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 Elkaîm (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
opening of a direct connection from the central navigation channel to the northern flank upstream
the Normandy bridge to rebuild meanders, (c) the prolongation of the northern breakwater by 750
m, and (d) the creation of a small artificial island in the southern flank to improve habitat
heterogeneity for sea birds. All these works thus took into consideration the overall current outflows
and generally improved circulation of water in the estuary. Despite these positive outcomes,
previous studies assessed a negative effect of Port2000 on the suprabenthos (mostly crustaceans, i.e.
decapods and peracarids that perform daily vertical migrations being in the benthos during the day
and in the water column at night), especially on the diversity and density of the dominant species
(Dauvin et al. 2010). Sedimentary changes were also identified in the area, especially at the
interface between the estuary and the Seine Bay (Dauvin et al. 2006), but these alone are not
conclusive to indicate changes on the overarching processes of the ecosystem.

Ecological network analysis (ENA) combines the calculation of a set of indices that joins
concepts from ecology, network geometry, and information theory to describe the functioning of a
food web. ENA has become a powerful toolbox for ecological and management studies, and it has
been proposed as a base for determining the “good ecological status” according to European
Union policies (Dame & Christian 2007, Niquil et al. 2012, Niquil et al. 2014b). For ENA to be applied, a
knowledge of the values of energy flows between all trophic compartments is required, including
external inputs into the ecosystem, exports to neighbouring habitats, and dissipative flows such as
respiration. To obtain an estimation of flow values, ecosystem-level linear inverse modelling (LIM)
can be used: a method to obtain values of all unknown flows starting from a reduced number of
known system parameters and local and global constraints on eco-physiological processes (Vézina
& Platt 1988, Niquil et al. 2011). Various approaches can be used to reach the objective of assessing
the changes in the Seine estuary functional properties in relation to Port2000 construction; the
successful approach for such a before/after impact study should however be one that provides not
only a single estimated value for each flow – by itself statistically untestable – but also its
associated uncertainty (Kones et al. 2009, Chaalali et al. 2015).
The levels of both anthropogenic and natural stress of aquatic ecosystems can be partially captured by ENA indices, although a general theory encompassing their different interpretations is still in progress (Saint-Béat et al. 2015). The stability of an estuarine food web – and by extension of its ecosystem – is its capacity of maintaining comparable levels of functioning, i.e. its provision of services to human populations which include, among many others, fishing resources, contaminant turnover, and participation in global biogeochemical cycles (Ulanowicz 2003, Lobry et al. 2008). Disturbance effects in estuarine biodiversity and food webs are known to influence ecosystem structure and functioning at various levels and might include, among others, an increase in total system activity (Baeta et al. 2011), increase in recycling rates (Odum 1985), and reduction in trophic flows specialisation which will be reflected in a higher system omnivory (Fagan 1997).

The main objective of this study was to perform a before/after evaluation of the impacts related to the construction of Port2000 on the Seine estuary functioning, based on the different anthropogenic pressures at play in the three main spatial estuarine habitats (northern, central, and southern). We have used linear inverse modelling to obtain estimations of ecosystem flows in the three habitats, and subsequently implemented the related network analysis.

2. Materials and methods

2.1. Study area

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

The marine part of the Seine estuary was split into three spatial boxes that were modelled separately, following previous assessments, and considered “habitats” as homogenous zones from the hydro-sedimentary and salinity points of view (Tecchio et al. 2015). These habitats were: (1) the central navigation channel (CH) upstream to the Tancarville bridge, separated from the flanks by breakwaters submerged at low tide, (2) the northern flank (FN) which includes the harbour of Le Havre and hosting the north intertidal flat, and (3) the southern flank (FS) shielded from the central channel current and hosting a large intertidal flat (Figure 1). The sediment composition of the two flanks is a combination of sandy and muddy bottoms. The central channel is dredged year-round and it is mainly composed by sandy bottoms with sparse rocks. Thus, the study spatial extent covers an area continuously under sediment resuspension and direct organic matter inflow from the Seine River (CH), one area subject to extensive anthropogenic impacts (FN), and a third area (FS) with
the least influence of human building works. We therefore considered the southern flank as the habitat that was least modified between the two periods (before/after Port2000), thus serving as a partial reference.

For each of the three habitats, two food-web models were constructed using data from two different periods: 1996–2002, representing the situation before the Port2000 construction, and 2005–2012, representing the present situation. Each model represents an average year, using averaged biomass of functional compartments from all available years in its corresponding period.

2.2. Linear inverse modelling

The estimation of energy flows between trophic compartments was performed with the LIM package for the R statistical programming framework (Van den Meersche et al. 2009, Van Oevelen et al. 2010). This approach reads a text declaration file for each model to set up and generates numerical matrices which define equalities (i.e. known flows) and inequalities (i.e. constraints) for the flows. It also automatically ensures that all flows take positive values, and establishes mass balances for all living and detritus compartments.

Each food web was composed of 15 internal trophic groups and 3 external compartments, i.e. inorganic carbon for photosynthesis, river input, and the respiration sink (Figure 2). Eighty-five (85) flows were described between these components. Each living compartment was linked with consumption flows (as input), excretion/mortality (output to detritus), respiration (exported outside the model), and production flows (predated by other compartments). The constraints on these flows, i.e. their minimum and maximum limits, were established using rates drawn from literature, from other modelling works (whenever their results were generalizable), or from local detailed studies for diet constraints (Table 1). Biomasses (Table 2) were taken from the same database as the previously performed modelling work (Tecchio et al. 2015): benthos and fish data came from a combination of Ifremer, CSLN, Le Havre Port Authority, GIP Seine-Aval, Wimereux marine station, and National
Natural History Museum Paris sampling programs, and were standardised as gC m\(^{-2}\) using conversion factors (Brey 2001, Oguz et al. 2008). Where available, biomasses were used to parameterise the production flows, by multiplying them with a range of production/biomass (P/B) rates, obtained from literature. Energy balance was defined as

\[
\text{production} (P) = \text{consumption} (Q) - \text{excretion} (U) - \text{respiration} (R).
\]

Consumption was defined as all flows entering a compartment. Excretion, i.e. flow from a living compartment to detritus, also included natural mortality. Two among the three energy balance ratios (among P/Q, U/Q, and R/Q), according to availability, were used to constrain flows for each living compartment. For example, suprabenthos production was set between 10% and 37% of its consumption: \(0.10 \cdot \text{SUPconsumption} < \text{SUPproduction} < 0.37 \cdot \text{SUPconsumption}\).

Bacterial flow to detritus was considered as the proportion of bacterial production that is shunted by viruses (Danovaro et al. 2008). For dietary constraints, single-sided inequalities were preferred, e.g. zooplankton (ZOO) consumption by planktivorous fish (FPV) was set higher than 30% of FPV total food intake: \(ZOO \rightarrow FPV > 0.30 \cdot FPV\text{consumption}\). This was more reflective of the typical predatory behaviour, allowing an automatic re-balancing of the diet when the biomass entered for a prey is lower than usual in a given habitat or when the estimated biomass is lower than usual in a particular solution (Table 3). Gross primary production, defined as the sum of carbon import for primary producers (i.e. phytoplankton and microphytobenthos), was constrained using minimum and maximum limits from literature (Videau et al. 1998).

Because this approach includes an inherent uncertainty in data input, the model was considered balanced simply when there were no incompatible constraints and, therefore, when at least one solution of flow values was present. This reduces to a minimum the use of arbitrary modifications of input data, and ensures that the solution found is not near the boundary of the poly-dimensional space of possible solutions.
After every model was checked to possess at least one solution, we used a Markov-Chain Monte Carlo (MCMC) procedure to sample 200,000 possible solutions of the flow values from the polytope of all possible solutions that satisfied the constraints. The starting position for the random walk algorithm was a parsimonious solution obtained by least-distance programming, i.e. minimizing the sum of squared unknowns. At each iteration, all flows were modified in a random direction by a normally-distributed jump length; their new position was then checked to lay inside the polytope and the flows for which this condition was not met were mirrored back inside the accepted space (Van den Meersche et al. 2009). When all flows were valid according to the constraints, the solution was saved and a new iteration commenced. Convergence of results was checked both by observing if the solution space was fully sampled and by comparing means and standard deviations of flows between increasing quantities of iterations. Each solution was then represented by a matrix of flows from each “source” compartment to the possible “sinks”, and was used to calculate ENA indices.

2.3. Ecological network analysis

Ecological network analysis was performed using the R software packages NetIndices (Kones et al. 2009) and enaR (Borrett & Lau 2014), along with personally-written complementary scripts (S. Tecchio). The following ENA indices were calculated:

- The Total system throughput (T..) was expressed as the sum of all flows occurring in the system, and interpreted as an indicator of system activity (Rutledge et al. 1976, Latham 2006).

- The Detritivory/Herbivory ratio (D/H) was obtained as the ratio between the sum of all predation flows on the detritus compartment (det) and the sum of all predation flows on primary producers (phy and mpb). An increase would indicate a shift to a more detritus-based food web, while a decrease would suggest an augmented importance of primary producers in trophic interactions (Ulanowicz 1992).
The **System Omnivory Index** (SOI) was calculated as the weighted mean of the omnivory indices of each consumer compartment, using the logarithm of their consumption as weights. It is an indicator of the overall dietary adaptation of the consumers, and an increase would generally indicate a response to an external pressure (Fagan 1997, Libralato 2008).

The **Finn’s Cycling Index** (FCI) was calculated as the ratio between flows generated by cycling over the total system throughput (Finn 1976, 1980). Although FCI definitions vary, this particular one was chosen to increase comparability with another modelling approach, *Ecopath with Ecosim*, which calculates the index using the same formula. See Guesnet et al. (2015) for comparison of ENA indices formulas between ecosystem modelling approaches.

The **Average Mutual Information** (AMI) expresses the degree of organisation of exchanges between functional groups, with increases indicating augmented specialisation and flow constraint (Hirata & Ulanowicz 1984).

The **Ascendency** was calculated as \[ A = AMI \cdot T.., \] and it is related to ecosystem growth and development (Ulanowicz & Abarca-Arenas 1997). Higher values would mean that the system is more active in constraining flows along more specific pathways, while low ascendancies have been related to system immaturity (Ortiz & Wolff 2002).

The **relative Redundancy** (R/DC) was calculated as the ratio between the internal flow overhead and the total development capacity of the ecosystem (Ulanowicz 2001) or, more formally, as:

\[ R/DC = \frac{\sum_{i,j=1}^{n} T_{ij} \cdot \log \left( \frac{T_{ij}^2}{T_{i..} \cdot T_{j..}} \right)}{\sum_{i=1}^{n+2} \sum_{j=0}^{n} T_{ij} \cdot \log \frac{T_{ij}}{T_{i..}}}. \]

The diversity of flows (H_r) was calculated as the Shannon-Wiener index of the flow values matrix and interpreted as both an indicator of redundancy of ecosystem processes and overall stability of the food web (Rutledge et al. 1976, Ulanowicz & Norden 1990).

The **Transfer Efficiency** (TE, Lindeman 1942) was obtained by first calculating the mean value of each flow for each spatial compartment, following the conclusions by Saint-Béat et al. (2013).
Then, the web was separated into discrete trophic levels (TL I, II, III, …) and TE was calculated as the proportion of outbound flows of a level that throughput into the next. In this case, the result is not a single value but one TE value for each trophic level, scaled from 0 to 1.

Indices were calculated for each solution of each model, obtaining distributions of 200,000 values each. Differences in the means of ENA indices between habitats and between the 2 periods of the same habitat (i.e. 1996–2002 and 2005–2012) were first tested by Student’s t-tests. Due to the large sample sizes, t-tests were finding differences even for tiny effects. Therefore, the non-parametric effect size statistic introduced by Cliff (1993) was applied to assess a statistical difference. Given two samples of size $n_1$ and $n_2$, the Cliff’s delta statistic, also called success rate difference, is expressed as:

$$\delta = \frac{P(x_{i1} > x_{i2}) - P(x_{i1} < x_{i2})}{n_1 n_2},$$

where $x_{i1}$ and $x_{i2}$ are scores within samples 1 and 2. This statistic estimates the probability that a randomly selected value in one sample is higher than a randomly selected value in the second sample minus the reverse probability, i.e. $\delta = P(x_1 > x_2) - P(x_1 < x_2)$. Note that a positive value indicates that all values in sample 1 are larger than all values in sample 2. Comparing the degree of overlapping of the two distributions can detect whether the significant difference is due to an effective ecological meaning or to the sample size alone. Significant differences were identified using thresholds provided by Romano et al. (2006): negligible for $|\delta| < 0.147$, small for $|\delta| < 0.33$, medium for $|\delta| < 0.474$, and large otherwise.

Differences in functioning between the two periods were also analysed by single flow values. We also calculated the percentage of difference in the means of each compartmental throughflow. The throughflow of a compartment is defined as the higher of its total inflow or outflow (which in our case were equal due to the models being at steady state). As the differences showed variations of over 4 orders of magnitude, a log transformation was applied to the percentages.
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 ($\text{FIX} \rightarrow \text{PHY}$), which globally averaged $411.2 \pm 55.4$ gC m$^{-2}$ y$^{-1}$ (Figures 3 and 4). The other primary production input flow was $\text{FIX} \rightarrow \text{MPB}$ and it was estimated at $61.0 \pm 28.1$ gC m$^{-2}$ y$^{-1}$. Respiration flows, which represented the export from the system, were dominated by bacterial respiration which was $141.4 \pm 84.2$ gC m$^{-2}$ y$^{-1}$ overall (BAC$\rightarrow$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
one, i.e. when mean flow values increased so did the variability, and vice versa. This reflects the non-normality of flows distributions.

The comparison of compartment throughflows (their total inflow or outflow, a proxy of activity) between the two periods showed that, in the CH system, activity in the benthos (from IDF to FBF) strongly increased over the whole food web in the later period (Figure 5). The compartments MPB, SUP, and FPI, always reduced their overall activity in the more recent period, while ZOO, IPR, and FBF always increased it. Worth mentioning is suprabenthos group (SUP) which decreased in all habitats, due to its above mentioned reduction in biomass and, therefore, in its production flows. Bacterial (BAC) activity also decreased in all spatial compartments in the more recent period. The rest of the groups had contrasting behaviour between habitats. The northern flank (FN) showed an increase in detritus feeding, zooplankton activity, and overall benthos dynamics (increase in IFF, IPR and FBF, with a decrease only in IDF).

3.2. Ecological network analysis

All t-tests performed on ENA indices showed extremely significant differences ($p < 10^{-15}$) except for the before/after comparison of SOI ($p = 0.10$). Thus, Cliff’s delta statistic was used for interpreting direction and significance of the comparisons (Table 4). We considered medium and large effect sizes to be indicative of a significant trend.

Comparing the before and after periods, the total system throughput ($T_{..}$) increased significantly in the CH and FN, and remained stable in FS (Figure 6 and Table 4). Ascendency increased significantly in CH and FN, while remaining stable in FS. Relative redundancy was the lowest in the CH before Port2000; it increased significantly up to the levels of the other two habitats after Port2000. Relative redundancy significantly increased in the FN and decreased in the FS between the two periods. The Average Mutual Information (AMI) showed high standard deviations in all
comparisons, with no contrasts being significant. Carbon recycling estimated by FCI increased in the after period in the three estuarine habitats, especially in CH and FN where contrasts were significant. The diversity of flows, estimated by $H_\alpha$, strongly increased from 3.02 to 3.27 in the CH, remained stable in the FN, and decreased in the FS. System omnivory remained stable in the CH and decreased in FN and FS, with the FS difference being significant. Finally, the detritivory/herbivory ratio (D/H) showed significant increases in the CH and FN, and remained stable in the FS. In CH and FN, this change in D/H was more due to an increase in detritus chain activity than to a decrease in consumption of primary producers (see again Figure 5).

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

The modelling approach applied in this work is not without caveats and aspects that could be
improved. A step forward might include an improved determination of primary production input,
which in the present work was characterised in coarse detail. In fact, gross phytoplankton
production was left estimated by the model and represented as such the necessary carbon input to
sustain the rest of the food web. For this reason, in the present study, transfer efficiency of level I
and the variety of primary producers were not considered for ecological network analysis. We also
did not take into account the exchange of organic carbon between the different habitats, such as
horizontal advection of food particles due to benthic currents, direct detritus export, and plankton
migration. These calculations would have been particularly computing-intensive if done in a
continuous way, and they might be better suited for other modelling approaches that already
integrate spatial and time-dynamics equations (e.g. Ecospace, Christensen et al. 2014).

Compared to the previous models of the different habitats of the Seine estuary (Rybarczyk &
Elkaïm 2003, Tecchio et al. 2015), the ones presented here better took into account bacterial flows
(such as bacterial mortality, i.e. viral shunt), and phytoplankton and microphytobenthos respiration
and exudation flows (which in the Ecopath approach are ignored). This translated into a direct
difference in the total system activity (estimated by T..) and, by connection, to differences in the
rest of the ENA indices calculated. A recent comparison between the two approaches, Ecopath and
LIM, found however lower estimates of T.. in the LIM-MCMC compared to the Ecopath model
(Chaalali et al. 2015), and explained this by differences in the number of compartments – generally
limited to 20 in LIM formulations – and by not considering cannibalism flows.
Finally, the inferential statistic applied here proved useful to compare ENA results when the large sample sizes did not allow the application of parametric statistical tests. To our knowledge, the use of Cliff’s delta for ecosystem modelling results is first presented here, and we hope it will be applied and criticised in future works.

### 4.2 Ecosystem functioning between periods

Ecosystems evolve towards maturity, which is the last state in the process of succession (Odum 1969). At maturity, we expect an increase in link connectivity and stability, and an accumulation of capital of nutrients and biomass which is usually stored at the higher trophic levels (Gunderson 2000). The link between system maturity and the observations by ENA has been done here by considering the limitations of using relatively small network with a high degree of aggregation of functional groups. However all models were built with the same link structure, thus permitting comparisons between them.

The construction of Port2000 was not the only changing condition between the two periods. Contrasting rates of river discharge were identified in the Seine, with the more recent period (after Port2000) marked by significantly lower river discharge (caused by the North Atlantic climatic Oscillation) than the first period (Dauvin & Pezy 2013). This reduced outflow might have shifted the maximum turbidity zone upstream and left the majority of organic matter within the navigation channel (CH), then favouring an increase in system activity especially on the benthic detritivorous compartments. The seasonal and inter-annual fluctuations inside each period were nevertheless too high to conclude that differences in ecosystem functioning before and after Port2000 would be due to multi-annual differences in organic matter input from river discharge. A complete deconvolution of the various external factors operating on the Seine estuary ecosystem will have to be achieved by a combination of other methods of ecosystem modelling, such as time-dynamics and/or spatial approaches, or the use of other sets of biological indicators. For the present work, the differences
between periods have been discussed without necessarily linking them directly to the Port2000 construction or to the mitigation measures.

The southern flank (FS) showed a reduction in both primary productivity requirements (herbivory) and detritivory, overall maintaining a stable system activity and D/H ratio. At the same time, the trophic flow specialisation increased. This step towards system maturation can be identified by a reduction of parallel pathways in the food web and of their flow evenness, i.e. reduced redundancy (Bondavalli et al. 2000), and by a change in system omnivory, as indicating a web-like structure of the food web. On the same line, according to Ulanowicz and Norden (1990), redundancy is a component of the overhead which can be seen as a reservoir of energy or possible “response” to perturbation without dramatic changes in functioning. High values of overhead are also associated with early ecosystem stages (Ulanowicz 1986). Thus, as the system evolves, it would become more efficient with a reduction of redundant pathways. Among others, this index has been proposed as an indicator of system resilience (Heymans et al. 2007). In the present work, the observed increase in efficiency (loss of redundancy and increase in flow diversity) could indeed be responsible for a decrease in resilience, which could act as an insurance against perturbation, in effect an adaptation capacity of the ecosystem. On the other hand, the interpretation of SOI in terms of ecosystem maturation is not consistent in literature: Odum (1969) postulated an increase in omnivory with maturation, while it was more recently related with the levels of system stress (Selleslagh et al. 2012). The transfer efficiency configuration by trophic levels was more linearized in the more recent period, but it was already showing a natural smooth slope before 2002. Marine ecosystems stressed by fishing activities show breaks in the decreasing pattern of TE with trophic level (Coll et al. 2009). In our case, the decrease of SOI should be interpreted as a reduction of system stress. In all cases, the FS showed all characteristics to be considered the least stressed area of the estuary, and at the same time, this condition was maintained and reinforced in the later period. This comforted our initial choice of considering FS as a reference compartment.
The northern flank (FN) is the habitat directly influenced by the construction of Port2000, as it was subject to several modifications and its overall surface was decreased from 25 to 20 km². The remediation works helped in the formation of a new intertidal flat and meanders but at the same time, they modified current dynamics and increased sand input and salinity (Cuvilliez et al. 2009). The direct observed effect, which was expected, was an increase in carbon recycling (mean FCI 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 have been compressed, increasing importance of lower trophic levels and detritus chain, which are indeed the levels with the highest contribution to carbon recycling. The improved water flow at the eastern side of FN might also have increased detritus input in the zone at the same time; however, in our models the estimation of input flows – both primary production and river input – was left unconstrained. Thus, it can be considered as the “required input to sustain the food web”, as energy balances of all living groups were instead constrained.

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
estuarine system can be stable even if it is far from maturity, i.e. not at ecological climax. The construction of Port2000 may have made the system recede to a previous step in ecological succession, but at the same time increase its stability at that particular system state. In fact, during reorganisation a system mobilises its biomass “assets”, stored at high trophic levels: this biomass is converted into flows linked more with the lower trophic levels (Pranovi & Link 2009). This process has two consequences; it increases recycling and detritivory, and it strengthens the connectivity of the remaining lower TLs (Rombouts et al. 2013). Transfer efficiency at TL IV in both FN and FS decreased after Port2000, supporting this possibility along with the straightening pattern of FN between the two periods.

Considering CH, we remember that ascendency is calculated as $A = TST \times AMI$ and that

$$\frac{A_I}{C} + \frac{R}{C} = 1,$$

thus all the elements are present to conclude if an increase in system activity is leading to an increase in system efficiency or just in parallel pathways. The AMI did not change significantly for any habitat between periods, therefore all changes in ascendency were due to changes in total system activity. In CH, ascendency increased and at the same time, the relative redundancy also increased. This effectively means that more redundant energy pathways were formed. Is this a signal that the system went back to a less resilient state? We suggest that the continuous reworking of the CH zone does not permit stable ecosystem dynamics at benthos level and consequently, the image that we can retrieve from ENA is one of a constantly shifting food web. The compartments that most changed their activity in the CH were indeed the benthic ones (suprabenthos and the 3 benthic groups). In fact, Garcia et al. (2011) found that ecosystem functioning of the English Channel is particularly sensitive to changes in benthos habitat characteristics, which in our case were highly variable between periods. Again, Patrício et al. (2004) showed that this condition of high instability can be found in other human-impacted estuaries. The pattern from transfer efficiency with a break at TL III is the confirmation that the system was stressed in 1996–2002, and that it still remains so in the later period.
4.3 Conclusions

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

Acknowledgements

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choices? Annual Meeting of the Southern Association for Institutional Research, October 14-17, 2006, Arlington, Virginia


**Figure legends**

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

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

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

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

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

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

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

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<th></th>
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<th>R/Q</th>
<th>U/Q</th>
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<td>min</td>
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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).

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<td>NEM Meiofauna</td>
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<td>BAC Bacteria</td>
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<td>PHY Phytoplankton</td>
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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).

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30
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).

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<td>δ = 0.825 (large)</td>
<td>δ = 0.638 (large)</td>
<td>δ = 0.031 (none)</td>
<td>δ = 0.583 (large)</td>
<td>δ = 0.973 (large)</td>
<td>δ = 0.619 (large)</td>
<td>δ = 0.066 (none)</td>
<td>δ = 0.981 (large)</td>
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<td>δ = 0.661 (large)</td>
<td>δ = 0.542 (large)</td>
<td>δ = -0.286 (small)</td>
<td>δ = 0.480 (large)</td>
<td>δ = 0.409 (medium)</td>
<td>δ = 0.692 (large)</td>
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<td>δ = -0.059 (none)</td>
</tr>
<tr>
<td><strong>FS</strong></td>
<td>δ = -0.143 (none)</td>
<td>δ = -0.296 (small)</td>
<td>δ = -0.612 (large)</td>
<td>δ = -0.188 (small)</td>
<td>δ = -0.595 (large)</td>
<td>δ = 0.254 (small)</td>
<td>δ = 0.200 (small)</td>
<td>δ = -0.643 (large)</td>
</tr>
</tbody>
</table>
Figure 4
Click here to download high resolution image

2005-2012 after Port2000

- GPP
- Detritivory
- Respiration
- Mortality

Carbon flow (g m⁻² d⁻¹)