



Mapping and monitoring intertidal benthic habitats: a review of techniques and a proposal for a new visual methodology for the European coasts

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Abstract: Mapping seafloors is a fundamental step for managing and preserving coastal zones. Moreover, in a context of current global environmental changes, new methods allowing long-term monitoring are increasingly required. Various methods have been used to map seafloors, primarily benthic macrofauna and sediment sampling along regular grids or transects, and remote sensing methods. These methods map very different things, do not have the same accuracy levels, and have different costs in time and money. Furthermore, such methods often require the competencies of highly skilled scientists and exclude non-specialists otherwise best placed to perform them. In this paper, we test a method based on Direct Field Observations ('DFO method'), which can be used by non-specialists, and assess if it is sufficient for mapping and monitoring intertidal habitats. We further compare this method with other conventional ones. The results show that such a simple method is relatively rapid and inexpensive given the results obtained. Moreover, it is particularly suitable for highly fragmented intertidal landscapes where other methods are often very limited. In consequence, in areas such as the European coasts, it can be used by non-specialists, such as protected-area managers, and because it is an inexpensive and quick method long-term monitoring is also possible.

Key words: benthic habitats, Chausey archipelago, citizen science, direct field observation, intertidal sandflats, habitat mapping, habitat monitoring, macrofaunal sampling, remote sensing.

I Introduction

Mapping seafloors is an essential preliminary step for managing and conserving coastal

areas, fulfilling both a conservation and a scientific need. From a conservation point of view, increasing marine littoral space and

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resource consumption (Gray, 1997) raises an urgent need for identifying the highest conservation status places and the most disturbed or threatened areas. From an operational viewpoint, stakeholders, managers and politicians are all involved in selecting the best sites to be conserved. For instance, littoral states of the European Union have to select sites to implement marine natural parks (eg, France has to create 10 marine natural parks by 2010). In this context, maps are one of the most important data supports to achieve such new challenges. From a scientific point of view, seafloor maps are the basis of both pattern (spatial distribution) and process (such as spatial dynamics, impacts of human and natural perturbations) assessments. For example, the first seafloor maps of the European coasts (Petersen, 1913) enabled identification of both the European benthic communities and their spatial distribution.

However, the current context of global changes (enhanced environmental dynamism and large-scale human sea use) induces new challenges for seafloor mapping. Unfortunately, the great majority of the available European seafloor maps are old, the information they contain is often incomplete and the diversity of investigators involved in the mapping has led to a great variety of aims and methods, which makes the assessment of long-term changes a challenge (but see, for example, Reise, 1982; Frid *et al.*, 2000). Moreover, as underlined by several authors (eg, Kvernevik *et al.*, 2002), most of the methods used to map seafloors are expensive with respect to both time and money. Consequently, few long-term monitoring methods exist in the marine environment beyond those pertaining to 'structured habitats' such as coral reefs or mangroves in tropical areas (Green *et al.*, 1996; Chauvaud *et al.*, 1998; Holden and Le Drew, 1998; Manson *et al.*, 2003; Philipson and Lindell, 2003; Proisy *et al.*, 2007) and seagrass beds in temperate or tropical areas (Larkum *et al.*, 2006; Orth *et al.*, 2006; Wabnitz *et al.*, 2008),

for which the long-term spatiotemporal dynamics can be monitored by remote sensing methods (eg, Godet *et al.*, 2008). The study of spatiotemporal dynamics of such habitats is very useful as potential ecological indicators, but, by definition, global changes affect all marine benthic species and habitats, including common and widespread species and habitats (Edwards and Richardson, 2004). The new challenge for the twenty-first century is, therefore, to effect a shift from the sole seafloor maps of a few set of habitats to a long-term monitoring of a large range of habitats (Malthus and Mumby, 2003).

Large temporal and spatial scale data are required to track global changes. One of the best ways to get such data is to involve volunteers in so-called 'citizen science' (see Cohn, 2008). Citizen science programmes can traditionally involve any volunteer citizen, and are increasingly popular with protected area managers (see, for example, the data set provided both by citizens and a protected area manager network in the French Breeding Bird Survey – Godet *et al.*, 2007). Participatory surveys mainly exist in terrestrial areas but have also recently been developed in the marine littoral area (eg, Pattengill-Semmens and Semmens, 2003; Kawabe, 2004; Delaney *et al.*, 2008). In principle, a protected area manager network, monitoring by themselves the areas they manage, would be able to perform a habitat mapping/monitoring programme in coastal areas. However, to achieve this end, new mapping/monitoring methods would have to be developed to be used by the largest number of protected area managers, and this implies the development of a user-friendly and low-cost (in time and money) method. In this scientific and social context, we assume that a 'good' mapping/monitoring method consists of an efficient trade-off between the need for accurate results (spatial resolution, number of detected elements, physical and biological validity) and the effort involved

(economic costs, time and technical skills required) to perform the method. Moreover, non-destructive methods are preferred to destructive ones.

In addition to biological entities, 'seafloor mapping' may concern a wide range of mapped entities such as elevation (eg, Cracknell, 1999) and sedimentary features (eg, Yates *et al.*, 1993; Rainey *et al.*, 2003; Deronde *et al.*, 2006). In this paper, we focus on benthic *habitat* mapping. In this context, *habitat* is used to mean 'a place in which both the physical and biological characteristics are homogeneous, and are different from those of the surrounding area(s)'. In other words, these characteristics vary less within than they do between habitats. This biophysical entity is commonly used in the marine conservation field, although international typologies (eg, EUNIS, Natura 2000) describe marine habitats more precisely (Ekeboom and Erkkila, 2003). Moreover, we focus on intertidal sandflat habitats, which include estuaries, known to support rich resident assemblages of invertebrate and vertebrate organisms providing important economic, aesthetic and conservational value (Hatcher *et al.*, 1989; Heip *et al.*, 1995). These areas are increasingly subjected to anthropogenic pressures inducing rapid changes in habitat distribution and functionality. Nowadays, although large national mapping programmes of coastal areas exist (eg, Dobson *et al.*, 1995), they are designed to cover large areas and may not provide enough details on seascape structure for individual estuarine sites, and detailed thematic mappings of estuarine environments are still uncommon (Zharikov *et al.*, 2005). Monitoring accurately such anthropogenically disturbed systems has, therefore, become a real challenge.

The aim of this paper is to address two main objectives: we first put forward a brief critical review of the methods available to map and monitor intertidal habitats; then we test at a specific site whether a new simplified method (mainly based on georeferenced direct field observations) is sufficient and

suitable to be applied by 'non-specialists' for benthic habitat mapping and monitoring. This method is further compared with existing, more conventional, methods.

II A brief review of the principal techniques for mapping and monitoring intertidal benthic habitats

An exhaustive review of all the techniques used to map seafloors is not the subject of the present paper. Here, we focus on the techniques that can be applied in intertidal sandflats both for mapping and monitoring benthic habitats. For each technique, we first give a description of the technique itself, together with its main applications. We then highlight the strengths and weaknesses of this method to map and monitor intertidal habitats with respect to the trade-off between the expected results and the required effort.

1 Traditional methods using macrofaunal and sediment sampling

In Europe, the spatial patterns of benthic 'habitats' (initially considered to be 'communities') have been studied since the early 1900s by Danish researchers, first by Petersen (1913; 1915) and subsequently by Thorson in the 1950s. Other studies include authors such as Molander (1930), Holme (1950), Cabioch (1968) and Cabioch *et al.* (1978). The sampling methods mainly involved grabs, cores and anchor dredges used along regular grids or transects. The habitats were determined *a posteriori* according to different methods that clustered the similar stations based on their physical and biological data. More recent studies discriminate between different habitats by using the methods recommended by Clarke and Warwick (1994) and as used in the Plymouth Routines in Multivariate Research (PRIMER) software (Clarke and Gorley, 2001).

These studies not only provided large inventories and seafloor maps, but they also constitute the foundations of current knowledge on the structure and the spatial

distribution of benthic assemblages and their control by environmental factors (eg, Thorson, 1957). The methodology remains useful today and is one of the few to determine the spatial patterns of benthic habitats on a large scale in subtidal areas when other data such as remote sensing data are not available. However, these methods are highly time-consuming due to the laboratory processing required for sorting the biological material and subsequently identifying the organisms which the samples contain. They also require highly skilled biologists accustomed to invertebrate taxonomy. For all these reasons, high-resolution survey designs are often impossible, small-scale patterns of heterogeneity are often ignored and long-term habitat monitoring is left aside. Macrofaunal and sediment sampling is also mainly deployed in subtidal areas, which are not easily accessible to humans. These methods are also unfortunately intrusive, whereas nowadays other modern methods, mainly including imaging, can avoid any benthic sampling especially in small fragile habitats, which was summed up by Solan *et al.* (2003) in their paper with the sentence 'A picture is worth a thousand worms'!

By contrast, the intertidal domain is accessible and visible at low tide, giving to an investigator the opportunity to directly visualize the habitat's spatial patterns, as in terrestrial systems, and to use stratified random sampling design. Moreover, European intertidal species and habitats have been well described by many authors so that a benthic 'naturalist' investigator is able to identify directly in the field habitats such as the eelgrass beds (*Zostera marina* or *Zostera noltii* beds), the *Arenicola marina* sands, the *Lanice conchilega* areas or the *Hediste diversicolor* mudflats, without performing any macrofaunal or sediment benthic sampling.

2 Remote sensing methods

Over the last several decades, many remote sensing techniques have been developed to

map seafloors. They involve: (1) aerial pictures, (2) satellite images, (3) hyperspectral data, or (4) acoustic data (see review by Diaz *et al.*, 2004). All these data are generally georeferenced and integrated into Geographic Information Systems (GIS). Generally, these methods have been used in conjunction with direct or indirect (via photo or video imaging) observations or biological/sedimentological sampling (see, for example, Magorrian *et al.*, 1995; Sotheran *et al.*, 1997; Pinn *et al.*, 1998; Smith and Greenhawk, 1998; Downie *et al.*, 1999; Kloser *et al.*, 2001; Kostylev *et al.*, 2001; Brown *et al.*, 2002; Freitas *et al.*, 2003).

- (1) Aerial photographs are the oldest remote sensing methods commonly used for intertidal area mapping (Ekebom and Erkkila, 2003). Although large intertidal areas have been mapped using photo-interpretation (eg, Gallagher and Reimold, 1973), the first maps generated by photo-interpretation mainly focused on small intertidal areas (eg, Perry and Hershner, 1999; Bonnot-Courtois *et al.*, 2005). Coupled with GIS, however, large areas are more commonly mapped, especially for mapping intertidal vegetation (eg, Higinbotham *et al.*, 2004). The use of aerial photographs and GIS also allows the tracking of changes in the distribution of different habitats over long time periods (eg, Donoghue *et al.*, 1994; Bonnot-Courtois *et al.*, 2004; Godet *et al.*, 2008).
- (2) Satellite images have been used in the marine environment for several years. Among the first accurate maps of intertidal sandflats using satellite data, Bartholdy and Folving (1986) used a 16-band Landsat multitemporal data set in Denmark. Today, the most commonly used satellites for intertidal areas are IKONOS (eg, Mumby and Edwards, 2002; Andréfouët *et al.*, 2003), SPOT (eg, Marchand and Cazoulat, 2003; Pasqualini *et al.*, 2005) and Landsat

TM/ETM+ (Foster Larsen *et al.*, 2004; Sorensen *et al.*, 2006), or, alternatively, radar (Baghdadi *et al.*, 2004).

- (3) Hyperspectral data are increasingly used on intertidal sandflats. Most of the studies use Compact Airborne Spectrographic Imager (CASI) or Daedalus Airborne Thematic Mapper (ATM) data, and mainly focus on seaweeds and micro-phytobenthos (eg, Zacharias *et al.*, 1992; Combe *et al.*, 2005) and/or humidity and sediment gradients mapping (Hunter and Power, 2002; Rainey *et al.*, 2003; Thomson *et al.*, 2003).
- (4) In the 1940s, the first sonographs had a low resolution and were able to detect only large physical targets. In the 1970s and 1980s, however, new development in acoustic electronics enabled high-resolution images of near-photographic resolution to be obtained (Kenny *et al.*, 2003). Later, digital electronics and new software enabled additional features such as real-time visualization and geo-corrected mosaics of the seabed. Among the main acoustic seabed mapping technologies Kenny *et al.* (2003) distinguish: (1) broad-acoustic beam systems, such as side scan sonar (SSS); (2) ground-discriminating single-beam echo-sounders, such as RoxAnn and QTC-View, (3) multiple narrow-beam swath bathymetric systems, and (4) multiple-beam sidescan sonar (SSS) systems (Komatsu *et al.*, 2003). Acoustic systems are mainly deployed in subtidal areas and there is little interest in using acoustic method in intertidal areas, because airborne imaging at low tide gives much better results. The only interest in using acoustics in intertidal areas is experimental – for example, in order to test their accuracy by comparing these technologies with airborne imaging or with a direct ground control.

Remote sensing methods allow large areas to be mapped relatively quickly, and can be suitable for both highly fragmented

and monotonous benthic systems (Freitas *et al.*, 2003). Compared to habitat mapping methods involving fauna and sediment sampling, remote sensing methods have clear advantages such as avoiding any physical or biological disturbance, and they allow a much finer spatial discrimination due to almost continuous sampling (Freitas *et al.*, 2006).

Remote sensing allows the accurate mapping of the spatial patterns of different coastal species, especially for seagrasses, which are most commonly studied in temperate climates (see Duarte, 1999). So-called ‘structured habitats’ such as coral reefs can be quickly and inexpensively mapped (Kvernevik *et al.*, 2002). Hyperspectral data, such as CASI data, enable the separation of even subtle differences in land cover because the numerous and narrow spectral bands can be chosen to suit particular applications (Hunter and Power, 2002). Highly fragmented habitats may now be clearly detected and monitored using hyperspectral data, such as intertidal *Z. noltii* beds or micro-phytobenthos (Combe *et al.*, 2005; Méléder *et al.*, 2005; Barillé *et al.*, 2007).

When mapping benthic habitats, methods using remote sensing often focus on bathymetry and sediment structures, and thus consider habitats as ‘dwelling places’ or ‘preferred substrates’ for plants or animals, with the biota representing a kind of cover overlying the physical bottom features (Diaz *et al.*, 2004). Biological data are only used to test the presumed conformability of species distributions with these characteristics. For this reason, the mapping methods concern mainly the preservation of particular species through their habitat, which is considered therefore as their preferred environment (eg, Cochrane and Lafferty, 2002; Whaley *et al.*, 2007). In fact, all these methods consist simply of (1) mapping the main homogeneous patches in terms of texture or morphology and sediment stability/disturbance (Diaz *et al.*, 2004) and (2) relating this information to the dependence of species on a particular set of substrate characteristics (Diaz *et al.*, 2004).

When considering satellite remote sensing, the most important problems concern data costs (even if some old images are now freely available), and the lack of flexibility in acquisition time, which may exclude long-term monitoring programmes. Moreover, satellite imagery resolution is often too coarse (eg, 10–20 m, SPOT; 15–30 m Landsat TM) for site-specific mapping of intertidal environments due to potential habitat patchiness, and satellites are thus more appropriate for mapping general land-cover type (eg, vegetated versus unvegetated, reef versus non-reef) (Higinbotham *et al.*, 2004; Zharikov *et al.*, 2005). Finally, even for structured habitats such as coral reefs, a greater number of narrower spectral bands is still required to be able to separate reef species or to differentiate between parameters visible in the field such as dead corals invaded by algae versus living corals (Philipson and Lindell, 2003).

With respect to hyperspectral data, the main disadvantage is the necessity for very highly skilled scientists and the elevated cost of the material and data. Moreover, the process of acquisition of the images is very

complex. One part of the process requires that ground reference data be collected simultaneously with the sensor over-flight. These ground reference data are Ground Control Point of target gathered with DGPS (Differential Global Positioning System, accuracy of ± 1 cm) and a large collection of radiometric data of field objects gathered with a spectrometer. Post-treatment is highly complex and only few scientific teams can use and apply this technology. Even if long-term habitat monitoring is theoretically possible, it cannot be carried out by non-specialists.

III Case study: proposed new visual methodology, and methodology for comparison with existing methods

1 Study site

The Chausey Islands are located in the Normand-Breton Gulf (France). This archipelago is subject to an extreme megatidal regime, with a tidal range up to 14 m during spring tides (Figure 1). It covers roughly 4500 ha, with 1410 ha of sandflats exposed during extreme low water spring tides and 829 ha

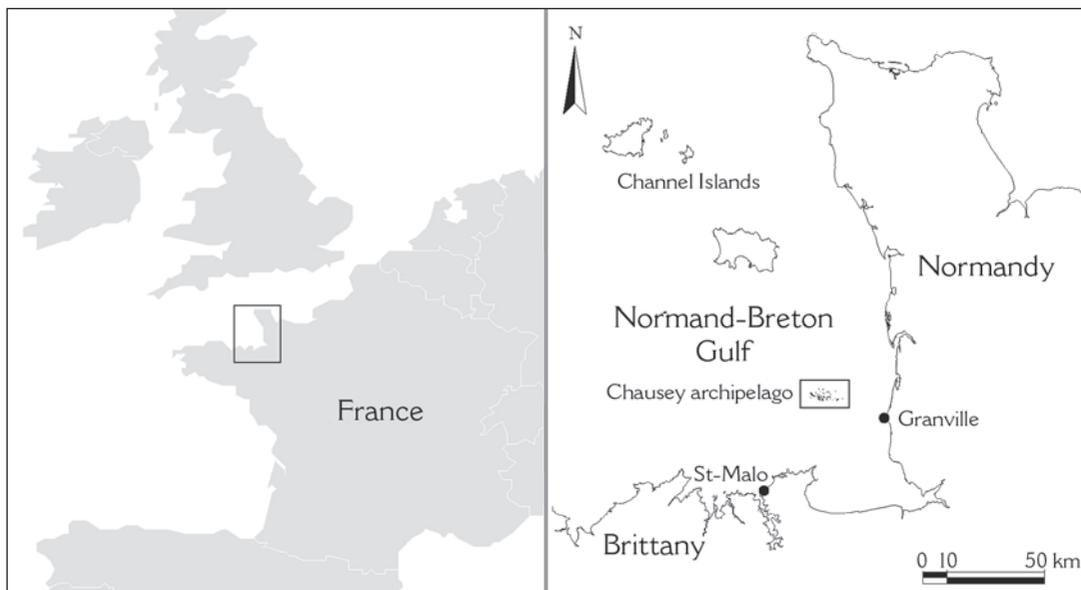


Figure 1 Location of the study site

during mean low water spring tides. The complexity of this archipelago, with over 300 islets and extreme megatidal regime, gives rise to a highly fragmented intertidal benthic landscape.

2 The new visual methodology 'Direct Field Observation' (DFO) method

An aerial photo mosaic was assembled from a 42-photograph set with a spatial scale of 1:10,000. These photos were taken on 13 August 2002, rectified using ER Mapper Software 6.1, and imported into the Geographic Information System (GIS) Arcview 3.1 Software (ESRI).

Using GIS on the aerial photo mosaic, 49 km of transects were plotted, covering the largest possible area of the site's intertidal sandflats and crossing over the main benthic features identified on the aerial photograph. In the spring of 2005, field observations were made along a 100 m band on both sides of the transects at 50 m intervals or at points where visible changes in the biological or sedimentary features could be detected

(the area surveyed was equal to 1072.84 ha, or 76% of the site's sandflats.) These observations were tabulated, generating a total of 980 descriptions, which were then completed with photographs of the sediment and landscapes in each of the four cardinal directions. These data were georeferenced using a Global Positioning System (GPS) and then integrated into a GIS.

The field descriptions include both abiotic and biotic data and can be grouped into five categories: (1) the main topographic characteristics of the tidal flat; (2) the sediment characteristics; (3) the hard or soft substrata vegetation (phanerogams and algae) known to be good indicators of specific bathymetric levels (selected from Lewis, 1964); (4) soft-bottom flora species identified in the field; and (5) soft-bottom fauna species identified in the field. (See Table 1 for the detailed list of data.)

Once the 980 field descriptions had been generated, a correspondence analysis was performed on the data. Next, a hierarchical clustering, measuring the Euclidian distance

Table 1 Criteria used for the field descriptions of the DFO method (* indicates the species collected and identified in the laboratory)

Categories					Abbr.	'note'	
1st level	2nd level	3rd level	4th level	5th level			
Abiotic criteria	Topography characteristics	Slope			Low Wea Stro	0=nul 1=weak 2=strong	
		Ripplemarks			Ripp	0/1	
		Ridges			Ridg	0/1	
		Mounds and depressions			Moun	0/1	
	Sediment characteristics	Texture	Silt			Silt	0/1
			Fine sands			Fine	0/1
			Medium sands			Medi	0/1
			Coarse sands			Coar	0/1
			Muddy			Mudd	0/1
		Structure	Limp			Limp	0/1
			Soft			Soft	0/1
			Indurate			Indu	0/1
		Oxidation	Oxidized			Oxid	0/1
			Anoxic	In surface		Anox1	0/1
		In a depth of 10 cm		Anox2	0/1		

(Continued)

Table 1 Continued

Categories					Abbr.	'note'	
1st level	2nd level	3rd level	4th level	5th level			
Biological criteria	Vegetation indicating a specific bathymetric level	Soft bottom vegetation	Algae	<i>Fucus lutarius</i>	Fuclut	0/1	
				<i>Vaucheria</i> spp.	Vauc	0/1	
			Phanerogams	Halophilous vegetation	Halo	0/1	
				<i>Zostera noltii</i>	Zosnol	0/1	
				<i>Zostera marina</i>	Zosmar	0/1	
		Hard substrate vegetation on blocks among soft sediments	Algae	<i>Pelvetia canaliculata</i>	Pelv	0/1	
				<i>Fucus spiralis</i>	Fucspi	0/1	
				<i>Fucus vesiculosus</i>	Fucves	0/1	
				<i>Ascophyllum nodosum</i>	Asconod	0/1	
				<i>Fucus serratus</i>	Fucser	0/1	
	Other vegetation	Soft bottom vegetation	Algae	<i>Enteromorpha</i> spp.	Ente	0/1	
				<i>Ulva</i> spp.	Ulva	0/1	
	Animal tracks	<i>Arenicola marina</i> faeces or burrows				Aremar	0=absent 1=scattered 2=abundant
		<i>Hediste diversicolor</i> burrows (or living animals)				Heddiv	0/1
		<i>Lanice conchilega</i> sand-fringes				Lancon	0=absent 1=scattered 2=abundant
		<i>Petaloproctus terricola</i> tubes				Peta	0/1
		<i>Sabella pavonina</i> tubes				Sabe	0/1
	Living animals	Cnidairs	<i>Anemonia viridis</i>		Anem	0/1	
			<i>Cereus pedunculatus</i>		Cere	0/1	
			<i>Edwardsia</i> spp.		Edwa	0/1	
		Annelids	<i>Cirratulidae</i> spp.		Cirr	0/1	
			<i>Nephtys caeca</i> *		Nepcae	0/1	
			<i>Nephtys hombergii</i> *		Nephom	0/1	
			<i>Nephtys cirrosa</i> *		Nepcir	0/1	
			<i>Perinereis cultrifera</i> *		Peri	0/1	
		Platyhelminthes	<i>Convoluta roscoffensis</i>		Conv	0/1	
		Sipunculids	<i>Sipunculida</i> spp.		Sipu	0/1	
		Crustaceans	<i>Talitrus saltator</i>		Tali	0/1	
			<i>Carcinus maenas</i>		Carc	0/1	
<i>Liocarcinus</i> spp.			Lioc	0/1			
<i>Paguridae</i> spp.			Pagu	0/1			
Molluscs		<i>Capsella variegata</i>		Caps	0/1		
		<i>Cerastoderma edule</i>		Cer	0=absent 1=scattered 2=abundant		
		<i>Crepidula fornicata</i>		Crep	0/1		
		<i>Gibbula magus</i>		Gibb	0/1		
		<i>Nassarius reticulatus</i>		Nass	0/1		
		<i>Ensis ensis</i>		Ensi	0/1		
		<i>Glycymeris glycymeris</i>		Glyc	0/1		
		<i>Macra glauca</i>		Mact	0/1		
		<i>Mytilus edulis</i>		Myti	0/1		
	<i>Paphia rhomboides</i>		Paph	0/1			
	<i>Ruditapes philippinarum</i>		Rudi	0/1			
	<i>Spisula ovalis</i>		Spis	0/1			
<i>Venerupis aurea</i>		Vene	0/1				
<i>Venus verrucosa</i>		Venu	0/1				

between observations, was carried out on the coordinates of the first factors of the correspondence analysis in order to group stations in terms of their similarities based on the data used. The identified habitats, corresponding to homogeneous groups, were then displayed on the aerial photograph in the GIS, with a different symbol representing each habitat. The habitats were mapped according to the habitat points displayed, the georeferenced landscape photographs, and benthic features visible on the aerial photograph. The entire mapping process was performed on the same 1:1000 scale. The 'real scale' (1:10,000) corresponds to the spatial resolution of the aerial photographs, and the 1:1000 scale corresponds to the zoom used with the GIS to facilitate the mapping process. Using the 1:1000 scale allowed polygons of terrain as small as 9 m² to be mapped, derived from the smallest-sided polygons (with side lengths of ≥ 3 mm) which could reliably be drawn on a computer screen.

Figure 2 presents the details of the Direct Field Observation survey, including the hardware, software and special skills required to use such a method, the various steps, and the expected time for each step. For reasons of simplicity, the habitats identified using this method are designated as Directly Field Observed habitats = DFO habitats.

3 Comparison of the DFO habitats with the benthic assemblages identified through a traditional benthic survey

Benthic habitat mapping is traditionally based on macrofaunal benthic sampling surveys emphasizing the different benthic assemblages. In this section, we evaluate the equivalence of the results coming from the DFO survey and traditional benthic surveys by comparing the DFO habitats with macrofaunal benthic assemblages identified by the more traditional survey methods.

Macrofaunal benthic sampling was conducted in autumn 2005 in the six largest DFO habitats. Three stations in each of the five main habitats (*Hediste diversicolor* muds;

Arenicola marina sands; *Lanice conchilega* beds; *Glycymeris glycymeris* coarse sands; and *Zostera marina* beds) and one station in the more localized habitat (*Cerastoderma edule* coarse sands) were sampled. At each station, four 0.1 m² cores were collected. Samples were then washed through a 2 mm-mesh circular sieve. After sieving, all samples were immediately preserved in 4% buffered formaldehyde mixed with seawater. In the laboratory, the material retained by the mesh sieve was sorted twice, the second time after Rose Bengal staining. All the macrozoobenthos components were identified to the lowest possible taxonomic order using standard taxonomic keys, and were then enumerated. Benthic-demersal species were not included in our results.

We followed methods recommended by Clarke and Warwick (1994) and used the Plymouth Routines in Multivariate Research (PRIMER) version v5.2.2 software (Clarke and Gorley, 2001) to analyse the structure of macrozoobenthic assemblages. Non-metric multidimensional scaling ordinations (nMDS) were done on the basis of Bray-Curtis similarity matrices calculated from 4th root transformed species density data and from presence-absence transformed species density data. Stress values were shown for each nMDS plot to indicate the accuracy of the representation of distances between samples (Clarke, 1993). Significant differences between groups were tested using the ANOSIM subroutine (Clarke and Green, 1988).

4 Comparison of the time required for the DFO method and for a traditional macrofaunal sampling survey

We assessed both the mesh size and the time required to provide a high-resolution map from regular grid benthic sampling that would be as accurate as the one provided by the DFO method. Using the GIS software, we created six regular grids of six different square mesh sizes (2000 m, 1000 m, 500 m, 250 m, 125 m, 62.5 m) overlapping the

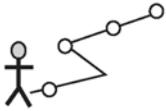
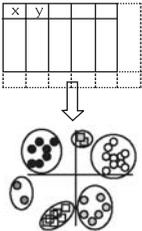
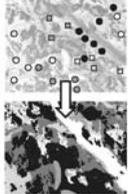
STEPS	TIME (day/person)	EQUIPMENT REQUIRED		SPECIAL SKILLS REQUIRED
		Hardware	Software	
<p>Georeferenced airphoto mosaic</p>  <ul style="list-style-type: none"> - Airphoto mission - Image processing - Creation of an airphoto mosaic - Mosaic georeferencing - Integration of the mosaic into a GIS 	10–15 days	<ul style="list-style-type: none"> - Personal Computer 	<ul style="list-style-type: none"> - Geospatial imagery processing software (eg, ER Mapper) - Geographic Information System (GIS) software (eg, ESRI-Arcview) 	<ul style="list-style-type: none"> - Intermediate photogrammetry skills - Intermediate GIS skills
↓				
<p>Field survey preparation</p>  <ul style="list-style-type: none"> - Development of a standard field form - Design of the naturalist transects on the airphoto mosaic - Preliminary field survey along a transect with all the team, with at least one experienced naturalist 	<ul style="list-style-type: none"> - 2 days - 1 day - 1 day 	<ul style="list-style-type: none"> - Personal Computer - Global Positioning System (GPS) - Field form - Plastic vials - Camera - Spade - 0.25m² quadrat 	<ul style="list-style-type: none"> - Geographic Information System (GIS) software (eg, ESRI-Arcview) 	<ul style="list-style-type: none"> - Intermediate GIS skills - Naturalistic skills (field identification of the main biological and sedimentological features of the area)
↓				
<p>Field survey</p>  <ul style="list-style-type: none"> - Field descriptions along transects by following the field form - Photographs of the landscapes, fauna and flora and sedimentological features - Sampling of the large unidentified macrofauna individuals 	40 days	<ul style="list-style-type: none"> - Global Positioning System (GPS) - Field form - Plastic vials - Camera - Spade - 0.25m² quadrat 		<ul style="list-style-type: none"> - Naturalistic skills
↓				
<p>Data analysis</p>  <ul style="list-style-type: none"> - Integrating all the data (descriptions, photographs) into the GIS - Correspondence analysis and hierarchical clustering on all the field descriptions - Identification and description of the biotic and abiotic characteristics of all the identified habitats 	<ul style="list-style-type: none"> - 5 days - 1–2 day - 1 day 	<ul style="list-style-type: none"> - Personal Computer 	<ul style="list-style-type: none"> - Geographic Information System (GIS) software (eg, ESRI-Arcview) - Statistical software (eg, R) 	<ul style="list-style-type: none"> - Intermediate statistical knowledge (exploratory statistic)
↓				
<p>Habitat mapping</p>  <ul style="list-style-type: none"> - Display of the identified habitats on the airphoto mosaic - Habitat mapping on a 1:1000 scale with the identified habitats display and photo interpretation 	30 days	<ul style="list-style-type: none"> - Personal Computer 	<ul style="list-style-type: none"> - Geographic Information System (GIS) software (eg, ESRI-Arcview) 	<ul style="list-style-type: none"> - Basic GIS skills

Figure 2 The DFO method step-by-step

DFO habitats. We attributed to each cell the largest habitat present in the cell. For each mesh size, we calculated:

- (1) a mean error ' α ' percentage, corresponding to the surface of the remaining DFO habitats in each cell (ie, all the DFO habitats within the cell, except the largest one);
- (2) a mean error ' β ' percentage, corresponding to 1 minus the ratio of the total area assessed using the regular grid method over the total area assessed using DFO method.

α and β were only calculated for cells covered by at least one quarter of intertidal soft sediments. Based on our own benthic sampling surveys, we assume that the mean time required for one person to collect benthic samples, sort the biological material, and identify the different invertebrate species is equal to 10 days per station (four replicates).

5 Comparison of the DFO method with a classic remote sensing method

In order to compare the DFO method to remote sensing methods, we mapped the different benthic features visible on the aerial photo mosaic using distinct layers of polygons with the GIS software, zooming in to a 1:1000 scale. Field validations with GPS were performed for every class identified on the intertidal sandflats. For each class of less than 20 ha, each polygon was checked in the field and boundaries were determined with GPS. For classes of more than 50 ha, quadrats-transects were plotted across the principal mapped polygons. For the class of more than 300 ha (*Z. marina* beds), only the main patches were checked in the field because these beds are known to be accurately mapped with photo-interpretation methods (Robbins, 1997).

6 Comparison of the DFO method and methods mapping bathymetric and sedimentary features

Because many modern benthic mapping techniques focus on bathymetric and sedimentological features (two factors strongly

controlling benthic species distribution – Thorson, 1971; Ysebaert *et al.*, 2002) to map habitats (Diaz *et al.*, 2004), we decided to compare DFO method to methods used to map bathymetric and sedimentary features. To do so, we collected two kinds of data:

- *Bathymetric data* – A bathymetric map was generated from bathymetric data for the test site acquired by Tocquet *et al.* (1957); six bathymetric levels were mapped and integrated into the GIS.
- *Sedimentary data* – 384 sediment cores were sampled across the archipelago using a 10 cm deep core with a diameter of 50 mm. The sediment size class distribution was analysed for all samples, which were rinsed repeatedly with distilled water allowing fine sediments to settle overnight prior to decanting. Clean sediments were dried at 60°C for 24h. Grain-size analyses were conducted using dry sieving through AFNOR standard sieves with 1, 0.8, 0.63, 0.50, 0.40, 0.315, 0.25, 0.20, 0.16, 0.125, 0.100 mm and 80, 63, 50, 40 μ m meshes. Sediments smaller than 40 μ m were collectively retained as a pan fraction. The weight of each size fraction was recorded as a percentage of the total sample weight.

Grain size parameters were calculated arithmetically and geometrically (in microns) with the Gradistat v.4.1. program (Blott and Pye, 2001), modified by Fournier (unpublished data, 2004) according to the Moment and Folk and Ward method. This program provides the sediment names and a physical description of the textural groups to which the sample belongs (eg, Slightly Gravelly Sand) according to Folk (1954). Textural groups were then displayed on the aerial photograph through the GIS, using a different symbol for each group. Each group was then mapped according to the groups displayed on the photograph and photo-interpretation.

On the GIS, the intersection of the different layers – corresponding either to the bathymetric levels and sedimentological

textural groups or to the DFO habitats – was used to determine the equivalence between these different data. In order to propose a synthetic overview of these equivalences, we focused on the four bathymetric levels and five textural groups. Consequently, a bathymetric-sedimentary group may correspond to one or more different DFO habitats.

For each bathymetric-sedimentary group, we calculated the corresponding area of each DFO habitat. We then attributed to each bathymetric-sedimentary group the identity of the main DFO habitat composing it. For example, if the bathymetric-sedimentary group 1 is composed of 15% of *G. glycymeris* coarse sands, and 85% of *Z. marina* beds, we identify group 1 as a *Z. marina* beds habitat. The % of area in the other habitats included in the bathymetric-sedimentary group was considered as a habitat mapping error probability. For example, the error probability associated to group 1 is equal to 15% (ie, 15% of this bathymetric-sedimentary group covers other habitats than the main one from which the group's name was derived).

IV Results and discussion

1 The DFO method

A first correspondence analysis (CA) was performed on the 980 field descriptions. The first two factors explain 17.95% of the total inertia, with 23.77% for the first three factors. The hierarchical clustering performed on the coordinates of the first three factors distinguished two main groups, A and B, with 2 DFO habitats (A1 and A2) within the group A (Figure 3).

A second CA was performed on group B, with the first two factors explaining 19.11% of the total inertia and the first three factors explaining 25.28%. The hierarchical clustering performed on the coordinates of the first three factors distinguished seven other main DFO habitats (Figure 3). The first factorial plane (Axis 1 and 2) is characterized by a Guttman effect (ie, a 'horseshoe effect'), revealing a sediment-bathymetry gradient

that ranges from muddy sediments of a high bathymetric level in the top left-hand corner to ridged coarse sediment of a low bathymetric level in the top right-hand corner. The factor projection on the first factorial plane revealed the main factors characterizing each group. All the codes/names of all the DFO habitats and the factors characterizing them are shown in Figure 3.

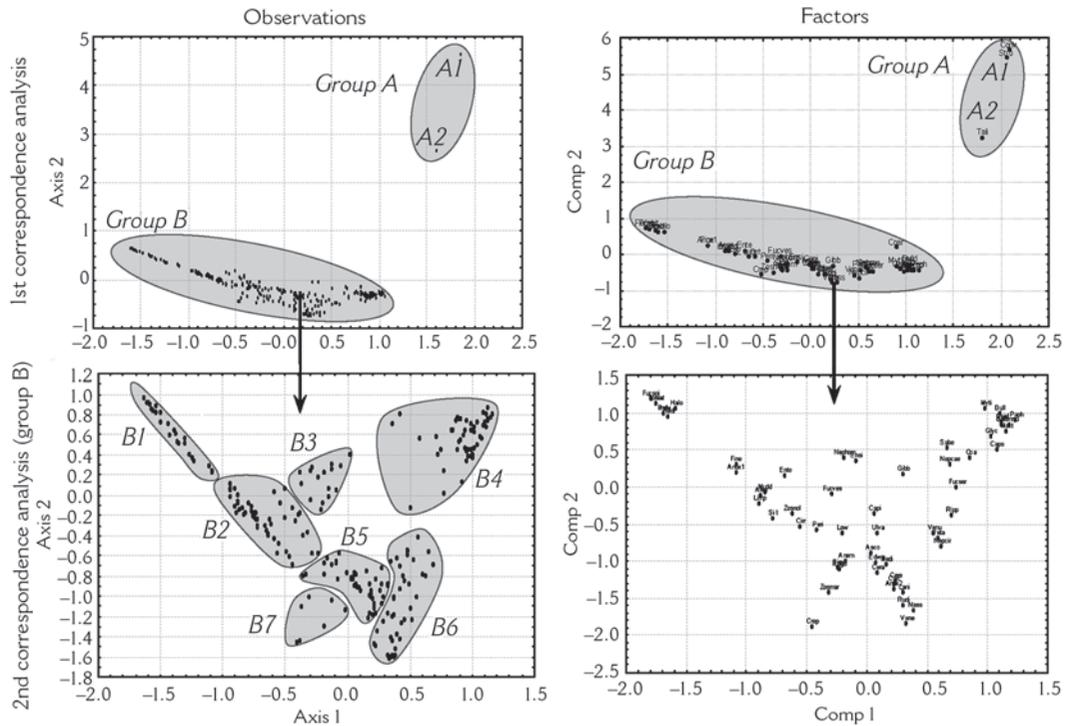
The map of the nine DFO habitats is presented in Figure 4. This map represents more than 90% of the sandflats exposed during mean low water spring tides and 60% of the sandflats exposed during extreme low water spring tides.

2 DFO habitats and benthic assemblages

A total of 209 macroinvertebrate taxa were identified from the 64 samples. The dendrogram of the hierarchical cluster analysis (Figure 5A) and the corresponding nMDS plot based on 4th root transformed data (Figure 5B) reveal three or eight groups (namely groups 'a' to 'h'), isolated at similarity levels of 18% or 41%, respectively (Figure 5B). Macrobenthic assemblages differ significantly between the groups with 41% similarity (ANOSIM $0.778 \leq R \leq 1$; $0.0001 \leq P \leq 0.029$) except for the clusters g and h (ANOSIM $R=0.067$; $P=0.304$).

The significantly different assemblages correspond to the different DFO habitats. Assemblage 'a' corresponds to the *H. diversicolor* muds, 'd' to *L. conchilega* beds, and 'e' to *Z. marina* beds. Assemblage 'c' includes one station from the *A. marina* sands and one from the *C. edule* coarse sands. The *G. glycymeris* coarse sands are split into two significantly different assemblages: 'f' and 'g'/h'.

The dendrogram of the hierarchical cluster analysis and the corresponding nMDS plot based on presence-absence transformed data reveal the same assemblages as with 4th root transformed data, except for two significantly different assemblages corresponding to the *A. marina* sands and *C. edule* coarse sands. Consequently, according to



Code	Factors	DFO habitat names
A1	Strong slopes; the platyhelminth <i>Convoluta roscoffensis</i>	<i>Convoluta roscoffensis</i> sands
A2	The amphipod <i>Talitrus saltator</i>	<i>Talitrus saltator</i> sands
B1	The algae of hard substratum: <i>Pelvetia canaliculata</i> and <i>Fucus spiralis</i> ; the algae of soft bottom: <i>Fucus lutarius</i> , <i>Vaucheria</i> spp.; Halophilous vegetation; the polychaete <i>Hediste diversicolor</i>	<i>Hediste diversicolor</i> muds
B2	Fine sands; muddy sands; anoxic sediment in surface; the algae <i>Enteromorpha</i> spp., <i>Fucus vesiculosus</i> ; the marine phanerogam <i>Zostera noltii</i> ; the polychaetes <i>Arenicola marina</i> , <i>Perinereis cultrifera</i> and polychaetes of the family Cirratulidae	<i>Arenicola marina</i> sands
B3	The polychaete <i>Nephtys hombergii</i> ; the gastropod <i>Gibbula magus</i> ; the bivalve <i>Ensis ensis</i>	<i>Ensis ensis</i> sands
B4	Soft sediments, oxidized, with ridges; the alga of hard substrate <i>Fucus serratus</i> ; the two polychaetes <i>Nephtys caeca</i> , <i>Sabella pavonina</i> ; the 6 bivalves <i>Glycymeris glycymeris</i> , <i>Capsella variegata</i> , <i>Macra glauca</i> , <i>Mytilus edulis</i> , <i>Paphia rhomboides</i> , <i>Spisula ovalis</i> ; and fishes of the genus <i>Ammodytes</i>	<i>Glycymeris glycymeris</i> coarse sands
B5	Medium sands; anoxic layer of the sediment to a depth of more than 10 cm; the alga of hard substratum <i>Ascophyllum nodosum</i> ; the anemone of the genus <i>Edwardsia</i> and the anemone <i>Cereus pedunculatus</i> ; the crab <i>Carcinus maenas</i> the bivalve <i>Cerastoderma edule</i>	<i>Cerastoderma edule</i> coarse sands
B6	Sediments with ripplemarks; algae of the genus <i>Ulva</i> ; the 3 polychaetes <i>Lanice conchilega</i> , <i>Nephtys cirrosa</i> and <i>Petaloproctus terricola</i> and other polychaetes of the family Cirratulidae; the gastropod <i>Nassarius reticulatus</i> ; the two bivalves <i>Venerupis aurea</i> and <i>Venus verrucosa</i>	<i>Lanice conchilega</i> beds
B7	The seagrass <i>Zostera marina</i> ; the gastropoda <i>Crepidula fornicata</i>	<i>Zostera marina</i> beds

Figure 3 Correspondence analysis performed on the 980 field descriptions of the DFO method

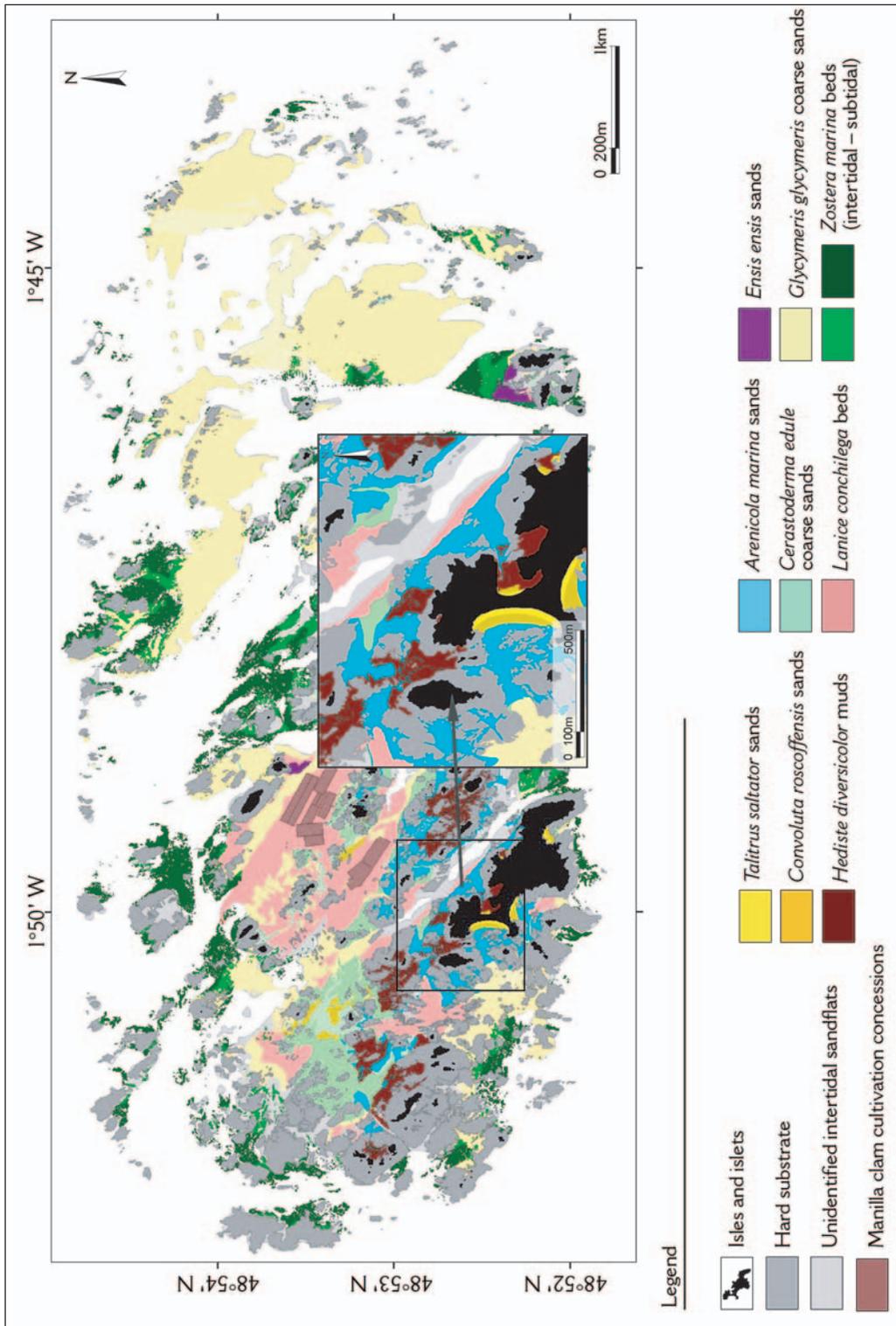


Figure 4 Habitats identified with the DFO method (= DFO habitats)

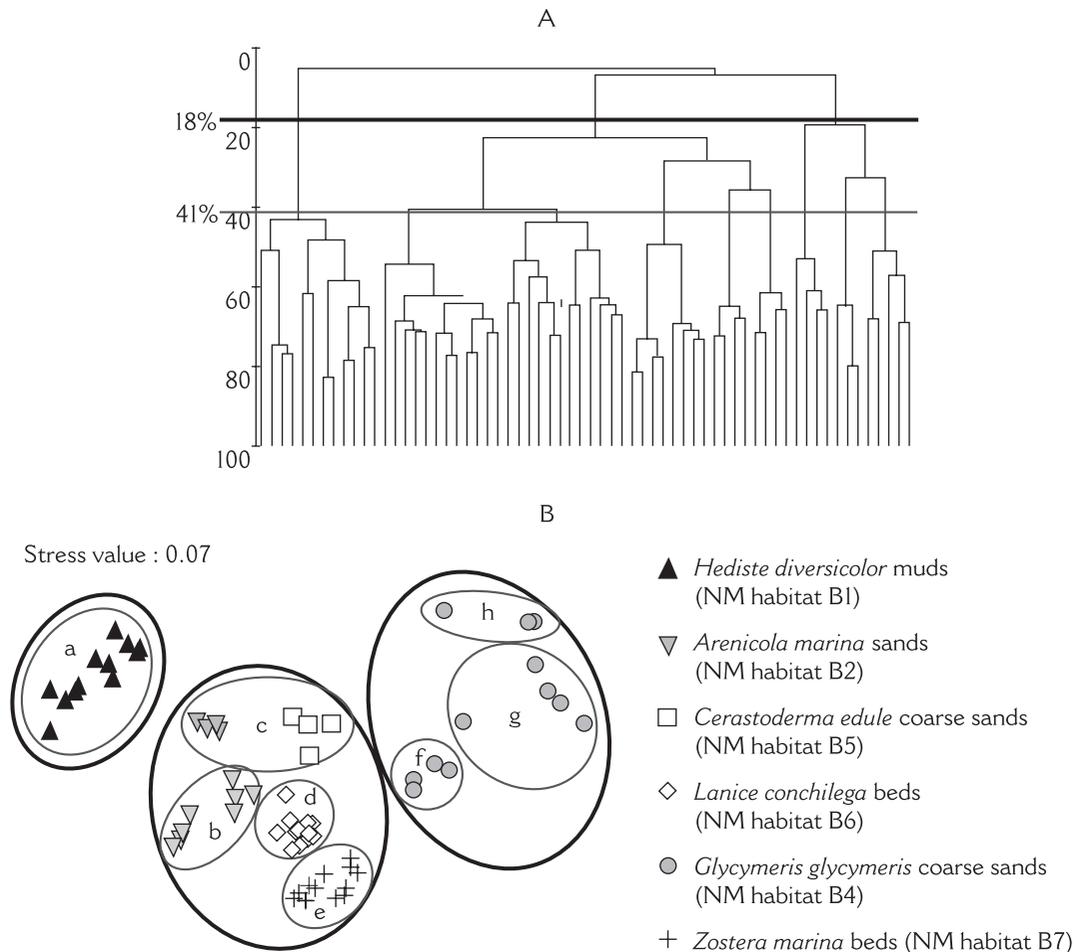


Figure 5 Dendrogram (A) and multidimensional scaling ordinations (B) performed on the basis of Bray-Curtis similarity matrix calculated from 4th root transformed species density data of 16 stations and 64 samples performed on the six main DFO habitats

this presence-absence transformation, the assemblages correspond exactly to the DFO habitats, except for the *G. glycymeris* coarse sands habitat, which is split into two significantly different assemblages.

3 Time required for the DFO method and a traditional macrofaunal sampling survey

The smaller the mesh size, the lower the α values (Figure 6A): the 62.5 m mesh size grid is the minimum grid needed to reach 10% α values. However, according to our

calculations, the total number of stations ($N = 69$) for even the smaller 500 m grid would mean three years of work for one person and would entail a relatively high error level ($\alpha = 24.5\%$), which is not a realistic scenario. Moreover, although relatively large and poorly fragmented habitats (eg, *G. glycymeris* coarse sands and *L. conchilega* beds; Figure 6B) may be accurately identified with large meshes, the others are imprecisely identified, even with the finest mesh size tested (Figure 6C).

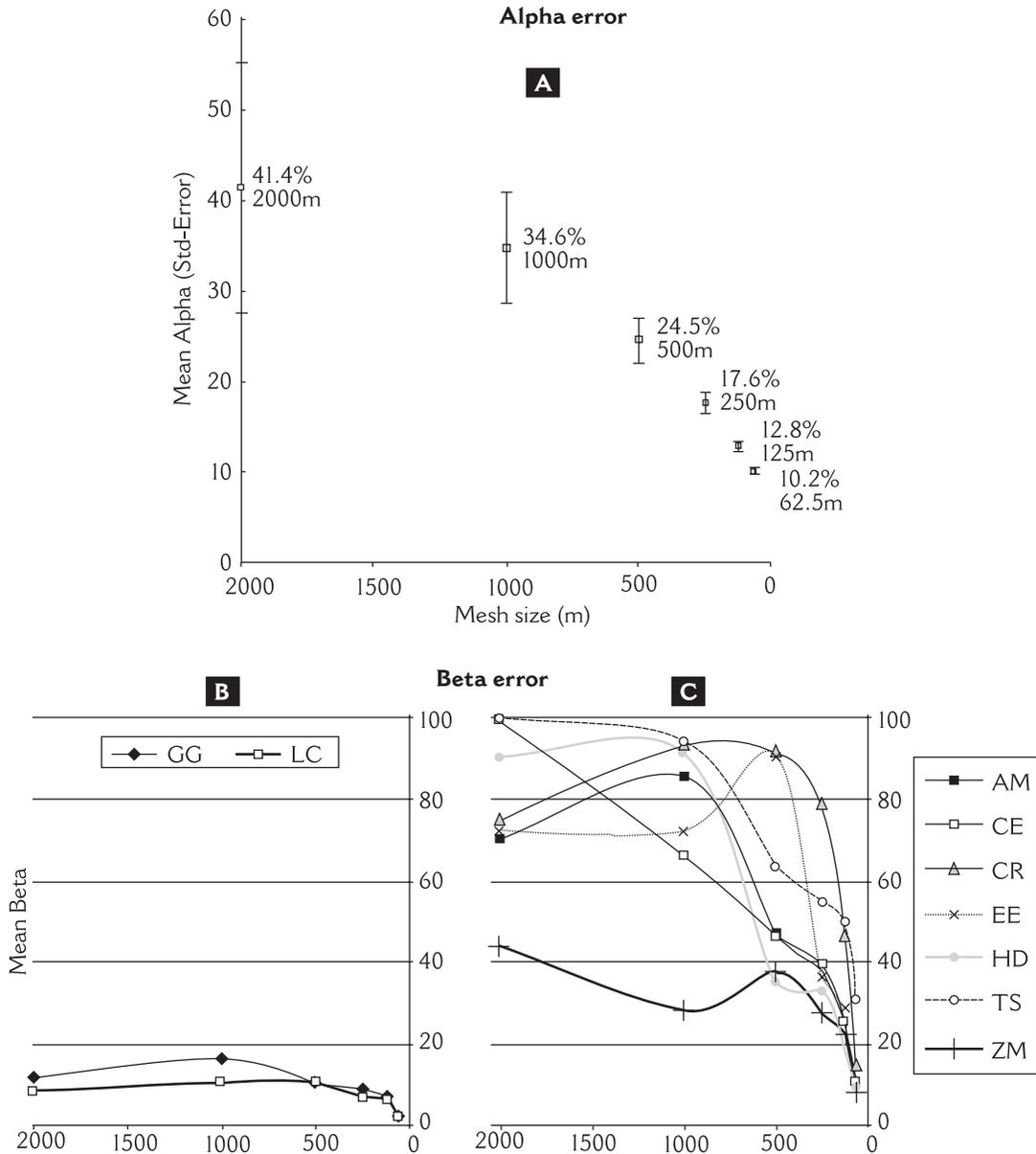


Figure 6 α and β % error, according to the mesh size

4 The DFO method and classic remote sensing methods

The remote sensing method allowed us to map all the islets, both rocky intertidal and subtidal areas, and six different soft-bottom classes on a 1:1000 scale, including salt marshes (2.63 ha), *Vaucheria* spp. (11.79 ha),

F. lutarius (1.94 ha), *L. conchilega* (90 ha), *Z. noltii* (1.55 ha) and *Z. marina* beds (119.46 ha intertidal and 223.69 ha subtidal). However, most of the intertidal sandflats were unidentified (1272 ha) so that the parts of the intertidal sandflats identified represented only 27% of the sandflats exposed during

mean low water spring tides and less than 16% of the sandflats exposed during extreme low water spring tides.

As a result, photo-interpretation allowed us to identify and map only two of the nine DFO habitats: the *L. conchilega* and *Z. marina* beds, which are associated with two specific benthic assemblages. Only a tiny part of the total intertidal sandflat area could be identified via the photo-interpretation method, and the identified entities did not necessarily correspond to original homogeneous biological or sedimentary groups. In fact, identified groups were essentially restricted to the visible flora or fauna found in high densities (ie, halophilous vegetation, *F. lutarius*, *Vaucheria* spp., *Z. noltii*, *Z. marina* and *L. conchilega*).

5 The DFO method and methods mapping bathymetric and sedimentary features

Figure 7 clearly shows that the DFO habitats correspond roughly to distinct bathymetric levels and to different sedimentary textures. For example, *T. saltator* sands are located at high bathymetric levels characterized by coarse sands. Nevertheless, several habitats may overlap the bathymetric levels and textural groups. If two bathymetric and sedimentary classes are almost covered by two different habitats (eg, the coarse sediment of low bathymetric levels are mainly covered by *G. glycymeris* coarse sands and the muddy sediments of low bathymetric levels are mainly covered by *Z. marina* beds), several DFO habitats may occur within a given bathymetric-sedimentary class.

Table 2 shows the habitat mapping error probability of each bathymetric-sedimentary group. Only three bathymetric-sedimentary groups have an error probability lower than 10%. These groups correspond to low-bathymetric level groups with coarse or fine muddy sands.

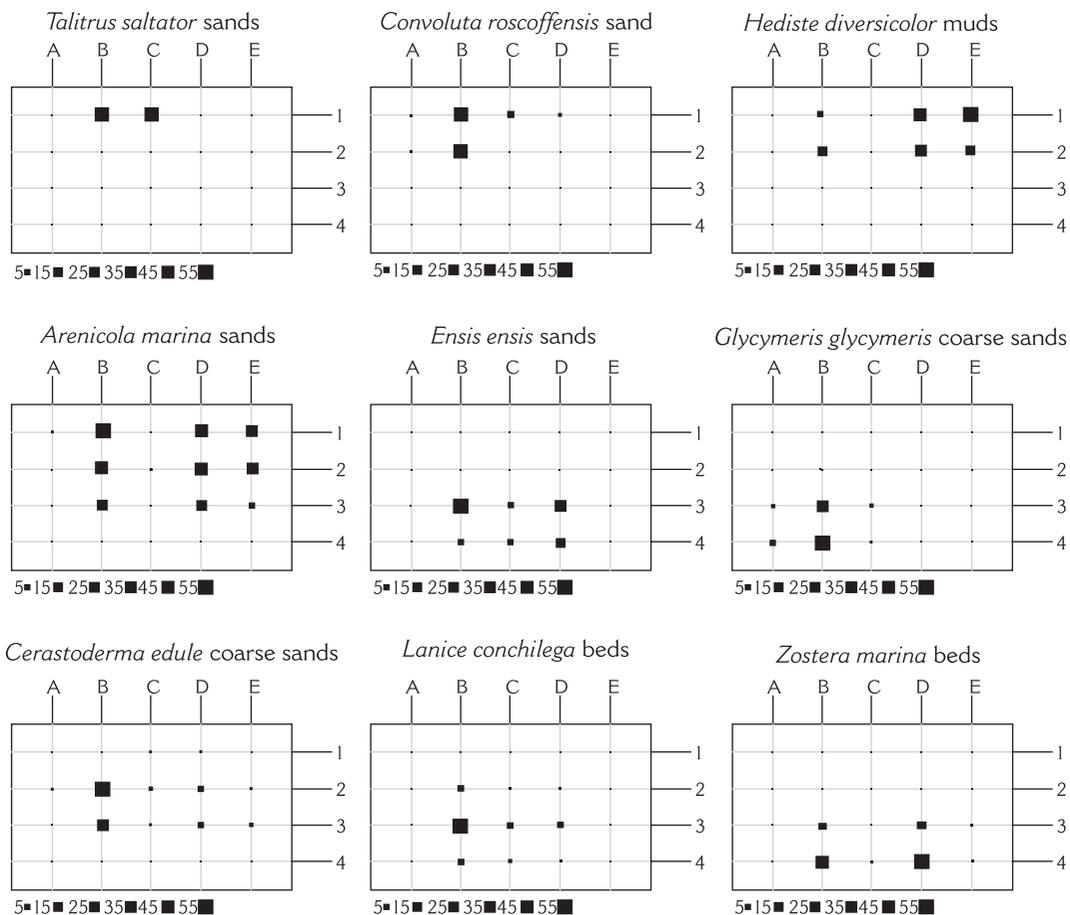
V Conclusions

Benthic mapping via photo-interpretation allows a very small number of natural entities to be mapped. These entities correspond

to visible biotic or abiotic features, but not necessarily to benthic habitats. Furthermore, unlike the DFO method, which identifies habitats using exploratory statistics, interpreting and selecting the different classes from aerial photos is a subjective process that is highly dependent on the user's experience and field knowledge. For this reason, we suggest using georeferenced aerial photo mosaics only as preliminary supports for benthic habitat mapping. The remote sensing techniques using satellite images performed for our test site (not presented in this paper) did not produce better results than the photo-interpretation. In fact, a preliminary evaluation of the SPOT5 satellite's ability to map benthic habitats was performed in 2005 on the Chausey archipelago (Cottonnec *et al.*, 2005). Using the usual image processing routines, 11 classes were detected, but they included only one soft-bottom intertidal habitat (the *L. conchilega* beds).

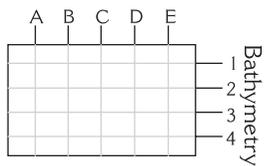
As demonstrated above, bathymetric and sedimentary features do not correspond precisely to DFO habitats. In fact, sediment types are known to control the benthic species distribution (Thorson, 1971), with similar groups of species commonly occurring on similar substrata, and grain size being the most commonly found correlative factor (Rhoads, 1976). However, as suggested by Newell *et al.* (1998), benthic community composition is not controlled by the simple granulometric properties of the sediment nor by the bathymetric features. For example, particle mobility and the association of biological and chemical factors operating over the long term must also be taken into account (Newell *et al.*, 1998). Nevertheless, these bathymetric and sedimentary data may be quite useful for identifying and/or modelling benthic habitats, if the word is used to mean the 'dwelling place' of particular species.

The DFO method, which is a skilled eye appraisal based on direct field observations, allows both highly accurate mapping and highly accurate identification of all the prospected sectors. In fact, the remaining



Legend

Sedimentary texture



Textural groups

- A Sandy gravel
- B ± Gravely sand
- C Sand
- D ± Gravely muddy sand
- E ± Gravely and ± sandy silt

Bathymetric levels

- 1 Above the mid-tide level
- 2 Between mid-tide level and mean low water neap level
- 3 Between mean low water neap level and mean low water spring level
- 4 Between mean low water spring level and extreme low water spring level

Figure 7 Percentage of the total area of each DFO habitat included in the different bathymetric levels and textural groups

unidentified sandflats could have been mapped by generating additional field descriptions along additional transects. Because the DFO habitats correspond to benthic biological realities, the DFO method should

allow expensive and time-consuming benthic and sedimentological benthic surveys to be avoided. Moreover, the DFO habitats conform to well-known benthic community classifications that have been described

Table 2 Habitat mapping error probability when using only bathymetric and sedimentological data (bold = >50%; normal = 10–50%; underlined = <10%)

	Sedimentary texture**				
	A	B	C	D	E
1	24.63	66.00	66.23	46.99	36.36
2	23.30	38.37	44.20	67.06	52.99
3	<u>1.15</u>	43.40	40.10	67.52	60.82
4	<u>0.62</u>	13.15	34.57	13.63	<u>5.08</u>

*1 Up to mid-tide level; 2 between mid-tide level and mean low water neap level; 3 between mean low water neap level and mean low water spring level; 4 between mean low water spring level and extreme low water spring level.

**A sandy gravel; B ± gravely sand; C sand; D ± gravely muddy sand; E ± gravely and ± sandy silt.

previously by several authors. Fifty years ago, Pérès (1957) proposed the first world-wide classification of benthic communities based on benthic bionomic studies conducted throughout the world (eg, Pruvot, 1895; de Beauchamp, 1914; Petersen, 1918; Ford, 1923; Le Danois, 1925; Pearse *et al.*, 1942; Stephenson and Stephenson, 1949; Jones, 1951; Thorson, 1952; Molinier and Picard, 1953; Costa and Picard, 1957). Almost all the DFO habitats correspond to the benthic communities previously described by Pérès (1957), and they also correspond to international typologies, such as the recent EUNIS (European Nature Information System) classification scheme (Table 3).

The DFO method is a relatively quick and inexpensive method, based mainly on intermediate naturalistic knowledge. Some particular skills are needed (eg, photogrammetrical and GIS skills), and there is a certain expense due to the cost of the aerial photography needed to produce the georeferenced aerial photo mosaic, but this comes into play essentially during the preliminary phase and is no more costly than the mapping support required by the majority of the other mapping methods.

There are several ways to compensate for either a lack of skill or a lack of money associated with the method. With enough money, no special photogrammetrical skills are

required: aerial photo mosaics that have already been georeferenced can be bought (€500 for 100 km² in France if the mosaic already exists, but more than €15,000 if the mosaic must be created), as can very high-resolution georeferenced satellite images, which are available for almost all the parts of the world (€3500 for 100 km² for a 0.8 m² resolution panchromatic image from the IKONOS Satellite). On the other hand, users with specific skills in photogrammetry and not much money could buy much more inexpensive sets of aerial photographs (€40 for one colour photograph in France, or €1760 for a set of 44 aerial photographs like the ones for the Chausey Islands, if the photographs already exist; €160 for one colour photograph, or €7040 for a 44-photo set if the photographs do not already exist and must be ordered). Free-access high-resolution satellite images and aerial photographs are becoming more and more easily available on the web (eg, Google EarthTM), and offer the possibility of creating aerial photo mosaics for no cost. The DFO method is all the more inexpensive because the required software can all be freely downloaded: there are many free GIS software (eg, SPRINGTM, www.inpe.br/spring/english/index.html; GRASSTM, www.grass.itc.it) and free statistical software (eg, RTM) packages now available on the internet.

Table 3 Correspondence between the DFO habitats, the benthic community classification of Pérès (1957) and the EUNIS classification

This article	Pérès (1957)	EUNIS classification scheme
<i>Talitrus saltator</i> sands	Jumping amphipods of the upper intertidal sandflats	Talitrids on the upper shore and strandline (A2.211)
<i>Convolvata roscoffensis</i> sands	<i>Nerine cirratulus</i> and <i>Bathyporeia</i> community of the mediolittoral sands and slightly muddy sands	<i>Scolecopsis</i> spp. in littoral mobile sand (A2.2231)
<i>Hediste diversicolor</i> muds	<i>Nereis diversicolor</i> , <i>Carcinus maenas</i> and <i>Corophium volutator</i> community of the western European shores	<i>Hediste diversicolor</i> and oligochaetes in littoral mud (A2.3223)
<i>Arenicola marina</i> sands	<i>Macoma</i> , <i>Cardium</i> and <i>Arenicola</i> community of the infralittoral sands and muddy sands. Higher densities of <i>Arenicola</i> in the muddy sands and sands with a high organic matter rate	<i>Macoma balthica</i> and <i>Arenicola marina</i> in muddy sand shores (A2.241)
<i>Cerastoderma edule</i> coarse sands	<i>Macoma</i> , <i>Cardium</i> and <i>Arenicola</i> community of the infralittoral sands and muddy sands. Higher densities of <i>Cardium</i> in high current velocity areas	<i>Cerastoderma edule</i> and polychaetes in littoral muddy sands (A2.242)
<i>Lanice conchilega</i> beds	?	<i>Lanice conchilega</i> in littoral sand (A2.244)
<i>Ensis ensis</i> sands	?	<i>Echinocardium cordatum</i> and <i>Ensis</i> spp. in lower shore and shallow sublittoral slightly muddy fine sand (A5.241)
<i>Glycymeris glycymeris</i> coarse sands	<i>Solenidae</i> , <i>Mactriidae</i> and <i>Donacidae</i> community of the infralittoral sands and muddy sands	<i>Mediomastus fragilis</i> , <i>Lumbrineris</i> spp. and venerid bivalves in circalittoral coarse sand or gravel (A5.132)
<i>Zostera marina</i> beds	<i>Zostera marina</i> community of the infralittoral sandflats	<i>Zostera marina</i> / <i>Zostera angustifolia</i> beds on lower shore or infralittoral clean or muddy sand (A5.5331)

Classic quantitative benthic sampling methods may be more precise and more appropriate for detecting the subtle biological differences that allow the different benthic assemblages living within a single DFO habitat to be distinguished. In fact, direct field observations may be less appropriate than benthic sampling methods for habitats characterized by small individuals, such as small amphipods or polychaetes. The DFO method primarily assesses macrofauna on the basis of visible bioturbations and structures or the tracks the fauna produce, and thus small bivalves or polychaete species are underestimated. In addition, we deliberately chose

to select a small number of megafaunal species that can be identified directly in the field, sometimes at the genus or family taxonomic level. However, we assume that the very large number of observations provided a counterbalance for this potential bias. Beyond what has been stated, several authors have shown that the family level is well suited for describing macrofaunal patterns (Warwick, 1988; Warwick *et al.*, 1990; Gray *et al.*, 1992).

In this study, we use direct field observations at a site characterized by highly fragmented landscapes. The DFO method would be less appropriate in more homogeneous

landscapes and might have to be modified slightly. First, it is clearly more difficult to detect gradual rather than abrupt sedimentary and biological changes in the field. Second, in many homogeneous sandflats, the bathymetric and sedimentary characteristics are very gradual and the DFO method would have to be adapted to ensure that the DFO transects cross the different principal bathymetric and sedimentary features. In addition, the accuracy of the benthic habitat mapping depends both on the spatial resolution of the aerial photographs and on the zoom scale used to map the habitats on the GIS. Therefore, we strongly recommend that potential DFO method users obtain photographs that are as accurate as possible and that they always apply the same zoom scale when mapping on the GIS.

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