



# Linking macrobenthic communities structure and zonation patterns on sandy shores: Mapping tool toward management and conservation perspectives in Northern France

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## ARTICLE INFO

### Article history:

Received 24 November 2014

Received in revised form

2 March 2015

Accepted 6 March 2015

Available online 11 March 2015

### Keywords:

Macrobenthic communities

Sandy shores

Mapping

EUNIS typology

Conservation

Eastern English Channel

## ABSTRACT

In a context of intensifying anthropogenic pressures on sandy shores, the mapping of benthic habitat appears as an essential first step and a fundamental baseline for marine spatial planning, ecosystem-based management and conservation efforts of soft-sediment intertidal areas. Mapping allows representing intertidal habitats that are basically characterised by abiotic (e.g. sediments, exposure to waves...) and biotic factors such as macrobenthic communities. Macrobenthic communities are known to show zonation patterns across sandy beaches and many studies highlighted the existence of three biological zones. We tested this general model of a tripartite biological division of the shore at a geographical scale of policy, conservation and management decisions (i.e. Northern France coastline), using multivariate analyses combined with the Direct Field Observation (DFO) method. From the upper to the lower shores, the majority of the beaches exhibited three macrobenthic communities confirming the existence of the tripartite biological division of the shore. Nevertheless, in some cases, two or four zones were found: (1) two zones when the drying zone located on the upper shore was replaced by littoral rock or engineering constructions and (2) four zones on beaches and estuaries where a muddy-sand community occurred from the drift line to the mid shore. The correspondence between this zonation pattern of macrobenthic communities and the EUNIS habitat classification was investigated and the results were mapped to provide a reference state of intertidal soft-sediment beaches and estuaries. Our results showed evidence of the applicability of this EUNIS typology for the beaches and estuaries at a regional scale (Northern France coastline) with a macroecological approach. In order to fulfil the requirements of the European Directives (WFD and MFS), this mapping appears as a practical tool for any functional study on these coastal ecosystems, for the monitoring of anthropogenic activities and for the implementation of management plans concerning effective conservation strategies.

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## 1. Introduction

The world's shoreline, interface between land and ocean, is dominated by sandy shores that are physically dynamic habitats (two-thirds of the world's ice-free coastlines according to McLachlan and Brown (2006)). These zones are of a prime importance

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for many animals since they provide permanent or transitory key habitats for zooplankton, macrofauna, insects, fishes, turtles or shorebirds for reproduction, nurseries, migration or feeding (Schlacher et al., 2008; Defeo et al., 2009; Schlacher et al., 2014a). Almost every beach on every coastline are threatened by some form of human activity (Brown and McLachlan, 2002); threats to sandy beach ecosystems range from the local spatio-temporal scale (e.g. weekly or seasonal recreational activities) to the global one (e.g. climate change; Defeo et al., 2009); as stressed by Schlacher et al. (2007), “sandy beaches are at the brink”.

Because these unique ecosystems are facing intensifying

anthropogenic pressures, Schlacher et al. (2007) stated that the continued existence of beaches as functional ecosystem is likely to depend on direct conservation efforts. The same conclusions were previously reached by McLusky and Elliott (2004) concerning the other major soft sediment areas in temperate regions, i.e. estuaries. In this framework, an ecological theory has to be developed and critical research directions required to improve sandy beach ecosystems management and conservation have been identified (Schlacher et al., 2007). Setting specifically-derived conservation targets for most ecosystems is a common practice; however, this has never been done for sandy shores (i.e. sandy beaches and estuaries; Harris et al., 2014a). Because of the complexity of ecosystems and hence biodiversity, surrogates approaches such as sub-sets of species, species assemblages and habitat typologies have to be used and plotted as measures of biodiversity (Pressey, 2004; Banks and Skilleter, 2007). Higher precision in the measurement and mapping of biodiversity across regions and biomes is an urgent need to improve systematic conservation planning (Margules and Pressey, 2000). In this context, species assemblages and/or habitat typologies appear as an appropriate surrogate for biodiversity estimation, but it needs to be mapped at a relevant scale that is sufficiently fine to be effective in a reserve design process and conservation (Harris et al., 2011). Mapping macrobenthic communities thus emerges as an essential initial step and a fundamental baseline for managing and conserving soft sediment intertidal areas (Shumchenia and King, 2010). As a prerequisite, multiple classification schemes have been developed internationally in an attempt to systematically classify habitats in different marine environments: e.g. NOAA (Allee et al., 2000) and CMES (Madden and Grossman, 2004) for the USA; the temperate benthic component of hierarchical classification scheme for Canada (Roff and Taylor, 2000); the national marine habitat classification scheme for Britain and Ireland (Connor et al., 2004); the EUNIS habitat classification for Europe (Davies et al., 2004) and the CSIRO Marine Research hierarchical scheme for habitat mapping and classification for Australia (CMR and DEP, 2002).

Intertidal soft-sediment macrofauna have long been known to show zonation patterns (Bally, 1983; McLachlan, 1990; Defeo et al., 1992; McLachlan and Jaramillo, 1995; Brazeiro, 1999; Raffaelli and Hawkins, 1999; Degraer et al., 2003; Rodil et al., 2006). The prime causes of zonation across a sandy beach are exposure, changing wave energy levels, sediment water content, grain size, beach slope and stability (Knox, 2001; Schlacher and Thompson, 2013a). These zones, with their associated fauna, shift with tides, storms and accretion/erosion cycles. Therefore, communities do not occupy fixed discrete area and/or time periods (Brazeiro and Defeo, 1996; Degraer et al., 1999). Thus, these areas are difficult to define in terms of tidal levels (Knox, 2001), notable exceptions being the sheltered shores and estuaries where zonation reflects biological responses to salinity gradient and its associated gradient of particle size (Raffaelli and Hawkins, 1999). Schlacher and Thompson (2013b), in a synopsis of the global literature, showed that most studies recognise a tripartite biological division of the shore, whereas Defeo and McLachlan (2005) characterised macroscale pattern (biogeographic pattern in community and populations) and mesoscale patterns (i.e. variations within a single beach). Thrush et al. (2005) stated that it is an issue of scale to represent all relevant habitats/communities in a meaningful way. A large scale analysis may not be suitable to describe habitats/communities efficiently in every regional area; a specific analysis at a regional scale is therefore necessary (Schiele et al., 2014) with temporal data on a large time window to get a full picture of zonation patterns (Haynes and Quinn, 1995; Defeo and McLachlan, 2005; Schlacher and Thompson, 2013b). In the present study, the existence of such a pattern in sandy beaches and estuaries communities zonation was therefore investigated at a regional spatial

scale (coastline length: 140 kms) corresponding to a geographical scale relevant for policy, conservation and management decisions (i.e. French county coastline). A macroecological approach is required to achieve such a goal (Brown, 1995; Gaston and Blackburn, 2000). In a research programme perspective, Brown et al. (2003) emphasised the focus of macroecology on trying to describe and explain the statistical phenomenology of ecologically informative variables among large number of species abundances within communities. The basis of the macroecological approach is to develop an understanding of complex systems through the study of the emergent properties of such systems in their entirety (MacArthur, 1972; Brown, 1995), but at the relevant spatio-temporal scales to reveal it (Luczak, 2012).

In order to fulfil the requirements of the European Marine Strategy Framework Directive (MSFD), each European Union member State has to identify its biotope within a common classification system (Schiele et al., 2014). A joint European reference set of habitat units with both a common description and hierarchical classification was therefore required to report habitat/community data in a comparable manner for use in nature conservation and management (Evans, 2012). The EUNIS habitat classification has been designed to achieve these purposes (Davies et al., 2004), although many studies faced difficulties with the applicability of the EUNIS system in the field (e.g. Galparsoro et al., 2012; Schiele et al., 2014). From the intertidal soft-sediment zonation and communities previously identified and described in the macroecological approach, it can be tested whether there is a reliable correspondence with the EUNIS habitats/communities.

Mapping intertidal macrobenthic communities based on the EUNIS habitat classification at a regional (or larger) spatial scale is a fundamental step and tool for managing and preserving intertidal areas in Europe. Traditional methods using macrofaunal and sediment sampling coupled, for instance, with a geostatistic method (Godet et al., 2009a; Defeo and Rueda, 2002) is unachievable at this scale; the number of samples needed to reliably apply spatial statistics is too huge and out of reach in this context. Furthermore, metrics concerning any type of invertebrate assemblage (meiofauna and macrofauna) are often expensive to use in modern environmental evaluations because of high labour costs incurred during sampling, sorting and identification (Schlacher et al., 2014b) and because of the time available to work in the field is limited to only a few hours during spring tides (Harris et al., 2011). Therefore, to map the macrobenthic communities (EUNIS habitat classification), the Direct Field Observation (DFO) method proposed by Godet et al. (2009a) can be used in combination with a classical macrofaunal and sediment analysis, since Godet et al. (2009a) demonstrated the consistency between the DFO method and the EUNIS classification scheme.

The aims of this paper, at a regional scale (Northern France), were: (1) to test the general model of beach zonation proposed by McLachlan and Jaramillo (1995), supported recently by Schlacher and Thompson (2013b) and to extent analysis to estuaries; (2) to search for a correspondence between the zonation observed and the EUNIS habitat classification (Evans, 2012; Galparsoro et al., 2012); and (3) to map the results to provide a reference state of intertidal soft-sediment beaches and estuaries at the spatial scale of Northern France using a combination of multivariate analysis and the 'DFO method' proposed by Godet et al. (2009a).

Finally, we discussed the protection status of the defined EUNIS communities at the Northern France scale in the frame of a Marine Protected Area (MPA) of 2300 km<sup>2</sup> along 118 km of coastline created in December 2012 under the Water Framework Directive (WFD) and the Marine Strategy Framework Directive (MSFD).

## 2. Materials and methods

### 2.1. Study area

The coastline of the Eastern English Channel and of the Southern Bight of the North Sea (Nord-Pas-de-Calais region, France) is composed of sandy beaches, two major estuaries (the Authie and the Canche estuaries) and two harbours with intertidal areas (Boulogne-sur-Mer and Dunkerque; Fig. 1). The tidal regime is semi-diurnal, macrotidal and decreases from 8.5 m in the Authie estuary to 5.45 m at the Belgium border (SHOM, 1968). Beaches are categorised as fully dissipative in morphodynamic state (McLachlan et al., 1993): the Dean's parameter ( $\Omega$ ; Wright and Short, 1983) is comprised between 5.06 to 7.93, the relative tidal range (RTR; Masselink and Short, 1993) between 9.08 to 14.17 and the Beach State Index (BSI; McLachlan et al., 1993) is always higher than 1.5 (Hequette, personal communication). The upper shores are composed of aeolian dunes between the Authie estuary and the Belgium border with the exception of Boulogne-sur-Mer, the Capes Gris-Nez and Blanc-Nez made up of cliffs (Anthony and Héquette, 2007).

### 2.2. Sampling design

A total of 358 macrobenthos samples were collected during low water of spring tides along the coastline of the study area between 1998 and 2012. Two hundred and five (205) macrobenthos samples were sampled on beaches (in 2002, 2008, 2010 and 2012 depending on sites), 75 in the Canche estuary (in 2000) and 78 in the Authie estuary (in 1998 and 2002; Fig. 2). To investigate the macrofaunal distribution, 3–5 stations were sampled along transects from the upper to the lower shore of each studied beach. For the two estuaries, a stratified random sampling approach was used (Luczak, 2002). All sampling stations were georeferenced using a Global Positioning System (GPS) and were then integrated into a Geographic Information System (GIS).

Before sampling and according to the DFO method (Direct Field Observation), field descriptions, including both abiotic and biotic data were listed: main topographic characteristics (e.g. absence/presence of ripples marks...), sediment characteristics (e.g. texture, oxidation...), vegetation (e.g. algae, phanerogams), animal tracks (e.g. *Lanice conchilega* sand-fringes, *Arenicola marina* faeces or burrows...) and living animals (See Table 1 in Godet et al. (2009a)). A photograph was also taken at each sampling station and macrobenthos samples (three replicates) were then collected with a corer (1/40 m<sup>2</sup> to a depth of 0.25 m) and washed through a

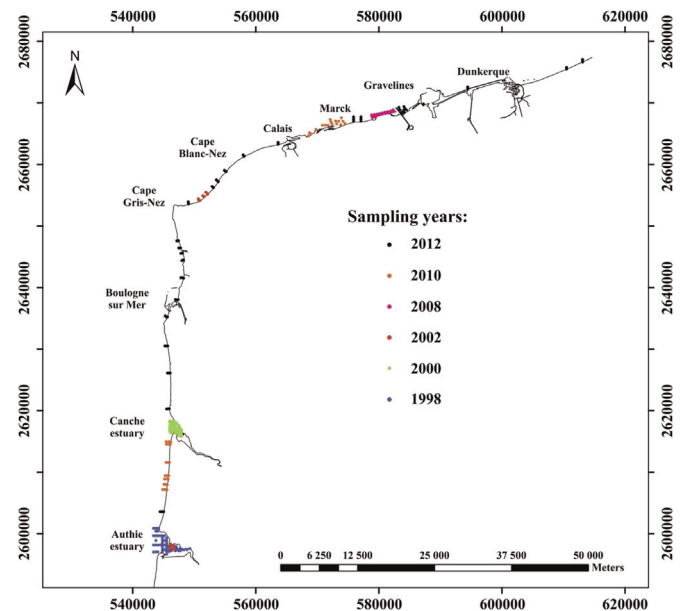


Fig. 2. Location of the stations sampled between 1998 and 2012. Color represent the sampling year.

1 mm mesh sieve. After sieving, all samples were immediately fixed and preserved in an 8% formaldehyde-seawater solution. At each station, one core was also sampled for granulometry analysis.

In the laboratory, the sieved samples were sorted and all macrobenthic organisms were counted and identified to the species level, whenever possible. Faunal densities were expressed as the number of individuals per m<sup>2</sup> (ind m<sup>-2</sup>). Biomass was determined as ash free dry weight (g of AFDW m<sup>-2</sup> after 6 h drying at 520 °C) for each station (ICES, 1986). Granulometry was analysed by dry sieving through a nested series of sieves with mesh sizes decreasing from 0.05 to 5 mm. Sediment grain size was classified in six categories: mud < 0.05 mm, fine sands [0.05–0.2], medium sands [0.2–0.5], coarse sands [0.5–2], fine gravels [2–5] and coarse gravels [5–20] according to the Larsonneur classification (1977).

### 2.3. Community analysis

Macrobenthic assemblages were identified following the methods recommended by Clarke and Warwick (2001). Average agglomerative clustering and non-metric multidimensional scaling (nMDS) were used on the basis of Bray–Curtis similarity matrices from 4th root transformed species density data and based on a data set with 347 samples and 108 taxa. Groups identified by cluster analysis were used as a first step to detect large macrobenthic communities. In a second step, the ‘Direct Field Observation’ DFO method (Godet et al., 2009a) was applied to investigate more precisely the obtained groups. ANOSIM randomisation test (Clarke and Green, 1988) was then performed to test the spatial differences in community structure along the coastline of the study site. Discriminating species, which significantly ( $p < 0.05$ ) contributed to segregate the different communities were identified using the similarity percentage routine (SIMPER). All analyses were performed with the Plymouth Routines in Multivariate Research (PRIMER<sup>®</sup>) software version v6 (Clarke and Gorley, 2006).

Mean densities, biomasses, species richness and sediment grain size categories (%) were calculated for each defined macrobenthic community. Kruskal–Wallis tests were finally performed to test differences ( $p < 0.05$ ; Zar, 2014) in densities, biomasses and species richness between macrobenthic communities. If differences were significant, multiple comparisons tests (post-hoc tests)

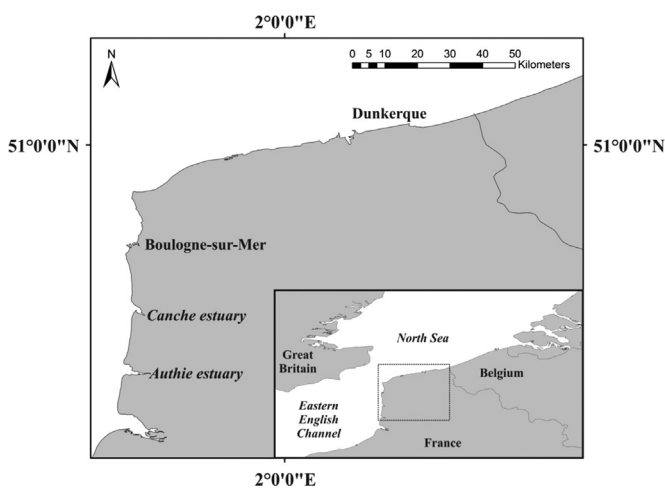


Fig. 1. Location of the study area.

**Table 1**  
 Characterisation of the identified macrobenthic communities: characterising species (%), the five most abundant species (%), densities (ind m<sup>-2</sup> ± SD), biomasses (g m<sup>-2</sup> ± SD), species richness (number of species ± SD), cover (km<sup>2</sup>), location, zonation on the shore, wave exposure and the correspondence between the identified communities and the EUNIS habitat classification (code and name). The common species between our identified communities and the EUNIS habitat classification are in bold.

Group	Identified community	Characterising species (%)	Most abundant species (%)	Densities (ind m <sup>-2</sup> ) ± SD	Biomasses (g m <sup>-2</sup> ) ± SD	Species richness ± SD	Cover (km <sup>2</sup> )	Location	Zonation	Wave exposure	EUNIS Code	EUNIS Classification	Characterising species EUNIS
1	<i>Scolecipis squamata</i> / <i>Eurydice pulchra</i> / <i>Bathyporeia</i> spp.	<b><i>Scolecipis squamata</i></b>	41 <i>Scolecipis squamata</i>	30	983 ± 1449	2.17 ± 3.70	5.3 ± 2.6	30.45	Beaches, bays	Mid-shore	Exposed	A2.223 Amphipods and <i>Scolecipis</i> spp. in littoral medium-fine sand	<b><i>Scolecipis squamata</i></b>
		<b><i>Eurydice pulchra</i></b>	17 <i>Eurydice pulchra</i>	19									<b><i>Eurydice pulchra</i></b>
		<b><i>Haustorius arenarius</i></b>	12 <i>Bathyporeia pilosa</i>	15									<b><i>Bathyporeia pilosa</i></b>
		<b><i>Bathyporeia pilosa</i></b>	10 <i>Bathyporeia sarsi</i>	9									<b><i>Haustorius arenarius</i></b>
		<i>Bathyporeia sarsi</i>	9 <i>Haustorius arenarius</i>	6									
2	<i>Nephtys cirrosa</i> / <i>Scolecipis squamata</i> / <i>Crangon crangon</i>	<b><i>Nephtys cirrosa</i></b>	48 <i>Spio martinensis</i>	30	682 ± 1835	6.59 ± 14.79	6.5 ± 3.6	55.90	Beaches, bays	Low-shore	Exposed	A2.23 Polychaete/Amphipod-dominated fine sand shores	<b><i>Nephtys cirrosa</i></b>
		<i>Scolecipis squamata</i>	14 <i>Nephtys cirrosa</i>	10									<b><i>Spio martinensis</i></b>
		<b><i>Crangon crangon</i></b>	7 <i>Bathyporeia pelagica</i>	6									<b><i>Crangon crangon</i></b>
		<b><i>Spio martinensis</i></b>	6 <i>Scolecipis squamata</i>	5									<b><i>Bathyporeia pelagica</i></b>
		<b><i>Bathyporeia pelagica</i></b>	6 <i>Urothoe poseidonis</i>	5									
3	<i>Peringia ulvae</i> / <i>Pygospio elegans</i> / <i>Macoma balthica</i>	<b><i>Peringia ulvae</i></b>	27 <i>Peringia ulvae</i>	57	6774 ± 11239	21.59 ± 72.36	6.3 ± 2.7	10.43	Beaches, bays	Upper and mid-shore	Moderately exposed, sheltered	A2.24 Polychaete/Bivalve-dominated muddy sand shores	<b><i>Pygospio elegans</i></b>
		<b><i>Corophium arenarium</i></b>	19 <i>Corophium arenarium</i>	12									<b><i>Peringia ulvae</i></b>
		<i>Bathyporeia pilosa</i>	14 <i>Pygospio elegans</i>	11									<i>Macoma balthica</i>
		<b><i>Pygospio elegans</i></b>	12 <i>Bathyporeia pilosa</i>	4									<i>Cerastoderma edule</i>
		<i>Eurydice affinis</i>	8 <i>Macoma balthica</i>	2									<b><i>Corophium arenarium</i></b>
4	Diptera larvae	<i>Diptera larvae</i>	47 <b><i>Oligochaeta</i></b>	45	124 ± 352	0.09 ± 0.17	0.8 ± 0.8	4.08	Beaches, bays	Upper-shore	Exposed, sheltered	A2.21 Strandline	<b><i>Oligochaeta</i></b>
		<i>Pygospio elegans</i>	33 <i>Pygospio elegans</i>	8									<i>Talitrus saltator</i>
		<i>Eurydice pulchra</i>	19 <i>Eurydice pulchra</i>	8									
			<i>Scolecipis squamata</i>	7									
	<i>Diptera larvae</i>	2											
5	<i>Pygospio elegans</i> / <i>Corophium arenarium</i>	<b><i>Pygospio elegans</i></b>	17 <i>Corophium arenarium</i>	30	4749 ± 3698	12.80 ± 10.81	17.5 ± 4.9	1.08	Harbours	Mid-shore	Sheltered	A2.242 <i>Cerastoderma edule</i> and Polychaete in littoral muddy sand	<b><i>Cerastoderma edule</i></b>
		<i>Corophium arenarium</i>	16 <i>Pygospio elegans</i>	28									<b><i>Macoma balthica</i></b>
		<b><i>Macoma balthica</i></b>	13 <i>Capitella capitata</i>	13									<b><i>Pygospio elegans</i></b>
		<i>Nephtys cirrosa</i>	9 <i>Lanice</i>	6									<i>Capitella capitata</i>

Table 1 (continued)

Group	Identified community	Characterising species (%)	Most abundant species (%)	Densities (ind m <sup>-2</sup> ) ± SD	Biomasses (g m <sup>-2</sup> ) ± SD	Species richness ± SD	Cover (km <sup>2</sup> )	Location	Zonation	Wave exposure	EUNIS Code	EUNIS Classification	Characterising species EUNIS
		<i>Cerastoderma edule</i>	6 conchilega Macoma balthica	5									<i>Scoloplos armiger</i>
6	<i>Corophium arenarium</i>	<i>Corophium arenarium</i>	100 Corophium arenarium Diptera larvae	57	0.07 ± 0.09	2.0 ± 1.4	0.28	Beaches	Upper-shore	Moderately exposed	A2.244	<i>Bathyporeia pilosa</i> and <i>Corophium arenarium</i> in littoral muddy sand	<i>Bathyporeia pilosa</i> <i>Corophium arenarium</i> <i>Peringia ulvae</i>
7	<i>Lanice conchilega</i>	<i>Lanice conchilega</i> <i>Nephtys cirrosa</i>	53 15 9 6 2 2 Nephtys cirrosa	82	5.17 ± 8.27	7.1 ± 4.7	0.85	Beaches, bays	Mid and low-shore	Moderately exposed, sheltered	A2.245	<i>Lanice conchilega</i> in littoral sand	<i>Lanice conchilega</i> <i>Scoloplos armiger</i> <i>Phyllodoce mucosa</i> <i>Pygospio elegans</i>

proposed by Siegel and Castellan (1988) were performed ( $p < 0.05$ ). All analyses were performed using R<sup>®</sup> (R Core Team, 2013).

#### 2.4. Allocation to the EUNIS classification and mapping

Macrobenthic communities identified through multivariate and statistical analyses and coupled with the DFO method were then characterised according to the EUNIS habitat classification (levels 4 and 5; Connor et al., 2004; Davies et al., 2004). To reach this goal, a comparison was performed regarding distribution pattern on the shore, sediment grain size, densities, biomasses, species richness and discriminating species.

The EUNIS habitat classification was developed in response to the implementation of the “Habitats Directive” of the European Union and aims to become the reference typology of habitats in Europe. It is organised in 6 hierarchical levels and was initially based on the “Marine Habitat Classification for Britain and Ireland” (Connor et al., 2004; Davies et al., 2004; Galparsoro et al., 2012). At level 1, habitats are distributed among marine habitats (code A) and other (terrestrial and freshwater habitats). The level 2 distinguishes marine habitats depending on the type of substrate (sediment or rock), depth and permanent or non-permanent immersion (e.g. A2 for coastal sediments). The level 3 allows classifying according to the abiotic conditions (e.g. nature of sediment, exposure or hydrodynamic energy, salinity: A2.2 for littoral sands or muddy-sands). At level 4, the classification is based on the biocenosis (the present fauna such as Polychaetes, Amphipods, and Bivalves...; e.g. A2.23 for “Polychaete/Amphipod-dominated fine sand shores”). At the levels 5 and 6, the resolution further increases in the description of the habitat with the macrobenthic species (e.g. at level 5 with A2.223 for “Amphipods and *Scolecopsis* spp. in littoral medium-fine sand” and at level 6 with A2.2232 for “*Eurydice pulchra* in littoral mobile sands”). We sought to allocate the macrobenthic communities at the finest hierarchical level.

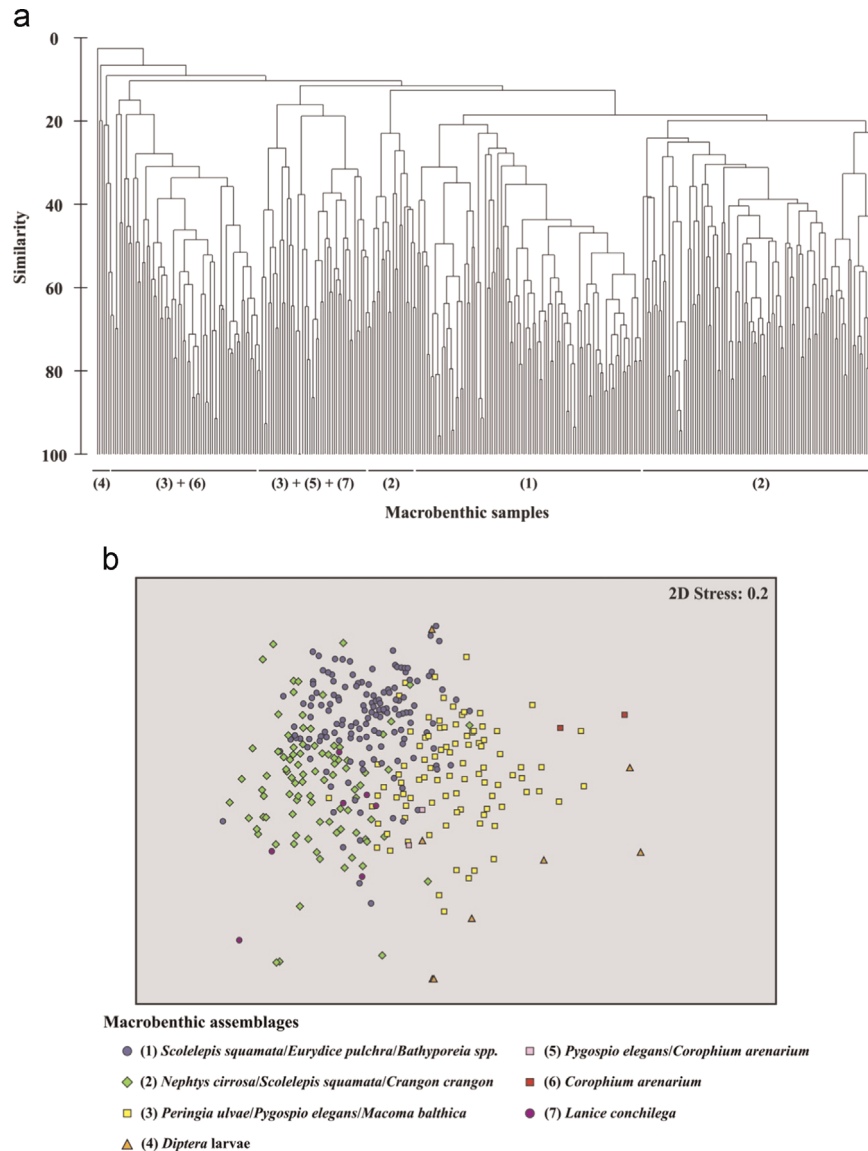
The final mapping of the macrobenthic communities of the sandy shores in the Eastern English Channel and the Southern Bight of the North Sea was performed using aerial photographs (©Ortho Littorale 2000) coupled with a GIS (Geographic Information System) software (ArcGIS 10<sup>®</sup>). From this mapping, areas occupied by each identified macrobenthic communities were calculated based on the surface of the beach during low waters of spring tides.

### 3. Results

#### 3.1. General description of the intertidal macrofauna

A total of 108 species was identified on the sandy shores of the study area (Appendix). With 45 species (42% of the macrobenthic species), Crustaceans were the dominant taxon: Amphipods represented 20% of the macrobenthic species (22 species), Decapoda 11% (12 species), Isopoda 5% (5 species), Cumacea 4% (4 species) and Mysidacea 2% (2 species). Polychaetes were the second taxa in number with 36 species (33% of the macrobenthic species); Molluscs were represented by 19 species (18%), Echinoderms 2 species (2%), Pycnogonids 1 species (1%), fishes 1 species (1%) and Insects, Nemertea, Nematoda and Oligochaeta 4 species (4%).

Densities ranged from 0 to 55,699 ind m<sup>-2</sup> with a mean of  $2422 \pm 6458$  ind m<sup>-2</sup> (mean ± SD). Samples with the lowest densities were located at the highest tidal levels (along the dunes) whereas the highest macrobenthic densities were found in estuaries and sandy beaches with muddy-sand. The highest biomasses were mainly found in estuaries and in the lower shores with a maximum of  $470 \text{ g m}^{-2}$  and a mean of  $8 \pm 37 \text{ g m}^{-2}$  for the entire study area. Species richness ranged from 0 to 21 species by station with a mean of  $5.7 \pm 3.3$  species.



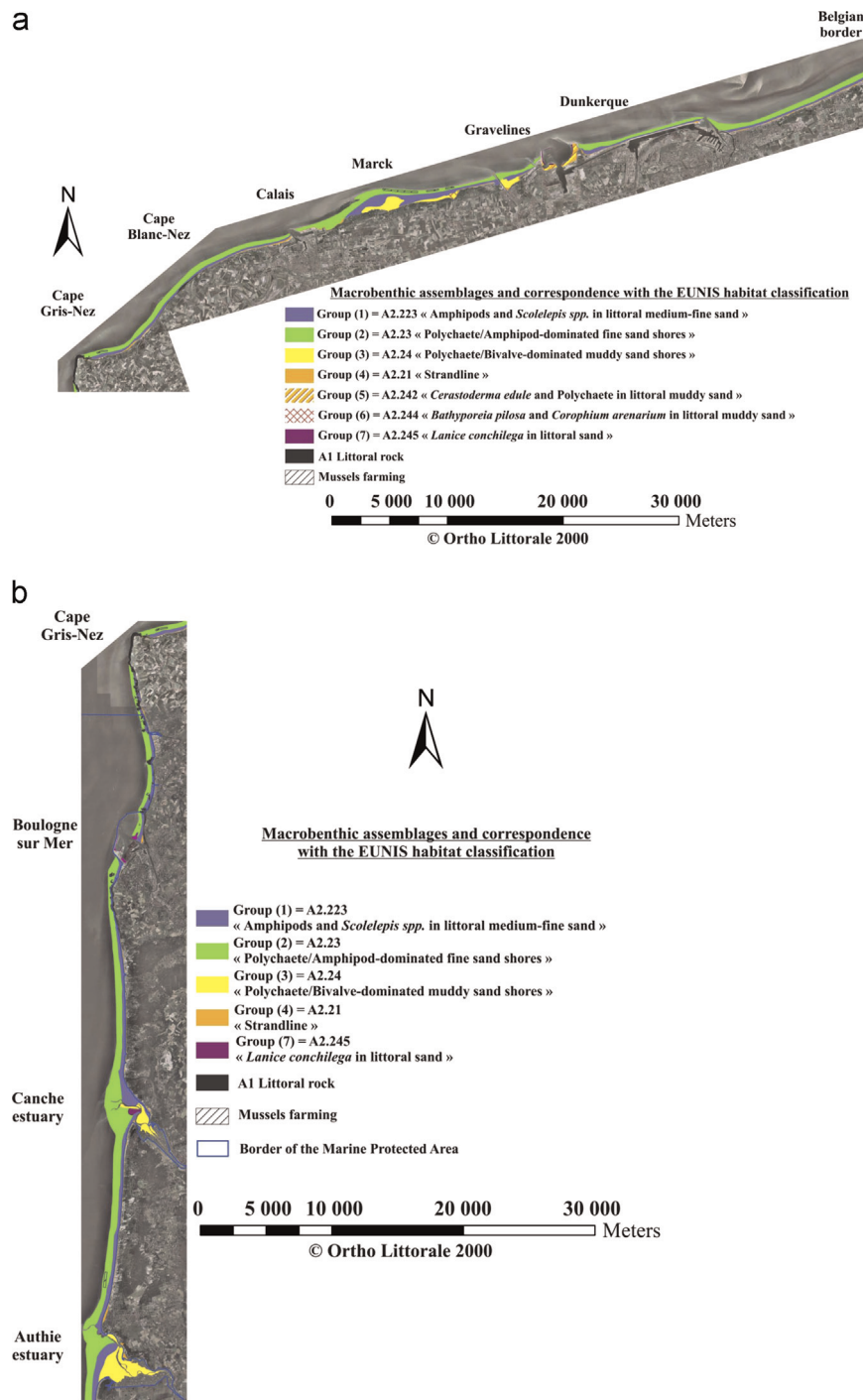
**Fig. 3.** (a) Dendrogram of the average agglomerative clustering and (b) Multidimensional scaling ordination performed on the basis of Bray–Curtis similarity matrix calculated from the 4th root transformed species density data of 347 stations and 108 taxa. Assemblages obtained by multivariate analyses were then combined with the DFO method (Godet et al., 2009a). This procedure distinguished seven macrobenthic communities: Group (1) *Scolecipis squamata*/*Eurydice pulchra*/*Bathyporeia* spp., group (2) *Nephtys cirrosa*/*Scolecipis squamata*/*Crangon crangon*, group (3) *Peringia ulvae*/*Pygospio elegans*/*Macoma balthica*, group (4) *Diptera* larvae, group (5) *Pygospio elegans*/*Corophium arenarium*, group (6) *Corophium arenarium* and group (7) *Lanice conchilega*.

### 3.2. Zonation patterns of macrofauna of the sandy shores

Based on the multivariate analyses combined with the biotic and abiotic parameters directly observed on the field (DFO method), used in a second step to determine more precisely the groups obtained in space, the dendrogram of the average agglomerative clustering (Fig. 3a) and the nMDS (Fig. 3b) distinguished seven macrobenthic assemblages (MDS stress 0.2; ANOSIM 0.42;  $p < 0.001$ ; Fig. 3). SIMPER analysis revealed the species primarily contributing to the observed pattern and helped to determine whether an assemblage was a distinct community or not. Cluster and MDS assemblages were therefore described with their most contributing species: (group 1) *Scolecipis squamata*/*Eurydice pulchra*/*Bathyporeia* spp community, (group 2) *Nephtys cirrosa*/*Scolecipis squamata*/*Crangon crangon* community, (group 3) *Peringia ulvae*/*Pygospio elegans*/*Macoma balthica* community, (group 4) *Diptera* larvae community, (group 5) *Pygospio elegans*/*Corophium arenarium* community, (group 6) *Corophium arenarium* community and (group 7) *Lanice conchilega* community.

Each sampling station was then allocated to a macrobenthic assemblage. As the location on the shore was known for each sampling station, the number of communities found on beaches and/or estuaries can be directly determined.

Based on these results, three main communities were recognised from the upper to the lower shore on most beaches (Fig. 4a and b). Stations sampled in the upper beach (supralittoral zone) were assigned to the *Diptera* larvae community (group 4) and stations sampled in the mid shore (from the drift line down to the mid shore) to the *Scolecipis squamata*/*Eurydice pulchra*/*Bathyporeia* spp community (group 1). Stations sampled in the lower shore were characterised by the *Nephtys cirrosa*/*Scolecipis squamata*/*Crangon crangon* community (group 2). Some beaches displayed two or four communities from the upper to the lower shore. In the case of two only communities, the *Diptera* larvae



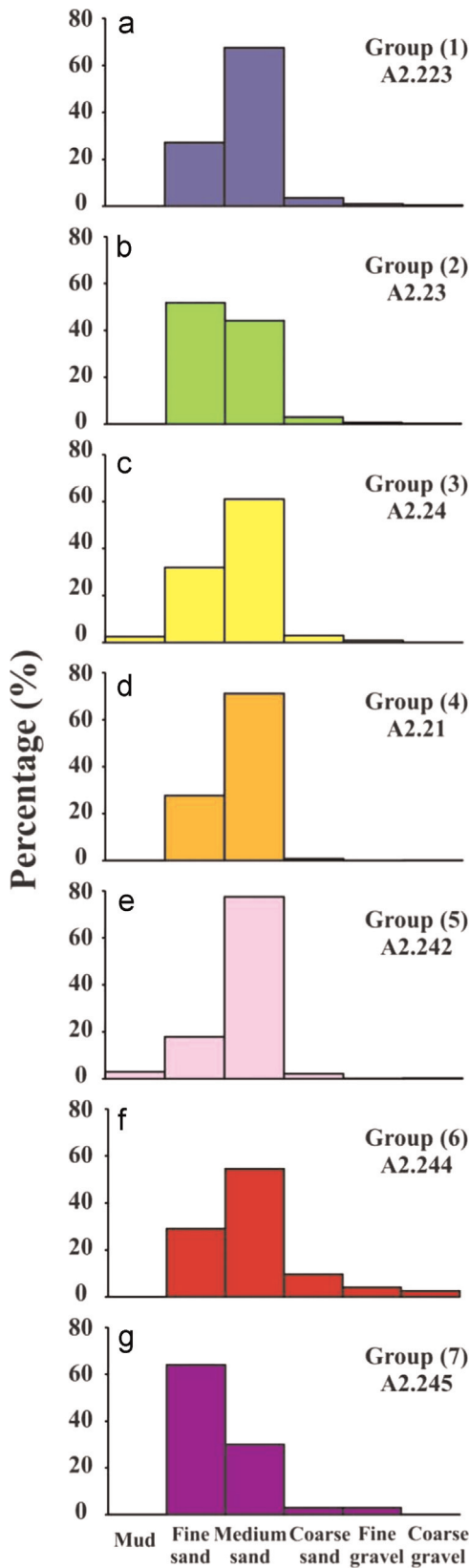
**Fig. 4.** (a) Map of the macrobenthic communities of the sandy shores in the Southern Bight of the North Sea (France) from the Cape Gris-Nez to the Belgium border according to the previous assemblages identified ("groups") and the correspondence with the EUNIS habitat classification. (b) Map of the macrobenthic communities of the sandy shores along the Eastern English Channel (Nord–Pas-de-Calais region, France) from the Authie estuary to the Cape Gris-Nez according to the previous assemblages identified ("groups") and the correspondence with the EUNIS habitat classification. The Marine Protected Area is bounded by the blue line and extends seaward. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

community was absent and replaced by littoral rock. In the second case, a fourth community was found from the drift line to the mid shore: the *Peringia ulvae*/*Pygospio elegans*/*Macoma balthica* community (group 3).

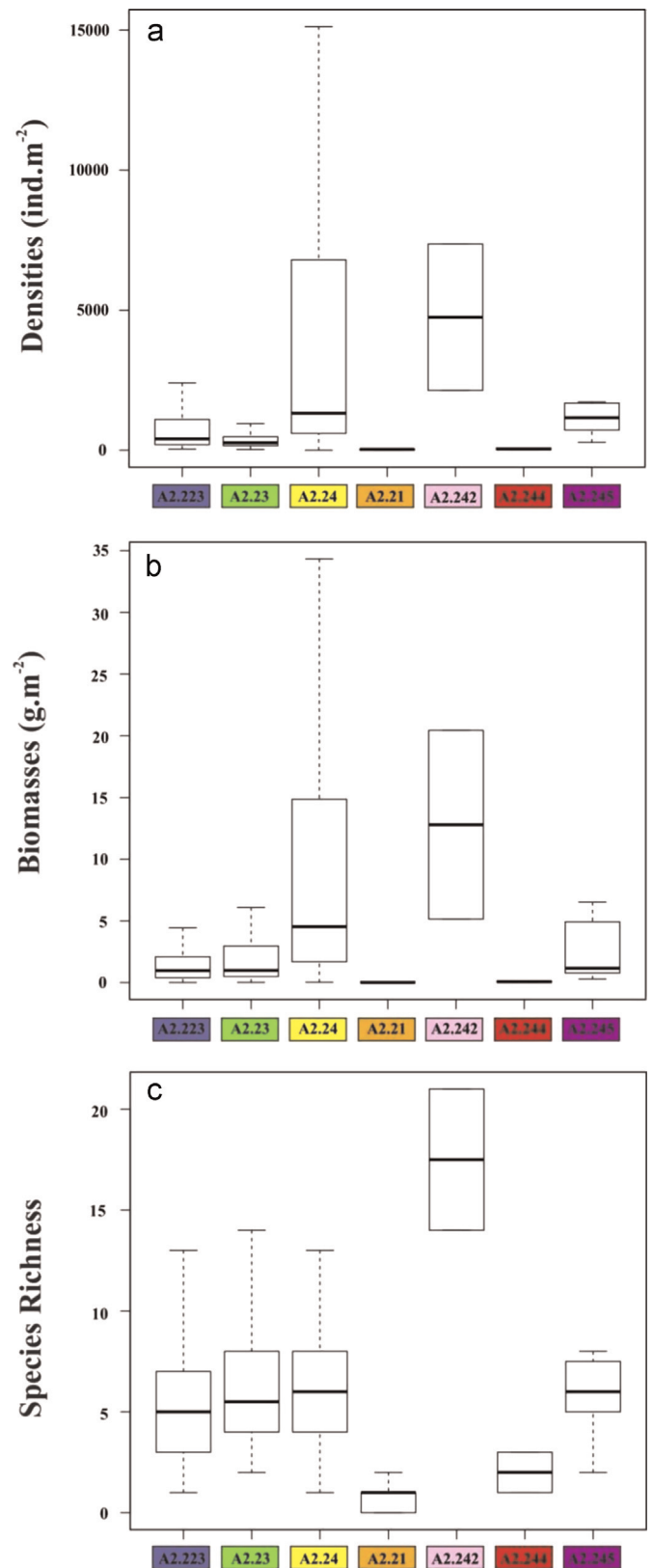
In estuaries (Canche estuary and Authie estuary), four communities were identified (Fig. 4b). From the high to the low intertidal zones of these estuaries were observed: the *Diptera* larvae community (group 4), the *Peringia ulvae*/*Pygospio elegans*/*Macoma balthica* community (group 3), the *Scolecipis squamata*/*Eurydice pulchra*/*Bathyporeia* spp

community (group 1) and the *Nephtys cirrosa*/*Scolecipis squamata*/*Crangon crangon* community (group 2). A fifth assemblage, characterised by the *Lanice conchilega* community (group 7), was also found in the middle of the Canche estuary.

In harbours (Dunkerque and Boulogne-sur-Mer; Fig. 4a and b), three macrobenthic assemblages were also recognised; the *Diptera* larvae community (group 4), the *P. elegans*/*C. arenarium* community (group 5) and the *Lanice conchilega* community (group 7) were observed from the upper to the lower shores.



**Fig. 5.** Sediment characteristics (%): contents in mud, fine sand, medium sand, coarse sand, fine gravel and coarse gravel for each defined macrobenthic community (“groups”) and the correspondence with the EUNIS habitat classification (i.e A2.223 “Amphipods and *Scolecipis* spp. in littoral medium-fine sand”, A2.23 “Polychaete/Amphipod-dominated fine sand shores”, A2.24 “Polychaete/Bivalve-dominated muddy sand shores”, A2.21 “Strandline”, A2.242 “*Cerastoderma edule* and Polychaete in littoral muddy sand”, A2.244 “*Bathyporeia pilosa* and *Corophium arenarium* in littoral muddy sand” and A2.245 “*Lanice conchilega* in littoral sand”).



**Fig. 6.** Box-Whisker plots showing the range of all 7 communities for: (a) densities (ind m<sup>-2</sup>), (b) biomasses (g m<sup>-2</sup>) and (c) species richness. Box-Whisker plots indicate median, minimum, maximum, lower and upper quartiles.



### 3.3. Correspondence between intertidal zonation patterns and the EUNIS habitat classification

The first assemblage “*Scolelepis squamata/Eurydice pulchra/Bathyporeia spp* community” (group 1 in Table 1) was located on the mid shore of all the exposed beaches of the study area, including the mouth of the Authie and Canche estuaries but was absent from harbours (Fig. 4a and b, in blue). This community covered 30.45 km<sup>2</sup> (Table 1) and presented a dominance of medium (68%) and fine sand (27%, Fig. 5a). Densities were  $983 \pm 1449$  ind.m<sup>-2</sup>, biomasses  $2.17 \pm 3.70$  g.m<sup>-2</sup> and species richness of  $5.3 \pm 2.6$  (Table 1; Fig. 6). A total of 60 species was sampled in this community that was characterised by five species which were also the most abundant: the polychaete *Scolelepis squamata* (41%), the isopods *Eurydice pulchra* (17%) and by three Haustoriid amphipods (a total of 31% for *Haustorius arenarius*, *Bathyporeia pilosa* and *sarsi*). According to the level 5 of the EUNIS habitat classification, this community was assigned to the Amphipods and *Scolelepis spp.* in littoral medium-fine sand (A2.223; Fig. 4a and b, in blue).

The “*Nephtys cirrosa/Scolelepis squamata/Crango crangon* community” (group 2 in Table 1) was spread over the entire study area except in harbours and extended from the mid to the lower shore (Fig. 4a and b, in green). It covered the greatest area of the sandy shore with 55.9 km<sup>2</sup> (Table 1). Sediment was mainly characterised by fine (52%) and medium sand (44%), mud was absent (Fig. 5b). This community exhibited a mean species richness of  $6.5 \pm 3.6$  with a total of 80 species identified, a mean density of  $682 \pm 1835$  ind m<sup>-2</sup> and a mean biomass of  $6.59 \pm 14.79$  g m<sup>-2</sup> (Table 1; Fig. 6). The five characterising species contributing to the community were: *Nephtys cirrosa* (48%), *Scolelepis squamata* (14%), the brown shrimp *Crango crangon* (7%), *Spio martinensis* (6%) and the Haustoriid amphipod *Bathyporeia pelagica* (6%, Table 1). This community was assigned to the Polychaete/Amphipod-dominated fine sand shores (A2.23; Fig. 4a and b, in green) according to the level 4 of the EUNIS habitat classification.

The third group “*Peringia ulvae/Pygospio elegans/Macoma balthica* community” (group 3 in Table 1) was mainly found in the upstream intertidal zone of the two estuaries (Canche and Authie; Fig. 4b, in yellow) and was also present from the upper to the mid shores of two moderately exposed beaches located between Calais and Dunkerque (i.e. Marck and Gravelines; Fig. 4a, in yellow); this group covered 10.43 km<sup>2</sup> (Table 1). Sediment was composed of medium sand (61%), fine sand (32%) and contained 3% of mud (Fig. 5c). Mean densities and biomasses were highly variable among samples but were significantly superior to the A2.223 and A2.23 communities (Table 1; Multiple Comparisons tests after KW  $p < 0.05$ ; Fig. 6a and b). A total of 37 species was identified and the species richness was  $6.3 \pm 2.7$  species. The discriminating species were the gastropod *Peringia ulvae* (27%), the crustacean amphipods *Corophium arenarium* (19%) and *Bathyporeia pilosa* (14%) and the worm *Pygospio elegans* (12%). The Baltic tellin *Macoma balthica* represented 2% of the total abundance (Table 1). This community was assigned to Polychaete/Bivalve-dominated muddy sand shores (A2.24 according to the level 4 of the EUNIS habitat classification; Fig. 4a and b, in yellow).

The fourth assemblage, corresponding to the *Diptera* larvae community (group 4 in Table 1), was located at and above the drift line (upper shore; Fig. 4a and b, in orange) on the entire study site (surface of 4.08 km<sup>2</sup>) but was sometimes replaced by littoral rock (Fig. 4a and b, in grey). Medium sand dominated the upper beach with 71%, fine sand with 28% and 1% of coarse sand (Fig. 5d). It presented the lowest species richness (a mean of 0.8 species, 16 species recorded in total) but also the lowest densities and biomasses (Table 1; Fig. 6; Multiple comparisons tests after KW  $p < 0.05$ ). Macrobenthic samples from this community were often azoic or with a single species (and only a few individuals). *Diptera*

larvae mainly contributed to the formation of this assemblage (47%). This community was assigned to the strandline (A2.21 according to the level 4 of the EUNIS habitat classification; Fig. 4a and b, in orange).

The fifth group “*Pygospio elegans/Corophium arenarium* community” (group 5 in Table 1) was only located in the mid shore of the intertidal area in Dunkerque harbour (sheltered zone) and covered 1.08 km<sup>2</sup> (Fig. 4b; hatched red/orange; Table 1). Medium and fine sand (77% and 18% respectively) characterised the sediment of this community; mud was also present with 2% (Fig. 5e). Although this community seemed to present the highest species richness of the study area with  $17.5 \pm 4.9$  species, no significant differences were observed for the species richness between the macrobenthic communities (Table 1; Fig. 6). Species most contributing to the assemblage were *Pygospio elegans* (17%), *Corophium arenarium* (16%), *Macoma balthica* (13%), *Nephtys cirrosa* (9%) and *Cerastoderma edule* (6%; Table 1). This community was assigned to the *Cerastoderma edule* and Polychaete in littoral muddy sand (A2.242 according to the level 5 of the EUNIS habitat classification; Fig. 4a, hatched red/yellow).

The sixth group “*Corophium arenarium* community” (group 6 in Table 1) was only found in the upper shore of one moderately exposed beach situated between Calais and Dunkerque (Fig. 4a, hatched red). It was the only community with a high proportion of coarse sediments (10% of coarse sand, 4% of fine gravel and 3% of coarse gravel; Fig. 5f). Species richness, densities and biomasses were as low as in the “Strandline” community (Multiple Comparisons tests after KW  $p > 0.05$ ; Fig. 6c). The characterising species was the amphipod *Corophium arenarium* (100%) and two other species were also abundant: *Diptera* larvae (29%) and the gastropod *Peringia ulvae* (14%; Table 1). Although *Bathyporeia pilosa* was not sampled during the surveys, the presence of this amphipod in this community was noted at several occasions (Rolet, personal observation). Therefore, this community was assigned to *Bathyporeia pilosa* and *Corophium arenarium* in littoral muddy sand (A2.244 according to the level 5 of the EUNIS habitat classification; Fig. 4a; hatched red).

The last group “*Lanice conchilega* community” (group 7 in Table 1) was located in the lower shores of two harbours (Boulogne-sur-Mer and Dunkerque) and in the centre of the Canche estuary (Fig. 4a and b, in purple). Fine sand dominated the sediment of this community (64%; Fig. 5g). A total of 26 species was identified in this community (on average  $7.1 \pm 4.7$  species). Densities and biomasses were important and highly variable among samples (Table 1; Fig. 6). Discriminating species were *Lanice conchilega* (53%), *Nephtys cirrosa* (15%), *Scolelepis squamata* (9%) and *Spiophanes bombyx* (6%; Table 1). This community was assigned to the *Lanice conchilega* in littoral sand (A2.245 according to the level 5 of the EUNIS habitat classification; Fig. 4a and b; in purple).

## 4. Discussion

For the first time, using multivariate analyses coupled with the DFO method, the zonation patterns of macrofauna in the sandy shores were successfully identified and connected with the EUNIS habitat classification at a regional scale. These EUNIS habitats were then mapped to provide a reference state of the intertidal soft-sediment beaches and estuaries at the scale of Northern France. Such maps are an essential component of systematic conservation planning, which have, to our knowledge, never been done for sandy shores at this spatial scale (Harris et al., 2014a).

### 4.1. Zonation patterns of the sandy shores

Zonation patterns on sandy beaches are a well-described phenomenon of intertidal areas (McLachlan and Jaramillo, 1995). The

main zonation schemes of macrofauna for sandy beaches were proposed by Dahl (1952) and Salvat (1964). Dahl (1952) defined three biological zones focusing on the typical crustacean fauna inhabiting each zone. Salvat (1964) defined four physical zones: drying, retention, resurgence and saturation, each zone characterised by changes in sand moisture content. Since these pioneered works, several zonation patterns of the macrofauna in sandy shores have been highlighted: (1) without a clear zonation (Haynes and Quinn, 1995; Rodil et al., 2006), (2) two zones with air-breathers above the drift line and water breathers below (Fernandes and Soares-Gomes, 2006); three zones focusing mainly on the distribution of crustaceans (Jaramillo et al., 1993; McLachlan and Jaramillo, 1995; Brazeiro and Defeo, 1996; Brazeiro, 1999; Degraer et al., 2003; Aerts et al., 2004; Defeo and McLachlan, 2005; Janssen and Mulder, 2005; Schlacher and Thompson, 2013b; Veiga et al., 2014) and (4) four zones (Salvat, 1964; McLachlan, 1990; Jaramillo and Gonzalez, 1991; Gheskiere et al., 2004).

The location on the shore of each sampling station and their allocation to a macrobenthic community allowed the identification of the number of communities present on beaches, estuaries and harbours of the study site. Thereby, three macrobenthic communities have been identified from the upper to the lower shores of most of the beaches in the study area. This intertidal zonation corresponded to the tripartite biological division found on the main sandy shores of the world (62% of the studies; Schlacher and Thompson, 2013b) and to the general model of beach zonation proposed by McLachlan and Jaramillo (1995). Our data lend broad support to this model in terms of faunistic identity of the zones: the community identified on the upper shore (at and above the drift line), “the Strandline” (A2.21), often azoic or colonised by *Diptera* larvae, Oligochaeta and some air-breathing crustaceans (e.g. *Talitrus saltator*), corresponds to the “supralittoral zone” described by McLachlan and Jaramillo (1995). The second community “Amphipods and *Scolecopsis* spp. in littoral medium-fine sand” is situated on the mid shore, between the drift line to around the effluent line, and corresponds to the “littoral zone” also dominated by amphipods (*Bathyporeia* spp. and *Haustorius arenarius*), isopods (*Eurydice* spp.) and spionid polychaetes (*Scolecopsis squamata*) as underlined by McLachlan and Jaramillo (1995). This macrobenthic community was also found on Belgian dissipative beaches (Degraer et al., 1999, 2003; Van Hoey et al., 2004). The third community assigned to “the Polychaete/Amphipod-dominated fine sand shores” located in the lower shore, extending from near the effluent line into the sublittoral, corresponds to the “sublittoral zone” (McLachlan and Jaramillo, 1995). It was characterised by several species of polychaetes (e.g. *Nephtys cirrosa*, *Spio martinensis*), amphipods and by crustaceans such as crabs and shrimps (e.g. *Crangon crangon*). Moreover, this low intertidal community (A2.23) can be considered as an intertidal extension of a typically subtidal community (the subtidal *Nephtys cirrosa* community in our case, Degraer et al., 1999; 2003; Desroy et al., 2003; Van Hoey et al., 2004).

Harbours within the study area (i.e. Boulogne-sur-Mer and Dunkerque) also exhibited a tripartite biological division, but the identified communities were different due to the sheltered configuration of these sites. On the upper shores, the strandline (A2.21) was detected. Two muddy-sand communities were then observed from the mid to the lower intertidal zone: the *Cerastoderma edule* and Polychaete in littoral muddy sand community (A2.242; mid shore) and the *Lanice conchilega* in littoral sand community (A2.245, lower shore). Even if, as underlined by Schlacher and Thompson (2013b), our results at a regional scale are overall in accordance with the tripartite biological division of the shore proposed by McLachlan and Jaramillo (1995), several exceptions were found locally, i.e. at the scale of beaches. This result is congruent with the horizontal source of variation at scales

of 1000 s of meters described by Veiga et al. (2014).

On the beaches located between Boulogne-sur-Mer and the Cape Gris-Nez, two macrobenthic communities were found: the “Amphipods and *Scolecopsis* spp. in littoral medium-fine sand” community situated on the mid shore and the “Polychaete/Amphipod-dominated fine sand shores” community on the lower shore. On the same type of dissipative beaches (de Panne, Belgium), Degraer et al. (1999) also found two species communities (i.e. the *Scolecopsis squamata*/*Eurydice pulchra* community between the MHS and MT level; the *Nephtys cirrosa* community between the MT and MLWS level) but this result should be interpreted with caution since no sampling was conducted in the subterrestrial fringe (e.g. strandline). In our case, this bipartite biological zonation was due to the absence of the strandline (A2.21) that was replaced by littoral rock (cliffs, boulders and/or pebbles) or by engineering constructions (dykes, seawalls).

On two beaches (Gravelines and Marck) and in the two estuaries (Canche and Authie), four macrobenthic communities were detected with the presence of a muddy-sand community dominated by polychaetes and bivalves (A2.24) located on the upper/mid shore following the strandline (A2.21). A fifth community was also identified in the centre of the Canche estuary in the form of patch: the *Lanice conchilega* in littoral sand (A2.245). Four macrobenthic communities, with similar biotic and abiotic parameters (fauna and sediment grain size), have been identified at the mouth of the Scheldt estuary (NW Europe; Ysebaert et al., 2003). Mudflats are characteristic of the upper shores of sheltered beaches (Knox, 2001). In our study, the muddy areas identified on beaches and outside estuaries are characteristics of flats with gentle slopes and sediments that vary from muddy-sand to muddy deposits predominantly composed of a silt/clay fraction. This specificity gives its ecological singularity and value to these shores, especially for wintering shorebirds (Rolet et al., 2015, in press).

On the sandy shores of the Eastern English Channel and the Southern Bight of the North Sea (Nord—Pas-de-Calais region, Northern France), two, three or four biological divisions were found. These different zonation patterns in sandy beaches showed that the number of biological zones may vary from small to large scales (beaches to regions; Giménez and Yannicelli, 1997; Rodil et al., 2006; Schlacher and Thompson, 2013b; Veiga et al., 2014) and mainly depends on physical factors that controlled the beach morphology (Schlacher and Thompson, 2013a). Many studies have shown that beach face slope was a dominant factor in community composition (McLachlan et al., 1993; Jaramillo and McLachlan, 1993; Rodil et al., 2006). Although all the studied beaches were categorized as fully dissipative in morphodynamic state (McLachlan et al., 1993), when the slopes were comprised between 0.7 and 1.7° (Hequette, personal communication), three biological zones were identified (i.e. A2.21, A2.223 and A2.23) except when the strandline (A2.21) was replaced by littoral rock in the upper shore (i.e. two zones). Nevertheless, four biological zones were identified when the slope of the beach was gentle such as in the “Marck” beach (slope: 0.4°) with the presence of a fourth muddy-sand community (A2.24). These findings support the hypothesis that physical factors are the main structuring components of sandy beach communities, a model that has gained quasi-paradigmatic status in sandy beach ecology (Schlacher et al., 2008; Schlacher and Thompson, 2013a).

It has been also shown that differences in the number of biological zones can be attributed to seasonal variations (Brazeiro and Defeo, 1996; Degraer et al., 1999), to the mobility of the intertidal fauna (McLachlan and Brown, 2006; Veiga et al., 2014) or to changes in the sampling effort and/or methodology (Schoeman et al., 2003; McLachlan and Dorvlo, 2005; Schooler et al., 2014). In our study, macrobenthos sampling has always been conducted following the same methodology (triplicate, corer of 1/40 m<sup>2</sup> to a

depth of 0.25 m, mesh sieve of 1 mm) and during the spring season (low water of spring tides). The different number of biological zones found here should not be attributed to any bias in the sampling methodology and/or to seasonal variations. Nevertheless, even if inter-annual variations might be present because our study was based on data collected over 15 years (1998–2012), this strengthened our results by incorporating community variations in the resulting clusters, which is one of the characteristic of macroecological studies (Brown, 1995; Gaston and Blackburn, 2000). The morphology of each beach and engineering constructions (dykes, seawalls...) are probably of the major components explaining the different biological zones found on the beaches of our study site (i.e. Northern France scale).

Veiga et al. (2014) concluded that zonation of macrofauna across the intertidal area is very variable on exposed sandy beaches (at several spatial scales), making difficult to describe a general pattern. In this case, even classification and ordination (MDS) are not of any help, because of a high degree of subjectivity in their interpretation (Veiga et al., 2014). Here, we showed that multivariate analyses (MDS, cluster) coupled with the DFO method (in a macroecological framework) was a reliable method to identify and describe macrofauna zonation on sandy beaches and estuaries at a regional scale.

#### 4.2. Applicability of the EUNIS classification with zonation patterns of intertidal macrofauna

Macrobenthic communities identified by multivariate analyses combined with the DFO method (Godet et al., 2009a) matched with habitats of the EUNIS classification (Davies et al., 2004) on the French sandy shores of the Eastern English Channel and the Southern Bight of the North Sea. To date and to our knowledge, no study has been conducted to test the applicability of the EUNIS habitat classification with the zonation patterns of intertidal macrofauna. In the English Channel, the EUNIS habitat classification was mainly used in subtidal areas both for direct mapping of observed habitats and for habitat modelling to produce predictive maps of habitat distribution for both research and practical applications (Coltman et al., 2008; Diesing et al., 2009; Coggan and Diesing, 2011; Galparsoro et al., 2012; Delavenne et al., 2013). This classification was initially based on the “Marine Habitat Classification for Britain and Ireland” (Connor et al., 2004) which was most developed in coastal regions where the majority of the data was available (Galparsoro et al., 2012).

Our results showed that dominant habitats could be related to the zonation patterns of intertidal macrofauna at levels 4 and/or 5 of the EUNIS habitat classification. Macrobenthic species which contributed to the similarity of each defined group in our analyses were often the same characterising species described by the EUNIS habitat classification and the “Marine Habitat Classification for Britain and Ireland” (Davies et al., 2004; Connor et al., 2004). When non-characterising species were detected by SIMPER analyses, it was due to an overlap between two macrobenthic communities resulting from a sampling realised at the boundary between two communities (i.e. ecotone; Frontier et al., 2008). Indeed, a high degree of overlap may be due to the transition from a species assemblage to another; transition which is gradual and not abrupt (Ysebaert et al., 2003). Zonation, exposure to wave currents and sediment grain size also matched between our groups and the typology of the EUNIS classification. For example, the description of the “Amphipods and *Scolecopsis spp.* in littoral medium-fine sand” community given by the EUNIS habitat classification matches with biotic and abiotic parameters observed for our “*S. squamata*/*Eurydice pulchra*/*Bathyporeia spp.*” group. Characterising species were the same: *Scolecopsis squamata*, *Eurydice pulchra*, *Bathyporeia pilosa* and *Haustorius arenarius*. This habitat was described as mobile

clean sandy beaches on exposed and moderately exposed shores, occurred mainly on the mid shore, with sediment grain sizes ranging from medium to fine, often with a fraction of coarse sediment (e.g. 68% of medium, 27% of fine and 4% of coarse sand for the A2.223 community of our study site). Nevertheless, assessing the EUNIS typology to the upper shore remained more difficult at a regional scale because of spatial variability at small scales. It is however not surprising, because the macroscopic study that was required to address regional (and global) problems of ecosystems change necessarily trades off the precision of small scale science to seek robust solutions to big problems (Brown, 1995). Some beaches of our study site were composed of medium and fine sand with *Oligochaeta* as infaunal assemblage; corresponding to the “*Oligochaetes in littoral mobile sand*” (A2.222; level 5 of the classification). Others were also constituted of medium to fine sand but with a community of sandhoppers (*Talitrid* amphipods) which occurred where driftlines of decomposing seaweed and other debris accumulated on the strandline (e.g. *Talitrids* on the upper shore and strand-line A2.211; level 5 of the classification). To avoid errors of assessment, we decided to assign the level 4 of the EUNIS habitat classification “Strandline” (A2.21) to the upper shore.

We thereafter identified reasons to explain why all of the macrobenthic communities previously identified could be assigned to a corresponding habitat of the EUNIS classification. Geology, sediments and external forcing (wind, waves, storms and tides) are factors controlling the morphology of the beaches. These factors are similar between the Northern coastline of France and the south-east coastline of Great Britain (Scott et al., 2011; Dauvin, 2012). A common geological history, a common climate (temperate), a same biogeographic entity between the Great Britain and the Northern France (Dauvin, 2012; Luczak and Spilmont, 2012) could be the explanation of the very good match between communities first described and founded in the Great Britain for the EUNIS habitat classification and those identified in the sandy shores of the Northern France.

#### 4.3. On the usefulness of the sandy shore mapping and EUNIS classification for marine conservation and management

Benthic habitat mapping is a fundamental step towards ecosystem-based management, conservation and marine spatial planning (Shumchenia and King, 2010; Pressey, 2004; Harris et al., 2011, 2014a). The present mapping provides a reference state of intertidal soft-sediment beaches and estuaries at the spatial scale of Northern France and is a prerequisite for any functional study of these coastal ecosystems. Since the creation of a Marine Protected Area (MPA) “le Parc Naturel Marin des Estuaires Picards et de la mer d’Opale” (2300 km<sup>2</sup>) along the coasts of Northern France in 2012, our study conducted at a regional scale will also be a practical tool for policy makers, managers and users of the littoral area even if this study was undertaken after the design of the MPA. Estimating and quantifying the protection/conservation status of the defined EUNIS communities at this scale will allow defining effective management and conservation plans for the preservation of the sandy shores.

Approximately half of the intertidal area is included in the MPA (51.73%, Table 2). On the seven identified macrobenthic communities, two muddy-sand communities are not included in the MPA (A2.242 and A2.244). The other macrobenthic communities have more than 50% of their surface included in the MPA: 67% for the strandline (A2.21), 50% for both the Amphipods and *Scolecopsis spp.* in medium-fine sand community (A2.223) and the Polychaete/Amphipod-dominated fine sand community (A2.23), 65% for the muddy-sand community (A2.24 but concerning only the two estuaries) and 68% for the *Lanice conchilega* in littoral sand

**Table 2**

Cover (km<sup>2</sup> and %) of each macrobenthic community into and outside of the Marine Protected Area (MPA). Contribution (%) of the MPA for each macrobenthic community.

Spatial distribution	MPA		OUT MPA		Conservation by the MPA
	Km <sup>2</sup>	%	Km <sup>2</sup>	%	
A2.21	2.74	2.66	1.34	1.30	<b>67</b>
A2.223	15.15	14.70	15.30	14.84	<b>50</b>
A2.23	28.09	27.25	27.81	26.98	<b>50</b>
A2.24	6.76	6.56	3.67	3.56	<b>65</b>
A2.242	–	–	1.08	1.05	<b>0</b>
A2.244	–	–	0.28	0.27	<b>0</b>
A2.245	0.58	0.56	0.27	0.26	<b>68</b>
<b>Total</b>	<b>53.32</b>	<b>51.73</b>	<b>49.75</b>	<b>48.27</b>	

community (A2.245; Table 2).

Contrary to the common perception, a high diversity of species is observed on sandy shores, with many species not found elsewhere such as regional endemic ones (Harris et al., 2014b). These highly adapted invertebrates (i.e. macrofauna species) are part of trophic networks including many vertebrate species (e.g. birds, turtles, fishes, mammals) that are dependent on these sandy shores for feeding and nesting (Schlacher et al., 2014a; Huijbers et al., 2015). Birds are usually the most abundant and diverse vertebrate species encountered in these sandy shores (Burton, 2012). Together with estuaries, sandy beaches with muddy patches are intertidal areas known to be attractive and of prime importance for migratory/wintering shorebirds which feed on macrobenthic organisms (Burger et al., 1997; McLusky and Elliott, 2004; Van de Kam et al., 2004; Spruzen et al., 2008; Spilmont et al., 2009). At our regional scale, this has been demonstrated for the two muddy-sand communities found in Northern France (A2.242 in Dunkerque harbour and A2.244 on the upper zone of a beach between Calais and Dunkerque) which represent an attractive feeding ground for numerous shorebirds during refuelling on their migration route and in winter (Marzec and Luczak, 2005; Rolet et al., in press). However, these sites are not included in the MPA; a risk when planners are forced to use surrogate measures based on broad scale in the design of marine reserve systems (Banks and Skilleter, 2007). Indeed, some habitats or communities will not be represented in the reserve network (Harris et al., 2011). Therefore, management and conservation efforts should be taken to preserve these two muddy-sand communities, as food resources for these species. Even if more than 60% of both the Polychaete/Bivalve in muddy-sand shores (A2.24) and the *Lanice conchilega* in littoral sand (A2.245) communities, known to be “oasis” in the shores for many shorebird species (Godet et al., 2009b; De Smet et al., 2013) are included in the MPA, providing a good protection status for numerous wintering and staging shorebirds, these are restricted to both estuaries.

## 5. Conclusions

The macroecological approach appeared relevant in our study to discover, describe and explain patterns of variations at the regional spatio-temporal scale of observation, i.e. to identify emergent and statistical properties of Complex Adaptive Systems (soft-sediment shore ecosystems in our case; Rombouts et al., 2013). For the first time, the zonation patterns of macrofauna in the sandy shores were connected with the EUNIS habitat classification. All the macrobenthic communities identified by multivariate analyses coupled with the Direct Field Observation (DFO) method (Godet et al., 2009a), were assigned to a biotope of the EUNIS habitat classification. Our results demonstrated that this typology was

suitable to characterise both beaches and estuaries at the Northern France scale. With the implementation of the European Directives (WFD and MFSO), this study should be a major tool to implement management plans for effective conservation strategies (design of MPAs and marine spatial planning) and to monitor anthropogenic activities impacting intertidal areas at the Northern France scale (recreational activities, engineering constructions on the coastline, pollution, aquaculture...). The methodology used could be applied and tested in adjacent areas of Europe shorelines (e.g. the Belgian and Dutch sandy shores and to the French Atlantic and western English Channel shorelines) but it may also be extent to sandy shores of other regions of the world with their own classification scheme.

The macrobenthic community maps provide a reference state of intertidal soft-sediment habitats that is a prerequisite for any functional study of these coastal ecosystems. As physical factors locally govern how communities in sandy shores are structured, if species assemblages and/or habitat typologies are to be used as a surrogate of biodiversity, the data should be collected at spatial scales reflecting the processes that control biodiversity patterns to contribute efficiently to the achievement of systematic conservation planning. Moreover, the design and planning of marine and adjacent terrestrial (e.g. dunes) protected areas systems should not be undertaken independently of each other because it is likely to lead to inadequate representation of intertidal habitats in either system (Banks et al., 2005). Thereby, the development of reserve systems specially designed to protect sandy shore ecosystems should be integrated into the design of terrestrial and marine protected area frameworks.

## Acknowledgements

This work was carried out in the framework of the MACROFONE programme funded by the region Nord-Pas-de-Calais and FRB (No. 12 000 447). The authors are grateful to those who contributed to this work by, providing their field data and/or by providing helpful manpower during sampling surveys in 2012. We are also grateful to Thomas Schlacher and the anonymous referee for their helpful comments and suggestions, which improved this paper.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.csr.2015.03.002>.

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