenthic species.

The density of the hyperbenthos varied from 0 in Asseca (R4), the most upstream station of the river, to more than 2000 animals per 37.5 m² in Esteiro do Ramalhete (L2), a station in the eastern part of the Ria Formosa, where the mysid *Mesopodopsis slabberi* (van Beneden, 1851) dominated the fauna (figure 2). Because no hyperbenthos was found in Asseca (R4), this station was omitted from further analyses. The highest biomass (33 g AFDW per

Table 2. List of species caught with the handsledge and the abbreviations used. The average density (N/37.5m^2) and biomass (mg AFDW/37.5m^2) per species as well as the average diversity numbers of Hill of the stations (N_0, N_1, N_2, $N\infty$; see text for definitions) are given for each community.

Tableau 2. Liste des espèces récoltées. La densité moyenne (N/37.5m^2) et la biomasse (mg AFDW/37.5m^2) par espèce ainsi que les indices moyens de diversité de Hill des stations (N_0, N_1, N_2, $N\infty$; voir texte pour les définitions) sont données pour chaque communauté.

| Name and stage	Code	Lagoon Density	Lagoon Biomass	River Density	River Biomass	Ocean Density	Ocean Biomass
Opisthobranchia							
Elysia viridis	Elys viri	1.25	0.13				
Haminea navicula	Hami navi	0.13	0.01				
Mysidacea							
Gastrosaccus spinifer	Gast spin					5.00	3.30
Leptomysis mediterranea	Lept medi	0.50	0.39				
Mesopodopsis slabberi	Meso slab	252.38	140.32				
Paramysis nouveli	Para nouv	23.63	20.59	0.33	0.54		
Schistomysis parkeri	Schi park					7.00	5.35
Schistomysis assimilis	Schi assi					19.00	7.47
Siriella clausii	Siri clau	0.88	0.23				
Tanaidacea							
Apseudes latreillii	Apse latr	0.38	0.04				
Leptochelia savignyi	Lept savi			1.00	0.02		
Cumacea							
Iphinoe tenella	Iphi tene	3.13	6.64				
Isopoda							
Cymothoinae species	Cymo Spec			1.00	0.08		
Cyathura carinata	Cyat cari			1.00	0.23		
Gnathiidae species (praniza)	Gnat Spec	0.13	0.01				
Idotea chelipes	Idot chel	1.88	2.01				
Idotea linearis	Idot line	0.13	0.39			2.00	1.53
Sphaeroma hookeri	Spha hook	0.13	0.04	6.67	1.88		
Amphipoda							
Ampelisca brevicornis	Ampe brev	0.13	0.03				
Atylus guttatus	Atyl gutt					1.00	0.77
Caprella acanthifera	Capr acan	5.13	0.31				
Corophium acherusicum	Coro ache	0.25	0.02				
Corophium species	Coro Spec			3.33	0.69		
Dexamine spinosa	Dexa spin	1.63	0.99				
Gammarus insensibilis	Gamm inse	2.00	2.58				
Gammarus locusta	Gamm locu	1.75	7.43				
Leptocheirus pilosus	Lept pilo			1.00	0.09		
Melita palmata	Meli palm	2.63	0.91				
Microdeutopus gryllotalpa	Micr gryl	0.25	0.08				
Microdeutopus species	Micr Spec	1.75	0.32				
Perioculodes longimanus	Peri long	0.63	0.05				
Pontocrates arenarius	Pont aren					6.00	0.69
Siphonoecetes species	Siph Spec	10.75	1.04				
Decapoda							
Carcinus maenas	Carc maen	0.75	1283.93				
Crangon crangon	Cran cran	8.38	173.11			1.00	61.78
Crangon crangon (postlarva)	Cran Post	9.13	2.77				
Diogenes pugilator	Diog pugi	0.25	3.30				
Palaemon adspersus	Pala adsp	1.38	14.33				
Palaemon elegans	Pala eleg	1.63	21.27	1.00	14.11		
Palaemon longirostris	Pala long			0.33	12.34		
Palaemonetes varians	Pala vari	12.25	137.68	1.33	14.11		
Pilumnus hirtellus	Pilu hirt	0.13	0.03				
Diptera							
Chironomus salinarius	Chir sali	0.25	0.03	0.33	0.03		
Thaliacea							
Salpa democratica	Salp demo	0.13	0.01				
Pisces							
Pisces egg	Pisc Spec	0.88	0.02			30.00	0.75
Pomatoschistus microps	Poma micr	19.75	4358.85	6.00	64.70		
Syngnathus typhle	Syng typh	0.50	20.70				
TOTAL		366,75	6 200.58	22.33	108.73	72.00	81.73
N_0		13.38		5.33		9.00	
N_1		5.64		4.13		5.02	
N_2		4.06		3.55		3.76	
$N\infty$		2.58		2.53		2.40	
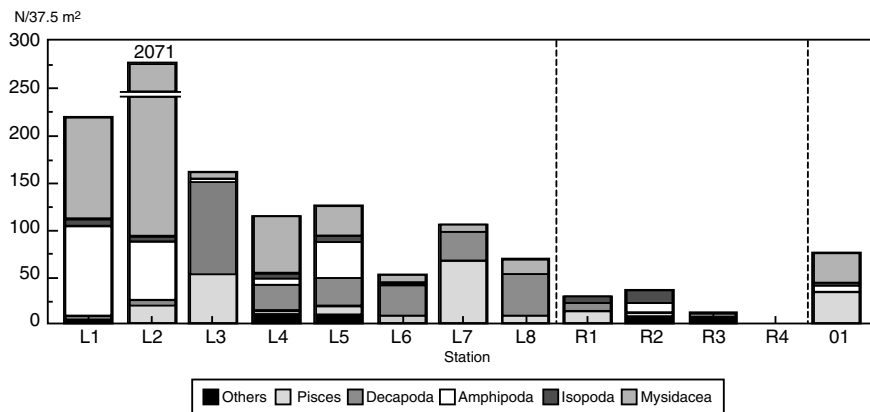
Figure 2. Faunal composition of the stations (replicates pooled).
Figure 2. Composition faunistique des stations (prélèvements regroupés).

37.5 m²) was found in Canal de Tavira (L7), the station where the Rio Gilão discharges in the lagoon. Here, the common goby *Pomatoschistus microps* (Krøyer, 1838) made up the bulk of the biomass.

Hill's diversity numbers were calculated for each station. The eastern stations of the lagoon contained the highest number of species and the upstream stations along the river the lowest number of species. The station Arroteiade Baixo (L5) in Olhão showed the highest values for all diversity numbers.

II. Analysis of the spatial patterns

The results of the TWINSPAN analysis performed on the density data are presented in figure 3. In the first division the samples taken in the Atlantic Ocean (O1) were separated from the other samples. Indicator species for the ocean are

Schistomysis assimilis (Sars, 1877), *S. parkeri* (Norman, 1892) and *Pontocrates arenarius* (Bate, 1858). Due to the strong currents no quantitative samples could be taken on the seaward side of Praia de Faro. Although these samples were not used in the data analysis, it should be noted that a very similar fauna was found: only three additional species were recorded, namely *Gastrosaccus sanctus* (van Beneden, 1861), *Eurydice pulchra* (Leach, 1815) and *Pontocrates altamarinus* (Bate & Westwood, 1862). In the subsequent division of the remaining samples one replicate from the Rio Séqua (R3), which only contained the species *Leptocheirus pilosus* (Zaddach, 1844), was split off. The subsequent division separated the samples from the river and those from the lagoon. The samples taken where the river flows into the Ria Formosa (L7) were classified together with the stations from the lagoon. One replicate from the Rio Gilão (R1), which only contained three species, was classified together with the lagoon. *Sphaeroma hookeri* (Leach, 1814) is the indicator species for the riverine samples while *Pomatoschistus microps*, *Paramysis nouveli* (Labat, 1953), *Mesopodopsis slabberi* and *Crangon crangon* (Linnaeus, 1758) were the indicator species for the lagunar samples. Further divisions of the samples did not yield any meaningful clusters. The analysis with the biomass data yielded almost the same picture (not presented). The difference was that all the samples from the Rio Gilão (R1) were clustered together with the samples
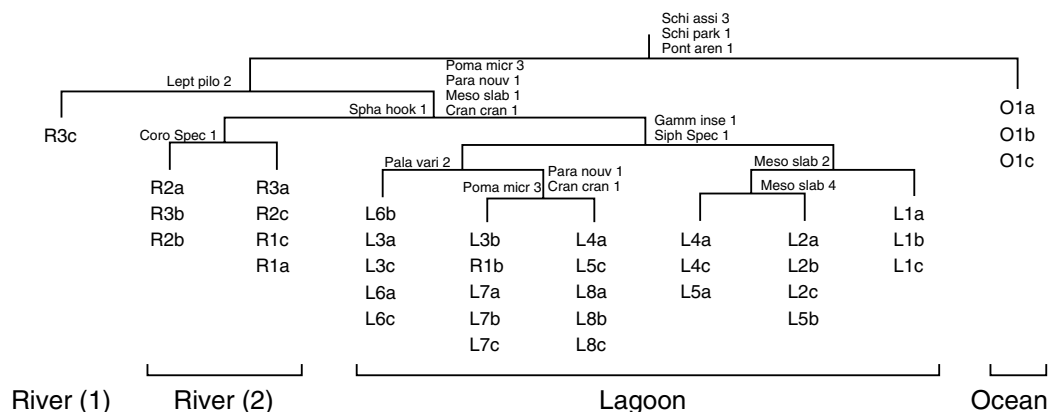

Figure 3. TWINSPAN with the density data of the replicates (a to c). Indicator species with pseudospecies cutlevel are given for each division.
Figure 3. Analyse TWINSPAN sur les abondances des différents réplicats (a - c). Les espèces indicatrices avec le niveau de division des pseudo-espèces sont indiquées pour les différents seuils.
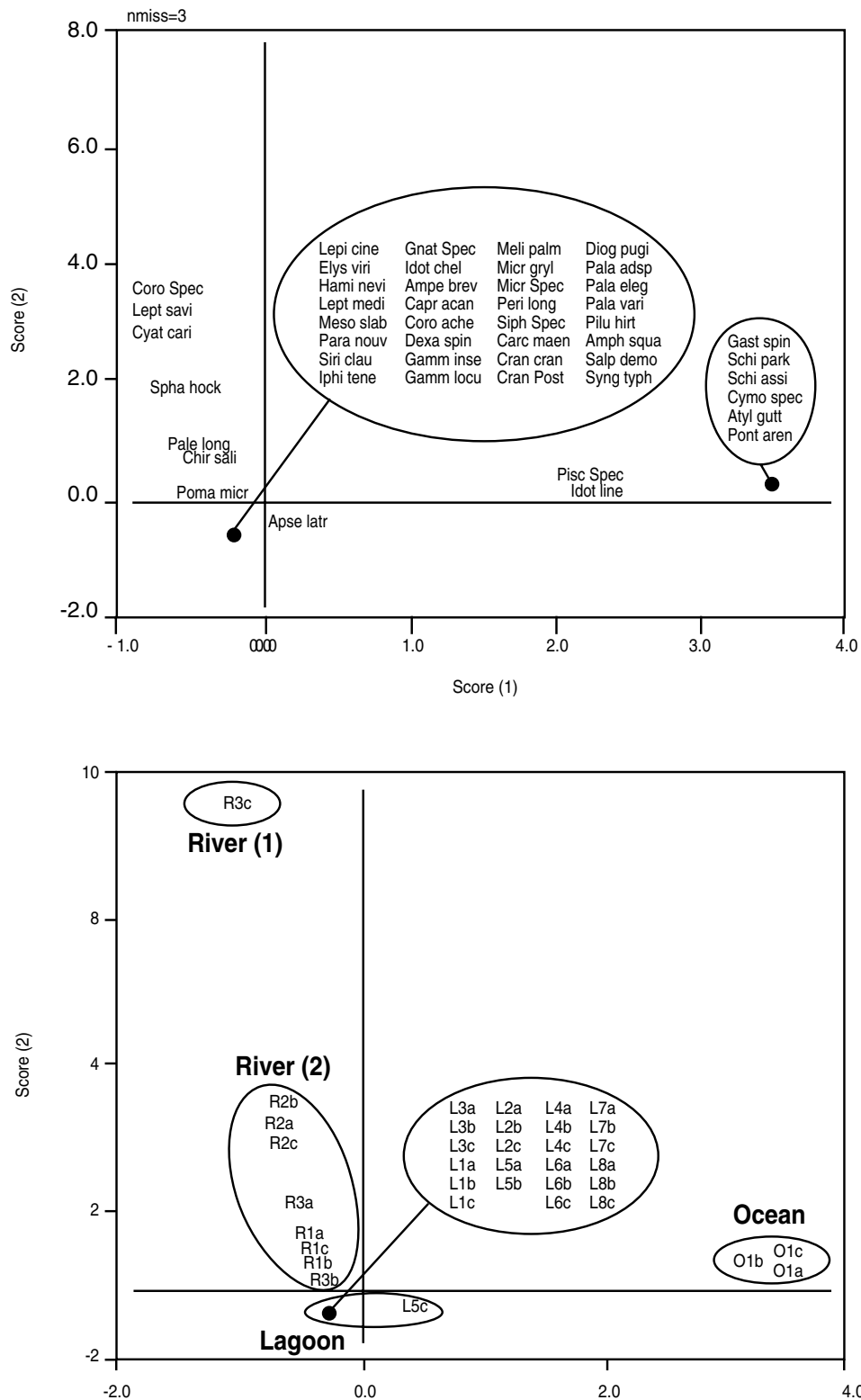
nmiss=3

Score (2) (top plot, vertical axis)

8.0

6.0

4.0

Coro Spec
Lept savi
Cyat cari

Spha hock

Pale long
Chir sali

Poma micr

Apse latr

Lepi cine	Gnat Spec	Meli palm	Diog pugi
Elys viri	Idot chel	Micr gryl	Pala adsp
Hami nevi	Ampe brev	Micr Spec	Pala eleg
Lept medi	Capr acan	Peri long	Pala vari
Meso slab	Coro ache	Siph Spec	Pilu hirt
Para nouv	Dexa spin	Carc maen	Amph squa
Siri clau	Gamm inse	Cran cran	Salp demo
Iphi tene	Gamm locu	Cran Post	Syng typh

Gast spin
Schi park
Schi assi
Cymo spec
Atyl gutt
Pont aren

Pisc Spec
Idot line

2.0

0.0

-2.0

-1.0   0000   1.0   2.0   3.0   4.0

Score (1)

Score (2) (bottom plot, vertical axis)

10

R3c

River (1)

8

River (2)

R2b
R2a
R2c

L3a	L2a	L4a	L7a
L3b	L2b	L4b	L7b
L3c	L2c	L4c	L7c
L1a	L5a	L6a	L8a
L1b	L5b	L6b	L8b
L1c		L6c	L8c

Ocean

4

R3a

2

R1a
R1c
R1b
R3b

O1b   O1c
O1a

L5c

Lagoon

-2

-2.0   0.0   2.0   4.0

Figure 4. Species scores (top) and sample scores (bottom) in the ordination plane formed by the first (horizontal) and second (vertical) axes of the CA with the log-transformed density data of the replicates; communities as identified by group average sorting are circled.

Figure 4. Positions des espèces (en haut) et des échantillons (en bas) dans le plan des deux premiers axes de l'analyse des correspondances (premier axe horizontal et deuxième axe vertical) après transformation logarithmique des abondances des taxa dans les réplicats. Les différentes communautés trouvées avec la méthode du triage des groupes moyens sont encerclées.

from the lagoon and no replicates from the Rio Séqua (R3) were split off from the other samples taken in the river.

Dendrograms of the group-average sorting cluster analyses (not presented) had similar configurations. The analyses with the density data and with the biomass data showed that the samples from the ocean were faunistically very different from the other samples. Then, again, one replicate of the Rio Séqua (R3c) was found to be quite different from the rest. The remaining samples were grouped into river samples and lagoon samples.

The ordination with the density data is in general agreement with the classifications: the four clusters identified by TWINSPAN and cluster analysis could also be identified in the ordination plane formed by the first (eigenvalue 0.86) and the second (eigenvalue 0.76) axes (figure 4). The eigenvalues for the third and the fourth axes were lower (0.63 and 0.53 respectively) and yielded no

additional information. Along the first and most important axis, the samples from the Atlantic Ocean are clearly separated from the other samples that are subsequently separated along the second axis into a group of samples from the river and the samples taken in the lagoon. Roughly, the species in the right half of the plot of the species scores are 'marine' species (figure 4). The spreading of the species in the plot along the second axis is most pronounced in the left half of the diagram. The species in the top of the plot are typical for the river, while the species typical for the lagoon are found in the bottom left quadrat. An ordination with the biomass data gave exactly the same picture for both the species and the sample scores (not presented).

For the characterization of the assemblages, the replicate R3c of the Rio Séqua, which clustered apart in the classifications and the replicate R1b of the Rio Gilão, which clustered together with the samples from the lagoon in
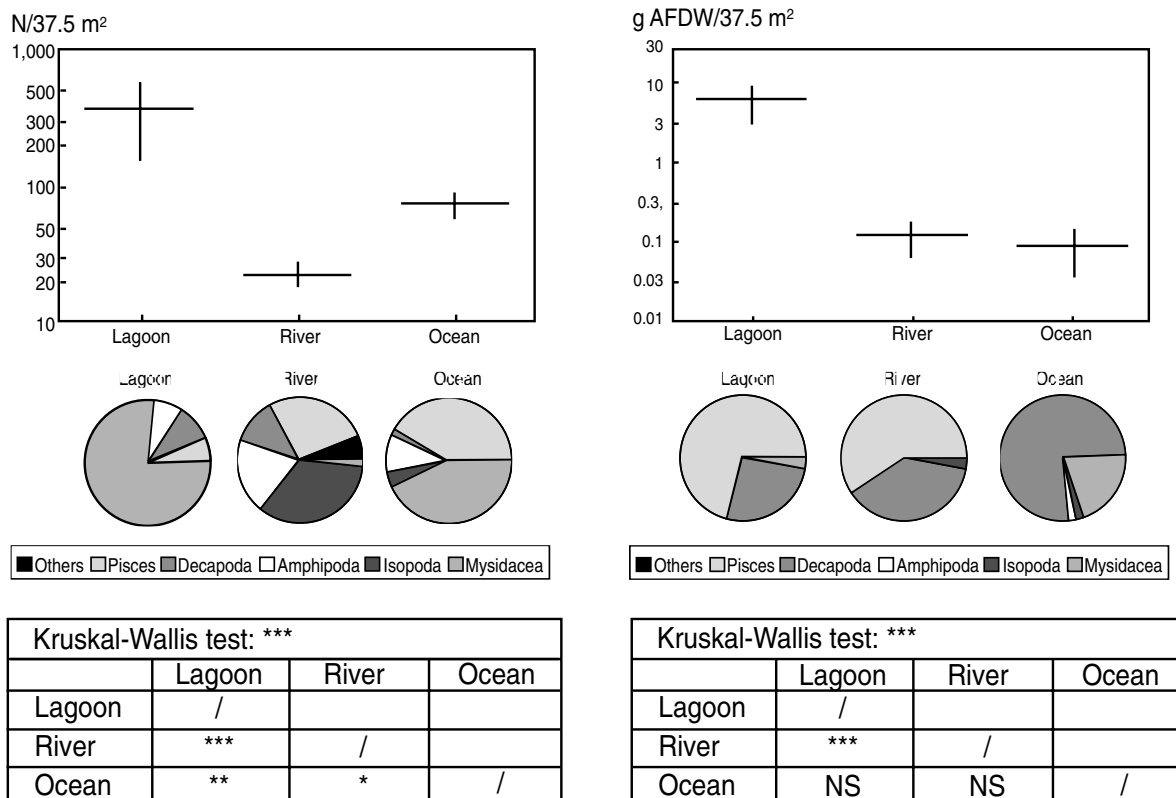

Kruskal-Wallis test: ***			
	Lagoon	River	Ocean
Lagoon	/		
River	***	/	
Ocean	**	*	/

Kruskal-Wallis test: ***			
	Lagoon	River	Ocean
Lagoon	/		
River	***	/	
Ocean	NS	NS	/

Figure 5. Average density and biomass of the three communities as identified by the multivariate analyses with indication of the standard error. The faunal composition is shown in the pie charts below each graph and the results of the Kruskal-Wallis test and the ad-hoc multiple comparisons are shown in the tables below the pie charts. Not significant = NS, significant = * (P<0.05) highly significant = ** (P<0.01) and very highly significant = *** (P<0.001).

Figure 5. Abondances et biomasses moyennes des trois communautés identifiées par l'analyse des correspondances avec indication de leur erreur standard. La composition faunistique est donnée sous forme de diagramme pour chaque communauté, ainsi que les résultats du test de Kruskal-Wallis et des comparaisons multiples pour chaque communauté. N.S. : non significatif, * significatif (p<0.05), ** très significatif (p<0.01) et *** hautement significatif (p<0.001).

TWINSPAN, were taken together with the other replicates from the respective stations. In this way the samples could be divided into three different communities: ocean, river and lagoon.

III. Characterization of the communities

The communities of the river and the ocean clearly differed from each other since they had not a single species in common (see also table 2). The river had six species in common with the lagoon while five were restricted to the river. The ocean, on the other hand, had six endemic species; three other species were also caught in the lagoon. Finally, the lagoon-community contained 28 endemic species.

The observation of *Schistomysis assimilis* is the first record from the Atlantic Ocean: this species was previously only found in the Mediterranean (San Vicente & Sorbe, 1993; Munilla & Corrales, 1995).

The average biomass and abundance of the different communities identified by the multivariate analyses, are shown in table 2 and figure 5. The hyperbenthos of the lagoon mainly consisted of mysids which made up 76% of the total density: *Mesopodopsis slabberi* (69%D), *Paramysis nouveli* (6.4%D), *Siriella clausii* (Sars, 1876) (0.24%D) and *Leptomysis mediterranea* (Sars, 1877) (0.14%D). Fishes {mainly *Pomatoschistus microps* (70%B)} and decapods {*Carcinus maenas* (Linnaeus, 1758) (21%B), *Crangon crangon* (2.7%B), *Palaemonetes varians* (Leach, 1814) (2.2%B), *Palaemon elegans* (Rathke, 1837) (0.34%B) and *P. adspersus* (Rathke, 1837) (0.23%B)} made up the bulk of the biomass in the lagoon. The density and the biomass in the lagoon were a lot higher (P<0.001) than in the river and the density in the lagoon was high in comparison with that of the ocean (P<0.01).

The hyperbenthic fauna of the river was composed of isopods {*Sphaeroma hookeri* (30%D) and *Cyathura carinata* (Krøyer, 1848) (4.5%D)}, fishes {*Pomatoschistus microps* (27%D)} and, to a lesser extent, amphipods {*Corophium* species (15%D) and *Leptocheirus pilosus* (4.5%D)} and decapods {*Palaemonetes varians* (6.0%D), *Palaemon elegans* (4.5%D) and *P. longirostris* (Milne Edwards, 1837) (1.5%D)}. The biomass however was almost exclusively made up by fishes {*Pomatoschistus microps* (60%B)} and decapods {Palaemonidae (37%B)}.

On the shore of the Atlantic Ocean, the hyperbenthos was also dominated by mysids {*Schistomysis assimilis* (26%D), *S. parkeri* (9.7%D) and *Gastrosaccus spinifer* (Goës, 1864) (6.9%D)}, while decapods {*Crangon crangon* (76%B)} followed by mysids (20%B) were the most important groups in terms of biomass. Although the densities in the ocean were lower than those in the lagoon (P<0.01) they were significantly higher than in the river (P<0.05).

Table 3. The hyperbenthos of shallow waters in the Northeastern Atlantic and the Western Mediterranean. When available, daytime data from winter are provided. The dominant taxa are Mysidacea (M), Amphipoda (A), Isopoda (I), Cumacea (C), Decapoda (D) and Pisces (P).

Tableau 3. L'hyperbenthos des eaux littorales de l'Atlantique Nord-Est et de la Méditerranée occidentale. Les données diurnes hivernales sont indiquées lorsqu'elle sont disponibles. Les taxa dominants sont les Mysidacea (M), Amphipoda (A), Isopoda (I), Cumacea (C), Decapoda (D) et Poissons (P).

Sampling area	Depth (m)	Density (N/100 m²)	# species	Dominant taxa	Remarks	Reference
Lagoon NE Atlantic	0.5 - 1	979	36	M>D>A>P	8 stations winter	This study
River NE Atlantic	0.5 - 1	60	11	I>P>A>D	3 stations winter	This study
Ocean NE Atlantic	0.5 - 1	192	9	M>P>A>I	1 station winter	This study
INTERTIDAL						
Robin Hood's Bay NE Atlantic	1	17	NA	A>M>I	1 station, July average of 6 daytime samples	Colman & Segrove (1955)
Creixell W Mediterranean	1	1926	36	M>C>A	2 stations	San Vicente & Sorbe (1993)
Brackish marsh Westerschelde NE Atlantic	< 3	269	NA	M>D>P	1 station average of 4 winter samples	Cattrijsse et al. (1994)
Playa de Rosa E Mediterranean	1	572	22	M>A>P>I	1 station july	Munilla & Corrales (1995)
ESTUARINE						
Westerschelde NE Atlantic	5 - 10	470	14	M>D>A	13 stations winter	Mees & Hamerlynck (1992) Mees et al. (1993)
Oosterschelde NE Atlantic	5 - 10	1	6	M	4 stations winter	Mees & Hamerlynck (1992)
Gironde NE Atlantic	6 - 15	2500	36	M>A>D>I	15 stations August	Mees et al. (1995)
Ems NE Atlantic	7.5 - 10.5	1400	32	M>A>P	12 stations August	Mees et al. (1995)
SHALLOW COASTAL						
Voordelta NE Atlantic	5 - 10	150	34	M>A	24 stations winter	Hamerlynck & Mees (1991) Mees & Hamerlynck (1992)
Bay of Seine Eastern English Channel NE Atlantic	8 - 13	63	15	M>C>A>D	1 station, June average of 31 daytime samples lowest net	Wang & Dauvin (1994)

The average diversity numbers of Hill per community are presented in table 2. The mean number of species found in the river was much lower than in the lagoon (P<0.001). The number of species was also higher in the ocean in comparison with the river (NS). Hill's diversity number N1 was higher in the lagoon than in the river (P<0.01) but the diversity of the ocean was only slightly higher than that of the river (NS). The diversity of the lagoon and the ocean did not differ significantly.

Discussion

The structural characteristics of the three hyperbenthic communities identified in this study (lagoon, river and ocean) are compared with those described in other studies conducted in shallow (<15 m depth) coastal areas of the Northeastern Atlantic and the Western Mediterranean in table 3. When possible, winter densities have been extracted from the cited papers. Although different sampling devices were deployed, densities per surface area are generally quite comparable to those reported from other areas. The difference in the height of the used net, which varied from 10 cm to 1.45 m, didn't seem to play an important role. This can be explained by the fact that hyperbenthic animals are known to concentrate in the water layers close to the bottom, as demonstrated by Wang & Dauvin (1994), who used different nets mounted on top of each other. Monthly sampling revealed that hyperbenthic densities and diversities are lowest during winter (Hamerlynck & Mees, 1991; Mees et al., 1993; Cattrijsse et al., 1994). Density and number of species found in the lagoon community were quite high as compared to other winter values, while the number of species in the ocean and the river communities were quite low. Only the Oosterschelde contained less species (Mees & Hamerlynck, 1992). The beach of the ocean community was very exposed to currents which is probably the main reason why this community contains less species: only species that are adapted to the strong currents in the surf zone can survive on such an exposed shore. On the other hand, species from the river community have to cope with reduced and fluctuating salinities. The number of hyperbenthic species gradually decreased from 11 in Canal de Tavira (L7), where the river flows into the Ria Formosa, to 0 in Asseca (R4), the most upstream station, while the density decreases from 275 animals per 100 m^2 to no animals at all. The river was probably to small to develop a typical estuarine hyperbenthic community with *Neomysis integer* (Leach, 1814) as the dominant species, as is the case of the Westerschelde, the Gironde and the Ems (Mees et al., 1993, 1995).

The time of the day is also an important factor influencing the density: in the Eastern English Channel densities in nightsamples were three times higher than in daysamples (Wang & Dauvin, 1994) and Colman & Segrove (1955) also reported much higher densities during the night.

Mysids always dominated the hyperbenthos in shallow waters in the Northeastern Atlantic and the Mediterranean: only in the river community and Robin Hood's Bay (Colman & Segrove, 1955), mysids were not the most abundant group. Other important taxa are Amphipoda, Isopoda, Cumacea, Decapoda and fishes.

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