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Evaluating ecosystem-level anthropogenic impacts in a stressed transitional environment: The case of the Seine estuary

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Abstract :

During 2002–2005, a new container terminal in the commercial harbour of Le Havre, named “Port2000”, was built on the northern flank of the Seine estuary, northern France. This extension is already known to have modified the estuary current and sediment dynamics, as well as reducing biomass of the suprabenthos assemblage, for the whole downstream part of the system. However, studies on other biotic communities were largely inconclusive, and an ecosystem-wide analysis was still lacking. Here, we performed a before/after study of ecosystem dynamics of the different habitats of the Seine estuary, using a Linear Inverse Modelling technique (LIM-MCMC) to estimate all flows occurring in the food web. Ecological Network Analysis indices were calculated, summarising ecosystem functioning traits and giving indications about the habitat health status. Results showed that the southern flank (FS, Fosse Sud) exhibits all characteristics to be considered as the least stressed habitat of the estuary: system activity and functional specialisation of flows were stable between periods, ecosystem recycling processes and detrital dynamics were also stable; an increase in trophic specialisation (decrease in system omnivory) was the only change confirming a general ecological succession. The northern flank (FN, Fosse Nord), where the actual terminal was built, showed a food web with increased importance of lower trophic levels (increased detritivory and carbon recycling), increased stability and flow efficiency, but possibly regressed to a previous step in ecological succession. In the central navigation channel (CH), patterns of network indices were overall inconclusive and the general image is one of a constantly shifting food web, a condition possibly caused by the year-round dredging activities. The functioning of

the Seine estuary – especially of FN and FS – seems to have been modified by the combination of harbour construction and the related mitigation measures. Network indices partially captured this combination of changes and, although not fully operational yet, they are promising tools to comply with the European Union mandate of defining ecosystem health status.

Highlights

► Six food web models of the Seine estuary, before and after harbour extension works. ► Ecological network analysis indices showed regression of stability in affected area. ► Other least affected habitat showed specialisation and normal ecological succession. ► ENA for ecosystem health indication is progressing towards operability.

Keywords : Linear inverse model, Estuarine ecosystem, Seine estuary, English Channel

1. Introduction

Anthropogenic disturbances are exerting a stronger and stronger pressure on marine and freshwater ecosystems (Halpern et al. 2008). These pressures, which include fishing, dredging, mining, organic and metallic contamination, among others, are known to modify the general ecosystem structure and functioning (De Lange et al. 2010). Estuarine environments are particularly responsive to these pressures, because they host communities with high productivity and, at the same time, a relatively low biodiversity compared to coastal ecosystems (McLusky & Elliott 2004). This means that, while they are of primary importance as providers of ecosystem services to humans, their capacity of resisting external stressors has not been completely clarified yet.

The Seine estuary is a transitional water system in northern France (Meybeck et al. 1998) that is commonly brought as an example of a productive habitat highly modified by human activities (Dauvin & Desroy 2005). Previous results of food web modelling studies in the downstream part of the estuary were provided by Rybarczyk and Elkaïm (2003) who identified an ecosystem still under ecological succession; the final point being a mature ecosystem. The different habitats of the Seine estuary and the adjacent Seine Bay were also the subject of a complementary and more recent food web modelling study, which considered the period 1996–2002 before the extension of the existing commercial harbour had started (Tecchio et al. 2015). Among its core conclusions, the estuary was not seen as a unitary system but rather described as a network of habitats each with its own internal emergent properties. This structure highlights the joint utility of the ecosystem approach in definition of ecological status and the consideration of explicit spatial subdivisions for impact assessment.

The Port2000 works were the extension of the existing commercial harbour of Le Havre, constructed in 2002–2005, with the purpose of optimising its access and expanding the available estate for container ships. The construction was performed including a series of mitigation measures and accessory works: (a) dredging in the northern flank to improve water recirculation, (b) the

72 opening of a direct connection from the central navigation channel to the northern flank upstream
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273 the Normandy bridge to rebuild meanders, (c) the prolongation of the northern breakwater by 750
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474 m, and (d) the creation of a small artificial island in the southern flank to improve habitat
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775 heterogeneity for sea birds. All these works thus took into consideration the overall current outflows
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976 and generally improved circulation of water in the estuary. Despite these positive outcomes,
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1277 previous studies assessed a negative effect of Port2000 on the suprabenthos (mostly crustaceans, i.e.
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1478 decapods and peracarids that perform daily vertical migrations being in the benthos during the day
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1779 and in the water column at night), especially on the diversity and density of the dominant species
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1980 ([Dauvin et al. 2010](#)). Sedimentary changes were also identified in the area, especially at the
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2281 interface between the estuary and the Seine Bay ([Dauvin et al. 2006](#)), but these alone are not
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2482 conclusive to indicate changes on the overarching processes of the ecosystem.
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2783 Ecological network analysis (ENA) combines the calculation of a set of indices that joins
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3084 concepts from ecology, network geometry, and information theory to describe the functioning of a
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3285 food web. ENA has become a powerful toolbox for ecological and management studies, and it has
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3586 been proposed as a base for determining the “good ecological status” according to European Union
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3787 policies ([Dame & Christian 2007](#), [Niquil et al. 2012](#), [Niquil et al. 2014b](#)). For ENA to be applied, a
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4088 knowledge of the values of energy flows between all trophic compartments is required, including
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4289 external inputs into the ecosystem, exports to neighbouring habitats, and dissipative flows such as
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4490 respiration. To obtain an estimation of flow values, ecosystem-level linear inverse modelling (LIM)
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4791 can be used: a method to obtain values of all unknown flows starting from a reduced number of
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4992 known system parameters and local and global constraints on eco-physiological processes ([Vézina](#)
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5293 [& Platt 1988](#), [Niquil et al. 2011](#)). Various approaches can be used to reach the objective of assessing
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5494 the changes in the Seine estuary functional properties in relation to Port2000 construction; the
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5795 successful approach for such a before/after impact study should however be one that provides not
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5996 only a single estimated value for each flow – by itself statistically untestable – but also its
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6297 associated uncertainty ([Kones et al. 2009](#), [Chaalali et al. 2015](#)).
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98 The levels of both anthropogenic and natural stress of aquatic ecosystems can be partially
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299 captured by ENA indices, although a general theory encompassing their different interpretations is
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100 still in progress (Saint-Béat et al. 2015). The stability of an estuarine food web – and by extension
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101 of its ecosystem – is its capacity of maintaining comparable levels of functioning, i.e. its provision
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102 of services to human populations which include, among many others, fishing resources,
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103 contaminant turnover, and participation in global biogeochemical cycles (Ulanowicz 2003, Lobry et
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104 al. 2008). Disturbance effects in estuarine biodiversity and food webs are known to influence
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105 ecosystem structure and functioning at various levels and might include, among others, an increase
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106 in total system activity (Baeta et al. 2011), increase in recycling rates (Odum 1985), and reduction
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107 in trophic flows specialisation which will be reflected in a higher system omnivory (Fagan 1997).
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2508 The main objective of this study was to perform a before/after evaluation of the impacts related
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2809 to the construction of Port2000 on the Seine estuary functioning, based on the different
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3100 anthropogenic pressures at play in the three main spatial estuarine habitats (northern, central, and
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3301 southern). We have used linear inverse modelling to obtain estimations of ecosystem flows in the
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3602 three habitats, and subsequently implemented the related network analysis.
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4114 2. Materials and methods

445 2.1. Study area

4816 The Seine estuary in northern France is a system heavily influenced by tides (almost 8 m at
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5117 spring tide at the estuary mouth), with the presence of a strong maximum turbidity zone compared
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538 to other macrotidal estuaries (Le Hir et al. 2001). Over the past century, water pollution levels –
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5619 among the highest in the continent – and frequent hypoxic events have increased management
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5820 concerns; furthermore, the fisheries operating in the marine part of the estuary have nowadays
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6021 collapsed (Dauvin 2008). Nevertheless, the estuary remains a nursery area for several species,
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122 especially for flatfish (Riou et al. 2001). Over the last 30 years, the Seine River has undergone
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123 fluctuations in its outflow, with a period of high variability before the Port2000 construction and a
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124 more stable period after Port2000 characterised by low outflow (Dauvin & Pezy 2013). In addition,
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125 the Port2000 construction brought changes to the structural aspects of the Seine estuary and,
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126 therefore, to the overall water circulation. The main construction consisted in closing out an area of
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127 approximately 5 km² adjacent to the older part of the harbour, in the northern flank (20% of its
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128 initial surface). An opening was created on the estuarine side to improve river flow into the FN.
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129 This measure has been favouring the formation of two new meanders and a general increase in
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130 intertidal surface. Water circulation was significantly increased; however, according to the latest
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131 observations in 2014, the new intertidal zone remains still poor in faunal abundance (CSLN Le
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132 Havre, unpublished data). The central navigation channel was further dredged and deepened to
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133 increase water flow, and it is still subject to continuous dredging to improve access to Rouen,
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134 another maritime port 120 km upstream. The southern flank, on the other hand, has been the least
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135 reworked area, with the only addition of an artificial island built as seabirds reserve, and it remains
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136 better separated from the central channel than the northern flank.

37 The marine part of the Seine estuary was split into three spatial boxes that were modelled
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138 separately, following previous assessments, and considered “habitats” as homogenous zones from
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139 the hydro-sedimentary and salinity points of view (Tecchio et al. 2015). These habitats were: (1) the
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140 central navigation channel (CH) upstream to the Tancarville bridge, separated from the flanks by
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141 breakwaters submerged at low tide, (2) the northern flank (FN) which includes the harbour of Le
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142 Havre and hosting the north intertidal flat, and (3) the southern flank (FS) shielded from the central
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143 channel current and hosting a large intertidal flat (Figure 1). The sediment composition of the two
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144 flanks is a combination of sandy and muddy bottoms. The central channel is dredged year-round
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145 and it is mainly composed by sandy bottoms with sparse rocks. Thus, the study spatial extent covers
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146 an area continuously under sediment resuspension and direct organic matter inflow from the Seine
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147 River (CH), one area subject to extensive anthropogenic impacts (FN), and a third area (FS) with
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148 the least influence of human building works. We therefore considered the southern flank as the
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149 habitat that was least modified between the two periods (before/after Port2000), thus serving as a
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150 partial reference.
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151 For each of the three habitats, two food-web models were constructed using data from two
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152 different periods: 1996–2002, representing the situation before the Port2000 construction, and
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153 2005–2012, representing the present situation. Each model represents an average year, using
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154 averaged biomass of functional compartments from all available years in its corresponding period.
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18 2.2. Linear inverse modelling 19

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22 The estimation of energy flows between trophic compartments was performed with the *LIM*
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24 package for the R statistical programming framework (Van den Meersche et al. 2009, Van Oevelen
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26 et al. 2010). This approach reads a text declaration file for each model to set up and generates
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28 numerical matrices which define equalities (i.e. known flows) and inequalities (i.e. constraints) for
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30 the flows. It also automatically ensures that all flows take positive values, and establishes mass
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32 balances for all living and detritus compartments.
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37 Each food web was composed of 15 internal trophic groups and 3 external compartments, i.e.
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39 inorganic carbon for photosynthesis, river input, and the respiration sink (Figure 2). Eighty-five (85)
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41 flows were described between these components. Each living compartment was linked with
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43 consumption flows (as input), excretion/mortality (output to detritus), respiration (exported outside
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45 the model), and production flows (predated by other compartments). The constraints on these flows,
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47 i.e. their minimum and maximum limits, were established using rates drawn from literature, from
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49 other modelling works (whenever their results were generalizable), or from local detailed studies for
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51 diet constraints (Table 1). Biomasses (Table 2) were taken from the same database as the previously
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53 performed modelling work (Tecchio et al. 2015): benthos and fish data came from a combination of
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55 Ifremer, CSLN, Le Havre Port Authority, GIP Seine-Aval, Wimereux marine station, and National
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172 Natural History Museum Paris sampling programs, and were standardised as gC m^{-2} using
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173 conversion factors (Brey 2001, Oguz et al. 2008). Where available, biomasses were used to
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174 parameterise the production flows, by multiplying them with a range of production/biomass (P/B)
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175 rates, obtained from literature. Energy balance was defined as
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176 $production (P) = consumption (Q) - excretion (U) - respiration (R)$. Consumption was
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1277 defined as all flows entering a compartment. Excretion, i.e. flow from a living compartment to
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178 detritus, also included natural mortality. Two among the three energy balance ratios (among P/Q,
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179 U/Q, and R/Q), according to availability, were used to constrain flows for each living compartment.
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180 For example, suprabenthos production was set between 10% and 37% of its consumption: $0.10 \cdot$
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21
281 $SUPconsumption < SUPproduction < 0.37 \cdot SUPconsumption$.
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24
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282 Bacterial flow to detritus was considered as the proportion of bacterial production that is shunted by
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283 viruses (Danovaro et al. 2008). For dietary constraints, single-sided inequalities were preferred, e.g.
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284 zooplankton (ZOO) consumption by planktivorous fish (FPV) was set higher than 30% of FPV total
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385 food intake: $ZOO \rightarrow FPV > 0.30 \cdot FPVconsumption$. This was more reflective of the typical
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386 predatory behaviour, allowing an automatic re-balancing of the diet when the biomass entered for a
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387 prey is lower than usual in a given habitat or when the estimated biomass is lower than usual in a
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388 particular solution (Table 3). Gross primary production, defined as the sum of carbon import for
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389 primary producers (i.e. phytoplankton and microphytobenthos), was constrained using minimum
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490 and maximum limits from literature (Videau et al. 1998).
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491 Because this approach includes an inherent uncertainty in data input, the model was considered
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502 balanced simply when there were no incompatible constraints and, therefore, when at least one
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503 solution of flow values was present. This reduces to a minimum the use of arbitrary modifications
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504 of input data, and ensures that the solution found is not near the boundary of the poly-dimensional
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505 space of possible solutions.
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196 After every model was checked to possess at least one solution, we used a Markov-Chain Monte
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197 Carlo (MCMC) procedure to sample 200,000 possible solutions of the flow values from the
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198 polytope of all possible solutions that satisfied the constraints. The starting position for the random
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199 walk algorithm was a parsimonious solution obtained by least-distance programming, i.e.
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200 minimizing the sum of squared unknowns. At each iteration, all flows were modified in a random
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201 direction by a normally-distributed jump length; their new position was then checked to lay inside
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202 the polytope and the flows for which this condition was not met were mirrored back inside the
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203 accepted space (Van den Meersche et al. 2009). When all flows were valid according to the
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204 constraints, the solution was saved and a new iteration commenced. Convergence of results was
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205 checked both by observing if the solution space was fully sampled and by comparing means and
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23
206 standard deviations of flows between increasing quantities of iterations. Each solution was then
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207 represented by a matrix of flows from each “source” compartment to the possible “sinks”, and was
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208 used to calculate ENA indices.
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32 2.3. Ecological network analysis 33 34

35 Ecological network analysis was performed using the R software packages *NetIndices* (Kones et
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37
38 al. 2009) and *enaR* (Borrett & Lau 2014), along with personally-written complementary scripts (S.
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41 Tecchio). The following ENA indices were calculated:
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- 43 • The *Total system throughput* (T..) was expressed as the sum of all flows occurring in the system,
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46 and interpreted as an indicator of system activity (Rutledge et al. 1976, Latham 2006).
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- 48 • The *Detritivory/Herbivory ratio* (D/H) was obtained as the ratio between the sum of all predation
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50 flows on the detritus compartment (*det*) and the sum of all predation flows on primary producers
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52 (*phy* and *mpb*). An increase would indicate a shift to a more detritus-based food web, while a
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54 decrease would suggest an augmented importance of primary producers in trophic interactions
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58 (Ulanowicz 1992).
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- 220 • The *System Omnivory Index* (SOI) was calculated as the weighted mean of the omnivory indices
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 221 of each consumer compartment, using the logarithm of their consumption as weights. It is an
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 222 indicator of the overall dietary adaptation of the consumers, and an increase would generally
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 223 indicate a response to an external pressure (Fagan 1997, Libralato 2008).
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 224 • The *Finn's Cycling Index* (FCI) was calculated as the ratio between flows generated by cycling
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 225 over the total system throughput (Finn 1976, 1980). Although FCI definitions vary, this
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 226 particular one was chosen to increase comparability with another modelling approach, *Ecopath*
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 227 *with Ecosim*, which calculates the index using the same formula. See Guesnet et al. (2015) for
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 228 comparison of ENA indices formulas between ecosystem modelling approaches.
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 229 • The *Average Mutual Information* (AMI) expresses the degree of organisation of exchanges
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 230 between functional groups, with increases indicating augmented specialisation and flow
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 231 constraint (Hirata & Ulanowicz 1984).
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 232 • The *Ascendency* was calculated as $A = AMI \cdot T_{..}$, and it is related to ecosystem growth and
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 233 development (Ulanowicz & Abarca-Arenas 1997). Higher values would mean that the system is
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 234 more active in constraining flows along more specific pathways, while low ascendancies have
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 235 been related to system immaturity (Ortiz & Wolff 2002).
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 236 • The *relative Redundancy* (R/DC) was calculated as the ratio between the internal flow overhead
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 237 and the total development capacity of the ecosystem (Ulanowicz 2001) or, more formally, as:
- $$R/DC = \frac{\sum_{i,j=1}^n T_{ij} \cdot \log\left(\frac{T_{ij}^2}{T_{i.} \cdot T_{.j}}\right)}{\sum_{i=1}^{n+2} \sum_{j=0}^n T_{ij} \cdot \log\frac{T_{ij}}{T_{..}}}$$
- 238 • The diversity of flows (H_r) was calculated as the Shannon-Wiener index of the flow values
 239 matrix and interpreted as both an indicator of redundancy of ecosystem processes and overall
 240 stability of the food web (Rutledge et al. 1976, Ulanowicz & Norden 1990).
 241 • The *Transfer Efficiency* (TE, Lindeman 1942) was obtained by first calculating the mean value
 242 of each flow for each spatial compartment, following the conclusions by Saint-Béat et al. (2013).

243 Then, the web was separated into discrete trophic levels (TL I, II, III, ...) and TE was calculated
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244 as the proportion of outbound flows of a level that throughput into the next. In this case, the
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245 result is not a single value but one TE value for each trophic level, scaled from 0 to 1.
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246 Indices were calculated for each solution of each model, obtaining distributions of 200,000
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247 values each. Differences in the means of ENA indices between habitats and between the 2 periods
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248 of the same habitat (i.e. 1996–2002 and 2005–2012) were first tested by Student's *t-tests*. Due to the
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249 large sample sizes, *t-tests* were finding differences even for tiny effects. Therefore, the non-
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250 parametric effect size statistic introduced by Cliff (1993) was applied to assess a statistical
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251 difference. Given two samples of size n_1 and n_2 , the *Cliff's delta statistic*, also called success rate
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252 difference, is expressed as:
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$$\hat{\delta} = \frac{P(x_{i1} > x_{i2}) - P(x_{i1} < x_{i2})}{n_1 n_2},$$

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253 where x_{i1} and x_{i2} are scores within samples 1 and 2. This statistic estimates the probability that a
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354 randomly selected value in one sample is higher than a randomly selected value in the second
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365 sample minus the reverse probability, i.e. $\delta = P(x_1 > x_2) - P(x_1 < x_2)$. Note that a positive value
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3856 indicates that all values in sample 1 are larger than all values in sample 2. Comparing the degree of
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257 overlapping of the two distributions can detect whether the significant difference is due to an
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4358 effective ecological meaning or to the sample size alone. Significant differences were identified
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259 using thresholds provided by Romano et al. (2006): negligible for $|\hat{\delta}| < 0.147$, small for $|\hat{\delta}| <$
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47
260 0.33, medium for $|\hat{\delta}| < 0.474$, and large otherwise.
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261 Differences in functioning between the two periods were also analysed by single flow values.
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262 We also calculated the percentage of difference in the means of each compartmental throughflow.
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263 The throughflow of a compartment is defined as the higher of its total inflow or outflow (which in
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264 our case were equal due to the models being at steady state). As the differences showed variations
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265 of over 4 orders of magnitude, a log transformation was applied to the percentages.
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3. Results

3.1. Analysis of the flow estimates

The biomasses used to parameterise production flows showed variations between periods. Invertebrate predators increased in all habitats, with the strongest increase in the FS where they increased from 9.83 to 41.65 gC m⁻². Suprabenthos showed an extreme biomass decline in all three habitats, with a 87.2% decrease in the CH and a 90.4% decrease in FN and FS. Invertebrate biomass over the whole estuary was two orders of magnitude higher than fish biomass, in both periods. The exception was in CH where the biomass of fishes changed from 9.43% of invertebrate biomass to 2.82% in the more recent period. Averaging over the three habitats, the ratio between fish and invertebrate biomass (considering only megabenthos as invertebrates) changed from 0.84% before Port2000 to 1.02% after its construction. Finally, meiofauna biomass was left unchanged between periods due to unavailability of data.

In all models, the most important estimated flow of the food web, in terms of magnitude, was the gross primary production of phytoplankton (FIX→PHY), which globally averaged 411.2 ± 55.4 gC m⁻² y⁻¹ (Figures 3 and 4). The other primary production input flow was FIX→MPB and it was estimated at 61.0 ± 28.1 gC m⁻² y⁻¹. Respiration flows, which represented the export from the system, were dominated by bacterial respiration which was 141.4 ± 84.2 gC m⁻² y⁻¹ overall (BAC→RES). The main internal flow matrices (i.e. consumption/predation between living compartments) were dominated by zooplankton ingestion and production flows. The analysis of differences in mean flows and in their standard deviations between periods yielded similar results. In the habitats where an overall increase in flows means was present, so did the overall flows variability. The general pattern for flows standard deviations followed approximately the mean's

289 one, i.e. when mean flow values increased so did the variability, and vice versa. This reflects the
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290 non-normality of flows distributions.
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291 The comparison of compartment throughflows (their total inflow or outflow, a proxy of activity)
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292 between the two periods showed that, in the CH system, activity in the benthos (from IDF to FBF)
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293 strongly increased over the whole food web in the later period (Figure 5). The compartments MPB,
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294 SUP, and FPI, always reduced their overall activity in the more recent period, while ZOO, IPR, and
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295 FBF always increased it. Worth mentioning is suprabenthos group (SUP) which decreased in all
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296 habitats, due to its above mentioned reduction in biomass and, therefore, in its production flows.
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297 Bacterial (BAC) activity also decreased in all spatial compartments in the more recent period. The
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298 rest of the groups had contrasting behaviour between habitats. The northern flank (FN) showed an
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299 increase in detritus feeding, zooplankton activity, and overall benthos dynamics (increase in IFF,
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300 IPR and FBF, with a decrease only in IDF).
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302 3.2. Ecological network analysis 35 36

303 All t-tests performed on ENA indices showed extremely significant differences ($p < 10^{-15}$) except
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304 for the before/after comparison of SOI ($p = 0.10$). Thus, Cliff's delta statistic was used for
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305 interpreting direction and significance of the comparisons (Table 4). We considered medium and
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306 large effect sizes to be indicative of a significant trend.
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307 Comparing the before and after periods, the total system throughput (T..) increased significantly
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308 in the CH and FN, and remained stable in FS (Figure 6 and Table 4). Ascendency increased
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309 significantly in CH and FN, while remaining stable in FS. Relative redundancy was the lowest in
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310 the CH before Port2000; it increased significantly up to the levels of the other two habitats after
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311 Port2000. Relative redundancy significantly increased in the FN and decreased in the FS between
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312 the two periods. The Average Mutual Information (AMI) showed high standard deviations in all
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313 comparisons, with no contrasts being significant. Carbon recycling estimated by FCI increased in
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314 the after period in the three estuarine habitats, especially in CH and FN where contrasts were
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315 significant. The diversity of flows, estimated by H_r , strongly increased from 3.02 to 3.27 in the CH,
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316 remained stable in the FN, and decreased in the FS. System omnivory remained stable in the CH
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317 and decreased in FN and FS, with the FS difference being significant. Finally, the
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318 detritivory/herbivory ratio (D/H) showed significant increases in the CH and FN, and remained
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319 stable in the FS. In CH and FN, this change in D/H was more due to an increase in detritus chain
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320 activity than to a decrease in consumption of primary producers (see again Figure 5).
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Transfer efficiencies by discrete trophic levels showed a more linear pattern after Port2000 construction for both northern and southern flanks (Figure 7). The transfer efficiencies at level I did not show particular differences and are omitted here, as their values were always close to 1. The decreasing pattern of transfer efficiency in FN was segmented before the construction, and it moved to a straighter pattern in the recent period (2005–2012). Transfer efficiency at level II strongly increased in CH after Port2000, while remaining stable in the FS. Furthermore, transfer efficiency at level III always increased after Port2000. In all habitats, trophic level V did not show changes in transfer efficiency between the two periods.

4. Discussion

4.1 Appropriateness of the methodology

The use of separate food web models to analyse the functioning of an estuarine ecosystem has been considered pertinent, even if each spatial box has been defined geographically rather than by a single habitat type (Tecchio et al. 2015). Here, the northern and southern flanks (FN and FS) included both intertidal and subtidal zones. However, the particular topography of the estuary, with these flanks separated from the central navigation channel and thus subject to specific current

337 regimes, means that this approximation is appropriate. Regarding the source data for biomasses, the
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338 variety of samplers used does not guarantee a perfect sampling efficiency *per se*, but field trips were
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339 numerous and distributed across seasons and years, and the same samplers were used between the
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340 two periods. A Pedigree analysis of the source dataset has been performed previously, obtaining
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341 results at the highest range of values reported in literature ([Tecchio et al. 2015](#)).

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1342 The modelling approach applied in this work is not without caveats and aspects that could be
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2045 improved. A step forward might include an improved determination of primary production input,
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2346 which in the present work was characterised in coarse detail. In fact, gross phytoplankton
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2547 production was left estimated by the model and represented as such the necessary carbon input to
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3049 sustain the rest of the food web. For this reason, in the present study, transfer efficiency of level I
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351 and the variety of primary producers were not considered for ecological network analysis. We also
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352 did not take into account the exchange of organic carbon between the different habitats, such as
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353 Compared to the previous models of the different habitats of the Seine estuary ([Rybarczyk &](#)
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4344 [Elkaim 2003](#), [Tecchio et al. 2015](#)), the ones presented here better took into account bacterial flows
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362 Finally, the inferential statistic applied here proved useful to compare ENA results when the
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363 large sample sizes did not allow the application of parametric statistical tests. To our knowledge,
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364 the use of Cliff's delta for ecosystem modelling results is first presented here, and we hope it will be
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365 applied and criticised in future works.
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366 *4.2 Ecosystem functioning between periods*

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367 Ecosystems evolve towards maturity, which is the last state in the process of succession ([Odum](#)
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368 [1969](#)). At maturity, we expect an increase in link connectivity and stability, and an accumulation of
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369 capital of nutrients and biomass which is usually stored at the higher trophic levels ([Gunderson](#)
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374 The construction of Port2000 was not the only changing condition between the two periods.
375 Contrasting rates of river discharge were identified in the Seine, with the more recent period (after
376 Port2000) marked by significantly lower river discharge (caused by the North Atlantic climatic
377 Oscillation) than the first period ([Dauvin & Pezy 2013](#)). This reduced outflow might have shifted
378 the maximum turbidity zone upstream and left the majority of organic matter within the navigation
379 channel (CH), then favouring an increase in system activity especially on the benthic detritivorous
380 compartments. The seasonal and inter-annual fluctuations inside each period were nevertheless too
381 high to conclude that differences in ecosystem functioning before and after Port2000 would be due
382 to multi-annual differences in organic matter input from river discharge. A complete deconvolution
383 of the various external factors operating on the Seine estuary ecosystem will have to be achieved by
384 a combination of other methods of ecosystem modelling, such as time-dynamics and/or spatial
385 approaches, or the use of other sets of biological indicators. For the present work, the differences

386 between periods have been discussed without necessarily linking them directly to the Port2000
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387 construction or to the mitigation measures.
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388 The southern flank (FS) showed a reduction in both primary productivity requirements
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389 (herbivory) and detritivory, overall maintaining a stable system activity and D/H ratio. At the same
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390 time, the trophic flow specialisation increased. This step towards system maturation can be
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391 identified by a reduction of parallel pathways in the food web and of their flow evenness, i.e.
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392 reduced redundancy (Bondavalli et al. 2000), and by a change in system omnivory, as indicating a
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393 web-like structure of the food web. On the same line, according to Ulanowicz and Norden (1990),
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394 redundancy is a component of the overhead which can be seen as a reservoir of energy or possible
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395 “response” to perturbation without dramatic changes in functioning. High values of overhead are
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396 also associated with early ecosystem stages (Ulanowicz 1986). Thus, as the system evolves, it
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397 would become more efficient with a reduction of redundant pathways. Among others, this index has
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398 been proposed as an indicator of system resilience (Heymans et al. 2007). In the present work, the
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399 observed increase in efficiency (loss of redundancy and increase in flow diversity) could indeed be
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400 responsible for a decrease in resilience, which could act as an insurance against perturbation, in
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401 effect an adaptation capacity of the ecosystem. On the other hand, the interpretation of SOI in terms
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402 of ecosystem maturation is not consistent in literature: Odum (1969) postulated an increase in
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403 omnivory with maturation, while it was more recently related with the levels of system stress
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404 (Selleslagh et al. 2012). The transfer efficiency configuration by trophic levels was more linearized
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405 in the more recent period, but it was already showing a natural smooth slope before 2002. Marine
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406 ecosystems stressed by fishing activities show breaks in the decreasing pattern of TE with trophic
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407 level (Coll et al. 2009). In our case, the decrease of SOI should be interpreted as a reduction of
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408 system stress. In all cases, the FS showed all characteristics to be considered the least stressed area
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409 of the estuary, and at the same time, this condition was maintained and reinforced in the later
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410 period. This comforted our initial choice of considering FS as a reference compartment.
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411 The northern flank (FN) is the habitat directly influenced by the construction of Port2000, as it
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412 was subject to several modifications and its overall surface was decreased from 25 to 20 km². The
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413 remediation works helped in the formation of a new intertidal flat and meanders but at the same
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414 time, they modified current dynamics and increased sand input and salinity (Cuvilliez et al. 2009).
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415 The direct observed effect, which was expected, was an increase in carbon recycling (mean FCI
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416 went from 9.6% to 13.9%) and in the D/H ratio (0.589 to 0.775 in average). The food web seems to
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417 have been compressed, increasing importance of lower trophic levels and detritus chain, which are
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418 indeed the levels with the highest contribution to carbon recycling. The improved water flow at the
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419 eastern side of FN might also have increased detritus input in the zone at the same time; however, in
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420 our models the estimation of input flows – both primary production and river input – was left
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421 unconstrained. Thus, it can be considered as the “required input to sustain the food web”, as energy
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422 balances of all living groups were instead constrained.
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What do the FN changes mean in terms of response to stress and disturbance levels in northern temperate estuaries? In another ecosystem modelling study, the efforts undertaken to restore a *Zostera* seagrass bed increased the system activity but at the same time, the ecosystem still showed signs of being stressed (Patrício & Marques 2006, Baeta et al. 2011). This suggests that an ecosystem can be on its way to restoration, but with a functioning not yet completely adapted to the new state. Similarly, changes in FN were probably not due to a natural restoration process – evolving to a more mature stage – but rather to a simple response to change that amplified opportunistic behaviours. In fact, disturbance can intensify the structural reworking of a food web, favouring the formation of parallel energy pathways and, therefore, increasing system redundancy (Bondavalli et al. 2000, Ulanowicz 2001) as the flow structure become more uncertain. As the system is not completely adapted to the new situation, an increase in redundancy as predicted after Port2000 may allow the system to become more flexible and less vulnerable to potential stress generated by this new situation. On the same line, the slight decrease in SOI evidences a system more resistant to pulse perturbations in the more recent period. Lobry et al. (2008) proposed that an

437 estuarine system can be stable even if it is far from maturity, i.e. not at ecological climax. The
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438 construction of Port2000 may have made the system recede to a previous step in ecological
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439 succession, but at the same time increase its stability at that particular system state. In fact, during
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440 reorganisation a system mobilises its biomass “assets”, stored at high trophic levels: this biomass is
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441 converted into flows linked more with the lower trophic levels (Pranovi & Link 2009). This process
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442 has two consequences; it increases recycling and detritivory, and it strengthens the connectivity of
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443 the remaining lower TLs (Rombouts et al. 2013). Transfer efficiency at TL IV in both FN and FS
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444 decreased after Port2000, supporting this possibility along with the straightening pattern of FN
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445 between the two periods.
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446 Considering CH, we remember that ascendancy is calculated as $A = TST \times AMI$ and that
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447 $\frac{A_i}{C} + \frac{R}{C} = 1$, thus all the elements are present to conclude if an increase in system activity is leading
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448 to an increase in system efficiency or just in parallel pathways. The AMI did not change
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449 significantly for any habitat between periods, therefore all changes in ascendancy were due to
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450 changes in total system activity. In CH, ascendancy increased and at the same time, the relative
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451 redundancy also increased. This effectively means that more redundant energy pathways were
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452 formed. Is this a signal that the system went back to a less resilient state? We suggest that the
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453 continuous reworking of the CH zone does not permit stable ecosystem dynamics at benthos level
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454 and consequently, the image that we can retrieve from ENA is one of a constantly shifting food
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455 web. The compartments that most changed their activity in the CH were indeed the benthic ones
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456 (suprabenthos and the 3 benthic groups). In fact, Garcia et al. (2011) found that ecosystem
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457 functioning of the English Channel is particularly sensitive to changes in benthos habitat
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458 characteristics, which in our case were highly variable between periods. Again, Patrício et al. (2004)
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459 showed that this condition of high instability can be found in other human-impacted estuaries. The
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460 pattern from transfer efficiency with a break at TL III is the confirmation that the system was
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461 stressed in 1996–2002, and that it still remains so in the later period.
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462 **4.3 Conclusions**

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463 The use of a simultaneous combination of Ecological Network Analysis indices can increase our
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464 perception of ecosystem evolution, especially regarding the definition of its current position in the
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465 ecological succession, and, therefore, allowing ones to partially infer its ecological status. ENA
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466 indices directly derived from Lindeman (1942) theory (transfer efficiency, D/H ratio) seem
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467 promising tools – although not yet fully operational – to comply with the European Union mandate
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468 of defining ecosystem health status, in accordance with what has been recently found by Niquil et
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469 al. (2014a). In this case, multiple stressors have been operating on each spatial compartment of the
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470 Seine estuary, rendering interpretation of the ENA patterns difficult. This effort is further
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471 compromised by the fact that most ENA indices respond in a non-monotonous way to external
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472 influences. Present results evidenced a combination of changes in the Seine estuary structure and
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473 functioning – especially in its two flanks – between the two periods before and after the
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474 construction of Port2000. However, to better discriminate between the different factors that acted in
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475 the estuary over the same period of time, we argue the inclusion of temporally-varying
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476 hydrodynamics to be considered in the future modelling efforts of the Seine estuary ecosystem.
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650 **Figure legends**

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651 **Figure 1.** Map of the study area in the Seine estuary and its position in northern Europe, with
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652 indication of the three modelled spatial compartments. The same colour coding is used in the
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653 subsequent figures. Also indicated (red line) is the area enclosed in the new Port2000 commercial
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654 harbour extension, which reduced the FN surface from 25 to 20 km².

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655 **Figure 2.** Representation of a generic food-web model of the three spatial compartments of the
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656 Seine Bay, sketched at the start of the modelling effort to establish the identity and direction of
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657 predatory and mortality flows. Respiration flows, present in all living groups, are not explicitly
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658 indicated and are summarised by the RES box. The two external inputs are FIX, for the carbon
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659 fixed by photosynthesis, and POC, for the input from river flow.

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660 **Figure 3.** Estimates of means and standard deviations of flows in the Seine estuary for the period
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661 1996–2002, before Port2000 construction. A log scale is used for the vertical axis.

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662 **Figure 4.** Estimates of means and standard deviations of flows in the Seine estuary for the period
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663 2005–2012, after Port2000 construction. A log scale is used for the vertical axis.

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664 **Figure 5.** Differences in compartment throughflows between before and after construction of
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665 Port2000 harbour, in the three spatial compartments of the Seine estuary. Note that the scales are
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666 log-modulus transformed, and that this percentage analysis does not consider the difference in
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667 absolute values between functional groups. Colours identify detritus (black), primary producers
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668 (green), and consumers (grey) groups.

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669 **Figure 6.** Ecological network analysis indices for all modelled compartments, comparing the before
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670 (first bars) and after (second bars) Port2000 construction periods. Error bars represent standard
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671 deviation. Asterisks indicate comparisons that were considered significant (medium and large
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672 effects) using Cliff's delta. Note the scaling difference in vertical axes.

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673 **Figure 7.** Transfer efficiencies by discrete trophic levels for the mean solution of each of the 6
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674 models, divided by spatial compartment and distinguished between before Port2000 construction
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675 (1996–2002, dashed line and white circles) and after construction (2005–2012, solid line and black
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676 circles).

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Table 1. Coefficients of production (P/B), food conversion efficiency (P/Q), respiration (R/Q), and excretion/mortality (U/Q) for all living compartments included in the models. Note that the whole range is presented here; the actual range for fish and invertebrates used in each model was slightly varied according to species composition and during balancing.

			P/B		P/Q		R/Q		U/Q		Literature
			min	max	min	max	min	max	min	max	
1	OIS	Seabirds	-	-	0.30	0.80	-	-	-	-	Saint-Béat (2012)
2	FPI	Fish, piscivores	0.12	1.20	0.09	0.24	-	-	0.10	0.50	Leguerrier et al. (2004), P/Q and U/Q generated using confidence intervals around standard Ecopath parameters (Christensen & Pauly 1993)
3	FPV	Fish, planktivores	0.48	1.60	0.10	0.30	-	-	0.10	0.50	
4	FBF	Fish, benthos feeders	0.19	3.05	0.11	0.30	-	-	0.10	0.50	
5	IPR	Invertebrates, predators	1.00	5.00	0.05	0.30	-	-	0.12	0.28	Christensen and Pauly (1993), Brey (2001)
6	IFF	Invertebrates, filter feeders	1.00	5.00	0.05	0.30	-	-	0.18	0.42	
7	IDF	Invertebrates, deposit feeders	1.00	5.00	0.05	0.30	-	-	0.18	0.42	
8	SUP	Suprabenthos	0.40	15.00	0.10	0.37	-	-	0.20	0.50	Brey (2001), Lobry et al. (2008), Lassalle et al. (2011)
9	ZOO	Zooplankton	-	-	-	-	0.10	0.30	0.10	0.50	Vézina and Savenkoff (1999), Tortajada et al. (2012)
10	NEM	Meiofauna	10.10	35.00	0.05	0.40	-	-	0.13	0.30	Heip et al. (1990), Van Oevelen et al. (2006)
11	BAC	Bacteria	-	-	0.11	0.60	-	-	0.05	0.35	delGiorgio and Cole (1998), Danovaro et al. (2008), Tortajada et al. (2012)
12	MPB	Microphytobenthos	4.20	30.00	-	-	0.05	0.30	0.05	0.73	Vézina and Platt (1988), Corrales et al. (2015)
13	PHY	Phytoplankton	-	-	-	-	0.05	0.30	0.05	0.50	Vézina and Platt (1988), Vézina and Savenkoff (1999)

Table 2. Biomasses used to constrain the production flows, presented for the 1996–2002 period (upper values) and for the 2005–2012 period (lower values).

			Biomass (gC m⁻²)		
			CH	FN	FS
1	OIS	Seabirds			
2	FPI	Fish, piscivores	0.019	0.060	0.057
3	FPV	Fish, planktivores	0.044	0.054	0.065
4	FBF	Fish, benthos feeders	0.040	0.037	0.025
5	IPR	Invertebrates, predators	0.010	0.026	0.029
6	IFF	Invertebrates, filter feeders	0.003	0.005	0.230
7	IDF	Invertebrates, deposit feeders	0.073	0.312	0.251
8	SUP	Suprabenthos	0.163	17.150	9.830
9	ZOO	Zooplankton	1.118	26.880	41.650
10	NEM	Meiofauna	0.442	1.897	22.320
11	BAC	Bacteria	1.963	4.340	5.262
12	MPB	Microphytobenthos	0.052	1.587	3.140
13	PHY	Phytoplankton	1.420	1.466	0.865
			0.713	1.070	1.070
			0.091	0.103	0.103
			0.427	0.119	0.119
			0.427	0.119	0.119
			0.050	1.725	1.720
			0.050	1.725	1.720

Table 3. Diet constraints for all models, expressed as minimum (upper value) and maximum (lower value) contribution of each prey (rows) in the total consumption of each predator (columns). Values of 0 or 1 mean that the contribution was left unconstrained to the right (if min = 0) or left (if max = 1).

Prey/predator	OIS	FPI	FPV	FBF	IPR	IFF	IDF	SUP	ZOO	NEM	BAC
FPI	0.00 1.00										
FPV	0.00 1.00	0.10 1.00									
FBF		0.11 1.00									
IPR	0.00 1.00	0.00 1.00		0.07 1.00							
IFF	0.00 1.00	0.00 1.00		0.00 1.00	0.10 1.00						
IDF		0.00 1.00	0.00 1.00	0.04 1.00	0.00 1.00						
SUP		0.00 1.00	0.00 1.00	0.05 1.00	0.00 1.00						
ZOO		0.00 1.00	0.30 1.00		0.00 1.00	0.00 1.00	0.00 0.10	0.00 1.00			
NEM			0.00 1.00	0.00 1.00	0.00 0.32	0.00 0.07	0.00 1.00				
BAC						0.00 0.20	0.00 1.00	0.00 0.13		0.00 1.00	
MPB				0.00 1.00	0.00 0.05	0.00 1.00	0.00 1.00	0.00 1.00		0.00 1.00	
PHY			0.20 1.00			0.40 1.00	0.00 0.25		0.00 1.00		0.00 1.00
DOC											0.00 0.55
DET				0.00 0.22	0.00 0.13	0.10 0.20	0.40 1.00	0.00 1.00	0.00 1.00	0.00 1.00	

Table 4. Statistical comparison of ENA indices for each habitat between the two modelled periods, using Cliff's delta. Effects are described with “none”, “small”, “medium”, and “large” according to Romano et al. (2006).

	D/H	T..	SOI	A	R/DC	FCI	AMI	H _r
CH	$\delta = 0.825$ (large)	$\delta = 0.638$ (large)	$\delta = 0.031$ (none)	$\delta = 0.583$ (large)	$\delta = 0.973$ (large)	$\delta = 0.619$ (large)	$\delta = 0.066$ (none)	$\delta = 0.981$ (large)
FN	$\delta = 0.661$ (large)	$\delta = 0.542$ (large)	$\delta = -0.286$ (small)	$\delta = 0.480$ (large)	$\delta = 0.409$ (medium)	$\delta = 0.692$ (large)	$\delta = -0.060$ (none)	$\delta = -0.059$ (none)
FS	$\delta = -0.143$ (none)	$\delta = -0.296$ (small)	$\delta = -0.612$ (large)	$\delta = -0.188$ (small)	$\delta = -0.595$ (large)	$\delta = 0.254$ (small)	$\delta = 0.200$ (small)	$\delta = -0.643$ (large)

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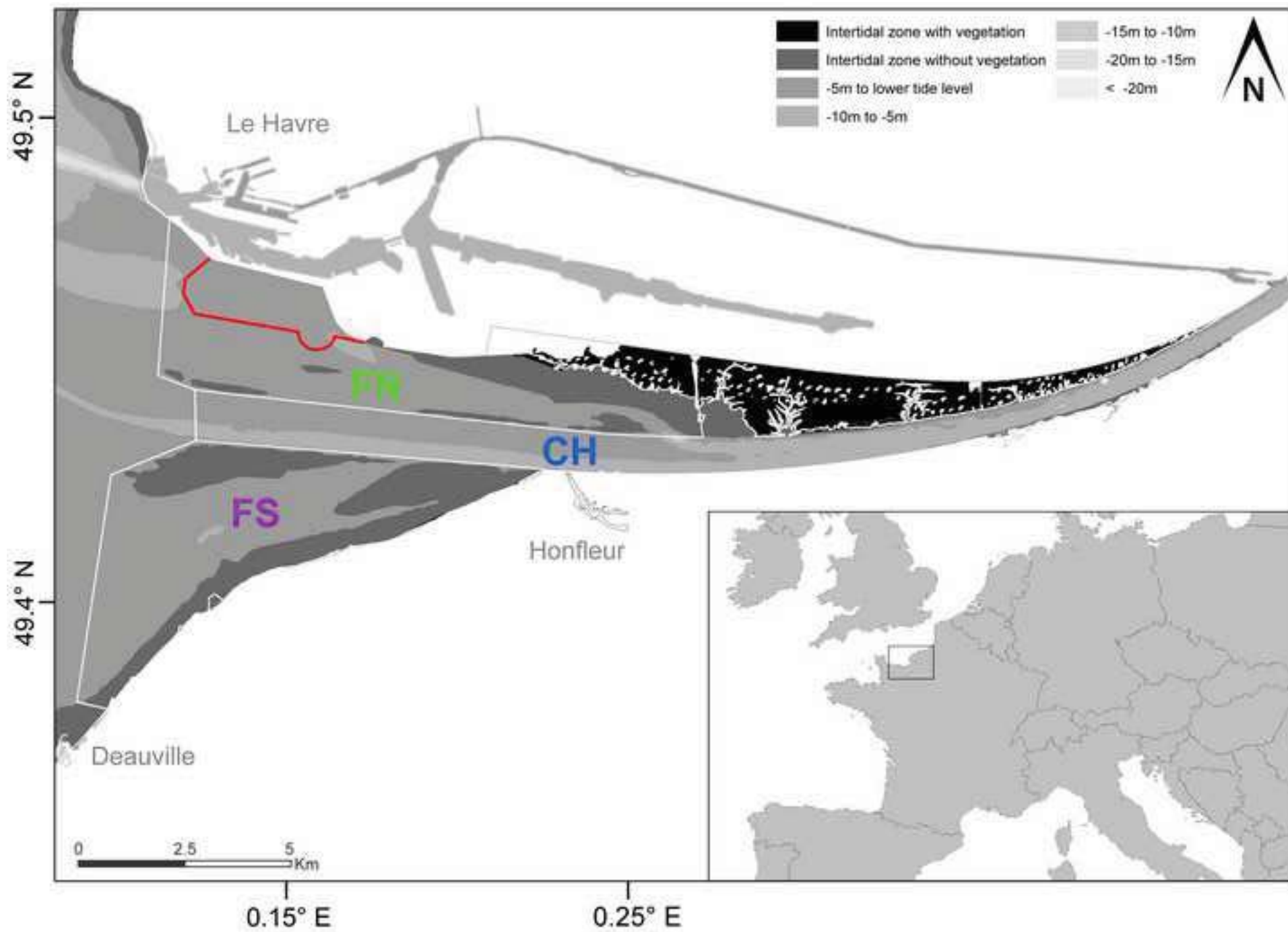


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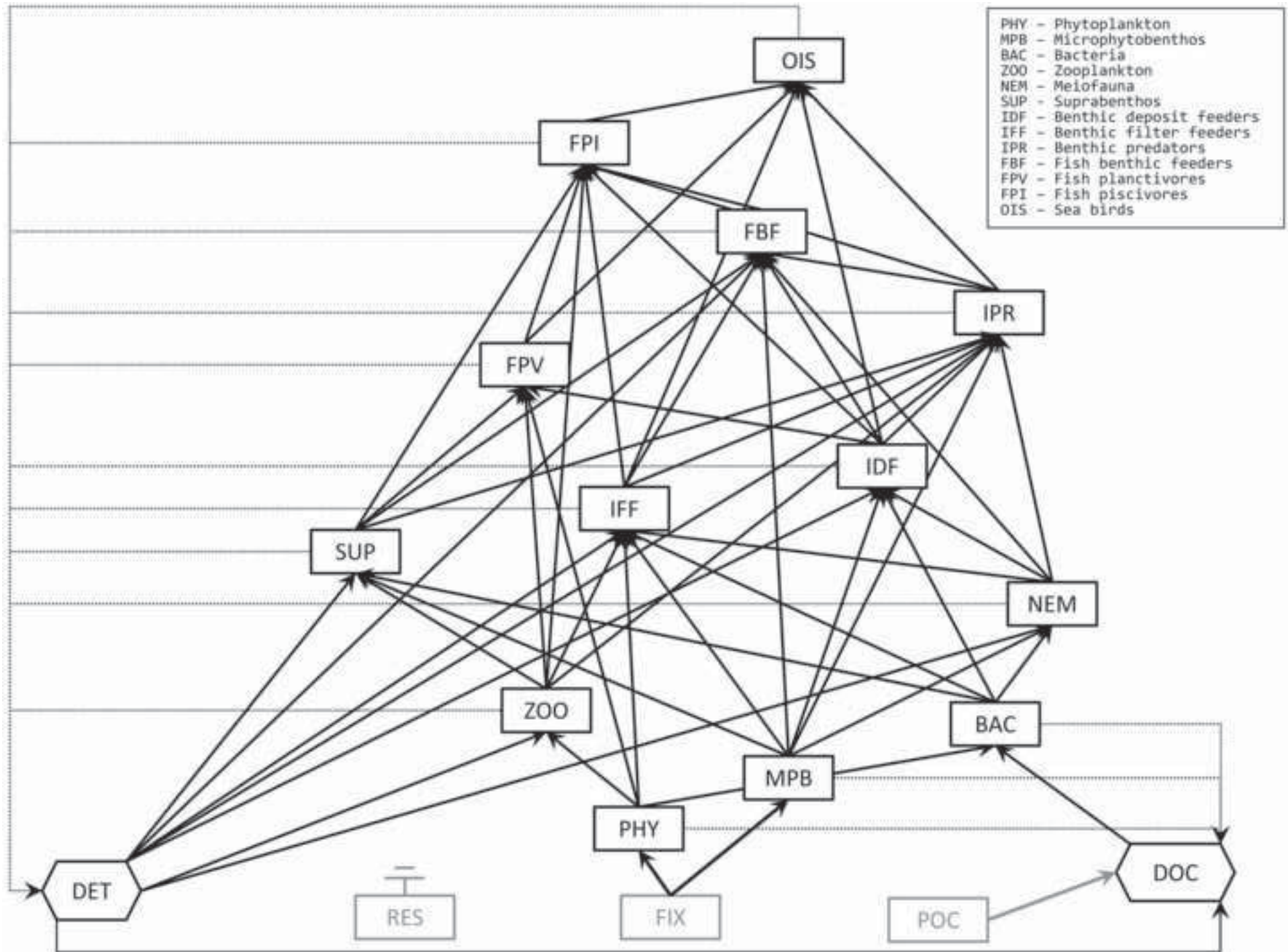


Figure 5

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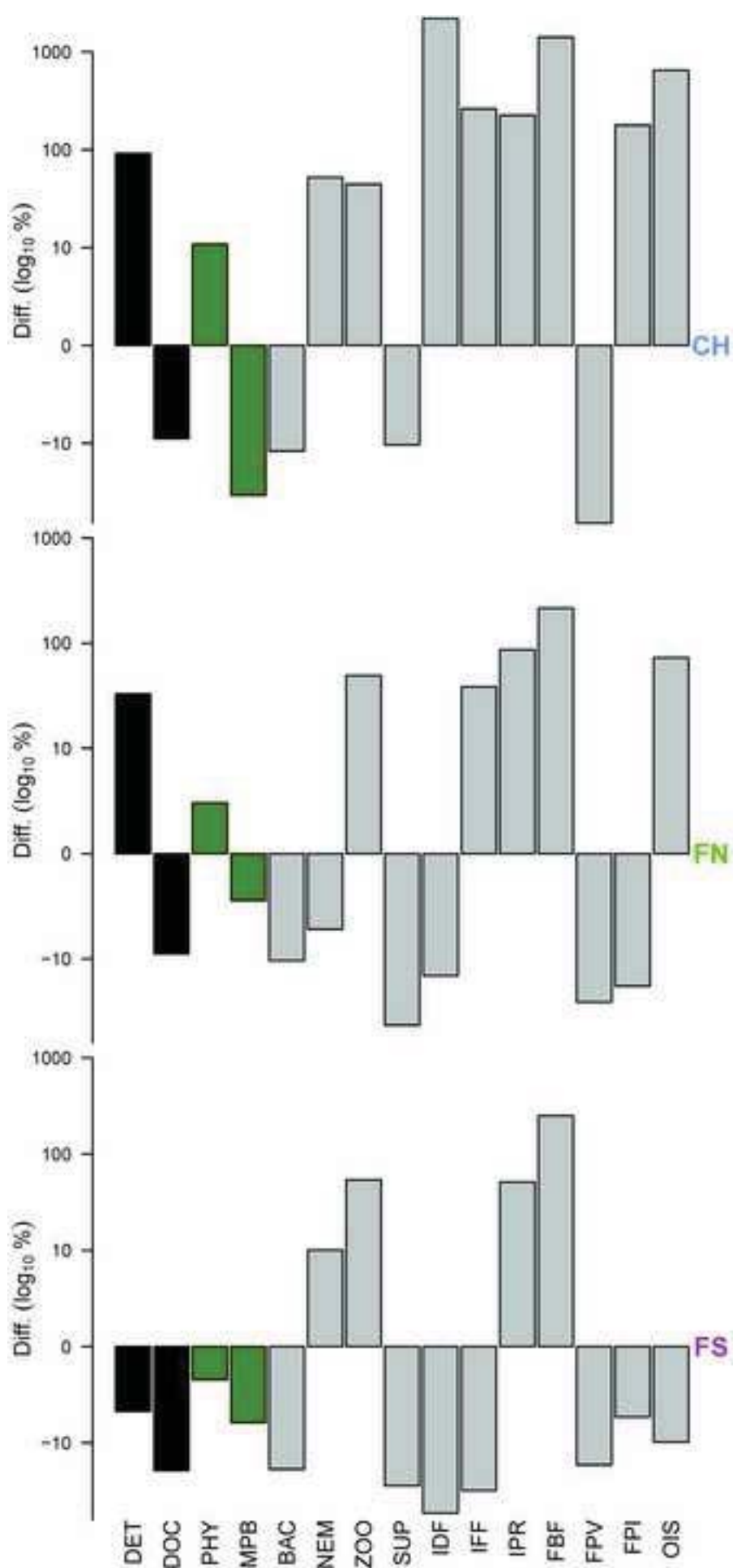


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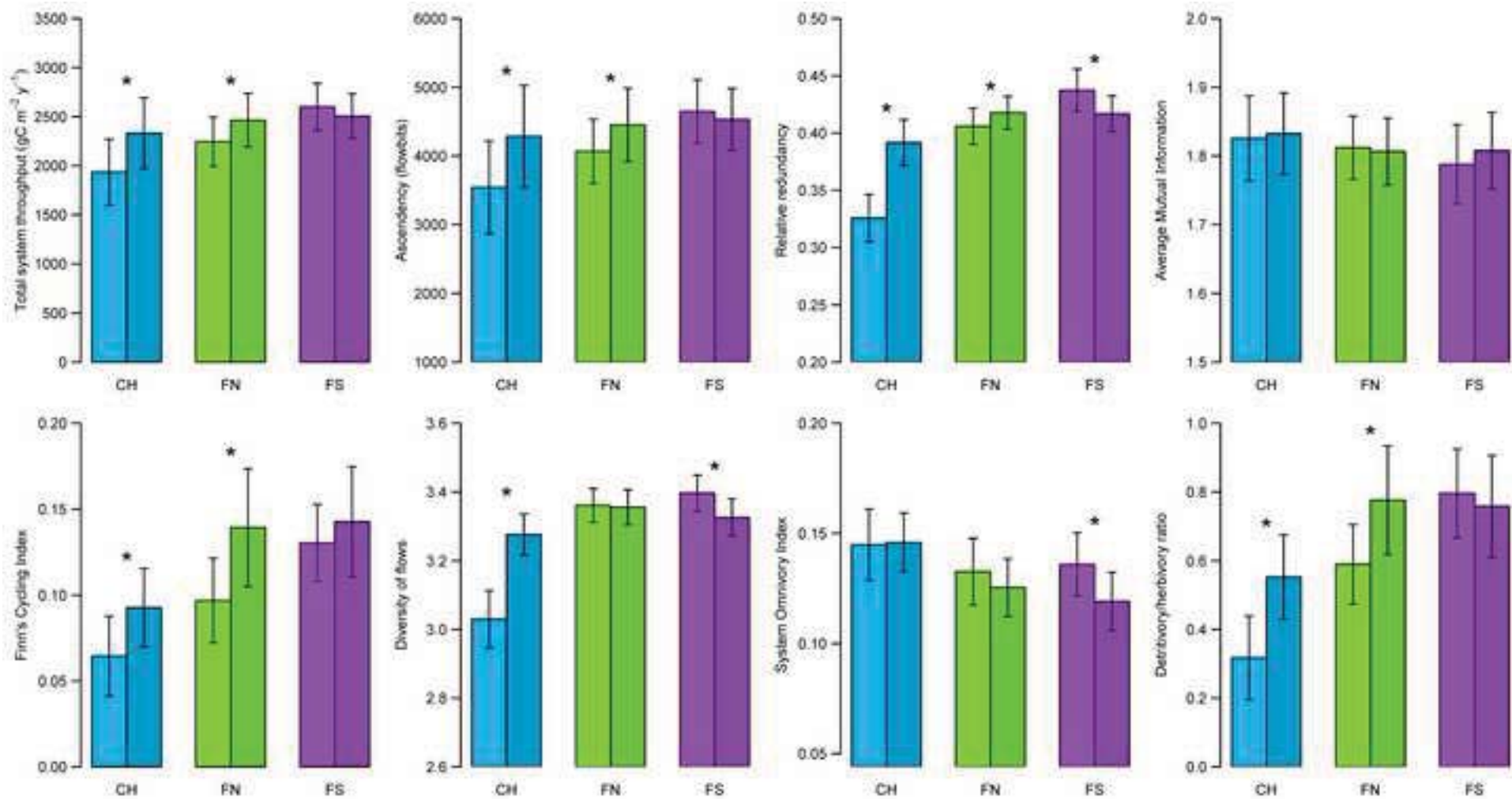


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