



## Projet Seine-Aval 5 **ANTROPOSEINE**

« ANalyse de la structure TROPhique et  
cONtribution des habitats de l'estuaire de la  
SEINE »

Annexes du rapport de recherche

Mars 2018

Coordination : Nathalie Niquil

### **1 Article Niquil et al 2014**

Niquil, N., Baeta, A., Marques, J. C., Chaalali, A., Lobry, J., & Patrício, J. (2014). Reaction of an estuarine food web to disturbance: Lindeman's perspective. *Mar Ecol Prog Ser*, 512, 141-154

Disponible ici : <http://www.int-res.com/articles/theme/m512p141.pdf>

### **2 Article Guesnet et al 2015**

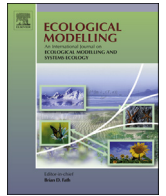
Guesnet V, Lassalle G, Chaalali A, Kearney K, Saint-Béat B, Karimi B, Grami B, Tecchio S, Niquil N, Lobry J (2015) Incorporating food-web parameter uncertainty into Ecopath-derived ecological network indicators. *Ecological Modelling* 313:29-40

### **3 Article Tecchio et al 2015**

Tecchio S, Tous Rius A, Dauvin J-C, Lobry J, Lassalle G, Morin J, Bacq N, Cachera M, Chaalali A, Villanueva MC, Niquil N (2015) The mosaic of habitats of the Seine estuary: Insights from food-web modelling and network analysis. *Ecological Modelling* 312: 91-101

### **4 Article Tecchio et al 2016**

Tecchio S, Chaalali A, Raoux A, Tous Rius A, Lequesne J, Girardin, V., Lassalle G, Cachera M, Riou P, Lobry J, Dauvin JC, Niquil N (2016). Evaluating ecosystem-level anthropogenic impacts in a stressed transitional environment: The case of the Seine estuary. *Ecological Indicators*, 61, 833-845.



# Incorporating food-web parameter uncertainty into Ecopath-derived ecological network indicators



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## ARTICLE INFO

### Article history:

Received 19 February 2015

Received in revised form 29 May 2015

Accepted 30 May 2015

### Keywords:

Ecopath with Ecosim

Ecosystem models

Network analysis

Parameter uncertainty

Comparative studies

## ABSTRACT

Ecological network analysis (ENA) provides numerous ecosystem level indices offering a valuable approach to compare and categorize the ecological structure and function of ecosystems. The inclusion of ENA methods in Ecopath with Ecosim (EwE) has insured their continued contribution to ecosystem-based management. In EwE, ENA-derived ecological conclusions are currently based on single values of ENA indices calculated from a unique input flow matrix. Here, we document an easy-to-use routine that allows EwE users to incorporate uncertainty in EwE input data into the calculation of ENA indices. This routine, named ENAtool, is a suite of Matlab functions that performs three main steps: (1) import of an existing Ecopath model and its associated parameter uncertainty values in the form of uncertainty intervals into Matlab; (2) generation of an ensemble of Ecopath models with the same structure as the original, and with parameter values varying based on the prescribed uncertainty limits; and (3) calculation of a set of 13 ENA indices for each ensemble member (one set of flow values) and of summary statistics across the whole ensemble. This novel routine offers the opportunity to calculate ENA indices ranges and confidence intervals, and thus to perform quantitative data analyses. An application of ENAtool on a pre-existing Ecopath model of the Bay of Biscay continental shelf is presented, with a focus on the robustness of previously published ENA-based ecological traits of this ecosystem when the newly introduced uncertainty values are added. We also describe the sensitivity of the ENAtool results to both the number of ensemble members used and to the uncertainty interval set around each input parameter. Ecological conclusions derived from EwE, particularly those regarding the comparison of structural and functional elements for a range of ecosystem types or the assessment of ecosystem properties along gradients of environmental conditions or anthropogenic disturbances, will gain in statistical interpretability.

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## 1. Introduction

Marine ecosystems are affected by climate change (Beaugrand, 2004; Hoegh-Guldberg and Bruno, 2010) and by other natural or human-caused disturbances (Pauly et al., 1998; Borja et al., 2010). Ecosystem models are useful to get a better understanding of the structure and function of a system and for predicting how it may change over time when facing single or multiple pressures (Plagányi, 2007). Ecopath with Ecosim (EwE) is a widely used modelling approach to represent marine food webs (Polovina, 1984; Christensen and Walters, 2004; Christensen et al., 2008). Since its

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development in the early 1980s, about 400 EwE models representing a wide variety of ecosystems worldwide have been published (Coll  ter et al., 2013a,b). Coupling EwE models to Ecological Network Analysis (ENA; Ulanowicz, 1986) was proposed as a relevant method to estimate energy flows and to characterize emergent properties of food webs, i.e. characteristics not directly observable that can only be detected by analysis of within-system interactions (Christensen and Pauly, 1992). ENA is a suite of tools that include input–output analysis, trophic structure analysis, pathway analysis, biogeochemical cycle analysis, and information analysis (Dame and Christian, 2006; Borrett and Lau, 2014). The main challenge for ENA is to capture the properties of entire food web in terms of a limited number of indices. In the scope of the European Marine Strategic Framework Directive (MSFD; <http://ec.europa.eu/directive-2008/56/EC>), the EU Member States have to report on the environmental status of the seas under their jurisdiction and to work on achieving “Good Environmental Status” (GES) using food-web indicators as one possible metric. In this direction, nine food-web indicators are currently under evaluation as potential indicators of GES; the Ecological Network Analysis indices are among these candidate indicators (Rombouts et al., 2013; Niquil et al., 2014).

The EwE network analysis plugin has been employed in many instances, notably to study the stability of ecosystems and their response to perturbations (Patricio et al., 2006; Lobry et al., 2008; Baeta et al., 2011; Selleslagh et al., 2012) or, more recently, to assess the dynamical food-web reorganization and redirection of energy flow pathways under environmental changes (Tomczak et al., 2013). Nonetheless, these holistic conclusions relied on single values of ENA indices which were derived from a single input data matrix with no specified uncertainty. Moreover, the ecological interpretation of these single values mostly relies on non-statistical comparisons with values obtained for ecosystems of the same type. Given that data uncertainties may translate to uncertainties in model outputs (e.g. Niiranen et al., 2012), it is generally agreed that important scientific questions should be scrutinized with as many models as possible (Fulton, 2010; G  r  mark et al., 2012). One method of incorporating uncertainty into Ecopath model analysis is to use an ensemble parameterization technique, building several Ecopath models each representing a potential manifestation of a food web and falling within the uncertainty ranges of the observed data (Aydin et al., 2007; Kearney, 2012). This approach results in distributions of parameters rather than specific values, while still meeting basic thermodynamic requirements. Kearney et al. (2012) provided a suite of Matlab functions to construct such a distribution of parameters based on an Ecopath model and its data pedigree, i.e. a quantification of the parameter certainty tied to the parameter’s origin. In this study, we extend the Kearney et al. (2012) code for generating this type of ensemble to feed into calculations of ENA indices. This work will allow parameter uncertainty to be incorporated into model-derived ENA indices, and will also improve interpretation of these indices by allowing statistical analyses. When overhauling the EwE source code between the release of EwE versions 5 and 6, the EwE developers chose not to continue support of the Ecoranger module, which had allowed users to explore parameter uncertainty ranges in a Bayesian context (Christensen et al., 2005). The code presented in this paper now offers an alternative method for analyzing this uncertainty.

The aim of this software development is to provide an easy-to-use routine to EwE users to generate a set of values for key ENA indices by explicitly taking into account uncertainty in model input data. To this end, two characteristics are identified as important: (i) a routine that can be called by a single line of Matlab code and can be run on all commonly used operating systems (recent Windows, Unix-based, and Mac platforms), independent of the EwE software versions used for the pre-existing ecosystem model construction

and (ii) a routine based on formulas of ENA indices currently in use in the last version of the EwE software. The present work is also the opportunity to harmonize ENA indices calculations derived from two main approaches for constructing ecological flow networks, i.e. EwE and linear inverse modelling (LIM; V  zina and Platt, 1988). Different formulas for the same index exist in the scientific literature and correspond to different interpretations of the same idea. We demonstrate the use of this tool by applying it to a pre-existing Ecopath model of the Bay of Biscay continental shelf (Lassalle et al., 2011) for which data quality is already categorized using Pedigree scores (Lassalle et al., 2014). ENA indices distributions derived from the ENAtool routine are compared with previous point estimate values obtained with this Ecopath model to test for robustness of ENA-derived ecological conclusions. Finally, we test sensitivity of ENA indices distributions to the number of balanced ensemble members underlying their calculation and to the level of uncertainty applied to specific Ecopath model parameters.

## 2. Materials and methods

### 2.1. The Ecopath concept and equations

The Ecopath with Ecosim (EwE) modelling software enables the building and analysis of food-web models (Polovina, 1984; Christensen and Walters, 2004; Christensen et al., 2008). The full software package includes several modules (e.g. Ecopath, Ecosim, Ecospace) to explore food webs across both space and time. However, for this study, we will focus only on the Ecopath component, which calculates a static mass-balanced snapshot of the biomass and energy fluxes between functional groups in a food web. In this context, a functional group refers to a species or group of species that occupy a particular niche in the food web, and can range in resolution from a broad grouping (e.g. pelagic fish) to specific life stage of a species (e.g. juvenile herring). The Ecopath model calculation is based on two “master” equations. The first equation decomposes the production term of each functional group:

$$\begin{aligned} \text{Production} = & \text{fishery catch} + \text{predation mortality} \\ & + \text{net migration} + \text{biomass accumulation} \\ & + \text{other mortality} \end{aligned}$$

“Other mortality” includes natural mortality factors such as mortality due to senescence and diseases.

The second equation describes the energy balance within each functional group:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food}$$

More formally, the two equations can be written as follows for functional group  $i$  and its predator  $j$ :

$$\begin{aligned} B_i \times \left(\frac{P}{B}\right)_i = & Y_i + \sum_j \left( B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ij} \right) \\ & + Ex_i + Bacc_i + B_i(1 - EE_i) \times \left(\frac{P}{B}\right)_i \end{aligned} \quad (1)$$

and

$$B_i \times \left(\frac{Q}{B}\right)_i = B_i \times \left(\frac{P}{B}\right)_i + R_i + U_i \quad (2)$$

where the main input parameters are biomass density ( $B$ , here in  $\text{kg C km}^{-2}$ ), production rate ( $P/B$ ,  $\text{year}^{-1}$ ), consumption rate ( $Q/B$ ,  $\text{year}^{-1}$ ), proportion of  $i$  in the diet of  $j$  ( $DC_{ij}$ ;  $DC$  = diet composition), net migration rate ( $Ex$ ,  $\text{year}^{-1}$ ), biomass accumulation ( $Bacc$ ,  $\text{year}^{-1}$ ), total catch ( $Y$ ;  $\text{kg C km}^{-2} \text{ year}^{-1}$ ), respiration ( $R$ ;  $\text{kg C km}^{-2} \text{ year}^{-1}$ ), amount of consumed food that is unassimilated



( $U$ ;  $\text{kgC km}^{-2} \text{ year}^{-1}$ ) and ecotrophic efficiency ( $EE$ ; amount of species production used within the system).

## 2.2. The generalized intra-model ensemble routine: ENAtool

In keeping with our goal to provide a single user-friendly tool for ENA index ensemble generation, we have packaged together a master Matlab script (ENAtool.m) and two data input templates, all of which are available via the supplementary materials. The ENAtool.m script grew out of, and now incorporates several sub-functions from, the Matlab implementation of Ecopath (Kearney, 2015; doi:10.5281/zenodo.17837), with additional routines added to calculate ENA indices from the resulting model ensemble. The key calculations performed by this tool are as follows. All the Matlab functions called during the ENAtool routine operate only on Ecopath data.

### 2.2.1. Import of a EwE model into Matlab

ENAtool first imports data from EwE6 databases into Matlab, storing them in a variable format we will refer to as EwE input structures (Fig. 1). The original data import function, *mdb2ewein*, relies on the 'mdbtools' (<http://mdbtools.sourceforge.net/>) set of utilities to read data from the MS Access file format used by EwE. As an alternative for those unwilling or unable to compile C source code, we have provided a companion import function, *excel2ewein*, which relies on an Excel template to provide the necessary input data (Fig. 1). This function is based on a template (see Template A provided in supplementary material 1) that must be filled with key input parameters and other related information by first opening the pre-existing EwE model with a database program such as Microsoft Access or OpenOffice Base. The template was provided as an Excel file and can be completed using any spreadsheet program (e.g. Microsoft Excel, OpenOffice Calc, etc.) but must be in the end saved as an Excel file (.xlsx). Both functions import all necessary Ecopath data, including basic inputs, diet compositions, fleet catches and discards, and multi-stanza group parameters, to the EwE input structure.

### 2.2.2. Generation of a set of balanced ensemble members

This second step can be decomposed into two phases: first, the definition of uncertainty around input parameters and then the construction of an ensemble of balanced Ecopath models (Fig. 1). A probability distribution for all or certain input parameters (i.e. field biomasses ( $B$ ), production over biomass ratios ( $P/B$ ), consumption over biomass ratios ( $Q/B$ ), ecotrophic efficiencies ( $EE$ ), and diet compositions ( $DC$ )) in the EwE input structure has to be defined. To do so, a level of uncertainty around each single value entered in the EwE input structure needs to be fixed. Uncertainty values were assigned as a percentage of the point estimate of each parameter. Minimum and maximum values of the parameter distribution can then be calculated as follows:

Limits = single value of the parameter

$$\pm(\text{percentage} * \text{single value of the parameter}) \quad (3)$$

In the present work, the *createpedigree* function was developed to ease this step, particularly in the case of pre-existing EwE models for which Pedigree scores were already estimated (Fig. 1 and Table 1). The Pedigree index (Funtowicz and Ravetz, 1990; Pauly et al., 2000) was designed to evaluate whether an EwE model was based on extensive field sampling performed within the boundaries of the system during specific dates. The Pedigree component in the EwE software allows marking/categorizing the data origin of each single input using pre-defined tables; the key criterion being that inputs from local data have the best confidence and the highest

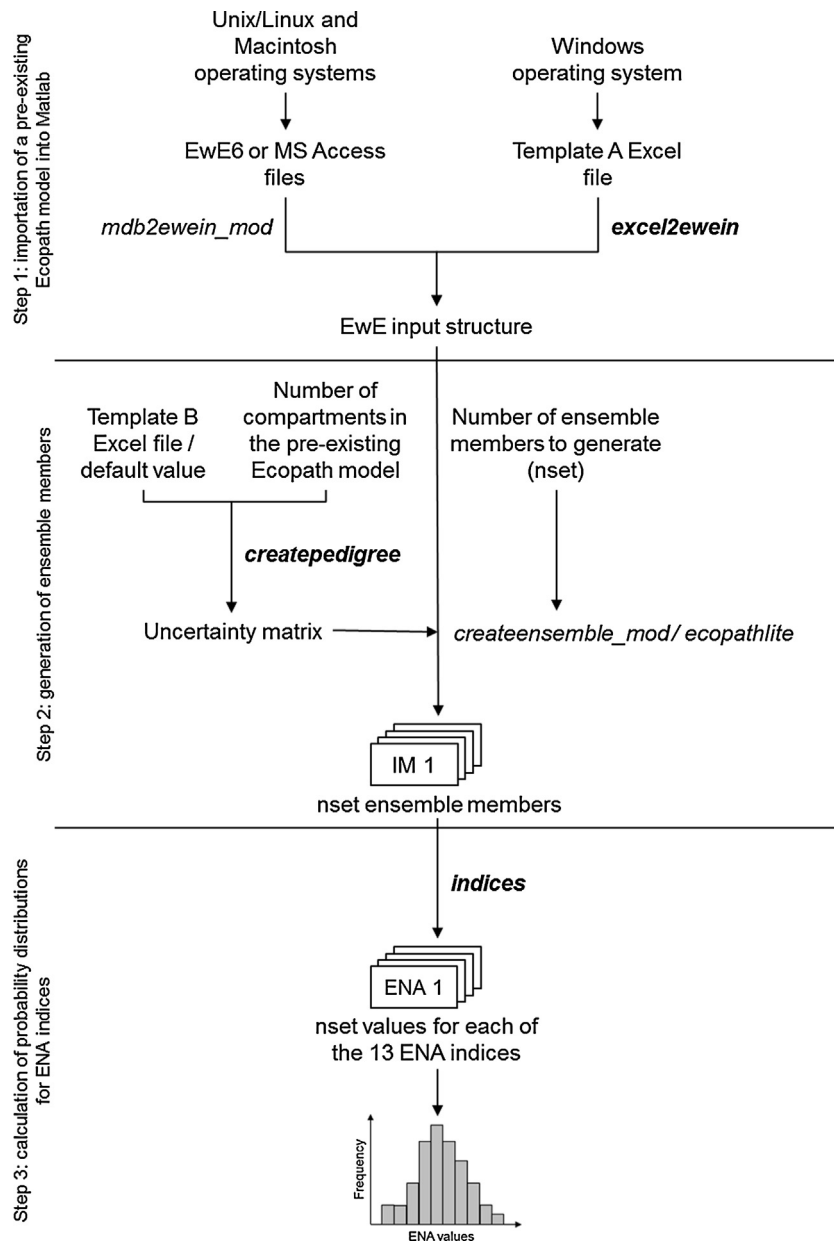
**Table 1**

Uncertainty applied to input parameters of the pre-existing Ecopath model of the Bay of Biscay continental shelf by Lassalle et al. (2011) (i.e. term 'percentage' in Eq. (3)). Values were derived from pre-defined tables provided by Christensen et al. (2005) associating a Pedigree score to each given level of uncertainty for each basic input parameter. Blank cells correspond to parameters left to be estimated by the model, where the parameter did not apply (e.g.  $Q/B$  for primary producers), or where the EwE software did not allow setting Pedigree scores (e.g.  $P/B$  of primary producers). To run the ENAtool routine, blank cells were replaced by zeros.

	$B$	$P/B$	$Q/B$	$DC$
Pursuit divers seabirds	0.1	0.9	0.5	0.8
Surface feeders seabirds	0.1	0.9	0.5	0.8
Striped dolphins	0.1	0.8	0.5	0.3
Bottlenose dolphins	0.1	0.8	0.5	0.3
Common dolphins	0.1	0.8	0.5	0.3
Long-finned pilot whales	0.1	0.8	0.5	0.3
Harbour porpoises	0.1	0.8	0.5	0.3
Piscivorous demersal fish	0.1	0.5	0.5	0.4
Piscivorous and benthivorous demersal fish 0.1	0.5	0.5	0.4	
Suprabenthivorous demersal fish	0.1	0.5	0.5	0.4
Benthivorous demersal fish	0.1	0.5	0.5	0.4
Mackerel	0.6	0.5	0.5	0.3
Horse mackerel	0.6	0.5	0.5	0.3
Anchovy	0.1	0.5	0.5	0.3
Sardine	0.1	0.5	0.5	0.3
Sprat	0.1	0.5	0.5	0.3
Benthic cephalopods	0.8	0.8	0.5	
Pelagic cephalopods	0.8	0.8	0.5	
Carnivorous benthic invertebrates	0.4	0.5		0.3
Necrophagous benthic invertebrates	0.4	0.5		0.3
Sub-surface deposit feeders invertebrates	0.4	0.5		0.3
Surface suspension and deposit feeders inv.	0.4	0.5		0.3
Benthic meiofauna	0.4	0.5		0.3
Suprabenthic invertebrates	0.4	0.5		0.3
Macrozooplankton	0.1		0.8	0.3
Mesozooplankton	0.1		0.8	0.3
Microzooplankton	0.1		0.8	0.3
Bacteria	0.1	0.1		0.3
Large phytoplankton	0.1			
Small phytoplankton	0.1			
Discards				
Detritus				

level in the scale (Christensen et al., 2005). In the pre-defined tables, each Pedigree score is associated with a default level of uncertainty expressed as  $\pm\%$ . For example, a Pedigree score of 1 (e.g. for a local biomass value) indicates a 10% uncertainty value. The *createpedigree* function builds a table of uncertainties based on an Excel file which contains for each parameter and each functional group the level of uncertainty to be applied to the single value (see Template B in supplementary material 2). Again, this Excel file can be opened with any spreadsheet program but must be finally saved as an Excel file. This Excel file can be also an export of the Pedigree table from the EwE software. If the user has no estimate of the uncertainty surrounding the input parameters in the pre-existing EwE model, a level of uncertainty can be set and a matrix of the same dimension as the uncertainty table will be automatically generated. With no specification from the user, the default values will be 20% around single values (Richardson et al., 2006).

As inputs, the *createensemble* function requires the uncertainty table built using the *createpedigree* function and the model imported into Matlab using *mdb2ewein* or *excel2ewein* (Fig. 1). The *createensemble* function generates a defined number of ensemble members that all fall within the prescribed uncertainty ranges. Parameter values can be sampled from a uniform distribution within limits fixed by the uncertainty table or a lognormal distribution with the mean and standard deviation set according to the uncertainty table. Both Latin hypercube and Monte-Carlo sampling methods can be used for random sampling in this interval. In the present application case, parameter values were randomly sampled using a Monte Carlo method from a uniform distribution with bounds directly related to the level of uncertainty.



**Fig. 1.** Schematic representation of the different Matlab functions that compose the ENAtool routine. The functions that were previously developed by Kearney (2012) are given in *italics*. In agreement with the developer, some modifications were made to these functions to enhance their applicability to all operating systems and to all EwE model versions. These modifications were specified in the name of the function by “\_mod”. The functions that were specifically built for the present work were marked in **bold**. The origins of formulas used in the *indices* functions are listed in Table 2.

The *ecopathlite* function called by the *createensemble* function is the one that reproduces the main calculations performed by the Ecopath module of the EwE software (Fig. 1). This function is a ‘stripped-down’ version of the Ecopath algorithms allowing an estimation of missing parameters by solving the system of  $n$  equations with  $n$  unknowns (see Eqs. (1) and (2)). Users can also choose whether they want ensemble members that respect the biomass conservation hypothesis, i.e. here, that met the ecotrophic efficiency balance requirements ( $EE < 1$ ). Combining *createensemble* and *ecopathlite* functions allows the user to compute a specific number (referred to henceforth as *nset*) of balanced ensemble members before calculating any ENA indices. For multi-stanza configurations, adjustments of parameters are made when calling *subecopathens.m* to calculate Ecopath values and check for balance. So the resulting ENA index values stemming from this code will incorporate the same multi-stanza relationships as in EwE.

### 2.2.3. Calculation of an ensemble of values for ENA indices

Finally, the *indices* function was developed in this present work to calculate a set of 13 ENA indices (Fig. 1; Table 2) for each ensemble member generated by the *createensemble* function. The mathematical formulas for these indices required a harmonization between the EwE and LIM ecosystem modelling communities. We compared the formulas in use in EwE with those currently in use by modellers working with linear inverse models (LIMs) in Matlab (Leguerrier et al., 2007; Johnson et al., 2009; Niquil et al., 2011; Saint-Béat et al., 2013) (Table 2). Most formulas were shared in common between both communities and were as such already available in Matlab. Ecological interpretations of ENA indices are summarized in Table 2. Full details regarding their links with ecosystem ecology theories can be found, for instance, in Ulanowicz (2004), Kones et al. (2009), and Saint-Béat et al. (2015).

**Table 2**

Formulas to calculate the 13 ENA indices in the *indices* function of the ENAtool routine. Formulas and their origins are presented for EwE software v.6 as well as for the linear inverse modelling approach. For each ENA index, its single value calculated using the EwE model of the Bay of Biscay continental shelf of Lassalle et al. (2011) was presented.  $TL_i$  is the trophic level of the  $i$ th functional group,  $Y_i$  the captures (i.e. landings and discards) for functional group  $i$ ,  $TST_c$  the sum of flows involved in cycles,  $T_{ij}$  the magnitude of the unidirectional flow from  $i$  to  $j$  (inflow),  $Q_i$  the consumption of functional group  $i$ ,  $DC_{ji}$  the proportion of  $j$  in the diet of  $i$  and  $BQB_i$  (or  $Ol_i$ ) is the omnivory index for  $i$ . The internal ascendancy  $A_i$ , internal capacity  $C_i$  and internal relative ascendancy  $A_i/C_i$  were also calculated by only considering internal flows to the system and constitute indices 11, 12 and 13, respectively.

Indices	General interpretation	EwE software formula	References	Single value of ENA index	Linear inverse modelling formula	References
Mean trophic level of captures (MTL)/no units	Fishing down, up or through the food web	$\frac{\sum_i TL_i \times Y_i}{\sum_i Y_i}$	Pauly et al. (1998)	3.753	~	
Total system throughput (TST)/kg C km <sup>-2</sup> year <sup>-1</sup>	Global activity of the system	Sum of all flows, i.e. consumption, respiration, imports and exports	Ulanowicz (1986)	935,578	~	
Finn cycling index (FCI)/no units	Proportion of flows in a system that is recycled	$\frac{TST_c}{TST} = \sum_j \frac{\sum_i T_{ij} + \text{Imports}_j}{TST}$	Finn (1980)	34.61	~	
Comprehensive cycling index (CCI)/no units	Proportion of all flows in a system that is recycled	$1.142 \times FCI$	Allesina and Ulanowicz (2004)	39.53	~	
Averaged path length (APL)/no units	Average number of functional groups that an atom of carbon passes through between its entry into the system and its exit	$\frac{TST}{\sum_i \text{Exports} + \sum_i \text{Respiration}}$	Finn (1980)	4.857	$\frac{TST - \sum_i \text{Imports}}{\sum_i \text{Imports}}$	Kay et al. (1989) and Baird et al. (1991)
Ascendancy (A)/flowbits	Quantification of the system activity in association with the degree of flows specialization	$\sum_i \sum_j T_{ij} \times \log \left[ \frac{TST \times T_{ij}}{\sum_j T_{ij} \times \sum_i T_{ij}} \right]$	Ulanowicz (1986)	860,882	~	
Capacity (C)/flowbits	Maximum potential ascendancy	$-\sum_i \sum_j T_{ij} \times \log \left[ \frac{T_{ij}}{TST} \right]$	Patricio et al. (2006)	3,808,206	$-TST \times \sum_i \frac{\sum_j T_{ij}}{TST} \times \log \left[ \frac{T_{ij}}{TST} \right]$	Ulanowicz (1986)
Relative ascendancy (A/C)/no units	Fraction of the system that is organized	$\frac{A}{C}$	Ulanowicz (1986)	0.226	~	
Overheads (O)/flowbits	Unorganized part of the system	$C - A$	Ulanowicz (1986)	2,947,325	~	
System Omnivory Index (SOI)/no units <sup>a</sup>	Omnivory	$\begin{cases} \sum_i \log \left[ \frac{Q_i}{\min(Q)} \right] \times BQB_i \\ \sum_i \log \left[ \frac{Q_i}{\min(Q)} \right] \times BQB_i \end{cases} \text{ si } s > 0$ <p>with <math>s = \sum_i \log \left[ \frac{Q_i}{\min(Q)} \right]</math> and</p> $BQB_i = Ol_i = \sum_j (TL_j - (\sum_j TL_j \times DC_{ji}))^2$	Villy Christensen (pers. comm.)	0.195	$\frac{\sum_i Ol_i \times \log[Q_i]}{\sum_i \log[Q_i]}$	Christensen and Pauly (1993)

<sup>a</sup> See <http://sources.ecopath.org/trac/Ecopath/ticket/1348> for issues regarding calculation of OI when imports are set in the diet matrix in Ecopath with Ecosim v.6.

### 2.3. The ENAtool application

#### 2.3.1. Description of the Bay of Biscay Ecopath model

A full description of the Bay of Biscay Ecopath parameterization can be found in [Lassalle et al. \(2011\)](#). The model considered for this zone was restricted to the central part of the shelf between the 30-m and 150-m isobaths with a surface area of 102,585 km<sup>2</sup> ([Fig. 2](#)). The model represented a typical year between 1994 and 2005, i.e. before the collapse of the European anchovy (*Engraulis encrasicolus*) and the subsequent five-year closure of the fishery for this species. Thirty-two *functional groups* were retained, including two seabirds, five marine mammals, nine fish, eight invertebrates, three zooplankton, two primary producers, one bacteria, discards from commercial fisheries, and pelagic detritus. Cephalopods were included in the form of two classes relating to their main oceanic domain (pelagic/benthic). The five main pelagic forage fish were given their own *functional groups* and demersal fish were divided into four multi-species *functional groups* on the basis of their diet regime. Marine mammals were included in the form of five mono-specific *functional groups* representing the small-toothed cetaceans most frequently encountered in the area.

#### 2.3.2. Summary of previous ENA-derived results

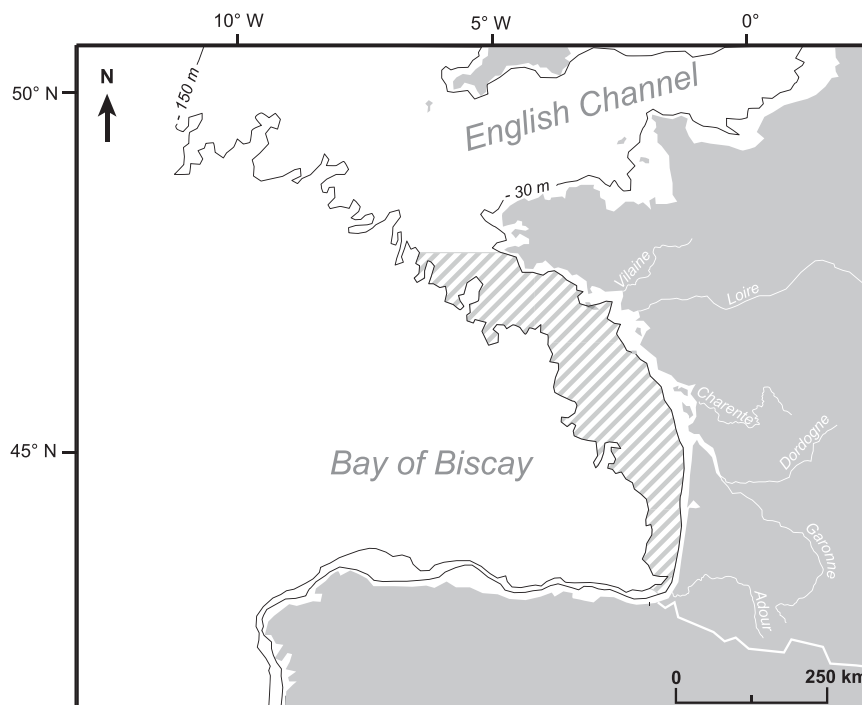
Some insights regarding the Bay of Biscay structure and function have been derived from ENA indices calculated with the EwE model of [Lassalle et al. \(2011\)](#) (see [Table 2](#) for single estimates). In this previous work, single point estimates were interpreted by comparison to those obtained for ecosystems of the same type or for other Ecopath models of the same ecosystem. The high Finn's Cycling Index (FCI) value, which measures the relative importance of cycling to the total flow ([Finn, 1980](#)), highlighted the strategic position of detritus as a perennial reservoir of energy in the Bay of Biscay. The System Omnivory Index (SOI) was regarded as an index reflecting the complexity of the inner linkages within the ecosystem ([Christensen and Pauly, 1992](#)). It is correlated with system maturity, since the internal network organization is expected

to increase as the system matures ([Odum, 1969](#)). The relatively moderate value for this output suggested a “web-like” food chain with an intermediate level of internal flow complexity. The Bay of Biscay also appeared as relatively immature, as indicated by the Ascendency (A), and has a high resistance to external perturbations according to System Overhead (O). Ascendency (A) merges the quantification of the system activity and the degree of specialization of flows in the network ([Ulanowicz, 1986; Ulanowicz and Wulff, 1991](#)). During maturation, ecosystem structure evolves towards an increase in ascendency ([Ulanowicz et al., 2006](#)). System Overhead (O) represents the amount of development capacity that does not appear as organized structure or constraints ([Ulanowicz, 1986](#)) and as such it corresponds to the system reserves when facing perturbations ([Heymans and Baird, 2000](#)).

#### 2.3.3. The Bay of Biscay Ecopath ensemble and ENA ensemble

The ENAtool routine was used to generate 1000 balanced ensemble members based on the uncertainty values assigned to each input parameter according to Pedigree scores ([Table 1](#)) ([Lassalle et al., 2014](#)); for this particular food web, the search for 1000 balanced ensemble members took between three and five days to run on a single-processor machine. For each ENA index listed in [Table 2](#), the single value obtained with the EwE software was graphically compared to the 1000 values derived from the ENAtool routine as to whether it falls between the boxplot whiskers. Then, the coefficient of variation between the mean value and the single Ecopath estimate was calculated.

The ‘balance’ constraint can move the parameter distribution of the balanced ensemble members away from the initial sampling distribution. It could make a crucial difference as to whether the ensemble experiment applied to the Bay of Biscay is simply adding error bars onto the input to the ENA index equations, or if it is adding error bars and shifting the mean/median value of the inputs variables. As such, an additional 1000-member ensemble based on the Bay of Biscay input dataset and Pedigree scores was generated, with keeping both balanced and unbalanced members. Then, the



**Fig. 2.** Study area of the Bay of Biscay continental shelf and locations of the main rivers flowing into it. The shaded area corresponds to the French part of the continental shelf between 30 and 150 m depth, and represents the spatial extent of the Ecopath model.



**Table 3**

Summary of results from the application of the ENAtool routine to the Bay of Biscay continental shelf ecosystem model and of results from the preliminary sensitivity analyses. 'Global' means that all input parameters were simultaneously changed according to the level of uncertainty and 'Local' that  $B$ ,  $P/B$ ,  $Q/B$  and  $DC$  were alternatively modified.

Application of the ENAtool routine ( $nset$ of 1000 and levels of uncertainty based on pedigrees)	Preliminary sensitivity analyses	
	Global/all combinations of $nset$ (10, 100, 1000) and levels of uncertainty (20, 40, 60%)	Local/ $nset$ of 1000 and level of uncertainty of 20%
<ul style="list-style-type: none"> <li>The single ENA indices values obtained from the pre-existing Ecopath model using the EwE software all fell within the boxplot whisker intervals.</li> <li>The coefficients of variation between the single ENA indices values obtained from the pre-existing Ecopath model using the EwE software and the mean distribution values were comprised between 0.08 (MTL) and 11.45% (Ci).</li> </ul>	<ul style="list-style-type: none"> <li>No influence of <math>nset</math> on the variance of ENA indices distributions.</li> <li>The variance of ENA indices distributions systematically increased with the level of uncertainty.</li> </ul>	<ul style="list-style-type: none"> <li>The variance of ENA indices distributions changed the most when variations were applied to <math>B</math> and <math>DC</math>.</li> </ul>

ensemble mean parameter values of these two ensembles were statistically compared using two-sample Kolmogorov–Smirnov goodness-of-fit tests ( $\alpha = 0.05$ ).

### 2.3.4. The preliminary sensitivity study

The ENAtool routine requires as main input arguments the number of ensemble members to generate and the level of uncertainty to be applied on  $B$ ,  $P/B$ ,  $Q/B$ , and  $DC$ . Therefore, it was important to study the influence of these arguments on the output variables, namely ENA indices. 1. A first exercise was performed to assess in which proportions ENA indices distributions were impacted by the number of ensemble members to generate and by the uncertainty set around input parameters in the ENAtool routine. Values for  $nset$  of 1000, 100 and 10 were tested. The point value of each parameter was changed by 20/40/60% up or down following Eq. (3). All combinations of  $nset$  and levels of uncertainty were run for the pre-existing Ecopath model of the Bay of Biscay continental shelf. 2. A second exercise tested which type of input parameter (i.e.  $B$ ,  $P/B$ ,  $Q/B$ , and  $DC$ ) influenced the ENA index distributions most strongly. To do so, the ENAtool routine was run with a  $nset$  of 1000 and a level of uncertainty of 20% alternatively applied to each input parameter type of the pre-existing Ecopath model of the Bay of Biscay continental shelf (Richardson et al., 2006).

In both exercises, the variance of ENA indices distributions (i.e. standard deviation squared) was the metric used to analyze the sensitivity results through graphical representations.

## 3. Results

First, based on the exploratory statistical comparisons of the parameter distributions between the balanced ensemble and the mixed ensemble (i.e. balanced and unbalanced), 52 of the basic estimates parameters shifted mean and 169 of the non-zero diet components shifted too.

For the pre-existing Ecopath model of the Bay of Biscay continental shelf, the value derived from the EwE software for each ENA index was compared to the range of values obtained following the application of the ENAtool routine to this model with a  $nset$  of 1000 and levels of uncertainty in accordance with Pedigree scores (Table 3). For  $A$ ,  $A_i/C_i$ , and MTL, the EwE single estimates fell within the range defined by the 1st (25%) and the 3rd (75%) quartile of ENA values (Fig. 3; Table 2 for the list of ENA indices with their abbreviations). For 9 of the 10 remaining ENA indices, the EwE single estimates fell in the upper boxplot whiskers calculated as 1.5 times the interquartile range. Regarding more specifically at the ENA indices used by Lassalle et al. (2011) in their assessment of the Bay of Biscay functioning, we calculated an FCI value with a mean of 33.09% across ensembles, compared to the single value of 34.61% obtained by Lassalle et al. (2011) (Fig. 3). The System Omnivory Index (SOI) presented the broader difference between the Ecopath

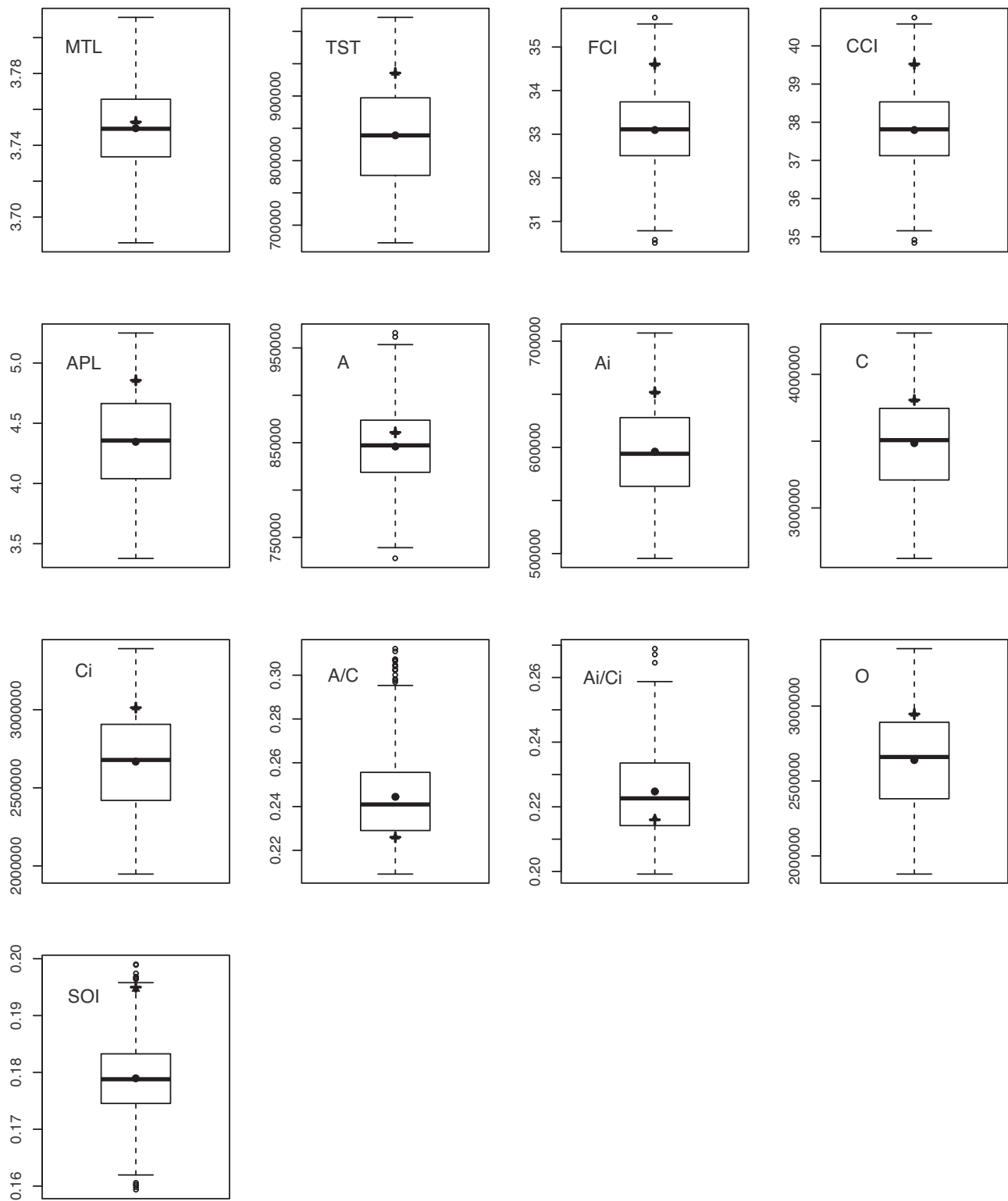
single estimate and the mean value, i.e. 0.195 versus 0.179, respectively (Fig. 3); the Ecopath SOI estimate being at the upper end of the distribution. The mean Ascendency ( $A$ ) was of 846,015 versus 860,882 flowbits for the pre-existing Ecopath model. The mean Overhead ( $O$ ) and the single Overhead estimate were of 2,639,671 and 2,947,325 flowbits, respectively. The coefficients of variation between the mean values and the single Ecopath estimates for those four indices were no greater than 10% (Table 3).

The first sensitivity exercise performed on the outputs of the ENAtool routine showed that the number of ensemble members generated induced no trend on the variance of ENA indices calculated as the standard deviation squared (Fig. 4 and Table 3). Indeed, for all of the three levels of uncertainty applied in the routine, i.e. 20, 40 and 60% on all parameters, and for all ENA indices, the variance of the distribution did not systematically increase with the number of ensemble members generated as first suspected (Fig. 4). On the contrary, when looking at a given number of ensemble members to generate, i.e. at a specific shade of grey, the variance of the distribution systematically increased with the level of uncertainty applied to the input parameters (Table 3). This trend was particularly marked for the Total System Throughputs (TST) with variances that almost doubled when the level of uncertainty was changed from 40 to 60% (Fig. 4). These results were in line with the method, as parameters for the ensemble members were here randomly sampled from a uniform distribution with bounds directly related to the level of uncertainty; every value in the interval having the same probability of being picked.

In the second sensitivity exercise, two input parameters appeared to be the most influential on ENA indices (Fig. 5). On the one hand, the Comprehensive Cycling Index (CCI), the Finn Cycling Index (FCI), the Mean Trophic Level of captures (MTL) and the System Omnivory Index (SOI) were the most sensitive to less constrained diet compositions ( $DC$ ) (Fig. 5). On the other hand, the relative Ascendency ( $A/C$ ), the Ascendency ( $A$ ), the Capacity ( $C$ ), the Averaged Path Length (APL), the Overheads ( $O$ ) and the Total System Throughput (TST) were the most sensitive to uncertainty in the Biomass ( $B$ ) parameter (Fig. 5).

## 4. Discussion

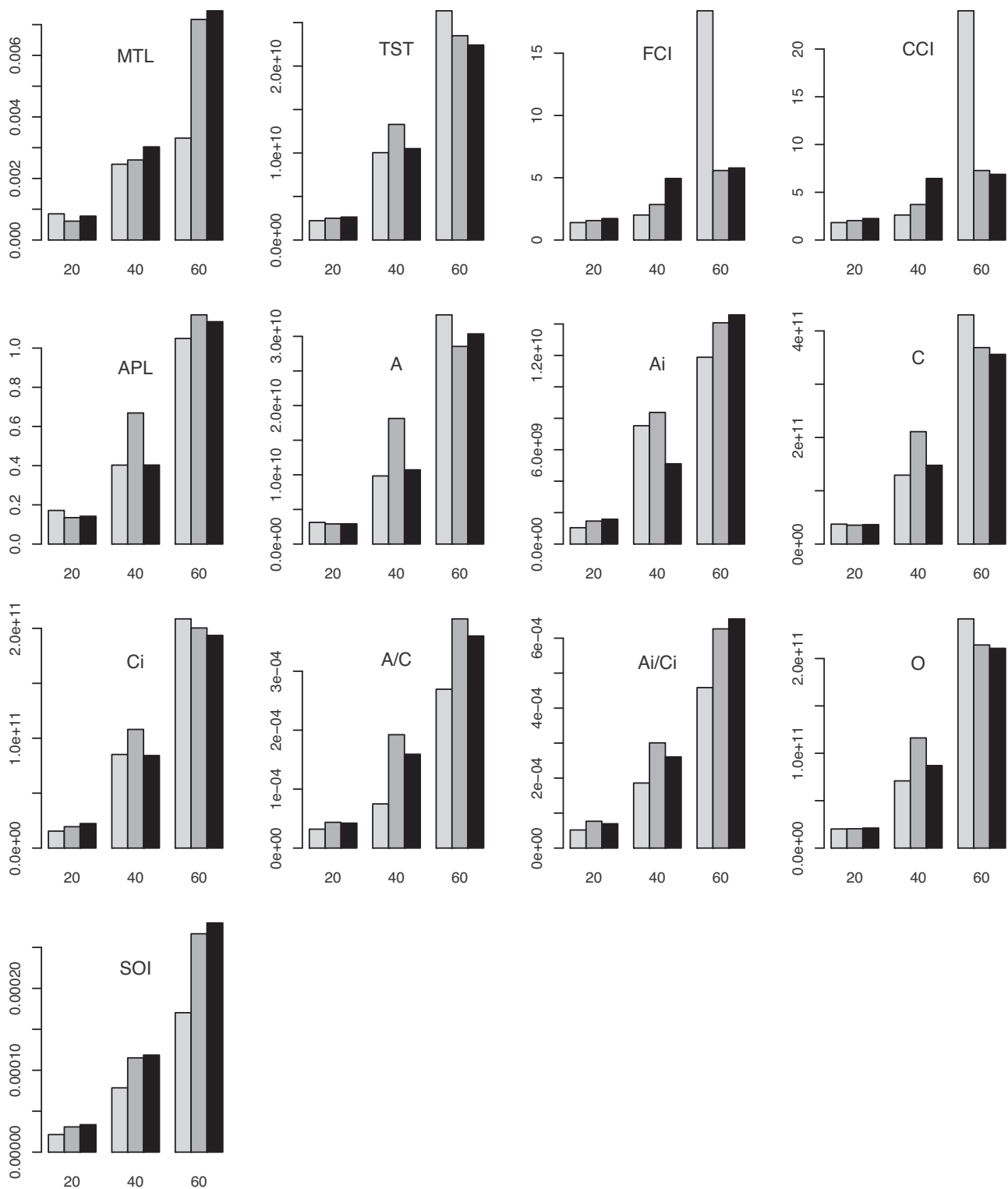
The present work provides EwE modellers, and more broadly ecosystem ecologists, with a routine that generates distributions of values for a set of well-known indices synthesizing structural and functional properties of ecosystems by taking into account uncertainty in model input parameters. In the first place, reanalyzing the Bay of Biscay continental shelf food web in the light of the most probable estimates of uncertainty around input parameters for this ecosystem supported the main ENA-derived ecological conclusions. Indeed, ENA index distributions all encompassed the single ENA values derived from the EwE software with mean values



**Fig. 3.** Boxplot of ENA indices values obtained from the ENAtool routine, run with a *nset* of 1000 and a level of uncertainty specific to each input parameter according to Pedigree scores for the pre-existing Ecopath model of the Bay of Biscay continental shelf of [Lassalle et al. \(2011\)](#). A black circle corresponds to the mean of the 1000 ENA indices values. A black cross represents the single ENA indices values obtained from the pre-existing Ecopath model using the EwE software. A black triangle is used for the ENA indices values calculated after the importation of the pre-existing Ecopath model to Matlab with no change on the input parameters. Results are depicted for the 13 ENA indices. Graphics are organized following the order of [Table 2](#).

in the same range as the initial Ecopath estimates ([Table 3](#)). The Bay of Biscay ensemble approach as such supported and strengthened the main conclusion of a detritus-based, and relatively mature ecosystem ([Lassalle et al., 2011](#)). In addition, when interpreting

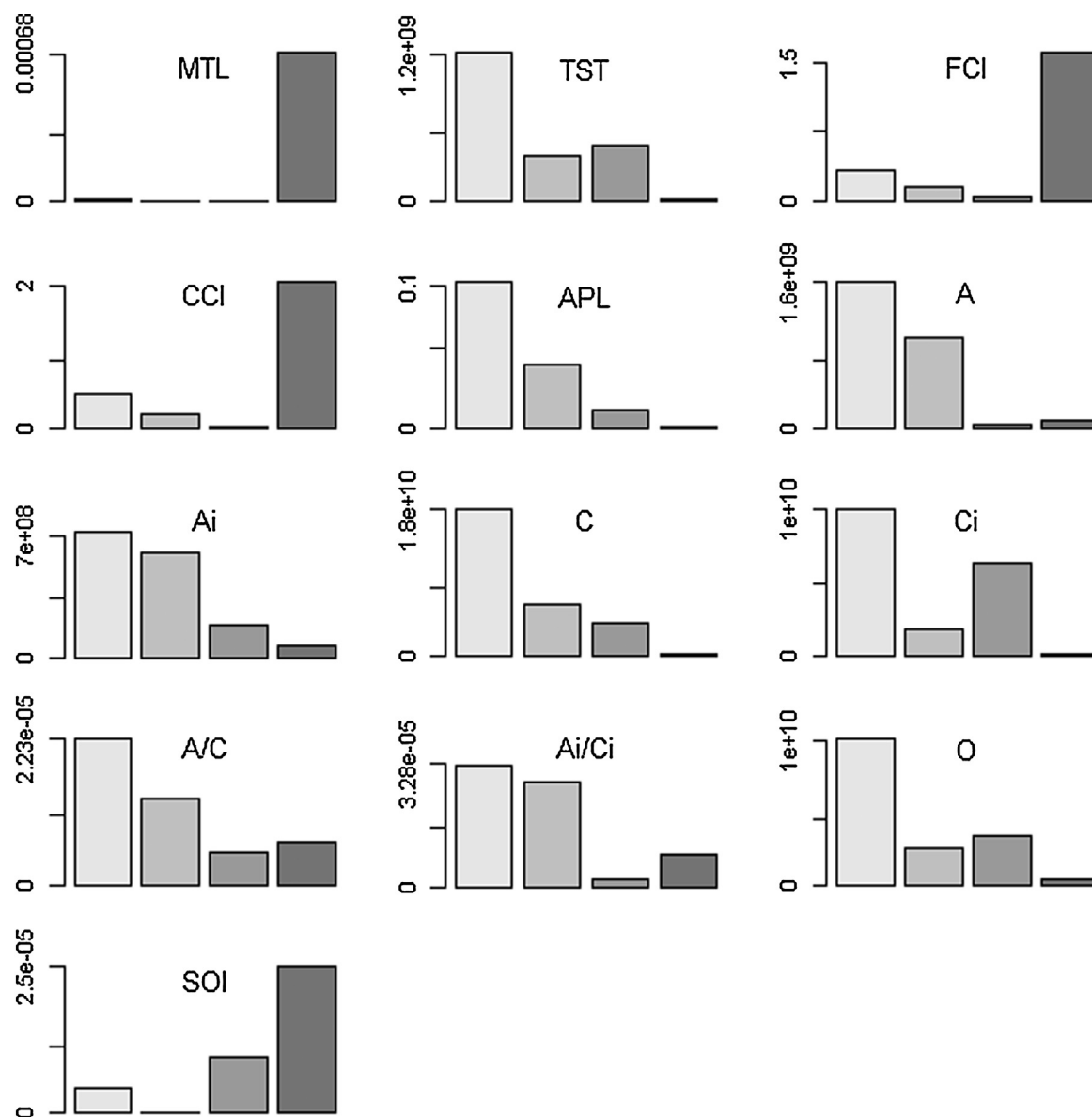
and using ENA distributions, it should be kept in mind that those values are derived from the propagation of parameter uncertainty forward but also, to some point, to the interplay in parameters required to keep the models balanced when any changes are made.



**Fig. 4.** Variance of ENA indices values obtained from the ENAtool routine run with every combinations of *nset* equal to 10 (light-grey bars), 100 (medium-grey bars) and 1000 (dark-grey bars) and levels of uncertainty of 20, 40 and 60% on the pre-existing Ecopath model of the Bay of Biscay continental shelf of Lassalle et al. (2011). Results are depicted for the 13 ENA indices. Graphics are organized following the order of Table 2.

The ENAtool routine was developed with the primary goal of strengthening ecological conclusions derived from comparative studies and before/after impact evaluations. Interpretation will no longer rely only on single value comparisons. The routine will permit one to test differences between ENA indices through statistical tests as performed in Saint-Béat et al. (2013) with LIM models.

The LIM models have evolved in the last decade from a single-solution method (Vézina and Platt, 1988) to statistical approaches with outputs composed of uncertainty intervals (density probability functions) of the flows and allowing the definition of uncertainty intervals of ENA indices. These methods first based on Monte Carlo approaches (Kones et al., 2006) are now used with a Monte Carlo



**Fig. 5.** Variance of ENA indices values obtained from the ENAtool routine run with a *nset* equal to 1000 and a level of uncertainty of 20% alternatively applied on each key input parameter. The application case is the pre-existing Ecopath model of the Bay of Biscay continental shelf of Lassalle et al. (2011). For each histogram, from the left to the right, the field biomasses are modified by  $\pm 20\%$ , then production to biomass ratios, consumption to biomass ratios, and finally diet compositions. Results are depicted for the 13 ENA indices. Graphics are organized following the order of Table 2.

Markov Chain routine (Kones et al., 2009). Several meta-analyses, based on a selection of EwE models, have been done, focusing either on theoretical ecology and ecological concepts, or on ecosystems and species of particular interest (see details in Colléter et al., 2013b), a growing proportion being based on ENA indices (e.g. Christensen, 1995; Pérez-España and Arreguín-Sánchez, 2001; Lobry et al., 2008; Coll and Libralato, 2012; Selleslagh et al., 2012). In the present work, complementary analyses were performed on the ENAtool routine to determine how much the ENA indices distributions were sensitive to the main routine arguments, namely the number of ensemble members to be generated (*nset*) and the level of uncertainty to apply on the EwE input parameters (Pedigree). The first induced no remarkable trend on the distributions whereas the latter was found positively related to the variance of the distributions (Table 3). As such, in future applications of the ENAtool routine, we recommend keeping the levels of uncertainty within a range compatible with known uncertainties on parameters. If no Pedigree scores were filled for the EwE model, model builders

or experts of the study area should be interviewed regarding the quality of data used during model construction. This was even more strongly suggested for field biomasses (*B*) and diet compositions (*DC*) that appeared as the most influential input parameters (Table 3). This last result can be also interpreted as an uncertainty analysis, showing that less constrained biomasses and diet compositions in input matrices both had a marked influence on ecosystem-level EwE model outputs such as ENA indices. This reinforces the well-known need for extra care to be used when setting these two parameters in EwE models, and more importantly for better information to be collected on these key characteristics of biological taxa. In the particular case of the Bay of Biscay, biomasses and diet compositions were both associated with low levels of uncertainty in the pre-existing Ecopath model, meaning they were already relatively well constrained by data. Within the four ENA indices that were strongly influenced by variations in diet compositions, the Mean Trophic Level (MTL) and the System Omnivory Index (SOI) were directly linked to trophic levels of functional groups

compared to the Finn Cycling Index (FCI) and the Comprehensive Cycling Index (CCI) for which interpretation of diet compositions influence was less intuitive. Nonetheless, FCI and CCI were both calculated from a matrix of internal exchanges that portrays the diet compositions of predators (Allesina and Ulanowicz, 2004). Indeed, both of these indices include the term  $T_{ij}$  (i.e. flow between functional groups  $i$  and  $j$ ) in their definition, which is the same as  $Q_{ij}$  in Ecopath, with  $Q_{ij} = B_j \times DC_{ij}$ . FCI, CCI and SOI were commonly used to assess key ecosystem structural and functional features such as system maturity (Christensen, 1995), complexity, and stability (Libralato, 2008). From an applied perspective, in a comparative study by Selleslagh et al. (2012), the SOI was also demonstrated to be positively correlated with the degree of anthropogenic perturbations in estuaries. In the context of the European Water Framework Directive, the development of more functional indicators based on fluxes of matters and energy, and trophic networks at the scale of the ecosystem was recently listed as a critical way to improve the implementation of European policies (Reyjol et al., 2014). In this scope, by using the ENAtool routine and by applying variations more specifically to the diet compositions, the robustness of this relationship 'SOI/anthropogenic impacts' is planned to be statistically tested in an upcoming comparative study before presentation as a potential indicator of "Good Environmental Status". Attention will have to be paid to the topology and the degree of aggregation among functional groups in the compared models as these two factors were demonstrated to influence ENA values (Johnson et al., 2009).

Application of the ENAtool routine is not strictly limited to the generation of ENA indices distributions for comparative studies; it can be also used to performed conventional uncertainty analyses. There is a need to assess parameter uncertainty of EwE outputs for decision making processes. In this scope, all balanced ensemble members derived from the resampling procedure in the ENAtool routine can be stored. And then, the various graphical representations proposed in the present work and more sophisticated statistical analyses can be performed to assess the influence of less constrained parameters on model estimates. Parameter uncertainty testing is also under development by the CEFAS (UK) where alternate balanced EwE models are generated to assess the impact of parameter uncertainty on fishing policies. A new R package, called 'Rpath', is currently under development and will address uncertainty in input parameters allowing for a creditable interval around model outputs (Lucey et al., 2014).

## 5. Conclusion

ENA indices are increasingly considered as potential indicators of ecosystem status. They express, alone or in combinations, key structural and functional aspects of a given system. The ENAtool routine will help to go a step further in ecosystem-based fisheries management (EBFM) by communicating to natural resources managers the distribution and mean values of ecosystem-level indices surrounded by confidence intervals. Statistical comparison of ENA index distributions, either between neighbouring ecosystems or under various management scenarios within a single ecosystem (i.e. before/after management action evaluations) can be performed using this tool, improving ecological diagnosis for a given system. Because the ENAtool routine is based on an ensemble parameterization technique, it will also contribute to the effort of the EwE community for parameter uncertainty testing.

## Acknowledgments

This research has been mainly supported by the project ANTRO-POSEINE (ANalysis of the TROPhic structure and cOntribution of

habitats from the SEINE River estuary) financed by the GIP-Seine Aval (<http://seine-aval.crihan.fr/web/>). It was also supported by the project DEVOTES (DEvelopment Of innovative Tools for understanding marine biodiversity and assessing good Environmental Status) funded by the European Union under the 7th Framework Programme, "The Ocean for Tomorrow" Theme (grant agreement no. 308392; [www.devotes-project.eu](http://www.devotes-project.eu)). The authors wanted to thank the two anonymous reviewers for their constructive remarks on the manuscript.

## Appendix A. Supplementary data

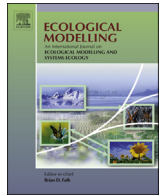
Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2015.05.036>

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# The mosaic of habitats of the Seine estuary: Insights from food-web modelling and network analysis



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## ARTICLE INFO

### Article history:

Received 30 January 2015

Received in revised form 19 May 2015

Accepted 23 May 2015

### Keywords:

Trophic network

Estuary

Ecological network analysis

*Ecopath with Ecosim*

Food web

Ecosystem health indicators

## ABSTRACT

Ecological network analysis was applied in the Seine estuary ecosystem, northern France, integrating ecological data from the years 1996 to 2002. The *Ecopath with Ecosim* (EwE) approach was used to model the trophic flows in 6 spatial compartments leading to 6 distinct EwE models: the navigation channel and the two channel flanks in the estuary proper, and 3 marine habitats in the eastern Seine Bay. Each model included 12 consumer groups, 2 primary producers, and one detritus group. Ecological network analysis was performed, including a set of indices, keystone, and trophic spectrum analysis to describe the contribution of the 6 habitats to the Seine estuary ecosystem functioning. Results showed that the two habitats with a functioning most related to a stressed state were the northern and central navigation channels, where building works and constant maritime traffic are considered major anthropogenic stressors. The strong top-down control highlighted in the other 4 habitats was not present in the central channel, showing instead (i) a change in keystone roles in the ecosystem towards sediment-based, lower trophic levels, and (ii) a higher system omnivory. The southern channel evidenced the highest system activity (total system throughput), the higher trophic specialisation (low system omnivory), and the lowest indication of stress (low cycling and relative redundancy). Marine habitats showed higher fish biomass proportions and higher transfer efficiencies per trophic levels than the estuarine habitats, with a transition area between the two that presented intermediate ecosystem structure. The modelling of separate habitats permitted disclosing each one's response to the different pressures, based on their a priori knowledge. Network indices, although non-monotonously, responded to these differences and seem a promising operational tool to define the ecological status of transitional water ecosystems.

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## 1. Introduction

Estuaries are at the interface of marine and freshwater ecosystems, and are usually characterised by high human activities and, accordingly, by high levels of anthropogenic pressure (Fairbridge, 1980; McLusky and Elliott, 2004). At the same time, they are among the most productive water ecosystems, of extreme importance

for biogeochemical cycles and for marine resources exploitation (Wilson, 2002). The importance of studying the effects of anthropogenic impact on estuarine ecosystems has increased in the last decade, especially in light of the Water Framework Directive, which mandates achieving "good environmental status" of all European water bodies by 2015–2021. However, the methods for evaluating environmental status are varied, addressing the issue at different scales (i.e. from populations to ecosystems), while a standardised methodology is still under discussion.

The Estuarine Quality Paradox refers to the issue of discerning human-driven stress in estuarine ecosystems, which are by

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baseline subject to high levels of natural environmental stress (Dauvin, 2007; Elliott and Quintino, 2007). Stress, in this context, is defined as a modification of ecosystem processes due to a response to an extended pressure from an external event or variable change (Odum, 1985). The paradox was identified particularly in the use of benthic community indicators, which are based on biodiversity assessments (Dauvin and Ruellet, 2009). In addition, the complexity of an estuary calls for a comprehensive consideration of both its internal dynamics and its ecological connections with the proximal marine biota (Able, 2005; Vinagre and Costa, 2014). A possible solution is the application of the ecosystem approach to ecological analysis, by which all species in the system are considered together, along with all flows and processes. Food-web modelling uses a series of linear equations to estimate values of all carbon flows occurring in a natural system, which can then be analysed with Ecological Network Analysis (ENA) indicators. The holistic ENA indices derived from food-web models were shown to partially discriminate natural from human pressures, and their use has been successfully applied in estuaries around European seas (Baird and Ulanowicz, 1993; Christian et al., 2005; Lobry et al., 2008; Patrício and Marques, 2006).

The Seine estuary is a mega-tidal estuary located in northern France, the third largest estuarine ecosystem in the country after the Gironde and Loire along the French Atlantic coast, discharging its waters into the English Channel (Meybeck et al., 1998). Anthropogenic pressures in the forms of water pollutants, landscape engineering, bridges and port building works, have all been identified as major shapers of the Seine estuary macrofauna assemblages (Dauvin et al., 2008, 2010). The Seine is the most polluted river in France, receiving human pressures from a highly-industrialised watershed, with important agricultural activities and inhabited by approximately 17 million people. The Seine estuary represents a typical estuarine ecosystem, highly stressed both by natural fluctuations and anthropogenic pressures, while at the same time hosting high levels of productivity (Dauvin and Desroy, 2005). A large part of the mouth of the estuary is included in a Natura2000 common interest area of the European Union and in a national natural reserve; however, no particular restrictions are in effect in the area. In addition, a new expansion of the Le Havre harbour (Port2000) was built in recent years, further eroding the surface of intertidal zones and increasing maritime traffic. Using ecological quality indicators, a previous assessment provided no definite findings on ecological status and concluded on the inability of discriminating between human pressures and habitat characteristics (Blanchet et al., 2008).

Various modelling efforts related to the English Channel have been performed over the years. In 2003, a first estimation of the trophic flows and biomasses in the Seine estuary was published, representing the state of the coastal system in the years 1996–1999 (Rybarczyk and Elkaïm, 2003). Their results showed a highly-productive ecosystem, far from ecological maturity as indicated by network analysis – an indication of stress (Christensen, 1995) – and more dependent than other estuaries on external sources such as river discharge. Rybarczyk et al. (2003) applied the same modelling approach in the Bay of Somme, another large estuarine system along the French coast of the eastern part of the English Channel. Another inverse modelling effort studied the whole eastern English Channel, finding a dominance of benthic carnivores in the food web, and evidences of differences in ecosystem functioning when the sediment benthic habitats were taken into account (Garcia et al., 2011). In particular, productivity and biological richness of estuaries were related to the capacity of their mosaic of habitats to perform functions essential to the life cycles of species inhabiting them (McLusky and Elliott, 2004). However, a more detailed analysis of the various habitats forming the Seine estuary, working at the ecosystem scale, has not been performed to date.

Moreover, the use and applicability of ENA to discern natural from anthropogenic stress, and thus their capability of circumventing the Estuarine Quality Paradox, although promising, has not been unequivocally demonstrated yet (Niquil et al., 2012).

In this work, we first describe the set up and balancing of 6 food-web models for different habitats of the Seine estuary, northern France, using the *Ecopath with Ecosim* approach. Modelling an ecosystem as a mosaic of habitats has been infrequently attempted (Baird et al., 2007; Vinagre and Costa, 2014). Then, we perform ENA on the resulting flow webs, to: (a) analyse the contribution of habitats and their key roles to the Seine estuary functioning, and (b) discuss the goodness of fit of ENA indices to environmental and anthropogenic stress and their use for ecosystem health management. This second objective is timely to recent European Union calls on assessing the applicability of ENA as ecosystem health indicators, considering the particular situation and scale of the Seine estuary as a case-study.

## 2. Materials and methods

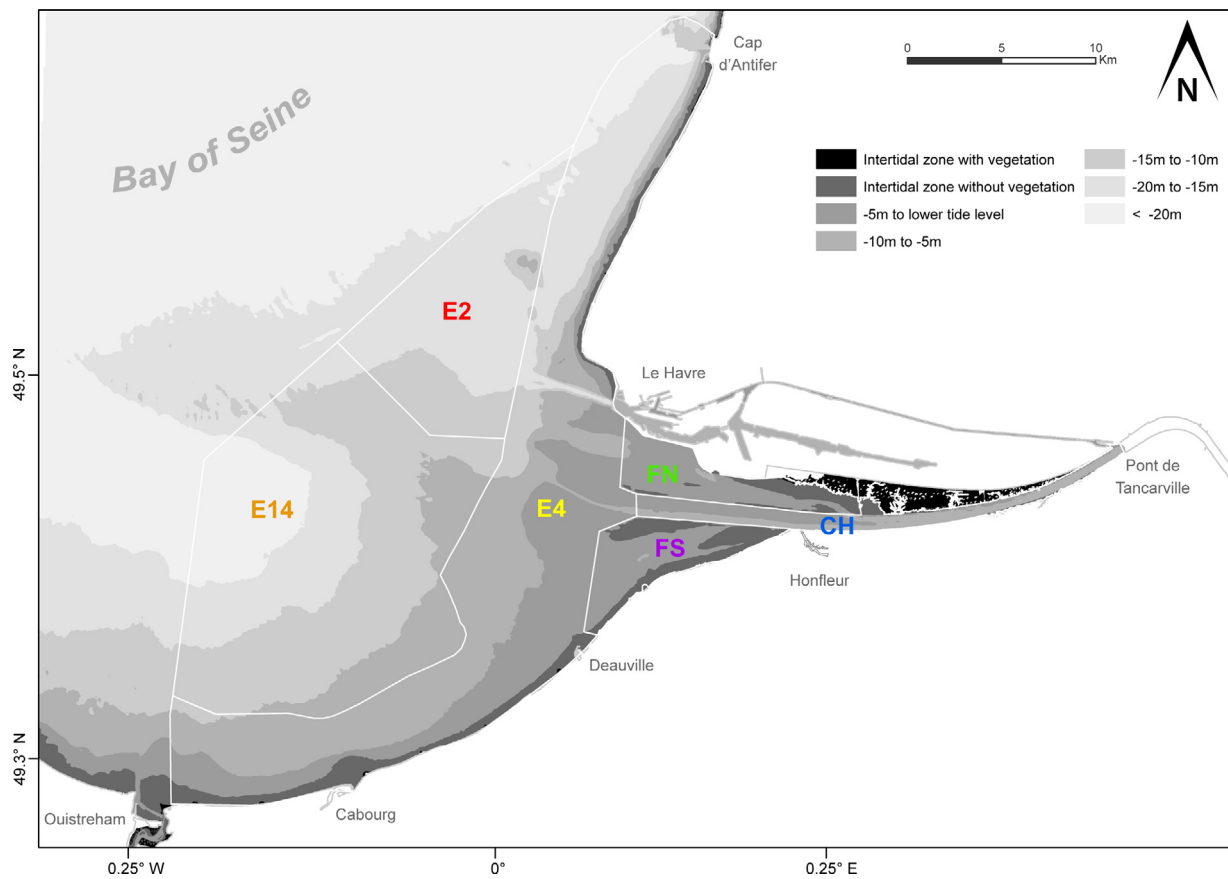
### 2.1. Study area

The Seine estuary and the adjacent western part of the Seine Bay were split into 6 spatial compartments, which were modelled separately (Fig. 1). Within the downstream part of the estuary proper, we identified three estuarine habitats, i.e. the northern channel (*Fosse Nord*, FN), the southern channel (*Fosse Sud*, FS) and the central navigation channel (*Chenal*, CH). Extending into the eastern Seine Bay, we identified 3 other spatial marine compartments based on their sediment composition and benthic habitat type (E4, E14, and E2), following guidelines by the European Union Nature Information System (EUNIS classification of benthic habitats). Due to the general current regimes in the Bay, and as the discharge plume of the Seine river flows primarily adjacent to the southern coast, the marine habitats under its influence were mainly E4 and E14, while the E2 was considered the habitat under the least influence of the plume (Salomon and Breton, 1991). We will refer to “habitats” from now on as the modelled spatial compartments, which represent homogenous zones from the hydro-sedimentary and salinity points of view. To better disclose this, we identified and summarised the levels of external pressures on each of the 6 habitats, by using a qualitative scale that ranged from – (no impact) to +++ (very high impact), according to both a literature review and the expert judgement of J.C. Dauvin.

The construction of the Le Havre harbour extension, called Port2000, started in the year 2002 and finished in 2005. As our objective was to exclude the impact of the harbour construction, which will be evaluated at a later date, models were set up representing the condition of each spatial compartment in the years before Port2000 construction, i.e. 1996–2002, for which an extensive dataset is available. The qualitative recollection of data above described was also relative on the same period.

### 2.2. Modelling approach

We used the *Ecopath with Ecosim* approach and software to estimate the carbon flows in the food webs. *Ecopath* is a mass-balance, single-solution model that uses linear equations to estimate flows between a number of functional groups established a priori (Christensen and Walters, 2004). Each group is parameterised with, at least, its biomass ( $B$ ,  $\text{gC m}^{-2}$ ), its production rate over biomass ( $P/B$ ,  $\text{year}^{-1}$ ), its consumption rate over biomass ( $Q/B$ ,  $\text{year}^{-1}$ ), its assimilation efficiency (or excretion rate,  $U/Q$ ), and the interactions with its prey and predators in the form of a diet matrix ( $DC$ ), which also establishes the identity of the trophic flows (Christensen and



**Fig. 1.** Map of the study area in the Seine estuary, northern France, with bathymetry and showing the subdivision of the six modelled habitats.

Source: Le Havre and Rouen port authorities, SHOM, and GIP Seine-Aval.

Pauly, 1992). Two linear equations for each functional group are solved to ensure mass and energy balance (Fig. 2) (Christensen and Walters, 2004). Eq. (1) expresses production ( $P$ ) as a function of predation, fishing mortality ( $Y$ ), net migration ( $E$ ), biomass accumulation ( $BA$ ), and natural mortality. Eq. (2) ensures energy balance, calculating consumption of the  $i$ th group ( $Q$ ) as the sum of its production, respiration ( $R$ ), and excretion ( $U$ ).

$$B \left( \frac{P}{B} \right)_i = \sum_j B_j \left( \frac{Q}{B} \right)_j DC_{ij} + Y_i + E_i + BA_i + B_i \left( \frac{P}{B} \right)_i (1 - EE_i) \quad (1)$$

$$Q_i = P_i + R_i + U_i \quad (2)$$

The models were considered at steady state, thus biomass accumulations and net migration rates were considered negligible compared to the rest of the flows and were set to zero. Each model included 15 functional groups, including one detritus group and two primary producers, i.e. phytoplankton and microphytobenthos. Consumer groups included bacteria, zooplankton, meiofauna, four benthic invertebrates groups, four fish groups, and seabirds. The groups were represented in all habitats to allow comparability.

Tables 1 and 2 show the input parameters used for all functional groups in the 6 habitats. Production, consumption, and excretion rates were obtained from literature, or from empirical equations (Pauly, 1980; Pauly et al., 1993) when data were available. All source data used for obtaining model parameters are listed in Supplementary Material Table 1. The maximum level of detail was available for fish and benthic invertebrates groups, as source data for biomasses and diets was compiled from a series of past research projects conducted in the area. Biomasses of fishes, which were generally available as wet weight ( $\text{g m}^{-2}$ ), were converted to carbon content ( $\text{gC m}^{-2}$ ) using a conversion factor of 0.11 from Oguz et al. (2008).

For benthic invertebrates, biomasses were converted from ash-free dry weight to carbon content using a conversion factor of 0.518 (Brey, 2001).

We also summarised the quality of source data for biomasses,  $P/B$ ,  $Q/B$ , and diet compositions into the Pedigree routine, which calculates a value between 0 and 1 related to the overall quality of the data (with 0 indicating that data is of low quality, and 1 indicating that data is highly precise and fully rooted in local studies).

All models had to be manually and slightly modified in their input data to equalise the mass balances. The balancing approach was top-down, starting modifications from top predators down to the lowest trophic levels. Balancing was performed taking into account the quality of source data as described by the Pedigree. When modifications had to be made, diet compositions were varied before other parameters. Each model was considered balanced when: (a) it did not violate mass balance, i.e. all  $EE$  were  $<1$ , (b) it did not violate energy balance, and (c) metabolic coefficients were reasonably within the known limits for each group (respiration/biomass ratio of 1–10 for fishes, and food-conversion efficiencies in the range 0.1–0.3 for consumers in general).

### 2.3. Network analysis

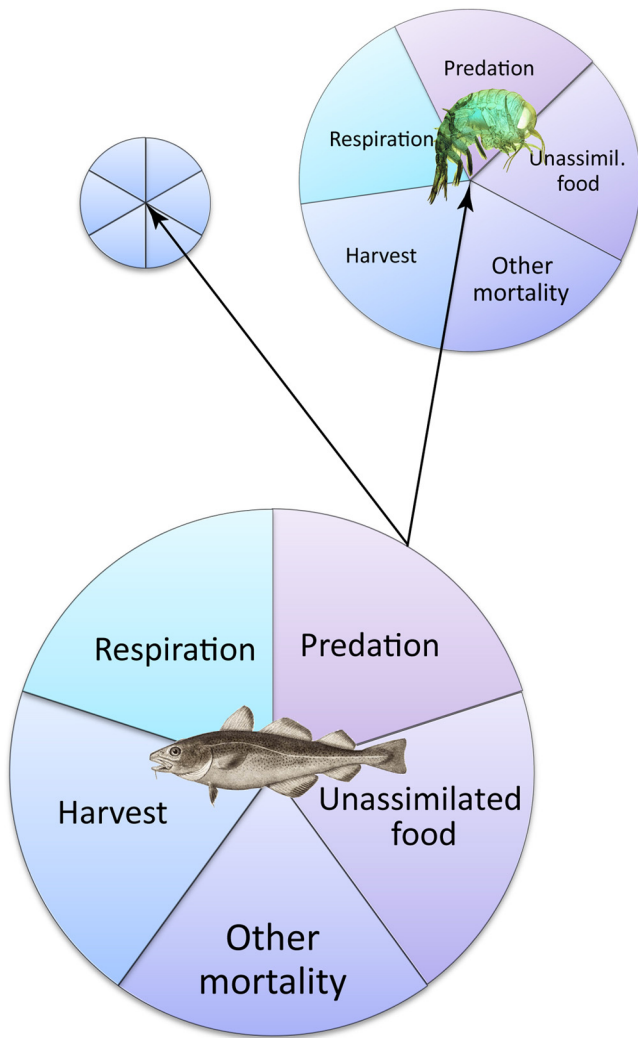
After models were balanced, the trophic level ( $TL$ ) of each functional group ( $i$ ) was calculated as the weighted average of the trophic levels of its prey ( $j$ ), according to:

$$TL_i = 1 + \sum_{j=1}^N DC_{ij} TL_j \quad (3)$$









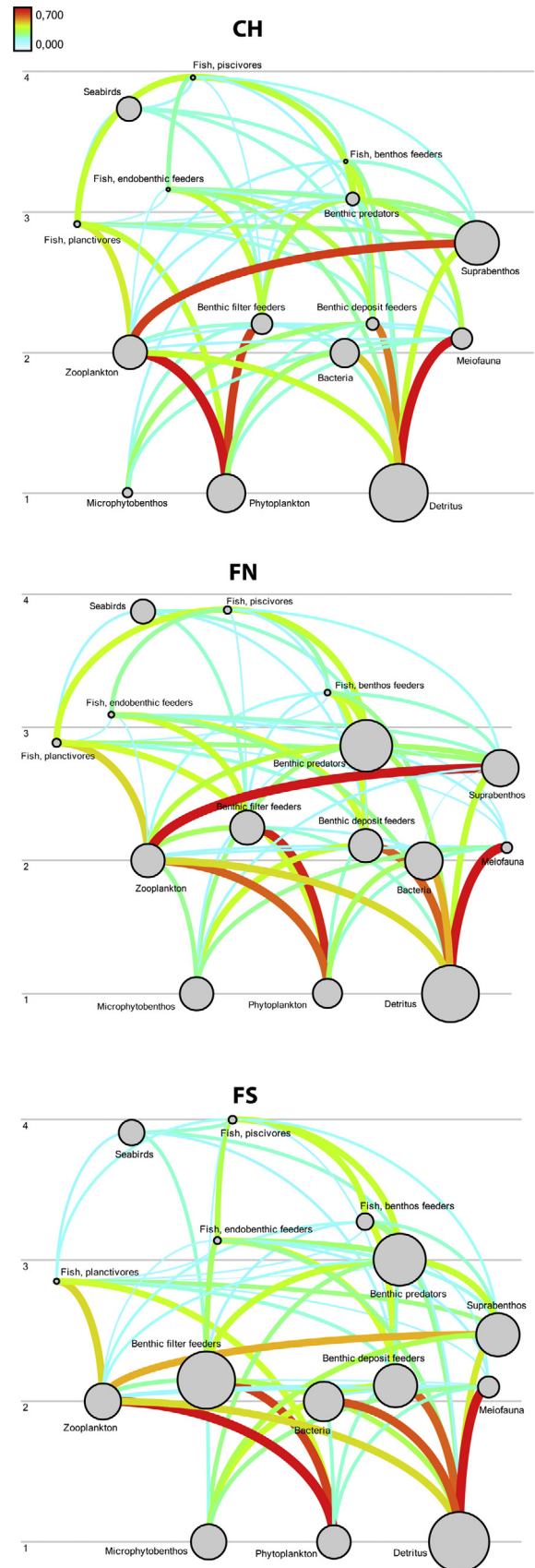
**Fig. 2.** Conceptual diagram explaining how Ecopath splits the production flows into the energy balance, and how the various functional groups (represented by the pies) are connected, as production for a prey is consumption for a predator. In our work, harvest ( $Y$  in Eq. (1)) was assumed zero.

estimates were always considerably lower than in other areas where field biomasses were measured, confirming the initial assumption of reduced prevalence. More generally, as biomass estimations are obtained from the mass balance equations, this accordance between assumption and estimation suggests a correct parameterisation of the predatory flows through the whole food web.

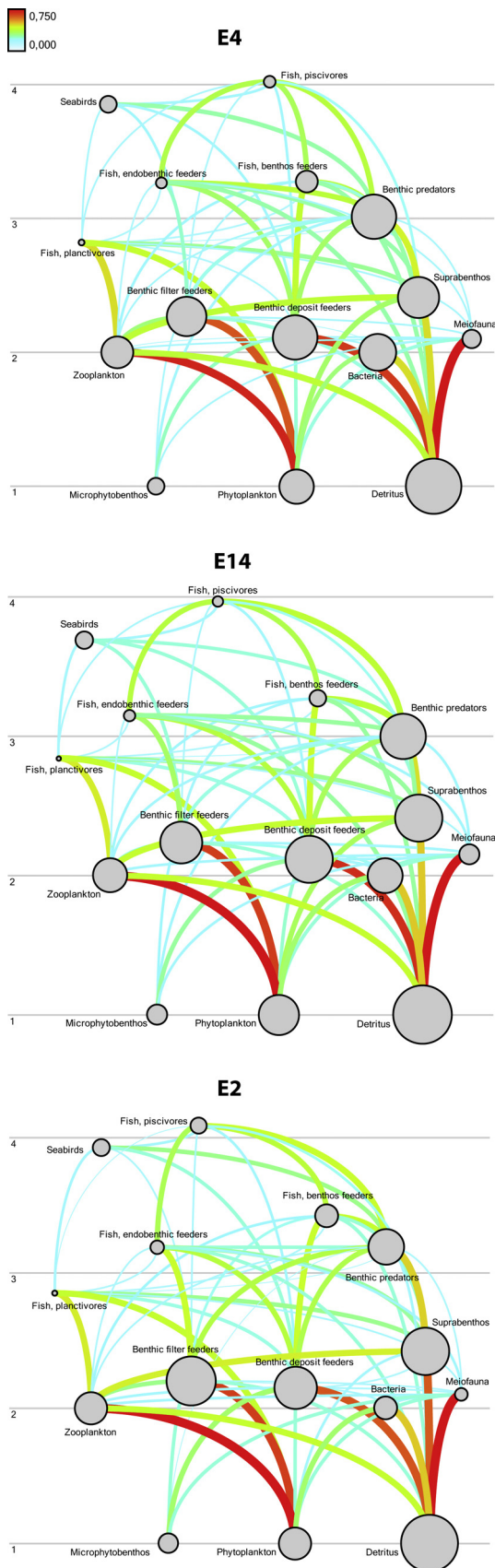
### 3.2. Ecosystem flow structure

Trophic levels (TL) ranged from 1.0 to a maximum of 4.1, represented in all models by fish piscivores that can be thus considered as top predators in the area (Figs. 3 and 4). Also at the top of the food webs were seabirds, which however acquired a large percentage of their diet from external sources. Trophic levels varied slightly between habitats, maintaining however the same rank order between functional groups. This shows that the balancing procedures did not change the relative importance of prey/predator interactions introduced with the diet matrix.

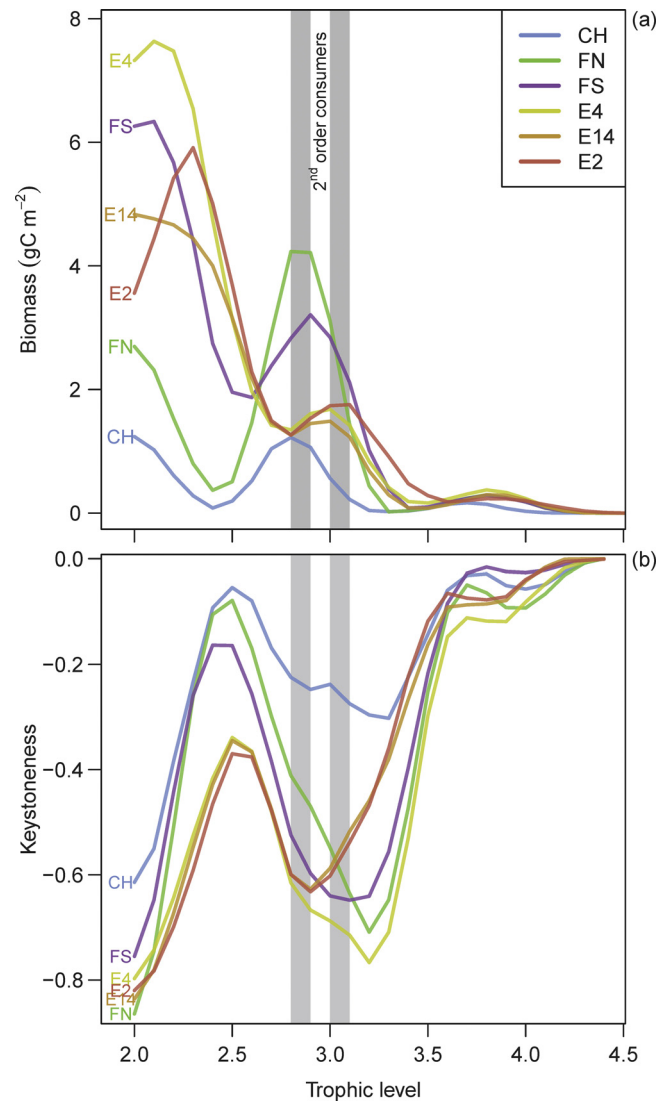
The majority of the functional groups maintained approximately the same omnivory between habitats, with the widest variations in omnivory index between habitats shown by the benthic predators (0.11–0.52). The groups with the highest omnivory were seabirds,



**Fig. 3.** Flows and biomasses of the three estuarine habitats (CH, FN, FS). Flows values by diet are indicated by the colour scale, while group biomasses are logarithmically proportional to the area of their respective circles. Groups are vertically positioned by their calculated trophic level.



**Fig. 4.** Flows and biomasses of the three marine habitats (E4, E14, E2). Flows values by diet are indicated by the colour scale, while group biomasses are logarithmically proportional to the area of their respective circles. Groups are vertically positioned by their calculated trophic level.



**Fig. 5.** Continuous trophic analysis of (a) biomass and (b) keystoneity, by trophic levels, for the six modelled habitats of the Seine Bay. Grey rectangles indicate the position of peaks identified in (a) as second-order consumers, and are repeated in (b) for reference. The first grey bar represents the peak of second-order consumers in estuarine habitats and the second one the peak in marine habitats.

fish planktivores, and fish benthos feeders, while the most specialised groups in terms of trophic habits were fish piscivores and, to a lesser degree, benthic deposit feeders (Supplementary Material Table 3). Meiofauna also showed low omnivory, due to them feeding mainly on detrital sources.

In terms of ENA overall indices, the total ecosystem activity (measured with the sum of all flows,  $T_{..}$ ) was the highest in the southern channel, mainly due to high values of export and flows to detritus (Table 3). The rest of the habitats had comparable activity levels, ranging from 1161 to 1826  $\text{gC m}^{-2} \text{y}^{-1}$ . The net system production and the ratio of primary production over total biomass were however the lowest in the southern channel, suggesting a less efficient utilisation of the inputted production, compared to the other modelled areas. The highest production over total biomass ratio was found in the central navigation channel, where the total biomass was the lowest.

The ratio of fish biomass over invertebrate biomass was reduced in the estuarine zones compared to the marine zones, with values ranging 1.14–1.48 in the former while ranging 2.27–4.56 in the Seine Bay. The total transfer efficiency (TE) between discrete

**Table 3**

General system statistics and ecological network analysis (ENA) indices of the 6 modelled ecosystems in the Seine Bay.

	CH	FN	FS	E4	E14	E2
Model area (km <sup>2</sup> )	24	25	28	270	232	90
Sum of all consumption (g m <sup>-2</sup> y <sup>-1</sup> )	413.05	575.62	706.82	633.78	703.92	697.84
Sum of all exports (g m <sup>-2</sup> y <sup>-1</sup> )	123.14	100.81	1681.98	183.34	300.59	84.54
Sum of all respiratory flows (g m <sup>-2</sup> y <sup>-1</sup> )	123.14	188.65	257.83	220.56	258.82	232.21
Sum of all flows into detritus (g m <sup>-2</sup> y <sup>-1</sup> )	535.92	295.98	1938.30	417.92	563.11	356.79
Total system throughput (T <sub>s</sub> ) (g m <sup>-2</sup> y <sup>-1</sup> )	1469.04	1161.05	4584.92	1455.60	1826.44	1371.39
Sum of all production (g m <sup>-2</sup> y <sup>-1</sup> )	635.75	417.10	492.31	541.72	707.27	483.24
Calculated total net primary production	498.10	229.34	280.70	343.82	499.31	256.71
Total primary production/total respiration	2.59	1.22	1.09	1.56	1.93	1.11
Net system production (g m <sup>-2</sup> y <sup>-1</sup> )	374.97	40.70	22.87	123.26	240.50	24.50
Total primary production/total biomass	48.68	8.99	6.95	12.02	16.68	9.15
Total biomass/total throughput	0.007	0.022	0.009	0.020	0.016	0.020
Total biomass (excluding detritus) (g m <sup>-2</sup> )	10.23	25.52	40.40	28.60	29.94	28.05
Fish biomass/invertebrate biomass (%)	1.48	1.17	1.14	4.36	2.27	4.56
Total transfer efficiency (%)	4.50	5.20	6.80	9.10	7.40	9.90
System Omnivory index (SOI)	0.184	0.193	0.160	0.186	0.177	0.160
Finn's cycling index (FCI) (% of T <sub>s</sub> )	8.52	18.94	3.65	13.86	11.23	20.65
Average path length (APL)	2.825	4.011	2.634	3.604	3.265	4.330
Relative redundancy (R/C)	0.556	0.535	0.380	0.580	0.590	0.542

trophic levels behaved similarly, with the estuarine zones (CH, FN, and FS) having overall lower efficiencies than the 3 marine habitats. The mean TE for the estuarine habitats was  $5.50 \pm 1.17\%$ , while in the marine habitats it was  $8.80 \pm 1.27\%$ . Zooming on the southern channel, its TE was 6.8%, the highest of the 3 estuarine habitats.

The system omnivory index (SOI) ranged 0.160–0.193, at the lower end of the range for marine ecosystems of the northern Europe (0.14–0.36, Mackinson and Daskalov, 2007). Omnivory was highest in the FN, was lowest in the FS and E2 habitats, and showed comparable intermediate values in the other habitats. High system omnivory in FN was mainly caused by high omnivory of benthic predators, while the lower SOI in FS and E2 were caused by lower contributions of benthic filter feeders and benthic predators, respectively. Finn's cycling index (FCI) was the index with the widest range between habitats. FCI ranged from 3.65% to 20.65%, with the highest values present in the E2 and FN sites, while being lowest in the FS. The average path length, which is calculated using the same logic as FCI, showed again higher values in the E2 and FN while being the lowest in the FS; path length in general ranged between 2.63 and 4.33. The relative redundancy index evidenced a single habitat, FS, which showed the lowest value (0.380) while the rest of the habitats with values comprised between 0.535 and 0.590, presenting more than half of their flow paths in parallel.

### 3.3. Ecological roles

Trophic spectrum of biomass showed differences mainly between the estuarine and the marine zones, with the latter showing biomass peaks at approximately one quarter of trophic level higher than the estuarine systems (Fig. 5a). The biomass peak of the second-order consumers was located at TL 2.75–2.95 for the three estuarine habitats, whereas it was visible at TL 3.05–3.15 for the marine habitats. These peaks were mainly produced by invertebrate benthic predators, in all habitats but the CH, where it was caused by increased biomass of suprabenthos (mainly due to the decapod *Palaemon longirostris*). The peaks for top predators were also shifted towards the same direction, but more overlapped due to their reduced contribution in biomass. The highest levels of keystone-ness were concentrated in all habitats in a peak at TL=2.5, and at TL>3.5 (Fig. 5b). Between these two peaks, the CH habitat behaved differently from all others, decreasing only down to -0.3. The biomass peak of second-order consumers was therefore not reflected in a higher trophic impact of their components over the rest of the food web, as the peaks of the two spectra did not superpose.

Keystoneness patterns showed variations between the different food webs (Fig. 6). Fish piscivores were always present at the highest positions in all 6 habitats, along with seabirds. Seabirds had the highest keystone-ness in all habitats except E4, where they stand considerably lower, and CH, where they had similar position as meiofauna. The northern channel (FN) had also zooplankton and phytoplankton occupying the third and fourth position, respectively, following seabirds and fish piscivores.

In the marine habitats, key roles were subject to wider variations, and benthic predators showed high keystone-ness. However, they appeared as structuring species rather than keystone, due to their high biomass in all three habitats. This was especially evident in E4, where benthic predators dominated the biomass along with benthic deposit feeders, and both showed high values of keystone-ness.

## 4. Discussion

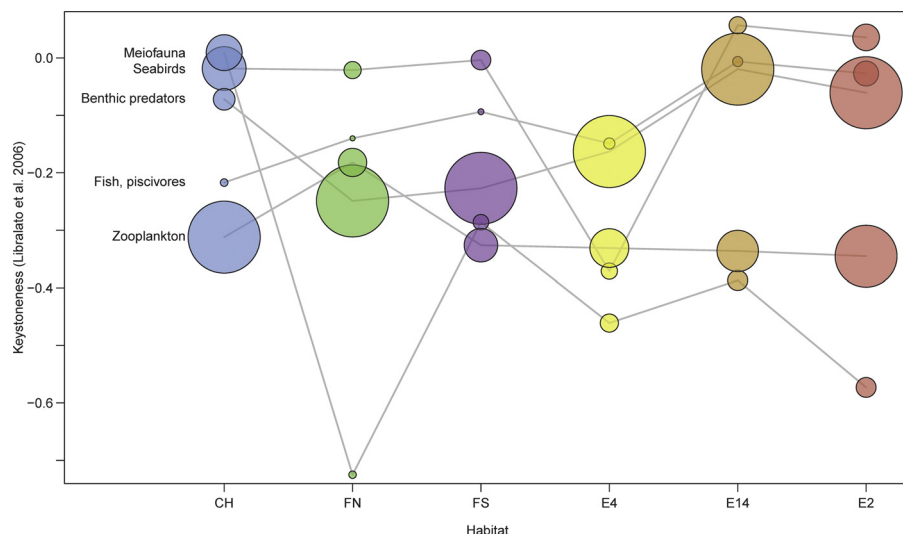
### 4.1. Advantages and limitations of the models

The usefulness of comparing snapshot ecosystem models, representing different habitats of a same biogeographical region, became evident over the last decade (Baeta et al., 2011; Baird et al., 2007; Lassalle et al., 2013; Patrício et al., 2004). In this study, we presented the most updated and comprehensive modelling effort for the Seine estuary food web. The models were rooted in high-quality source data as evidenced by the high Pedigree value, compared to literature, and by the consistent estimates of the missing biomasses. Also, by studying a continuum of estuarine and marine habitats (in the proximity of the Seine Bay) this approach provided one of the first insights of the differences between food-web structure and function along the estuarine-coastal gradient, from which future studies of inter-habitat connectivity through flows of energy will be possible.

The sampling programmes used as biomass source data focused particularly on benthic megafauna and fishes. Small-sized trophic groups, such as bacteria, microphytobenthos, and meiofauna, were mainly parameterised using data from other models of the same area or of similar regions (see Supplementary Table 1). However, the same pattern of knowledge was available for all six habitats, thus permitting relevant comparisons between them.

Estuarine and marine habitats are known to have ostensibly different abiotic conditions between them and, following from it, different community structures and functions (Fairbridge, 1980; Heip and Herman, 1995; Wilson, 2002). For this reason, it is pivotal





**Fig. 6.** Keystoneness index by Libralato et al. (2006) by functional group for each of the six modelled habitats (indicated also by colour codes). The area of circles is proportional to each group biomass, relative to its habitat. Only groups with high keystoneness ( $>0.55$ ) are represented.

to characterise each habitat along an estuarine-coastal gradient as it would provide useful information for spatial management planning. In addition, setting a baseline of ecological index values will allow for subsequent before/after impact evaluations, such as in the case of the construction of Port2000 harbour extension. Using models to represent a mean multi-annual condition also helps reducing noise from low-scale temporal trends, and will allow for a more thorough observation of long-term patterns.

#### 4.2. Characterisation of habitats in the Seine estuary

In the central navigation channel (CH) meiofauna was shown to play a keystone role, indicating an increased importance of substrate processes. In fact, the sediment of CH is constantly reactivated due to high levels of resuspension caused by the year-round maintenance dredging to keep the channel navigability and by maritime traffic for the Rouen harbour 120 km upstream (Dauvin and Desroy, 2005). Maintenance dredging causes smothering and removal of bed organisms, and increased turbidity with impact to fishes (Elliott and Hemingway, 2002). In fact, the biomass of both fishes and macrobenthic invertebrates in the CH was the lowest of the estuary, leaving detritus-driven dynamics as the main active compartment. To better disclose this process, more detailed approaches should be undertaken: to date, the *Ecopath* approach does not allow focusing on the fine details of flows to and from detritus, and the bacterial dynamics are also modelled in coarse detail (Christensen and Walters, 2004). More complex inverse modelling techniques, possibly coupled with in situ measurements of sediment community functioning and quantification of uncertainty, might be better suited to solve this critical issue in terms of system productivity.

In the keystoneness analysis, two habitats – FN and E4 – behaved differently from the rest. The highest levels of impact were registered in the FN according to ENA, which is in reality a combination of both anthropogenic and environmental stress (Table 4). The highest levels of system omnivory (SOI) and high carbon recycling (FCI) compared to the other estuarine habitats logically revealed that FN is therefore a highly impacted area, where benthic invertebrate predators dominate the community, and where the food web is associated with a more web-like structure.

In E4, top-down control was reduced by the low keystoneness of seabirds and by the increased importance of phytoplankton. This

evidences a particularly interesting condition, with E4 being a possible ecotone and mediating the transition from estuarine to marine environments by hosting changes in keystone species with respect to the neighbouring habitats. The Seine estuary is particular in the sense that the gradient of salinity is limited than in other estuaries and it is concentrated at the mouth of the estuary, while the fluvial part of the watershed is shifted up flow (Meybeck et al., 1998). In addition, estuarine and marine zones differed in their overall community composition and discrete trophic levels structure: the estuarine habitats hosted a lower proportion of fish biomass over invertebrate biomass than the marine habitats, and lower transfer efficiency between trophic levels. A difference between these two regions suggested that the E4 habitat might indeed be considered as a transition, ecotone-like, zone. Apart from their ecological interest, estuarine ecotones are considered as key areas for stability and functioning of water ecosystems (Elliott and Whitfield, 2011) and thus host interesting conditions to be specifically tested by means of ENA.

In the analysis of the biomass trophic spectrum, a movement of biomass peaks towards lower trophic levels would theoretically indicate a response to stress (Gascuel and Pauly, 2009). However, this paradigm was studied in relation to fishing impact, where the removal of biomass of high TL would shift the structure of the community “down” the food web (Pauly et al., 1998). In this study, the second-order consumers indeed occupied slightly lower trophic positions, evidencing a response from stress with respect to the marine habitats. However, it is unlikely that this response is caused by fishing because the estuarine habitats are subjected to considerably less fishing effort than the marine ones, apart from the fishery on the decapod *Crangon crangon*. More generally, the Seine estuary is the ecosystem least exploited by fishing in the southern English Channel (Martin et al., 2009). Rather, it is more probable that this analysis can evidence multiple stresses with potential synergistic effects, such as the ones caused by wide-spread anthropogenic disturbance from construction, marine traffic, and water pollution. In fact, the peak of second-order consumers was mainly caused by suprabenthos in the CH, while benthic predators dominated the peak in all other habitats, in accordance to what was found in a more extended study of the English Channel (Garcia et al., 2011). This confirms results from the keystoneness analysis, and further suggests the particular importance of sediment community processes in the CH habitat.

**Table 4**

Qualitative analysis of impacts for each of the 6 modelled habitats. Categories ranged from – for no impact to +++ for very high impact.

	CH	FN	FS	E4	E14	E2	References
Dredging	+++	–	–	–	–	–	Marmin et al. (2014)
Deposit	+	+++	–	+++	–	–	Marmin et al. (2014)
Dyke	+++	++	++	–	–	–	Guezennec (1999) and Cuvilliez et al. (2009)
Loss of intertidal zones	–	+++	–	–	–	–	Cuvilliez et al. (2009) and Dauvin and Desroy (2005)
Shrimp fishing	+	+	+	+++	–	–	Morin et al. (2010)
Other commercial trawling	–	–	+	++	++	++	Morin et al. (2010)
Granulate extraction	–	–	–	–	–	+	Marmin et al. (2014)
Salinity decrease	+++	++	+	+	–	–	Dauvin and Pezy (2013)
Port construction	+	+++	–	–	–	–	Dauvin et al. (2006)
Bridge construction	–	+++	–	–	–	–	Cuvilliez et al. (2009)
Siltation (arrival of fine terrestrial particulate)	+	+	++	+++	–	–	Guezennec (1999)
Increase in sandy sediments	–	+++	+	–	–	–	Cuvilliez et al. (2009) and Dauvin et al. (2006)
Presence of maximal turbidity zone	+++	+	+	++	–	–	Guezennec (1999)
Residual currents (disturbance)	+++	+++	++	+	+	+	Le Hir (2001)

#### 4.3. Fitting stress to ENA

The ENA indices usually respond to stress, defined as a negative response from disturbance produced by an external pressure (Odum, 1985). When an ecosystem is influenced by an external pressure, its response depends on its levels of resistance, defined as the extent of functioning variations, and resilience, corresponding to the time needed to return to a comparable state (Pimm, 1991). ENA indices can, with varying sensitivities, inform on these two characteristics of marine ecosystems and provide a numerical basis for comparing between habitats. However, for systems that are already under stress such as estuaries, the differences may be subtle or at least masked by the baseline effects of natural disturbance (Dauvin, 2007; Elliott and Quintino, 2007). Here, we collected qualitative data on current knowledge of the levels of stress in the 6 studied habitats (Table 4), to perform a first, although still coarse, analysis of the fitting of ENA to anthropogenic and natural impact levels.

As previously described, the Seine estuary is one of the most man modified and contaminated estuary in France. As expected, the northern channel habitat (FN) evidenced the highest levels of ecological stress, according to ENA values. The indices that most captured this stressed condition were FCI and SOI, in accordance to the classical interpretation of ecosystem responses with stress, i.e. higher recycling and shorter food chains in stressed areas (McCann and Hastings, 1997; Odum, 1985; Scharler and Baird, 2005). The second-most impacted area in the Seine estuary appears to be the highly-dredged navigation channel (CH), where maritime traffic is present year-round, the substrate is constantly resuspended, and a constant maximum turbidity zone is present. In addition, central channels in estuaries usually present high levels of natural variability, especially close to the mouth where tidal forces and water mixing are maximal (McLusky and Elliott, 2004). Here, indications of system immaturity were found, such as high net system production and keystone species shifts, while overall ENA indices did not completely reflect this condition.

Low-to-intermediate levels of physical disturbance, such as those found in the southern channel (FS), are known to increase benthic diversity and complexity and, consequently, favour an increase of ecosystem activity (Baeta et al., 2011; Hall, 1994). The FS also hosts a wide intertidal area, a trait that might probably increase ecosystem activity. This is indeed what was evidenced by T., the highest levels of biomass, the high trophic specialisation compared to other areas (shown by SOI), and low system stress (indicated by lower FCI and R/C).

Concerning the ENA indicators applied in this study, we found an acceptable fitting of SOI, FCI, and to a lesser extent R/C to the levels of supposed stress of each spatial compartment. SOI was already identified as a relevant indicator of stress in a previous

meta-analysis of estuarine food webs (Selleslagh et al., 2012). A general trend for system omnivory in estuaries is, however, still to be determined. In this study, values of SOI were generally considerably higher, for instance, to those found in the Mondego estuary, Portugal, which however did not consider the fish community in the model (Baeta et al., 2011). These indices have been recently proposed as possible methods to comply the EU mandate as ecological status indicators (Niquil et al., 2012). Although the results presented here are promising, however, a more specific analysis will be necessary in this sense, including statistically-testable comparisons and possibly considering other ENA candidate indices such as Ascendency and its derived indicators (Ulanowicz and Abarca-Arenas, 1997). Furthermore, the average path length (APL) did respond to the same gradients as FCI, thus suggesting that either index would be sufficient for ecological status studies.

Another important reason to model separate habitats can be drawn from comparing these results with a previous food-web model of the Seine estuary (Rybarczyk and Elkaïm, 2003). This previous model is approximately overlapping with the three estuarine habitats considered here (CH, FN, FS) using the same number of functional groups, although with different subdivisions between them and not considering bacteria which can influence recycling estimations. In the 2003 study, SOI and R/C indices showed values outside the range showed in the present study (SOI = 0.11 and R/C = 0.281, Rybarczyk and Elkaïm, 2003) while other two indices, FCI and T., which here responded to the levels of habitat pressure, had values inside the range obtained in this study (FCI = 16.1 and T. = 3603 gC m<sup>-2</sup> y<sup>-1</sup> in the 2003 study). Differences are then present between considering separate habitats and a larger area, and might change the direction and interpretation of results especially in relation to assessing the ecological status.

#### 5. Conclusions

In this study, an analysis of the contribution of the Seine habitats and their key roles to the estuary functioning was done based on the analysis of emergent ENA properties. The two habitats with a functioning most related to a stressed state were the northern and central navigation channels, where building works and constant maritime traffic are considered major anthropogenic stressors. Regarding our second objective, the combined use of ENA indices and keystone analysis can respond fairly adequately to the distinct levels of pressure in an estuarine ecosystem, seeming thus a promising candidate indicator of “ecosystem health status”. The ENA response alone was not completely unequivocal, meaning that further studies are needed to fully disclose the response patterns of ENA indices to the levels of ecosystem stress. Furthermore, while acknowledging that a holistic approach considering the whole estuary might disclose previously unknown properties, results here



point to a spatial complexity of the Seine estuary ecosystem, where distinct habitats present distinct emergent traits. In the framework of assessing environmental status of ecosystems subject to the European Union Water Framework Directive, we argue for including the habitat-level spatial observation when planning conservation strategies.

## Acknowledgements

This work was funded by the project ANTROPOSEINE (G.I.P. Seine-Aval, 5th programme, France). We also acknowledge, for their help in compiling the dataset and for giving specific expert advices: Aurore Raoux (UMR BOREA Caen), Chloé Dancie (CSLN Le Havre), Philippe Riou and Mathilde Schapira (IFREMER Port-en-Bessin), Anik Brind'Amour (IFREMER Nantes), Bruno Ernande (IFREMER Boulogne-sur-Mer), Sami Souissi (Station Marine de Wimereux), Sandrine Alizier (UMR LOG Wimereux), Stella Marmin (UMR M2C Caen), Franck Gentil and Eric Thiébaud (Station Biologique de Roscoff), Nicolas Desroy (IFREMER Dinard), and the Port Authorities of Le Havre and Rouen.

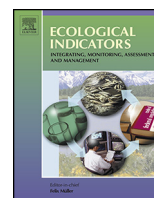
## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2015.05.026>

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



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## ARTICLE INFO

### Article history:

Received 30 June 2015

Received in revised form 12 October 2015

Accepted 14 October 2015

Available online 6 November 2015

### Keywords:

Linear inverse model

Estuarine ecosystem

Seine estuary

English Channel

## 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.

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## 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 and Elliott, 2004). This means that, while they are of primary importance as providers of ecosystem services to humans, their capacity of resisting external stressors is not yet fully understood.

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The Seine estuary is a transitional water system in northern France (Meybeck et al., 1998) that is commonly referred to as an example of a productive habitat highly modified by human activities (Dauvin and 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 space 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 and Christian, 2007; Niquil et al., 2012, 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 and 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.

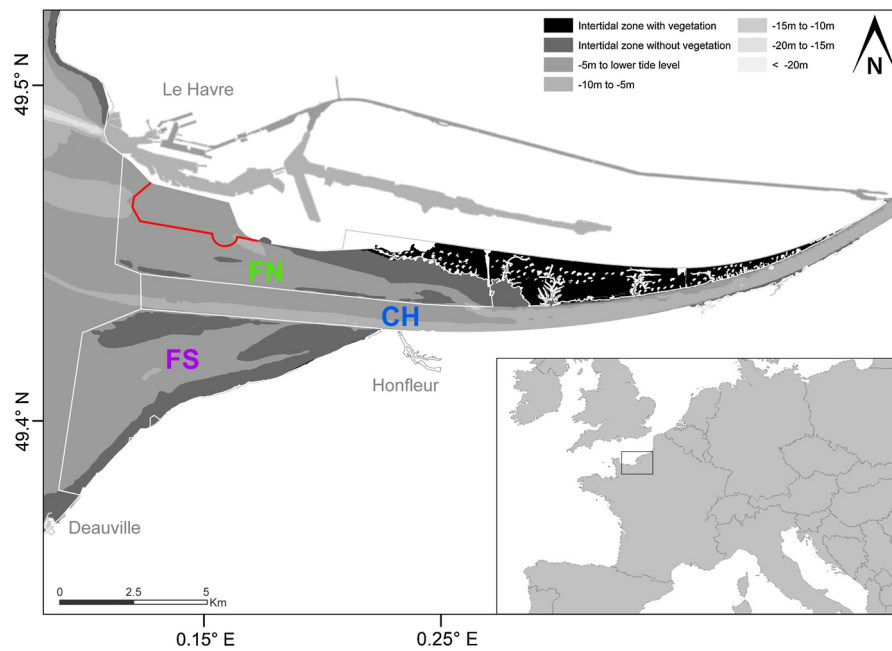
## 2. Materials and methods

### 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 and 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 km<sup>2</sup> 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 (Fig. 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



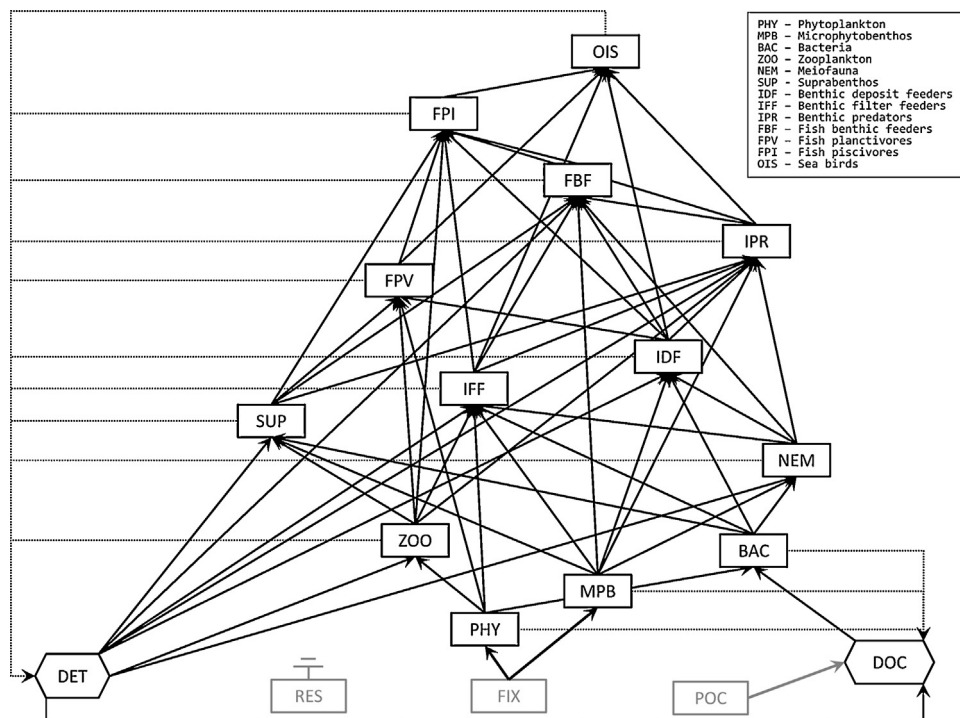


**Fig. 1.** Map of the study area in the Seine estuary and its position in northern Europe, with indication of the three modelled spatial compartments. The same colour coding is used in the subsequent figures. Also indicated (red line) is the area enclosed in the new Port2000 commercial harbour extension, which reduced the FN surface from 25 to 20 km<sup>2</sup>. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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



**Fig. 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.



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 (Fig. 2). Eighty-five (85) flows were described between these components. Each living compartment was linked with consumption flows (as input), flows to detritus (excretion and mortality), 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 generalisable), 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 programmes, and were standardised as  $\text{gCm}^{-2}$  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:  $0.10 \text{ SUPconsumption} < \text{SUPproduction} < 0.37 \text{ SUPconsumption}$ . Bacterial flow to detritus was considered as the proportion of bacterial production that is utilised by viruses, or “viral shunt” (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:  $\text{ZOO} \rightarrow \text{FPV} > 0.30 \text{ FPVconsumption}$ . 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

**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) Leguerrier et al. (2004), P/Q and U/Q generated using confidence intervals around standard Ecopath parameters (Christensen & Pauly, 1993)
2	FPI	Fish, piscivores	0.12	1.20	0.09	0.24	–	–	0.10	0.50	
3	FPV	Fish, planktivores	0.48	1.60	0.10	0.30	–	–	0.10	0.50	Christensen and Pauly (1993), Brey (2001)
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	
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	
10	NEM	Meiofauna	10.10	35.00	0.05	0.40	–	–	0.13	0.30	Vézina and Savenkoff (1999), Tortajada et al. (2012)
11	BAC	Bacteria	–	–	0.11	0.60	–	–	0.05	0.35	
12	MPB	Microphytobenthos	4.20	30.00	–	–	0.05	0.30	0.05	0.73	delGiorgio and Cole (1998), Danovaro et al. (2008), Tortajada et al. (2012)
13	PHY	Phytoplankton	–	–	–	–	0.05	0.30	0.05	0.50	

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

**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	

position for the random walk algorithm was a parsimonious solution obtained by least-distance programming, i.e. minimising 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 and 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 and Ulanowicz, 1984).
- The *Ascendency* was calculated as  $A = AMIT..$ , and it is related to ecosystem growth and development (Ulanowicz and 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 and Wolff, 2002).
- The *relative Redundancy* (R/DC) was calculated as the ratio between the internal flows overhead and the total development capacity of the ecosystem (Ulanowicz, 2001). Considering only internal flows, usually indicated by a subscript *i*, means excluding from the calculation export, import, and dissipation flows.
- The *diversity of flows* ( $H_f$ ) 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 and 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 trophic level to the next higher one. 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:

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

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  $|\hat{\delta}| < 0.147$ , small for  $|\hat{\delta}| < 0.33$ , medium for  $|\hat{\delta}| < 0.474$ , and large otherwise.

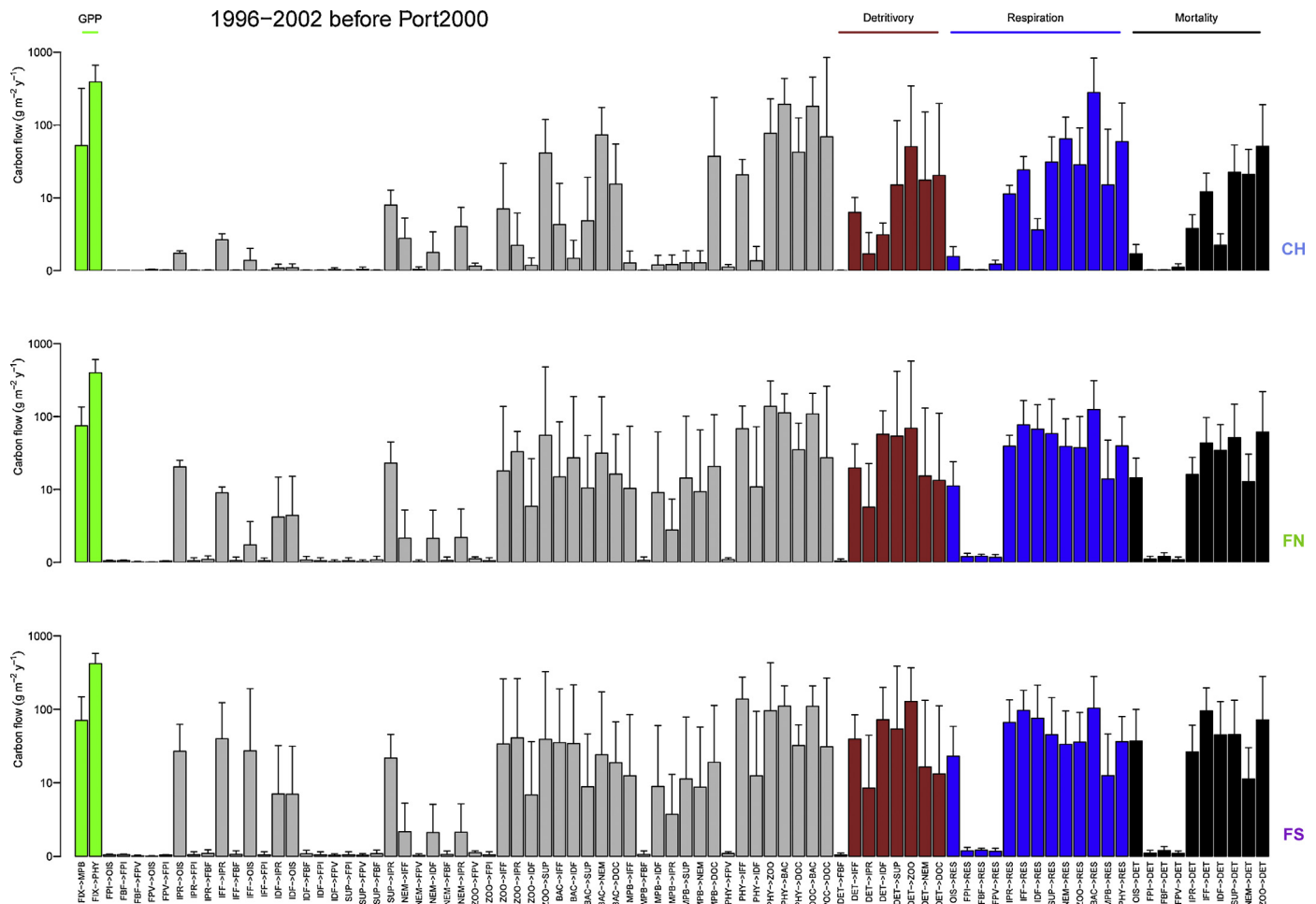
Differences in functioning between the two periods were also analysed by single flow values. We also calculated the percentage of difference in the means of each compartmental throughflow. The throughflow of a compartment is defined as the higher of its total inflow or outflow (which in our case were 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<sup>-2</sup>. Suprabenthos showed an extreme biomass decline in all three habitats, with an 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<sup>-2</sup> y<sup>-1</sup> (Figs. 3 and 4). The other primary



**Fig. 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.

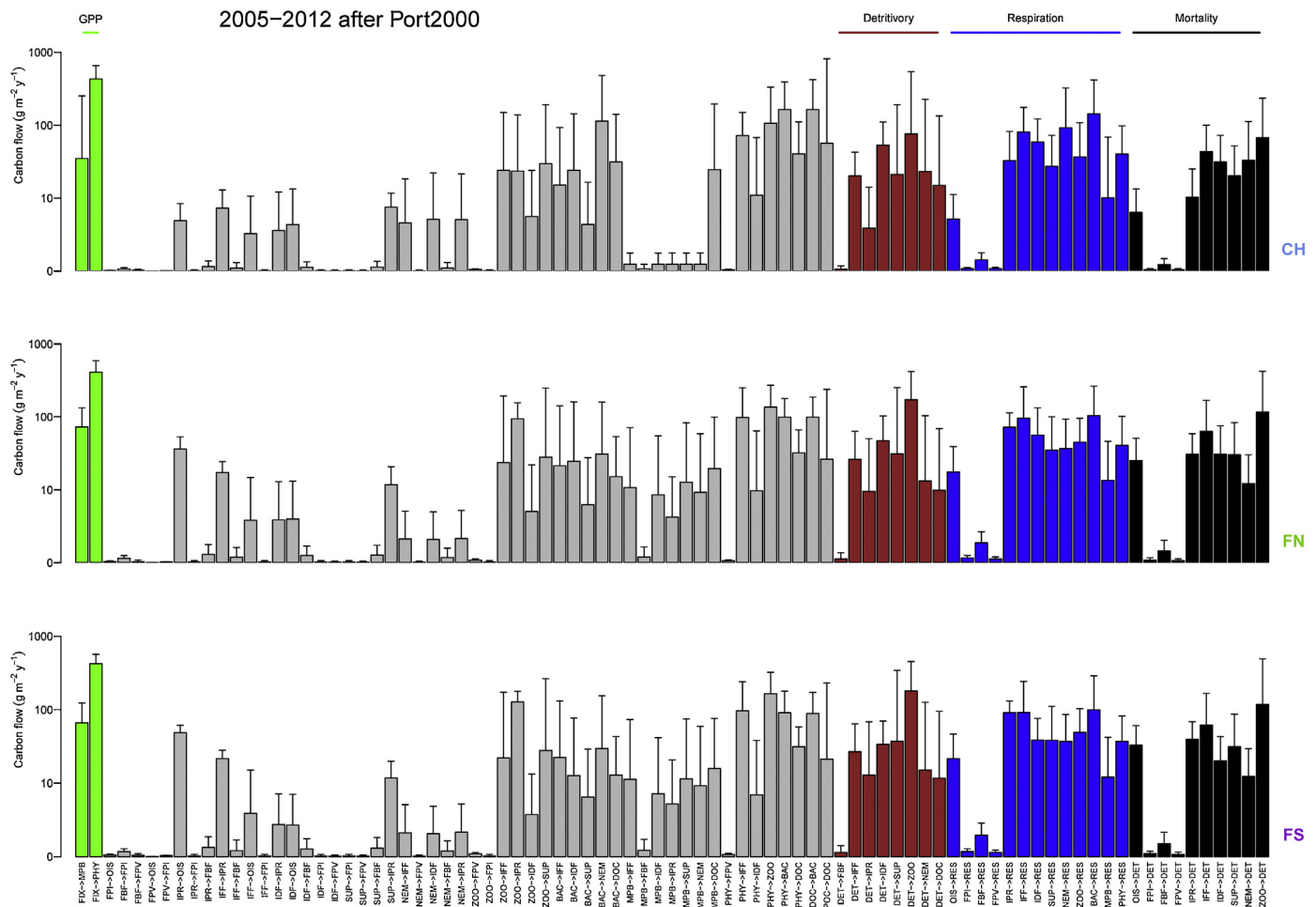
production input flow was  $\text{FIX} \rightarrow \text{MPB}$  and it was estimated at  $61.0 \pm 28.1 \text{ gC m}^{-2} \text{ y}^{-1}$ . Respiration flows, which represented the export from the system, were dominated by bacterial respiration which was  $141.4 \pm 84.2 \text{ gC m}^{-2} \text{ y}^{-1}$  overall ( $\text{BAC} \rightarrow \text{RES}$ ). 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 (Fig. 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 ( $T_s$ ) increased significantly in the CH and FN, and remained stable in FS (Fig. 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  $H_r$ , 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 Fig. 5).



**Fig. 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.

Transfer efficiencies by discrete trophic levels showed a more linear pattern after Port2000 construction for both northern and southern flanks (Fig. 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

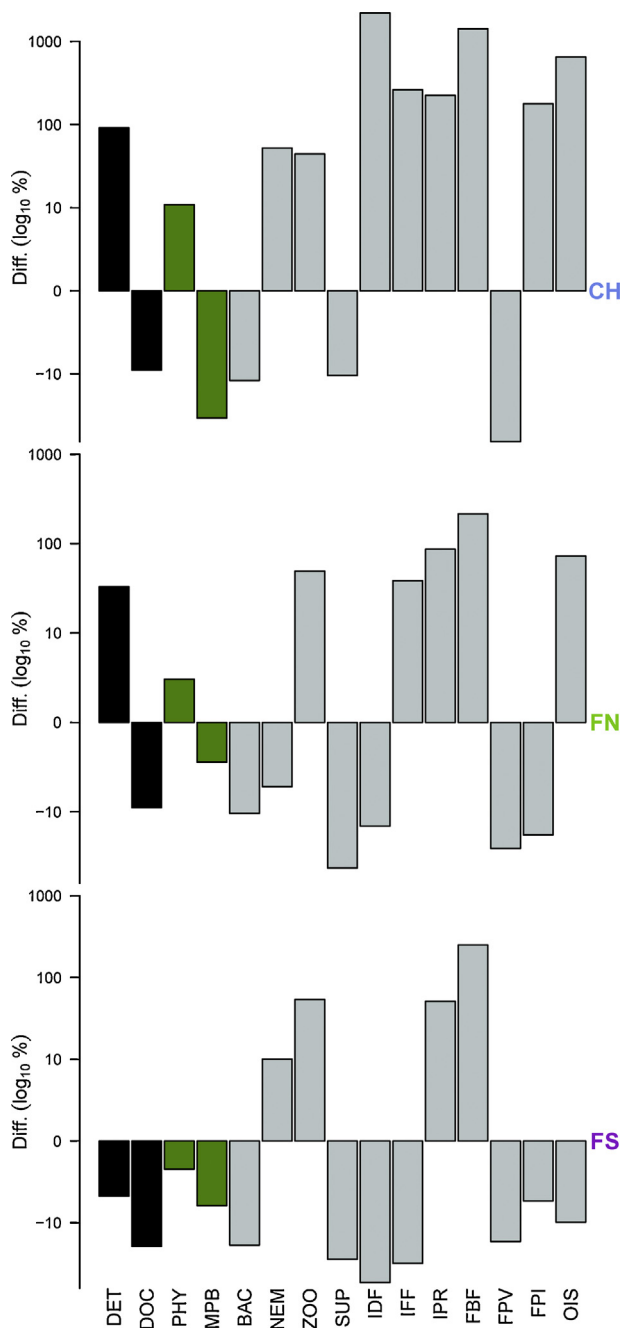
The use of separate food web models to analyse the functioning of an estuarine ecosystem has been considered pertinent, even if each spatial box has been defined geographically rather than by a single habitat type (Tecchio et al., 2015). Here, the northern and southern flanks (FN and FS) included both 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 and 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





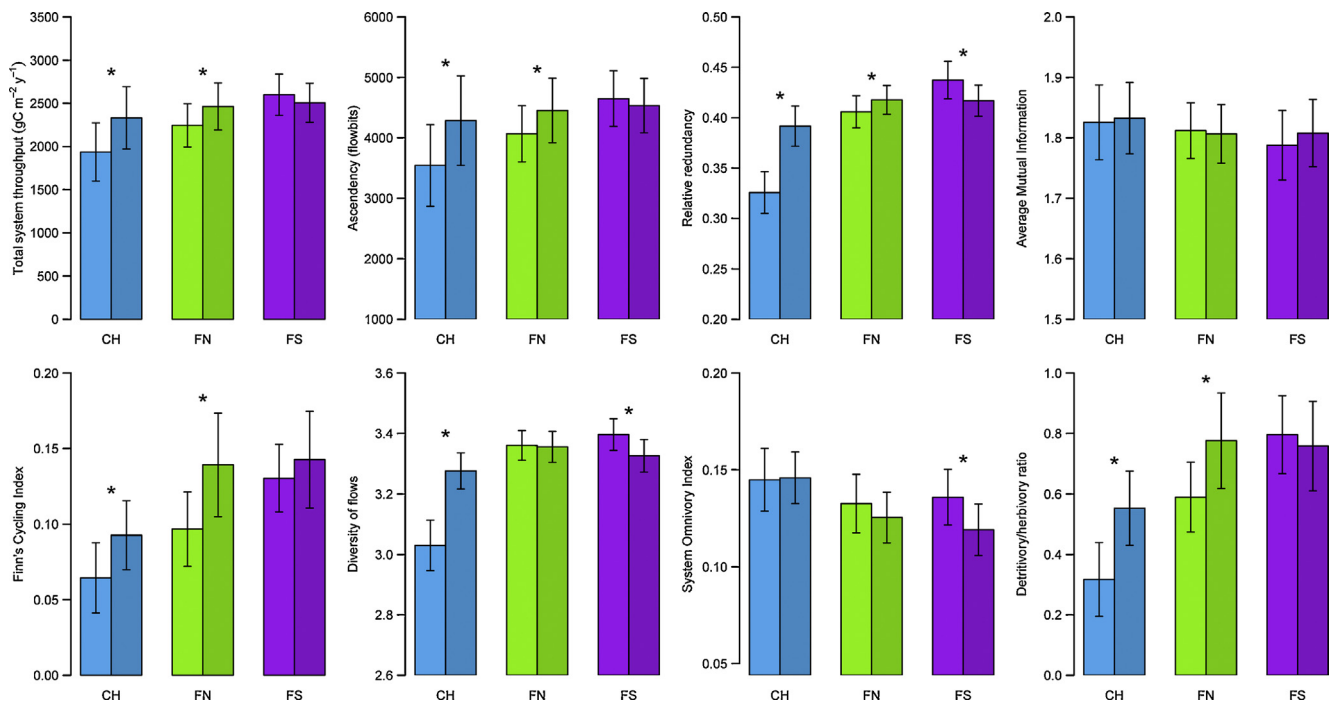
**Fig. 5.** Differences in compartment throughflows between before and after construction of Port2000 harbour, in the three spatial compartments of the Seine estuary. Note that the scales are log-modulus transformed, and that this percentage analysis does not consider the difference in absolute values between functional groups. Colours identify detritus (black), primary producers (green), and consumers (grey) groups. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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

**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)



**Fig. 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.

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.

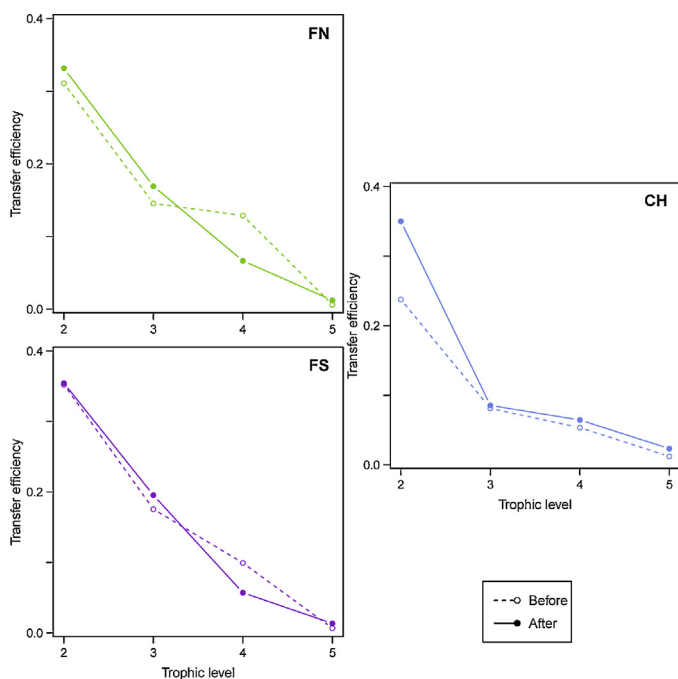
#### 4.2. Ecosystem functioning between periods

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 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 and 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



**Fig. 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).

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 linearised 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 km<sup>2</sup>. 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 (0.589–0.775 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 and 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 and Link, 2009). This process has two consequences; it increases recycling and detritivity, 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 ascendancy is calculated as  $A = T_{..} \times AMI$  and that  $(A_i/DC_i) + (R/DC_i) = 1$ , 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 ascendancy were due to changes in total system activity. In CH, ascendancy 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.

## 5. 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

This study was funded by the project ANTROPOSEINE (G.I.P. Seine-Aval, France). We thank the *EuroSquid* computer for helping in polytopes exploration, and Prof Jean-Paul Robin for providing us with its computing time. The authors also thank all the

colleagues who participated in data collection, mainly under the G.I.P. Seine-Aval scientific programmes.

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*Niquil N. (coord.), Tecchio S., Dauvin J.C., Lassalle G., Lobry J., 2018. Projet ANTROPOSEINE : ANalyse de la structure TROPhique et cONtribution des habitats de l'estuaire de la SEINE. Annexes du rapport de recherche du programme Seine-Aval 5, 39 p.*

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