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## Assessing the ecological status of an estuarine ecosystem: linking biodiversity and food-web indicators

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8 3 **Assessing the ecological status of an estuarine ecosystem:**

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10 4 **linking biodiversity and food-web indicators**  
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12 5

13  
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62 **Highlights**  
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28 The Seine estuary ecosystem was described before and after the Port2000 extension.

29 A toolbox of various indices was used, describing complementary characteristics.

30 Port2000 effects were complex to separate from other human-induced and natural effects.

31 Ecological Network Analysis was useful in defining functional indicators.

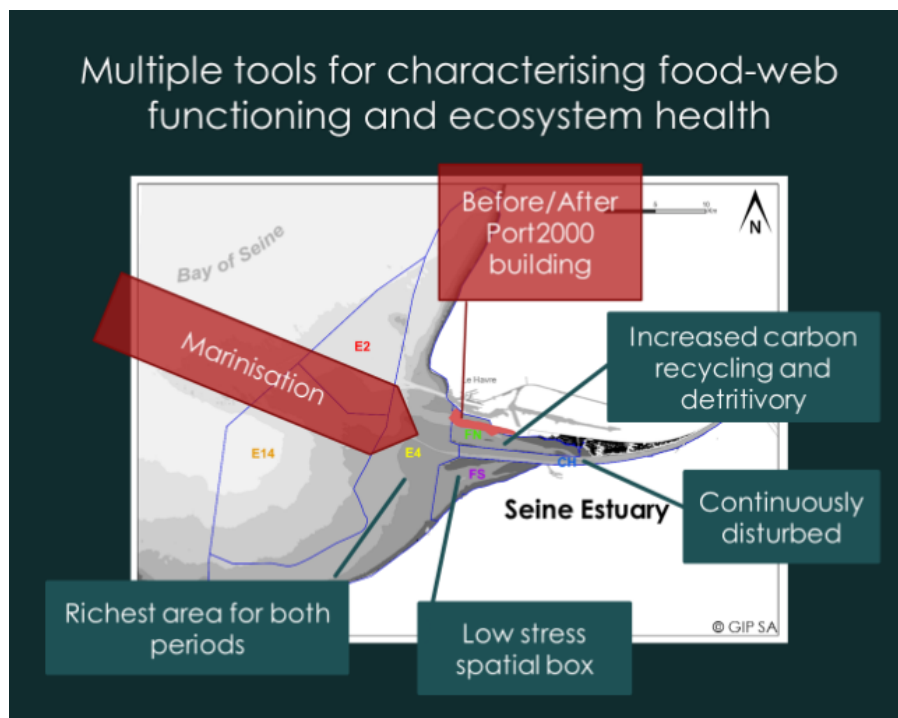
32 The need to continue long-term monitoring and to use multiple tools is emphasized.

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35 **Graphical abstract**  
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121 **Abstract**  
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125 44 During the last decades, the highly-anthropized Seine estuary has been impacted by  
126 45 modification of its habitats (building of a major extension of Le Havre harbour, i.e. Port2000)  
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128 46 and a significant natural decrease in freshwater discharge. A Before/After analysis, using a  
131  
132 47 toolbox of indicators, was applied to characterize the effects of both events on the estuarine  
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134 48 ecosystem status. We selected from existing tool boxes several indicators derived from food  
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136 49 web modelling or community composition data, such as biodiversity indicators, a guild-based  
137  
138 50 index (*i.e.* Estuarine and Lagoon Fish Index ELFI) and ecological network analysis (ENA)  
139  
140 51 indices. ENA and biodiversity indicators were applied on six spatial boxes describing the Seine  
142  
143 52 estuary and its outlet. Results showed an increase in taxonomic and functional richness over  
144  
145 53 time, mainly due to marinisation, and significant changes in food-web properties in relation to  
146  
147 54 Port2000. ENA indices appeared as a promising method in ecological status assessment,  
148  
149 55 especially for estuaries considered as inherently disturbed.  
150

151 56

152  
153 57 **Keywords:** ecology, biodiversity, food web, ecosystem functioning, ecosystem health  
154  
155 58 indicators  
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157 59

159 60 **1. Introduction**  
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164 62 Areas at the land-sea interface are often strongly impacted by human activities (e.g. Borja *et*  
165  
166 63 *al.*, 2012). Because estuaries are of great economic importance, they are commonly subject to  
167  
168 64 physical modifications such as port development and channelization to enhance harbour and  
169  
170 65 industrial activities (Marmin *et al.*, 2014). In addition, pollution and other anthropogenic  
171  
172 66 disturbances may cause modifications in aquatic communities (*i.e.* group of species or taxa  
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180 67 present in a given area that can be characterised by the distribution of individuals or biomasses  
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182 68 among those species (Borja *et al.*, 2012)), that could in turn influence the whole ecosystem  
183  
184 69 functioning. A stressed ecosystem is here defined as an ecosystem undergoing changes in its  
185  
186 70 structure (e.g. productivity of its species) or functioning (e.g. food-web dynamics) following  
187  
188 71 physical, chemical or biological constraints or perturbations, either of a natural or an  
189  
190 72 anthropogenic origin. A stressed ecosystem is therefore expected to show modifications in both  
191  
192 73 its structure (e.g. species assemblages) and functioning (e.g. food-web properties), compared to  
193  
194 74 a defined baseline. Estuarine ecosystems are constituted of a mosaic of habitats linked to natural  
195  
196 75 (e.g. tide, freshwater input) and anthropogenic factors (McLusky and Elliott, 2004; Elliott and  
197  
198 76 Whitfield, 2011). However, it is difficult to distinguish between natural and human-induced  
199  
200 77 disturbances in estuaries due to their naturally high stress level and inherent variability: a  
201  
202 78 concept known as estuarine quality paradox (Dauvin, 2007; Elliott and Quintino, 2007; Dauvin  
203  
204 79 and Ruellet, 2009).

207  
208 80 Multiple tools exist to derive various indicators describing and reflecting the structure and  
209  
210 81 functioning of ecosystems (Rombouts *et al.*, 2003; de la Vega *et al.*, 2018). Biodiversity and  
211  
212 82 guild-based indices are the most commonly used and were largely developed for application to  
213  
214 83 coastal and transition water masses in Europe under the EU Water Framework Directive (WFD)  
215  
216 84 (EU, 2000; Hering *et al.*, 2010). Biodiversity indices aim to describe communities'  
217  
218 85 characteristics and enable comparisons at different spatial scales (e.g. species richness, *alpha*,  
219  
220 86 *beta* and *gamma*, diversities). Guild-based indicators are generally developed to assess the  
221  
222 87 response of ecosystems to specific or more general disturbances (*i.e.* the comparison between  
223  
224 88 the Ecology Quality Status of an estuary or a part of an estuary to a reference ecosystem with  
225  
226 89 or without moderate disturbances) (Perez-Dominguez *et al.*, 2012; Lepage *et al.*, 2016).  
227  
228 90 Delpech *et al.* (2010) suggested using a fish-based indicator called Estuarine and Lagoon Fish  
229  
230 91 Index (ELFI) to assess the ecological status of French estuaries. ELFI was based on pressure-

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92 impact models and the purpose was to select relevant metrics that were known to be sensitive  
93 to anthropogenic pressures (Tableau *et al.*, 2013; Pasquaud *et al.*, 2013). However, this  
94 ecological quality indicator is mainly based on structural or taxonomic elements and do not  
95 sufficiently reflect neither the functioning of ecosystems (de Jonge *et al.*, 2006; Rombouts *et*  
96 *al.*, 2013) nor the biodiversity patterns between and within ecosystems (e.g. Vasconcelos *et al.*,  
97 2013).

98 Ecological Network Analysis (ENA) corresponds to a collection of mathematical indices  
99 describing the structure and functioning of a trophic network and characterise the overall  
100 structural properties of food webs (Ulanowicz, 1997; Niquil *et al.*, 2014). Mass-balanced food-  
101 web models such as Linear Inverse Modelling (Vézina and Platt, 1988; Niquil *et al.*, 2011;  
102 Tecchio *et al.*, 2016) and Ecopath with Ecosim (Polovina, 1984) compute values of all carbon  
103 flows in a given food web and then calculate ENA indices to assess the properties emerging  
104 from the food-web architecture.

105 A common feature of both biodiversity indices and holistic ENA indicators is that they can  
106 be related to concepts of stress, stability, resistance and resilience (Fath *et al.*, 2019; Safi *et al.*,  
107 2019). The stability of an ecosystem corresponds to its ability to maintain a comparable  
108 functioning in the presence of perturbations that drive it away from its original state  
109 (Vasconcellos *et al.*, 1997; Lobry *et al.*, 2008; Saint-Béat *et al.*, 2015). Grimm & Wissel (1997)  
110 defined resistance as the property of populations, communities or ecosystems to remain  
111 “essentially unchanged”. Resilience is the ability or the time taken by a system to recover from  
112 a change due to perturbations and is linked to stability (Pimm, 1984; Mathevet and Bousquet,  
113 2014). Although ENA indices have great potential to inform management decisions in estuaries  
114 and large tidal areas (de la Vega *et al.*, 2018), their implementation in ecosystem health  
115 assessment is not sufficiently established yet.

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298 116 The objective of the present study was to investigate the contribution of ENA indices to the  
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300 117 assessment of the Seine estuarine ecosystem quality by confronting them to some more  
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302 118 commonly used indicators (i.e. biodiversity and guild-based indices). The Seine estuary is a  
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304 119 good example of a highly anthropogenic transitional area (Dauvin and Desroy, 2005; Dauvin  
305  
306 120 *et al.*, 2006). For more than 150 years, the Seine estuary has undergone many transformations,  
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308 121 such as shores linearization and calibration of the navigation channel from Le Havre (i.e.  
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310 122 entrance of the estuary) to port of Rouen (120 km upstream). Port2000 is an extension of the  
311  
312 123 existing commercial port of Le Havre, located in the Northern Channel of the Seine estuary,  
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314 124 that was constructed between 2002 and 2005 and that modified the morphological and  
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316 125 hydrological characteristics of the estuary (Dauvin *et al.*, 2006; Tecchio *et al.*, 2016). This  
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318 126 extension aimed to optimise the access of long-distance trade ships and to expand the available  
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320 127 area for those vessels in the harbour. Moreover, the navigation channel is also continuously  
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322 128 dredged to ensure maritime access of ships up to the port of Rouen (Marmin *et al.*, 2014). A  
323  
324 129 recent study using Ecopath models has shown that before the construction of Port2000, the  
325  
326 130 northern and navigation channels of the Seine estuary already presented signs of disturbance  
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328 131 (i.e. an effect, either biotic or abiotic, inducing a perturbation such as stress in an ecosystem;  
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330 132 relative to a specified reference state, (Rykiel JR, 1985)) due to maritime traffic, dredging, and  
331  
332 133 building works leading to a lack of connectivity between estuarine areas (Tecchio *et al.*, 2015).  
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334 134 Later, Tecchio *et al.* (2016) used a statistically more-advanced modelling framework (LIM-  
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336 135 MCMC) to estimate flows in the Seine estuary food web and compute ENA indices describing  
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338 136 its functional properties before and after Port2000. They showed that the northern channel  
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340 137 evolved towards a shorter food web and increased its resistance property. This was considered  
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342 138 as a potential impact of the Port2000 construction. Results from ENA indices also evidenced  
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344 139 that the food web in the navigation channel was constantly changing, probably due to  
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357 140 continuous dredging activities, and that the southern channel could be seen as the least disturbed  
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359 141 area for both periods (Tecchio *et al.*, 2016).

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361 142 In addition to these anthropogenic disturbances, the Seine Estuary is also subject to an  
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363 143 increase of salinity in the lower part of the estuary, called marinisation. Marinisation is due to  
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365 144 a decrease in freshwater input coming from the river, associated with intrusion of marine water  
366  
367 145 in the lower part of the estuary. Marinisation is a common evolution in estuaries receiving water  
368  
369 146 from rivers and influenced by human activities (e.g. irrigation, dams) (David *et al.*, 2007;  
370  
371 147 Goberville *et al.*, 2010; Chaalali *et al.*, 2013).

372  
373 148 We used here an original combination of methods to assess the ecosystem health of the Seine  
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375 149 estuary before and after the construction of Port2000. These analyses were performed on six  
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377 150 spatial boxes previously defined to describe the estuary (Tecchio *et al.*, 2016).

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381 151 We first addressed the methodological question “Do the different indicators used in this  
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383 152 study (species-based, guild-based and ecosystem-based indices) bring similar, complementary  
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385 153 or different information on the ecological status of this estuarine ecosystem?” We then  
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387 154 addressed two ecological questions using this set of indicators: (i) How did physical distinct  
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389 155 areas of the estuary (spatial boxes) react to perturbations? (ii) Can we distinguish the effects  
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391 156 due to Port2000 from global change effects in the context of the estuary’s natural marinisation?

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## 394 395 158 **2. Materials and Methods**

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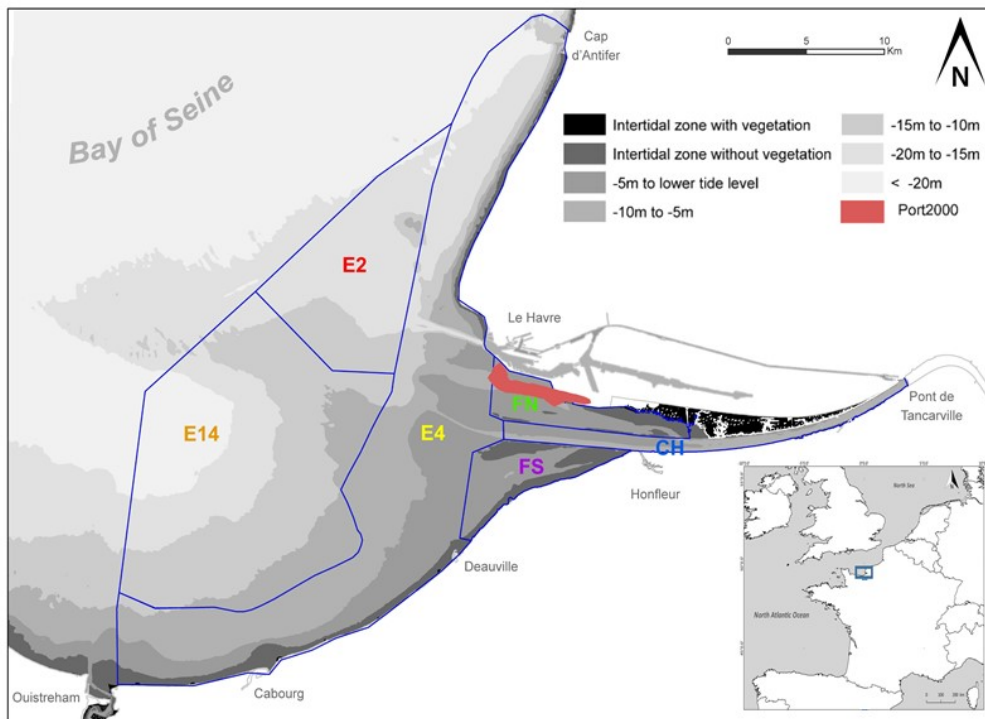
### 400 160 *2.1. Study site and periods*

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404 162 Six spatial boxes, based on habitat characteristics and sediment types of the Seine estuary  
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406 163 and the adjacent eastern part of the Seine Bay, previously defined in Tecchio *et al.* (2015) were  
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408 164 considered: (a) three estuarine boxes: the navigation channel (CH), the northern channel (FN),  
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 416 165 and the southern channel (FS); (b) an intermediate box located at the mouth of the estuary (E4),  
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 418 166 and (c) two marine spatial boxes (E2 and E14) (Fig. 1). Hydro-sedimentary and salinity  
 419  
 420 167 conditions were considered homogenous within each spatial box (Tecchio *et al.*, 2015). For  
 421  
 422 168 each zone, two sets of data were gathered corresponding to two different periods: 1996–2002,  
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 424 169 representing the situation before the Port2000 construction, and 2005–2012, corresponding to  
 425  
 426 170 the recent situation, after the Port 2000 construction.



454 171  
 455  
 456 172 **Fig. 1.** Map showing the geographical position of the Seine estuary in France. The spatial boxes  
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 458 173 are composed of the navigation channel (CH), the northern channel (FN), and the southern  
 459  
 460 174 channel (FS) as estuary boxes; an intermediate box located at the mouth of the estuary (E4),  
 461  
 462 175 and two marine boxes (E2 and E14). Source: GIP Seine-Aval and SHOM.

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474  
475 178 2.2. Indicators based on taxonomic diversity  
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477 179 2.2.1. Data  
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479 180 For the subsequent indices' calculations, both fish data (from beam trawl) and  
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481 macrozoobenthos data (from 0.1 m<sup>2</sup> Smith McIntyre or Van Veen grabs) were collected  
482 181  
483 following identical sampling protocols between both periods, as results were standardised to  
484 182  
485 take into account differences in sampling effort. This allows quantitative and qualitative  
486 183  
487 comparisons to be made.  
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491  
492 186 2.2.2. Indicators  
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494 187 The taxonomic richness is defined as the total number of taxa sampled at a given scale. It  
495  
496 was computed by pooling all sampled taxa by spatial box and period (Before Port2000 = 1996-  
497 188  
498 2002 vs After Port2000 = 2005-2012). To limit bias due to sampling design, taxonomic richness  
499 189  
500 was standardized with relation to the sampling effort by dividing it by the log-transformed total  
501 190  
502 number of samples realised for a given space-time unit (Nicolas *et al.*, 2010).  
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504

505 192 Alpha ( $\alpha$ ), beta ( $\beta$ ) and gamma ( $\gamma$ ) diversity indices give information on changes in  
506  
507 community composition and the processes driving them, between spatial units or periods  
508 193  
509 (Barros *et al.*, 2014).  $\alpha$ -diversity describes the taxonomic diversity on a local scale (calculated  
510 194  
511 for each spatial box),  $\gamma$ -diversity corresponds to the taxonomic diversity of the entire region of  
512 195  
513 interest (all six spatial boxes considered in the study) and  $\beta$ -diversity represents the variation in  
514 196  
515 taxonomic composition among the spatial boxes of the studied area (Barros *et al.*, 2014). The  
516 197  
517 mean  $\alpha$ -diversity ( $\bar{\alpha}$ ) of a region or area comprising several spatial boxes was calculated as the  
518 198  
519 average of  $\alpha$ -diversity in each spatial box (Eq. 1).  
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521

522 200  $\bar{\alpha} = \sum_{i=1}^N \alpha^i / N$  (1); with  $\alpha_i$  the taxonomic richness in the spatial box  $i$ , and  $N$  the number of  
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524  
525 201 spatial boxes.  
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534 202  $\beta$ -diversity is the ratio between  $\gamma$  and  $\bar{\alpha}$  (Eq. 2) (Anderson *et al.*, 2011) and represents the  
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536 203 number of times by which the taxonomic richness in the whole region considered (*i.e.* the entire  
537  
538 204 estuary) is greater than the average taxonomic richness in the different spatial boxes. In other  
539  
540 205 words, it corresponds to the ratio between regional and local species diversity and is related to  
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542 206 compositional heterogeneity.

543  
544  
545 207 
$$\beta = \gamma / \bar{\alpha} \quad (2)$$
  
546

547 208 with  $\gamma$ -diversity = taxonomic diversity of the entire region of interest and  $\bar{\alpha}$  = mean  $\alpha$ -diversity.

549 209 Biodiversity analyses were performed using the software package PRIMER-E v.6 (Clarke  
550  
551 210 & Gorley, 2006). A two-dimensional non-metric Multi-Dimensional Scaling (nMDS)  
552  
553 211 ordination was implemented for the six spatial boxes for each of the two periods, based on  
554  
555 212 square-root-transformed biomasses to reduce the asymmetry in species distributions, and a  
556  
557 213 Bray-Curtis similarity index computed on a species composition matrix. The nMDS plot gives  
558  
559 214 a visual representation of the proximity in species composition between samples: the closer  
560  
561 215 they are on the plot, the more similar they are in their species composition (Clarke and Warwick,  
562  
563 216 2001). The ‘stress’ index calculated by the routine in PRIMER reflects how well the ordination  
564  
565 217 is capable of preserving the rank of similarities in a bi-dimensional space, providing information  
566  
567 218 on the quality of the representation.

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### 571 572 220 *2.3. Multimetric fish-based indicator ELFI*

#### 573 574 221 *2.3.1. Data*

575  
576 222 Fish data ‘After Port2000’ were standardized data, collected from surveys following a  
577  
578 223 normalized protocol especially designed for fish monitoring in the French estuaries for the  
579  
580 224 WFD (Appendix A). Fish data used for multimetric fish-based indicator ELFI (Delpech *et al.*,  
581  
582 225 2010) calculation ‘Before Port2000’ were collected from surveys designed for various other  
583  
584 226 monitoring purposes but were obtained using similar sampling gear (*i.e.* beam trawls with  
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593 227 similar net features). For standardization and comparison, we accounted for sampling effort  
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595 228 (trawled surface area and time spent trawling) and considered that the spatial design was  
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597 229 relevant regarding WFD fish sampling protocol (> 6 samples by haline zone, defined by salinity  
598  
599 230 level) following the Venice estuarine system: oligohaline (0-5); mesohaline (5-18), polyhaline  
600  
601 231 (18-30) and euhaline (<30) zones (Venice System, 1958; Elliott & McLusky, 2002). This  
602  
603 232 allowed for comparison of ELFI values between both periods.  
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### 608 234 2.3.2. Indicator calculation

609  
610 235 ELFI has already been used to assess the ecological status of French estuaries (Tableau *et*  
611  
612 236 *al.*, 2013; Teichert *et al.*, 2018) (ecological status categories described in Appendix B). The  
613  
614 237 ELFI indicator is composed of seven metrics: density of (1) benthic fish (DB), (2) diadromous  
615  
616 238 migrant species (DDIA), (3) marine juveniles migrants (DMJ), (4) freshwater species (DFW),  
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618 239 (5) resident species (DER), (6) total density of fish (DT) and (7) standardised taxonomic  
619  
620 240 richness (RT/lnS) (Pasquaud *et al.*, 2013). Indeed, taxonomic richness (RT) was divided by the  
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622 241 log-transformed total number of samples in each spatial box (lnS) to limit the bias due to  
623  
624 242 sampling design, defining RT/lnS as the standardised taxonomic richness. These metrics are  
625  
626 243 proxies that reflect the physical quality of the habitat (DB, DER), the chemical quality of water  
627  
628 244 and sediment (DB, DMJ, DFW), but also the habitat connectivity (i.e. the degree to which  
629  
630 245 separate patches of habitat are connected; DDIA) (Hall *et al.*, 2011) and the general degradation  
631  
632 246 level, which reflects a general dysfunction in ecosystem health due to accumulation of negative  
633  
634 247 impacts (DT, RT/lnS). Contrary to the diversity indices calculated at the spatial box level, ELFI  
635  
636 248 represents the estuary level due to the high number of samples required to calculate this index.  
637  
638 249 ELFI values were computed using R (R Development Core Team, 2015). This fish index was  
639  
640 250 inter-calibrated at the European level with seven other fish indices in use in the North East  
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642 251 Atlantic region of Europe (Lepage *et al.*, 2016) in order to ensure that assessments provided by  
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651  
652 252 these indices are consistent. Data were provided by ‘*Agence de l’Eau Seine Normandie*’ for the  
653  
654 253 ‘After Port2000’ period whereas values were computed from Ifremer and CSLN (*Cellule de*  
655  
656 254 *Suivi du Littoral Normand*) fish surveys for the ‘Before Port2000’ period.  
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## 660 256 *2.4. Indicators based on food-web models: Ecological Network Analysis (ENA)*

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### 664 258 *2.4.1. Data sources and model construction*

667 259 We used the LIM model from Tecchio *et al.* (2016) for the three estuarine spatial boxes (FN,  
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669 260 FS and CH; Fig. 1) for both periods, using 13 functional groups. A summary of data sources is  
670  
671 261 given in Appendices C and D. Biomasses are expressed in gC.m<sup>-2</sup>. We constructed three  
672  
673 262 additional LIM models representing the spatial boxes E2, E4 and E14 based on the same  
674  
675 263 functional groups (Appendix C) and the same types of input data, including production, food  
676  
677 264 conversion efficiency (i.e. ratio of the biomass produced by one compartment compared to its  
678  
679 265 food intake (Christensen & Walters, 2004)), respiration, and excretion ratios. Data sources and  
680  
681 266 references used for the construction of the LIM-MCMC models are presented in detail in  
682  
683 267 Tecchio *et al.* (2015, 2016). Briefly, a system of linear equations was set up, linking species  
684  
685 268 metabolic ratios (such as production/biomass, respiration/biomass, excretion/consumption  
686  
687 269 ratios), species biomass, and diet compositions. In these equations, the unknowns were the  
688  
689 270 flows connecting the compartments. The flow constraints were established using data from  
690  
691 271 literature or other modelling works (Appendix C). Known equalities such as those including  
692  
693 272 the biomass stocks were included to constrain the model into a finite multi-dimensional space.  
694  
695 273 Metabolic parameters as well as dietary constraints (i.e. proportion of prey in predator diet)  
696  
697 274 were implemented as "inequalities": minimum and maximum values were included in the linear  
698  
699 275 equations to partially constrain the related flows. This approach produces solutions that are  
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701 276 robust to the effect of parameterisation uncertainty (Hines *et al.*, 2015; Hines *et al.*, 2018).  
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711 277 Then, this space was sampled by using a Markov-Chain Monte Carlo routine to obtain 200,000  
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713 278 solutions of the set of flow values. Ecological Network Analysis was applied to these 200,000  
714  
715 279 solutions, using the R software packages *NetIndices* (Soetaert *et al.*, 2015) and *enaR* (Borrett  
716  
717 & Lau, 2014), along with scripts developed for the present study [see Tecchio *et al.* (2016) for  
718 280  
719 additional methodological details].  
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722 282 To assess statistical differences in ENA indices between both periods, the non-parametric  
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724 283 effect size statistic introduced by Cliff (1993) was applied [see Tecchio *et al.* (2016) for  
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726 284 methodological details] as we were dealing with a situation of large amount of data (each ENA  
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728 285 index was calculated 200,000 times before Port2000 and the same number after Port2000)  
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730 286 which renders the estimation of classical parametric test statistics unfeasible (Mulholland &  
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732 287 Jones, 1968).  
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#### 736 289 2.4.2. *Indices*

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739 290 We calculated six relevant ENA indices: the Total System Throughput (T..), the System  
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741 291 Omnivory Index (SOI), the Finn's Cycling Index (FCI), the Ascendency (A), the relative  
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743 292 Redundancy (R/DC) and the Detritivory/Herbivory ratio (D/H). This set of indices was used by  
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745 293 Tecchio *et al.* (2016) to characterize the inner part of the Seine estuary and most of them have  
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747 294 been proposed as management tools in the OSPAR Convention context (Safi *et al.*, 2019). The  
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749 295 Total system throughput (T..) corresponds to the sum of all flows occurring in the system, and  
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751 296 acts as an indicator of system size and activity (Rutledge *et al.*, 1976; Aoki, 1988; Latham,  
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753 297 2006). The Finn's Cycling Index (FCI) represents the fraction of the flows in the system that is  
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755 298 generated by recycling and was calculated as the proportion of T.. generated by cycling (Finn,  
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757 299 1976; Finn, 1980). Although other FCI definitions exist, this particular one was chosen to  
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759 300 remain consistent with previous work and another common modelling approach, *Ecopath with*  
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761 301 *Ecosim*. The Ascendency was calculated as the product of the Total system throughput (T..)

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770 302 and the Average Mutual Information (AMI), where AMI expresses the degree of organisation  
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772 303 of exchanges between the different functional groups (increasing AMI indicates higher dietary  
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774 304 specialisation; Hirata & Ulanowicz, 1984). High ascendancy values mean that the system is  
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776 305 more actively channelling flows along more specific pathways, whereas low values have been  
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778 306 linked to system immaturity (Ortiz & Wolff, 2002). Relative redundancy (R/DC) was calculated  
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781 307 as the ratio between the internal flows overhead and the total development capacity of the  
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783 308 ecosystem (Ulanowicz, 1986; Ulanowicz, 2001) and measures the amount of parallel trophic  
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785 309 pathways connecting the trophic compartments. R/DC acts as an indicator of inefficiency of the  
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787 310 network (Hirata & Ulanowicz, 1984; Bondavalli *et al.*, 2000) but it is also a way to increase  
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789 311 ecosystem resilience because parallel pathways can replace each other (Ulanowicz, 1997). The  
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791 312 System Omnivory Index (SOI) was calculated as the mean of the omnivory indices of each  
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793 313 consumer compartment, weighted by the logarithm of their consumption (Christensen &  
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795 314 Walters, 1993; Libralato, 2008). Omnivory is defined as the variability of prey trophic levels  
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797 315 where high SOI values correspond to a food web with a web-like structure (i.e. with several  
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799 316 pathways between compartments) whereas low SOI values reflect a chain-like structure with  
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801 317 fewer pathways (Dimitrios *et al.*, 2018). Therefore, SOI is an indicator of the overall dietary  
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803 318 adaptation of the consumers, and an increase in SOI generally corresponds to a stabilizing  
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805 319 response to an external disturbance (Fagan, 1997; Libralato, 2008). The Detritivory/Herbivory  
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807 320 ratio (D/H) was calculated as the ratio between the sum of all predation flows on the detritus  
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809 321 compartment (detritivory, flows from detritus to consumers) and the sum of all predation flows  
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811 322 on primary producers (herbivory, flows from phytoplankton and microphytobenthos to  
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813 323 consumers). An increase in D/H would indicate that the ecosystem shifts towards a more  
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815 324 detritus-based food web, depending less on plant material for trophic interactions (Ulanowicz,  
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817 325 1992; Luong *et al.*, 2014; Niquil *et al.*, 2014).  
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829 **3. Results**  
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833 329 Results concern “species-based” (species diversity and biomasses), “community-based”  
834 330 (fish index ELFI) and “ecosystem-based” (Ecological Network Analysis) indicators, which  
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836 331 provide information at different levels.  
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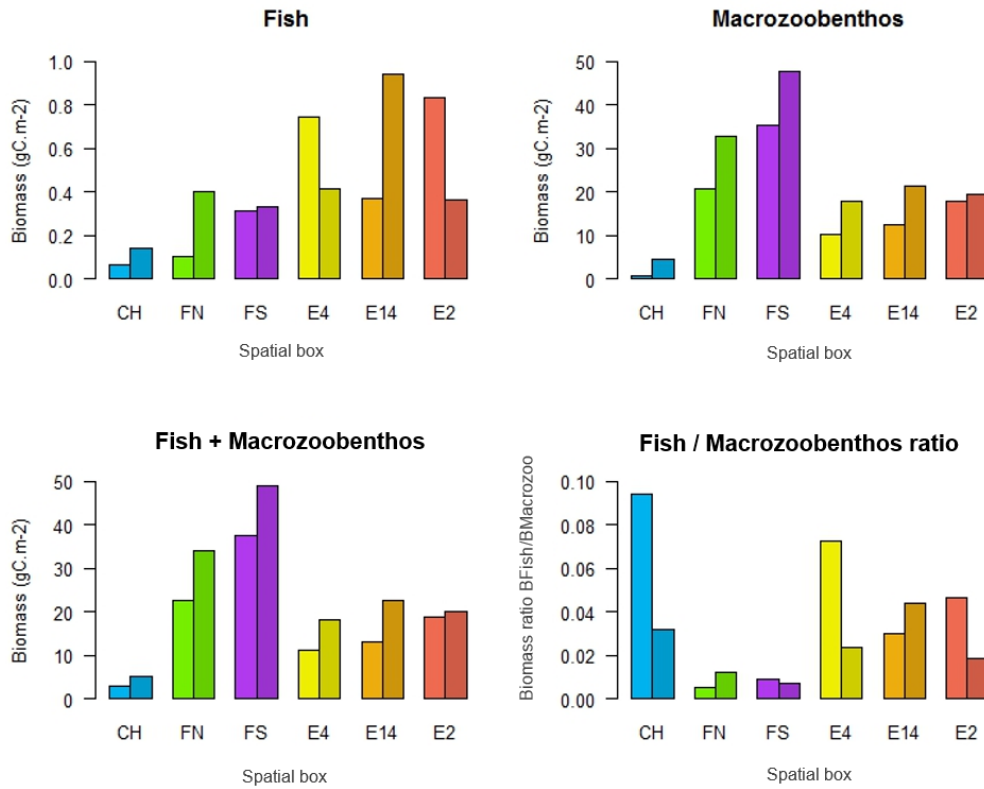
841 333 *3.1. Species-based indices related to diversity and biomasses*

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843 334 *3.1.1. Biomass trend*

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846 335 In the estuary boxes CH and FN, fish and macrozoobenthos biomasses increased between  
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848 336 periods (Fig. 2, Table 1). For the southern channel (FS), while macrozoobenthos biomass  
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850 337 increased, fish biomass remained stable, and it appeared that this was the case for all fish groups  
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852 338 (Fig. 2). For instance, the biomass of piscivorous fish in FS averaged 0.057 g C.m<sup>-2</sup> in the first  
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854 339 period and approached 0.055 g C.m<sup>-2</sup> in the second one. In CH, while total fish biomass  
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856 340 increased, the biomass of planktivorous fish decreased (Fig. 2). This was mainly related to two  
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858 341 pelagic species: *Clupea harengus* and *Sprattus sprattus*. In the same way, for FN, while the  
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860 342 total fish biomass increased, the biomass of piscivorous and planktivorous fishes slightly  
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862 343 decreased (Fig. 2). This was quantitatively compensated by a strong increase in benthos feeders’  
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864 344 biomass. The decrease in planktivorous fish biomass in FN was due to four species *Clupea*  
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866 345 *harengus*, *Gasterosteus aculeatus*, *Osmerus eperlanus* and *Sprattus sprattus*. The overall  
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868 346 biomass (including fish, macrozoobenthos and the suprabenthos) increased for the three  
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870 347 estuarine spatial boxes. Among the three estuarine boxes, the ratio of fish biomass on benthic  
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872 348 invertebrate biomass (BFish/BMacrozoobenthos) was the highest in CH (0.09 in the first period  
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874 349 and 0.03 in the second one). Nonetheless, this ratio was divided by three in CH congruently to  
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876 350 the sharp increase in benthic macrofauna biomass between periods that was multiplied by 7  
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878 351 (Fig. 2, Table 1).  
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353 **Fig. 2.** Barplots representing fish biomass, macrozoobenthos biomass, the sum of fish and  
 354 macrozoobenthos biomasses, and the ratio  $B_{Fish}/B_{Macrozoobenthos}$ , for all spatial boxes  
 355 before the construction of Port2000 (first bars) and after (second bars). The spatial boxes are  
 356 composed of the navigation channel (CH), the northern channel (FN), and the southern channel  
 357 (FS) as estuary boxes; an intermediate box located at the mouth of the estuary (E4), and two  
 358 marine boxes (E2 and E14).

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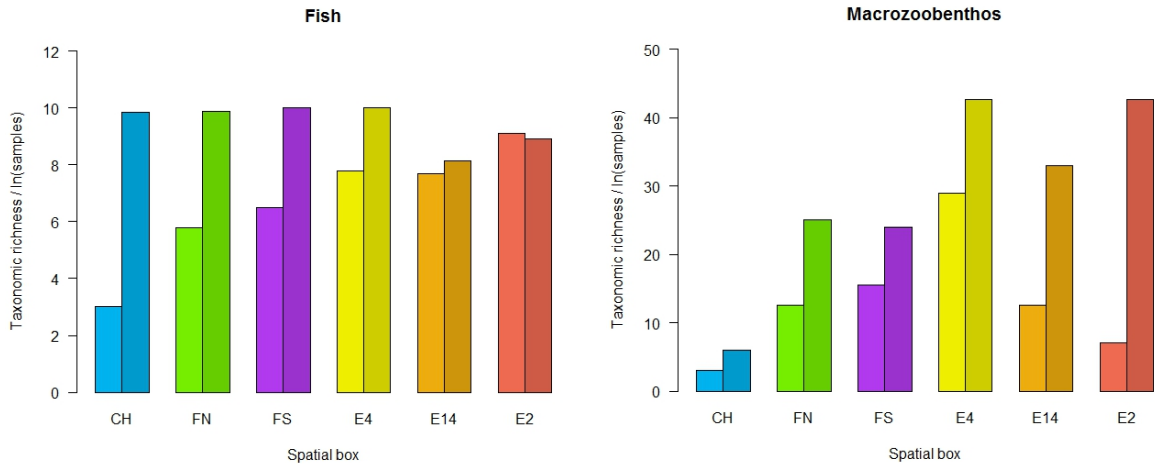
**Table 1.** Summary of comparisons between periods (Before and After Port2000 construction) for biomass values, biodiversity indices, and the ELFI index. See text for details on the indices. < indicates that the value of the index is lower Before than After Port2000; > indicates that the value of the index is greater Before than After Port2000.

		Spatial boxes					
		CH	FN	FS	E4	E14	E2
Biomass	Fish	<	<	<	>	<	>
	Benthos	<	<	<	<	<	<
TR	Fish	<	<	<	<	>	>
	Benthos	<	<	<	<	<	<
$\alpha$	Fish	<	<	<	<	>	>
	Benthos	<	<	<	<	<	<
Diversity	$\square^*$	Fish			<		
		Benthos			<		
	$\beta^*$	Fish			<		
		Benthos			>		
	$\gamma^*$	Fish			<		
		Benthos			<		
ELFI*					<		

\*  $\square$ ,  $\beta$  and  $\gamma$  diversity indices are computed for the whole estuary

### 3.1.2. Taxonomic richness and species composition

The taxonomic richness increased between periods, from 16 to 47 fish taxa and from 5 to 29 macrozoobenthos taxa in the navigation channel (CH) (Fig. 3). The same trend was observed in the Northern and Southern channels (FN and FS; Fig. 3). The estuary box CH showed particularly low values of macrozoobenthos taxonomic richness compared to the other spatial boxes (Fig. 3). The intermediate box E4 was the richest spatial box in terms of fish (with 51 taxa during the first period and 59 taxa during the second one) and benthic macrofauna (with 177 taxa during the first period and 307 during the second one). No strong changes were observed for the fish taxonomic richness in the marine spatial boxes E14 and E2. All taxa that were gained between periods, both for fish and macrozoobenthos, were exclusively of marine origin. Results on standardised taxonomic richness are given in Figure 3.



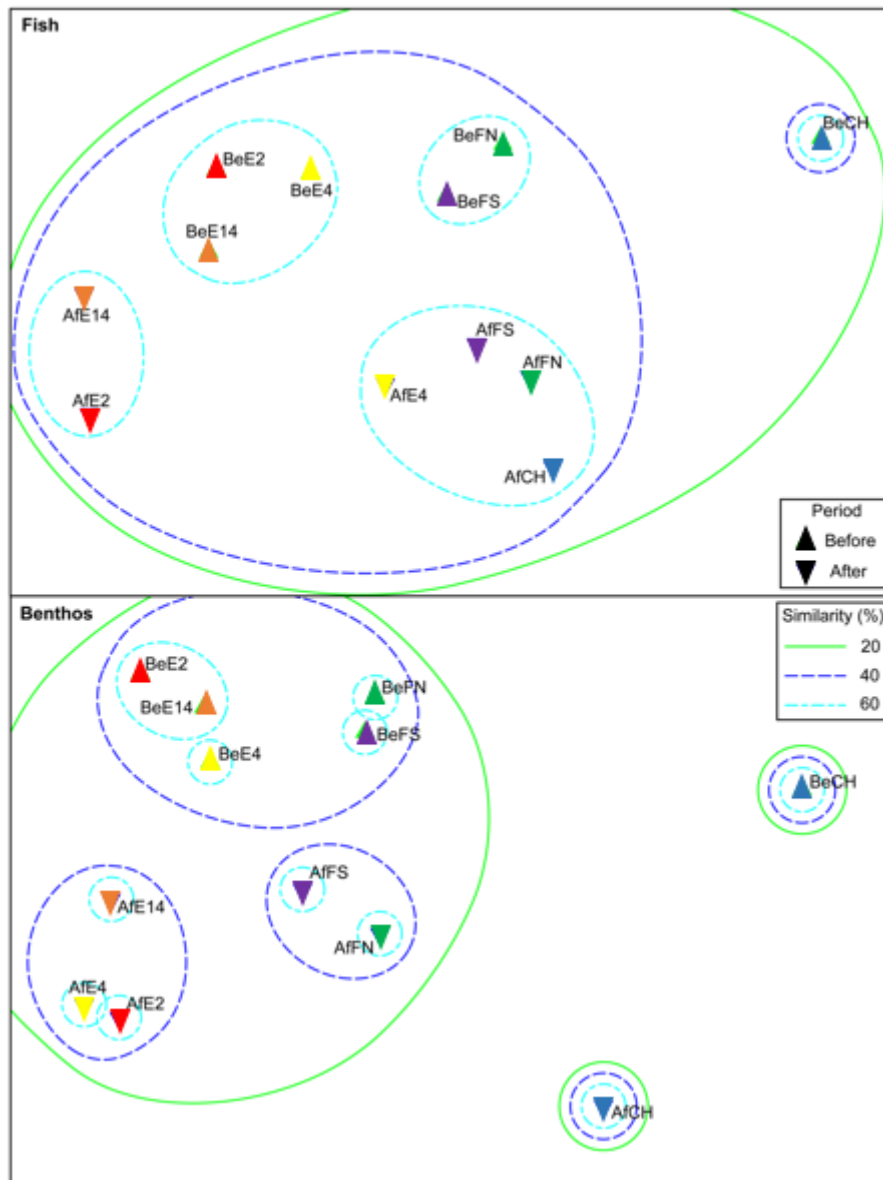
**Fig. 3.** Barplots representing taxonomic richness divided by the log-transformed total number of samples realised within the six spatial boxes before (first bars) and after (second bars) the construction of Port2000 for fish and macrozoobenthos. The spatial boxes are composed of the navigation channel (CH), the northern channel (FN), and the southern channel (FS) as estuary boxes; an intermediate box located at the mouth of the estuary (E4), and two marine boxes (E2 and E14).

### 3.1.3. Diversity indices

The  $\alpha$ ,  $\beta$  and  $\gamma$  taxonomic diversity analyses between periods showed that the average number of fish species  $\alpha$  increased from 32.8 to 41 species, and from 65.7 to 177.2 for macrozoobenthos.  $\gamma$ -diversity increased from 54 to 71 taxa for fish and from 195 to 353 taxa for macrozoobenthos, and  $\beta$ -diversity increased from 1.65 to 1.73 for fish and decreased from 2.97 to 1.99 for macrozoobenthos (Table 1).

The MDS ordination based on fish composition data showed a remarkable spatial segregation according to the salinity gradient between the estuarine and the marine spatial boxes (Fig. 4 top). The same pattern was observed with the MDS ordination based on macrozoobenthos species (Fig. 4 bottom). The ‘stress’ value of 0.05 was very low, underlying the good quality of the representation.

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**Fig. 4.** MDS ordination based on Bray-Curtis similarity matrices from biomass data (square-root transformed) for fish (on the upper part) and for macrozoobenthos (on the lower part), for all spatial boxes during the first (first bars), before Port2000, and the recent (second bars) periods.

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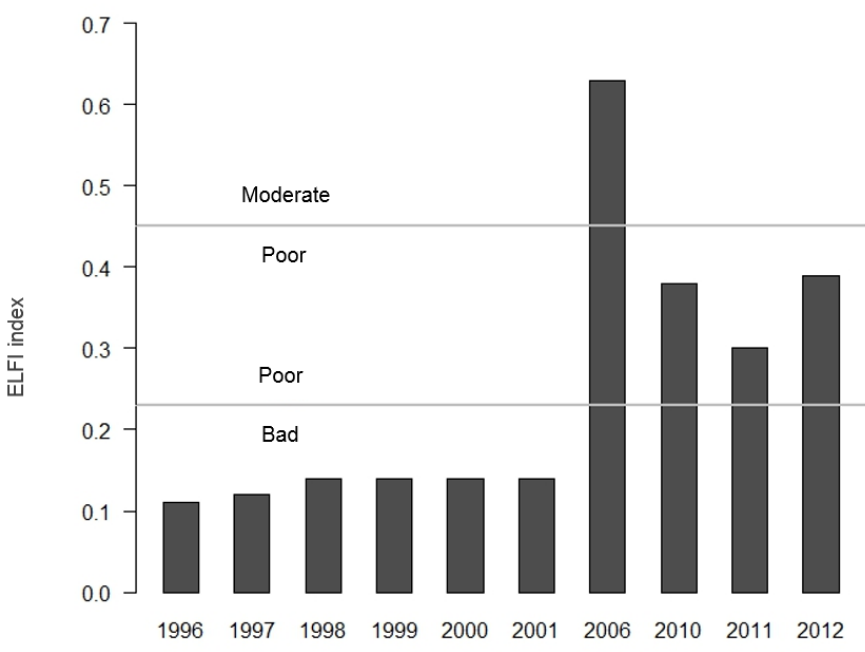
405 CH appeared as the spatial box that has experienced the greatest change in fish composition  
 406 between periods, with less than 20% similarity in the community composition before and after  
 407 Port2000. In addition, the benthic macrofauna composition in this estuary box demonstrated  
 408 few similarities with the other spatial boxes, and this for both periods. For fish in the ‘Before’  
 409 period, marine boxes E2, E4 and E14 formed a group well separated from the inner estuary,

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410 where FN and FS were grouped and CH isolated from these two other estuarine boxes. Similar  
411 results were obtained for macrozoobenthos. But in the ‘After’ period, the marine box E4 was  
412 grouped, for fish, with not only the estuary boxes FN and FS, but also CH (Fig. 4). This  
413 similarity in biodiversity composition was only limited to fish compartment; the benthos  
414 remained structured in a very similar way, in both periods.

415  
416 *3.2. A community-based index for fish: ELFI*

417 During the period before Port2000, the Seine estuary showed lower values of ELFI (from  
418 0.1 to 0.14) compared to the period after Port2000, the highest value recorded being 0.68 in  
419 2006 (Fig. 5). The metric DDIA, indicator of habitat connectivity related to diadromous species,  
420 showed strong changes in the recent period (after Port2000), with a value of 0.88 in 2006, 0.70  
421 in 2010 and 0.71 in 2012 (missing value in 2011), meaning that this metric gradually decreased  
422 after the Port2000 construction.



423  
424 **Fig. 5.** ELFI values for the whole estuary for 10 years, between 1995 and 2012, with the class  
425 boundaries of the Water Framework Directive.  
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427 3.3. *Ecosystem-based indicators: food webs and ENA*

428 ENA indices showed that all indices in the two marine zones (E2 and E14) remained similar  
429 between the two periods (Table 2). R/DC and SOI decreased between before and after “Port  
430 2000” in the estuary box (FS). All indices, except SOI, increased between the two periods in  
431 the intermediate box E4 and in the estuary boxes CH and FN.

432 Total System Throughput (T..), representing the size and activity of the system, significantly  
433 increased in the estuary boxes CH and FN as well as in the intermediate box E4 and remained  
434 stable in all the other spatial boxes (Table 2); Cliff’s delta; Fig. 6).

435 The SOI, reflecting the omnivory in the system, significantly decreased in the estuary box  
436 FS between the two periods. (Fig. 6). The D/H ratio significantly increased in the estuary boxes  
437 CH, FN and in the intermediate box E4, while remaining stable in the marine boxes E14, E2  
438 and in FS (Table 2, Fig. 6).

439 The FCI reflecting the recycling in the system, significantly increased between the two  
440 periods in the estuary boxes CH, FN and in the intermediate box E4 (Table 2, Fig. 6).

441 The ascendancy (A) and relative redundancy (R/DC) indices significantly increased in CH  
442 between the two periods. The ascendancy also significantly increased in the intermediary box  
443 E4 between the two periods (Table 2, Fig. 6).

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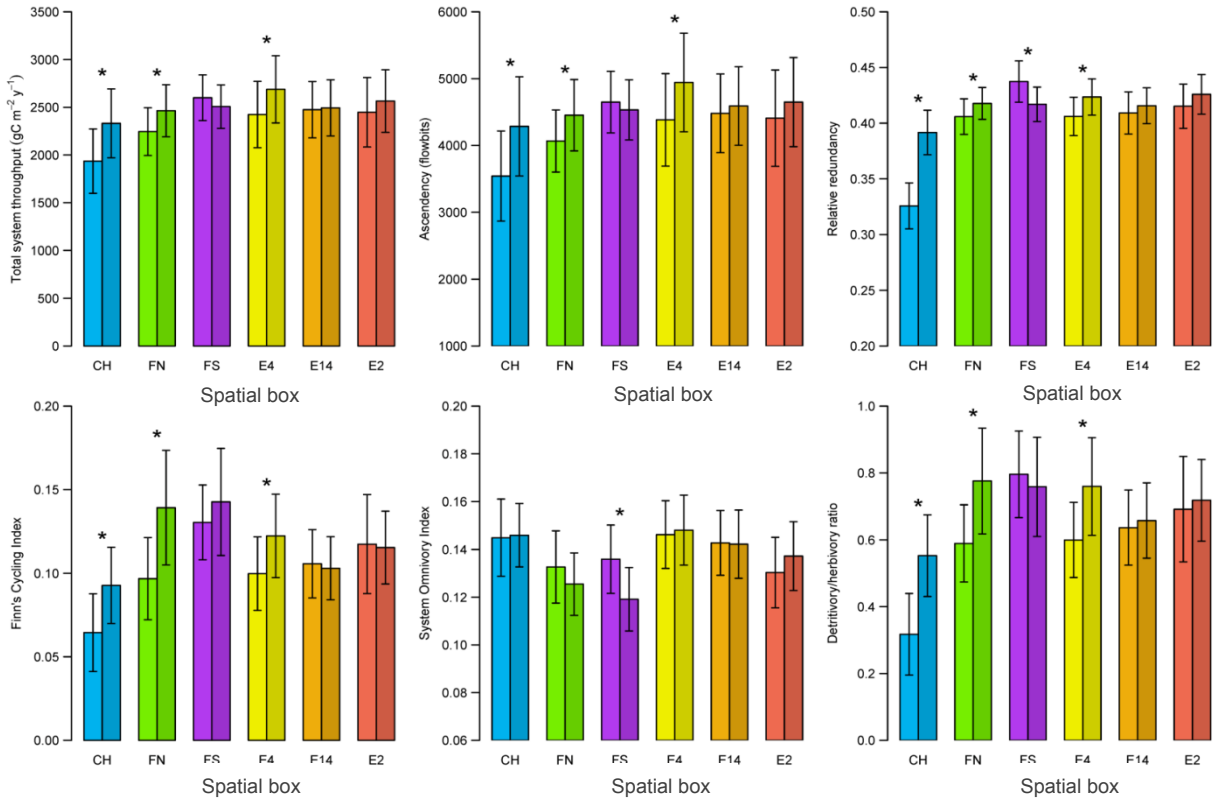
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**Table 2.** ENA means and standard deviations, derived from LIM-MCMC models, for all spatial boxes before (1996-2002) and after (2005-2012) Port2000 construction. < indicates that the value of the index is lower Before than After Port2000; > indicates that the value of the index is greater Before than After Port2000. Only statistically significant results based on Cliff's delta are listed. ns: non-significant.

ENA	Period	CH	FN	FS	E4	E14	E2
T..	Before	1935 ± 337	2244 ± 251	2600 ± 240	2424 ± 347	2475 ± 296	2447 ± 364
T..	After	2332 ± 361	2463 ± 273	2507 ± 227	2687 ± 352	2494 ± 294	2564 ± 328
<b>Evolution T..</b>		<	<	ns	<	ns	ns
FCI	Before	0.087 ± 0.03	0.124 ± 0.03	0.163 ± 0.03	0.128 ± 0.03	0.135 ± 0.02	0.149 ± 0.04
FCI	After	0.119 ± 0.03	0.175 ± 0.04	0.178 ± 0.04	0.153 ± 0.03	0.131 ± 0.02	0.145 ± 0.03
<b>Evolution FCI</b>		<	<	Ns	<	ns	ns
Ascendency	Before	3542 ± 675	4066 ± 465	4648 ± 461	4382 ± 692	4480 ± 589	4408 ± 721
Ascendency	After	4285 ± 742	4453 ± 534	4532 ± 450	4942 ± 737	4590 ± 588	4649 ± 667
<b>Evolution Ascendency</b>		<	<	Ns	<	ns	ns
R/DC (%)	Before	32.6 ± 2	40.6 ± 2	43.7 ± 2	40.6 ± 2	40.9 ± 2	41.5 ± 2
R/DC (%)	After	39.2 ± 2	41.8 ± 1	41.7 ± 2	42.4 ± 2	41.6 ± 2	42.6 ± 2
<b>Evolution R/DC(%)</b>		<	<	>	<	ns	ns
SOI	Before	0.145 ± 0.02	0.133 ± 0.02	0.136 ± 0.01	0.146 ± 0.01	0.143 ± 0.01	0.130 ± 0.01
SOI	After	0.146 ± 0.01	0.125 ± 0.01	0.119 ± 0.01	0.148 ± 0.01	0.142 ± 0.01	0.137 ± 0.01
<b>Evolution SOI</b>		ns	ns	>	ns	ns	ns
D/H	Before	0.317 ± 0.12	0.589 ± 0.12	0.796 ± 0.13	0.600 ± 0.11	0.637 ± 0.11	0.692 ± 0.16
D/H	After	0.553 ± 0.12	0.776 ± 0.16	0.758 ± 0.15	0.760 ± 0.15	0.658 ± 0.11	0.718 ± 0.12
<b>Evolution D/H</b>		<	<	ns	<	ns	ns

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**Fig. 6.** Ecological network analysis (ENA) indices for all spatial boxes for the period before (first bars) and after (second bars) Port2000. The spatial boxes are composed of the navigation channel (CH), the northern channel (FN), and the southern channel (FS) as estuary boxes; an intermediate box located at the mouth of the estuary (E4), and two marine boxes (E2 and E14). Means and standard deviations are represented. Asterisks represent significant changes assessed from Cliff's delta statistics (level 0.05; between before and after construction).

**4. Discussion**

*4.1. Limitations*

Fish species were sampled using beam trawls, which target the first 50cm above the seafloor. The fish assemblage was therefore biased, the pelagic species likely being underestimated. In addition, the edges of each habitat were not sampled. Therefore, a few fish species might not have been sampled. However, the sampling gears and methods were similar between periods



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469 and among spatial boxes, allowing comparison between time periods and spatial boxes. ELFI  
470 values, for both periods, need to be considered with some caution, given the differences in  
471 sampling protocol between periods that may slightly affect the comparability.

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473 *4.2. Signs of estuarine marinisation*

474 The biomasses of marine species increased between both periods in the Seine estuary. For  
475 example, *Pomatoschistus minutus* biomass increased in two estuarine boxes (FN, FS), and in  
476 the intermediate box (E4), and *P. microps* was newly observed in these areas after Port2000.  
477 These two fish species, especially *P. minutus* are mostly marine species (Leitão *et al.*, 2006),  
478 suggesting a tendency of marinisation. Previously termed by David *et al.* (2007) and later used  
479 in several papers (Pasquaud *et al.*, 2012; Chevillot *et al.*, 2016, 2017), « marinisation »  
480 describes the process whereby marine waters flow far upstream into the basin along with a  
481 higher abundance of marine species in the estuarine transitional zone. The Seine estuary, as  
482 many north-eastern Atlantic Ocean estuarine ecosystems (Goberville *et al.*, 2010), is going  
483 through a process of ‘marinisation’. The time period 2005-2012 was characterised by a  
484 significantly lower discharge of the Seine river (Dauvin and Pezy, 2013), resulting in an  
485 increase of salinity up to 5 in the estuarine boxes (Bacq *et al.*, 2013). The salinity in the marine  
486 boxes remained stable between periods. The arrival of marine species finding newly suitable  
487 conditions in most spatial boxes might explain the increase in taxonomic richness. This  
488 marinisation tendency was supported by the MDS ordination showing a clear spatial (along the  
489 salinity gradient) and temporal (before and after Port2000) segregation, indicating that  
490 marinisation modified the ecological structure of communities. This is also supported by the  
491 higher ELFI values in the Seine estuary after Port2000 which is likely a consequence of the  
492 marinisation enhancing the taxonomic richness and biomass of fish in the estuarine spatial  
493 boxes. The same trend has already been observed in the Gironde estuary where changes in fish

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1419 494 assemblages and an increase of the ELFI index were attributed to an increase in temperature  
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1421 495 and salinity indicating marinisation (Pasquaud *et al.* 2012; Chevillot *et al.*, 2016, 2017).  
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1426 497 *4.3. Signs of anthropogenic impacts*

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1428 498 *4.3.1. The global estuary*

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1430 499 In the Seine estuary, the ELFI indicator increases with ecosystem quality (Le Pape *et al.*,  
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1432 500 2015). The ecological status of the Seine estuary therefore improved from a ‘bad’ status before  
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1434 501 Port2000 to a ‘poor’ status after Port2000. Diadromous species abundance was associated to  
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1436 502 habitat connectivity, as opposed to habitat fragmentation (barriers to migratory fish) (Pasquaud  
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1438 503 *et al.*, 2013). After Port2000, the highest DDIA value recorded was 0.88 in 2006 and then the  
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1440 504 general pattern of this metric for that period was characterized by an overall decrease of DDIA,  
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1442 505 with values dropping down to 0.71 in 2012, likely due to a lower connectivity for migrant  
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1444 506 species such as eel *Anguilla anguilla* or grey mullet *Liza ramada*, associated with the extension  
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1446 507 of the breakwaters between FN and CH during the Port2000 construction. As an example, smelt  
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1448 508 *O. eperlanus* is a diadromous species which was formerly abundant in the upper part of the  
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1450 509 northern channel for reproduction (Morin *et al.*, 2015). Extending the breakwaters between FN  
1451  
1452 510 and CH during the Port2000 construction might have impacted the connectivity between these  
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1454 511 two zones, and *O. eperlanus* has been negatively affected by this rupture of connectivity.  
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1456 512 Moreover, it seemed that the differences in fish assemblages between the spatial boxes widened  
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1458 513 ( $\beta$ -diversity increased from 1.65 to 1.73), which might be related to availability of new habitats  
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1460 514 for marine species inside the estuary. Concerning benthic species, the diversity trend between  
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1462 515 spatial boxes showed the reverse trend, showing signs of standardisation ( $\beta$ -diversity decreased  
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1464 516 from 2.97 to 1.99).  
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1470 518 *4.3.2. Estuarine disturbed boxes*  
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1478 519 Comparatively to the rest of the estuary, strong effects of perturbations were expected in the  
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1480 520 navigation channel (CH) because of the continuous dredging and the high hydrodynamics. The  
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1482 521 estuarine box FN was the spatial box the most directly affected by the construction of Port2000  
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1484 522 and by the mitigation measures such as the artificial formation of meanders, which might have  
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1486 523 modified the hydrodynamics (Cuvilliez *et al.*, 2015). In addition, an increase in water turbidity  
1487  
1488 524 was noted in this box (S. Lesourd, personal communication).

1490  
1491 525 The increase in detritivory/herbivory ratio (D/H) observed in both CH and FN between the  
1492  
1493 526 two periods suggests an ecosystem more stressed after the Port2000 construction (Niquil *et al.*,  
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1495 527 2014), probably reacting to perturbations by enhancing opportunistic behaviours such as  
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1497 528 detritivory. The higher carbon recycling (FCI) observed after Port2000 in these two estuarine  
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1499 529 spatial boxes can also be a sign of increasing stress (Vasconcellos *et al.*, 1997). However,  
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1501 530 increasing FCI and D/H values could also be interpreted by a sign of increasing maturity  
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1503 531 (Odum, 1969; Christensen, 1995; Allesina and Ulanowicz, 2004; Vasconcelos *et al.*, 2007) but  
1504  
1505 532 other ENA indices support the statement of increasing stress. Indeed, the relative redundancy  
1506  
1507 533 (R/DC) significantly increased across periods in CH and FN, highlighting the fact that the  
1508  
1509 534 system was enduring a higher level of stress (Hirata & Ulanowicz, 1984; Bondavalli *et al.*,  
1510  
1511 535 2000) but was also more able to resist to disturbances as the energy transfers could be  
1512  
1513 536 maintained through the trophic network via other pathways (Ulanowicz, 1997; Rybarczyk &  
1514  
1515 537 Elkaïm, 2003).

#### 1518 538 1519 1520 1521 539 *4.3.3. Estuarine reference box*

1522  
1523 540 The FS, which was initially considered as the least varying spatial box (Tecchio *et al.*, 2015)  
1524  
1525 541 and thus a reference, showed a reduction in redundancy (R/DC), omnivory (SOI) and detritivory  
1526  
1527 542 (D/H), while maintaining a stable system activity (T..) and carbon recycling (FCI). The trophic  
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1529 543 specialisation was evidenced by the congruent reduction in omnivory (leading to a more chain-

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544 like structure of the food web) and redundancy (reduction of parallel pathways), which can be  
545 a sign of maturity. Results for FS therefore suggested that the reduced disturbance conditions  
546 here favoured an expected ecological succession.

4.3.4. *Intermediate box*

549 E4 is the transitional area between the inner estuary and the marine environment. Results  
550 from ENA indices show an increase in system activity (T..), redundancy (R/DC), carbon cycling  
551 (FCI), omnivory (SOI) and detritivory (D/H). Therefore, as for CH and FN, following the same  
552 interpretation framework, we could assume that the system in E4 was increasing its stabilizing  
553 mechanisms when facing stronger disturbances.

4.3.5. *Marine boxes*

556 Results from ENA indices show no significant differences between the two periods for both  
557 spatial boxes E14 and E2. Therefore, we can assume that the construction of Port2000 has no  
558 negative effect on the food web dynamics of these two marine boxes. However, the spatial box  
559 E2 contains the dumping site of Octeville for dredged sediments from the Le Havre harbour  
560 (Marmin *et al.*, 2014). For these two spatial boxes, we noticed that the fish taxonomic richness  
561 decreased whereas the benthic macrofauna richness increased. The relative importance of  
562 benthic communities had intensified in E2, as shown by the decrease in the  
563 BFish/BMacrozoobenthos ratio between both periods, contrary to what was noticed in E14.  
564 This might be explained by a potential increasing turbidity in E2 due to the dumping of  
565 sediments that could affect fish more than the benthic communities. However, the effect of the  
566 Port2000 construction on these two marine boxes cannot be evidenced.

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568 4.4. Relative effects of marinisation and port construction

569 4.4.1. The global estuary

570 The higher taxonomic diversity and ELFI index values observed after Port2000 in a context  
571 of marinisation suggest a decrease of ecosystem stress after Port2000, as taxonomic richness is  
572 considered a key factor in ecosystem stability in response to anthropogenic pressures (e.g.  
573 McCann, 2000; Chapin *et al.*, 2000). However, investigations in the different spatial boxes were  
574 necessary to detect potential effects of the Port2000 construction.

576 4.4.1. Estuarine disturbed boxes

577 The food web in CH is continuously disturbed due to the dredging activity, greatly limiting  
578 the colonisation of the seafloor by benthic organisms, as seen in other locations (e.g. in the  
579 Venice lagoon: Pranovi *et al.*, 2003). In CH, the community was characterized by an extremely  
580 low benthos richness and biomass compared to the other spatial boxes. Nonetheless,  
581 communities subjected to regular disturbances are also more adapted, less sensitive, and recover  
582 more quickly than undisturbed communities (Dernie *et al.*, 2003; Marmin *et al.*, 2014). Results  
583 from ENA indices in the two boxes CH and FN suggest an ecosystem more stressed after the  
584 Port2000 construction. Species-based indices were very useful to detect the effects of dredging  
585 activities which directly affect the settlement of benthic communities. This effect was also  
586 reflected in the ENA indices.

588 4.4.2. Estuarine reference box

589 In FS, both fish and macrozoobenthos taxonomic richness increased. However, the ratio  
590 B<sub>Fish</sub>/B<sub>Macrozoobenthos</sub> remained stable. The MDS analysis showed that the fish  
591 composition in this spatial box did not deeply change between periods. ENA indices suggest a  
592 mature system for FS for both periods. Therefore, this estuarine spatial box could be confirmed

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593 as the least stressed area of the Seine estuary, as previously assessed by Tecchio *et al.* (2016),  
594 and that species-based indicators, ELFI and ENA indices bring similar information for this  
595 spatial box.

596  
597 *4.4.3. Intermediate box*

598 We assumed that E4 should exhibit the highest taxonomic richness and biomasses given its  
599 intermediate position between marine and estuarine waters (Dauvin & Desroy, 2005). It had the  
600 highest fish and benthic macrofauna taxonomic richness of all spatial boxes. Similar results  
601 were found by Martino and Able (2003), who showed that in the Mullica river-Great Bay  
602 (USA), fish species richness increased from the marine stations to the ones at the mouth of the  
603 estuary, and then strongly decreased towards the estuarine sampling stations. The MDS analysis  
604 put forward that E4 could be seen as an intermediate spatial box for fish, but as a marine box  
605 for the macrobenthos community. Indeed, this confirmed that E4 itself can be considered as an  
606 ‘ecocline’, i.e. a boundary of progressive changes (spatial and ecological) between two different  
607 systems, the ocean and the estuary (Attrill and Rundle, 2002; Basset *et al.*, 2013). Finally,  
608 results from ENA indices demonstrated an increase in system activity, redundancy, cycling,  
609 omnivory and detritivory between the two periods. Therefore, as for CH and FN, ENA indices  
610 enabled us to identify that the system was increasing its stabilizing mechanisms, probably to  
611 face stronger disturbances.

612  
613 *4.4.4. Marine boxes*

614 Finally, in the bay, E14 and E2 marine boxes appeared similar in terms of fish and  
615 macrozoobenthos taxonomic composition between the two periods. Results from ENA indices  
616 show no significant differences between the two periods for both spatial boxes. Indices based

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617 on diversity and biomasses showed the importance of benthic communities has intensified in  
618 E2 but the origin of this change remains unknown.

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620 *4.4.5. Summary*

621 The estuarine marinisation effects are potentially stronger than the effects of the Port2000  
622 construction. Indeed, on the one hand, the marinisation of the Seine estuary mostly changed the  
623 species assemblages, therefore affecting the ecosystem structure (i.e. biological and physical  
624 architecture of an ecosystem), due to the arrival of numerous marine species. On the other hand,  
625 the anthropogenic pressures affected habitat connectivity and food-web dynamics (i.e. transfer  
626 of energy from one part of the food web to another, Lindeman, 1942), assessed with ENA  
627 indicators such as system activity, omnivory, recycling or detritivory. The main information  
628 brought by the combination of indices was summarized in Table 3.

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**Table 3.** Main information about the functioning and the status of the six spatial boxes.

Method	Main results	Conclusions
Biotic indices based on diversity and biomasses => <b>give information about the structure of communities</b>	Increase of the taxonomic richness between periods for the estuarine spatial boxes (CH, FN, FS) and the biomass of fish and macrozoobenthos increased	<b>Arrival of marine species</b> such as <i>P. minutus</i> in relation to the marination of the estuary (lower river discharge in the second period)
	CH: low values of macrozoobenthos richness	Low benthos biomass due to dredging and high hydrodynamics in this part of the estuary
	E4: the richest area for both periods	This corresponds to the rich <i>Abra alba-Lagis koreni</i> macrobenthic community and the feeding zone for fish (mainly flatfish).
	The MDS ordination showed a spatial segregation between CH and the other zones, and a temporal change between periods, both for fish and macrozoobenthos	<b>Evolution in salinity plays a determinant role in the spatial gradient of the fauna; both periods were clearly distinguished</b>
Biotic indices based on the classification of species in trophic groups => <b>give information about the functioning of the food web</b>	FN: higher carbon recycling and detritivory (increase in detritus input) + higher redundancy (more species)	<b>Stress increased in the estuary mainly for CH and FN zones. The other zones were less disturbed.</b>
	CH: increase in system activity, carbon cycling, ascendancy, redundancy and detritivory	
Biotic index based on the classification of species in ecological groups => <b>give information about the health status of ecosystems</b>	FS: still in 'high ecological status'	Reference box
	Increase in ELFI values between periods	The ecological status was supposed to have improved but it is likely due to the arrival of marine species only
	Decrease of the metric DDIA (diadromous species) in the second period, indicator of a lower habitat connectivity	<b>Lower connectivity due to the extension of the breakwaters</b> between FN and CH during the Port2000 construction

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ELFI was sensitive to the arrival of marine species and therefore was highly relevant in a context of marination of the estuary. ENA indices appeared as good 'surveillance indicators', that Shephard *et al.* (2015) proposed as indicators that would be a good complement to operational indicators, for example in the context of the Marine Strategy Framework Directive application. ENA indices are also useful to take ecosystem-based management measures for



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1832 640 such ecosystems (de la Vega *et al.*, 2018; Safi *et al.*, 2019). In addition, their association with  
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1834 641 biodiversity indicators made the analysis more robust as suggested by Rombouts *et al.* (2013).  
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1836 642 For instance, the arrival of new species and the higher biomasses observed in some spatial boxes  
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1839 643 between periods can also explain increases in some ENA indicators such as system activity,  
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1841 644 omnivory or redundancy but this cannot be evidenced and requires further investigations.  
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## 1843 645

### 1844 646 **5. Conclusions**

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1849 648 The effects of the Port2000 construction were not as evident as expected due to the presence  
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1851 649 of other natural (e.g. marinisation) and anthropogenic (e.g. continuous harbour activities)  
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1853 650 perturbations, which makes the interpretation of ecological indicators difficult. ELFI was  
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1855 651 particularly relevant in a context of marinisation, as this index is sensitive to the arrival of new  
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1857 652 marine species. But the different metrics used to calculate ELFI are also indicative of  
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1859 653 anthropogenic impacts (e.g. DDIA and habitat connectivity affected by the construction of  
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1861 654 Port2000), making ELFI a very powerful tool to assess the health status of this estuary. The use  
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1863 655 of ENA indices alone was not sufficient to describe changes in ecosystem functioning between  
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1865 656 the two periods, distinguishing the effects of the Port2000 construction and the process of  
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1867 657 marinisation, but they appeared as an interesting complementary set of tools for characterising  
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1869 658 the evolution of food-web dynamics. Indeed, ENA indices allowed us to observe changes that  
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1871 659 occurred in specific ecosystem processes and to identify how an ecosystem becomes more  
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1873 660 stable (e.g. by increasing omnivory) under increasing stress. We showed that detecting changes  
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1875 661 related to anthropogenic disturbances alone in the Seine requires using ecological indicators at  
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1877 662 different levels (species, communities and ecosystem) and at multiple scales of observations.  
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1879 663 This work emphasizes the need to use several metrics to assess ecosystem health status and to  
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1881 664 continue long-term monitoring of such complex and reactive ecosystems.  
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937 **Figure legends**

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**Fig. 1.** Map showing the geographical position of the Seine estuary in France. The spatial boxes are composed of the navigation channel (CH), the northern channel (FN), and the southern channel (FS) as estuary boxes; an intermediate box located at the mouth of the estuary (E4), and two marine boxes (E2 and E14). Source: GIP Seine-Aval and SHOM.

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**Fig. 2.** Barplots representing fish biomass, macrozoobenthos biomass, the sum of fish and macrozoobenthos biomasses, and the ratio B<sub>Fish</sub>/B<sub>Macrozoobenthos</sub>, for all spatial boxes before the construction of Port2000 (first bars) and after (second bars). The spatial boxes are composed of the navigation channel (CH), the northern channel (FN), and the southern channel (FS) as estuary boxes; an intermediate box located at the mouth of the estuary (E4), and two marine boxes (E2 and E14).

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**Fig. 3.** Barplots representing taxonomic richness divided by the log-transformed total number of samples realised within the six spatial boxes before (first bars) and after (second bars) the construction of Port2000 for fish and macrozoobenthos. The spatial boxes are composed of the navigation channel (CH), the northern channel (FN), and the southern channel (FS) as estuary boxes; an intermediate box located at the mouth of the estuary (E4), and two marine boxes (E2 and E14).

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**Fig. 4.** MDS ordination based on Bray-Curtis similarity matrices from biomass data (square-root transformed) for fish (on the upper part) and for macrozoobenthos (on the lower part), for all spatial boxes during the first (first bars), before Port2000, and the recent (second bars) periods.

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**Fig. 5.** ELFI values for the whole estuary for 10 years, between 1995 and 2012, with the class boundaries of the Water Framework Directive.

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**Fig. 6.** Ecological network analysis (ENA) indices for all spatial boxes for the period before (first bars) and after (second bars) Port2000. The spatial boxes are composed of the navigation channel (CH), the northern channel (FN), and the southern channel (FS) as estuary boxes; an intermediate box located at the mouth of the estuary (E4), and two marine boxes (E2 and E14). Means and standard deviations are represented. Asterisks represent significant changes assessed from Cliff's delta statistics (level 0.05; between before and after construction).

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2658 **Appendices**  
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2660 **Appendix A.** Data sources used in the calculation of ELFI index  
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<b>Indicator</b>	<b>Before Port2000</b>	<b>After Port2000</b>	<b>Boundary classes</b>
	Biomasses from		
	Ifremer and CSLN.	Index values from	
ELFI	Use of an R script	Agence de l'Eau Seine-	Delpech et al., 2010
index	provided by Mario	Normandie	
	Lepage (Irstea, UR		
	EABX)		

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2684 Fish data ‘After Port2000’ are standardized data from surveys designed for ELFI calculation  
2685 following normalized protocol. Fish data used for ELFI calculation ‘Before Port2000’ were  
2686 obtained using similar sampling gear (beam trawls with similar net features), accounting for  
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2690 sampling effort (trawled surface area) and considering a relevant spatial design regarding WFD  
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2692 fish sampling protocol (> 6 tows by haline zone)  
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**Appendix B.** Range values between the five ‘Ecological Quality Status’ levels considered for the ELFI indicator (Delpech et al., 2010). Five levels of EQS classified as ‘high’, ‘good’, ‘moderate’, ‘poor’, and ‘bad’ were used. ‘High status’ means very low human pressure. ‘Good status’ means a ‘slight’ deviation from this condition, ‘moderate status’ means moderate deviation, ‘poor status’ means high deviation and ‘bad status’ means very high human pressure.

Range values for	
EQS level	ELFI
High	$0.90 \leq \text{ELFI} \leq 1.00$
Good	$0.68 \leq \text{ELFI} < 0.90$
Moderate	$0.45 \leq \text{ELFI} < 0.68$
Poor	$0.23 \leq \text{ELFI} < 0.45$
Bad	$0.00 \leq \text{ELFI} < 0.23$



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**Appendix C. Data sources used in the calculation of the different indicators**

<b>Group</b>	<b>Compartment</b>	<b>Biomass data</b>	<b>Biodiversity indicators</b>	<b>ENA indices</b>	<b>ELFI</b>
1	Seabirds	-		X	
2	Fish, piscivores	Ifremer, CSLN, Le Havre port authority sampling	X	X	X
3	Fish, planktivores	programs (Liteau, Port2000, Grand Canal,	X	X	X
4	Fish, benthos feeders	COLMATAGE 2008-2009-2010), and GIP Seine-Aval	X	X	X
5	Benthic predators		X	X	
6	Benthic filter feeders	PECTOW, BENTHOSEINE, and COLMATAGE projects, Le Havre port authority, and GIP Seine-Aval	X	X	
7	Benthic deposit feeders		X	X	
8	Suprabenthos	National Natural History Museum Paris, Wimereux marine station, Caen University, Le Havre port authority, and GIP Seine-Aval sampling programs		X	
9	Zooplankton	From Rybarczyk and Elkaïm (2003)		X	
10	Meiofauna	Le Guellec and Bodin (1992); Ratsimbazafy, (1998); Spilmont <i>et al.</i> (2005)		X	
11	Bacteria	Chardy (1987); Chardy and Dauvin (1992)		X	
12	Microphytobenthos	Spilmont <i>et al.</i> (2005), Napoleon <i>et al.</i> (2012)		X	
13	Phytoplankton	SURVAL database ( <a href="http://envlit.ifremer.fr/resultats/surval">http://envlit.ifremer.fr/resultats/surval</a> )		X	
14	Detritus	Seine-Aval sampling program		X	

**Appendix D.** Biomasses entered in LIM-MCMC models for all trophic compartments and for both periods, before (1996-2002) and after (2005-2012) Port2000 construction. The values of biomass are mean over the years. Data sources are presented in Appendix A. More information can be found in Tecchio et al. 2016. For the spatial boxes, see Fig.1.

	Trophic compartments		Period	Biomass (gC m <sup>-2</sup> y <sup>-1</sup> )					
				CH	FN	FS	E4	E14	E2
1	<b>OIS</b>	Seabirds	1996-2002						
			2005-2012						
2	<b>FPI</b>	Fish, piscivorous	1996-2002	0.019	0.060	0.057	0.143	0.103	0.264
			2005-2012	0.044	0.048	0.055	0.061	0.543	0.004
3	<b>FPV</b>	Fish, planktivorous	1996-2002	0.040	0.037	0.025	0.043	0.026	0.016
			2005-2012	0.012	0.027	0.028	0.047	0.013	0.004
4	<b>FBF</b>	Fish, benthos feeders	1996-2002	0.003	0.005	0.230	0.560	0.244	0.554
			2005-2012	0.088	0.327	0.252	0.307	0.387	0.358
5	<b>IPR</b>	Invertebrates, predators	1996-2002	0.163	17.15	9.830	1.000	2.590	0.981
			2005-2012	1.118	26.88	41.65	1.109	14.69	2.817
6	<b>IFF</b>	Invertebrates, filter feeders	1996-2002	0.442	1.897	22.32	3.08	3.81	12.71
			2005-2012	1.963	4.340	5.262	9.425	3.123	10.82
7	<b>IDF</b>	Invertebrates, deposit feeders	1996-2002	0.052	1.587	3.140	6.134	6.134	4.255
			2005-2012	1.420	1.466	0.865	7.200	3.705	5.923
8	<b>SUP</b>	Suprabenthos	1996-2002	2.208	2.030	2.010	0.101	0.101	0.101
			2005-2012	0.542	0.960	0.930	0.020	0.020	0.020
9	<b>ZOO</b>	Zooplankton	1996-2002						
			2005-2012						
10	<b>NEM</b>	Meiofauna	1996-2002	0.427	0.119	0.119	0.377	0.402	0.167
			2005-2012	0.427	0.119	0.119	0.377	0.402	0.167
11	<b>BAC</b>	Bacteria	1996-2002						
			2005-2012						
12	<b>MPB</b>	Microphytobenthos	1996-2002	0.050	1.725	1.720	0.300	0.350	0.380
			2005-2012	0.050	1.725	1.720	0.300	0.350	0.380
13	<b>PHY</b>	Phytoplankton	1996-2002						
			2005-2012						