



The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management

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Dutertre, M., Hamon D., Chevalier C., and Ehrhold, A. 2013. The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management – ICES Journal of Marine Science, 70: 294–308.

Received 5 November 2011; accepted 8 October 2012; advance access publication 30 November 2012.

Relationships between benthic macrofauna and natural abiotic factors were studied along the coastal fringe of South Brittany, situated north of the Gulf of Biscay on the French Atlantic continental shelf. Within the framework of the REBENT network, sediment characteristics, depth, and macrofaunal abundance were determined for 95 stations spread over five subtidal sectors, using a combination of seabed acoustic remote sensing systems and grab sampling. The physico-chemical properties of the water column and the hydrodynamic conditions were generated by validated three-dimensional environmental models which take into account variations over shorter temporal scales. Multivariate analyses ranked 16 natural abiotic variables according to the significance of their influence on the macrofauna. Together these variables explained 51% of spatial variation in the macrofauna, with morpho-sedimentological and hydrological factors contributing 22% and 26%, respectively. The outputs from validated three-dimensional environmental models appear to be useful interpretational tools for benthic ecology studies, especially in estuarine and coastal ecosystems with high environmental variability due to regular freshwater inputs. Ten major species assemblages were identified using biological and physical characteristics. The results provide important baseline knowledge for future ecosystem and resource management.

Keywords: benthos, coastal management, environmental factors, models, South Brittany, spatial variations.

Introduction

The macrofauna play many important roles in marine ecosystems, such as nutrient cycling, dispersion and burial of sediments, and secondary production (Snelgrove, 1998). Over the past few decades, interest in biological diversity and increasing anthropogenic pressure have led to an expansion of applied ecological research and impact studies on the macrobenthic communities residing in coastal and estuarine areas (Le Bris and Glémarec, 1996; Desroy *et al.*, 2002; Ysebaert and Herman, 2002). In fact, macrobenthic species are considered good indicators because most of them cannot migrate out of their habitat and they exhibit different tolerances to environmental stress (Dauer, 1993). Among the primary goals of many marine benthic ecology studies are the identification of factors responsible for spatial patterns in macrofaunal assemblages, especially those which help to distinguish between natural and man-induced

changes (Ysebaert and Herman, 2002; Ellis *et al.*, 2006; Bolam *et al.*, 2008). In general, abiotic factors determine the broad distributional patterns of benthic organisms at a larger scale, while abiotic and biotic factors operate together at a smaller scale (Sanvicente-Añorve *et al.*, 1996, 2002; Rees *et al.*, 1999; Ellingsen, 2002). In non-isolated marine ecosystems susceptible to the influence of human activities, such as coastal and estuarine areas, the importance of studies at large spatial scales has recently been recognized in order to manage habitats and resources better, especially for the development of the relatively new ecosystem-based approach and the establishment of marine protected area networks (Desroy *et al.*, 2002; Ysebaert and Herman, 2002; Ellis *et al.*, 2006; Fraschetti *et al.*, 2011). Relationships between the macrobenthos and natural environmental factors can therefore be used to characterize seabed habitats, defined as the physical and chemical environment in which a species or a community

lives, and to establish baseline knowledge enabling the detection of spatial and temporal variations (Van Hoey *et al.*, 2004; Bolam *et al.*, 2008; Shumchenia and King, 2010).

In many studies, sediment characteristics have been identified as important factors responsible for macrofaunal distribution (Ellingsen, 2002; Van Hoey *et al.*, 2004; Hily *et al.*, 2008). However, on large spatial scales, other natural environmental factors such as the hydrodynamic conditions and physico-chemical properties of the water column directly or indirectly affect the presence and abundance of benthic species (Warwick and Uncles, 1980; Ysebaert and Herman, 2002; Moulart *et al.*, 2007; Bolam *et al.*, 2008). These factors control food supply, larval dispersion, and metabolism (Pearson and Rosenberg, 1987; Shanks *et al.*, 2003). While sediment characteristics and depth are relatively stable over time, hydrodynamic factors (including tidal current strength, freshwater outflow, and wave action) and physico-chemical properties vary over shorter temporal scales (e.g. seasonal, fortnightly, and semi-diurnal tidal cycles) in macrotidal temperate regions. In coastal regions subject to estuarine inputs, the degree of tolerance of benthic species to the short-term variability of abiotic factors greatly influences their spatial distribution (Green, 1968; Laprise and Dodson, 1993). However, as real-time monitoring of such factors is labour intensive and expensive in many situations, their importance may be underestimated in benthic ecological studies. Using three-dimensional hydrodynamic models, measures of tidal current velocity and wave action can be generated with fine spatial and time resolutions near the seabed, which may help to explain macrofaunal distribution (Warwick and Uncles, 1980; Bolam *et al.*, 2008). The development of validated three-dimensional environmental models generating continuous data on the variability of a large variety of environmental factors, including hydrodynamic conditions and physico-chemical properties (Cugier and Le Hir, 2002; Ménesguen *et al.*, 2007), can therefore greatly improve the identification of abiotic factors responsible for macrofaunal distribution (Warwick and Uncles, 1980; Gogina and Zettler, 2010).

Due to its geomorphological characteristics, the coastal fringe of South Brittany, situated north of the Gulf of Biscay on the French Atlantic continental shelf, corresponds to a transitional zone between relatively small estuaries and semi-enclosed marine areas (Glémarec *et al.*, 1986; Le Bris and Glémarec, 1996). Exposed to both continental and marine influences, this region shows a high diversity of soft-bottom macrobenthic communities, which were qualitatively described previously by Glémarec (1969) using a Rallier du Baty dredge. Because it was greatly affected by the successive oil spills of the “Erika”, in 1999, and the “Prestige”, in 2000, and has a high European conservation value, this zone was explored as a priority by the REBENT (“Réseau Benthique”) network, launched by IFREMER in 2000, in order to provide consistent baseline knowledge about French coastal benthic habitats and to permit monitoring to detect changes at various spatial- and time-scales (Ehrhold *et al.*, 2006; REBENT, 2011). A stratified sampling strategy was adopted, based on the results of earlier geophysical surveys, which was appropriate for the high diversity of explored substrata. A combination of marine remote sensing systems, grab sampling, and sediment analysis was then used to perform fine-scale (30–80 km²) seabed habitat mapping by comparing morpho-sedimentary data and macrofaunal distribution. From the results, a temporal monitoring strategy was then developed for benthic habitats of special ecological interest. Considering that site-specific environmental

conditions can lead to ecological misinterpretations at a small spatial scale (Ellis and Schneider, 2008), a clear classification and large-scale (150 km) comparison between the species assemblages of the different sectors of the REBENT network appears necessary to better understand the overall spatial patterns of macrofaunal distribution and for marine resource management (Thrush *et al.*, 1998; Przeslawski *et al.*, 2011). Moreover, seabed habitat maps obtained from the REBENT network did not take into account highly variable environmental factors or quantify the influence of each environmental factor.

The aim of this study is to identify and rank the natural abiotic factors responsible for the soft-bottom macrofaunal distribution along the coastal fringe of South Brittany taking into account highly variable hydrological factors (hydrodynamic conditions and physico-chemical properties of the water column) generated by validated recently developed three-dimensional environmental models. These results, obtained by integrating fine-scale studies into a broad-scale spatial analysis, were used to determine the biotic and physical characteristics of the major seabed habitats found in this region in order to improve the baseline knowledge of benthic habitats for ecosystem and resource management.

Material and methods

Study area

This investigation collected macrofaunal data from the coastal fringe of South Brittany, extending over 150 km from east to west along the northern part of the French Atlantic continental shelf (Figure 1a). This subtidal zone is predominantly covered by soft sediments and bordered by a southern rocky belt from which a succession of islands emerges. The hydrodynamic conditions, showing an increasing complexity near the islands, are mainly influenced by the swell from the west due to the relatively weak tidal currents (mean tidal range ~ 3 m). The coastal fringe of South Brittany is also subject to the influence of eastern river plumes (Loire and Vilaine Rivers) which can extend to the western limit of South Brittany. Within the framework of the REBENT monitoring network, five subtidal sectors were investigated between 2003 and 2005 (Table 1, Figure 1b–f). In each sector, the localization and number of sampling stations were based on morpho-sedimentary units or distinct biocenoses determined during previous acoustic surveys using a differential Global Positioning System THALES AQUARIUS[®] and a digital sidescan sonar EDGETECH DF-1000[®] (see the full description of the protocol in Ehrhold *et al.*, 2006).

Biological data

In the five subtidal sectors, marine benthic macrofauna was sampled with a 0.125 m² Hamon grab, deployed from the coastal vessel Thalia. This grab is recommended for mixtures of sediment including coarse gravel, as well as macrofauna sampling up to a sediment depth of 30 cm (Dauvin *et al.*, 2007). Three replicates were collected per station, and each of them was washed on board over a circular 2 mm mesh sieve. In contrast to the long-term monitoring strategy of the REBENT network, a 1 mm circular mesh sieve was not used for the fine-scale habitat mapping in order to reduce the amount of retained sediment, especially for the study of heterogeneous coarse substrata. The retained macrofauna was then fixed in a 5% buffered formaldehyde solution for later identification to the lowest taxonomic level (predominantly species) and enumeration in the laboratory. The World Register

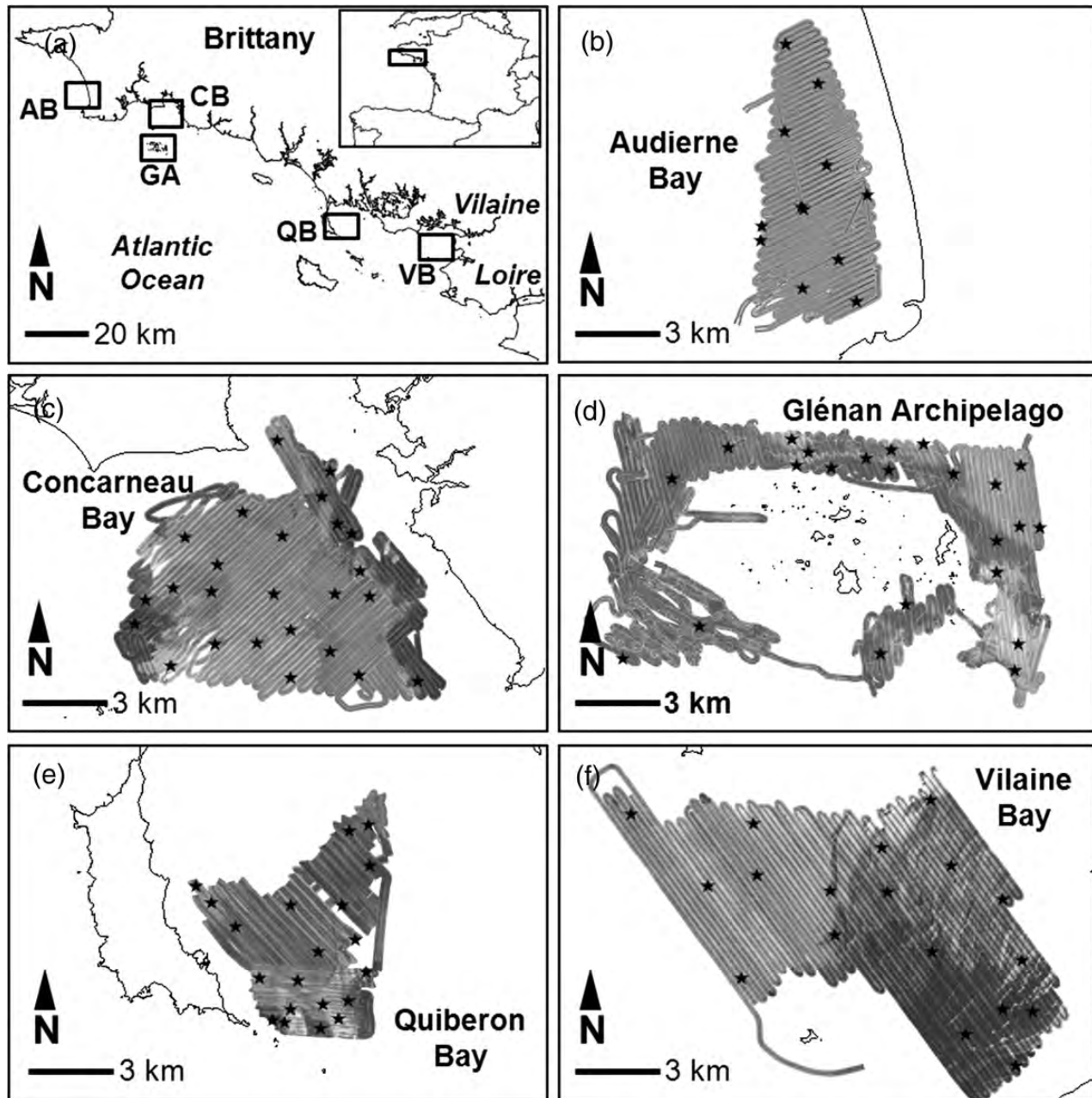


Figure 1. Localization of the five subtidal sectors monitored within the framework of the REBENT network (a), and image mosaics obtained from sidescan sonar in each of these sectors (b–f). Sampling stations are indicated by stars. AB, Audierne Bay; CB, Concarneau Bay; GA, Glénan Archipelago; QB, Quiberon Bay; VB, Vilaine Bay.

of Marine Species (WORMS, 2011) was used to harmonize species names. Biological traits, corresponding to feeding habit, living habit, relative adult mobility, and larval life duration, were assigned to most of the species in order to provide a functional description of macrobenthic communities.

Environmental data

Sediment samples were collected at each station with a 0.042 m² Shipek grab deployed from the coastal vessel *Thalia*, put into a plastic bag, and frozen during their storage. In the laboratory, ~200 g of each sediment sample were first wet-sieved on a 50 µm stainless steel sieve. The fraction above 50 µm was dry-sieved

using a sieve shaker, on a range of stainless steel sieves placed at –4 phi intervals, down to 4 phi (63 µm). The retained fractions were weighed in order to give a full particle size distribution, and GRADISTAT 4.0 software was used to calculate the mean grain diameter, sorting index, and mud content of the distribution.

Temporal and spatial variations in hydrological factors were generated at the bottom layer, over a year, using MARS three-dimensional and wind–wave WAVEWATCH III environmental models in their operational configurations (Tolman, 2002; Lazure and Dumas, 2008). MARS three-dimensional code uses regular orthogonal grids with square meshes aligned with geographic axes, on the horizontal plane (Ménésguen et al., 2007).

Table 1. Sampling plan of the REBENT monitoring network along the coastal fringe of South Brittany.

Subtidal sector	Sampling date	Area covered by sonar (km ²)	Number of sampling stations
Audierne Bay	June 2005	30.19	12
Concarneau Bay	October 2003	68.00	25
Glénan Archipelago	October 2003	67.90	22
Quiberon Bay	October 2003	32.72	20
Vilaine Bay	November 2004	80.88	16

For each mesh, the water column is divided into ten layers on which thickness follows the bathymetry (σ -coordinates). According to the recent development of the models in the framework of the PREVIMER project and the possibility of having good validations by means of satellite observations and seawater measurements, the year 2009 was chosen as the “reference” year to generate hydrological variations because of the absence of exceptional climatic events. Thus, temperature ($^{\circ}\text{C}$), salinity, oxygen saturation (%), suspended particulate matter (SPM, mg l^{-1}) and chlorophyll *a* ($\mu\text{g l}^{-1}$) concentrations were derived from the ECOMARS 3D-BRETAGNE model (resolution grid = 3 km, period = 12 h), while current velocity (m s^{-1}) was obtained from the MARS 3D-MANGA model (resolution grid = 4 km, period = 1 h). Significant wave agitation (m s^{-1}) was derived from the SUDBZH (resolution grid = 200 m, period = 3 h) and LOIRE (resolution grid = 370 m, period = 3 h) models for the three western and two eastern sectors, respectively. For each hydrological factor, annual descriptive statistics (mean, standard deviation, maximum, and minimum) were determined in each square of the resolution grid covering a sampling station and included in the environmental matrix. Annual standard deviation was used as an indicator of environmental variability.

Data analysis

A Bray–Curtis similarity matrix was generated based on a square root-transformed species abundance matrix. Hierarchical, agglomerative classification (CLUSTER) employing group-average linking was conducted using the abundance similarity matrix to produce a dendrogram, while non-metric multidimensional scaling (MDS) was performed to produce an ordination plot (Clarke and Warwick, 1997). The statistical significance of the genuine clusters was then tested with a series of “similarity profile” permutation tests (SIMPROF). Each significant species assemblage, resulting from the multivariate analyses, was characterized by its species richness (S), density of individuals (N, ind. m^{-2}), Shannon’s diversity index (H' , $\log 2$), and Pielou’s evenness index (J'). The main indicator species and associated percentage of indication were determined for each significant species assemblage using the IndVal method, which compared the relative abundance and frequency of the species between different combinations of stations (De Cáceres *et al.*, 2010).

Draftsman plots were used to remove environmental variables showing a high degree of correlation with others. Spatial variations in the environmental conditions over the study area were analysed using normalized principal components analysis (PCA) in order to determine which variables differed the most between stations. The BIOENV procedure was used to identify which combination of environmental variables best explained the differences in

macrofaunal distribution. The relative importance of each environmental variable in accounting for the community variation was determined by forward selection using the DISTLM procedure (Legendre and Anderson, 1999). The above macrofaunal and environmental data were analysed using the PRIMER[®] V6 software package. Natural abiotic variables significantly influencing the macrofaunal distribution were averaged for the stations showing similar species assemblages in order to determine the associated benthic habitats, and compared using one-way analyses of variance (ANOVAs).

Results

General characteristics of the macrofauna

A total of 551 species was identified at the 95 subtidal sampling stations of South Brittany. Polychaetes were the most diverse group with 244 species (44.3%), crustaceans comprised 136 species (24.7%), molluscs 122 species (22.1%), and echinoderms 19 species (3.4%). Other species belonged to the following groups: anthozoans, platyhelminths, nemertean, sipunculids, echiurids, phoronids, tunicates, and protochordates. The species most frequently observed were the polychaetes *Notomastus latericeus* and *Lumbrineris gracilis*, found in 78% and 66% of the stations, respectively. Over the study area, 148 species, including 109 singletons, were only recorded at single stations. Predator (31.6%) and deposit-feeding (29.9%) species were dominant, followed by suspension-feeders (23.9%), scavengers (10.5%), and grazers (4.1%). Most of the species were free living (68%), 19.2% were permanent burrow dwellers, and 12.9% were tube dwellers. Epifauna and infauna corresponded to 63.9% and 36.1% of the species, respectively. At 26% similarity, the dendrogram produced by hierarchical agglomerative clustering distinguished ten major species assemblages, named A–J (Figure 2). The SIMPROF test confirmed that these assemblages were different at 1% significance. Four species assemblages (C, D, G, and J) showed restricted geographical distributions, whereas the others were more widely distributed (Figure 3). Most of the species assemblages exhibited clear indicator species, except for the species assemblages E and I (Table 2). Shannon’s diversity index (H' , Table 2) ranged from 3.50 to 6.21, while Pielou’s evenness index (J') ranged from 0.52 to 0.86.

Environmental conditions

PCA revealed that environmental conditions mainly distinguished stations according to an east–west gradient, especially between eastern (Quiberon and Vilaine) and western (Audierne, Concarneau, and Glénan) sectors (Figure 4). The separation along principal component axis 1 (PC1), explaining 43% of the total variation, mainly reflected the influence of environmental variability, maximum salinity, and mean SPM concentration, and highlighted the effect of freshwater inputs from eastern estuaries. The separation along axis 2 (PC2), explaining 18% of the total variation, was mainly due to oxygen saturation, mean temperature, and hydrodynamic conditions.

Being located near the path of the Vilaine River, Vilaine Bay showed an environmental setting with a pronounced estuarine influence near the seabed. In 2009, annual mean salinity and annual mean SPM concentration were 32.5 ± 0.4 and $6.0 \pm 0.7 \text{ mg l}^{-1}$, respectively. During winter floods, salinity fell to 24.4 while SPM concentration showed several peaks between 13.2 and 23.6 mg l^{-1} . Regular freshwater inputs and the relatively low depth

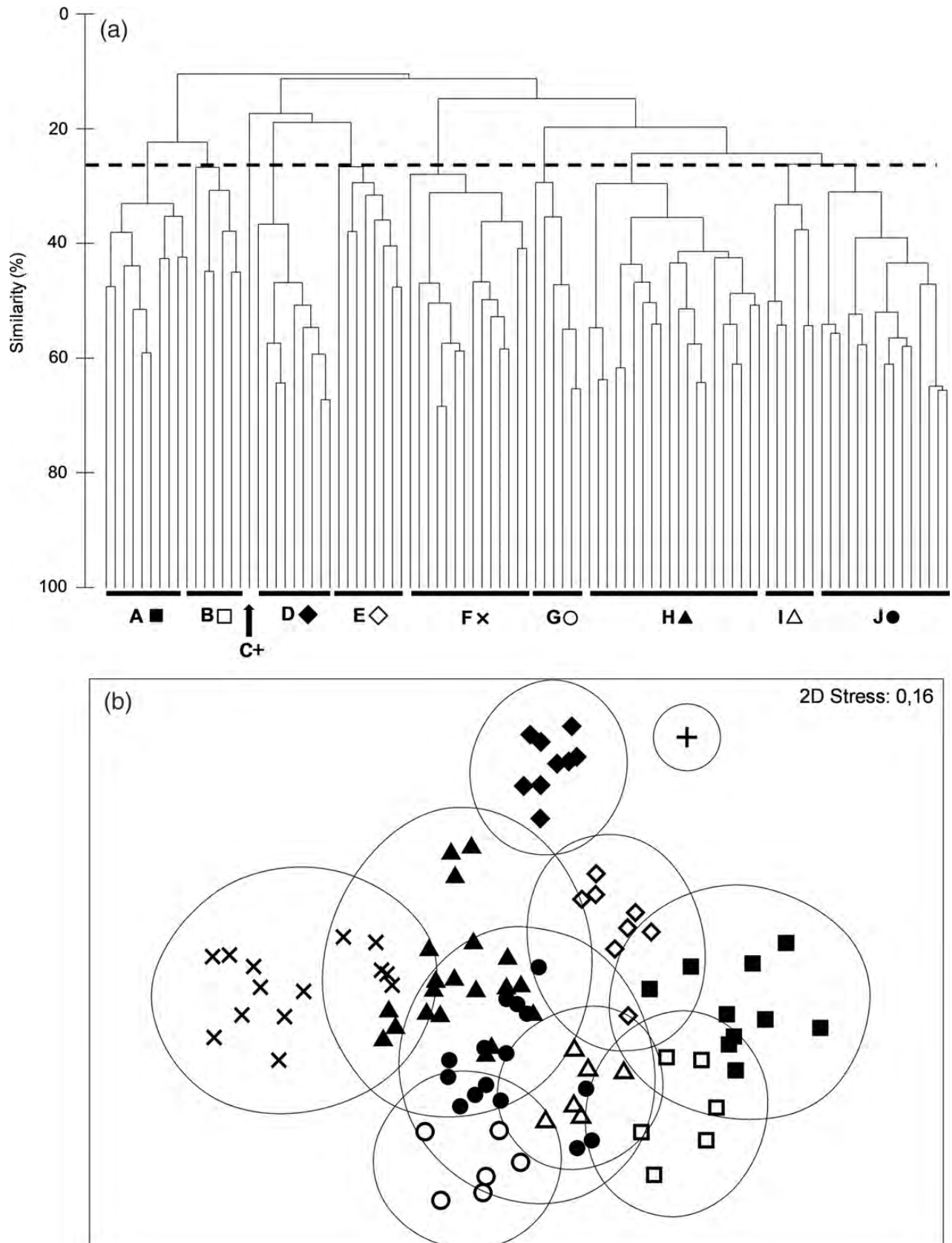


Figure 2. Dendrogram (a) and MDS ordination plots (b) based on the species abundance data determined from 95 sampling stations along the coastal fringe of South Brittany. Ten station clusters (= species assemblages) were identified at the 26% similarity level, and named A–J.

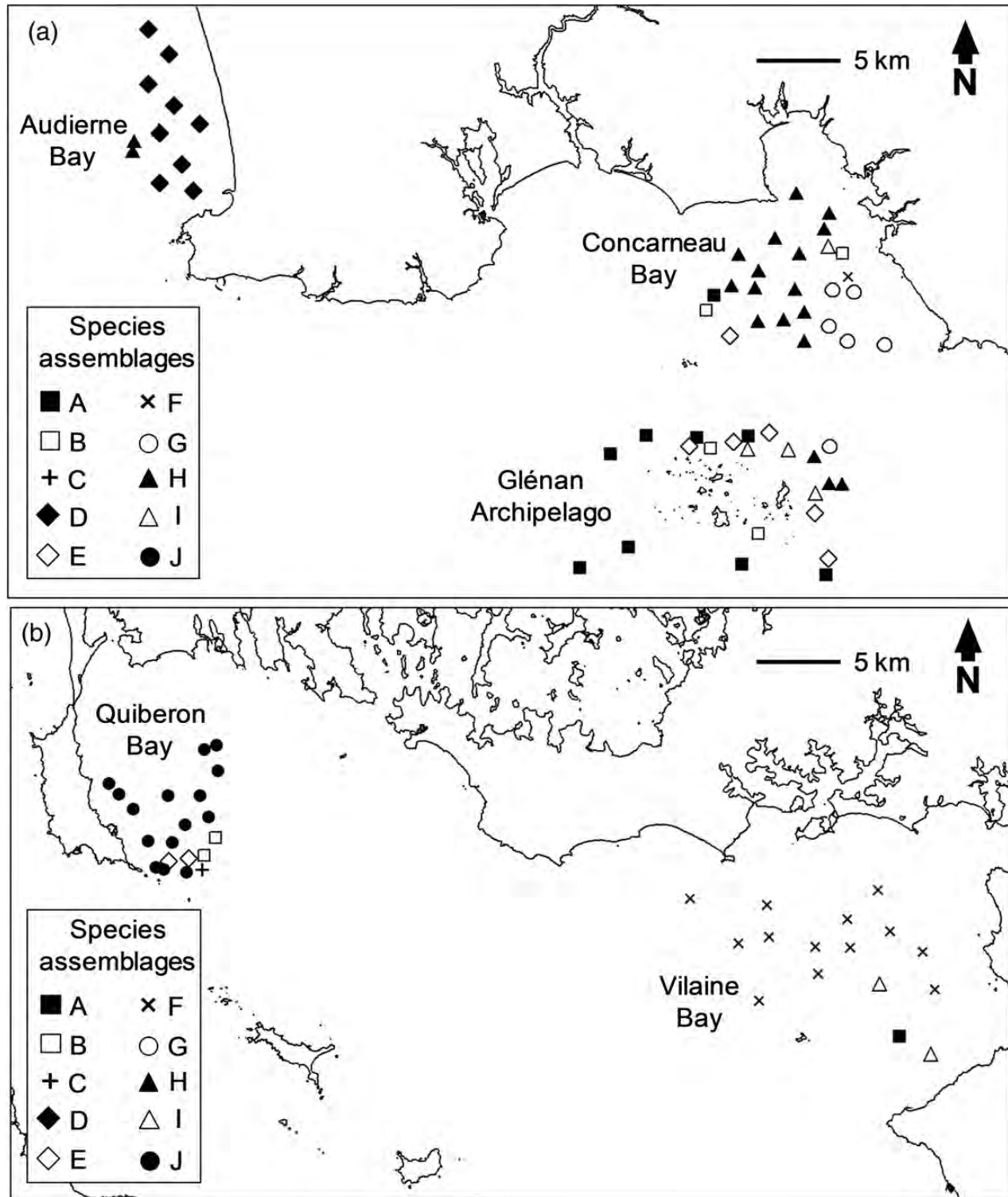


Figure 3. Geographic distribution of the ten species assemblages identified in the western oceanic (a) and eastern estuarine (b) parts of the coastal fringe of South Brittany.

(between 5.8 and 14.4 m) of Vilaine Bay also led to elevated primary production highlighted by an annual mean chlorophyll *a* concentration equal to $3.0 \pm 0.5 \mu\text{g l}^{-1}$, with peaks between 4.2 and $16.8 \mu\text{g l}^{-1}$ during the spring period (April–May). Hydrodynamics were relatively low near the bottom, with

annual mean current velocity equal to $0.08 \pm 0.02 \text{ m s}^{-1}$ and annual mean wave agitation equal to $0.20 \pm 0.03 \text{ m s}^{-1}$. The mudiest stations (mud content >90%) of the coastal fringe of South Brittany were found in the seabed of Vilaine Bay, where oxygen saturation fell to 64% during summer 2009. The southeastern

Table 2. Biotic characteristics of the ten species assemblages (Sp. Ass.) identified along the coastal fringe of South Brittany.

Sp. Ass.	Indicator species	S	N	H'	J'
A	<i>Pisone remota</i> (76%), <i>Protodorvillea kefersteini</i> (71%), <i>Lumbrinereides amoureuxi</i> (54%), <i>Polygordius appendiculatus</i> (50%)	167	405	5.88	0.80
B	<i>Aonides oxycephala</i> (85%), <i>Animoceradocus semiserratus</i> (82%), <i>Clausinella fasciata</i> (77%), <i>Pisidia longicornis</i> (63%), <i>Tapes rhomboides</i> (52%), <i>Spirobranchus triqueter</i> (38%), <i>Gammarella fucicola</i> (27%), <i>Limaria hians</i> (17%), <i>Limatula</i> <i>subauriculata</i> (17%)	218	1838	5.13	0.66
C	<i>Travisia forbesii</i> (100%), <i>Bathyporeia elegans</i> (90%), <i>Glycera oxycephala</i> (89%)	17	96	3.53	0.86
D	<i>Scolecopsis cantabra</i> (97%), <i>Magelona johnstoni</i> (91%), <i>Iphinoe trispinosa</i> (89%), <i>Donax</i> <i>vittatus</i> (67%), <i>Owenia fusiformis</i> (54%)	88	418	4.11	0.64
E	<i>Scoloplos armiger</i> (55%), <i>Gari</i> <i>fervensis</i> (48%), <i>Poecilochaetus</i> <i>serpens</i> (42%), <i>Aponuphis</i> <i>bilineata</i> (33%)	186	443	6.11	0.81
F	<i>Sternaspis scutata</i> (100%), <i>Nephtys</i> <i>hystricis</i> (68%), <i>Kurtiella</i> <i>bidentata</i> (60%), <i>Lagis koreni</i> (34%), <i>Alitta succinea</i> (30%), <i>Virgularia mirabilis</i> (28%)	86	390	4.16	0.65
G	<i>Haploopsis sp.</i> (100%), <i>Pista</i> <i>elongata</i> (60%), <i>Terebellides</i> <i>stroemi</i> (60%), <i>Ampelisca spinipes</i> (49%), <i>Maldane glebifex</i> (26%), <i>Macroclymene santandarensis</i> (23%)	105	588	3.50	0.52
H	<i>Amphiura filiformis</i> (81%), <i>Thyasira flexuosa</i> (45%), <i>Pholoe</i> <i>inornata</i> (37%)	208	778	4.78	0.62
I	<i>Pista cristata</i> (54%), <i>Sthenelais boa</i> (53%), <i>Leptochiton asellus</i> (48%)	174	807	5.77	0.78
J	<i>Ampharete finmarchica</i> (81%), <i>Dipolydora coeca</i> (78%), <i>Drilonereis filum</i> (70%), <i>Crepidula fornicata</i> (47%), <i>Asterias</i> <i>rubens</i> (20%), <i>Ocenebra erinaceus</i> (14%)	300	1340	6.21	0.75

The first three indicator species (bold characters) and secondary indicator species are given with their percentage of indication (IndVal).

H', Shannon's diversity index; J', Pielou's evenness index; N, density (ind. m⁻²); S, species richness.

part of Vilaine Bay was relatively sheltered from the estuarine influence and directly exposed to wave and tidal current action.

In 2009, the environmental setting of Quiberon Bay showed attenuated estuarine effects near the bottom, involving annual mean salinity and annual mean SPM concentration equal to 33.4 ± 0.2 and 3.5 ± 0.2 mg l⁻¹, respectively. Chlorophyll *a* concentration showed an annual mean equal to 2.3 ± 0.3 µg l⁻¹, with spring peaks ranging from 6.3 to 9.0 µg l⁻¹. Quiberon Bay is a

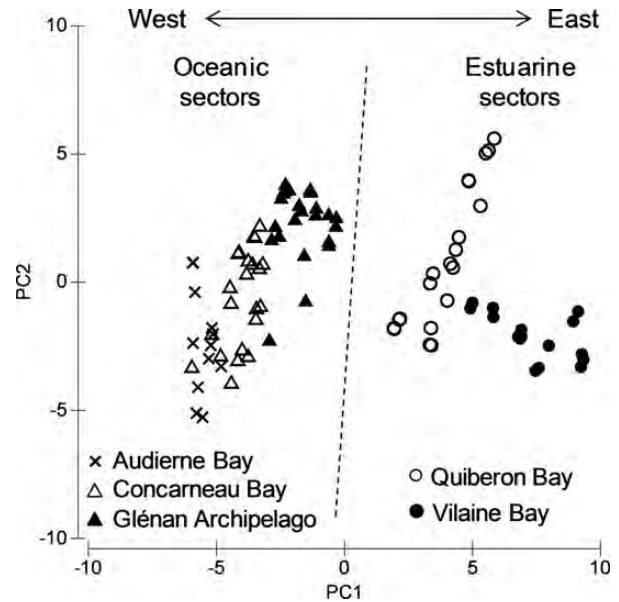


Figure 4. Principal components analysis plot based on normalized physical data for the 95 sampling stations along the coastal fringe of South Brittany. Symbols correspond to the five subtidal sectors monitored within the framework of the REBENT network.

shallow area (between 5.4 and 13.1 m) with a mud content ranging from 0 to 45.5%. In summer 2009, oxygen saturation fell to 45% in the muddy areas. Hydrodynamics were relatively low (annual mean current velocity = 0.11 ± 0.02 m s⁻¹ and annual mean wave agitation = 0.20 ± 0.03 m s⁻¹) in the major part of Quiberon Bay, while geomorphological characteristics were related to an increase in current velocity (annual mean = 0.14 ± 0.01 m s⁻¹) at the southeastern part.

The western and eastern parts of Concarneau Bay correspond to large pits (between 14.3 and 25.7 m) separated by shoals (<10 m). The western part was strongly influenced by hydrodynamic conditions generated by the Atlantic Ocean, with a relatively high current velocity (annual mean = 0.15 ± 0.02 m s⁻¹) which can be associated with the predominance of coarse sediments. On the other hand, sediments of the eastern part of Concarneau Bay were muddier, especially due to the sedimentation of fine particles brought by the eastern rivers' plumes during winter floods. Indeed, during this period, the SPM concentration was almost four times higher (6.4 mg l⁻¹) near the seabed, while salinity decreased from 34.6 to 32.5. Except in the northeastern part, where sedimentation of fine particles brought by the eastern rivers' plumes occurs, the periphery of the Glénan Archipelago, which showed a mean depth of 25.9 ± 8.1 m, was dominated by coarse sediments in relation to the direct exposure to the influence of hydrodynamic conditions generated by the Atlantic Ocean. In Concarneau Bay and at the periphery of the Glénan Archipelago, the annual mean SPM concentration was 1.6 ± 0.4 and 1.1 ± 0.1 mg l⁻¹, respectively, while the annual mean chlorophyll *a* concentration was 1.8 ± 0.2 and 1.7 ± 0.1 µg l⁻¹, respectively. In summer, oxygen saturation fell to 59% in the eastern muddy parts of Concarneau Bay, while it remained higher than 70% in the other seabed habitats of Concarneau Bay and the Glénan Archipelago. Along the eastern coast of Concarneau Bay, shoals (<11 m) were covered by dense

accumulations of live and dead unattached coralline algae also known as maerl.

In Audierne Bay, both depth and mud content progressively increased from 8 to 40 m and from 1.3 to 5.6 mg l⁻¹, respectively, with distance from the coast. Above a depth of 30 m, a well-sorted fine sandy bottom and relatively low mud content can be associated with the strong wave agitation, which was the highest (annual mean = 0.43 ± 0.12 m s⁻¹) reported along the coastal fringe of South Brittany.

Relationships between macrobenthos and environmental conditions

The BIOENV procedure indicated that the variations in macrofaunal distribution of South Brittany can best be explained by a combination of eight variables (Table 3, correlation = 0.60). These corresponded to sediment characteristics (mud content, mean grain diameter, and sorting index), hydrodynamic conditions (maximum current velocity and mean wave agitation), and environmental variability (standard deviations in temperature, SPM concentration, and oxygen saturation). Mud content individually showed the highest correlation with species distribution (correlation = 0.34). Although it increased with the number of combined environmental variables, the correlation was relatively similar using 4–8 variables. Forward selection indicated that 16 of the tested environmental variables had a significant influence

Table 3. Best correlations obtained between an increasing number of environmental variables and macrofaunal distribution along the coastal fringe of South Brittany, as revealed by the BIOENV procedure.

No. of variables	Correlation	Selections
8	0.60	Mud content, mean wave agitation, mean grain diameter, variability of temperature, maximum current velocity, variability of SPM concentration, variability of oxygen saturation, sorting index
7	0.59	Mud content, mean wave agitation, mean grain diameter, variability of temperature, maximum current velocity, variability of SPM concentration, variability of oxygen saturation
6	0.59	Mud content, mean wave agitation, mean grain diameter, variability of temperature, maximum current velocity, variability of SPM concentration
5	0.58	Mud content, mean wave agitation, mean grain diameter, variability of temperature, maximum current velocity
4	0.57	Mud content, mean wave agitation, mean grain diameter, variability of temperature
3	0.54	Mud content, mean wave agitation, mean grain diameter
2	0.47	Mud content, mean wave agitation
1	0.34	Mud content

The maximum correlation (0.60) was obtained associating eight variables. SPM, suspended particulate matter.

($p < 0.01$) on macrofaunal distribution and together explained 51% of the total variation in the spatial patterns (Table 4). Sediment characteristics together explained 20% of this variation, environmental variability 13%, and hydrodynamic conditions 4%.

Significant differences (ANOVA, $p < 0.01$) in the mean values of environmental variables having a significant influence on macrofaunal distribution enabled the distinction of the benthic habitats supporting each of the ten species assemblages (Figures 5 and 6).

Species assemblages and associated seabed habitats

Species assemblages A and B were characteristic of clean coarse sediments (Figure 5, mean grain diameter >1.5 mm, mud content <1%), as confirmed by the presence of the cephalochordate *Branchiostoma lanceolatum* and the polychaete *Aonides paucibranchiata* in these two assemblages only. Species assemblage A was found on clean gravels and under high tidal current velocities (Figure 5), such as at the stations of the Glénan Archipelago exposed to appreciable tidal/wave action and near the mouth of the Vilaine River (Figure 3). Such an environment favoured highly mobile (52.7%) and epifaunal (58.4%) species such as the polychaetes *Pisone remota*, *Protodorvillea kefersteini*, and *Polygordius appendiculatus* (Table 2). On the other hand, clean coarse sediments supporting species assemblage B corresponded to maerl beds showing a complex structure, with spaces between

Table 4. Hierarchical classification of environmental variables having a significant influence ($p < 0.01$) on macrofaunal distribution along the coastal fringe of South Brittany, as revealed by forward selection in the DISTLM procedure.

Variable	Adjusted R ²	Pseudo-F	p-value	Cumulative proportion
Mud content	0.10	11.48	0.001	0.11
Minimum oxygen saturation	0.15	7.10	0.001	0.17
Mean grain diameter	0.20	6.17	0.001	0.22
Variability of temperature	0.23	5.62	0.001	0.26
Sorting index	0.26	4.12	0.001	0.30
Mean wave agitation	0.28	3.72	0.001	0.32
Variability of SPM concentration	0.30	3.58	0.001	0.35
Variability of salinity	0.32	3.89	0.001	0.38
Maximum current velocity	0.34	3.01	0.001	0.40
Mean SPM concentration	0.35	2.59	0.001	0.42
Variability of chlorophyll <i>a</i> concentration	0.36	2.39	0.001	0.44
Depth	0.37	2.23	0.001	0.46
Mean temperature	0.37	2.03	0.002	0.48
Maximum salinity	0.38	1.85	0.002	0.49
Variability of oxygen saturation	0.39	1.78	0.010	0.50
Minimum chlorophyll <i>a</i> concentration	0.40	1.79	0.007	0.51

Cumulative proportion corresponds to the percentage of the macrofaunal variation explained by the associated environmental variables. SPM, suspended particulate matter.

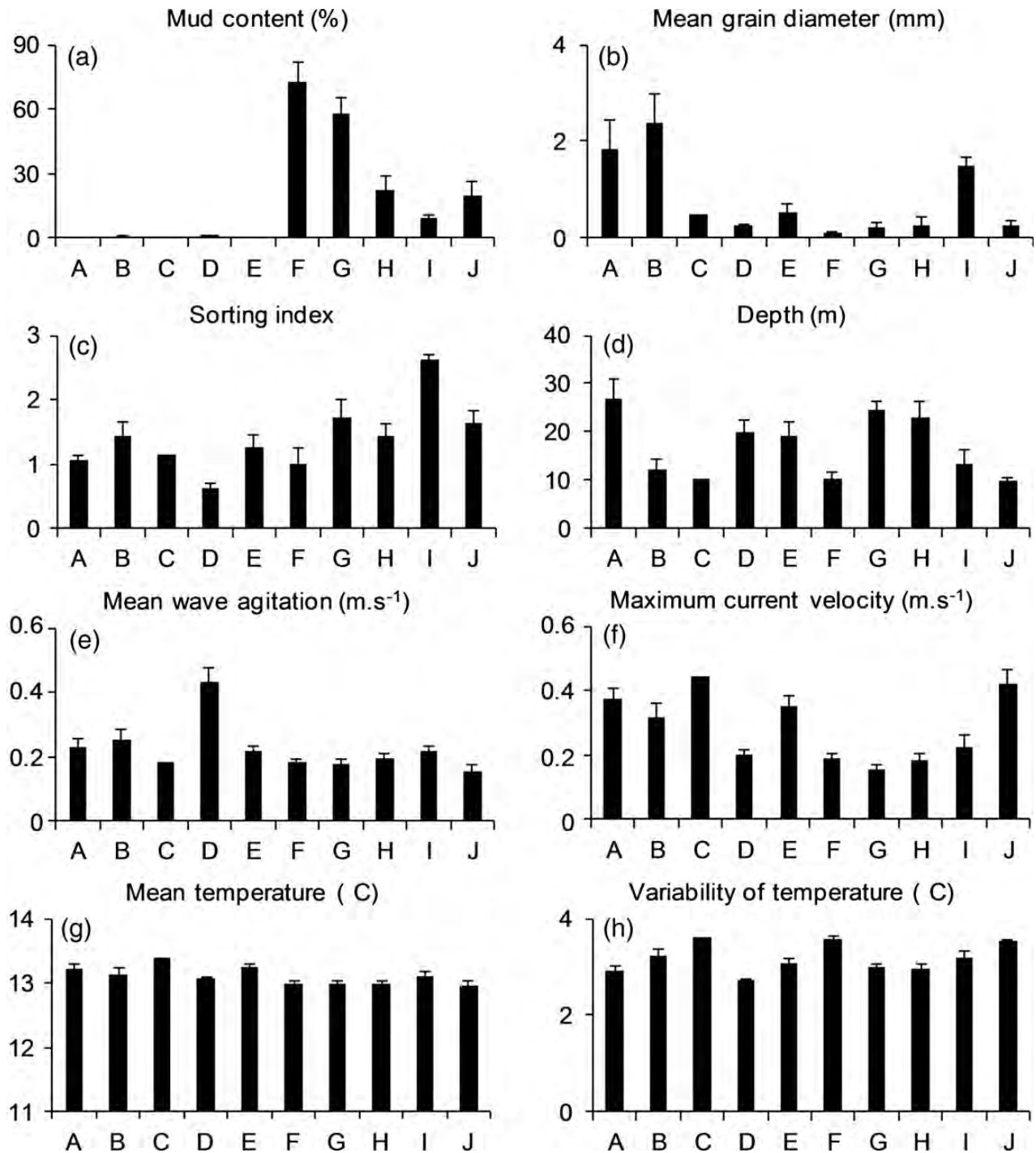


Figure 5. Natural abiotic factors influencing the ten species assemblages (A–J) identified along the coastal fringe of South Brittany. Values correspond to the average abiotic conditions of sampling stations clustered according to their species assemblages, and are given with their 95% confidence intervals.

branched forms and hard calcareous surfaces for sessile organisms and borers, resulting in the highest density of individuals (Table 2), mainly represented by suspension-feeders such as the decapod *Pisidia longicornis* (762 ind. m⁻²), the polychaete *Spirobranchus triqueter* (231 ind. m⁻²), and the bivalves *Clausinella fasciata* (44 ind. m⁻²) and *Tapes rhomboides* (22 ind. m⁻²). Although environmental conditions were similar to those supporting species

assemblage A (Figures 5 and 6), species assemblage B was found at reduced depth and in lower current velocities. The amphipoda *Animoceradocus semiserratus* and *Gammarella fucicola*, as well as bivalves of the Limidae family (*Limaria hians* and *Limatula subauriculata*), were only observed in species assemblage B.

Species assemblages C, D, and E were supported by clean fine sediments (Figure 5, mean grain diameter <1 mm, mud content

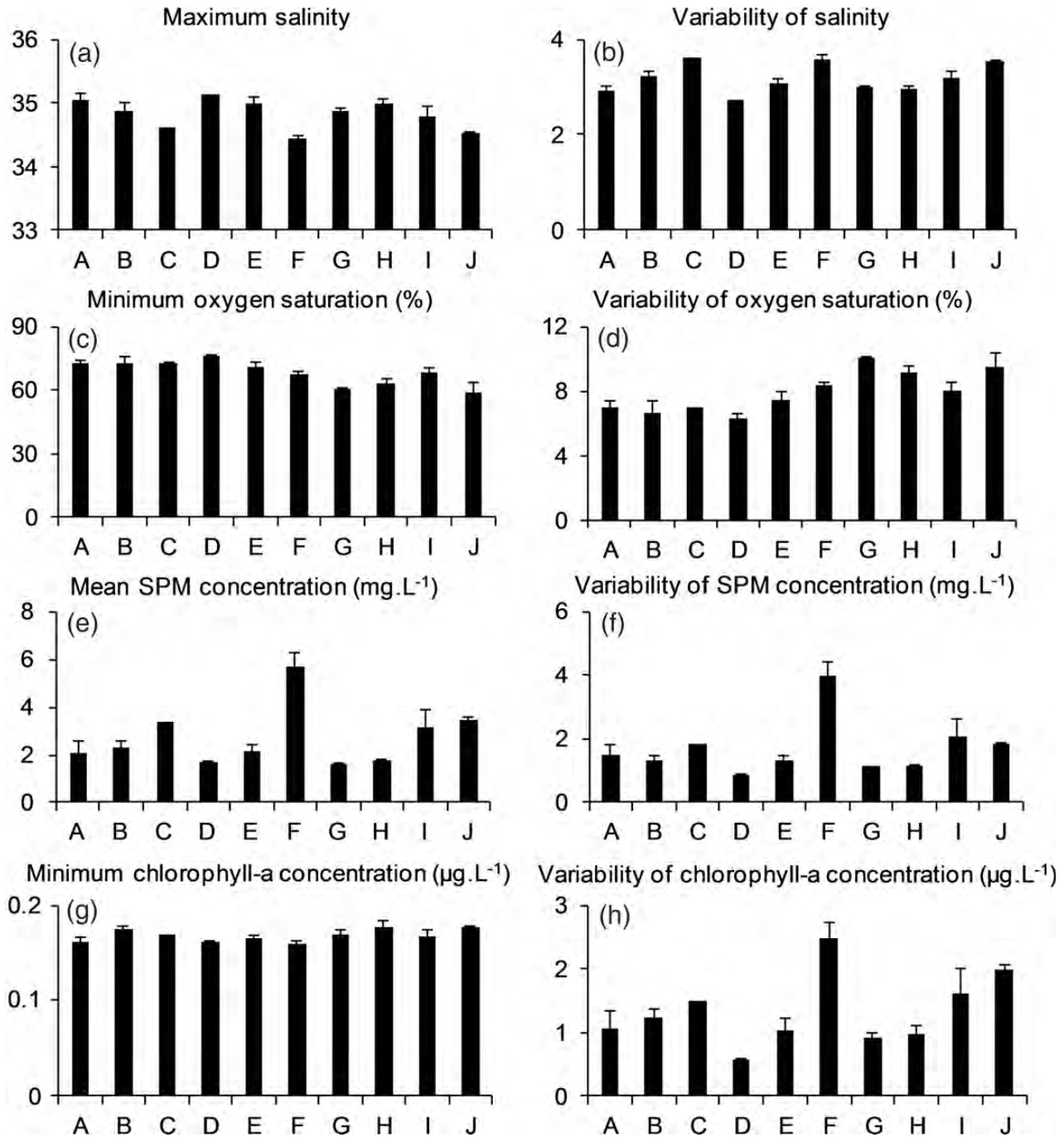


Figure 6. Natural abiotic factors influencing the ten species assemblages (A–J) identified along the coastal fringe of South Brittany. Values correspond to the average abiotic conditions of sampling stations clustered according to their species assemblages, and are given with their 95% confidence intervals. SPM, suspended particulate matter.

<1.5%) and showed a relatively high abundance of the polychaete *Nephtys cirrosa* (14–24 ind. m⁻²). Species assemblage C was only observed at a single station in the southern part of Quiberon Bay where mean grain diameter was equal to 0.5 mm (Figure 3). This corresponded to an isolated shallow sandbank (–10 m) subject to high tidal current velocities and was characterized by the polychaete *Travisia forbesii* (19 ind. m⁻²) which was not observed at other stations (Table 2). Species assemblage D was only found on the well-sorted (sorting index <1) fine sandy bottom (mean

grain diameter varying between 0.18 and 0.29 mm) of Audierne Bay (Figure 3), down to 30 m depth, and numerically dominated by the polychaete *Owenia fusiformis* (147 ind. m⁻²). Species assemblages C and D were dominated by infauna which represented 62.0% and 59.3% of the species, respectively. Species assemblage E was numerically dominated by the polychaete *Aponuphis bilineata* (58 ind. m⁻²) but did not show clear indicator species (Table 2). This assemblage was found in high current velocities, on fine sediments (mean grain diameter varying between

0.29 and 0.94 mm) showing the lowest mud content (average mud content = 0.11%; Figure 5).

Species assemblages F and G were found in fine muddy sediments (mean grain size <1 mm, mud content >50%) subject to weak hydrodynamic conditions (Figure 5). Species assemblage F, characterized by the presence of the polychaete *Sternaspis scutata* (Table 2), was found in highly variable shallow estuarine areas showing a mud content >70% and a mean grain diameter varying between 0.05 and 0.23 mm (Figures 5 and 6), such as Vilaine Bay and the eastern part of Concarneau Bay (Figure 3). As for assemblage D, homogeneous sediments supporting species assemblage F were associated with relatively low species richness (Table 2), mainly comprising deposit-feeding (42.5%) and infaunal (60.9%) species. On the other hand, species assemblage G was found in deeper areas (>20 m) showing a mean grain diameter varying between 0.08 and 0.88 mm, and characterized by a low summer oxygen saturation down to 60% (Figures 5 and 6). Highly dominated by the tubicolous suspension-feeding amphipod *Haploops* sp. (321 ind. m⁻²), this species assemblage was the least diverse and had the lowest equitability in species abundance (Table 2). Species showing the highest abundance, such as *Haploops* sp., *Ampelisca spinipes*, *Terebellides stroemi*, *Maldane glebifex*, and *Macroclymene santandarensis*, have a direct development.

Species assemblages H, I, and J were supported by sandy-muddy sediments, with mud content ranging between 4% and 50% (Figure 5). Assemblage H, dominated by the suspension-feeding ophiuroid *Amphiura filiformis* (282 ind. m⁻²), was found mainly in deep areas (>20 m) with an average mud content close to 26% and relatively weak hydrodynamic conditions (Table 2 and Figure 5). Species of this assemblage were predominantly infaunal (58.4%), deposit-feeding (43.6%), and of low mobility (46.9%). The most heterogeneous sediment (sorting index >2) supported species assemblage I which appeared as a transitional stage between coarse and muddy sediments (Figure 5). Species assemblage J was characterized by the polychaete *Ampharete finmarchica* and was only found in shallow areas of Quiberon Bay (Table 2 and Figure 3), showing less pronounced estuarine conditions than those supporting assemblage F (Figures 5 and 6).

Discussion

Relationships between macrobenthos and natural abiotic factors

The spatial distributions of the 551 species found along the subtidal coastal fringe of South Brittany showed a relatively high correlation with environmental factors and can be 51% explained by a combination of 16 natural abiotic variables. Although there was a degree of interdependence among some of these environmental variables (Figures 5 and 6), statistical analysis highlighted the additional contribution of each of them to the variations in the spatial patterns. Sediment characteristics, bathymetry, and hydrodynamic conditions (current velocity and wave agitation), which are generally used in benthic studies (Warwick and Uncles, 1980; Ysebaert and Herman, 2002; Van Hoey et al., 2004; Moulaert et al., 2007; Bolam et al., 2008), contributed to 26% of the explanation of the broad-scale macrofauna spatial pattern. As they explained 25% of the spatial pattern, the physico-chemical properties of the water column appear essential in order to understand the broad-scale species distribution in estuarine and coastal

ecosystems. Although the output from mathematical models may not fully represent the complex functioning of the coastal environment, highly variable hydrological factors generated by three-dimensional environmental models greatly contributed to the relatively high correlation between the environment and species distributions, and, therefore, significantly improved understanding of the causes of spatial patterns of the macrobenthos at the South Brittany scale. Considering the diversity of the environmental factors used and the reliability of the three-dimensional models at a large spatial scale (Ménésguen et al., 2007), our results provide a good estimation of the percentage of macrofaunal spatial variations which can be explained by natural abiotic conditions. There was some evidence to suggest that sampling stations characterized by similar natural abiotic conditions also supported similar species assemblages, even when they were situated far away from each other. However, the spatial patterns of macrofaunal distribution also revealed that a large number of stations sharing similar species assemblages were concentrated in small areas. The sampling design of the REBENT network could be partly responsible for this geographical clustering. Nevertheless, continuous macrofauna sampling performed by Glémarec (1969) all over the coastal fringe of South Brittany showed similar location-specific assemblages. As discussed below, this mainly results from the great diversity of substrata and the progressive east-west transition between “estuarine” and “oceanic” conditions.

Taken together, mud content, mean grain diameter, and sorting index were responsible for 20% of the variation in the soft-bottom macrofaunal distribution along the coastal fringe of South Brittany. Relationships between sediments and the macrobenthos have often been described in terms of the range of granulometric variations tolerated by each species (Ellingsen, 2002; Van Hoey et al., 2004; Hily et al., 2008). According to their lifestyle, benthic organisms require specific sediment characteristics for tube building, burrowing, or feeding (Self and Jumars, 1988; Pinedo et al., 2000). For example, *Owenia fusiformis*, a polychaete needing a large quantity of fine particles to build its tube and to grow, was the dominant species in the well-sorted fine sandy bottom of Audierne Bay (Pinedo et al., 2000). Fine particles, easily re-suspended by water movements, are known to affect the feeding processes of benthic species (Wildish, 1977; Snelgrove, 1999). Moreover, in nearshore ecosystems, organic content tends to increase with the fineness of the particles (Gray and Elliot, 2009), thereby enhancing the food supply for many benthic species. However, in the present study, homogeneous fine sediment showed a relatively low value of species richness (< 100 species) and no interstitial fauna such as hesionid and syllid polychaetes, and sipunculids.

The influence of the Vilaine and Loire estuaries induced marked gradients in the environmental conditions between riverine-influenced coasts and coasts without this influence, and can be related to 16% of the explanation of the spatial patterns of species distribution provided by the physico-chemical properties of the water column. Freshwater inputs led to regular decreases in temperature and salinity, involving the lowest maximum salinity as well as the highest variability in salinity and temperature, in the shallow areas of Vilaine and Quiberon Bays. Moreover, SPM and chlorophyll *a* concentrations showed their highest values and variability in these areas. High physico-chemical variability resulted in the presence of euryhaline and/or eurythermal species such as *Alitta succinea*, *Lagis koreni*, *Heteromastus filiformis*, *Marphysa sanguinea*, and *Thalassema thalassenum*. Independently

of the influence of the major eastern estuaries, a high environmental variability and associated macrofauna (species assemblage F) were also observed in a shallow station near the mouth of small rivers east of Concarneau Bay.

Maximum current velocity and mean wave agitation each explained 2% more of the macrofauna spatial pattern. Under strong hydrodynamic conditions, physical erosion and suspension of soft sediment favour infauna and active burrowers, as observed in species assemblages C and D submitted to the highest maximum current velocity and to the highest wave agitation, respectively. For example, the bivalve *Donax vittatus*, which can rapidly return into the soft sediment after being dislodged and is characteristic of wave-exposed sand bottoms (Allen and Moore, 1987), was only found in Audierne Bay. Such types of benthic habitats, with high environmental selectivity due to strong hydrodynamic conditions, were associated with relatively low species richness (< 100 species). Variations in the hydrodynamic conditions can also modify the functional features of some species as observed in the ophiurid *A. filiformis*, which generally feeds on suspended particulate matter but can change to deposit-feeding in areas of low water flow (Ockelmann and Muus, 1978). Hydrodynamic conditions influenced the sediment characteristics and physico-chemical properties of the water column. Areas with high hydrodynamic energy also showed higher mean temperatures and high oxygen saturation. On the other hand, shallow estuarine areas were characterized by low values of oxygen saturation, which could be attributed to eutrophic conditions induced by organic matter enrichment (Le Bris and Glémarec, 1996). In Quiberon Bay, organic enrichment caused by effluent from shellfish activities occurring in the north of this bay probably increases summer oxygen depletion (Bouchet and Sauriau, 2008). As for environmental variability, hydrodynamic influence generally declined with depth.

As natural abiotic factors do not fully explain the macrofaunal distribution, other explanatory factors could be taken into account in order to understand better the structuring of marine soft-bottom communities. In the estuarine and coastal areas of South Brittany, anthropogenic pressure has not yet been quantified, but activities such as trawling, dredging, and shellfish farming which take place here are known to impact strongly on macrobenthic communities at small and large spatial scales (Thrush *et al.*, 1998; Hartstein and Rowden, 2004; Hily *et al.*, 2008). Moreover, some species can cause modifications of the environmental conditions, which are not usually accounted for in the output from mathematical models (Reise, 2002). For example, high densities of the ophiuroid *A. filiformis* can significantly increase the oxygen flux in the sediment by ventilating their burrows (Vopel *et al.*, 2003).

A baseline for the management of marine ecosystems and resources

While traditional management of marine ecosystems has mainly concerned single threats along single portions of ecosystems, the relatively new ecosystem-based approach is now considered a promising requirement for sustainable environmental management and the establishment of marine protected area networks (Fraschetti *et al.*, 2011). This approach needs to take into account the influence of some important environmental factors, such as estuarine outputs, climate change, pollution, habitat degradation, and fishery impacts, occurring at a wider spatial scale than that considered by local surveys generally performed in

marine benthic ecology. Moreover, while local environmental conditions can lead to misinterpretations of benthic habitat characteristics at a small spatial scale (Ellis and Schneider, 2008), site to site comparisons of the physical environment associated with distant similar species assemblages reduce site-related artefacts and enable a more realistic physical characterization of benthic habitats. As demonstrated in the present study, the integration of local ecological surveys, using the same data sources and methodology, into a large-scale ecosystem-based approach greatly improves the understanding of the relationship between species distribution and environment, and provides a consistent baseline compatible with management concerns and the detection of spatial and temporal changes. The quantification of such species–environment relationships also represents the core of predictive modelling, which provides an overall integrated vision compatible with ecosystem management (Gogina and Zettler, 2010; Méléder *et al.*, 2010). Allowing the use of a large variety of environmental data at different spatial and temporal scales, three-dimensional environmental models appear as useful tools to take into account highly variable hydrological factors in order to better explain the spatial distribution of macrobenthic species.

Along the coastal fringe of South Brittany, the strong influence of the outputs of the eastern estuaries was only highlighted by the integration of local ecological surveys into a large-scale ecosystem-based approach. The *Sternaspis scutata* community (species assemblage F), which appeared clearly dependent on the estuarine outputs and corresponds to a major nursery for the Gulf of Biscay's demersal fish, can be affected by Vilaine's estuary planning. Since the 1970s, the commissioning of the Arzal barrage, situated 6 km upstream from the mouth of the Vilaine River, has involved the silting of Vilaine Bay and has probably played a role in the drastic reduction of the spatial distribution of the erected pennatulid *Virgularia mirabilis* compared with the previous observations performed in the *S. scutata* community (Glémarec, 1969). In the eastern part of Concarneau Bay, modifications of the outputs of the major eastern estuaries can also affect the sedimentation of fine particles brought by the river's plumes during the winter floods, and therefore the *Amphiura filiformis* and *Haploops* sp. communities (species assemblages H and G). Such alterations may partly explain the expansion of the *Haploops* sp. community at the expense of that of *Maldane glebifex* between 1964 and 1974 (Glémarec *et al.*, 1986), according to the silting requirements of these two structuring species. While low oxygen levels observed in this study do not seem to have negative effects on the *Haploops* sp. community, more severe hypoxia could be responsible for the decrease in *Haploops* spp. abundance in Øresund bottom waters, between Denmark and Sweden (McDermott, 1993). Moreover, in South Brittany, the dominance of species with direct development probably limits the geographical dispersion of the *Haploops* sp. community.

When anthropogenic pressures are not spatially quantified, such as in the coastal fringe of South Brittany and many other nearshore ecosystems, their qualitative impacts can be indirectly detected by the analysis of benthic communities. In Quiberon Bay, the presence of the *Ampharete finmarchica* community (species assemblage J), which was not reported before (Glémarec, 1969), seemed to be the result of the intensification of oyster production since the introduction of the Pacific oyster *Crassostrea gigas* in the 1970s. Indeed, the two main species of this community, *A. finmarchica* and *Dipolydora coeca*, are considered as indicators of organic enrichment (Gray and Pearson,

1982), which is a phenomenon often associated with oyster farming (Bouchet and Sauriau, 2008). The influence of oyster farming on the *A. finmarchica* community was also attested to by the presence in this study of the invasive slipper-limpet *Crepidula fornicata* and predators of farmed bivalves such as the oyster drill *Ocenebra erinaceus* and the starfish *Asterias rubens*. In the present study, heterogeneous sediments and organic enrichment due to shellfish farming supported the highest species richness. Moreover, silting due to oyster farming could also be responsible for the disappearance of the maerl bed identified by Glémarec (1969) at the south of Quiberon Bay. Indeed, the large-scale approach implemented in our study revealed the presence of a residual maerl community (species assemblage B) in this zone, while maerl accumulations were not observed during the oceanographic surveys. Being hot spots for marine biodiversity and nurseries for commercially exploited species, maerl beds are amongst the main concerns of European conservation policies despite the lack of knowledge about their dependence on environmental factors (Grall and Hall-Spencer, 2003). In South Brittany, the comparisons of the physical setting of different maerl beds showed that depth and current velocity are determinant abiotic factors for the establishment of this type of habitat, probably in relation to the biological requirements of photosynthetic coralline algae. In fact, light intensity decreases with depth and SPM concentration, while hydrodynamic conditions can be limiting for the development of coralligenous algae (Wilson et al., 2004).

Both *S. scutata* and *A. filiformis* communities (species assemblages F and H) showed high proportions of infauna (60.9% of the species and 84.9% of the individuals) and active burrowers (19.2% of the species and 49.8% of the individuals), suggesting physical disturbances. In contrast to species assemblages C and D, where similar biological traits can be associated with strong current velocity or wave agitation, the functional structure of species assemblages F and H can partly result from dredging and trawling activities which occurred in the areas supporting these benthic communities, and have created numerous furrows clearly visible on acoustic recordings (Talidec et al., 2000; AE, unpublished data). Although these functional traits have often been associated with towed fishing (Tillin et al., 2006; de Juan et al., 2007), further investigations, including notably a spatial quantification of the fishing effort by means of vessel monitoring systems, will determine whether the proportions of infauna and active burrowers are effectively enhanced by dredging and trawling activities.

Conclusion

The present study integrated local ecological surveys in an ecosystem-based approach in order to identify and rank a range of natural abiotic factors determining soft-bottom macrofaunal distribution at a variety of spatial scales along the subtidal coastal fringe of South Brittany. The relatively high correlation between macrofaunal and physical data suggests that validated three-dimensional environmental models can be useful tools to support ecosystem management in particular by enabling the generation of summary statistics to quantify highly variable hydrological factors, which can be important in determining benthic species distributions (Gogina and Zettler, 2010; Méléder et al., 2010). Providing a consistent description of the macrofaunal communities and associated seabed habitats, these results are useful in establishing a baseline for the detection of ecological changes and anthropogenic impacts.

Acknowledgements

This work was jointly funded by IFREMER and the French Agency for Protected Marine Areas (AAMP). The authors wish to thank Philippe Cugier, Alain Ménesguen, and Fabrice Lecornu, coordinator of the PREVIMER project, for the use of the 3D environmental models, as well as Jean-Dominique Gaffet for his help in the field. Aline Blanchet is also thanked for her great contribution to the taxonomic identification and species enumeration. We also thank anonymous reviewers for their valuable comments on the manuscript.

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Handling editor: Rochelle Seitz