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# Regional and latitudinal patterns of soft-bottom macrobenthic invertebrates along French coasts: Results from the RESOMAR database

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## ABSTRACT

This study aims to describe the patterns of soft bottom macrozoobenthic richness along French coasts. It is based on a collaborative database developed by the "*Réseau des Stations et Observatoires Marins*" (RESOMAR). We investigated patterns of species richness in sublittoral soft bottom habitats (EUNIS level 3) at two different spatial scales: 1) seaboards: English Channel, Bay of Biscay and Mediterranean Sea and 2) 0.5° latitudinal and longitudinal grid. Total observed richness, rarefaction curves and three incidence-based richness estimators (Chao2, ICE and Jacknife1) were used to compare soft bottom habitats species richness in each seaboard. Overall, the Mediterranean Sea has the highest richness and despite higher sampling effort, the English Channel hosts the lowest number of species. The distribution of species occurrence within and between seaboards was assessed for each major phylum using constrained rarefaction curves. The Mediterranean Sea hosts the highest number of exclusive species. In pairwise comparisons, it also shares a lower proportion of taxa with the Bay of Biscay (34.1%) or the English Channel (27.6%) than that shared between these two seaboards (49.7%). Latitudinal species richness patterns along the Atlantic and English Channel coasts were investigated for each major phylum using partial LOESS regression controlling for sampling effort. This showed the existence of a bell-shaped latitudinal pattern, highlighting Brittany as a hotspot for macrobenthic richness at the confluence of two biogeographic provinces.

## 1. Introduction

Accurately describing contemporary large-scale patterns of marine macrobenthic diversity is one of the major objectives of marine ecological research (Renaud et al., 2009, Vandepitte et al., 2010). It is particularly relevant in the context of climate change as the distribution of some crustaceans (e.g. Pezy and Dauvin, 2016), bivalves (Philippart et al., 2003), gastropods (Mieszkowska et al., 2007) and polycheates (Wethey and Woodin, 2008) are reported to move further North following temperature increase. However benthic species response to increasing temperature seems to be complex (Hawkins et al., 2009) and slow (Hinz et al., 2011). Indeed, differences in distribution change rates have been reported

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among taxa as well as among life traits (see Pinsky et al., 2013; Poloczanska et al., 2013), illustrating differential responses to climate change among marine life compartments (e.g. highly motile vs slightly motile). Furthermore, global change also includes the introduction of alien species and anthropogenic pressures to coastal ecosystems, which are another major threats for marine biodiversity (Harley et al., 2006; Occhipinti-Ambrogi, 2007) that modifies species composition at the regional scale.

While it is still unclear exactly how global change will modify the regional distribution of species, it seems likely that these changes will occur mostly along latitudinal gradients. In order to track and understand these changes it is necessary to describe and analyze recent and contemporary macrobenthic diversity patterns in this context. Only in doing so can we address the challenge of proposing plausible proximate and historical causes acting at different scales. Furthermore, the assessment of the global distribution of species richness may help to understand differences across region in the context of invasive species propagation (Occhipinti-Ambrogi, 2007). French coastlines offer an interesting case study to address these questions as they cover a large latitudinal gradient including different biogeographical regions from the Northern European seas down to the Lusitanian province.

Species richness is the most elementary, easy to interpret and widely used measure of biodiversity (e.g. Dornelas et al., 2014). It has been shown to follow a – generally unimodal – large-scale (>45°) latitudinal gradient for marine benthic invertebrates with a peak in equatorial regions (Chaudhary et al., 2016).

Marine benthic species richness patterns have scarcely been studied simultaneously on the entirety of French seaboards (from 42°N to 51°N). Indeed, existing studies either had either limited geographic scope (e.g. eastern English Channel, Foveau et al., 2013; English Channel and Bay of Biscay estuaries, Blanchet et al., 2014; Gulf of Lion, Labrune et al., 2008), or focused only on single taxonomic groups (e.g. polychaetes, Dauvin et al., 2006; amphipods, Dauvin and Bellan-Santini, 2004). French coasts are constituted by three seaboards spread over three distinct biogeographical provinces with contrasted hydro-climatic characteristics: i) the English Channel (hereafter EC) including the 60 km of the southern part of the North Sea in the cold temperate Northern European seas, ii) the Bay of Biscay (hereafter BB) in the Lusitanian province and iii) the sub-tropical North-West Mediterranean Sea (hereafter MS) (Spalding et al., 2007). These three seaboards harbor a large panel of sedimentary features (Dauvin, 2015 for the EC; Le Loc'h et al., 2008 for the BB; Aloïsi et al., 1973 for the MS). On the one hand, local and regional abiotic variables – temperature, salinity, hydrodynamics and sedimentary features – exert strong environmental control on species distributions from the local to the regional scale (Warwick and Uncles, 1980; Roy et al., 2000; Levin et al., 2001; Gray, 2002; Bonsdorff, 2006; McArthur et al., 2010) and should have a strong impact on species richness patterns at these scales. On the other hand, broad-scale climatic and hydrodynamics systems should play a role at broader scales (Wiens, 1989; Dinter, 2001; McArthur et al., 2010).

The combination of local, regional and broad-scale processes should result in partially overlapping sets of species as well as richness differences among the three seaboards. Furthermore, because of their adjacency we also expect the EC and BB to share more species than either does with the MS. Indeed, the fluid marine environment offers a wide variety of means to disperse from one location to another (Cowen and Sponaugle, 2009) and most benthic invertebrates (70%) have a larval stage that facilitates to their dispersion. However, hydrological characteristics of marine biogeographical provinces often lead to the creation of frontal structures limiting larval dispersal (Ayata et al., 2010).

The present study aims to verify the alleged decrease of diversity towards higher latitudes using a large historical database. However, because it includes the transition between the Northern European seas and the Lusitanian province, we also expect the latitudinal pattern along French Atlantic coasts to be more complex than a simple linear model (e.g. Roy et al., 1998; Hummel et al., 2016). Indeed, biogeographic boundaries potentially host high species richness by combining the diversity of the adjoining biogeographic areas and sustaining species not found elsewhere (Kark and van Rensburg, 2006). Therefore, the present's objectives are threefold (1) to compare species richness of soft-bottom communities between the three French seaboards, (2) to investigate species composition and proportions of shared species among these regional species pools and, (3) to examine latitudinal patterns along French Atlantic coasts. This work was conducted using historical and recent data from a macrobenthic fauna database compiled by the French *Réseau des Stations et Observatoires Marins* (RESOMAR). This national database was set up within the context of contemporary efforts leading to the constitution of similar large global and regional databases compiling marine biodiversity datasets (e.g. OBIS, Macroben, LargeNet).

## 2. Materials and methods

### 2.1. RESOMAR database

The RESOMAR Benthos Database (http://resomar-benthos.epoc.u-bordeaux1.fr/) compiles historical and current benthic macrofauna datasets collected along the metropolitan France seaboards: English Channel, Bay of Biscay and Mediterranean Sea. It currently holds 106 datasets for a total of 9990 sampling occasions (or station-date dyads) over a 50-year time period (1961–2011) (Fig. 1). In the RESOMAR Benthos Database sampling tools are disparate, however >60% of sampling occasions were sampled by grabs (e.g. Day, Eckman, Hamon, Shipeck, Smith McIntyre). Thus we assumed that, at large-scale, the sampling tools effect was outweighed by that for the sampling effort. The systematic nomenclature of the database was checked following the World Register of Marine Species (WoRMS, http://www.marinespecies.org/). An Expert Committee composed of French experts in taxonomy from the EC, BB and MS was formed to solve possible misidentification issues. International experts were also consulted when needed.

Stations were assigned a habitat type (sensu the European Nature Information System classification - EUNIS, http://eunis.eea.europa.eu/, Davies et al., 2001; Galparsoro et al., 2012) using granulometry (when available) and most abundant species. Otherwise, in the absence of granulometric data, habitat type was derived from sedimentary maps (e.g. CARtographie des HAbitats Marins, REseau BENthique). The EUNIS structure is based on three levels of environmental variables (substrate, biological zone, energy) that define a 'habitat envelope'. Concerning marine habitat types, EUNIS constitutes a hierarchical structure up to six levels combining habitats physical attributes and biological communities, with the levels 1 to 4 informing about the abiotic factors. A total of 67.1% of sampling occasions were assigned to EUNIS level 4, 17.7% to EUNIS level 5, and 0.8% to EUNIS level 6. However, 0.1% could only be assigned to EUNIS level 2 and 1.2% to EUNIS level 3. For the remaining 13.1% sampling occasions neither sediment grain size data nor geographical coordinates were available and no habitat type was assigned.

### 2.2. Subtidal soft bottom subset

This study focuses on large-scale species richness patterns in sublittoral sedimentary habitats (A5. EUNIS) because numerous sampling occasions from these habitats are distributed among the three seaboards. The analysis was conducted at EUNIS level 3 as it was the best compromise between precision and the number of available sampling occasions (86.8% of the database). To capture the most information on species richness and to control for seasonal variability (e.g. storms, winter mortalities…), we only selected sampling occasions collected between March and October because this period coincides with the recruitment period of most benthic species. We excluded from our analysis stations that were clearly known as being impacted by pollution or other strong human-induced stress and thus consider that pollution does not play an important role when comparing the species lists from the 3 seaboards.

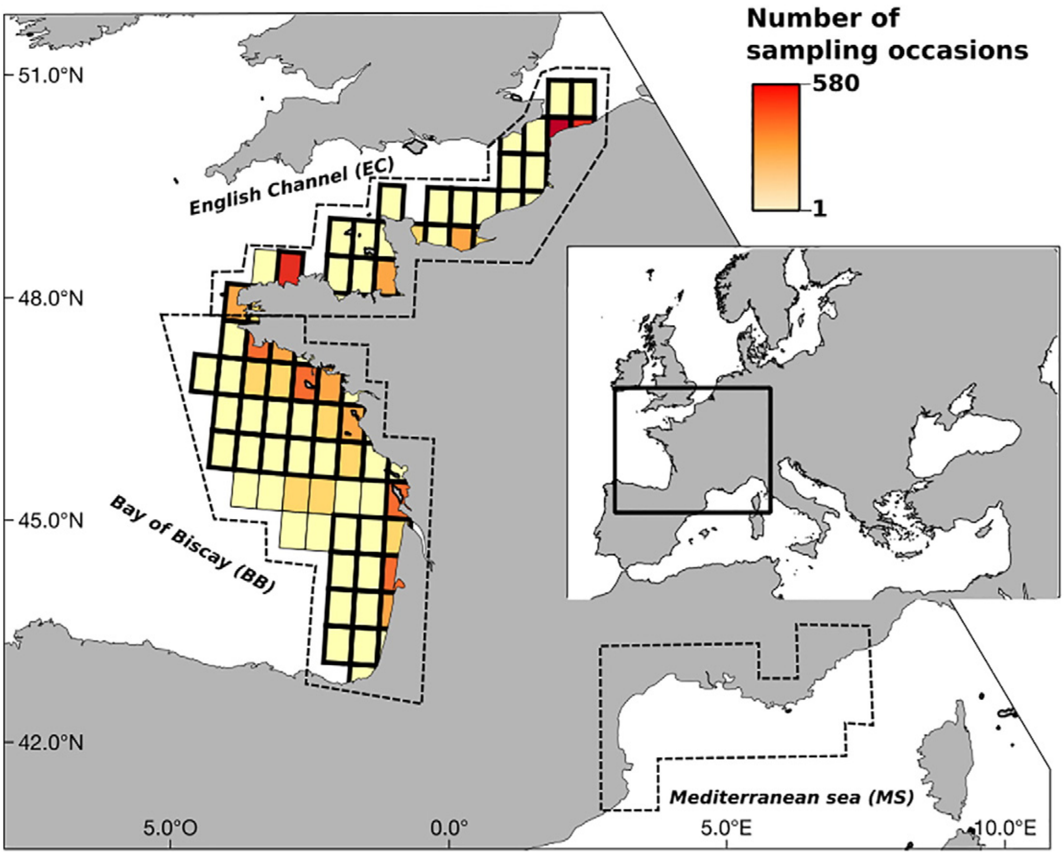

**Fig. 1.** Spatial scope of the RESOMAR Benthos Database. Records cover a 50-years period (1961 to 2011). Sampling effort expressed as the number of sampling occasions is represented in each cell (0.5 × 0.5° grid size). Only cells used to investigate latitudinal pattern of microbenthic richness were shown. Stations selected in this study are located in cells with thick borders.

The selected subset contains 4635 (46.4%) of the 9990 sampling occasions (Table 1). *Sublittoral sand sediments* (A5.2: 2207 sampling occasions) were the most frequent habitat, while *sublittoral mud sediments* (A5.3: 964 sampling occasions) and *sublittoral coarse sediment* (A5.1: 759 sampling occasions) were somewhat less frequent. *Mixed sediments* (A5.4: 463 sampling occasions) were the least abundant. A total of 923 sediment habitats (A5) sampling occasions were not assigned to EUNIS level 3. The distribution of habitat types differed among the three seaboards (Table 1). In the EC, sand sediments (A5.2) were intensively sampled (1069 of sampling occasions) relative to the other habitats. In the BB, 993 sampling occasions were in A5.2, 680 in A5.1, 700 in A5.3, and 241 in A5.4. In the MS, mud (A5.3; 184 sampling occasions) and sand sediments (A5.2; 145 sampling occasions) were more frequent than other habitats (A5.4: 59 sampling occasions; A5.1: 31 sampling occasions). This discrepancy warrants the use of methods controlling for sampling effort in the analyses described below. Finally, when the identification of specimens was ambiguous, taxa were designated as their parent taxa (e.g. genus), either across the entire database, or for a specific seaboard.

**Table 1**
Observed species richness (S), total number of individuals (N), estimates of total species richness (ICE, Chao2, Jackknife1) and number of sampling occasions for the three seaboards and subtidal sediment habitats (A5.1: sublittoral coarse sediment; A5.2: sublittoral sand; A5.3: sublittoral mud; A5.4: sublittoral mixed sediments, NA: subtidal sediment habitats defined to higher level).

| | S | N | ICE | Chao2 | Jackknife1 | Number of sampling occasions |
|---|---|---|---|---|---|---|
| English Channel (EC) | 1042 | 1,654,849 | 1104.9 | 1239.9 | 1237.9 | 1520 |
| A5.1 | 281 | 5810 | 318.5 | 364.8 | 375.3 | 47 |
| A5.2 | 729 | 1,253,050 | 789.7 | 922.9 | 894.9 | 1069 |
| A5.3 | 377 | 202,207 | 419.0 | 482.1 | 484.9 | 80 |
| A5.4 | 490 | 91,065 | 528.7 | 590.1 | 606.3 | 163 |
| NA | 664 | 102,717 | 723.8 | 827.7 | 834.4 | 161 |
| Bay of Biscay (BB) | 1607 | 620,577 | 1692.1 | 1850.1 | 1877.9 | 2954 |
| A5.1 | 573 | 8864 | 659.9 | 811.4 | 777.7 | 680 |
| A5.2 | 1040 | 119,527 | 1124.5 | 1268.6 | 1293.8 | 993 |
| A5.3 | 860 | 208,133 | 942.4 | 1130.1 | 1095.7 | 700 |
| A5.4 | 703 | 22,552 | 777.5 | 887.7 | 912.3 | 241 |
| NA | 971 | 261,501 | 1039.3 | 1143.4 | 1171.8 | 340 |
| Mediterranean Sea (MS) | 1765 | 604,706 | 1895.4 | 2137.3 | 2150.8 | 841 |
| A5.1 | 326 | 13,672 | 389.0 | 478.0 | 458.9 | 31 |
| A5.2 | 655 | 36,594 | 743.2 | 966.8 | 872.4 | 145 |
| A5.3 | 861 | 48,741 | 963.5 | 1135.4 | 1119.5 | 184 |
| A5.4 | 730 | 21,120 | 843.5 | 1073.8 | 993.0 | 59 |
| NA | 1254 | 484,579 | 1357.2 | 1595.3 | 1558.4 | 422 |

### 2.3. Data analysis

#### 2.3.1. Benthic richness across French seaboards

Species richness estimates for the three seaboards were obtained with: 1) total observed richness, 2) expected richness as obtained from sample-based taxon sampling curves (Gotelli and Colwell, 2001), and, 3) three incidence-based richness estimators (Chao2: Chao, 1987; ICE: Lee and Chao, 1994; Jackknife1: Burnham and Overton, 1978, 1979) adapted to datasets with varying sample sizes and large sample grain size (Brose et al., 2003; Hortal et al., 2006).

The proportions of shared species between regions were estimated using a constrained rarefaction procedure accounting for differences in sampling effort in the three seaboards. For each seaboard and each comparison, two sample-based rarefaction curves were computed: one for species shared with the other seaboard(s) under consideration, and another for species found only in the considered seaboard. These curves are strictly additive: for a given sampling effort the sum of their expected richness gives the expected richness for the seaboard rarefaction curve, i.e. the one computed using all species in the seaboard. In the two seaboards case four rarefaction curves were computed, two for each seaboard. This procedure thus yielded one estimate for each of the two numbers of species found in a single seaboard and two estimates for the number of species shared between the two seaboards. The lowest of the latter was used as the number of shared species and the exceeding species were simply transferred to the seaboard of origin (see Appendix 1 for further details and R code). Proportions of shared species were estimated for the lowest number of sampling occasions across the three seaboards.

#### 2.3.2. Macrobenthic richness latitudinal pattern

The latitudinal richness pattern in BB and EC was studied by first binning samples in 0.5° × 0.5° cells (ca. 2100 km$^2$ area). Linear models of richness and sampling efforts, as a function of latitude, were first computed to take into account the disparities in sampling effort along French seaboards. The relationship between species richness and latitude from the Northern EC to the Southern BB was then investigated with LOESS regression between the residuals of these two models (Cleveland et al., 1991).

All data analyses were executed with R 3.1.3 (R Core Team, 2015) using the fossil (Vavrek, 2011), iNEXT (Hsieh et al., 2016) and vegan (Oksanen et al., 2015) packages; the RESOMAR database was accessed with the RMySQL package (Ooms et al., 2016).

## 3. Results

### 3.1. Subtidal soft bottom subset

The 5315 sampling occasions in the subset accounted for 2,880,132 (47.8%) of the 6,021,856 individuals in the RESOMAR benthos database and contain 2624 (84.3%) of the 3111 taxa: 1958 taxa identified to the species level within 1126 genera, 471 families, 132 orders, 52 classes and 13 phyla. From this point on, and for clarity's sake, "species" and "species richness" refer to the lowest taxonomic level at which specimens were identified, either species or genus.

No species was ubiquitous (i.e. occurred in all sampling occasions), and 30.7% were restricted to 1 (20.0%) or 2 (10.7%) sampling occasions. Only 124 species (6.1%) were singletons (i.e. represented by a single individual) and 133 (6.5%) doubletons (i.e. represented by two individuals).

Overall, annelids and arthropods were the most abundant as well as the richest phyla, accounting for 32.5% and 28.7%, respectively, of the total observed richness. Molluscs followed with 20.7% and other less abundant phyla made up <5.3% of the total observed richness (Table 2). Annelids occurred in most (91.4%) sampling occasions, as well as molluscs (76.7%) and arthropods (73.9%). Echinoderms occurred in 61.4% of sampling occasions, but accounted for only 4.8% of the total observed species richness (Table 2).

**Table 2**
Observed species richness (S), total number of individuals (N), and Number of sampling occasions (F) for each taxonomic group of the soft-bottom subset. Numbers into brackets give the percentages of total observed richness for each group.

| | S | N | F |
|---|---|---|---|
| Annelida | 852 (32.5) | 1,431,006 (49.7) | 4858 (91.4) |
| Arthropoda | 754 (28.7) | 935,234 (32.5) | 3930 (73.9) |
| Mollusca | 543 (20.7) | 308,506 (10.71) | 4078 (76.7) |
| Cnidaria | 138 (5.3) | 10,387 (0.4) | 1613 (30.3) |
| Echinodermata | 127 (4.8) | 70,990 (2.46) | 3266 (61.4) |
| Chordata | 82 (3.1) | 3295 (0.1) | 776 (14.6) |
| Porifera | 43 (1.6) | 227 (0.01) | 101 (1.9) |
| Bryozoa | 32 (1.2) | 185 (0.01) | 143 (2.7) |
| Sipuncula | 24 (0.9) | 49,445 (1.7) | 1400 (26.3) |
| Echiura | 8 (0.3) | 117 (0.004) | 58 (1.1) |
| Brachiopoda | 8 (0.3) | 807 (0.03) | 59 (1.1) |
| Hemichordata | 7 (0.3) | 166 (0.01) | 72 (1.4) |
| Phoronida | 6 (0.2) | 69,769 (2.42) | 418 (7.9) |

All species richness analyses were first conducted using all phyla listed in Table 2. Species richness patterns were then restricted to the four most abundant and frequent phyla: annelids, arthropods, molluscs and echinoderms.

### 3.2. Benthic richness across French seaboards

There was no clear relationship between species richness and sampling intensity at the seaboard scale. This holds whether sampling effort was expressed as the number of sampling occasions or as the total number of individuals. Indeed, at the seaboard scale, observed and extrapolated species richness increased from north (EC) to south (MS) but the number of sampling occasions was higher in the BB (2274) than in the other seaboards (EC: 1520; MS: 841; Table 1). Moreover, the number of individuals was three times higher in EC (1,654,849) than in BB (620,577) and MS (604,706; Table 1) while species richness in MS was about twice that observed in EC for each subset (Table 1).

Also, as noted before, the distribution of sampling occasions across habitat types differed between seaboards (Table 2). Comparisons of habitat richness among seaboards yielded no consistent ordering considering either observed or extrapolated richness. Within coarse sediments (A5.1; 573 species) and sand sediments (A5.2; 1040 species), BB hosted the highest observed richness followed by the MS (A5.1: 326 species; A5.2: 655 species) and the EC (A5.1: 281 species; A5.2: 729 species; Table 1). For mud (A5.3) and mixed sediments (A5.4), EC was the poorest seaboard (Table 1). However, taking discrepancies in sampling effort into account gave a consistent pattern of ordering. Rarefied richness for the MS was consistently higher across all habitats (Fig. 2).

Using a constrained rarefaction procedure (see details above), the MS stands out with 954 unique species compared with either the EC or BB, while the BB showed 286 (12%), and the EC only 143 (6%) exclusive species (Fig. 3). About a quarter of the 2386 species in the dataset were shared by the three seaboards (555 species or 22%). In pairwise comparisons, the MS shared more species with BB (≈35%) than with EC (≈28%) regardless of phyla, while BB and EC shared about 50% of their species (Table 3).

To summarize, the MS was the least sampled but hosted the highest benthic macro-invertebrates species richness and was characterized by a large number of exclusive species. The EC had the lowest species richness but sampling occasions mostly comprised sand sediments. Despite a large number of sampling occasions, the BB had intermediate species richness. These two contiguous seaboards shared about half of their species.

### 3.3. Macrobenthic richness latitudinal pattern

After controlling for sampling effort, maximal species richness along the BB and EC seaboards was found at the confluence of these two

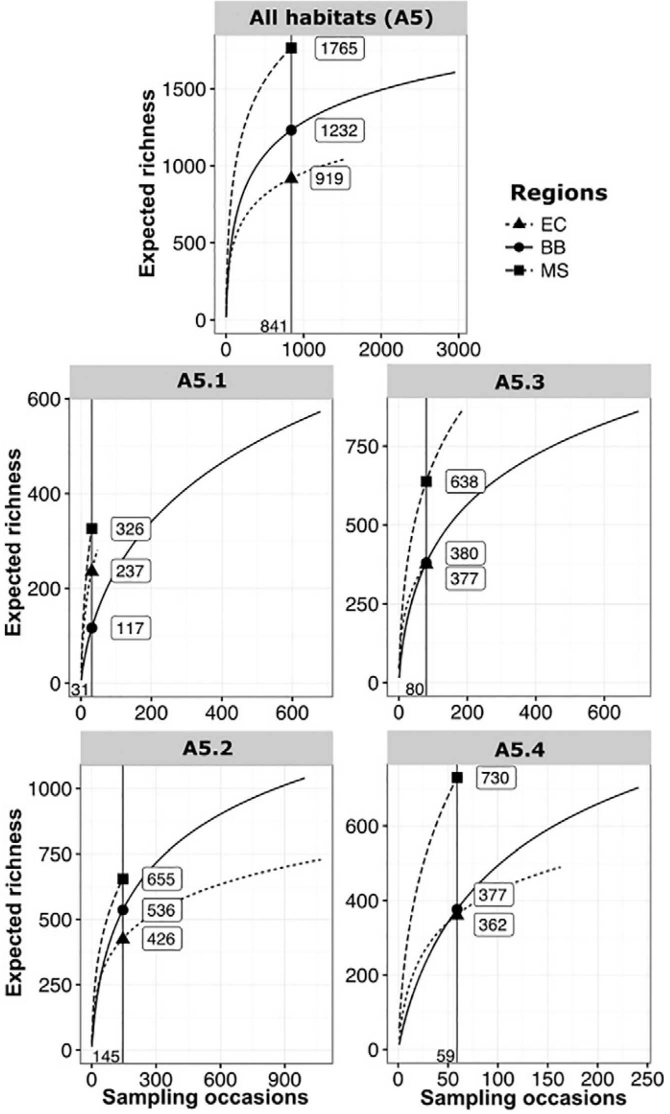

**Fig. 2.** Sample-based rarefaction of benthic macro-invertebrates on the subtidal soft sediments subset (A5.1: sublittoral coarse sediment; A5.2: sublittoral sand; A5.3: sublittoral mud; A5.4: sublittoral mixed sediments) within each seaboard (EC: English Channel; BB: Bay of Biscay; MS: Mediterranean Sea). The vertical line represents the minimum effort.

seaboards. Indeed, for all taxa combined, annelids, as well as molluscs, LOESS regression produced bell-shaped curves peaking at Brittany (Fig. 4). Total observed species richness at the 0.5° grid scale ranged from 30 to 804 taxa in Brittany, compared to richness of 42 to 290 species in the rest of EC and 6 to 406 species in the rest of BB (raw data not shown). The 148 species shared (7.9%; Fig. 3) between these two seaboards (and also absent from the MS) were mostly found along Brittany's coasts and scarcely elsewhere (results not shown). Moreover, grid cells in Brittany hosted more than twice as many species as those in the rest of BB and EC for dominant phyla: polychaetees 280, 154, and 133 species for Brittany, BB, and EC respectively; arthropods 257, 138, and 83 species; molluscs 210, 93, and 58 species; and, echinoderms 144, 39, and 15 species.

## 4. Discussion

Investigating species richness patterns of several high-level taxa at broad-scale and regional scale is an innovative aspect of the present paper. General dominance patterns of the major phyla were of the same order of magnitude as those reported in other studies that cover all, or part, of the area under study (Arvanitidis et al., 2002; Ellingsen and Gray, 2002; Le Loc'h et al., 2008; Sokołowski et al., 2012; Foveau et al., 2013). Annelids and arthropods tend to dominate these communities, in terms of abundance, and often species richness (Knox, 1977; Hutchings, 1998; Arvanitidis et al., 2002 for annelids – Dauvin et al., 1994; Prato and Biandolino, 2005; Lourido et al., 2008 for arthropods).

Explanations for observed richness patterns can be sougth at the local-scale, regional-scale and broader across seaboard-scale. Indeed, temperature influences period of reproduction, the number of cohorts and generations per period of reproduction (univoltism, plurivoltism), egg development, the survival of larvae and adults and the capacity of organisms to settle on substrates (Hiscock et al., 2004). Salinity strongly affects richness patterns: Bonsdorff (2006) revealed a decrease of diversity from the South to the North of the Baltic Sea. Along such gradients, marine species diversity decreases with decreasing salinity and conversely for freshwater diversity (Cognetti and Maltagliati, 2000). Hydrodynamic conditions drive the distribution of invertebrates via transport and dispersal of larvae and adults and can have important consequences on population dynamics (Levin et al., 2001). Furthermore, the physical stress resulting from hydrodynamics determines distribution patterns of sedimentary bed forms and therefore plays an important role in the distribution of benthic communities (Stride, 1973; Ellingsen and Gray, 2002; Van Hoey et al., 2004; Dauvin, 2015). Indeed, the 3D structure of sediments can provide refuge for numerous species, and heterogeneous sediments with more potential niches can foster higher diversity than homogeneous sediments (Ellingsen and Gray, 2002).

Although France's seaboards have contrasting hydro-climatic conditions, they are all strongly influenced by freshwater inputs – the Seine River in the Eastern part of the EC; the Vilaine, Loire and Gironde rivers in the BB; the Rhone river in the Gulf of Lion – establishing salinity gradients and dispersal barriers between the coast and the open sea (Bourrin and Durrieu de Madron, 2006; Ayata et al., 2011; Dauvin, 2012). They also share similar soft-bottom habitat types, i.e. coarse sediments (A5.1), sand sediments (A5.2), mud (A5.3) and mixed sediments (A5.4, EUNIS 2016, Habitat Classification level 3). Nonetheless, the prevalence and spatial distribution of these habitats differ from one seaboard to the other due to hydro-climatic and topographic features.

### *4.1. Benthic richness across French seaboards*

In accordance with our hypothesis, macrobenthic richness differs among French metropolitan seaboards with the MS having the highest exclusive species and total richness regardless of phyla. At nearly 40%, the proportion of exclusive species is twice the endemism rate reported by Bazairi et al. (2010), but this is certainly an artifact of the more restricted geographic scope of the present study. Still, its complex geological history and higher temperature, are probably responsible for the distinctness of the MS (Coll et al., 2010). The alternation of ice ages and warm interglacial during the Quaternary and the post-Pliocene "diversity pump" from the Atlantic are recognized to have promoted speciation processes in the MS (see Bianchi and Morri, 2000). Also, the MS subset is probably influenced by the influx of the NE Atlantic, inducing a wide range of physical and chemical conditions (Pérès, 1967; Coll et al., 2010; Dauvin et al., 2013), which may favor the settlement of both cold and warm water species (Koukouras et al., 2001). Finally, for the past thirty years, several new species have been brought to the MS by way of shipping, aquarium species propagation, and aquaculture (Coll et al., 2010; Nunes et al., 2014).

Because of its complex mosaic of habitats (Le Loc'h et al., 2008) the BB has the potential to host high species richness. Indeed, BB's "Grande Vasière" contributes to the region overall intermediate richness. Large inputs of freshwater that induce large amplitudes of physical and chemical conditions could also favor richness in the region as they allow for the settlement of both cold and warm water species as well as species adapted to brackish waters. The low proportion of species shared between BB and MS could also be an artifact of the RESOMAR database not covering

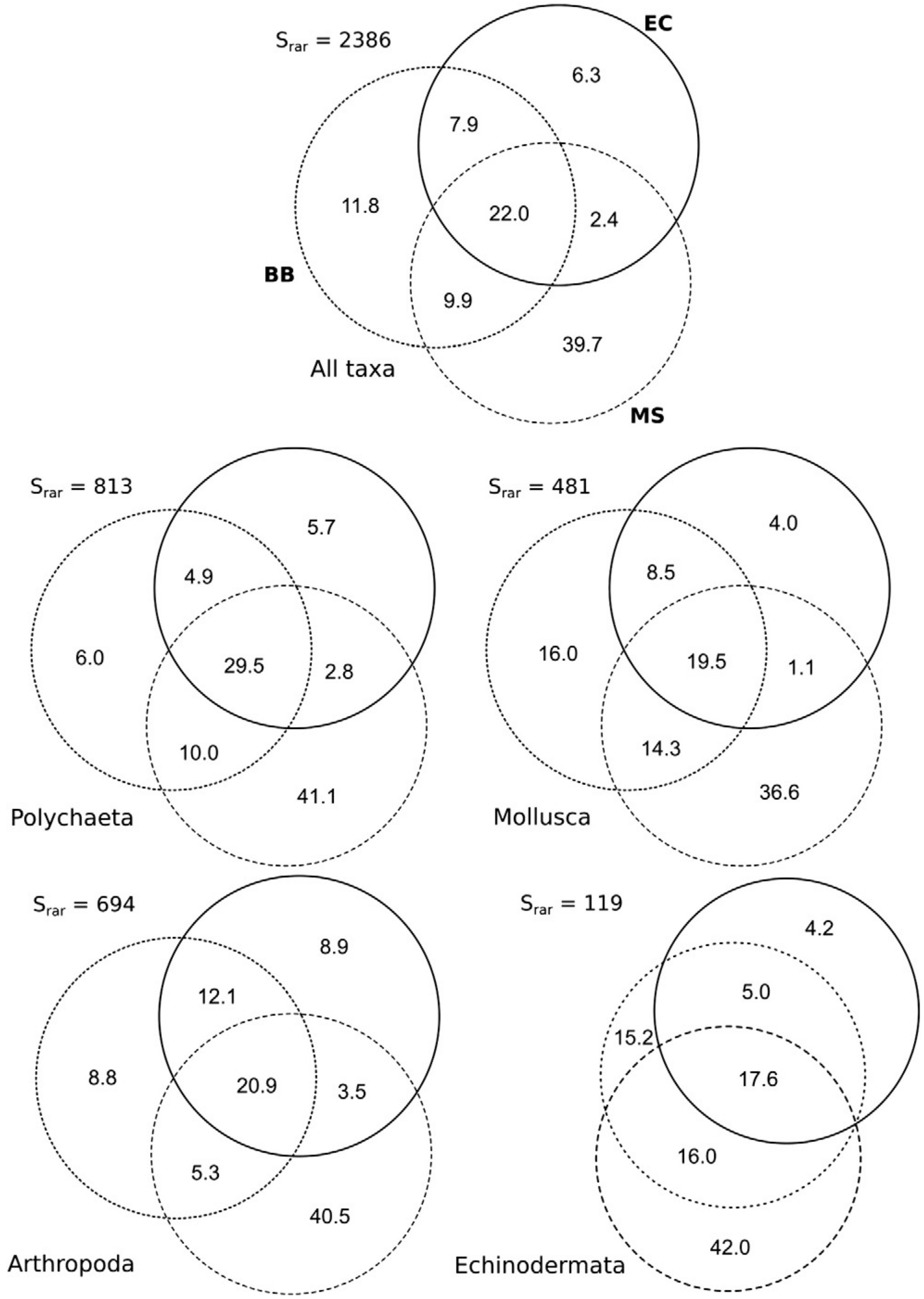

**Fig. 3.** Venn diagram obtained by a constrained rarefaction procedure (see Material and methods for details) describing the number of shared species between seaboards of the soft-bottom subset (EC: English Channel; BB: Bay of Biscay; MS: Mediterranean Sea).

Portuguese and Spanish coasts. Indeed, some holobenthic species originally described as endemic to the MS have been encountered along the Portuguese coast and in the BB which shows deep outputs of saltier waters that spread along the Atlantic coast to the south of Ireland (Dauvin, com. pers.).

In the present study, EC is the most species poor seaboards, with total richness lower than that previously reported for a similar sampling effort (i.e. 318 stations in Foveau et al., 2013, Fig. 2). However, this previous study willingly maximized richness by sampling a plethora of coastal and offshore habitats while the present effort is based strictly on coastal monitoring datasets and a restricted set of habitats: for example, the pebble and gravel habitats was the richest of those in Foveau et al. (2013), but is not considered here as they are scarcely present in the RESOMAR database. Interestingly, we report nearly twice as many species as Foveau et al. (2013) for sand sediments (729 vs. <400 species). At first sight the EC's low species richness could be linked to a north-south richness gradient. However, regional ecological, geological and evolutionary processes could also explain the low species richness in the EC. Indeed, after the last glacial maximum (15,000 BP), the English Channel was still land and was recolonized only very recently and probably through two different paths – the Celtic Seas and the North Sea – as reported for numerous invertebrate species (Jolly et al., 2006). This recent colonization could thus partly explain the low species richness in the south of the North Sea as species are still migrating to this area from glacial refugia (Ellingsen and Gray, 2002). Moreover, differences in richness between regions could also be related to within-region habitat distribution. While the BB offers a rich mosaic of habitats and the MS harbors contrasted habited along a depth gradient, strong

**Table 3**
Pairwise percentages of shared species between seaboards of the soft-bottom subset as obtained by a constrained rarefaction procedure (see Material and methods for details). Values correspond to proportions of species shared between two seaboards relative to the total number of species in the two seaboards. (EC: English Channel; BB: Bay of Biscay; MS: Mediterranean Sea).

| | | EC | BB |
|---|---|---|---|
| BB | All taxa | 49.7 | |
| | Polychaeta | 58.4 | |
| | Arthropoda | 55.5 | |
| | Mollusca | 44.2 | |
| | Echinodermata | 39 | |
| MS | All taxa | 27.6 | 34.1 |
| | Polychaeta | 34.4 | 41.9 |
| | Arthropoda | 26.8 | 28.8 |
| | Mollusca | 24.4 | 35.2 |
| | Echinodermata | 20.8 | 35.1 |

physical constraints in the EC lead to large extents of offshore continuous coarse and sandy sediments that dwarf other habitats and confine muddy habitats to bays and estuaries that cover a small part of this region (Dauvin, 2015). This is reflected in our database where sand sediments dominate the EC (79.8% of sampling occasions) while the proportions of each habitat are nearly balanced in the BB and MS (Table 1). The Liguro-Provencal current - flowing from east to west - maintains Rhône River particles on the continental shelf area where they undergo several deposition/resuspension cycles (Durrieu de Madron et al., 2000; Bonifácio et al., 2014). Coarse sediments of the MS are under-represented in the database because they are restricted to the edge of the shelf and are difficult to sample (Table 1).

The BB and EC share more species than BB and MS which can be explained by the fact that BB and EC form a continuum while the MS is separated from both areas by some 2000 km of coasts, namely Spanish and Portuguese coasts, not included in our dataset. This hypothesis is corroborated by Kinlan and Gaines (2003) who estimated that the genetic dispersion distance range of marine invertebrates varies between a few meters and several hundred kilometers (>500 km). Nevertheless, the Iroise Sea, located between BB and EC, hosts thermal and haline structures that can hinder dispersal between the EC and BB (Pingree et al., 1982; Boyer et al., 2009; Ayata et al., 2010) and thus potentially limit the number of shared species between the two seaboards. Indeed, the pelagic stages are strongly sensitive to hydrological discontinuities - i.e. where water bodies have different physical and chemical properties - such as thermic and haline fronts (Ayata et al., 2010). In the BB, the water column is mixed by climatic events during the winter period (storms) and it is stratified during summer (Ayata et al., 2010, 2011) inducing barriers. The Strait of Gibraltar separates the MS from the Atlantic and creates strong currents, as well as thermal and haline fronts (Millot, 1999; Cimmaruta et al., 2005) limiting larval propagation. At the western tip of Brittany, the Iroise Sea and water bodies between Le Conquet and Roscoff host thermic and haline frontal structures, and constitute a cold-water enclave that could favor the settlement of stenotherm species strongly impacted by large thermic amplitude especially in the Eastern Channel (Gallon et al., 2014; Dauvin, 2015). In addition to sea temperature increase, global change induces modifications in current and wind circulations, turbulence, and stratification (Harley et al., 2006). At broad-scale, these modifications could strongly affect connectivity patterns (e.g. time retention, currents speed) and thus deeply modify the current distribution of invertebrates between the three French seaboards. Among these changes, it can be expected that the number of species shared between seaboards will increase, mainly through the arrival of southern-species, eurytherm species, and alien species through shipping or other means of long distance transport. However, because of present hydrodynamic features along French coasts, these changes are not expected to be evenly distributed. Indeed western and north-western Brittany have been identified as the most stable areas for seaweeds (Gallon et al., 2014). In addition, aquaculture (e.g. oysters) induces transports of living organisms and associated

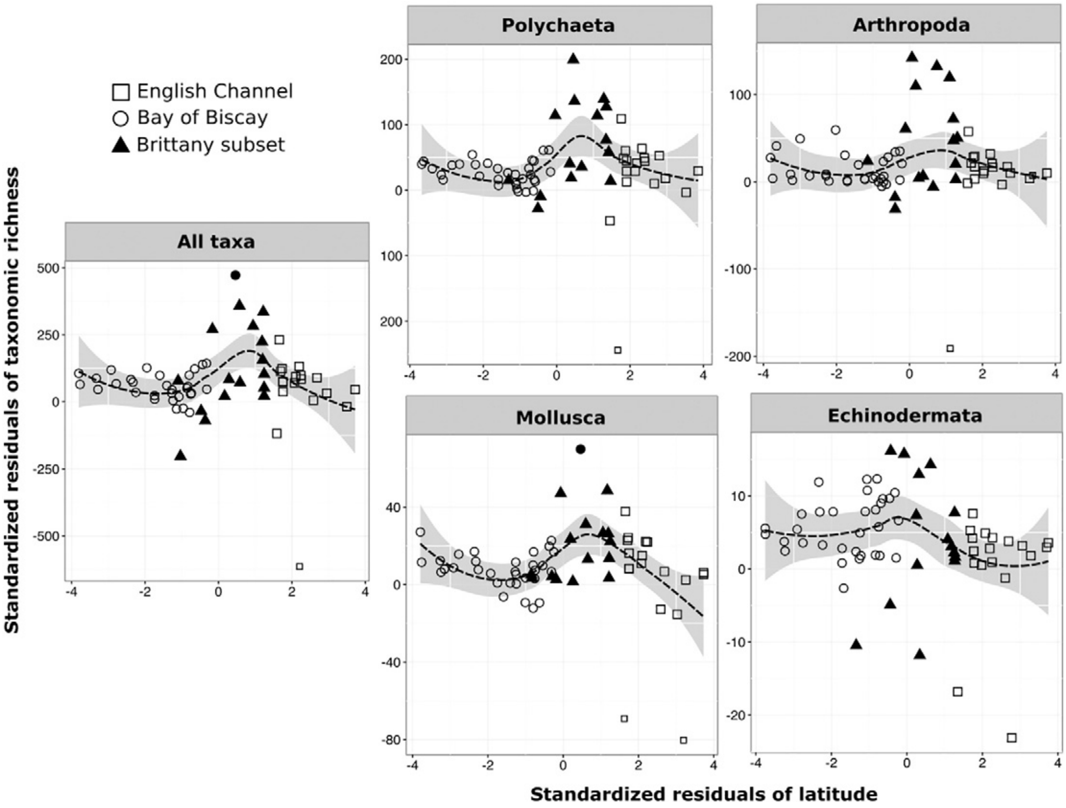

**Fig. 4.** LOESS regressions between species richness and latitudinal bins of the soft-bottom subset while controlling for sampling effort from the Northern English Channel to the Southern Bay of Biscay. Solid lines represent LOESS regressions and gray shades confidence intervals.

species between the MS and the BB/EC seaboards (e.g. Bachelet et al., 1990, 2004; Goulletquer et al., 2002). These activities constitute important vector of long distance species introduction between seaboards separated by several thousand kilometers of coastlines and hydrological barriers and, as such, could contribute to further homogeneisation of benthic invertebrate species assemblages among the MS and BB/EC (Olden and Rooney, 2006).

### *4.2. Macrobenthic richness latitudinal pattern*

By focusing on a similar latitudinal extent (42°N to 51°N) most studies conducted at large and medium scales revealed either linear relationship between richness and latitude (Crame, 2000; Rex et al., 1993; Roy et al., 1998; Clarke and Lidgard, 2000; Roy et al., 2000) or no relationship (Dauvin et al., 1994). By reviewing 27 published studies and based on the geographic distribution of 65,000 species within the Ocean Biogeographic Information System (OBIS), Chaudhary et al. (2016) revealed a bimodal distribution (peaks at 50°N to 55°N and 20°S to 25°S) that dips close to the equator. Most authors suggest that latitudinal gradients differ both between hemispheres (Crame, 2000; Macpherson, 2002) and marine taxa (Chaudhary et al., 2016). The different hydro-climatic conditions in both hemispheres could explain the geographic asymmetry (e.g. upwelling, rivers; Roy et al., 1998; Macpherson, 2002). Nonetheless, an analysis of data published from 1993 and 2003, taking account three major oceans (Pacific, Atlantic, and Indian), did not reveal any pattern differences between northern and southern hemispheres regarding either the slope or the strength of the richness gradient (Hillebrand, 2004). Overall, observed richness tends to decrease with increasing latitude such gradient being supported by data on molluscs (Rex et al., 1993; Roy et al., 1998, 2000; Crame, 2000), crustaceans (Dworschak, 2000) as well as bryozoans (Clarke and Lidgard, 2000). In addition, spatial scales of observation can have a great bearing on richness trends and patterns, as well as in the underlying factors governing them (Wiens, 1989; Dinter, 2001; Willig et al., 2003; Hillebrand, 2004). Indeed, at medium (<10°) and regional spatial scales (<3°), the existence of latitudinal gradients remains controversial as some authors have failed to detect any consistent patterns (Ellingsen and Gray, 2002). Some even reporting opposite trends – i.e. an increase of species richness with higher latitude (e.g. in the North Sea, Heip et al., 1992; Rees et al., 1999; along the Argentina coasts, Doti et al., 2014) or a bell-shaped trend (Gray, 2000; Hummel et al., 2016). Our study revealed a more complex pattern: a bell-shaped curve peaking in Brittany between 47°N to 49°N latitude (Fig. 4). This suggests that local hydroclimatic conditions could be key factors contributing to richness patterns at such a regional scale. Although Brittany was previously recognized as a hotspot for seaweed species biodiversity (Kerswell, 2006; Santelices et al., 2009) specifically because it is located in a biogeographic transition area, this study gives the first indications that Brittany as a whole, is a hotspot for benthic macrofauna biodiversity. Previous studies had focused on either southern or northern Brittany independently from one another (e.g. Glémarec, 1969; Cabioch et al., 1977) while this is the first study investigating the distribution of macrozoobenthic richness along the entire Atlantic and Channel coasts.

The causes for this pattern may be found in the topographic, hydrodynamic and oceanographic features of the area. Firstly, in Brittany, several coastal embayments (semi-enclosed areas) are characterized by a mosaic of benthic habitats created by the co-occurrence of fine sediments brought by coastal rivers and coarse sediments originating from strong tidal currents, e.g. the Normano-Breton Gulf (Retière, 1979; Cabral et al., 2015), the Bay of Morlaix (Ehrhold et al., 2011), the Bay of Brest (Grall and Glémarec, 1997), the Bay of Concarneau (Ehrhold et al., 2006) and the gulf of Morbihan (Glémarec, 1964). The heterogeneity of habitats and the co-existence of numerous microhabitats could provide a high number of potential niches and diverse ways to exploit the environmental resources, thus increasing species richness (Benedetti-Cecchi and Cinelli, 1995). Surrounding areas such as the eastern part of the EC and the central part of the BB are highly dominated by large and homogenous habitats (coarse sediments or fine sand) (Chassé et al., 1978; Cabioch, 1968 for the Western Channel). Secondly, the coexistence of sedimentary habitats with rocky habitats at small scales (km) could also explain the high diversity of benthic assemblages in Brittany. Moreover, macroalgae facilitate the distribution and the dispersion of numerous taxa by creating refuges from environmental stressors by providing substrate for settlement and growth (Thomsen and McGlathery, 2005; Thomaz and da Cunha, 2010). Finally, within the ‘temperate Northern Atlantic’ realm, Brittany is a biogeographic transition zone (sensu Morrone, 2004 in Ferro and Morrone, 2014) at the boundary between the cold temperate and boreal Northern European Seas and Lusitanian provinces (Spalding et al., 2007). As such it is expected to have high species richness by harboring species from the two biogeographic provinces. Interestingly, thermal and haline structures in the Iroise Sea can hinder dispersal between the EC and BB (Pingree et al., 1982; Boyer et al., 2009; Ayata et al., 2010) and numerous benthic species find their limit of distribution in Brittany (e.g. Cabioch et al., 1977; Grall et al., 2015; Le Duff and Grall, 2012; Quillien et al., 2012).

### *4.3. Limitations*

The RESOMAR database reflects the French synergy around studies on benthic compartments. This database not only allows for the safeguard of invaluable ecological datasets, but also opens new opportunities to investigate diversity patterns at spatial scales larger than that allowed by any of the individual datasets. Bringing together these numerous and diverse datasets, covering large spatial and temporal scales, in a readily usable format constituted a great challenge, but now offers great opportunities to study ecological pattern at bioregional scales. Despite our efforts to homogenize the database and reduce the impact of potential confounding factors, some remain such as those induced by the specificity of each dataset as each comes from a specific research program with its own sampling design.

## 5. Conclusion

In conclusion, this study reveals macrobenthic richness distribution along the three metropolitan France seaboards. Macrobenthic richness is shown to differ between seaboards regardless of benthic habitat and the MS has the highest richness and the highest number of exclusive species. The EC hosts the lowest number of species while it is the most sampled. Owing to their proximity and more moderate barriers to dispersal, the EC and BB share a higher proportion of taxa than either shares with the MS. Finally, the investigation of latitudinal gradient along French Atlantic coasts reveals Brittany as a whole as a hotspot for macrobenthic richness, according to its transitional location between BB and EC and its habitats high diversity. This pattern is mainly constrained by hydro-climatic and topographic conditions such as hydrodynamics, complexity of the mosaic of benthic habitats, amplitudes of physical and chemical conditions, and historical processes.

In the context of global change, one would anticipate that the degree of differentiation between seaboards and latitudinal patterns may change in years to come. In such context, the RESOMAR database will surely represent as a baseline for describing and comparing macrobenthic fauna diversity patterns along French coasts.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.seares.2017.03.011.

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