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Lise Bacouillard, Noémie Baux, Jean-Claude Dauvin, Nicolas Desroy, Katja Juliana Geiger, et al.. Long-term spatio-temporal changes of the muddy fine sand benthic community of the Bay of Seine (eastern English Channel). *Marine Environmental Research*, 2020, 161, pp.105062. 10.1016/j.marenvres.2020.105062 . hal-02916254

HAL Id: hal-02916254

<https://normandie-univ.hal.science/hal-02916254>

Submitted on 22 Aug 2022

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Long-term spatio-temporal changes of the muddy fine sand benthic community of the Bay of Seine (eastern English Channel)

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ABSTRACT

In the English Channel, the eastern Bay of Seine is exposed to numerous anthropogenic disturbances, in particular major changes in sediment dynamics, which are expected to greatly impact benthic communities. To assess the long-term effects of these stressors on the muddy fine sand benthic community, an original long-term monitoring program has been implemented since 1988. It is based on the sampling of a network of 60 stations during seven surveys over 28 years from 1988 to 2016. We investigate changes of species abundance, species composition and species diversity at different scales (α -diversity, β -diversity and γ -diversity). Contrary to results obtained in many coastal areas, our results showed a long-term persistence of the community in terms of species composition and structure although a general shift towards muddy sediment have resulted in increased colonisation by species associated with muddy habitats and a decrease in spatial beta diversity.

Keywords

Benthic ecology; Coastal zone; Temporal variability; Species composition; Macrofauna; α -diversity; β -diversity; γ -diversity

1. Introduction

Marine coastal ecosystems experience increasing pressures due to human activities including overexploitation of marine resources, eutrophication, contamination by organic and non-organic pollutants, coastal urbanization and introduction of non-indigenous species, which can overlap and interact with climate change (Airoldi and Beck, 2007; Halpern et al., 2008). The cumulative effects of these diverse pressures, which often vary in magnitude, spatial extent, temporal duration and frequency (Donohue et al., 2016), result in changes to the structure of marine communities (e.g. species richness, species composition, density and biomass of dominant species) which can alter ecosystem functioning and the delivery of ecosystem services (Cardinale et al., 2012; Gamfeldt et al., 2015). In this context, there is a growing need for analysis of long-term datasets to assess responses of communities to temporal changes in environmental conditions to facilitate management and conservation efforts (Magurran et al., 2010; Giron-Nava et al., 2017). Such datasets provide essential resources to address several issues: (1) describe and understand the complex long-term dynamics of community diversity in response to changing environmental conditions; (2) assess the effects of multiple stressors and disentangle the relative contributions of anthropogenic impacts and natural variability; (3) provide data for predictive models; (4) support the development of ecological indicators to evaluate the ecosystem; and (5) support the implementation of ecosystem-based management (Duffy et al., 2013).

For macrobenthic communities, two main strategies have been developed to monitor long-term ecological change over recent decades. The first approach consists of sampling one or multiple stations at a regular frequency, often yearly (e.g. Fromentin et al., 1997; Warwick et al., 2002; Frid et al., 2009; Clare et al., 2015), during several decades. It provides valuable information on the dynamics of macrobenthic

communities and their drivers, but requires continuous and long-term financial and human support. Furthermore, it does not allow consideration of the spatial heterogeneity of environmental conditions or responses of macrobenthic communities. A second approach consists of sampling a network of stations after a long time interval, generally exceeding a decade, which allows rapid detection of major changes in macrobenthic macrofauna without being able to statistically infer the causes of the observed changes (Hinz et al., 2011; Kröncke et al., 2011; Callaway, 2016; Bonifácio et al., 2018). An original alternative approach, which has been implemented in the eastern Bay of Seine, combines both of these strategies and is based on long-term large-scale sampling of a network of stations (i.e. ~ 60 stations) at regular intervals (i.e. every five years) over a long period (i.e. 1988 to 2016). Thus, it enables the detection of interactive effects between spatial and temporal processes on the dynamic of macrobenthic communities.

Macrobenthic communities in the Bay of Seine were first described from data collected during early 1970s (Cabioch and Gentil, 1975; Gentil and Cabioch, 1997) which identified seven macrobenthic communities in relation to the spatial distribution of the sediment substrates: (1) the coarse gravel and pebbles community, (2) the sandy gravels and gravels community, (3) the *Branchiostoma lanceolatum* coarse sand community, (4) the *Ophelia borealis* - *Nephtys cirrosa* fine and medium clean sands community, (5) the *Abra alba* - *Lagis koreni* muddy fine sand community, (6) the heterogenous muddy mixed community and (7) the *Limecola balthica* community in estuarine muddy fine sand and mud. Since these pioneering works, studies on the *Abra alba* - *Lagis koreni* muddy fine sand community in the eastern part of the Bay of Seine showed that the community was distinctly structured in space with patchy distribution of most dominant species and the identification of distinct faunal assemblages (Thiébaud et al., 1997;

Baffreau et al., 2017; Dauvin et al., 2017). Thiébaud et al. (1997) demonstrated that the spatial structure of the community resulted from the combination of several environmental gradients related to salinity, sediment grain size and food supply. These authors highlighted a relative stability of this spatial organization over a 5-year period. Over a longer period (1983-1992), the community structure at only one station was also relatively stable compared other sandy communities in the western English Channel (Bay of Morlaix) and in the south of the North Sea (Gravelines area), despite the influence of alternative periods of cold and mild conditions on the densities of some species (Fromentin et al., 1997). More recently, the introduction of non-indigenous species and the arrival of species associated with muddy sediment were observed without an assessment of their impacts on the community structure (Dauvin et al., 2007; Jourde et al., 2012). Thus, the non-indigenous razor clam *Ensis leei* (formerly *Ensis directus*) was first reported in 1998 and colonized the south-eastern coasts of the bay at moderate density ($< 100 \text{ ind.m}^{-2}$; Dauvin et al., 2007). The polychaete *Melinna palmata* has been observed since 2002 and has rapidly extended its population to reach densities of 277 ind.m^{-2} in March 2006 and between 625 and 2500 ind.m^{-2} in September 2008 and September 2009 in parallel to the increased siltation rates of the bay (Dauvin et al., 2007; Alizier, 2011). Likewise, another species inhabiting muddy sediment, the crab *Asthenognathus atlanticus*, was first sampled in 2008 (Jourde et al., 2012).

The concept of “stability/variability” is a focal point of ecological research that has received attention for decades by theoreticians and empiricists alike. Traditionally, stability was perceived as a binary measure based on the asymptotic stability of multispecies systems, with communities either stable or unstable (MacArthur, 1955). Recently, the concept of “multidimensional ecology stability” has emerged and multiple correlated or independent components of the stability were identified to capture the

different aspects of the responses of communities to diverse disturbances, e.g. variability, persistence, resistance, resilience, or robustness (Donohue et al., 2013).

As described in Donohue et al. (2013), temporal variability at the population or community levels is commonly quantified as coefficient of variation (CV) of density or biomass, with high variability corresponding to low stability. The “compositional turnover” which represents the (temporal) beta diversity is the reciprocal of persistence and measures the extent of change in community composition over time. It can be quantified using Jaccard or Bray-Curtis similarity index depending if changes are addressed in terms of presence/absence or relative abundances of species. Furthermore, these different metrics of stability/variability can be calculated at different spatial scales to understand how temporal variation may differ from one site to another within a community. Therefore these different components allow assessing stability/variability appropriately at both a small or large scale, temporarily or spatially.

Using the study site of the eastern Bay of Seine, which is highly representative of urbanized coastal areas exposed to numerous anthropogenic threats (Dauvin, 2008; Marmin et al., 2016; Tecchio et al., 2016; Baux et al., 2019), this study investigated the spatio-temporal changes of species abundance, species composition and species diversity at different scales (α -diversity, β -diversity, γ -diversity) between 1988 and 2016. Based on the analysis of spatio-temporal data provided by the original long-term monitoring program of the muddy fine sand benthic community implemented in this area, we address two specific questions: (1) how did the benthic community vary through time and space according to the scale of observation (i.e. local station vs. whole community) and (2) what was the degree of correlation of the different components of the stability?

2. Materials and methods

2.1. Study area

Along the north-western French coasts, the Bay of Seine forms a quadrilateral area of about 5000 km² largely open to the central English Channel in the north with a water depth never exceeding 30 m (Fig. 1). Within the bay, semi-diurnal tidal currents range between 1 and 3 knots and their velocity gradually diminishes towards the eastern part of the bay (Salomon and Breton, 1991). These currents combined with wave action are the main drivers for the distribution of superficial sediments (Larsonneur et al., 1982; Marmin et al., 2016) and macrobenthic communities (Gentil and Cabioch, 1997) resulting in an offshore-inshore gradient. Offshore sediments consist mainly of pebbles and gravels while coastal sediments are dominated by fine sand and muddy fine sand habitats. The shallow waters of the eastern part of the bay and the Seine estuary, the largest macrotidal estuary in the English Channel, are exposed to multiple anthropogenic disturbances such as maritime traffic, civil engineering works, fisheries, sediment dredging and dumping, and pollution (Dauvin, 2006). Since the middle of the 19th century, engineering works and dredging for the development of industrial and harbour activities have led to a decrease in the Seine river channel section, a lessening of the seawater exchanges and changes in the morpho-sedimentary dynamics (Le Hir et al., 2001; Lesourd et al., 2001, 2016). From the 70s to the 90s, an increase in fine-grained sedimentation in the subtidal shallow waters of the Bay of Seine in response to a downstream shift of the turbidity maximum has resulted in the evolution from sand-dominated seabed to one dominated by mud, with a threefold increase of the surface area covered by mud and sandy mud (Lesourd et al., 2001). More recently, following several years of low Seine river flows, a decrease in muddy area was

reported in parallel to an increase in sandy mud and muddy sand mostly in front of the estuary, which has spread over the bay in the form of fine-grained sediment and been incorporated within the sandy fraction (Lesourd et al., 2016). The sediment dynamics within the bay is also influenced by the dumping, in the Northern Channel of the Seine estuary (Kannik) and North of the Cap de la Hève (Octeville), of 6-7 million m³ per year (cumulated from two major harbours) of dredged material from Seine river and harbour basins (Marmin et al., 2016; Baux et al., 2019). In addition to the disturbances resulting from man-made modifications, the Seine estuary is placed among the most contaminated estuaries with high levels of heavy metals, particularly cadmium and lead, and organic contaminants (e.g. PAHs, PCBs, pesticides) which have highly variable effects on benthic organisms (Dauvin, 2008; Fisson, 2014). The study site can be considered as highly disturbed before and since the beginning of the monitoring program in 1988. But, since 1988, it has undergone significant changes in terms of sedimentary dynamics in response to the “Port 2000” project, which corresponded to the large expansion of Le Havre harbour, aimed at making it a major crossroads for maritime trade and contributed to the increasing siltation rates of this part of the Bay of Seine (Tecchio et al., 2016).

2.2. Sampling and laboratory strategy

The macrofaunal distribution in the eastern part of the Bay of Seine was established during seven sampling surveys (named “PECTOW” surveys) carried out over 28 years (i.e. 1988, 1991, 1996, 2001, 2006, 2011 and 2016) during winter time (February/March) before the recruitment period of the dominant species. Sixty stations were sampled six or seven times from 1988 to 2016 with a total of 403 sampling station-period combinations: 43 stations were sampled on each of the seven surveys whilst 17

stations were sampled during only six surveys (Fig. 1). At each station, two samples were collected using a 0.25 m² Hamon grab, except in 2016 where five samples were taken using a 0.1 m² Hamon grab for the same total sampling surface of 0.5 m². The Hamon grab has been used in previous studies undertaken within the Bay of Seine because it is effective in varied sedimentary environments, from mud to gravels (Eleftheriou and Moore, 2008), ensuring homogeneity in the protocol. An additional grab sample was collected for sediment grain analysis. Macrofauna was collected by sieving samples through a 2 mm circular mesh sieve on board, which is a sufficient mesh size to sample wintering adults of most macrofauna species (Thiébaud et al., 1997), and fixed with a 10% buffered formalin solution. Macrofaunal organisms were sorted and stored in 70% ethanol before being identified to the lowest possible taxa, generally to species level, and counted. Species or taxa names were checked against the World Register of Marine Species (WORMS, <http://www.marinespecies.org>) on February 2020. Densities of the different taxa are expressed as number of individuals per 0.5 m². Sediment samples of approximately 200 g were dried and sieved over sequentially arranged sieves following the Wentworth scale. Sediment type was then classified according to the silt content: fine sand (silt content < 5%), muddy fine sand (5% < silt content < 25%), sandy mud (25% < silt content < 75%) and mud (silt content > 75%) (Bachelet et al., 1997).

2.3. Data analysis

2.3.1. Temporal variability in species composition and densities

To quantify the temporal variability of species composition, the first 10 dominant taxa were identified for each survey. Then, the coefficient of variation (CV, i.e. the ratio of the standard deviation to the mean multiplied by 100) of their densities over time was

used to describe the variability of species densities at two spatial scales, i.e. the scale of the bay and the scale of a local station, from the 43 common stations sampled on every survey. The CV at the scale of the bay was calculated using the mean and the standard deviation of the average species densities at the 43 common stations for the seven surveys. The CV at the scale of a local station was calculated with the mean and the standard deviation of species densities at each station for the seven surveys. The CV was calculated at stations for which densities were non-zero at least three times because three values are needed to calculate a standard deviation. Spatial variations in CVs at the scale of local stations provided information on the spatial heterogeneity of temporal variability in species densities.

2.3.2. Gamma diversity

Gamma diversity (i.e. species diversity of the large sampling area; Whittaker, 1960) refers in this study to the total number of species sampled during each survey in the eastern Bay of Seine. For each survey, species accumulation curves were drawn after 999 permutations to describe its year-to-year variations.

2.3.3. Alpha diversity

At each station for each survey, alpha diversity (i.e. species diversity in a sampling site) was calculated using species diversity indices that cover its different facets, i.e. richness, heterogeneity and evenness. These indices include species richness (S), Shannon-Weaver index (H') using \log_2 in its formulation, and Pielou's evenness (J'). The number of individuals per 0.5 m² (N) at each station was also calculated. To assess the variations in univariate indices among surveys, a Kruskal-Wallis non-parametric test was computed with R language (R Core Team, 2014). For those indices presenting a significant difference among surveys, a Dunn multiple comparison test was applied to

identify which surveys are significantly different from the others (i.e. $p < 0.05$) (Zar, 1999).

2.3.4. Beta diversity

To analyse the beta diversity (i.e. the degree of change in species composition/structure among sampling sites; Anderson et al., 2011), different analyses have been carried out depending on whether we have considered presence/absence or relative abundance data, and focused on the changes in species composition/structure among sites (i.e. spatial beta diversity) or among sampling dates at each sampling site (i.e. temporal beta diversity). The Jaccard distance was used to measure the “composition” component of beta diversity while the Bray-Curtis coefficient provided a measure of the “community structure” component of beta diversity (Donohue et al., 2013).

First, the spatio-temporal changes in community structure have been visualized from a Hierarchical Cluster Analysis (HCA) performed using the group average linkage method and the Bray-Curtis similarity index commonly used for benthic macrofauna (Field et al., 1982). Species densities were first $\log_{10}(x+1)$ transformed to reduce the contribution of the most abundant species. The resulting sub-clusters were tested using a type 1 “similarity profile” permutation test (i.e. SIMPROF test) to determine if they could be interpreted as distinct macrofaunal assemblages. The assemblages were first characterized with distinct species diversity indices (S , H' and J') and then with a Similarity Percentage analysis (SIMPER; Clarke, 1993) to determine which species contribute the most to the similarity between station-period combinations (i.e. one station sampled during a given survey) of a given assemblage. For this analysis, 11 station-periods out of the 403 sampling station-periods were identified as outliers and

were excluded, leaving a total of 392 station-periods. These 11 station-periods corresponded to stations with very low species richness and low densities of individuals or dominance of a single species. The objective of this first analysis was to visualize the temporal changes in the spatial structure of the macrobenthic community at the scale of the eastern Bay of Seine, i.e. the spatial beta diversity.

Second, the changes in the community composition and structure over time at each station, i.e. the temporal beta diversity, were quantified using both the Jaccard similarity index calculated from species presence/absence data and the Bray-Curtis similarity index calculated from the $\log_{10}(x+1)$ transformed species densities. At each of the 43 common stations sampled on every survey and for both indices, a similarity matrix was generated between the seven surveys. One mean value of Jaccard and Bray-Curtis index was calculated from the corresponding similarity matrices at each of the 43 stations as a measure of the extent of change in the local community composition/structure over time. A high mean value indicated weak changes in the community composition/structure among surveys at the local scale while a low mean value showed large changes in the community composition/structure among surveys. Spatial variations in the mean value of similarity index at the scale of local stations documented the spatial heterogeneity of temporal variability in species composition/structure.

The proportion of variation in community structure related to sediment type was quantified using a Distance based Linear Model (DistLM) performed between the $\log_{10}(x+1)$ transformed species densities at each station-period and the fine sediment type data (i.e. fine sand, muddy fine sand, sandy mud, mud) at each station-period for a total of 390 station-periods. The analysis was performed using the Bray-Curtis similarity

index for the species similarity matrix and by transforming the “sediment type” nominal variable into binary variables (Anderson et al., 2008).

All analyses on diversity were performed using PRIMER 7® and Permanova+ for Primer softwares (Anderson et al., 2008; Clarke et al., 2014).

3. Results

3.1. Sediment grain size analysis

From 1988 to 2001, the silt content was below 10 % in the majority of the study area except closest to the Seine estuary where it reached 25-50 % at some stations (Fig.2). Silt content increased slightly in 1996, especially along the coasts of Pays de Caux, where it reached 10-25 %. The increased siltation of the eastern Bay of Seine became apparent in 2006 with silt content exceeding 25 % in a high number of stations and 75 % at three stations directly in front of the estuary, off Cabourg and in Antifer harbour. While most stations were composed of fine sand and muddy fine sand between 1988 and 2001, with less than 15 % of stations with sandy mud or mud, by 2006 there had been a shift towards muddier sediments with more than 25 % of stations composed of sandy mud or mud. In 2011, the silt content tended to decrease but remained high in front of the Seine estuary and at some stations along the coasts of the Pays de Caux. Further a decreased siltation was observed in 2016. However, in contrast to earlier observations (1988 - 2001), silt content exceeded 10 % in most stations. The consistently high silt content in Antifer harbour reported in most surveys could be explained by the structure of the harbour, which traps fine sediments coming from the Seine estuary.

3.2. Species composition and densities

A total of 221 taxa belonging to nine phyla were reported during the survey period, including Annelida Polychaeta with 85 taxa (38 %), Arthropoda, mostly Malacostraca, with 69 taxa (33 %), Mollusca with 41 taxa (19 %) and Echinodermata with 12 taxa (5 %). The five other phyla were far less abundant: Cnidaria with four taxa, Sipuncula with three taxa, and Chordata and Phoronida with only one taxon. Nemertea were not identified beyond phyla owing to difficulties in accurately identifying incomplete pieces of organisms. Of the 221 taxa, 40 were sampled only once during the seven surveys. Among the seven surveys, gamma diversity ranged from 90 taxa in 1988 to 158 taxa in 2016 and showed no temporal trend (Fig. 3). The proportion of rare species per year (i.e. species found at one or two station-periods throughout the monitoring program) varied among years, following a temporal pattern close to that of the species accumulation curves, with 13 rare species reported in 2016 and 2006, 7 in 2011 and 2001, 5 in 1991, 4 in 1988 and 1 in 1996.

Only twenty-one of the 221 taxa identified within the eastern Bay of Seine were ranked among the ten most abundant taxa in at least one survey (Table 1). Among the most abundant taxa, four species were common to the seven surveys (i.e. *Owenia fusiformis*, *Acrocnida brachiata*, *Lagis koreni* and *Nephtys hombergii*), two species six times (i.e. *Kurtiella bidentata* except in 2016 and *Abra alba* except in 2011), and one species five times (i.e. *Phaxas pellucidus* except in 1988 and 2006). These seven species represent the “typical” species of the *Abra alba* - *Lagis koreni* muddy fine sand community. *Owenia fusiformis* remained the most abundant species, except in 2001 and 2016 when it was ranked second, behind *Kurtiella bidentata* and *Phaxas pellucidus* respectively. The other taxa, which generally occurred in lower ranking positions, were (1) abundant only occasionally like *Aphelochaeta marioni* in 2001, 2006 and 2016, or *Nucula nitidosa* in 2001 and 2006, (2) rather dominant at the beginning of the study

period such as *Thyone fusus* and *Echinocardium cordatum* or (3) rather dominant at the end of the study period such as *Ampharete baltica*, *Magelona johnstoni* and *Melinna palmata*.

Regardless of the relative stability of the macrobenthic community in terms of species composition and relative densities of dominant species at the scale of the eastern Bay of Seine for the 28-year survey period, their average densities were highly variable over time, depending on the species. Thus, the CV of the most dominant species at the 43 common stations sampled on every survey ranged from 26% for *Lagis koreni* to 94% for *Phaxas pellucidus* (Table 1). The average densities of *Lagis koreni* varied by a factor of 2.2, from 13.0 ind.0.5m⁻² in 2011 to 29.2 ind.0.5m⁻² in 1988, while those of *Phaxas pellucidus* varied by a factor of 77.6, from 0.7 ind.0.5m⁻² in 1988 to 54.3 ind.0.5m⁻² in 2016. For the most abundant species, *Owenia fusiformis*, the CV reached 57% with average densities varying by a factor of 5.7, from 52.7 ind.0.5m⁻² in 2016 to 298.8 ind.0.5m⁻² in 1988.

At the local scale, the ranges of CV also differed between species (Fig. 4). Some species such as *Nephtys hombergii* or *Thyone fusus* had a limited range of low values while other species such as *Melinna palmata* and *Magelona mirabilis* had a limited range of high values, suggesting that the temporal variations of their densities varied little in space between stations. Conversely, for other species like *Owenia fusiformis*, *Acrocnida brachiata* and *Echinocardium cordatum*, the CV showed a wide range of values among stations. There was no spatial consistency in the CV values of the mean densities for the most abundant species during the 28 years of the study period. For a given station, some species exhibited low temporal variations in their densities while other species showed high variations.

3.3. Changes in local diversity

The number of individuals and species diversity indices measured at each of the 403 sampling station-periods showed significant differences between years (Kruskal-Wallis test; N: $p < 0.01$; S: $p < 0.001$; H': $p < 0.001$; J': $p < 0.001$) (Fig. 5). The number of individuals (N) varied between 1 and 4281 ind.0.5m⁻² with no temporal trend. There were no significant differences between the years 1988 and 1991 at the beginning of the study period and the years 2001, 2011 and 2016 at the end of the study period. N was significantly lower during 1996, compared to all other years and higher in 2006, compared to the two preceding and succeeding years. Maximal densities could locally exceed 2000 ind.0.5m⁻² except for the years 1996 and 2016. Species richness (S) ranged between 1 and 65 species and showed erratic variations with time. Dunn post-hoc tests indicated that S was significantly lower during years 1988 and 1996 compared to other surveys and significantly higher for the years 2006 and 2016. Intermediate values were reported for the years 1991, 2001 and 2011. Shannon index (H') varied between 0 and 5.07 while Pielou's evenness (J') varied between 0.07 and 0.97, both being significantly lower in 1988. H' and J' increased significantly between first and second surveys and remained constant for the last surveys (i.e. no significant differences between these last surveys).

3.4. Macrofaunal assemblages

On the basis of a compromise between the results of the SIMPROF test and the need to identify a limited number of assemblages on the 392 station-periods, five assemblages were identified from the HCA at a 21% similarity level (Supplementary material Fig. A): one major assemblage (IV) of 334 station-periods, two assemblages composed of about 20 station-periods (I, II), and two minor assemblages with only four

and six station-periods respectively (III, V) (Table 2). Four station-periods were isolated and not grouped within the five assemblages leaving a total of 388 station-periods spread across the assemblages. The main characteristics of these different assemblages and sub-assemblages and their spatial distribution are given in Table 2 and Figure 6. The results of the SIMPER analysis are provided in Table 3.

Assemblage I was characterized by the lowest mean density (22.3 ind.0.5m⁻²) and the lowest mean taxonomic richness (5.4 taxa; Table 2). Species which contributed the most to the similarity within each station-period of this assemblage were the polychaete *Nephtys hombergii* and in a lesser extent the bivalve *Abra alba* and the polychaete *Lagis koreni*. Each year, between one and six stations located in close proximity to the Seine estuary belonged to this assemblage (Fig. 6).

Assemblage II showed moderate values of N (110.6 ind.0.5m⁻²), S (15.3 taxa) and H' (2.7). Characteristic species of this assemblage were mainly those inhabiting clean fine and medium sand like the polychaetes *Nephtys cirrosa* and *Magelona johnstoni* and the echinoderm *Echinocardium cordatum* (Table 3). This assemblage was mainly observed off the Seine estuary, but in 2011, it was also reported at two stations off Deauville (Fig. 6).

Assemblage III was only observed at four stations in 2016 off Deauville (Fig. 6). It was characterized by the local presence of the bivalve *Donax* spp. in fine sand whose average densities reached 100 ind.0.5m⁻². As a result of dominance by a single species, the Shannon index and Pielou's evenness of this sub-assemblage were low (Table 2).

Assemblage IV was the core assemblage of the muddy fine sand benthic community of the eastern Bay of Seine. It was subdivided into a small sub-assemblage (sub-assemblage IVa) and a major sub-assemblage (sub-assemblage IVb) at a 25% similarity level (Supplementary material Fig. A). Sub-assemblage IVa was a small

assemblage observed only at five station-periods in 1988, 2011 and 2016 (Fig. 6). It was mainly dominated by one species, the brittle star *Acrocnida brachiata*, such that the Shannon index and Pielou's evenness were low (Table 2). Sub-assemblage IVb, which extended from Antifer harbour to Ouistreham, was divided further into three sub-assemblages which differed in terms of mean densities, mean species richness and the relative density of dominant species (Tables 2 and 3).

Sub-assemblage IVb₂, which was the most important in terms of the number of station-periods, showed the highest mean density (717 ind.0.5m⁻²) and the highest mean taxonomic richness (28.4 taxa; Table 2). It was characterized by dominance of the polychaete *Owenia fusiformis* and high densities of "typical" species of the community like the brittle star *Acrocnida brachiata*, the polychaetes *Nephtys hombergii* and *Lagis koreni*, and the bivalves *Phaxas pellucidus*, *Kurtiella bidentata* and *Abra alba* (Table 3). The polychaete *Ampharete baltica* which has had an increasing influence, being ranked amongst the ten most dominant species in all surveys since 2006 made a large contribution to the assemblage. Sub-assemblage IVb₁ differed from the previous one by a lower mean density (383.1 ind.0.5m⁻²) and a lower mean taxonomic richness (18.4 taxa; Table 2). Whilst *Owenia fusiformis* remained the most abundant species in this sub-assemblage, its mean density was about half that within sub-assemblage IVb₂. Only *Lagis koreni* was more abundant in this sub-assemblage than in the previous. According to SIMPER results, this sub-assemblage was characterised by five of the seven "typical" species of the community except *Acrocnida brachiata* and *Phaxas pellucidus* (Table 3). Finally, sub-assemblage IVb₃ showed a high mean taxonomic richness (27.2 taxa) but a lower mean density than sub-assemblages IVb₁ and IVb₂ (Table 2). The species contributing most to the similarity among station-periods of this sub-assemblage were species which were commonly observed in sandier environments such as *Phaxas*

pellucidus, *Glycinde nordmanni*, *Echinocardium cordatum*, *Chaetozone gibber* and *Euspira nitida* (Table 3). These three sub-assemblages should be defined as three different facies of the community: (1) a *Lagis koreni* facies for the sub-assemblage IVb₁, (2) an *Owenia fusiformis* - *Acrocnida brachiata* facies for the sub-assemblage IVb₂ and (3) an impoverished *Phaxas pellucidus* facies for the sub-assemblage IVb₃.

The relative importance and the distribution of these three sub-assemblages changed with time (Fig. 6). The sub-assemblage IVb₁ was reported each year off the Seine estuary and off Deauville and was slightly more extended in 2006. The sub-assemblage IVb₂ was observed from Antifer harbour to Ouistreham each year whereas the sub-assemblage IVb₃ was distributed at the western periphery of the sampling area, mostly from Cap de la Hève to Ouistreham, and disappeared from 2011 onwards. After this date, there was a tendency for homogenisation of the community with an extension of the sub-assemblage IVb₂.

Assemblage V was only found at coastal stations between the Cap de la Hève and Antifer harbour in 1991, 1996, 2011 and 2016 (Fig. 6). Its taxonomic richness and mean densities were low. However, due to the lack of dominant species, Shannon index (H') and Pielou's evenness (J') of this assemblage were high, with the most characteristic species being the polychaetes *Nephtys hombergii* and *Hilbigneris gracilis*, and the bivalve *Phaxas pellucidus*, which were sampled at relatively low densities (Table 3).

To assess the extent of change in the community structure over time at local scale, the mean value of the Bray-Curtis similarity coefficient was calculated at each station between all pairs of sampling surveys (Fig. 7). The less variable stations (i.e. Bray-Curtis similarity coefficient > 50 %) were located in the Northeast of the Bay of Seine, along the Pays de Caux between Antifer harbour and Le Havre, and to a lesser extent at some stations between Ouistreham and Deauville. These stations belonged

mostly to the sub-assemblage IVb₂ each year (Fig. 6). Conversely, the year-to-year changes were more marked at stations located in front of the estuary and at some stations between Deauville and Ouistreham. These patterns of relative stability/variability of community structure at the local scale remained consistent when quantifying only compositional change by using the Jaccard similarity coefficient (Supplementary material Fig. B). The relationship between average values of the Bray-Curtis and Jaccard similarity coefficients was positive and highly significant ($R^2 = 0.894$; $N = 43$; $p < 0.001$) (Supplementary material Fig. C).

The DistLM showed that the sediment type had a highly significant effect on the spatio-temporal changes in the community structure ($p < 0.001$) but explained only 4.6% in the variation of the community structure.

4. Discussion

4.1. Stability vs. variability at different scales

This study investigated the spatio-temporal changes in the composition and structure of the muddy fine sand benthic community of the eastern Bay of Seine between 1988 and 2016 to understand how the macrobenthic community varies according to the scale of observation (i.e. the “study area” scale, the “assemblage” scale and the “local station” scale) and the different measures of stability (e.g. variability of densities based on CV, β -diversity). Whilst the eastern Bay of Seine is exposed to multiple anthropogenic stressors that have persisted over time, the main changes during the study period have been the evolution of sediment dynamics, resulting in repercussions at different scales: widespread increased siltation in the eastern Bay of Seine since 2006 as evidenced by our results and Lesourd et al. (2016) at the regional

scale, and large volumes of dredged and dumped sediments at the local scale [4.5 million $\text{m}^3\cdot\text{y}^{-1}$ at the Kannik dumping site (Marmin et al., 2016) and 2-2.5 million $\text{m}^3\cdot\text{y}^{-1}$ at the Octeville dumping site (Baux et al., 2019)].

4.1.1. Variability at the study area scale

At the “study area” scale, only 10% of the total number of identified taxa (21 out of 221) was ever among the first ten most abundant taxa. A pool of only seven typical species were ranked among the most abundant taxa at least five times out of the seven surveys and drove the temporal evolution of the community composition: *Owenia fusiformis*, *Acrocnida brachiata*, *Lagis koreni*, *Nephtys hombergii*, *Kurtiella bidentata*, *Abra alba* and *Phaxas pellucidus*. However, the first observation of *Melinna palmata* in 2002 (Dauvin et al., 2007), its ranking within the ten dominant species since 2011 and the increase in density of the polychaete *Ampharete baltica*, which are both associated with mud and muddy sand habitats (Oyenekan, 1988; Zettler et al., 2013), reflect major effects of the recent siltation of the eastern part of the Bay of Seine. The siltation resulted from both alteration of the morpho-sedimentary dynamics of the Seine estuary *via* river flows and flood intensity, and the increase of dredged sediment deposit following the extension of Le Havre harbour along the Cap de la Hève-Antifer area (Lesourd et al., 2001; Méar et al., 2018; Baux et al., 2019).

At the scale of the whole study area, the total taxonomic richness as well as mean values of local diversity (i.e. local taxonomic richness, Shannon’s index and Pielou’s evenness) displayed no general trend of increasing alpha and gamma diversity although significant differences between years were observed, in particular alpha diversity was lowest at the beginning of the study in 1988 and in 1996. Such year-to-year differences could be partly explained by large variations in dominance patterns of some abundant

species like *Owenia fusiformis* for which mean densities varied from 214.8 ind.0.5m⁻² in 1991 to 90.3 ind.0.5m⁻² in 1996. Dauvin and Gillet (1991) already reported large year-to-year variations in *Owenia fusiformis* densities which were related to large year-to-year variations in the recruitment. They proposed several hypotheses to explain these variations: a failure in the reproduction, an export of most larvae outside the bay, a low survivorship of young recruits. The lowest local species richness in 1988 and 1996 was to be compared with lowest gamma diversity in the same years which was partly related to the proportion of rare species.

The five years sampling frequency precluded assessment of the effects of climatic oscillations on species densities or local diversity at decadal or sub-decadal scales as observed in the German Bight (North Sea) in response to the North Atlantic Oscillation (Kröncke et al., 1998; Shojaei et al., 2016) or in the Bay of Banyuls (Mediterranean Sea) in response to the Western Mediterranean Oscillation (Bonifácio et al., 2019). However, analysis of temporal changes in the benthic community at one station off the Seine estuary sampled yearly between 1978 and 1992 showed that greatest change occurs at seasonal time scales (Fromentin et al., 1997). Year-to-year changes in community structure, in response to the alternation of cold and mild winters, were of low amplitude.

4.1.2. Variations at the assemblage scale

At the “assemblage” scale, the overall community structure persisted over time with three dominant assemblages which differed in terms of taxonomic richness and relative densities of the dominant species: the *Lagis koreni* facies off the Seine estuary and off Deauville, the *Owenia fusiformis* - *Acrocnida brachiata* facies from Antifer harbour to Ouistreham and the impoverished *Phaxas pellucidus* facies at the periphery of the study area. These assemblages, which represent 84% of the sampling station-

periods from 1988 to 2016, were very similar in terms of distribution and characteristic species with those already described by Thiébaud et al. (1997) from observations carried out through four winter surveys between 1986 and 1991. The remaining assemblages included only a small number of station-periods, between 1 and 8 %, and were characterized by low internal similarity. They were interspersed within the other assemblages with no specific spatial identity and seemed to correspond to very local assemblage composition and structure.

The relative importance and the distribution of the three main assemblages changed little with time but the *Owenia fusiformis* - *Acrocnida brachiata* facies extended in 2016 to cover 58% of sampled stations. This extension led to a decrease in the spatial beta diversity and consequently a biotic homogenization of the community structure which is now recognized to be a major broad-scale consequence of anthropogenic stressors in both terrestrial and marine ecosystems (Thrush et al., 2006; Socolar et al., 2016). In soft sediments, biotic homogenization can be the result of various stressors including physical disturbance such as increased sediment inputs and deposition, the selective removal of habitat-forming species and the proliferation of engineer or non-indigenous species (Thrush et al., 2004; Rigolet et al., 2014). The recent spread of fine particles over the entire eastern Bay of Seine, corresponding to a decrease in the total muddy area and relative increases in sandy mud and muddy sand, is likely an important contributor to the observed biotic homogenization (Lesourd et al., 2016).

4.1.3. Variability at the local station scale

At a smaller scale, i.e. the “local station” scale, variability of species densities and community structure were more complex. Several patterns were observed regarding the spatio-temporal variations of species densities. For some species, temporal variation of

densities varied little in space (i.e. between stations), whether these were low variations as for *Nephtys hombergii* or high variations as for *Melinna palmata*. Conversely, for other species like *Owenia fusiformis*, temporal variation in density varied greatly in space, with some stations showing low temporal variation whilst others showed considerably higher levels of variation. Beyond temporal variation in density at the bay scale that could be attributed to inter-annual variation in recruitment intensity depending on the species biological traits, such spatial variability in temporal variations suggest that some stations are more stable than others. This population level observation was also observed at the community level, with high variability in temporal variation in community composition and community structure amongst stations. The least variable stations were reported along the Pays de Caux and between Ouistreham and Deauville within the *Owenia fusiformis* - *Acrocnida brachiata* facies, whilst those displaying highest variability were located in front of the Seine estuary and off Deauville. Higher temporal variability in these shallow parts of the bay could be related to their exposure to greater instability in morpho-sedimentary dynamics in response to several human and natural stressors. In particular, high seasonal variations in the sedimentary regime were reported with soft mud deposits in winter greatly reworked by waves and tidal currents, leading to alternations of deposition and erosion periods corresponding with the seasons and meteorological events (Lesourd et al., 2001; Garnaud et al., 2002). On the contrary, the high densities of the tubicolous worm *Owenia fusiformis* which dominated the assemblage reported along the Pays de Caux and off Ouistreham are expected to have sediment stabilizing effects with positive effects on the persistence of the community despite the presence of the Octeville dumping site off Cap de la Hève (Volkenborn et al., 2009).

4.2. Mechanisms involved in the long-term persistence of the community

At the regional scale, the composition and the structure of the macrobenthic community did not show any major changes over the 30 years of the study despite the presence of continuous anthropogenic pressures since the beginning of the monitoring program, in particular the redevelopment of Le Havre harbour with the “Port 2000” project. Contrary to what would be expected for a system exposed to multiple stressors including climate change which are known to have important non-linear effects on coastal benthic communities (Hewitt et al., 2016), a relative stability of the community is highlighted. For example in the North Sea, changes in the distribution of various species were reported at a large regional scale between 1986 and 2000, in response to environmental factors such as increased sea surface temperature and primary production (Kröncke et al., 2011). At shorter time scales, decadal changes in a local community structure have also been observed in different parts of the North Sea in response to climate change and eutrophication (Frid et al., 2009; Shojaei et al., 2016). At the scale of the Gulf of Lions (Mediterranean Sea), Bonifácio et al. (2018) showed important changes in macrofauna composition in a littoral fine sand community at a 12-year interval due to climatic events which control changes in the density of the dominant polychaete, *Ditrupa arietina*. These communities, although still present at the end of the studies, have undergone such changes that they could not be considered as “persistent” compared to the *Abra alba* - *Lagis koreni* community in the eastern Bay of Seine. However, the situation of a “persistent” community *sensu* Grimm & Wissel (1997), i.e. a stability property which considers a dynamic equilibrium within boundaries, is not unique. In Swansea Bay, a coastal area considered as a “heavily modified water body”

exposed to diffuse and point pollution, strong similarities in the spatial distribution and species composition of benthic communities occurred between 1984 and 2014 with a group of five common species particularly persistent over 30 years (Callaway, 2016).

Different mechanisms might explain the observed persistence of the macrobenthic community in the eastern Bay of Seine over 30 years. Whilst areas more heavily impacted by human activities are assumed to have a lower biodiversity than areas less impacted by the same activities (Johnston and Roberts, 2009), these observations from small-scale studies may not occur at a larger scale. Firstly, it has been shown that communities in modified estuaries exposed to high level of toxic contaminants can be comparable in diversity to those in unmodified estuaries for epibiota or infaunal polychaetes (Dafforn et al., 2013; Clark et al., 2015). The negative impacts of contaminants on species diversity observed at small scales in laboratory experiments are not necessarily observed within field experiments performed at larger spatial scales where they could be compensated by positive effects of organic enrichment and increases in productivity. Such a compensation mechanism could occur in the highly productive eastern Bay of the Seine where maximal primary production can exceed $20 \text{ mgC.m}^{-2}.\text{d}^{-1}$ during spring (Napoléon et al., 2014).

Secondly, as pointed out by Dauvin et al. (2017), the persistence of the community could be partly due to the benthic-pelagic life cycle of dominant species, with dispersal at larval and post-larval stages influencing the capacity of species to recover from local disturbances. In particular, post-settlement dispersal which has been reported for most dominant species (Olivier et al., 1996) and is frequent over long time periods could allow species to track environmental variations by escaping adverse conditions and colonizing quickly undisturbed areas, a mechanism which can be important for the persistence of benthic communities (Pilditch et al., 2015). Bi-monthly

monitoring of the sediment dynamics in the northern part of the Seine estuary showed rapid restructuring of benthic communities by juvenile drifters in response to intense episodes of sediment transport (Desroy et al., 2007). Each station evolves independently of the others, so one station can be affected by localized environmental change without others being affected, creating a small-scale mosaic. Such observations suggest that the turnover of individuals can be very high at local scale but contribute to the long-term persistence of the community at the regional scale.

Thirdly, we observed the integration of new species into the community, either in response to changes in the sedimentary environment like the polychaete *Melinna palmata* or as non-indigenous species like the North American bivalve *Ensis leei*. This assimilation occurred without any drastic changes in the community structure although the long-term risks of assimilating non-indigenous species are their influence on the recovery and the resilience of the community (Thrush et al., 2008). Introduced to the North Sea in the 1970's by the transport of its larvae in ballast water from North American Atlantic coasts and now present from Spain to Norway (Gollasch et al., 2015), the jack-knife clam *Ensis leei* was first reported in 1998 in the eastern Bay of Seine (Dauvin et al., 2007) and has become increasingly abundant with a maximum of 78 ind.m⁻² in 2001 and 200 ind.m⁻² in 2016. The consequences of *Ensis leei* introduction appeared highly variable among regions. In the Bay of Seine, its installation did not drastically disrupt the community, and its population remains at low to moderate densities, contrary to what has been observed in the southern part of the North Sea where *Ensis leei* changed dramatically the abundance and biomass of the fine sand community in this area (Ghertsos et al., 2000). In the *Abra alba* fine sand community along the Belgian coasts, *Ensis leei* has become the most common species causing a decline in the densities of other bivalves (Van Hoey et al., 2004). In the eastern German

Bight, it could facilitate the settlement of some deposit feeders by forming dense mats that stabilize the sediment and trap organic matter. Thus in this latter area, it seems to act positively by diversifying the community and not as a nuisance for other species (Dannheim and Rumohr, 2012).

Similar to *Ensis leei*, the tubicolous polychaete *Melinna palmata* was first recorded in 2002 in the eastern Bay of Seine (Dauvin et al., 2007) and reached maximum densities of 298 ind.m⁻² in 2011 in response to the siltation of the bay. Ranked amongst the 10 most abundant taxa since 2011, *Melinna palmata* has not significantly altered the community structure nor its spatial organization over the last three decades even if, in a recent description of benthic habitats in the Bay of Seine, Baffreau et al. (2017) have described a “*Melinna palmata* sandy mud community” defined as a very muddy facies of the *Abra alba* muddy fine sand community. Indeed, although the sediment type and consequently the silt content had a significant effect on the structure of the community, its role was minor over the last three decades. This result is consistent with the relative stability of the community. We hypothesized that the increase in silt content had modified the relative abundances of some secondary species inhabiting either muddy habitat (e.g. *Melinna palmata*) or sandy habitats (e.g. *Echinocardium cordatum*) but that the dominant typical species which structured the community occupied a relatively large sediment range that remained within the sediment range observed in the present study.

4.3. Sampling strategy and spatial scales

Historical data are very valuable to highlight the long-term persistence of the composition and structure of benthic communities (Callaway, 2016). The two main strategies developed to assess long-term changes in macrobenthic communities have advantages and disadvantages. The long-term monitoring of one or few stations on a

667 regular frequency has the advantage of describing the dynamics of macrobenthic
668 communities in relation to changes in climatic and environmental variables, which is not
669 possible from a comparison at long time intervals of a network of stations. Such an
670 approach is also favoured in monitoring programs dedicated to the assessment of the
671 ecological status of French coastal water bodies for the EU Water Framework Directive
672 (WFD). However, it raises the questions of the representativeness of the sampling
673 station and of the spatial heterogeneity in the long-term variability of a macrobenthic
674 community observed at a local scale. In the case study of the eastern Bay of Seine, the
675 magnitude of temporal variations in the density of dominant species and in the
676 community composition or structure varied greatly in space, suggesting that the
677 perception of stability/variability of a community can vary according to the sampling
678 station. In a heavily modified area exposed to multiple stressors acting at different
679 spatial and temporal scales, we recommend a management strategy based on a nested
680 sampling design that considers a variety of both spatial and temporal scales and is
681 economically sustainable. In the case of the eastern Bay of Seine, this hierarchical
682 strategy could be implemented as follows: (1) a network of 60 stations sampled every
683 five years to assess the long-term changes in the beta diversity (i.e. assemblages
684 distribution) which is now recognized as a major issue in marine ecosystems
685 management (Thrush et al., 2006, 2008) and is essential to determine how changes in
686 alpha diversity scale-up at larger scales (e.g. spreading of non-indigenous species); (2) a
687 small number of four or five stations sampled at least once a year to analyse the
688 heterogeneity in the responses of local community to multiple stressors (e.g climate
689 change, changes in the river flow) (Hewitt et al., 2016). These stations should be
690 representative of the main macrofaunal assemblages in the region and of areas
691 exhibiting different levels of temporal variability.

5. Conclusion

Like most European estuaries and coastal embayments, the eastern Bay of Seine has been exposed to strong human impacts since the 19th century in relation to the development of industrial activities and the continued need to ensure and improve maritime traffic. Therefore the oldest data collected in 1988 is unlikely to represent a pristine state of the community, nevertheless major morpho-sedimentary changes have occurred during the last 30 years in response to variations in the Seine river flow and the development of Le Havre harbour (Lesourd et al., 2016), and the introduction of new species has been reported (Dauvin et al., 2007). Despite its exposure to multiple stressors including climate change, the *Abra alba* - *Lagis koreni* muddy fine sand community of the eastern Bay of Seine and its facies have been persistent in terms of species composition, relative densities of the dominant species and spatial organization over the last 30 years of the study. The community is dominated by highly resilient species capable of quickly rebuilding their populations. This persistence of the benthic community was dependent on scales of space (i.e. local vs. regional scale), time (i.e. sampling frequency) and biological organization (i.e. population vs. assemblage) emphasizing the need to implement sampling strategies combining different scales. The regional persistence of the community observed in the eastern Bay of Seine differed from findings in other coastal areas where climate change drives major shifts in benthic communities at different biological levels of organisation. These results suggest that the sensitivity of benthic communities to climate change is not consistent across regions and might be reduced in heavily modified ecosystems exposed to multiple stressors. The macrobenthic community in the eastern Bay of Seine appears to be a very resilient system at a 30-year time scale, and it is likely that more time will be required to observe the consequences of climate change on the subtidal benthos in this area.

717 **Acknowledgments**

718 This study was successively supported by the “French National Program on the
719 Determinism of the Recruitment” (PNDR), the “French National Program on Coastal
720 Environment” (PNEC) and the “Seine-Aval” program coordinated by the GIP Seine-Aval.
721 It forms part of the research doctoral research work of Lise Bacouillard partly funded by
722 the Brittany region. We thank the crew of the research vessels “Pluteus II”, “Côtes
723 d’Aquitaine” and “Côtes de la Manche” for their valuable assistance during the different
724 field surveys. We also gratefully acknowledge all students, technicians and colleagues
725 who contribute to the sampling and laboratory works since 1988, and Louis Cabioch and
726 Christian Retière who initiated this long-term program in the eastern part of the Bay of
727 Seine in the 1980’s. We would like to express our gratitude to Céline Houbin for her help
728 in map production and to Lydia White for English proof reading. We thank three
729 anonymous referees for their valuable comments on a first version of this manuscript.

730 FIGURE CAPTIONS

- 731 Figure 1: Location of the study area and of the 60 stations sampled between 1988 and
 732 2016 during the seven sampling surveys in the eastern Bay of Seine. The black dots
 733 correspond to the 43 common stations sampled on every survey and the grey
 734 squares to the 17 stations sampled only during six surveys. The three dumping sites
 735 are indicated in grey line (Kannik, Machu, Octeville).
 736 Figure 2: Spatial distribution of the silt percentages (%) within the sediment, in the
 737 eastern Bay of Seine for each survey.
 738 Figure 3: Species accumulation curves for the seven surveys performed in the eastern
 739 Bay of Seine from 1988 to 2016. Plotted values are mean values of 999
 740 randomization of sample order.
 741 Figure 4: Coefficients of variation (CV) of species abundance expressed as a percentage
 742 calculated at each station for the 21 taxa ranked amongst the 10 most abundant
 743 species at least once, for each survey. The trend of CV values per station is given for
 744 five stations, each representative of different sectors of the study area.
 745 Figure 5: Boxplot representation of the species diversity indices calculated for each
 746 survey at each station: (A) number of individuals (N), (B) species richness (S), (C)
 747 Shannon-Weaver index (H') and (D) Pielou's evenness (J'). For each plot, similar
 748 letters (a, b, c and d) above each bar indicate no statistical differences among years
 749 following the Dunn tests ($p < 0.05$).
 750 Figure 6: Spatial distribution of assemblages and sub-assemblages identified with
 751 Hierarchical Cluster Analysis in the eastern Bay of Seine for each survey. The
 752 number of stations for each survey was 50 in 1988, 57 in 1991, 55 in 1996, 56 in
 753 2001, 58 in 2006, 56 in 2011 and 56 in 2016.
 754 Figure 7: Spatial distribution of the mean values of Bray-Curtis similarity coefficients
 755 (temporal beta diversity) at each of the 43 common stations sampled on every
 756 survey in the eastern Bay of Seine.
 757

758 TABLE CAPTIONS

759 Table 1: Rank of the 10 most abundant taxa (1 to 10), mean species density (M; ind.0.5m⁻²) ±
 760 SE (Standard Error) for each sampling survey and all station-periods, coefficient of
 761 variation (CV) of species densities at the scale of the bay expressed as a percentage only
 762 for the 43 common stations sampled on every survey.

763 Table 2: Characteristics of the assemblages and sub-assemblages identified with the
 764 Hierarchical Cluster Analysis with the number of station-periods, mean species
 765 density (ind.0.5m⁻²), mean species richness (S), mean Shannon-Weaver index (H')
 766 and mean Pielou's evenness (J') ± SE (Standard Error) with a total of 388 station-
 767 periods spread across the assemblages.

768 Table 3: Results of the SIMPER analysis with the percentage of similarity within each
 769 assemblage identified by Hierarchical Cluster Analysis, species contributions to the
 770 similarity between stations within the same assemblage and mean species densities.
 771

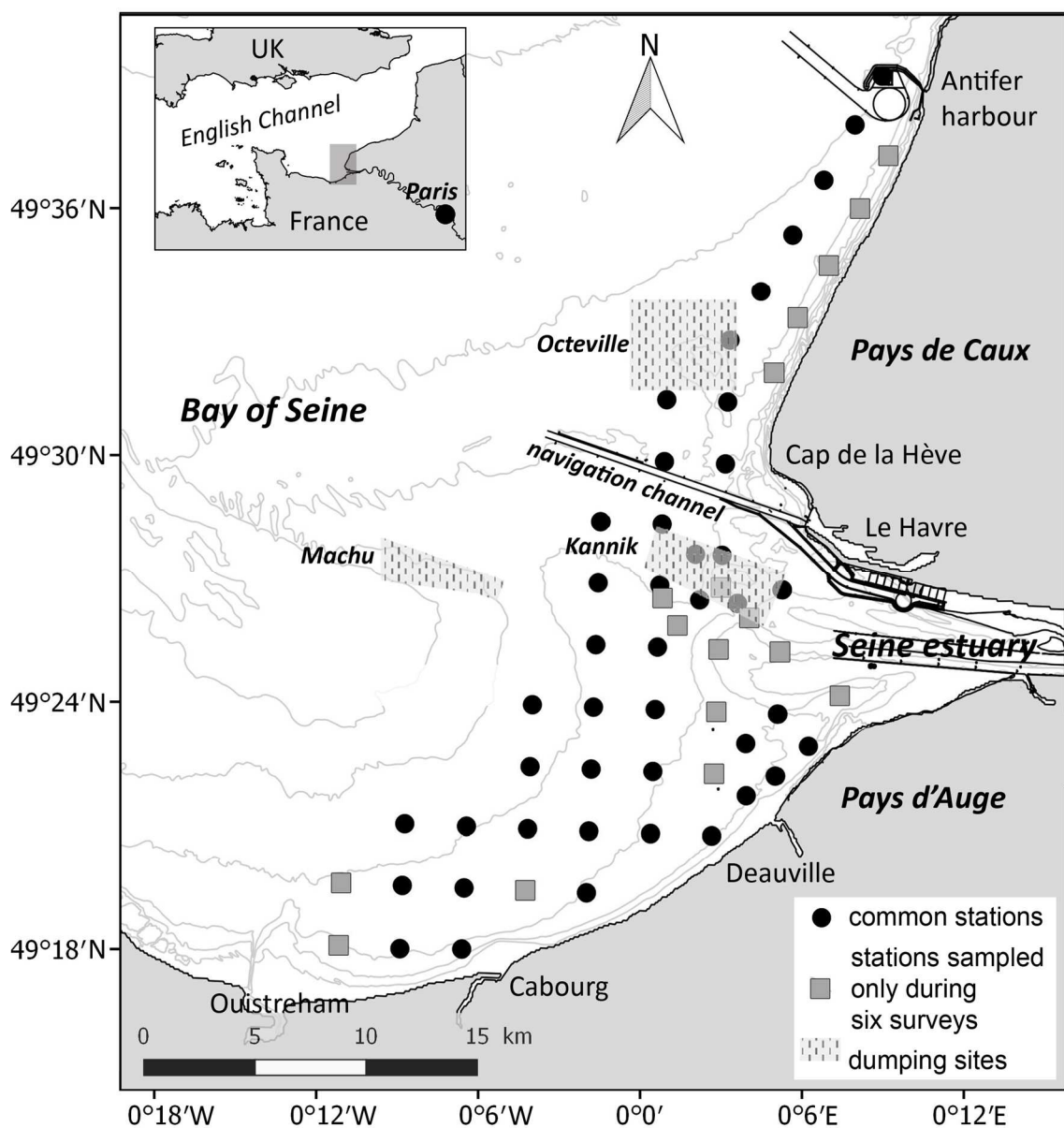


Figure 1: Location of the study area and of the 60 stations sampled between 1988 and 2016 during the seven sampling surveys in the eastern Bay of Seine. The black dots correspond to the 43 common stations sampled on every survey and the grey squares to the 17 stations sampled only during six surveys. The three dumping sites are indicated in grey line (Kannik, Machu, Octeville).

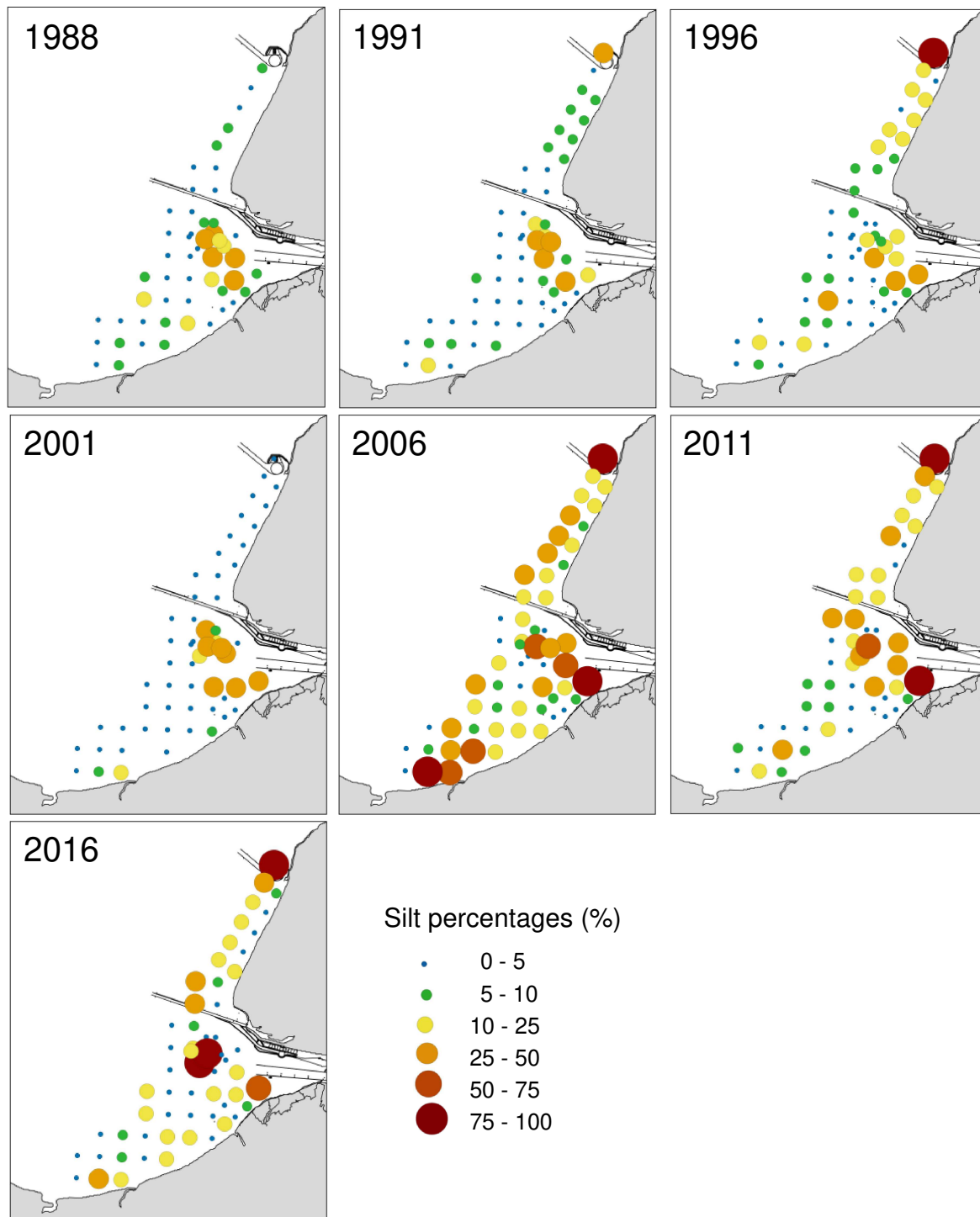


Figure 2: Spatial distribution of the silt percentages (%) within the sediment, in the eastern Bay of Seine for each survey.

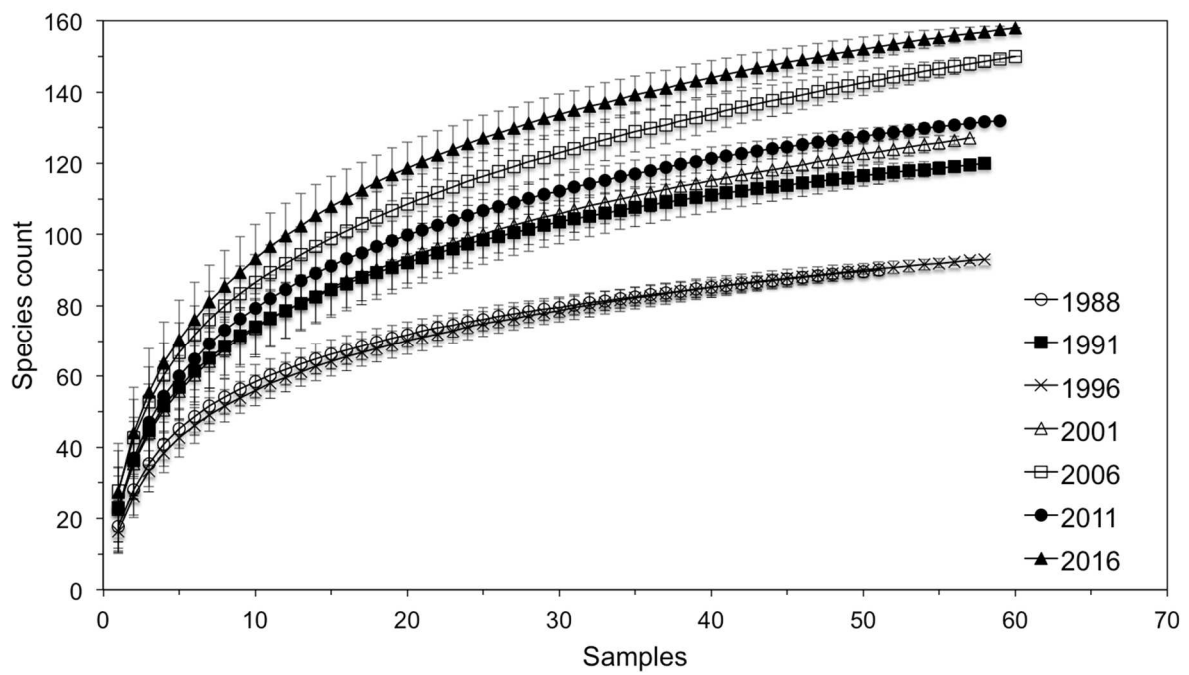


Figure 3: Species accumulation curves for the seven surveys performed in the eastern Bay of Seine from 1988 to 2016. Plotted values are mean values of 999 randomization of sample order.

873 **Table 1:** Rank of the 10 most abundant taxa (1 to 10), mean species density (M; ind.0.5m⁻²) ± SE
874 (Standard Error) for each sampling survey and all station-periods, coefficient of variation (CV) of
875 species densities at the scale of the bay expressed as a percentage only for the 43 common
876 stations sampled on every survey.

Taxa	CV (%)	Sampling survey													
		1988		1991		1996		2001		2006		2011		2016	
		M	±SE	M	±SE	M	±SE	M	±SE	M	±SE	M	±SE	M	±SE
<i>Owenia fusiformis</i>	57	1		1		1		2		1		1		2	
		298.8	74.7	214.8	50.1	90.3	21.2	64.6	15.3	190.9	51.5	153.5	46.4	52.7	14.0
<i>Acrocnida brachiata</i>	39	2		3		3		5		3		5		7	
		39.3	8.9	46.2	10.6	27.1	7.9	23.0	8.0	37.4	11.3	20.2	7.4	10.0	2.6
<i>Lagis koreni</i>	26	4		7		4		6		5		7		4	
		29.2	8.1	23.3	5.6	15.3	4.3	22.4	5.0	23.4	5.2	13.0	7.4	17.1	9.5
<i>Nephtys hombergii</i>	48	9		6		7		10		8		9		6	
		5.6	0.9	26.1	3.1	9.3	1.3	11.2	1.6	15.0	2.2	11.7	1.8	10.4	1.5
<i>Kurtiella bidentata</i>	86	5		2		2		1		2		3		-	
		17.7	6.7	109.7	39.5	28.4	11.8	121.1	35.5	148.4	48.5	28.2	8.6	-	-
<i>Abra alba</i>	78	6		4		6		3		9		-		5	
		13.5	7.8	34.9	9.8	10.1	2.6	37.8	8.2	11.3	2.6	-	-	10.7	3.2
<i>Phaxas pellucidus</i>	94	-		5		5		7		-		4		1	
		-	-	30.7	8.3	15.0	2.8	16.4	3.4	-	-	20.6	5.8	54.3	12.9
<i>Aphelocheata marioni</i>	139	-		-		-		4		6		-		8	
		-	-	-	-	-	-	34.6	8.7	19.6	8.1	-	-	9.2	2.4
<i>Ampharete baltica</i>	83	-		-		-		-		10		6		3	
		-	-	-	-	-	-	-	-	10.3	2.7	16.9	5.0	19.8	3.8
<i>Magelona johnstoni</i>	159	-		-		-		-		4		2		-	
		-	-	-	-	-	-	-	-	37.4	11.5	38.5	22.0	-	-
<i>Magelona mirabilis</i>	154	-		-		8		9		-		-		-	
		-	-	-	-	6.3	2.0	12.5	3.6	-	-	-	-	-	-
Nemertea	131	3		-		-		-		-		8		-	
		33.1	15.5	-	-	-	-	-	-	-	-	12.6	2.2	-	-
<i>Nucula nitidosa</i>	102	-		-		-		8		7		-		-	
		-	-	-	-	-	-	14.3	5.4	17.9	5.2	-	-	-	-
<i>Thyone fusus</i>	74	8		10		-		-		-		-		-	
		6.7	3.3	8.3	6.0	-	-	-	-	-	-	-	-	-	-
<i>Echinocardium cordatum</i>	53	10		-		9		-		-		-		-	
		4.8	1.1	-	-	6.3	1.2	-	-	-	-	-	-	-	-
<i>Melinna palmata</i>	140	-		-		-		-		-		10		9	
		-	-	-	-	-	-	-	-	-	-	9.7	3.0	8.5	1.5
<i>Lanice conchilega</i>	114	7		-		-		-		-		-		-	
		11.5	9.7	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chaetozone gibber</i>	113	-		8		-		-		-		-		-	
		-	-	18.1	6.0	-	-	-	-	-	-	-	-	-	-
<i>Fabulina fabula</i>	98	-		9		-		-		-		-		-	
		-	-	13.4	4.3	-	-	-	-	-	-	-	-	-	-
<i>Sagartia troglodytes</i>	37	-		-		10		-		-		-		-	
		-	-	-	-	4.6	1.6	-	-	-	-	-	-	-	-
<i>Corbula gibba</i>	175	-		-		-		-		-		-		10	
		-	-	-	-	-	-	-	-	-	-	-	-	7.8	2.1

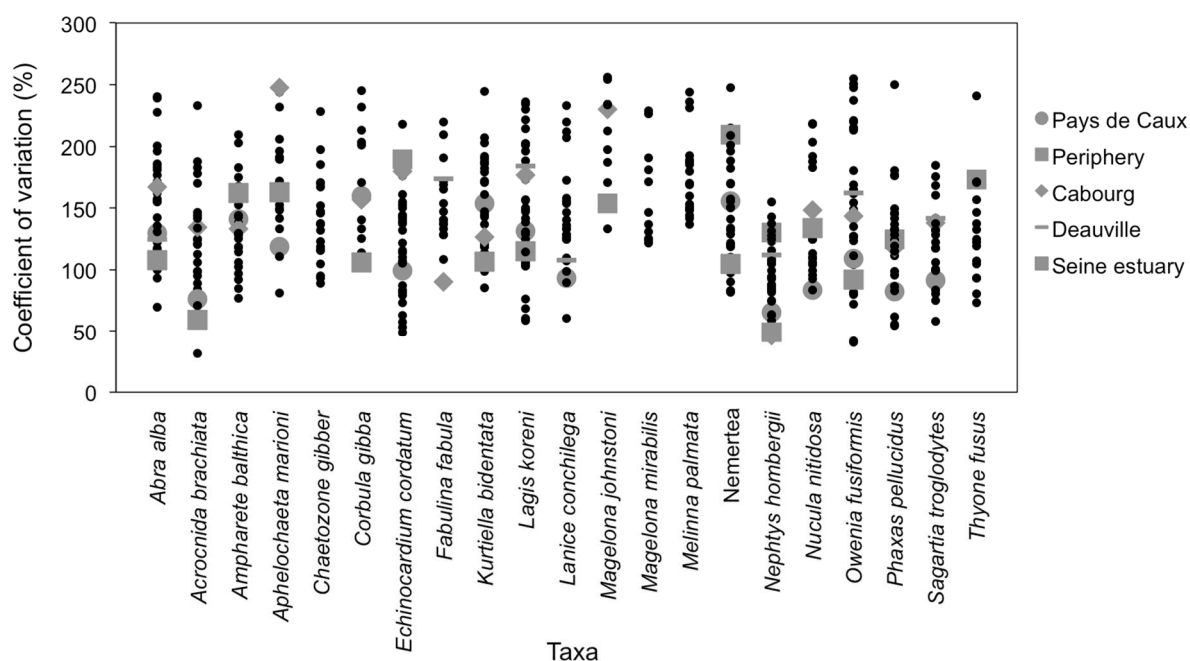


Figure 4: Coefficients of variation (CV) of species abundance expressed as a percentage calculated at each station for the 21 taxa ranked amongst the 10 most abundant species at least once, for each survey. The trend of CV values per station is given for five stations, each representative of different sectors of the study area.

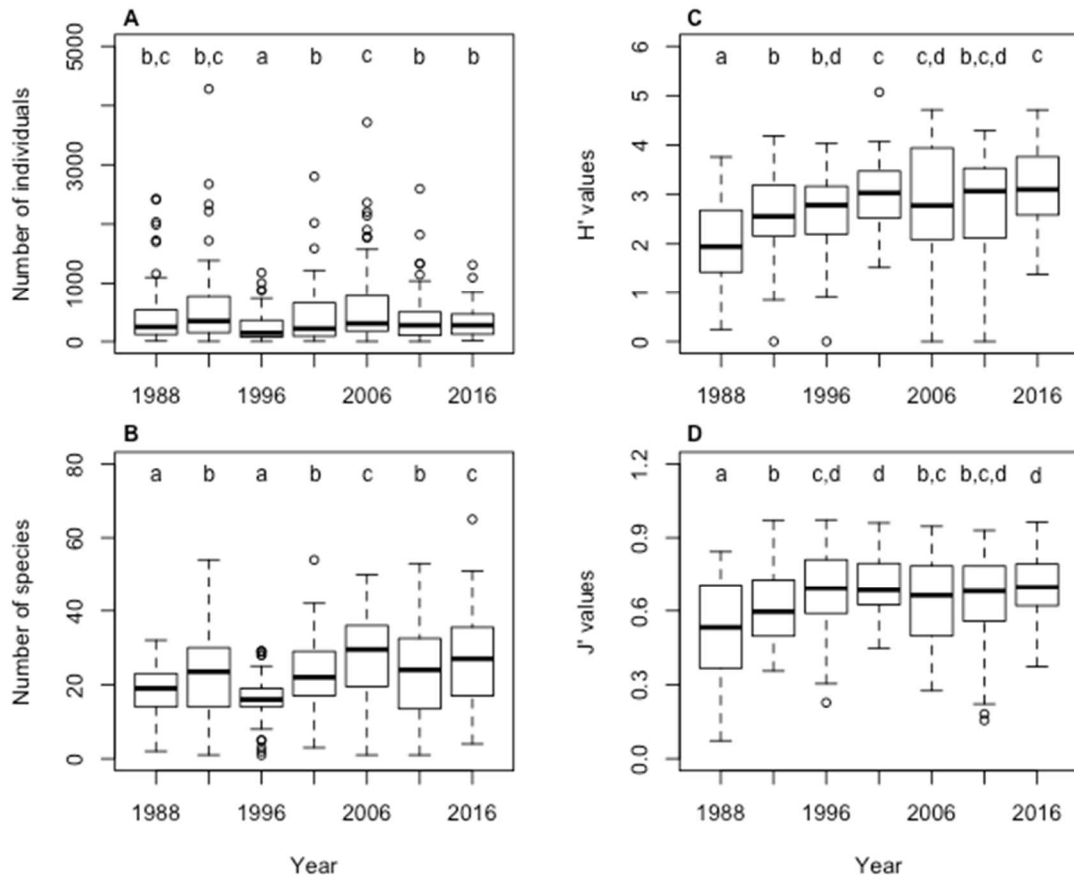


Figure 5: Boxplot representation of the species diversity indices calculated for each survey at each station: (A) number of individuals (N), (B) species richness (S), (C) Shannon-Weaver index (H') and (D) Pielou's evenness (J'). For each plot, similar letters (a, b, c and d) above each bar indicate no statistical differences among years following the Dunn tests ($p < 0.05$).

Table 2: Characteristics of the assemblages and sub-assemblages identified with the Hierarchical Cluster Analysis with the number of station-periods, mean species density (ind.0.5m⁻²), mean species richness (S), mean Shannon-Weaver index (H') and mean Pielou's evenness (J') \pm SE (Standard Error) with a total of 388 station-periods spread across the assemblages.

Assemblage	Number of stations	Mean density	\pm SE	S	\pm SE	H'	\pm SE	J'	\pm SE
I	23	22.3	3.1	5.43	0.42	1.78	0.14	0.76	0.04
II	21	110.6	38.2	15.29	1.39	2.73	0.19	0.72	0.04
III	4	216.3	35.3	20.50	2.40	0.71	0.11	0.16	0.02
IVa	5	128.2	22.4	14.20	1.07	0.48	0.07	0.12	0.02
IVb ₁	70	383.1	43.3	18.40	0.91	2.44	0.07	0.60	0.02
IVb ₂	190	717.0	49.9	28.43	0.69	2.90	0.06	0.60	0.01
IVb ₃	69	194.5	18.8	27.19	1.11	0.69	0.04	0.14	0.01
V	6	38.3	5.6	13.67	1.31	3.26	0.12	0.87	0.02

Table 3: Results of the SIMPER analysis with the percentage of similarity within each assemblage identified by Hierarchical Cluster Analysis, species contributions to the similarity between stations within the same assemblage and mean species densities.

Assemblage	Similarity (%)	Species	Contribution (%)	Density (ind.0.5m ⁻²)
I	36.6	<i>Nephtys hombergii</i>	51.9	6.6
		<i>Abra alba</i>	17.0	3.5
		<i>Lagis koreni</i>	11.3	2.
II	30.5	<i>Nephtys cirrosa</i>	21.1	6.6
		<i>Magelona johnstoni</i>	16.3	53.0
		<i>Nephtys hombergii</i>	10.3	4.4
		Nemertea	8.6	2.
		<i>Glycinde nordmanni</i>	7.0	2.0
		<i>Magelona filiformis</i>	5.6	4.2
		<i>Echinocardium cordatum</i>	5.2	9.5
III	42.6	<i>Donax spp.</i>	20.3	99.5
		<i>Lanice conchilega</i>	16.1	11.3
		<i>Owenia fusiformis</i>	9.4	7.8
		<i>Nephtys cirrosa</i>	8.8	24.2
		<i>Fabulina fabula</i>	7.7	3.0
		<i>Lagis koreni</i>	6.2	4.0
		<i>Tritia reticulatus</i>	5.0	5.3
IVa	36.3	<i>Acrocnida brachiata</i>	48.5	57.6
		<i>Echinocardium cordatum</i>	11.1	7.0
		Nemertea	7.4	1.8
		<i>Owenia fusiformis</i>	6.5	13.6
IVb ₁	39.7	<i>Owenia fusiformis</i>	23.5	119.3
		<i>Nephtys hombergii</i>	17.9	19.1
		<i>Lagis koreni</i>	12.2	48.5
		<i>Fabulina fabula</i>	7.3	16.7
		<i>Abra alba</i>	6.0	16.9
		<i>Kurtiella bidentata</i>	5.5	50.1
IVb ₂	41.7	<i>Owenia fusiformis</i>	13.3	264.0
		<i>Acrocnida brachiata</i>	9.5	52.8
		<i>Nephtys hombergii</i>	8.3	16.2
		<i>Phaxas pellucidus</i>	7.0	38.5
		<i>Ampharete baltica</i>	5.9	18.8
		<i>Lagis koreni</i>	5.7	22.1
		<i>Kurtiella bidentata</i>	5.2	120.7
		<i>Abra alba</i>	4.8	30.4
		Nemertea	4.4	9.1
		<i>Ophiura ophiura</i>	4.2	6.5
		<i>Echinocardium cordatum</i>	2.9	4.9
IVb ₃	39.6	<i>Nephtys hombergii</i>	8.6	6.9

		<i>Phaxas pellucidus</i>	8.3	10.7
		<i>Glycinde nordmanni</i>	8.0	6.7
		<i>Echinocardium cordatum</i>	7.8	6.2
		<i>Chaetozone gibber</i>	6.3	16.6
		<i>Euspira nitida</i>	5.7	3.0
		Nemertea	5.6	21.7
		<i>Magelona mirabilis</i>	5.1	12.2
		<i>Acrocrida brachiata</i>	5.0	16.1
		<i>Sigalion mathildae</i>	4.3	3.1
		<i>Caulerella alata</i>	3.7	6.1
		<i>Owenia fusiformis</i>	3.2	22.6
V	25.7	<i>Nephtys hombergii</i>	19.1	4.0
		<i>Hilbigneris gracilis</i>	18.4	4.0
		<i>Phaxas pellucidus</i>	16.3	4.2
		Nemertea	13.2	1.3
		<i>Ampharete baltica</i>	9.7	3.2

938

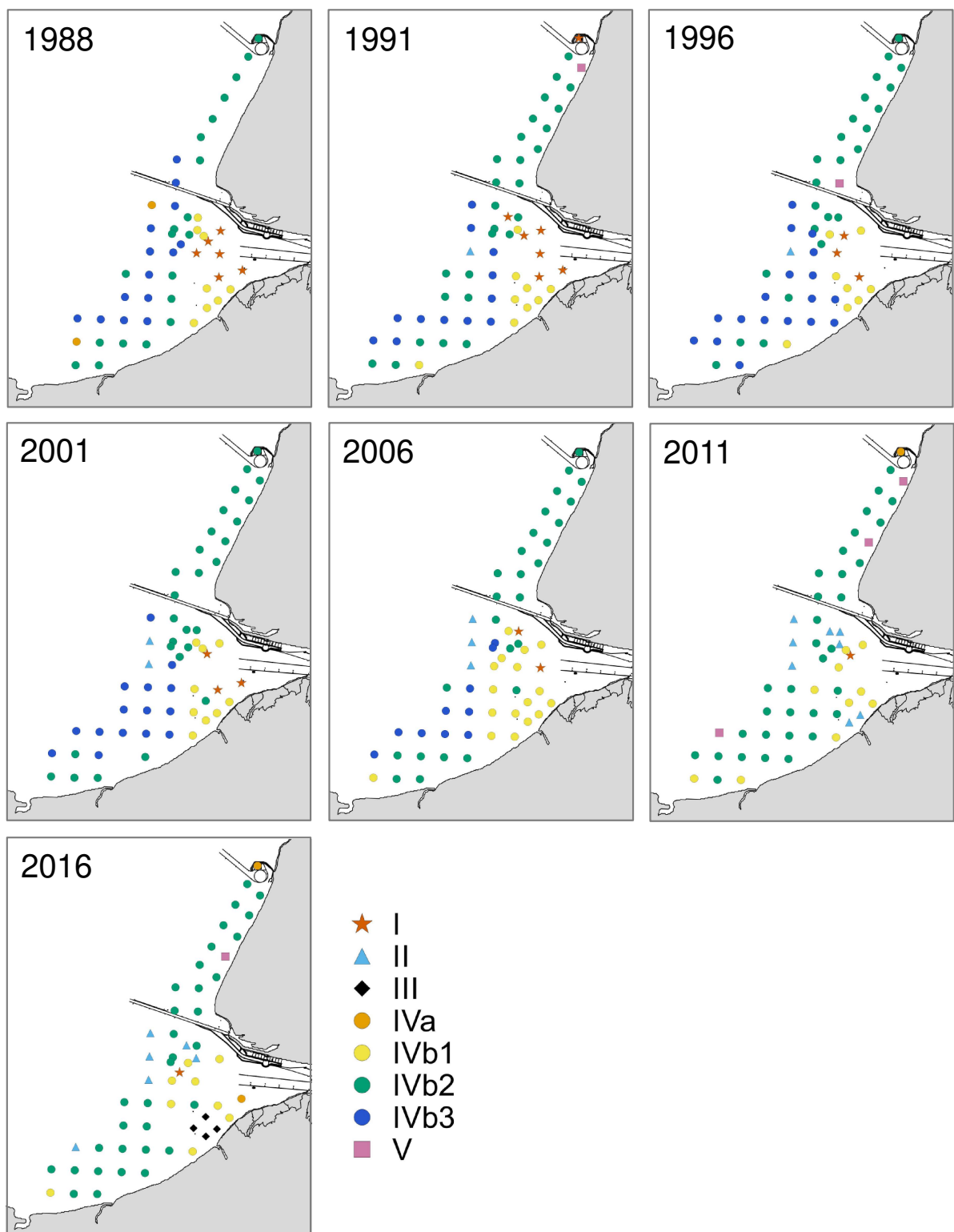


Figure 6: Spatial distribution of assemblages and sub-assemblages identified with Hierarchical Cluster Analysis in the eastern Bay of Seine for each survey. The number of stations for each survey was 50 in 1988, 57 in 1991, 55 in 1996, 56 in 2001, 58 in 2006, 56 in 2011 and 56 in 2016.

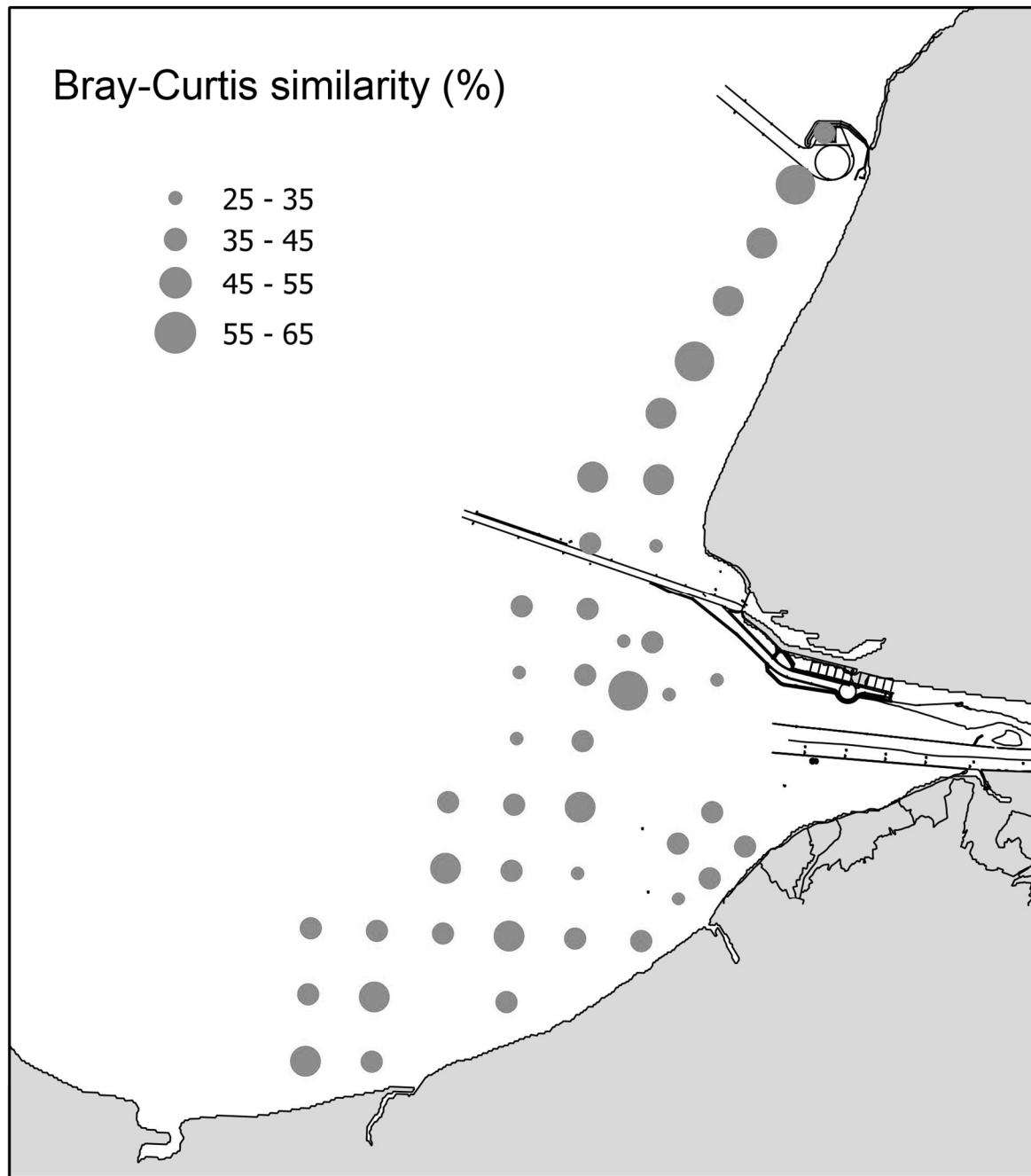


Figure 7: Spatial distribution of the mean values of Bray-Curtis similarity coefficients (temporal beta diversity) at each of the 43 common stations sampled on every survey in the eastern Bay of Seine.

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