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Morphospecies and taxonomic sufficiency of benthic megafauna in scientific bottom trawl surveys

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Abstract:

Scientific fisheries surveys routinely identify a large diversity of commercial and non-commercial benthic megainvertebrates that could provide useful information for Marine Strategy Framework Directive (MSFD) descriptors. Species is obviously the basic taxonomic level to which most ecological studies and theories refer. Identification at this level of organization is indeed always preferred over any other taxonomic level. Nevertheless, aggregation of species to higher taxonomic levels may be unavoidable sometimes, since errors of identification are known or suspected to occur in many surveys. Using analyses of taxonomic sufficiency (identification of organisms at various taxonomic resolutions) and groups of morphospecies (taxa identified easily by non-experts on the basis of evident morphological traits), this study aims to quantify the loss of ecological information incurred by partial identification of benthic megafauna in bottom trawl surveys in order to put such data to good use. The analyses were conducted on five scientific surveys representing a large range of geographical areas (from 150 km^2 to 150 000 km^2) and environmental conditions. Results show that genus, family and, particularly, morphospecies are good surrogates for species identification in community analyses. We suggest that bottom trawl surveys can provide reliable megafauna data that may usefully complete those obtained by grab surveys. The use of morphospecies could lead to new strategies, combining different datasets to provide indicators for MSFD descriptors (e.g. D6).

Highlights

► This study quantifies the ecological loss of misidentifying benthic megafauna. ► It suggests that the morphospecies is a good surrogate to species identification. ► Bottom-trawl surveys provide reliable data to inform MSFD benthic descriptors.

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1. Introduction

The main objective of the Marine Strategy Framework Directive (MSFD; 2008/56/EC) is to achieve or maintain good environmental status (GES) by 2020. To fulfil MSFD requirements, 11 qualitative descriptors and a suite of indicators associated with each descriptor have been selected (Rice et al., 2012). European Member States have already initiated the reviews required to provide information for these descriptors and the estimation of the related indicators that will be used to assess the GES (Borja et al., 2011; Rombouts et al., 2013). Among the MSFD descriptors, D6, which concerns Sea Floor Integrity, and three others (D1, D2 and D4) include indicators that refer directly or indirectly to macro- and megainvertebrates (EC, 2010).

In a recent report on the Sea Floor Integrity descriptor (D6), Rice et al. (2010) underlined that most time series and established monitoring programs of benthos are conducted relatively nearshore and have restricted spatial coverage. These authors called for new strategies to assess environmental status of the sea floor integrity at regional or sea-wide scales. Scientific bottom trawl surveys dedicated to stock assessment of bentho-demersal fish populations routinely identify commercial and non-commercial benthic macro- and megainvertebrates. These annual surveys often cover large geographic areas (e.g. the North Sea) and could thus be used as a complement to grab surveys in order provide more complete information for MSFD descriptors. Data collected from bottom trawl surveys are available rapidly, as the sizes of the invertebrates collected allow a rapid identification that can be mostly done at sea. This is a considerable advantage over grab samples, which are usually washed through 1 or 2 mm mesh screens and then require a large amount of laboratory time for sorting and identification. Ground fish surveys, particularly those conducted using beam trawls, have already proved efficient for sampling and studying the functional components of the benthic megainvertebrate communities, from filter feeders to detritivores and scavengers (Brind'Amour et al., 2009; Kopp et al., 2013; Tillin et al., 2006).

Despite the attractiveness of such "rapidly-collected" data, important issues regarding the accuracy of the species identification must be addressed before their widespread use. Ground fish surveys are mainly dedicated to fisheries, yet they are often limited by taxonomic and logistic constraints regarding zoobenthos identification. The survey coordinator has "parataxonomists" (sensu Gamez, 1991), rather than taxonomic experts, on board who can easily classify the macro- and megainvertebrate species into large recognizable taxonomic units or morphospecies (Oliver and Beattie, 1996), but hardly classify specimens to the species level. Morphospecies are defined as taxa distinguished solely on the basis of morphological differences easily identified by non-experts. This concept was used extensively in the mid-90s in the terrestrial realm (on plants and insects) and stimulated great debate at the time (Beattie and Oliver, 1999; Goldstein, 1999). However, as recently mentioned by Derraik et al. (2010), "*morphospecies can be a useful technique for invertebrate studies, particularly where time and financial constraints exist* […]". From an ecological point of view, the concept of morphospecies embraces some fundamental aspects of functional ecology. Species sharing similar morphological traits form functional groups that likely occupy similar habitats or respond similarly to a stress (Keddy, 1992; Zobel, 1997). In the case of marine megainvertebrates sampled in bottom trawl surveys, morphospecies may thus define an ecological unit as being as relevant as species to study macro- and megabenthic communities.

Similar to the notion of morphospecies, is the concept of taxonomic sufficiency, which aims to identify organisms to the level of taxonomic resolution sufficient to satisfy the objectives of a particular study (Ellis, 1985; Terlizzi et al., 2003). It is commonly used in environmental assessment studies where taxa other than species serve to detect changes in assemblages exposed to anthropogenic stress (Ellis, 1985; Terlizzi et al., 2003) or natural conditions (Anderson et al., 2005; Vanderklift et al., 1998; Wlodarska-Kowalczuk and Kedra, 2007).

The present study aims to quantify the loss of ecological information brought about by misidentification of the benthic macro- and megafauna in bottom trawl surveys. More specifically we (i) assess the loss of ecological information (taxa richness) with increasing taxonomic level and groups of morphospecies, (ii) compare the results among surveys conducted at different spatial scales (coastal bays to continental shelf), and (iii) provide a list of benthic invertebrate species, for which identification at the species level is crucial during bottom trawl surveys. Our study covers five different ecosystems sampled using different protocols (gear, time, area covered...), thereby precluding any direct comparison among these ecosystems. Our goal is thus not to compare the ecosystems with each other but rather to examine the results obtained in each system to verify the generalization of our conclusions.

2. Materials and Methods

2.1. Case studies and sampling surveys

The IBTSWG (International Bottom Trawl Surveys Working Group) is an ICES- (International Council for the Exploration of the Sea) coordinated working group aiming to improve standardization and collaboration between a number of national surveys (Fig. 1). Two areas can be distinguished: (1) the North Sea and English Channel IBTS and (2) the Western and Southern area IBTS. These areas differ slightly in terms of sampling protocol (ICES, 2012). In the present study, we used the French dataset from three of the IBTS surveys: EVHOE (*EValuation des ressources Halieutiques de l'Ouest Europe*) for the Bay of Biscay, CGFS (Channel Ground Fish Survey) for the English Channel, and IBTS for the southern North Sea (Fig.1C, 1D & 1E).

Simultaneously, France has carried out a number of dedicated coastal nursery surveys, mainly in estuaries, encompassing a variety of coastal habitats ranging from open shallow muddy estuarine areas, under the direct influence of freshwater inflows, to semi-enclosed sheltered muddy marsh areas with shellfish-farming, slightly affected by rivers (Gilliers et al., 2006).

We used the datasets from two of these small-scale surveys: the Bay of Seine and the Bay of Vilaine (Fig. 1A &1B). A technical description of the five sampling surveys is given in Table 1.

2.2. Species taxonomy and selection

Selection of the benthic megafauna in each case study was done prior to all analyses. We accounted for the selectivity of the sampling gear (GOV and beam trawl) and only taxa correctly identified at the species level and countable organisms were included in the analyses. Concurrently, we eliminated all pelagic species, clinging organisms such as barnacles, and species from the Cnidaria phylum from the datasets. Although these organisms represented a large proportion of species richness in two of the case studies (~ 38% in the Eastern English Channel basin and ~ 26% in the southern North Sea), we found it very difficult to estimate their densities precisely. It is thus worth mentioning that any values of species richness given in the present study should be interpreted with caution as the complete range of benthic species was not included in the analyses. The goal of the study was not to compare the species richness among the ecosystems, but to estimate the loss of information within an ecosystem when lowering the taxonomic resolution. Nevertheless, the species remaining in the dataset after this selection are still representative of the megafauna found in each case study: between 62% and 89% of the species richness depending on the case study. Species taxonomy was retrieved and updated from the World Register of Marine Species (WoRMS, 2011).

Taxonomic sufficiency was evaluated at four taxonomic levels (species, genus, family and order) and for the morphospecies (morph) groupings. As morphospecies are morphologically, and often functionally, similar species we sometimes grouped species from different genera and/or families together (Supplementary Material A). For instance, the morphospecies "swimming crabs" (G19 in Supplementary Material A) included all the swimming crabs that

look alike (e.g. *Liocarcinus holsatus*, *Liocarcinus depurator*, *Polybius henslowii*...). We estimated the differences between the morphospecies and the species level by calculating an error rate of identification using the formula from Derraik et al. (2010):

$$\text{Identification error} = \frac{(Ns - Nm)}{Ns}$$

where N_s is the number of species and N_m the number of morphospecies (i.e. morph). This formula is one way of quantifying the loss of ecological information when species are identified at the morphospecies level.

Analyses were restricted to a single year for each case study as our objective was to compare the spatial community structure of the megabenthic invertebrate fauna without considering annual variability. The selected year was chosen as the most representative of the spatial structure for each case study after visual examination of the major habitats identified using the Hierarchical Cluster Analysis (HCA) described in the following section.

2.3. Data analyses

Data analyses were done in three steps. We first assessed the taxonomic community characteristics of the six case studies by calculating the species richness (SR, i.e. number of species) in each case study and by station, as well as a species to higher-level taxa ratio. According to Wlodarska-Kowalczuk and Kedra (2007), the latter ratio index can be viewed as a measure of the applicability of taxonomic sufficiency without making a specific test for it. High ratios could reach values of 4 to 6 whereas low ratios would be below 3 or 4 (Giangrande et al., 2005; Wlodarska-Kowalczuk and Kedra, 2007). Secondly, we conducted HCA with Ward's algorithm (Ward, 1963) on the sites*species densities (individual m^{-2}) matrix of each case study to identify groups of stations (i.e. habitats) that were then used in the estimation of the taxonomic sufficiency. Results from the HCA were also compared with actual sedimentary and bathymetry strata in the five case studies. Thirdly, we assessed the

similarity between the habitats within each case study by comparing the clusters obtained from the HCA for the 4 taxonomic levels and the morphospecies using the Adjusted Rand Index (ARI; Rand, 1971). The species level was considered as the "taxonomic reference" from which deviation was assessed. The ARI is commonly used in data clustering as a measure of the similarity between two partitions (for instance P1 and P2):

$$\text{ARI} = \frac{(n/2)\ (a+d)\ -\ [(a+b)(a+c)-(c+d)(b+d)]}{(n/2)^2\ -\ [(a+b)(a+c)-(c+d)(b+d)]}$$

where n is the number of elements (here the number of stations) to be classified, a and b can be considered as the number of agreements between P1 and P2, whereas c and d are the number of disagreements between P1 and P2 (Table 2). P1 in our study was the result obtained from the species taxonomic level HCA, whereas P2 was the HCA result for the other taxonomic levels and morphospecies (i.e. genus, family, order and morph). A taxonomic level or morphospecies was deemed sufficient when the ARI at that taxonomic level or typology did not show great differences from the estimated ARI calculated at the species level (ARI = 70%). We also conducted Non-metric Multidimensional Scaling (nMDS) on the Bray-Curtis dissimilarities using double square root- ($\sqrt{\sqrt{}}$) transformed matrices of taxonomic abundance data; and graphically represented the results using the HCA groups previously identified. These analyses were done for each taxonomic level and morphospecies (i.e. species, genus, family, order, and morph). The nMDS was conducted using two dimensions because the stress values for that number of dimensions were always below 0.05, suggesting a good fit between the ordination and the Bray Curtis distances. The nMDS were done to assess and visualize the similarities and/or differences in community structure among the taxonomic levels and morphospecies. All the statistical analyses were conducted using R software (R Team, 2005)

3. Results

3.1. Species richness and habitat definition

1. The five case studies used different sampling strategies and consequently

displayed differences in their overall indices of community structure. They

had different species numbers and average species richness but showed

similarities in terms of species to higher-level taxa ratios (Table 3). As

expected under the species–area relationship, surveys conducted in the two

coastal bays (Bays of Seine and Vilaine) and the English Channel displayed a

lower overall species richness (SR) than the broad-scale surveys carried out

in the Bay of Biscay and North Sea. On average, the stations in the Bay of

Seine and English Channel were poor in terms of species richness (average

$SR_{stations}$ = 6.94 and 6.49, respectively) and displayed low and constant values

of species to higher level taxa ratios, suggesting that these surveys are mainly

characterized by a low number of non-redundant, closely related species. The

Bay of Vilaine was characterized by relatively high average $SR_{stations}$ values

and a small coefficient of variation (ratio of the standard deviation to the

mean) indicating a rich community with some evenness in SR distribution

across the sampling stations. Low and constant values of species to taxa

ratios were also observed, suggesting low taxonomic redundancy of species

by genus, family and morphospecies. The two broad-scale surveys (i.e. Bay

of Biscay and North Sea) generally displayed richer communities, with 130

and 111 species, respectively, and high average $SR_{stations}$ values, indicating

that these large-scale ecosystems encompass a large diversity of habitats, themselves composed of a large number of species. Just as for the other three surveys, the low and constant values of ratios of species to higher-level taxa observed in the Bay of Biscay and North Sea surveys (from 1.00 to 3.33) suggest a low number of related species.

All the habitats defined by HCA analyses in each case study generally corresponded to bathy-sedimentary strata (Fig. 1 & Table 4). The limits of each habitat were defined by grouping the stations corresponding roughly to HCA results. A full environmental description of the different habitats in each case study is given in Table 4 with references to the associated literature, but here we focus only on the main results. We defined three to four habitats in the two coastal bays and in the large-scale ecosystems (Table 4). All habitats described in each of the case studies were then used as a grouping variable in the analyses of the taxonomic sufficiency.

3.2. Analyses of morphospecies

The taxa richness computed using the morphospecies datasets gave similar results to those estimated using the species dataset: an increasing gradient of morphospecies richness in the following order: Bay of Seine, Bay of Vilaine, English Channel, Bay of Biscay and North Sea surveys. We then compared the morphospecies (morph) with the species identification by calculating an identification error rate; this ranged between 12.07% (in the Bay of Vilaine) and 18.75% (in the Bay of Seine) for the small-scale surveys. The large-scale fish surveys, such as those ones conducted in the Bay of Biscay and the North Sea, displayed error rates of 18.46 and 17.91%, respectively. Over the 47 morphospecies identified by the experts, 62% included multiple genera and 36% were composed of multiple families. Among these families, we specifically recognized 23 that included several morphospecies (morph, Table 5

& Supplementary Material A) that determine the benthic community structure of the five case studies.

3.3. Rand index and cluster comparisons: status of the benthic community

A general decrease in the ARI was observed for the five case studies as we moved away from the taxonomic reference (i.e. species level) towards the order level (Fig. 2). The morphospecies displayed correlation values close to those for the family and genus levels. Similar results were underlined by the nMDS ordinations, where a change in site distribution was observed at the order level. This result was observed in all the case studies, thus only the ordinations for the English Channel are presented (Fig. 3). The ordinations for the five case studies and for all the groupings are given in Supplementary Material B.

The highest similarities in the ordinations and in the ARI were found for the two coastal bays, where values never went below the 0.80 threshold (except for the order level). The lowest ARI was observed in the Bay of Biscay and North Sea ecosystems, where the values were never higher than 0.70. The English Channel followed the general pattern: decreasing values from species to order level but with ARI values ranging between the small- and large-scale case studies.

4. Discussion

4.1. Different ecosystems and spatial scales, similar responses

The five surveys were conducted at different spatial scales and showed differences in terms of habitat and community structure. As expected from the species–area relationships, the small-scale beam trawl surveys displayed lower species richness than the large-scale bottom trawl surveys (see Supplementary Material A for a species list from each case study). However, the five surveys displayed low and constant species to higher-taxa-level ratios (around 1.5) suggesting low species redundancy with increasing taxonomic level (for genus and family) in all the studied ecosystems. Furthermore, species richness in the five ecosystems was strongly

correlated with richness at other taxa levels (i.e. genus, family, and morphospecies), indicating that regardless of the scale of the survey and/or the taxonomic level used, the overall richness of the site was maintained. Concurrently, the general pattern of the ARI shared by the five surveys suggested that family-level and morphospecies groups are of sufficient morphological or functional dissimilarity to discriminate the different habitats in each of the survey areas. This finding is in agreement with Bacci et al. (2009), who compared taxonomic sufficiency approach in two contrasted case studies (shelf *vs.* estuarine Mediterranean ecosystems). They concluded that taxonomic sufficiency appears to be a valid instrument to analyse and describe the structure of benthic communities in the two ecosystems they studied and in cases of taxonomically complex communities. These findings also agree with those of other studies looking at the impact of using lower taxonomic levels in marine biodiversity assessment (Anderson et al., 2005; Gaston, 2000; Giangrande et al., 2005; Olsgard et al., 2003).

Although similar patterns in taxonomic sufficiency were observed among our case studies, differences in the absolute values of ARI were also visible. This suggests that lowering the taxonomic level in systems dominated by few families or orders and displaying low species richness will have less impact (in terms of correlation with the species level) than doing this in species-rich systems displaying high evenness across several families (Bowman and Bailey, 1997; Heino, 2008). In the five ecosystems studied, this pattern was particularly apparent where similar patterns of ARI and species to taxa ratios were observed, but where a quantitative loss of information (lower ARI values) was also noticeable from small-scale to large-scale surveys. Hawkins and Norris (2000) and Heino (2008) suggested that the relationship between species richness and the loss of information at low taxonomic resolution may be partly due to adaptive radiation in species taxa. Species in family-rich taxa would have a broader range of different ecological niches, displaying different responses to the

environment. Therefore, the loss of the species level in the assessment of such ecosystems such ecosystems would likely lead to significant functional erosion.

The five case studies differ not only in their community structures but also in the range of habitats they cover and in their sampling protocol (type of bottom trawl, area swept…). The two small-scale systems (Bay of Seine and Bay of Vilaine) are both composed of a limited number of sandy and muddy habitats in a similar range of depths, whereas the other three systems all cover a large latitudinal range displaying a broad gradient of environmental conditions (sediments, depth, salinity, see Table 4). Species in environment-rich systems will likely occupy a wider range of ecological niches than species inhabiting systems with less environmental heterogeneity (Baldi, 2008; Connor and McCoy, 1979), which might explain the decreasing gradient of taxonomic sufficiency as we move from "species-poor" ecosystems towards "species-rich" ones. It is worth mentioning that although the ARI values decrease in these large ecosystems, the range of absolute values is still highly satisfactory and comparable to other studies (Bevilacqua et al., 2009; Soares-Gomes et al., 2012; Wlodarska-Kowalczuk and Kedra, 2007).

4.2. The morphospecies: a functional concept

Habitat template theory proposes that species with similar morphological traits occupy similar habitats (Southwood, 1977). According to this hypothesis, habitat is the setting where evolution occurs, giving specific life history strategies to organisms thereby grouping similar functional attributes in similar habitats. This concept is closely related to the morphospecies and one could argue that grouping species according to their morphological similarities, as is done with morphospecies, is an indirect way of including functional aspects of the community in the analyses.

The use of morphospecies such as the one in the present study is quite widespread in the terrestrial realm (Derraik et al., 2010; Oliver and Beattie, 1996; Pik et al., 1999), remote

ecosystems (Barnes et al., 2009; Sabbatini et al., 2002) and estuaries (Soares-Gomes et al., 2012). For instance, morphospecies are used as Operational Taxonomic Units (OTU) in high-resolution seabed imagery or deep-sea areas where identification is often impractical and unreliable (Barnes et al., 2009), or when dealing with taxonomically difficult groups of rare and small species such as micro-gastropods (Albano et al., 2011). In these previous studies, the morphospecies were considered in the same way as they were in our study, i.e. as a unique group of (most likely) several species displaying sufficient morphological similarities to be classified together. Here, morphospecies were identified by experts, based on the similarity of their major morphological characteristics as well as the similarity in their functional attributes (Bremner, 2008; Bremner et al., 2003; Tillin et al., 2006).

Results from the ARI analyses coupled with the experts' identification of the morphospecies in each of the five case studies allowed an important practical issue to be addressed: the creation of a list of families and species for which adequate efforts of identification should be made on board (Table 5). The species included in this list are those that are structural for the benthic communities of the surveys; the morphological similarities they display thereby indicate similar underlying functional traits.

We deliberately excluded uncountable and clinging organisms from our analyses. These organisms are often viewed as problematic because they are difficult to assess quantitatively (Zettler et al., 2007). This is however a strong limitation of benthic studies, as these organisms may be structurally important species in some ecosystems (e.g. English Channel and North Sea). There is thus a need to develop statistical techniques or methods to jointly process these organisms along with the countable ones. Such parameters allow an integrated view of the macro and megabenthic communities of the marine realm, which is required to improve our knowledge of these communities.

4.3. Implications for the MSFD

In the MSFD, each Member State had to undertake an Initial Assessment of the current

ecological state by the end of 2012, and identify existing data that could be useful for the

Initial Assessment and development of the indicators. Some Member States have already

started to assess the environmental status of their marine waters (Borja et al., 2011) while

others are still compiling the data to inform the various descriptors (Rombouts et al., 2013).

Nevertheless, several indicators are still being developed and tested and are thus far from

being operational and directly implemented in the MSFD (Rombouts et al., 2013). For

instance, indicators from the Sea Floor Integrity descriptor (e.g. D6) require ecological

knowledge on data-poor habitats such as the offshore and deep-sea benthic communities

(Rice et al., 2012). These remote ecosystems represent large surfaces, and discrepancies are

expected between the large geographic areas covered by these surfaces in the various sub-

regions and the sampling gear traditionally used in benthic ecology (i.e. grabs). According to

(Rice et al., 2010), "*other strategy must be developed for general assessments of*

environmental status of sea floor integrity on regional and sea-wide scales." Fisheries science

bottom trawl surveys cover very broad geographic areas. For instance the surface of the study

areas of the IBTS (in the North Sea) and EVHOE (in the Bay of Biscay) surveys are about 11

112 km^2 and 150 000 km^2 respectively, thereby encompassing a large number of habitats and

indeed benthic communities. We showed that the data collected in these large-scale and other

small-scale bottom trawl fisheries surveys could correctly identify benthic habitats previously

described by other studies that used grab samples (Table 4). These findings underline that

data obtained from fisheries surveys may well complement those from grab samples to

provide useful information for MSFD benthic descriptors (e.g. D6: Sea Floor Integrity).

The use of morphospecies or lower taxonomic levels, such as genus or family, could thus be

used to homogenize the combined datasets. This was notably done by Dimitriou et al (2012)

in a recent meta-analysis conducted on a large database of macrofaunal samples compiled by assembling various data sets from the Eastern Mediterranean including sublittoral and continental shelf surveys of various types. Their final dataset inevitably comprised taxa identified at different taxonomic levels. They suggested a benthic index that could be calculated using the family level (Benthic Quality Index, BQI) and showed that this strongly agreed with the existing Water Framework Directive (WFD) indicators. In the same way, Munari et al. (2009) calculated four benthic indices to assess the water quality of the Adriatic coastal transitional ecosystems to eventually implement the WFD and concluded that "*A genus or family level of identification for the WFD implementation in the benthic compartment of Italian transitional waters might be sufficient for evaluating the status of such water bodies*".

The two aforementioned studies were conducted in the context of the WFD. However, as recently underlined by Borja et al. (2010), the MSFD provides a more holistic and functional approach than the WFD as it breaks down the ecosystems into a set of process-like components (i.e. functional descriptors) and recombines them in an integrated approach (the GES assessment). For instance, indicator 6.2.2 from the D6 addresses the condition of benthic communities using multi-metric indices such as species diversity and richness, or the ratio of opportunistic to sensitive species. We argue that this indicator could be well informed using the morphospecies identified in our study as morphological and anatomical attributes constrain the role a species may play in the community, and species sharing similar attributes form functional groups are likely to occupy similar habitats and respond similarly to anthropogenic pressures (Bremner, 2008; Tonn et al., 1990). Classification of species according to a suite of biological or morphological traits (i.e. Biological Traits Analysis, BTA) has been used to reflect the changes in the system functioning (Bremner, 2008). We therefore suggest that whenever it is impossible to identify taxa at the species level, BTA

could be compiled on a mixed species and morphospecies   trait matrix without losing any functional information (Bremner et al., 2003).

5. Conclusions

Species is the basic ecological unit in the ecological niche and succession theories; whilst identification at the species level is always preferred over any other taxonomic levels. Nevertheless, aggregation of species to higher taxonomic levels may sometimes be unavoidable, as we know or suspect that errors of identification occur in some surveys. In such cases, aggregation should be undertaken with caution, as the taxonomic sufficiency may be highly dependent on the community structure of the system under study (Giangrande et al., 2005), although this may also not be the case (Bacci et al., 2009). Furthermore, the use of any higher taxonomic level in species-rich ecosystems will inevitably and unfortunately lead to lower diversity estimations. This study has indicated that, although absolute values of diversity can be lowered, the general spatial patterns distinguishing benthic communities are still maintained. We confirm the conclusions reached in several other studies (Dethier and Schoch, 2006; Guzman-Alvis and Carrasco, 2005; Somerfield and Clarke, 1995; Terlizzi et al., 2008; Vanderklift et al., 1998; Wlodarska-Kowalczuk and Kedra, 2007), indicating that genus and family levels are generally good surrogates for species in benthic community analyses. We underline that analyses of morphospecies may be better suited than genus or family level analyses because morphospecies classification only increases the taxonomic level of a certain number of species, i.e. the misidentified ones, thereby keeping most of the ecological information for the rest of the community "intact". Nevertheless, the morphospecies classification offers no panaceas, only new and reliable solutions to counter the problem of misidentification that sometimes occurs on board fisheries science bottom trawl surveys.

From an applied perspective, this study suggests that bottom trawl survey data can be used as a reliable and complementary source of data to dedicated macrobenthos surveys (e.g. grab data), to provide information for MSFD benthic descriptors (D6 and, to a lesser extent, D1, D2, D4). The use of such complementary sources of data will likely require the combination and standardization of the various databases, which might be composed of several surveys using different gears, sampling strategies, and taxonomic levels of identification. Morphospecies could thus be an appropriate substitute in this context.

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Figure captions

Fig. 1. Map of geographic areas and sampling stations for each of the five French datasets: *Bay of Seine* (A), *Bay of Vilaine* (B), *Eastern English Channel basin* (C), *Bay of Biscay* (D), *North Sea* (E). The dotted lines delineate the habitats found in the present study using cluster analyses (see Materials and Methods for details). The habitats described here (H1 to H4) are a schematic view of the macro- and megabenthic communities in the studied ecosystems. These are described in detail for each ecosystem in Table 4.

Fig. 2. Adjusted Rand Index (ARI) values calculated for the five case studies. ARI is a measure of similarity between a taxonomic reference (here the species level) and another taxonomic level. It varies between 0 and 1 (see the Materials and Methods section for more details).

Fig. 3. NMDS ordination on Bray-Curtis similarities using $\sqrt{\sqrt{x}}$-transformed taxonomic densities for the English Channel. The legends correspond to the number of predefined habitats in each case study. Ordinations of all the case studies can be found in the figures included in Supplementary Material B.

Table 1   Technical description of the sampling surveys used in the five case studies.

Location	Bay of Seine	Bay of Vilaine	English Channel	Bay of Biscay	North Sea
Year	2008	2009	2007	2009	2011
Depth range (m)	5-20	5-35	5-100	30-600	15-200
Gear name	3 m beam trawl	3 m beam trawl	19.70/25.90 GOV	36/47 GOV	36/47 GOV
Vertical opening (m)	0.5	0.5	3	4	4
Cod size (mm)	20	20	20	20	20
Trawl duration (min)	15	15	30	30	30
Surface covered (m^2)	~ 4 500	~ 4 500	~ 27 750	~ 69 000	~ 35 000

Table 2   Match and mismatch matrix used in the calculation of the adjusted Rand Index (ARI). a, b, c, and, d are counts of unique pairs.

	Partition 1 (P1)		
Number of pairs	Same cluster	Different clusters	Sums
Same cluster	a	b	$a+b$
Different clusters	c	d	$c+d$
Sums	$a+c$	$b+d$	

Partition 2 (P2)

Table 3   Summary of the number of stations included in the analyses for each case study and the indices for community structure: total species richness (SR), average SR by sampling sites, and average species to higher-level taxa ratios (Ratio). Standard deviations given are in parenthesis.

Case study	Bay of Seine	Bay of Vilaine	English Channel	Bay of Biscay	North Sea
Number of stations	46	49	92	62	88
SR	32	58	58	130	111
Average $SR_{stations}$	6.94 (2.10)	13.76 (3.15)	6.49 (3.21)	19.50 (6.34)	11.23 (6.49)
Ratio Sp/Gen	1.143	1.123	1.158	1.095	1.437
Ratio Sp/Fam	1.209	1.323	1.365	1.453	1.640
Ratio Sp/Ord	2.201	2.157	2.442	2.628	3.330
Ratio Sp/morph	1.143	1.313	1.245	1.271	1.537

Table 4   Environmental and biological description of the different habitats observed in each case study. These habitats were generally associated with the bathy-sedimentary gradient, as identified in previous studies (Cabioch, 1968; Dauvin et al., 2006; Desroy et al., 2007; Elkaim et al. 1982; Foveau, 2009; Kopp et al., 2013; Laffargue and Martin, 2010; Le Bris and Glemarec, 1995; Sanvicente-Anorve et al., 2002; Vaz et al., 2007) and corresponded to the predefined groups used in the nMDS analyses.

Habitat	Bay of Seine	Bay of Vilaine	English Channel	Bay of Biscay	North Sea
H1	Muddy estuarine habitat under high river discharge influence. Benthic assemblage characterized by *Pectinaria*, *Cerastoderma*, and *Nephys*.	Muddy habitat ranging between 0 to 5 m under river discharge influence. Benthic assemblage dominated by *Cerastoderma edule*.	Shallow coastal habitat where fine sand and mud constitute the bulk of the sediment, characterized by the deposit feeder *Abra alba* and *Nephys cirrosa*.	Mixed sandy and muddy habitats ranging 150–350 m extending from the mid-shelf to shelf break, characterized by *e.g. Hyalinoecia tubicola*, *Leptometra celtica*, *Pagurus prideaux, Adamsia carciniopados*	Muddy and warm water habitat ranging 30–50 m depth, characterized by *Liocarcinus depurator*, *Paguridae* and *Pandalus*.
H2	Muddy and sandy euryhaline habitat. Benthic assemblage, characterized by *Owenia*, *Lanice*, and *Eteone*.	Muddy and sandy habitat ranging 5–10 m under river discharge influence in wet winters. Benthic assemblage dominated by *Owenia fusiformis*.	Sandbanks in fine to coarse grains and shallow (10–30 m) habitat dominated by *Ophelia borealis*, *Nereis cirrosa*, and *Spiophanes bombyx*.	Deep muddy grounds at the shelf slope around 500 m deep, characterized by *Pasiphaea sivado*, *Pagurus alatus, Polycheles typhlops* and *Actinauge sp.*	Sandy to coarser sediment habitats scattered with stones displaying high bed shear stress and depths ranging between 30–50 m. Benthic community characterized by *Hyas*, *Palaemon serratus*, *Buccinum*

					undatum, and Echinoidae.
H3	Muddy and sandy polyhaline habitat, characterized by *Asterias*, *Harmothoe*, and *Leptonereis*.	Muddy habitat ranging 10–15 m displaying a benthic assemblage dominated by *Sternaspis scutata*	Gravel and coarse sand habitat in deeper depths (50–60 m), dominated by *Verruca stroemia*, and *Sabellaria spinulosa*.	Heterogeneous coastal strata mostly less than 50 m deep, characterized by *Ophiura ophiura*, *Asterias rubens*	Sandy and shallow habitat (10–30 m) with high bed shear stress, dominated by a community of echinoderms (*Astropecten irregularis irregularis*, *Ophiura albida*, *Ophiura ophiura*).
H4		Deep muddy and sandy habitat ranging 15–30 m, under marine influence. Benthic assemblage dominated by *Abra alba*.	Pebble community in strong current areas, dominated by *Ophiotrix fragilis* and *Pisidia longicornis*.	Sand dominated habitats, mostly at depths greater than 100 m, characterized by *Astropecten irregularis*, *Macropipus tuberculatus*	Deep (>60 m) and warm water habitat scattered with pebbles, characterized by *Lithodes maja* and *Astropecten irregularis irregularis*.
H5				Sandy mudflats ('Grande-Vasière') from 100 to 120 m, characterized by burrowing crustaceans like *Nephrops norvegicus*, *Munida spp* and *Alpheus glaber*	

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Table 5   List of families and species regularly captured in scientific bottom trawl surveys to which special attention should be paid because they are important species structuring the megabenthic communities in the study surveys. For the complete list of morphospecies see Table S1 of Supplementary Material S1.

Family	Species	Morphospecies
Alpheidae	*Alpheus glaber*	Gr45
Amphiuridae	*Acrocnida brachiata*	Gr36
	Amphiura filiformis	Gr36
Anomiidae	*Pododesmus patelliformis*	Gr26
	Pododesmus squama	Gr26
Antedonidae	*Antedon petasus*	Gr1
	Leptometra celtica	Gr1
Atelecyclidae	*Atelecyclus rotundatus*	Gr21
	Atelecyclus undecimdentatus	Gr21
Calliostomatidae	*Calliostoma granulatum*	Gr31
	Calliostoma zizyphinum	Gr31
Carcinidae	*Liocarcinus depurator*	Gr19
	Liocarcinus holsatus	Gr19
	Liocarcinus marmoreus	Gr19
	Liocarcinus navigator	Gr19
	Liocarcinus pusillus	Gr19
	Liocarcinus vernalis	Gr19
	Polybius henslowii	Gr19
Crangonidae	*Crangon allmanni*	Gr18

	Crangon crangon	Gr18
	Philocheras echinulatus	Gr18
	Pontophilus spinosus	Gr18
Discodorididae	*Jorunna tomentosa*	Gr11
Dorididae	*Doris pseudoargus*	Gr11
Inachidae	*Inachus dorsettensis*	Gr4
	Inachus leptochirus	Gr4
	Inachus phalangium	Gr4
	Macropodia rostrata	Gr4
	Macropodia tenuirostris	Gr4
Majidae	*Ergasticus clouei*	Gr4
Naticidae	*Euspira catena*	Gr28
	Euspira pulchella	Gr28
Nephropidae	*Nephrops norvegicus*	Gr45
Onchidorididae	*Onchidoris bilamellata*	Gr11
Ophiuridae	*Ophiura albida*	Gr3
	Ophiura ophiura	Gr3
Pasiphaeidae	*Pasiphaea multidentata*	Gr17
	Pasiphaea sivado	Gr17
Pectinidae	*Aequipecten opercularis*	Gr20
	Mimachlamys varia	Gr20
Pharidae	*Pharus legumen*	Gr38
	Phaxas pellucidus	Gr38
Polynoidae	*Lepidonotus clava*	Gr27
	Lepidonotus squamatus	Gr27

	Gattyana cirrhosa	Gr27
Sigalionidae	*Sthenelais boa*	Gr27
Tritoniidae	*Tritonia hombergi*	Gr11
Velutinidae	*Lamellaria perspicua*	Gr11

Research highlights

- This study quantifies the ecological loss of misidentifying benthic megafauna
- It suggests that the morphospecies is a good surrogate to species identification
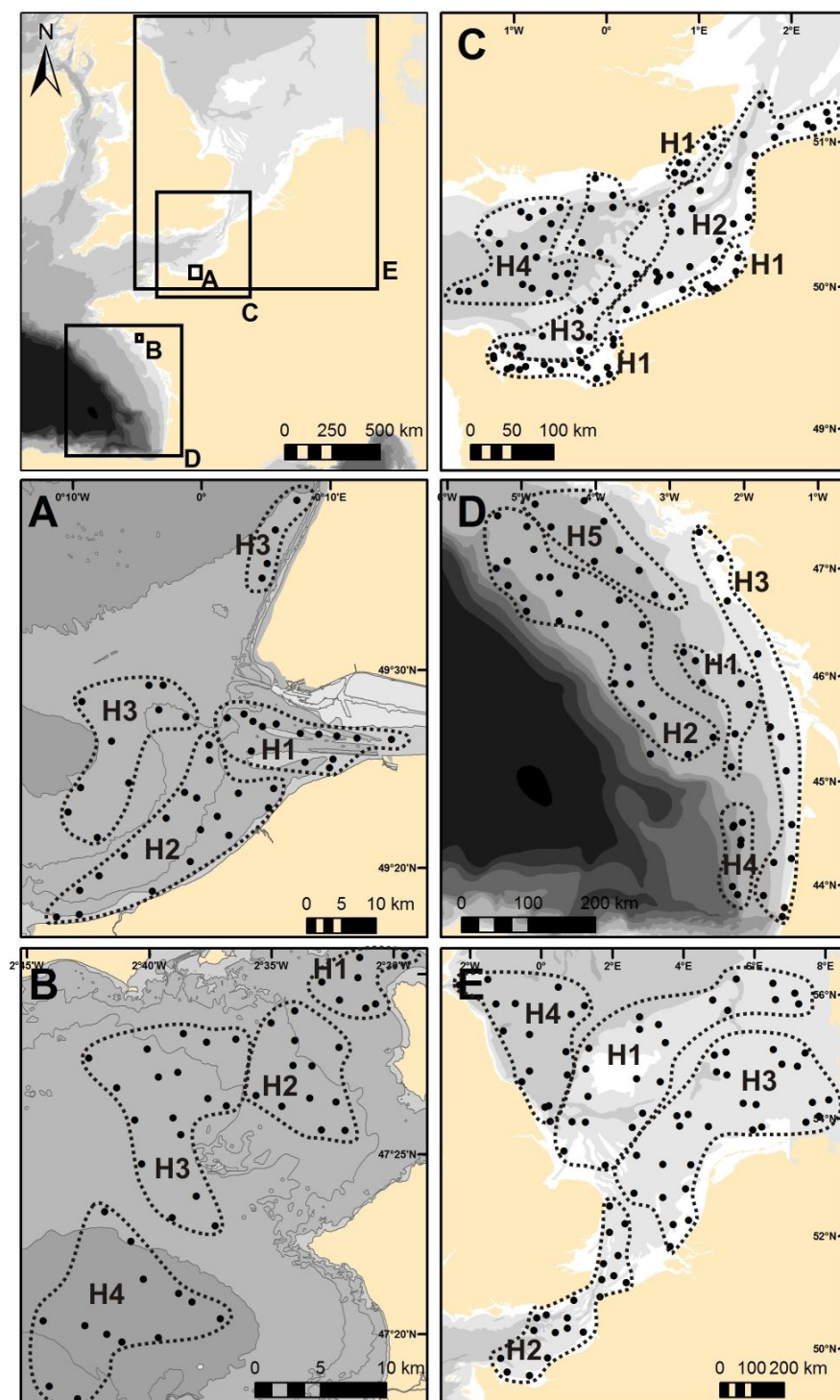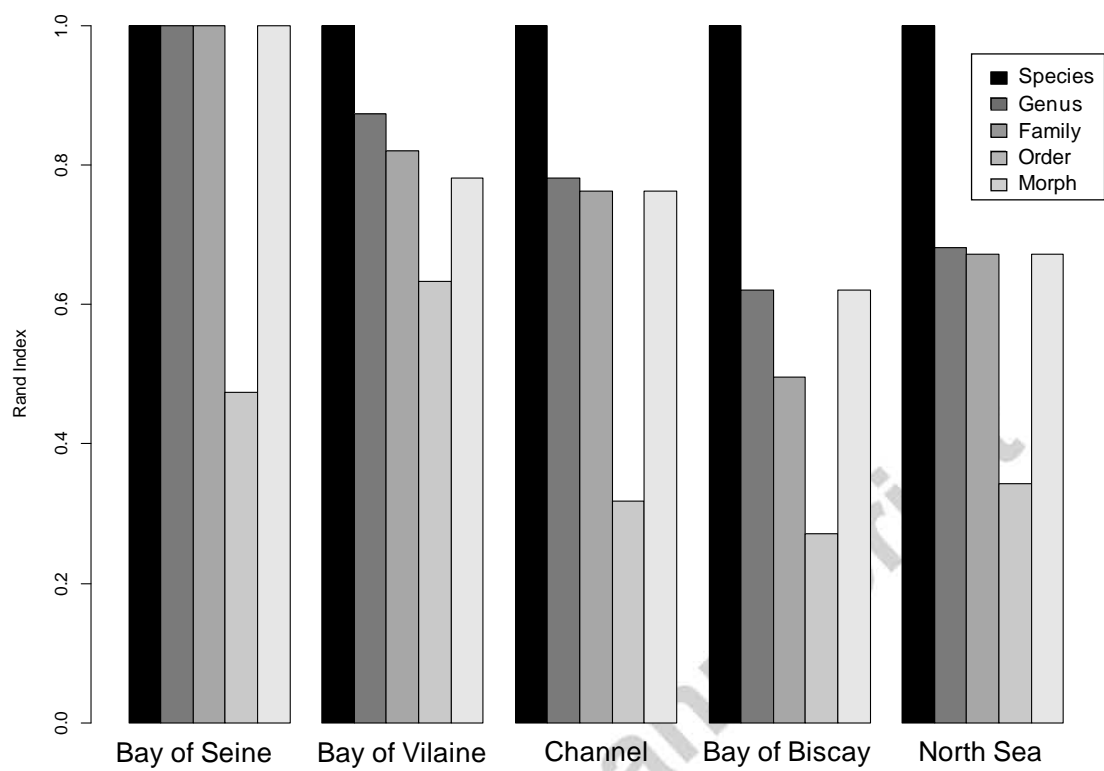- Bottom-trawl surveys provide reliable data to inform MSFD benthic descriptors
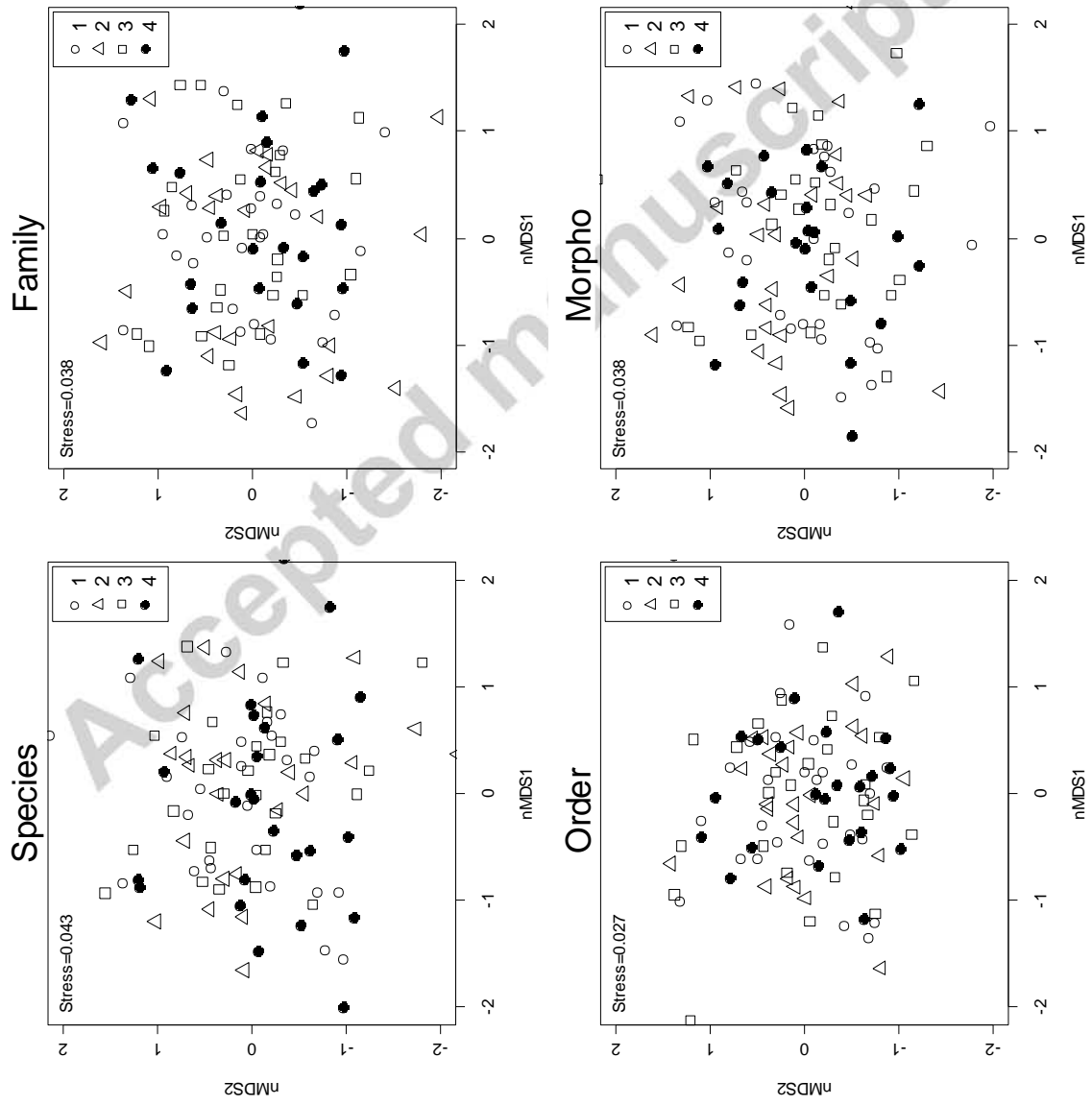
Fig. 1

Fig. 2

Fig. 3