

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

Bacouillard Lise ^{1,*}, Baux Noémie ^{2,3,4}, Dauvin Jean-Claude ², Desroy Nicolas ⁵, Geiger Katja Juliana ¹, Gentil Franck ¹, Thiébaud Éric ¹

¹ Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR7144, Adaptation et Diversité en Milieu Marin, Place Georges Teissier, CS90074, 29688, Roscoff Cedex, France

² Normandie Univ., UNICAEN, Laboratoire Morphodynamique Continentale et Côtière M2C, UMR, CNRS, 6143 M2C, 24 rue des Tilleuls, F-14000, Caen, France

³ Normandie Univ., UNICAEN, Laboratoire des Sciences Appliquées de Cherbourg, EA 4 253, 50100, Cherbourg, France

⁴ Conservatoire National des Arts et Métiers, INTECHMER, 50100, Cherbourg, France

⁵ IFREMER, Station de Dinard, LER Bretagne Nord, 38 rue du Port Blanc, 35800, Dinard, France

* Corresponding author : Lise Bacouillard, email address : lise.bacouillard@sb-roscoff.fr

noemie.baux@lecnam.net ; jean-claude.dauvin@unicaen.fr ; Nicolas.Desroy@ifremer.fr ; katjes.gecko@gmail.com ; gentil@sb-roscoff.fr ; eric.thiebaut@sb-roscoff.fr

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.

Highlights

► The community structure was highly persistent over the last three decades. ► Silting-up promoted changes in species composition and a decrease in β -diversity. ► Community stability differed according to the scale of observation. ► There is a need to implement a sampling strategy combining different scales.

Keywords : Benthic ecology, Coastal zone, Temporal variability, Species composition, Macrofauna, α -diversity, β -diversity, γ -diversity

36 **1. Introduction**

37 Marine coastal ecosystems experience increasing pressures due to human
38 activities including overexploitation of marine resources, eutrophication, contamination
39 by organic and non-organic pollutants, coastal urbanization and introduction of non-
40 indigenous species, which can overlap and interact with climate change (Airoldi and
41 Beck, 2007; Halpern et al., 2008). The cumulative effects of these diverse pressures,
42 which often vary in magnitude, spatial extent, temporal duration and frequency
43 (Donohue et al., 2016), result in changes to the structure of marine communities (e.g.
44 species richness, species composition, density and biomass of dominant species) which
45 can alter ecosystem functioning and the delivery of ecosystem services (Cardinale et al.,
46 2012; Gamfeldt et al., 2015). In this context, there is a growing need for analysis of long-
47 term datasets to assess responses of communities to temporal changes in environmental
48 conditions to facilitate management and conservation efforts (Magurran et al., 2010;
49 Giron-Nava et al., 2017). Such datasets provide essential resources to address several
50 issues: (1) describe and understand the complex long-term dynamics of community
51 diversity in response to changing environmental conditions; (2) assess the effects of
52 multiple stressors and disentangle the relative contributions of anthropogenic impacts
53 and natural variability; (3) provide data for predictive models; (4) support the
54 development of ecological indicators to evaluate the ecosystem; and (5) support the
55 implementation of ecosystem-based management (Duffy et al., 2013).

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

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

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

86 Baffreau et al., 2017; Dauvin et al., 2017). Thiébaud et al. (1997) demonstrated that the
87 spatial structure of the community resulted from the combination of several
88 environmental gradients related to salinity, sediment grain size and food supply. These
89 authors highlighted a relative stability of this spatial organization over a 5-year period.
90 Over a longer period (1983-1992), the community structure at only one station was also
91 relatively stable compared other sandy communities in the western English Channel
92 (Bay of Morlaix) and in the south of the North Sea (Gravelines area), despite the
93 influence of alternative periods of cold and mild conditions on the densities of some
94 species (Fromentin et al., 1997). More recently, the introduction of non-indigenous
95 species and the arrival of species associated with muddy sediment were observed
96 without an assessment of their impacts on the community structure (Dauvin et al., 2007;
97 Jourde et al., 2012). Thus, the non-indigenous razor clam *Ensis leei* (formerly *Ensis*
98 *directus*) was first reported in 1998 and colonized the south-eastern coasts of the bay at
99 moderate density ($< 100 \text{ ind.m}^{-2}$; Dauvin et al., 2007). The polychaete *Melinna palmata*
100 has been observed since 2002 and has rapidly extended its population to reach densities
101 of 277 ind.m^{-2} in March 2006 and between 625 and 2500 ind.m^{-2} in September 2008 and
102 September 2009 in parallel to the increased siltation rates of the bay (Dauvin et al.,
103 2007; Alizier, 2011). Likewise, another species inhabiting muddy sediment, the crab
104 *Asthenognathus atlanticus*, was first sampled in 2008 (Jourde et al., 2012).

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

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

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

124 Using the study site of the eastern Bay of Seine, which is highly representative of
125 urbanized coastal areas exposed to numerous anthropogenic threats (Dauvin, 2008;
126 Marmin et al., 2016; Tecchio et al., 2016; Baux et al., 2019), this study investigated the
127 spatio-temporal changes of species abundance, species composition and species
128 diversity at different scales (α -diversity, β -diversity, γ -diversity) between 1988 and
129 2016. Based on the analysis of spatio-temporal data provided by the original long-term
130 monitoring program of the muddy fine sand benthic community implemented in this
131 area, we address two specific questions: (1) how did the benthic community vary
132 through time and space according to the scale of observation (i.e. local station vs. whole
133 community) and (2) what was the degree of correlation of the different components of
134 the stability?

135 2. Materials and methods

136 2.1. Study area

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

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

176 **2.2. Sampling and laboratory strategy**

177 The macrofaunal distribution in the eastern part of the Bay of Seine was
178 established during seven sampling surveys (named “PECTOW” surveys) carried out over
179 28 years (i.e. 1988, 1991, 1996, 2001, 2006, 2011 and 2016) during winter time
180 (February/March) before the recruitment period of the dominant species. Sixty stations
181 were sampled six or seven times from 1988 to 2016 with a total of 403 sampling station-
182 period combinations: 43 stations were sampled on each of the seven surveys whilst 17

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

202 **2.3. Data analysis**

203 **2.3.1. Temporal variability in species composition and densities**

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

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

217 **2.3.2. Gamma diversity**

218 Gamma diversity (i.e. species diversity of the large sampling area; Whittaker,
219 1960) refers in this study to the total number of species sampled during each survey in
220 the eastern Bay of Seine. For each survey, species accumulation curves were drawn after
221 999 permutations to describe its year-to-year variations.

222 **2.3.3. Alpha diversity**

223 At each station for each survey, alpha diversity (i.e. species diversity in a
224 sampling site) was calculated using species diversity indices that cover its different
225 facets, i.e. richness, heterogeneity and evenness. These indices include species richness
226 (S), Shannon-Weaver index (H') using \log_2 in its formulation, and Pielou's evenness (J').
227 The number of individuals per 0.5 m^2 (N) at each station was also calculated. To assess
228 the variations in univariate indices among surveys, a Kruskal-Wallis non-parametric test
229 was computed with R language (R Core Team, 2014). For those indices presenting a
230 significant difference among surveys, a Dunn multiple comparison test was applied to

231 identify which surveys are significantly different from the others (i.e. $p < 0.05$) (Zar,
232 1999).

233 **2.3.4. Beta diversity**

234 To analyse the beta diversity (i.e. the degree of change in species
235 composition/structure among sampling sites; Anderson et al., 2011), different analyses
236 have been carried out depending on whether we have considered presence/absence or
237 relative abundance data, and focused on the changes in species composition/structure
238 among sites (i.e. spatial beta diversity) or among sampling dates at each sampling site
239 (i.e. temporal beta diversity). The Jaccard distance was used to measure the
240 “composition” component of beta diversity while the Bray-Curtis coefficient provided a
241 measure of the “community structure” component of beta diversity (Donohue et al.,
242 2013).

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

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

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

274 The proportion of variation in community structure related to sediment type was
275 quantified using a Distance based Linear Model (DistLM) performed between the \log_{10}
276 $(x+1)$ transformed species densities at each station-period and the fine sediment type
277 data (i.e. fine sand, muddy fine sand, sandy mud, mud) at each station-period for a total
278 of 390 station-periods. The analysis was performed using the Bray-Curtis similarity

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

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

283 **3. Results**

284 **3.1. Sediment grain size analysis**

285 From 1988 to 2001, the silt content was below 10 % in the majority of the study
286 area except closest to the Seine estuary where it reached 25-50 % at some stations
287 (Fig.2). Silt content increased slightly in 1996, especially along the coasts of Pays de
288 Caux, where it reached 10-25 %. The increased siltation of the eastern Bay of Seine
289 became apparent in 2006 with silt content exceeding 25 % in a high number of stations
290 and 75 % at three stations directly in front of the estuary, off Cabourg and in Antifer
291 harbour. While most stations were composed of fine sand and muddy fine sand between
292 1988 and 2001, with less than 15 % of stations with sandy mud or mud, by 2006 there
293 had been a shift towards muddier sediments with more than 25 % of stations composed
294 of sandy mud or mud. In 2011, the silt content tended to decrease but remained high in
295 front of the Seine estuary and at some stations along the coasts of the Pays de Caux.
296 Further a decreased siltation was observed in 2016. However, in contrast to earlier
297 observations (1988 - 2001), silt content exceeded 10 % in most stations. The
298 consistently high silt content in Antifer harbour reported in most surveys could be
299 explained by the structure of the harbour, which traps fine sediments coming from the
300 Seine estuary.

301 **3.2. Species composition and densities**

302 A total of 221 taxa belonging to nine phyla were reported during the survey
303 period, including Annelida Polychaeta with 85 taxa (38 %), Arthropoda, mostly
304 Malacostraca, with 69 taxa (33 %), Mollusca with 41 taxa (19 %) and Echinodermata
305 with 12 taxa (5 %). The five other phyla were far less abundant: Cnidaria with four taxa,
306 Sipuncula with three taxa, and Chordata and Phoronida with only one taxon. Nemertea
307 were not identified beyond phyla owing to difficulties in accurately identifying
308 incomplete pieces of organisms. Of the 221 taxa, 40 were sampled only once during the
309 seven surveys. Among the seven surveys, gamma diversity ranged from 90 taxa in 1988
310 to 158 taxa in 2016 and showed no temporal trend (Fig. 3). The proportion of rare
311 species per year (i.e. species found at one or two station-periods throughout the
312 monitoring program) varied among years, following a temporal pattern close to that of
313 the species accumulation curves, with 13 rare species reported in 2016 and 2006, 7 in
314 2011 and 2001, 5 in 1991, 4 in 1988 and 1 in 1996.

315 Only twenty-one of the 221 taxa identified within the eastern Bay of Seine were
316 ranked among the ten most abundant taxa in at least one survey (Table 1). Among the
317 most abundant taxa, four species were common to the seven surveys (i.e. *Owenia*
318 *fusiformis*, *Acrocnida brachiata*, *Lagis koreni* and *Nephtys hombergii*), two species six
319 times (i.e. *Kurtiella bidentata* except in 2016 and *Abra alba* except in 2011), and one
320 species five times (i.e. *Phaxas pellucidus* except in 1988 and 2006). These seven species
321 represent the “typical” species of the *Abra alba* - *Lagis koreni* muddy fine sand
322 community. *Owenia fusiformis* remained the most abundant species, except in 2001 and
323 2016 when it was ranked second, behind *Kurtiella bidentata* and *Phaxas pellucidus*
324 respectively. The other taxa, which generally occurred in lower ranking positions, were
325 (1) abundant only occasionally like *Aphelochaeta marioni* in 2001, 2006 and 2016, or
326 *Nucula nitidosa* in 2001 and 2006, (2) rather dominant at the beginning of the study

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

330 Regardless of the relative stability of the macrobenthic community in terms of
331 species composition and relative densities of dominant species at the scale of the
332 eastern Bay of Seine for the 28-year survey period, their average densities were highly
333 variable over time, depending on the species. Thus, the CV of the most dominant species
334 at the 43 common stations sampled on every survey ranged from 26% for *Lagis koreni*
335 to 94% for *Phaxas pellucidus* (Table 1). The average densities of *Lagis koreni* varied by a
336 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
337 *Phaxas pellucidus* varied by a factor of 77.6, from 0.7 ind.0.5m⁻² in 1988 to 54.3 ind.0.5m⁻
338 ² in 2016. For the most abundant species, *Owenia fusiformis*, the CV reached 57% with
339 average densities varying by a factor of 5.7, from 52.7 ind.0.5m⁻² in 2016 to 298.8
340 ind.0.5m⁻² in 1988.

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

351 **3.3. Changes in local diversity**

352 The number of individuals and species diversity indices measured at each of the
353 403 sampling station-periods showed significant differences between years (Kruskal-
354 Wallis test; N: $p < 0.01$; S: $p < 0.001$; H': $p < 0.001$; J': $p < 0.001$) (Fig. 5). The number of
355 individuals (N) varied between 1 and 4281 ind.0.5m⁻² with no temporal trend. There
356 were no significant differences between the years 1988 and 1991 at the beginning of the
357 study period and the years 2001, 2011 and 2016 at the end of the study period. N was
358 significantly lower during 1996, compared to all other years and higher in 2006,
359 compared to the two preceding and succeeding years. Maximal densities could locally
360 exceed 2000 ind.0.5m⁻² except for the years 1996 and 2016. Species richness (S) ranged
361 between 1 and 65 species and showed erratic variations with time. Dunn post-hoc tests
362 indicated that S was significantly lower during years 1988 and 1996 compared to other
363 surveys and significantly higher for the years 2006 and 2016. Intermediate values were
364 reported for the years 1991, 2001 and 2011. Shannon index (H') varied between 0 and
365 5.07 while Pielou's evenness (J') varied between 0.07 and 0.97, both being significantly
366 lower in 1988. H' and J' increased significantly between first and second surveys and
367 remained constant for the last surveys (i.e. no significant differences between these last
368 surveys).

369 **3.4. Macrofaunal assemblages**

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

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

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

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

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

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

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

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

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

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

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

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

450 mostly to the sub-assemblage IVb₂ each year (Fig. 6). Conversely, the year-to-year
451 changes were more marked at stations located in front of the estuary and at some
452 stations between Deauville and Ouistreham. These patterns of relative
453 stability/variability of community structure at the local scale remained consistent when
454 quantifying only compositional change by using the Jaccard similarity coefficient
455 (Supplementary material Fig. B). The relationship between average values of the Bray-
456 Curtis and Jaccard similarity coefficients was positive and highly significant ($R^2= 0.894$;
457 $N= 43$; $p < 0.001$) (Supplementary material Fig. C).

458 The DistLM showed that the sediment type had a highly significant effect on the
459 spatio-temporal changes in the community structure ($p < 0.001$) but explained only
460 4.6% in the variation of the community structure.

461 **4. Discussion**

462 **4.1. Stability vs. variability at different scales**

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

473 scale, and large volumes of dredged and dumped sediments at the local scale [4.5 million
474 $\text{m}^3\cdot\text{y}^{-1}$ at the Kannik dumping site (Marmin et al., 2016) and 2-2.5 million $\text{m}^3\cdot\text{y}^{-1}$ at the
475 Octeville dumping site (Baux et al., 2019)].

476 **4.1.1. Variability at the study area scale**

477 At the “study area” scale, only 10% of the total number of identified taxa (21 out
478 of 221) was ever among the first ten most abundant taxa. A pool of only seven typical
479 species were ranked among the most abundant taxa at least five times out of the seven
480 surveys and drove the temporal evolution of the community composition: *Owenia*
481 *fusiformis*, *Acrocnida brachiata*, *Lagis koreni*, *Nephtys hombergii*, *Kurtiella bidentata*, *Abra*
482 *alba* and *Phaxas pellucidus*. However, the first observation of *Melinna palmata* in 2002
483 (Dauvin et al., 2007), its ranking within the ten dominant species since 2011 and the
484 increase in density of the polychaete *Ampharete baltica*, which are both associated with
485 mud and muddy sand habitats (Oyenekan, 1988; Zettler et al., 2013), reflect major
486 effects of the recent siltation of the eastern part of the Bay of Seine. The siltation resulted
487 from both alteration of the morpho-sedimentary dynamics of the Seine estuary *via* river
488 flows and flood intensity, and the increase of dredged sediment deposit following the
489 extension of Le Havre harbour along the Cap de la Hève-Antifer area (Lesourd et al.,
490 2001; Méar et al., 2018; Baux et al., 2019).

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

497 species like *Owenia fusiformis* for which mean densities varied from 214.8 ind.0.5m⁻² in
498 1991 to 90.3 ind.0.5m⁻² in 1996. Dauvin and Gillet (1991) already reported large year-
499 to-year variations in *Owenia fusiformis* densities which were related to large year-to-
500 year variations in the recruitment. They proposed several hypotheses to explain these
501 variations: a failure in the reproduction, an export of most larvae outside the bay, a low
502 survivorship of young recruits. The lowest local species richness in 1988 and 1996 was
503 to be compared with lowest gamma diversity in the same years which was partly related
504 to the proportion of rare species.

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

514 **4.1.2. Variations at the assemblage scale**

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

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

528 The relative importance and the distribution of the three main assemblages
529 changed little with time but the *Owenia fusiformis* - *Acrocnida brachiata* facies extended
530 in 2016 to cover 58% of sampled stations. This extension led to a decrease in the spatial
531 beta diversity and consequently a biotic homogenization of the community structure
532 which is now recognized to be a major broad-scale consequence of anthropogenic
533 stressors in both terrestrial and marine ecosystems (Thrush et al., 2006; Socolar et al.,
534 2016). In soft sediments, biotic homogenization can be the result of various stressors
535 including physical disturbance such as increased sediment inputs and deposition, the
536 selective removal of habitat-forming species and the proliferation of engineer or non-
537 indigenous species (Thrush et al., 2004; Rigolet et al., 2014). The recent spread of fine
538 particles over the entire eastern Bay of Seine, corresponding to a decrease in the total
539 muddy area and relative increases in sandy mud and muddy sand, is likely an important
540 contributor to the observed biotic homogenization (Lesourd et al., 2016).

541 **4.1.3. Variability at the local station scale**

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

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

569 **4.2. Mechanisms involved in the long-term persistence of the**
570 **community**

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

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

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

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

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

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

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

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

662 **4.3. Sampling strategy and spatial scales**

663 Historical data are very valuable to highlight the long-term persistence of the
664 composition and structure of benthic communities (Callaway, 2016). The two main
665 strategies developed to assess long-term changes in macrobenthic communities have
666 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.

692 5. Conclusion

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

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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

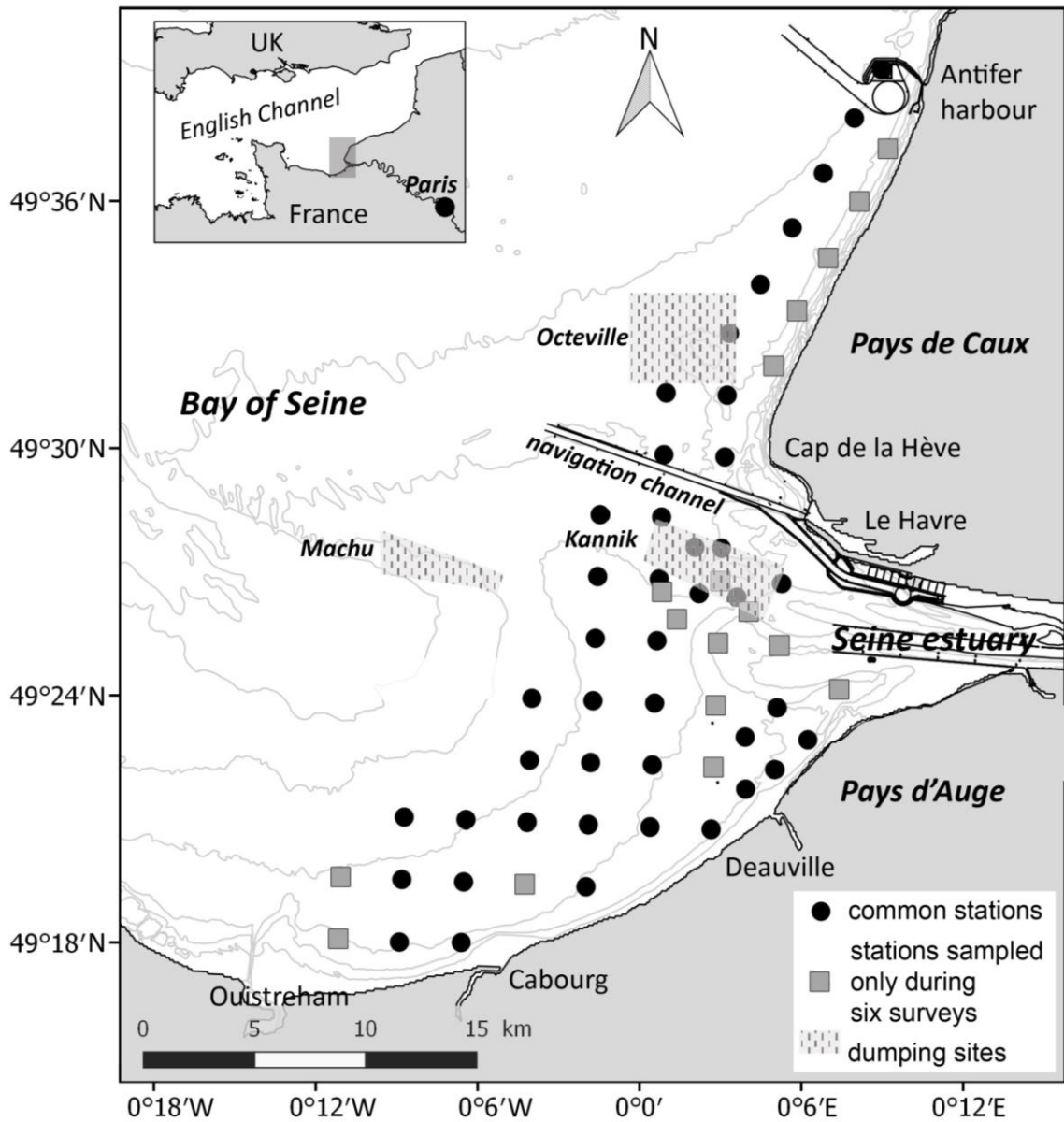
758 TABLE CAPTIONS

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



805 **Figure 1:** Location of the study area and of the 60 stations sampled between 1988 and 2016
806 during the seven sampling surveys in the eastern Bay of Seine. The black dots correspond to the
807 43 common stations sampled on every survey and the grey squares to the 17 stations sampled
808 only during six surveys. The three dumping sites are indicated in grey line (Kannik, Machu,
809 Octeville).

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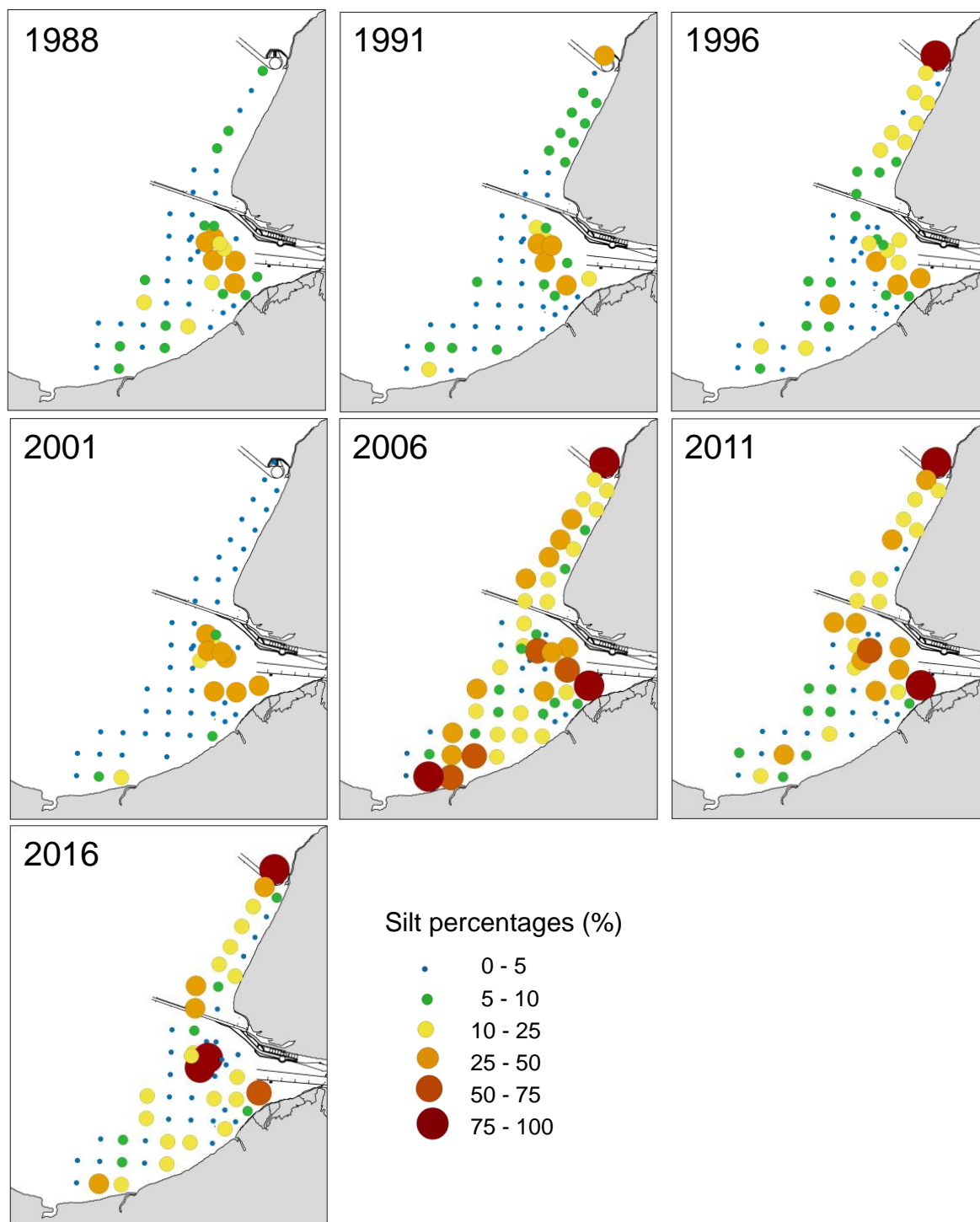


Figure 2: Spatial distribution of the silt percentages (%) within the sediment, in the eastern Bay of Seine for each survey.

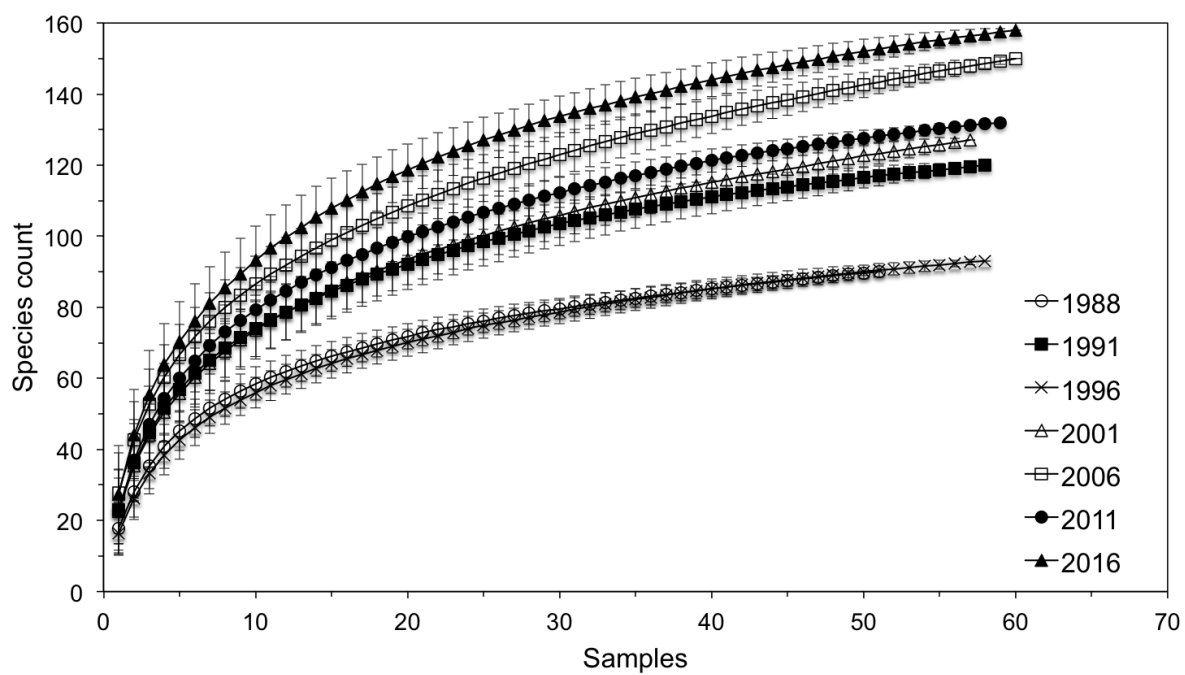


Figure 3: Species accumulation curves for the seven surveys performed in the eastern Bay of Seine from 1988 to 2016. Plotted values are mean values of 999 randomization of sample order.

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>Aphelochaeta 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

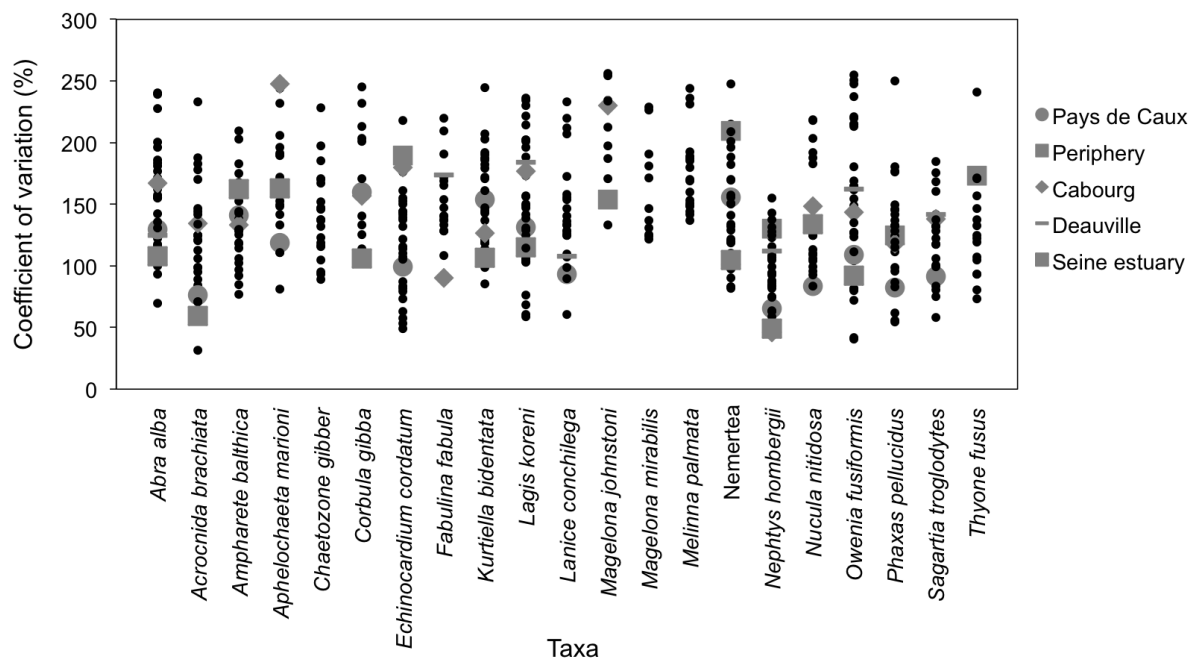


Figure 4: Coefficients of variation (CV) of species abundance expressed as a percentage calculated at each station for the 21 taxa ranked amongst the 10 most abundant species at least once, for each survey. The trend of CV values per station is given for five stations, each representative of different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

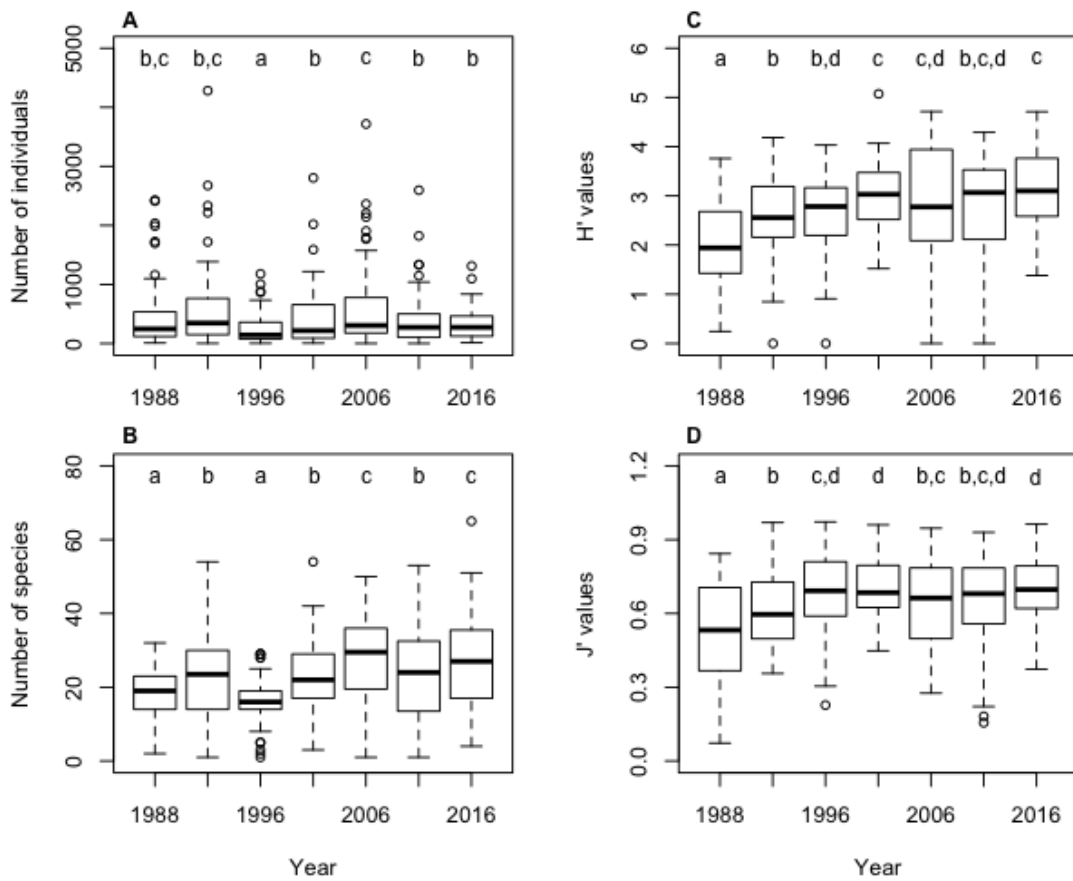


Figure 5: Boxplot representation of the species diversity indices calculated for each survey at each station: (A) number of individuals (N), (B) species richness (S), (C) Shannon-Weaver index (H') and (D) Pielou's evenness (J'). For each plot, similar letters (a, b, c and d) above each bar indicate no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

929 **Table 2:** Characteristics of the assemblages and sub-assemblages identified with the
 930 Hierarchical Cluster Analysis with the number of station-periods, mean species density
 931 (ind.0.5m⁻²), mean species richness (S), mean Shannon-Weaver index (H') and mean Pielou's
 932 evenness (J') \pm SE (Standard Error) with a total of 388 station-periods spread across the
 933 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

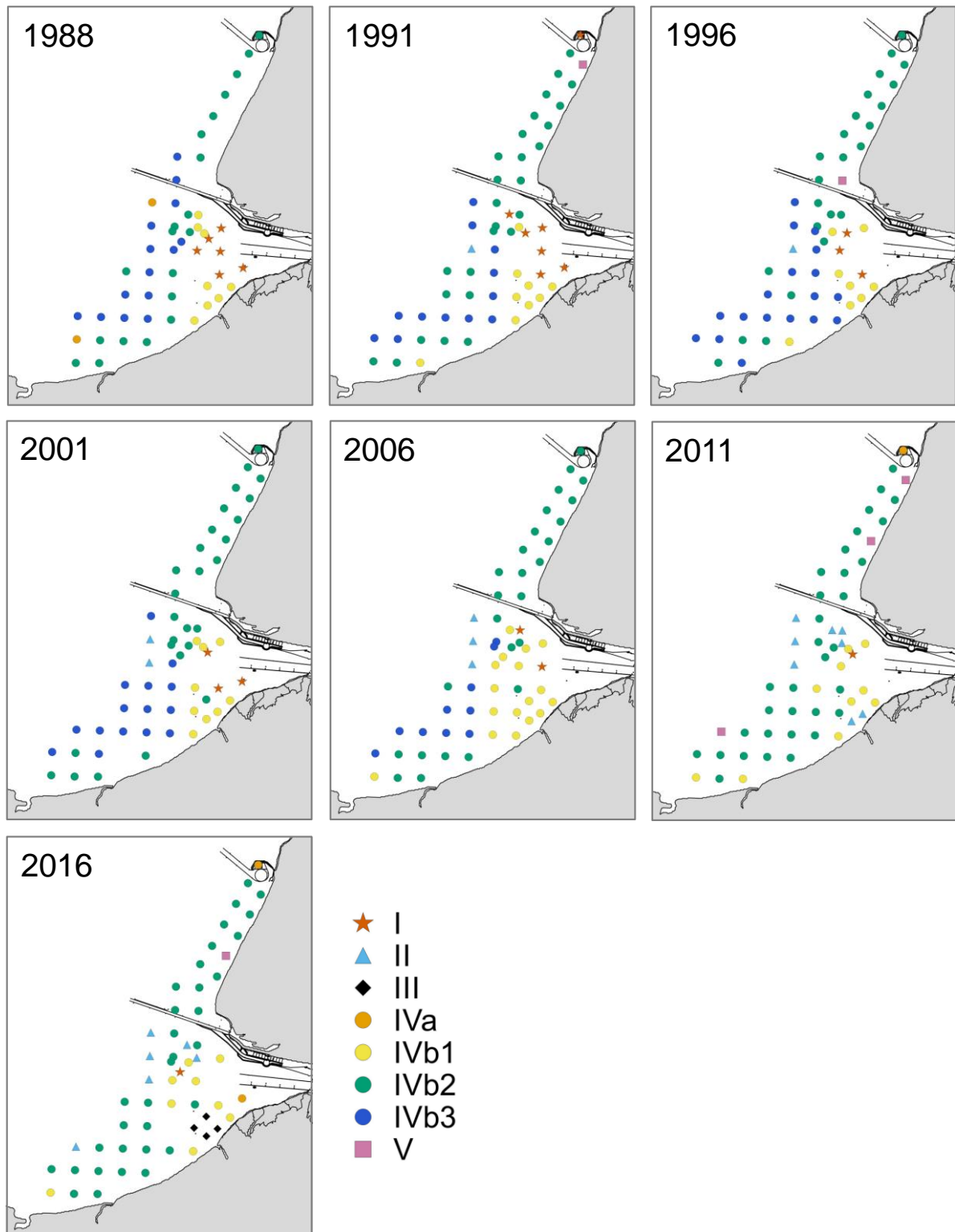
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935 **Table 3:** Results of the SIMPER analysis with the percentage of similarity within each
 936 assemblage identified by Hierarchical Cluster Analysis, species contributions to the similarity
 937 between stations within the same assemblage and 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>Acrocrida 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>Acrocrida 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
IVb ₃	39.6	<i>Echinocardium cordatum</i>	2.9	4.9
		<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>Acrocnida brachiata</i>	5.0	16.1
		<i>Sigalion mathildae</i>	4.3	3.1
		<i>Caulleriella 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

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

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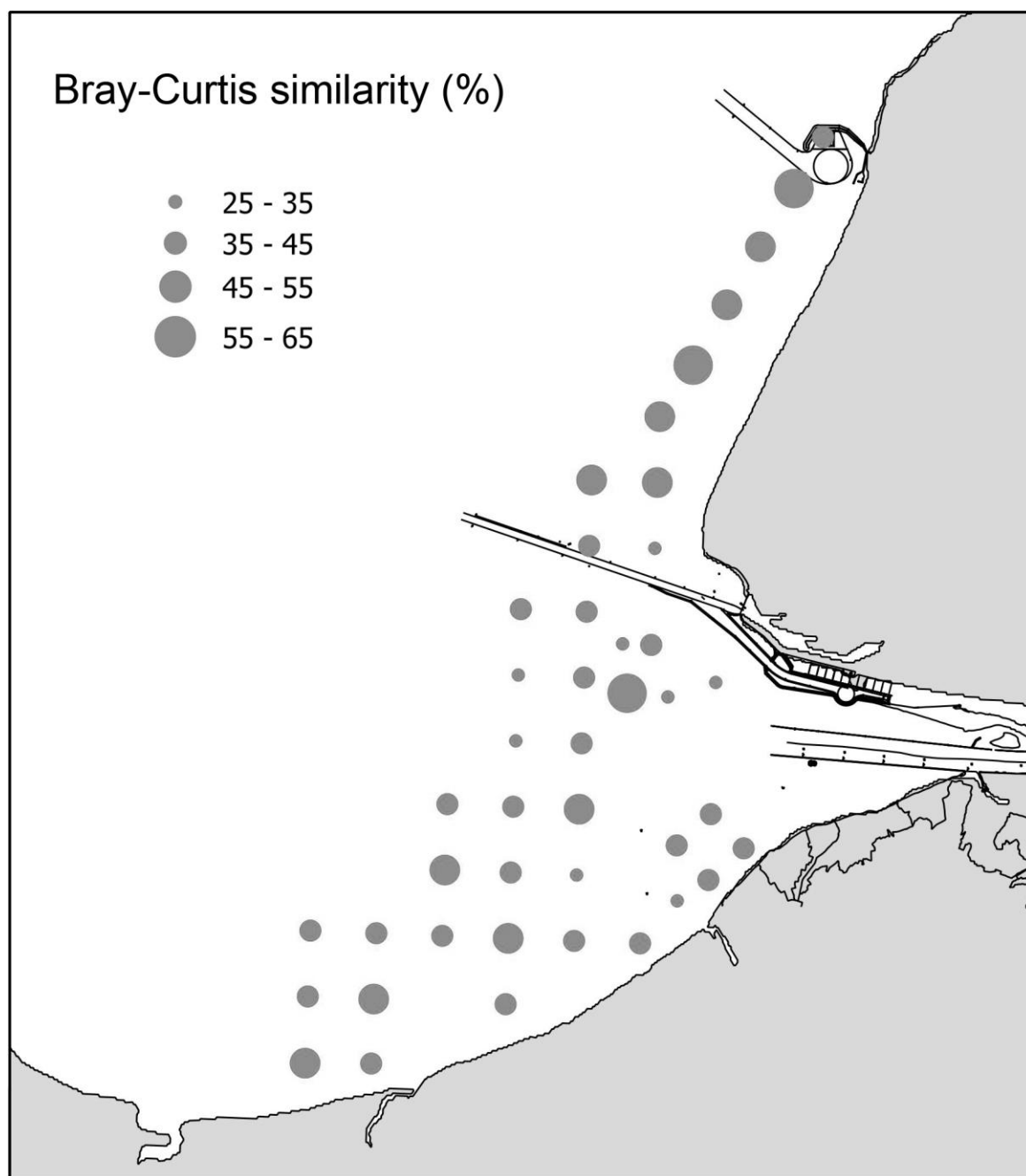


Figure 7: Spatial distribution of the mean values of Bray-Curtis similarity coefficients (temporal beta diversity) at each of the 43 common stations sampled on every survey in the eastern Bay of Seine.

1023 SUPPLEMENTARY MATERIALS FIGURE CAPTIONS

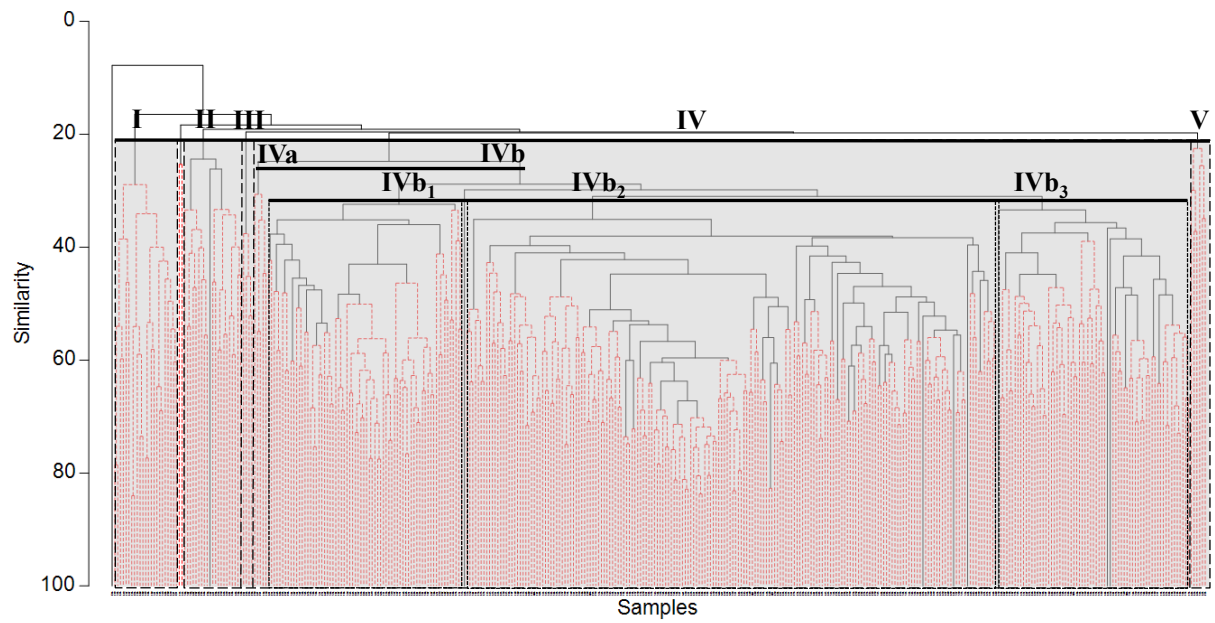
1024 Figure supp. A: Hierarchical Cluster Analysis of macrofaunal composition led to five
1025 assemblages and several sub-assemblages based on $\log_{10}(x+1)$ transformed species
1026 abundances using Bray-Curtis similarity index and result of the SIMPROF test in
1027 red.

1028 Figure supp. B: Spatial distribution of the mean values of Jaccard similarity coefficients
1029 (temporal beta diversity) at each of the 43 common stations sampled on every
1030 survey in the eastern Bay of Seine.

1031 Figure supp. C: Linear regression between mean values of Bray-Curtis and Jaccard
1032 similarity coefficients at each station ($R^2= 0.894$; $N= 43$; $p < 0.001$).

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1051 **Figure supp. A:** Hierarchical Cluster Analysis of macrofaunal composition led to five
1052 assemblages and several sub-assemblages based on $\log_{10}(x+1)$ transformed species abundances
1053 using Bray-Curtis similarity index and result of the SIMPROF test in red.

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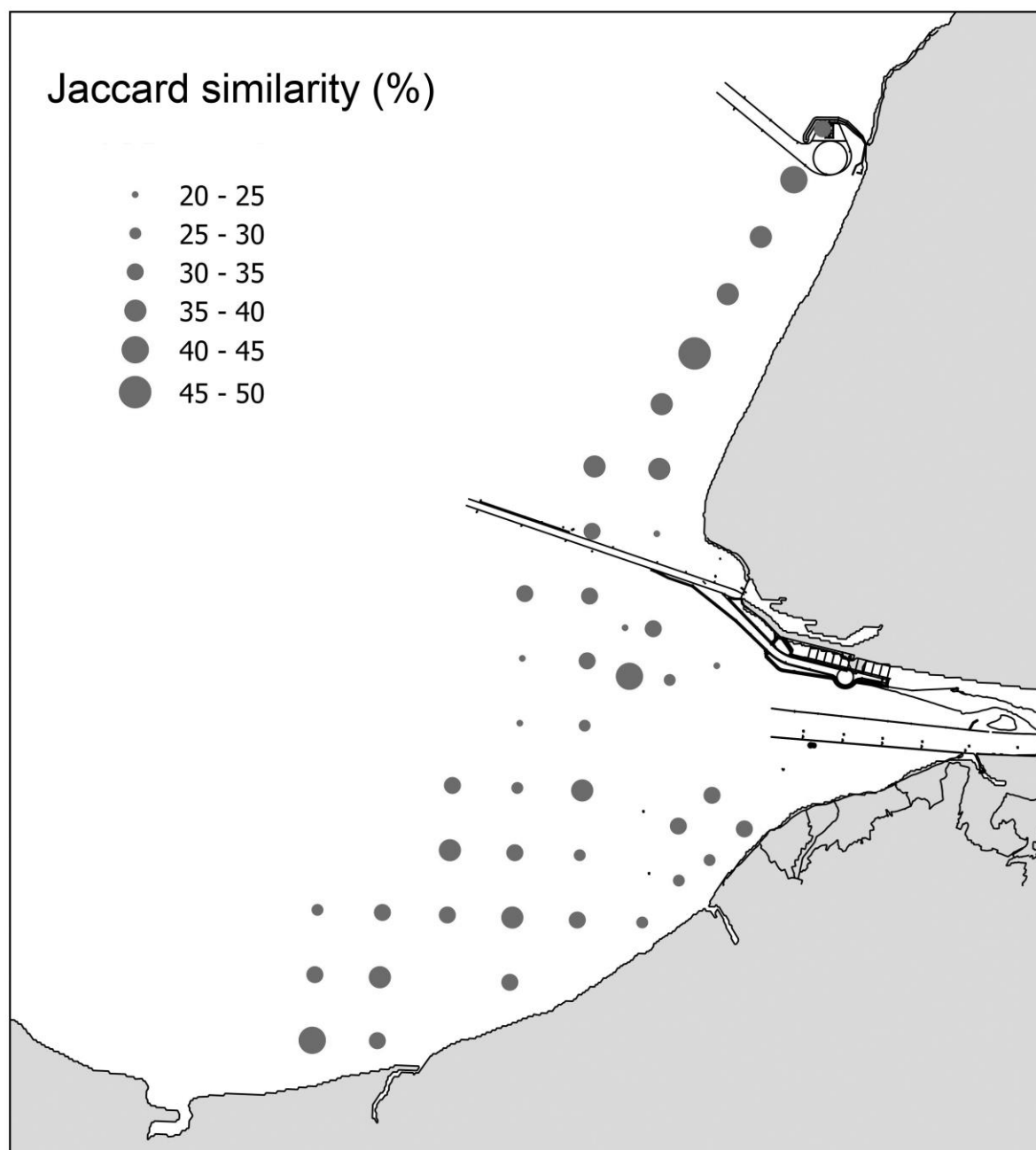


Figure supp. B: Spatial distribution of the mean values of Jaccard similarity coefficients (temporal beta diversity) at each of the 43 common stations sampled on every survey in the eastern Bay of Seine.

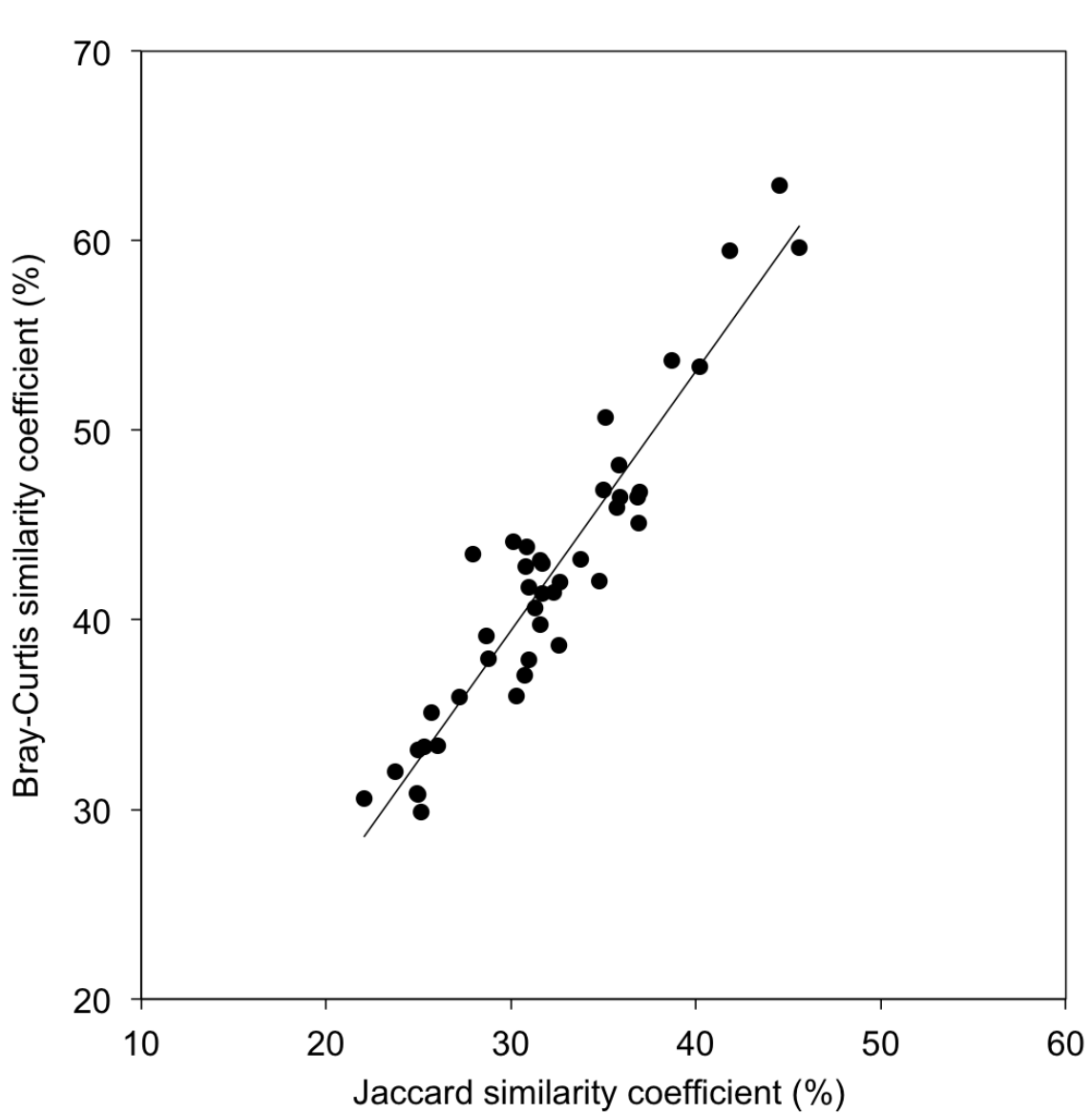


Figure supp. C: Linear regression between mean values of Bray-Curtis and Jaccard similarity coefficients at each station ($R^2= 0.894$; $N= 43$; $p < 0.001$).

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Highlights

- The community structure was highly persistent over the last three decades
- Silting-up promoted changes in species composition and a decrease in β -diversity
- Community stability differed according to the scale of observation
- There is a need to implement a sampling strategy combining different scales

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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