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

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1 Highlights:

- 2 • The ENAtool routine relies on an ensemble parameterization technique
- 3 • It incorporates the uncertainty in EwE inputs into the calculation of ENA indices
- 4 • The ENAtool routine was applied on the Bay of Biscay continental shelf Ecopath model
- 5 • The previously ENA-derived structural and functional properties were strengthened
- 6 • Ecosystem comparative studies will now integrate statistical analyses on ENA indices



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## 31 Abstract

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

54

55 Key words: Ecopath with Ecosim; ecosystem models; network analysis; parameter uncertainty;

56 comparative studies

57

## 58 1. Introduction

59 Marine ecosystems are affected by climate change (Beaugrand, 2004; Hoegh-Guldberg and  
60 Bruno, 2010) and by other natural or human-caused disturbances (Pauly et al., 1998; Borja et al.,  
61 2010). Ecosystem models are useful to get a better understanding of the structure and function of  
62 a system and for predicting how it may change over time when facing single or multiple  
63 pressures (Plagányi, 2007). Ecopath with Ecosim (EwE) is a widely-used modelling approach to  
64 represent marine food webs (Polovina, 1984; Christensen and Walters, 2004; Christensen et al.,  
65 2008). Since its development in the early 1980s, about 400 EwE models representing a wide  
66 variety of ecosystems worldwide have been published (Colléter et al., 2013a; Colléter et al.,  
67 2013b). Coupling EwE models to Ecological Network Analysis (ENA; Ulanowicz, 1986) was  
68 proposed as a relevant method to estimate energy flows and to characterize emergent properties  
69 of food webs, i.e. characteristics not directly observable that can only be detected by analysis of  
70 within-system interactions (Christensen and Pauly, 1992). ENA is a suite of tools that include  
71 input-output analysis, trophic structure analysis, pathway analysis, biogeochemical cycle  
72 analysis, and information analysis (Dame and Christian, 2006; Borrett and Lau, 2014). The main  
73 challenge for ENA is to capture the properties of entire food web in terms of a limited number of  
74 indices. In the scope of the European Marine Strategic Framework Directive (MSFD;  
75 <http://ec.europa.eu>; Directive 2008/56/EC), the EU Member States have to report on the  
76 environmental status of the seas under their jurisdiction and to work **on achieving** “Good  
77 Environmental Status” (GES) using food-web indicators as one possible metric. In this direction,  
78 nine food-web indicators are currently under evaluation as potential indicators of GES; the  
79 Ecological Network Analysis indices are among these candidate indicators (Rombouts et al.,  
80 2013; Niquil et al., 2014).

81 The EwE network analysis plugin has been employed in many instances, notably to study the  
82 stability of ecosystems and their response to perturbations (Patricio et al., 2006; Lobry et al.,  
83 2008; Baeta et al., 2011; Selleslagh et al., 2012) or, more recently, to assess the dynamical food-  
84 web reorganization and redirection of energy flow pathways under environmental changes  
85 (Tomczak et al., 2013). Nonetheless, these holistic conclusions relied on single values of ENA  
86 indices which were derived from a single input data matrix with no specified uncertainty.

87 **Moreover, the ecological interpretation of these single values mostly relies on non-statistical**  
88 **comparisons with values obtained for ecosystems of the same type.** Given that data  
89 uncertainties may translate to uncertainties in model outputs (e.g. Niiranen et al., 2012), it is  
90 generally agreed that important scientific questions should be scrutinized with as many models as  
91 possible (Fulton, 2010; Gårdmark et al., 2012). One method of incorporating uncertainty into  
92 Ecopath model analysis is to use an ensemble parameterization technique, building several  
93 Ecopath models each representing **a potential manifestation** of a food web and falling within the  
94 uncertainty ranges of the observed data (Aydin et al., 2007; Kearney, 2012). This approach  
95 results in distributions of parameters rather than specific values, while still meeting basic  
96 thermodynamic requirements. Kearney et al. (2012) provided a suite of Matlab functions to  
97 construct such a distribution of parameters based on an Ecopath model and its data pedigree, i.e. a  
98 quantification of the parameter certainty tied to the parameter's origin. In this study, we extend  
99 the Kearney et al. (2012) code for generating this type of ensemble to feed into calculations of  
100 ENA indices. **This work will allow parameter uncertainty to be incorporated into model-**  
101 **derived ENA indices, and will also improve interpretation of these indices by allowing**  
102 **statistical analyses. When overhauling the EwE source code between the release of EwE**  
103 **versions 5 and 6, the EwE developers chose not to continue support of the Ecoranger**  
104 **module, which had allowed users to explore parameter uncertainty ranges in a Bayesian**



105 **context (Christensen et al., 2005). The code presented in this paper now offers an**  
106 **alternative method for analyzing this uncertainty.**

107 The aim of this software development is to provide an easy-to-use routine to EwE users to  
108 generate a set of values for key ENA indices by explicitly taking into account uncertainty in  
109 model input data. To this end, two characteristics are identified as important: (i) a routine that can  
110 be called by a single line of Matlab code and can be run on all commonly-used operating systems  
111 (recent Windows, Unix-based, and Mac platforms), independent of the EwE software versions  
112 used for the pre-existing ecosystem model construction, and (ii) a routine based on formulas of  
113 ENA indices currently in use in the last version of the EwE software. The present work is also the  
114 opportunity to harmonize ENA indices calculations derived from two main approaches for  
115 constructing ecological flow networks, i.e. EwE and linear inverse modelling (LIM; Vézina and  
116 Platt, 1988). Different formulas for the same index exist in the scientific literature and correspond  
117 to different interpretations of the same idea. We demonstrate the use of this tool by applying it to  
118 a pre-existing Ecopath model of the Bay of Biscay continental shelf (Lassalle et al., 2011) for  
119 which data quality is already categorized using Pedigree scores (Lassalle et al., 2014). ENA  
120 indices distributions derived from the ENAtool routine are compared with previous point  
121 estimate values obtained with this Ecopath model to test for robustness of ENA-derived  
122 ecological conclusions. Finally, we test sensitivity of ENA indices distributions to the number of  
123 balanced ensemble members underlying their calculation and to the level of uncertainty applied  
124 to specific Ecopath model parameters.

125

## 126 2. Materials and Methods

### 127 2.1 The Ecopath concept and equations

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

138 Production = fishery catch + predation mortality + net migration + biomass accumulation + other  
 139 mortality

140 “Other mortality” includes natural mortality factors such as mortality due to senescence, diseases,  
 141 etc.

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

143 Consumption = production + respiration + unassimilated food

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

$$146 \quad B_i \times (P/B)_i = Y_i + \sum_j (B_j \times (Q/B)_j \times DC_{ij}) + Ex_i + B_{acc_i} + B_i(1 - EE_i) \times (P/B)_i \quad (1)$$

147 and

$$148 \quad B_i \times (Q/B)_i = B_i \times (P/B)_i + R_i + U_i \quad (2)$$

149 where the main input parameters are biomass density ( $B$ , here in  $\text{kg C} \cdot \text{km}^{-2}$ ), production rate  
 150 ( $P/B$ ,  $\text{year}^{-1}$ ), consumption rate ( $Q/B$ ,  $\text{year}^{-1}$ ), proportion of  $i$  in the diet of  $j$  ( $DC_{ij}$ ;  $DC$  = diet

151 composition), net migration rate ( $Ex$ , year<sup>-1</sup>), biomass accumulation ( $Bacc$ , year<sup>-1</sup>), total catch ( $Y$ ;  
152 kg C·km<sup>-2</sup> year<sup>-1</sup>), respiration ( $R$ ; kg C·km<sup>-2</sup>·year<sup>-1</sup>), amount of consumed food that is  
153 unassimilated ( $U$ ; kg C·km<sup>-2</sup>·year<sup>-1</sup>) and ecotrophic efficiency ( $EE$ ; amount of species production  
154 used within the system).

155

156 2.2 The generalized intra-model ensemble routine: ENAtool

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

165

166 2.2.1 Import of a EwE model into Matlab

167 ENAtool first imports data from EwE6 databases into Matlab, storing them in a variable format  
168 we will refer to as EwE input structures (Fig. 1). The original data import function, *mdb2ewein*,  
169 relies on the ‘mdbtools’ (<http://mdbtools.sourceforge.net/>) set of utilities to read data from the  
170 MS Access file format used by EwE. As an alternative for those unwilling or unable to compile C  
171 source code, we have provided a companion import function, *excel2ewein*, which relies on an  
172 Excel template to provide the necessary input data (Fig. 1). This function is based on a template  
173 (see Template A provided in Supplementary Material 2) that must be filled with key input  
174 parameters and other related information by first opening the pre-existing EwE model with a

175 database program such as Microsoft Access or OpenOffice Base. The template was provided as  
176 an Excel file and can be completed using any spreadsheet program (e.g. Microsoft Excel,  
177 OpenOffice Calc etc.) but must be in the end saved as an Excel file (.xlsx). **Both functions**  
178 **import all necessary Ecopath data, including basic inputs, diet compositions, fleet catches**  
179 **and discards, and multi-stanza group parameters, to the EwE input structure.**

180

### 181 2.2.2 Generation of a set of balanced ensemble members

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

188 Uncertainty values were assigned as a percentage of the point estimate of each parameter.

189 Minimum and maximum values of the parameter distribution can then be calculated as follows:

190 Limits = single value of the parameter +/- (percentage \* single value of the parameter) (3)

191 In the present work, the *createpedigree* function was developed to ease this step, particularly in  
192 the case of pre-existing EwE models for which Pedigree scores were already estimated (Fig. 1;  
193 Table 1). The Pedigree index (Funtowicz and Ravetz, 1990; Pauly et al., 2000) was designed to  
194 evaluate whether an EwE model was based on extensive field sampling performed within the  
195 boundaries of the system during specific dates. The Pedigree component in the EwE software  
196 allows marking/categorizing the data origin of each single input using pre-defined tables; the key  
197 criterion being that inputs from local data have the best confidence and the highest level in the  
198 scale (Christensen et al., 2005). In the pre-defined tables, each Pedigree score is associated with a

199 default level of uncertainty expressed as  $\pm\%$ . For example, a Pedigree score of 1 (e.g. for a local  
200 biomass value) indicates a 10% uncertainty value. The *createpedigree* function builds a table of  
201 uncertainties based on an Excel file which contains for each parameter and each **functional**  
202 **group** the level of uncertainty to be applied to the single value (see Template B in Supplementary  
203 Material 3). Again, this Excel file can be opened with any spreadsheet program but must be  
204 finally saved as an Excel file. This Excel file can be also an export of the Pedigree table from the  
205 EwE software. If the user has no estimate of the uncertainty surrounding the input parameters in  
206 the pre-existing EwE model, a level of uncertainty can be set and a matrix of the same dimension  
207 as the uncertainty table will be automatically generated. With no specification from the user, the  
208 default values will be 20% around single values (Richardson et al., 2006).

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

218 The *ecopathlite* function called by the *createensemble* function is the one that reproduces the  
219 main calculations performed by the Ecopath module of the EwE software (Fig. 1). This function  
220 is a 'stripped-down' version of the Ecopath algorithms allowing an estimation of missing  
221 parameters by solving the system of  $n$  equations with  $n$  unknowns (see equations (1) and (2)).

222 Users can also choose whether they want ensemble members that respect the biomass

223 conservation hypothesis, i.e. here, that met the ecotrophic efficiency balance requirements (EE  
224  $< 1$ ). Combining *createensemble* and *ecopathlite* functions allows the user to compute **a specific**  
225 **number (referred to henceforth as *nset*) of balanced ensemble members before calculating**  
226 **any ENA indices. For multi-stanza configurations, adjustments of parameters are made**  
227 **when calling *subecopathens.m* to calculate Ecopath values and check for balance. So the**  
228 **resulting ENA index values stemming from this code will incorporate the same multi-stanza**  
229 **relationships as in EwE.**

230

### 231 2.2.3 Calculation of an ensemble of values for ENA indices

232 Finally, the *indices* function was developed in this present work to calculate a set of 13 ENA  
233 indices (Fig. 1; Table 2) for each ensemble member generated by the *createensemble* function.  
234 The mathematical formulas for these indices required a harmonization between the EwE and LIM  
235 ecosystem modelling communities. We compared the formulas in use in EwE with those  
236 currently in use by modelers working with linear inverse models (LIMs) in Matlab (Leguerrier et  
237 al., 2007; Johnson et al., 2009; Niquil et al., 2011; Saint-Béat et al., 2013) (Table 2). Most  
238 formulas were shared in common between both communities and were as such already available  
239 in Matlab. Ecological interpretations of ENA indices are summarized in Table 2. Full details  
240 regarding their links with ecosystem ecology theories can be found, for instance, in Ulanowicz  
241 (2004), Kones et al. (2009), and Saint-Béat et al. (2015).

242

## 243 2.3 The ENAtool application

### 244 2.3.1 Description of the Bay of Biscay Ecopath model

245 A full description of the Bay of Biscay Ecopath parameterization can be found in Lassalle et al.  
246 (2011). The model considered for this zone was restricted to the central part of the shelf between

247 the 30-m and 150-m isobaths with a surface area of 102,585 km<sup>2</sup> (Fig. 2). The model represented  
248 a typical year between 1994 and 2005, i.e. before the collapse of the European anchovy  
249 (*Engraulis encrasicolus*) and the subsequent five-year closure of the fishery for this species.  
250 Thirty-two **functional** groups were retained, including two seabirds, five marine mammals, nine  
251 fish, eight invertebrates, three zooplankton, two primary producers, one bacteria, discards from  
252 commercial fisheries, and pelagic detritus. Cephalopods were included in the form of two classes  
253 relating to their main oceanic domain (pelagic/benthic). The five main pelagic forage fish were  
254 given their own **functional groups** and demersal fish were divided into four multi-species  
255 **functional** groups on the basis of their diet regime. Marine mammals were included in the form  
256 of five mono-specific **functional groups** representing the small-toothed cetaceans most  
257 frequently encountered in the area.

258

### 259 2.3.2 Summary of previous ENA-derived results

260 Some insights regarding the Bay of Biscay structure and function have been derived from ENA  
261 indices calculated with the EwE model of Lassalle et al. (2011) (see Table 2 for single estimates).  
262 In this previous work, single point estimates were interpreted by comparison to those obtained for  
263 ecosystems of the same type or for other Ecopath models of the same ecosystem. The high Finn's  
264 Cycling Index (FCI) value, which measures the relative importance of cycling to the total flow  
265 (Finn, 1980), highlighted the strategic position of detritus as a perennial reservoir of energy in the  
266 Bay of Biscay. The System Omnivory Index (SOI) was regarded as an index reflecting the  
267 complexity of the inner linkages within the ecosystem (Christensen and Pauly, 1992). It is  
268 correlated with system maturity, since the internal network organization is expected to increase as  
269 the system matures (Odum, 1969). The relatively moderate value for this output suggested a  
270 "web-like" food chain with an intermediate level of internal flow complexity. The Bay of Biscay

271 also appeared as relatively immature, as indicated by the Ascendency (A), and has a high  
272 resistance to external perturbations according to System Overhead (O). Ascendency (A) merges  
273 the quantification of the system activity and the degree of specialization of flows in the network  
274 (Ulanowicz, 1986; Ulanowicz and Wulff, 1991). During maturation, ecosystem structure evolves  
275 towards an increase in ascendency (Ulanowicz et al., 2006). System Overhead (O) represents the  
276 amount of development capacity that does not appear as organized structure or constraints  
277 (Ulanowicz, 1986) and as such it corresponds to the system reserves when facing perturbations  
278 (Heymans and Baird, 2000).

279

### 280 2.3.3 The Bay of Biscay Ecopath ensemble and ENA ensemble

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

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



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

297

#### 298 2.3.4 The preliminary sensitivity study

299 The ENAtool routine requires as main input arguments the number of ensemble members to  
300 generate and the level of uncertainty to be applied on  $B$ ,  $P/B$ ,  $Q/B$ , and  $DC$ . Therefore, it was  
301 important to study the influence of these arguments on the output variables, namely ENA indices.

302 1. A first exercise was performed to assess in which proportions ENA indices distributions were  
303 impacted by the number of ensemble members to generate and by the uncertainty set around  
304 input parameters in the ENAtool routine. Values for  $nset$  of 1000, 100 and 10 were tested. The  
305 point value of each parameter was changed by 20/40/60% up or down following equation (3). All  
306 combinations of  $nset$  and levels of uncertainty were run for the pre-existing Ecopath model of the  
307 Bay of Biscay continental shelf. 2. A second exercise tested which type of input parameter (i.e.  $B$ ,  
308  $P/B$ ,  $Q/B$ , and  $DC$ ) influenced the ENA index distributions most strongly. To do so, the ENAtool  
309 routine was run with a  $nset$  of 1000 and a level of uncertainty of 20% alternatively applied to  
310 each input parameter type of the pre-existing Ecopath model of the Bay of Biscay continental  
311 shelf (Richardson et al., 2006).

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

314

### 315 3. Results

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

319 For the pre-existing Ecopath model of the Bay of Biscay continental shelf, the value derived from  
320 the EwE software for each ENA index was compared to the range of values obtained following  
321 the application of the ENAtool routine to this model with a *nset* of 1000 and levels of uncertainty  
322 in accordance with Pedigree scores (**Table 3**). For A, Ai/Ci, and MTL, the EwE single estimates  
323 **fell** within the range defined by the 1<sup>st</sup> (25%) and the 3<sup>rd</sup> (75%) quartile of ENA values (Fig. 3;  
324 Table 2 for the list of ENA indices with their abbreviations). For 9 of the 10 remaining ENA  
325 indices, the EwE single estimates **fell** in the upper boxplot whiskers calculated as 1.5 times the  
326 interquartile range. Regarding more specifically at the ENA indices used **by Lassalle et al.**  
327 **(2011) in their assessment of the Bay of Biscay functioning**, we calculated an FCI value with a  
328 mean of 33.09% across ensembles, compared to the single value of 34.61% obtained by Lassalle  
329 et al. (2011) (Fig. 3). The System Omnivory Index (SOI) presented the broader difference  
330 between the Ecopath single estimate and the mean value, i.e. 0.195 *versus* 0.179 respectively  
331 (Fig. 3); the Ecopath SOI estimate being at the upper end of the distribution. The mean  
332 Ascendency (A) was of 846015 *versus* 860882 flowbits for the pre-existing Ecopath model. The  
333 mean Overhead (O) and the single Overhead estimate were of 2639671 and 2947325 flowbits,  
334 respectively. The coefficients of variation between the mean values and the single Ecopath  
335 estimates for those four indices were no greater than 10% (**Table 3**).

336 The first sensitivity exercise performed on the outputs of the ENAtool routine showed that the  
337 number of ensemble members generated induced no trend on the variance of ENA indices  
338 calculated as the standard deviation squared (Fig. 4; **Table 3**). Indeed, for all of the three levels of  
339 uncertainty applied in the routine, i.e. 20, 40 and 60% on all parameters, and for all ENA indices,  
340 the variance of the distribution did not systematically increase with the number of ensemble  
341 members generated as first suspected (Fig. 4). On the contrary, when looking at a given number  
342 of ensemble members to generate, i.e. at a specific shade of grey, the variance of the distribution

343 systematically increased with the level of uncertainty applied to the input parameters (**Table 3**).

344 This trend was particularly marked for the Total System Throughputs (TST) with variances that

345 almost doubled when the level of uncertainty was changed from 40 to 60% (Fig. 4). These results

346 were in line with the method, as parameters for the ensemble members were here randomly

347 sampled from a uniform distribution with bounds directly related to the level of uncertainty;

348 every value in the interval having the same probability of being picked.

349 In the second sensitivity exercise, two input parameters appeared to be the most influential on

350 ENA indices (Fig. 5). On the one hand, the Comprehensive Cycling Index (CCI), the Finn

351 Cycling Index (FCI), the Mean Trophic Level of captures (MTL) and the System Omnivory

352 Index (SOI) were the most sensitive to less constrained diet compositions (*DC*) (Fig. 5). On the

353 other hand, the relative Ascendency (*A/C*), the Ascendency (*A*), the Capacity (*C*), the Averaged

354 Path Length (*APL*), the Overheads (*O*) and the Total System Throughput (TST) were the most

355 sensitive to uncertainty in the Biomass (*B*) parameter (Fig. 5).

356

#### 357 4. Discussion

358 The present work provides EwE modellers, and more broadly ecosystem ecologists, with a

359 routine that generates distributions of values for a set of well-known indices synthesizing

360 structural and functional properties of ecosystems by taking into account uncertainty in model

361 input parameters. In the first place, reanalyzing the Bay of Biscay continental shelf food web in

362 the light of the most probable estimates of uncertainty around input parameters for this ecosystem

363 supported the main ENA-derived ecological conclusions. Indeed, ENA index distributions all

364 encompassed the single ENA values derived from the EwE software with mean values in the

365 same range as the initial Ecopath estimates (**Table 3**). The Bay of Biscay ensemble approach as

366 such supported and strengthened the main conclusion of a detritus-based, and relatively mature

367 ecosystem (Lassalle et al., 2011). In addition, when interpreting and using ENA distributions, it  
368 should be kept in mind that those values are derived from the propagation of parameter  
369 uncertainty forward but also, to some point, to the interplay in parameters required to keep the  
370 models balanced when any changes are made.

371 The ENAtool routine was developed with the primary goal of strengthening ecological  
372 conclusions derived from comparative studies and before/after impact evaluations.

373 **Interpretation will no longer rely only on single value comparisons.** The routine will permit  
374 one to test differences between ENA indices through statistical tests as performed in Saint-Béat et  
375 al. (2013) with LIM models. The LIM models have evolved in the last decade from a single-  
376 solution method (Vézina and Platt, 1988) to statistical approaches with outputs composed of  
377 uncertainty intervals (density probability functions) of the flows and allowing the definition of  
378 uncertainty intervals of ENA indices. These methods first based on Monte Carlo approaches  
379 (Kones et al., 2006) are now used with a Monte Carlo Markov Chain routine (Kones et al., 2009).

380 Several meta-analyses, based on a selection of EwE models, have been done, focusing either on  
381 theoretical ecology and ecological concepts, or on ecosystems and species of particular interest  
382 (see details in Colléter et al., 2013b), a growing proportion being based on ENA indices (e.g.  
383 Christensen, 1995; Pérez-España and Arreguín-Sánchez, 2001; Lobry et al., 2008; Coll and  
384 Libralato, 2012; Selleslagh et al., 2012). In the present work, complementary analyses were  
385 performed on the ENAtool routine to determine how much the ENA indices distributions were  
386 sensitive to the main routine arguments, namely the number of ensemble members to be  
387 generated (*nset*) and the level of uncertainty to apply on the EwE input parameters (Pedigree).

388 The first induced no remarkable trend on the distributions whereas the latter was found positively  
389 related to the variance of the distributions (**Table 3**). As such, in future applications of the  
390 ENAtool routine, we recommend keeping the levels of uncertainty within a range compatible

391 with known uncertainties on parameters. If no Pedigree scores were filled for the EwE model,  
392 model builders or experts of the study area should be interviewed regarding the quality of data  
393 used during model construction. This was even more strongly suggested for field biomasses (*B*)  
394 and diet compositions (*DC*) that appeared as the most influential input parameters (**Table 3**). This  
395 last result can be also interpreted as an uncertainty analysis, showing that less constrained  
396 biomasses and diet compositions in input matrices both had a marked influence on **ecosystem-**  
397 **level** EwE model outputs such as ENA indices. This **reinforces the well-known** need for extra  
398 care to be used when setting these two parameters in EwE models, and more importantly for  
399 better information to be collected on these key characteristics of biological taxa. In the particular  
400 case of the Bay of Biscay, biomasses and diet compositions were both associated with low levels  
401 of uncertainty in the pre-existing Ecopath model, meaning they were already relatively well  
402 constrained by data. Within the four ENA indices that were strongly influenced by variations in  
403 diet compositions, the Mean Trophic Level (MTL) and the System Omnivory Index (SOI) were  
404 directly linked to trophic levels of **functional groups** compared to the Finn Cycling Index (FCI)  
405 and the Comprehensive Cycling Index (CCI) for which interpretation of diet compositions  
406 influence was less intuitive. Nonetheless, FCI and CCI were both calculated from a matrix of  
407 internal exchanges that portrays the diet compositions of predators (Allesina and Ulanowicz,  
408 2004). Indeed, both of these indices include the term  $T_{ij}$  (i.e. flow between **functional** groups *i*  
409 and *j*) in their definition, which is the same as  $Q_{ij}$  in Ecopath, with  $Q_{ij} = B_j \cdot DC_{ij}$ . FCI, CCI and  
410 SOI were commonly used to assess key ecosystem structural and functional features such as  
411 system maturity (Christensen, 1995), complexity, and stability (Libralato, 2008). From an applied  
412 perspective, in a comparative study by Selleslagh et al. (2012), the SOI was also demonstrated to  
413 be positively correlated with the degree of anthropogenic perturbations in estuaries. In the context  
414 of the European Water Framework Directive, the development of more functional indicators

415 based on fluxes of matters and energy, and trophic networks at the scale of the ecosystem was  
416 recently listed as a critical way to improve the implementation of European policies (Reyjol et al.,  
417 2014). In this scope, by using the ENAtool routine and by applying variations more specifically  
418 to the diet compositions, the robustness of this relationship ‘SOI/anthropogenic impacts’ is  
419 planned to be statistically tested in an upcoming comparative study before presentation as a  
420 potential indicator of “Good Environmental Status”. Attention will have to be paid to the  
421 topology and the degree of aggregation among **functional groups** in the compared models as  
422 these two factors were demonstrated to influence ENA values (Johnson et al., 2009).

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

435

436 5. Conclusion

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

448

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457 **the manuscript.**

458

459 Figure captions

460

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

468

469 Figure 2: Study area of the Bay of Biscay continental shelf and locations of the main rivers  
470 flowing into it. The shaded area corresponds to the French part of the continental shelf between  
471 30 and 150m depth, and represents the spatial extent of the Ecopath model.

472

473 Figure 3: Boxplot of ENA indices values obtained from the ENAtool routine, run with a *nset* of  
474 1000 and a level of uncertainty specific to each input parameter according to Pedigree scores for  
475 the pre-existing Ecopath model of the Bay of Biscay continental shelf of Lassalle et al. (2011). A  
476 black circle corresponds to the mean of the 1000 ENA indices values. A black cross represents  
477 the single ENA indices values obtained from the pre-existing Ecopath model using the EwE  
478 software. A black triangle is used for the ENA indices values calculated after the importation of  
479 the pre-existing Ecopath model to Matlab with no change on the input parameters. Results are  
480 depicted for the 13 ENA indices. Graphics are organized following the order of Table 2.

481



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

487  
488 Figure 5: Variance of ENA indices values obtained from the ENAtool routine run with a *nset*  
489 equal to 1000 and a level of uncertainty of 20% alternatively applied on each key input  
490 parameter. The application case is the pre-existing Ecopath model of the Bay of Biscay  
491 continental shelf of Lassalle et al. (2011). For each histogram, from the left to the right, the field  
492 biomasses are modified by  $\pm 20\%$ , then production to biomass ratios, consumption to biomass  
493 ratios, and finally diet compositions. Results are depicted for the 13 ENA indices. Graphics are  
494 organized following the order of Table 2.

495

496 Table 1: Uncertainty applied to input parameters of the pre-existing Ecopath model of the Bay of  
 497 Biscay continental shelf by Lassalle et al. (2011) (i.e. term ‘percentage’ in equation (3)). Values  
 498 were derived from pre-defined tables provided by Christensen et al. (2005) associating a Pedigree  
 499 score to each given level of uncertainty for each basic input parameter. Blank cells correspond to  
 500 parameters left to be estimated by the model, where the parameter did not apply (e.g.  $Q/B$  for  
 501 primary producers), or where the EwE software did not allow setting Pedigree scores (e.g.  $P/B$  of  
 502 primary producers). To run the ENAtool routine, blank cells were replaced by zeros.

	$B$	$P/B$	$Q/B$	$DC$
505 Pursuit divers seabirds	0.1	0.9	0.5	0.8
506 Surface feeders seabirds	0.1	0.9	0.5	0.8
507 Striped dolphins	0.1	0.8	0.5	0.3
508 Bottlenose dolphins	0.1	0.8	0.5	0.3
509 Common dolphins	0.1	0.8	0.5	0.3
510 Long-finned pilot whales	0.1	0.8	0.5	0.3
511 Harbour porpoises	0.1	0.8	0.5	0.3
512 Piscivorous demersal fish	0.1	0.5	0.5	0.4
513 Piscivorous and benthivorous demersal fish	0.1	0.5	0.5	0.4
514 Suprabenthivorous demersal fish	0.1	0.5	0.5	0.4
515 Benthivorous demersal fish	0.1	0.5	0.5	0.4
516 Mackerel	0.6	0.5	0.5	0.3
517 Horse mackerel	0.6	0.5	0.5	0.3
518 Anchovy	0.1	0.5	0.5	0.3
519 Sardine	0.1	0.5	0.5	0.3
520 Sprat	0.1	0.5	0.5	0.3
521 Benthic cephalopods		0.8	0.8	0.5
522 Pelagic cephalopods		0.8	0.8	0.5
523 Carnivorous benthic invertebrates	0.4	0.5		0.3
524 Necrophageous benthic invertebrates	0.4	0.5		0.3
525 Sub-surface deposit feeders invertebrates	0.4	0.5		0.3
526 Surface suspension and deposit feeders inv.	0.4	0.5		0.3
527 Benthic meiofauna	0.4	0.5		0.3
528 Suprabenthic invertebrates	0.4	0.5		0.3
529 Macrozooplankton	0.1		0.8	0.3
530 Mesozooplankton	0.1		0.8	0.3
531 Microzooplankton	0.1		0.8	0.3
532 Bacteria	0.1	0.1		0.3
533 Large phytoplankton	0.1			
534 Small phytoplankton	0.1			
535 Discards				
536 <u>Detritus</u>				

537

538 Table 2: Formulas to calculate the 13 ENA indices in the *indices* function of the ENAtool routine. Formulas and their origins are  
 539 presented for EwE software v.6 as well as for the linear inverse modelling approach. For each ENA index, its single value calculated  
 540 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  $i^{\text{th}}$   
 541 **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  
 542 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  
 543 of  $i$  and  $BQB_i$  (or  $OI_i$ ) is the omnivory index for  $i$ . The internal ascendancy  $A_i$ , internal capacity  $C_i$  and internal relative ascendancy  
 544  $A_i/C_i$  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)	935578	~	
Finn cycling index (FCI) / no units	Proportion of flows in a system that is recycled	$\frac{TST_c}{TST} = \sum_j \frac{\sum_i T_{ij} + Imports_j}{TST}$	Finn (1980)	34.61	~	

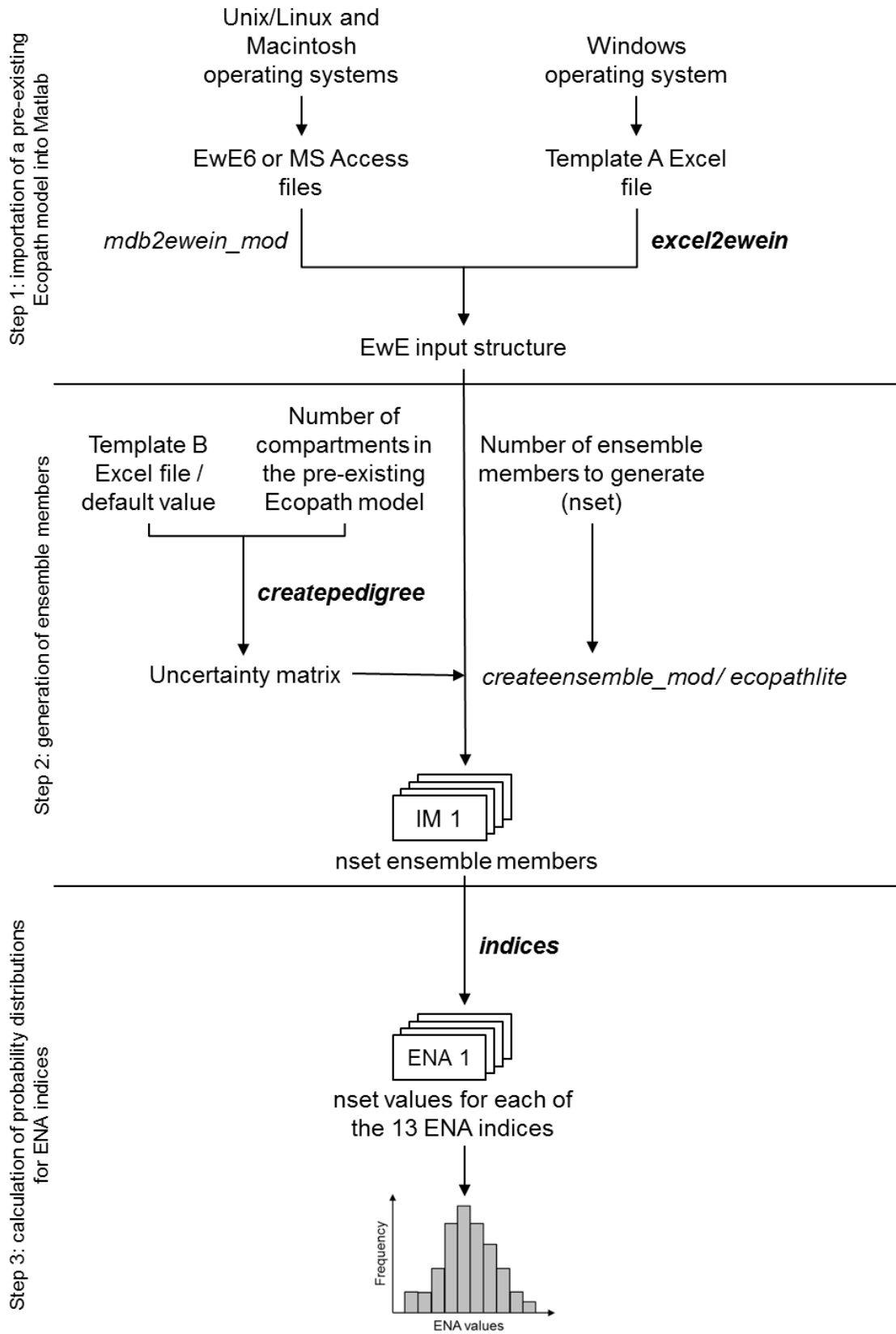
Comprehensive cycling index (CCI) / no units	Proportion of all flows in a system that is recycled	$1.142 \times FCI$	Allesina and Ulanowicz (2004)	39.53	~	
Averaged path length (APL) / no units	Average number of functional groups that an atom of carbon passes through between its entry into the system and its exit	$\frac{TST}{\sum_i Exports + \sum_i Respiration}$	Finn (1980)	4.857	$\frac{TST - \sum_i Imports}{\sum_i Imports}$	Kay et al. (1989); Baird et al. (1991)
Ascendency (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)	86088 2	~	
Capacity (C) / flowbits	Maximum potential ascendency	$-\sum_i \sum_j T_{ij} \times \log \left[ \frac{T_{ij}}{TST} \right]$	Patricio et al. (2006)	38082 06	$-TST \times \sum_i \frac{\sum_j T_{ij}}{TST} \times \log \left[ \frac{1}{i} \right]$	Ulanowicz (1986)
Relative ascendency	Fraction of the system	$\frac{A}{C}$	Ulanowicz (1986)	0.226	~	

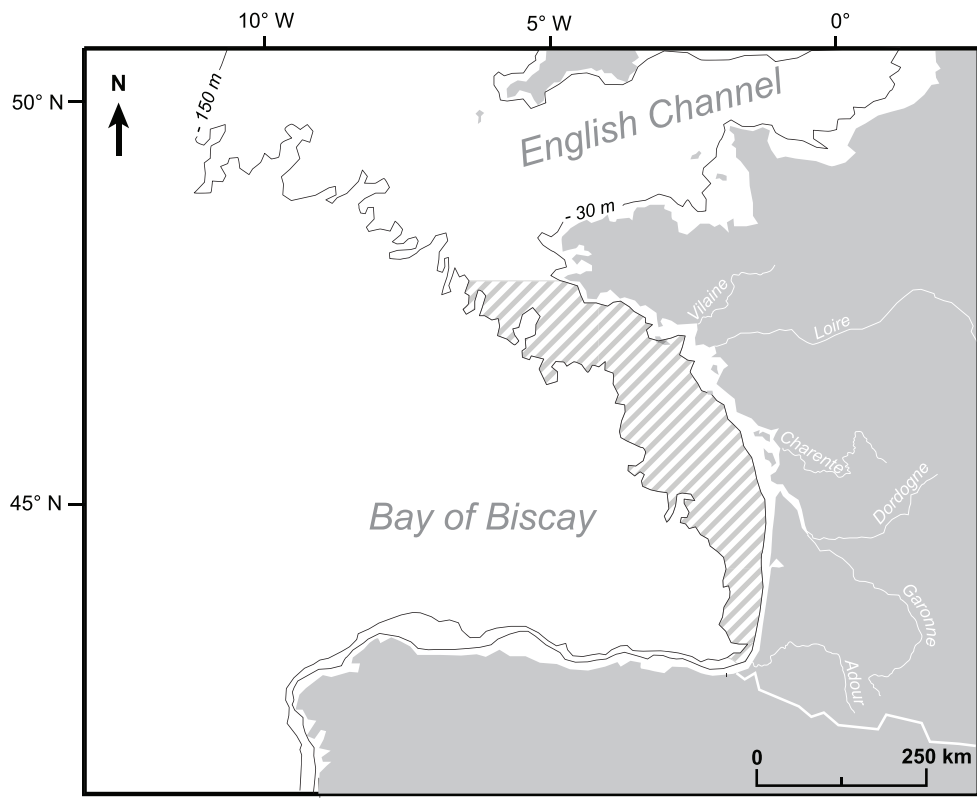
(A/C) / no units	that is organized					
Overheads (O) / flowbits	Unorganized part of the system	$C - A$	Ulanowicz (1986)	29473 25	~	
System Omnivory Index (SOI) / no units *	Omnivory	$\left\{ \begin{array}{l} \frac{\sum_i \log \left[ \frac{Q_i}{\min(Q)} \right] \times BQB_i}{s} \quad \text{if } s > 0 \\ \sum_i \log \left[ \frac{Q_i}{\min(Q)} \right] \times BQB_i \end{array} \right.$	Villy Christensen, pers. comm.	0.195	$\frac{\sum_i OI_i \times \log[Q_i]}{\sum_i \log[Q_i]}$	Christensen and Pauly (1993)
		with $s = \sum_i \log \left[ \frac{Q_i}{\min(Q)} \right]$ and				
		$BQB_i = OI_i = \sum_j \left( TL_j - \left( \sum_j TL_j \times DC_{ji} \right) \right)^i$				

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

547 **Table 3: Summary of results from the application of the ENAtool routine to the Bay of Biscay continental shelf ecosystem**  
 548 **model and of results from the preliminary sensitivity analyses. ‘Global’ means that all input parameters were simultaneously**  
 549 **changed according to the level of uncertainty and ‘Local’ that  $B$ ,  $P/B$ ,  $Q/B$  and  $DC$  were alternatively modified.**  
 550

<b>Application of the ENAtool routine</b> ( <i>nset</i> of 1000 and levels of uncertainty based on pedigrees)	<b>Preliminary sensitivity analyses</b> Global / All combinations of <i>nset</i> (10, 100, 1000) and levels of uncertainty (20, 40, 60%)      Local / <i>nset</i> 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 <i>nset</i> 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>

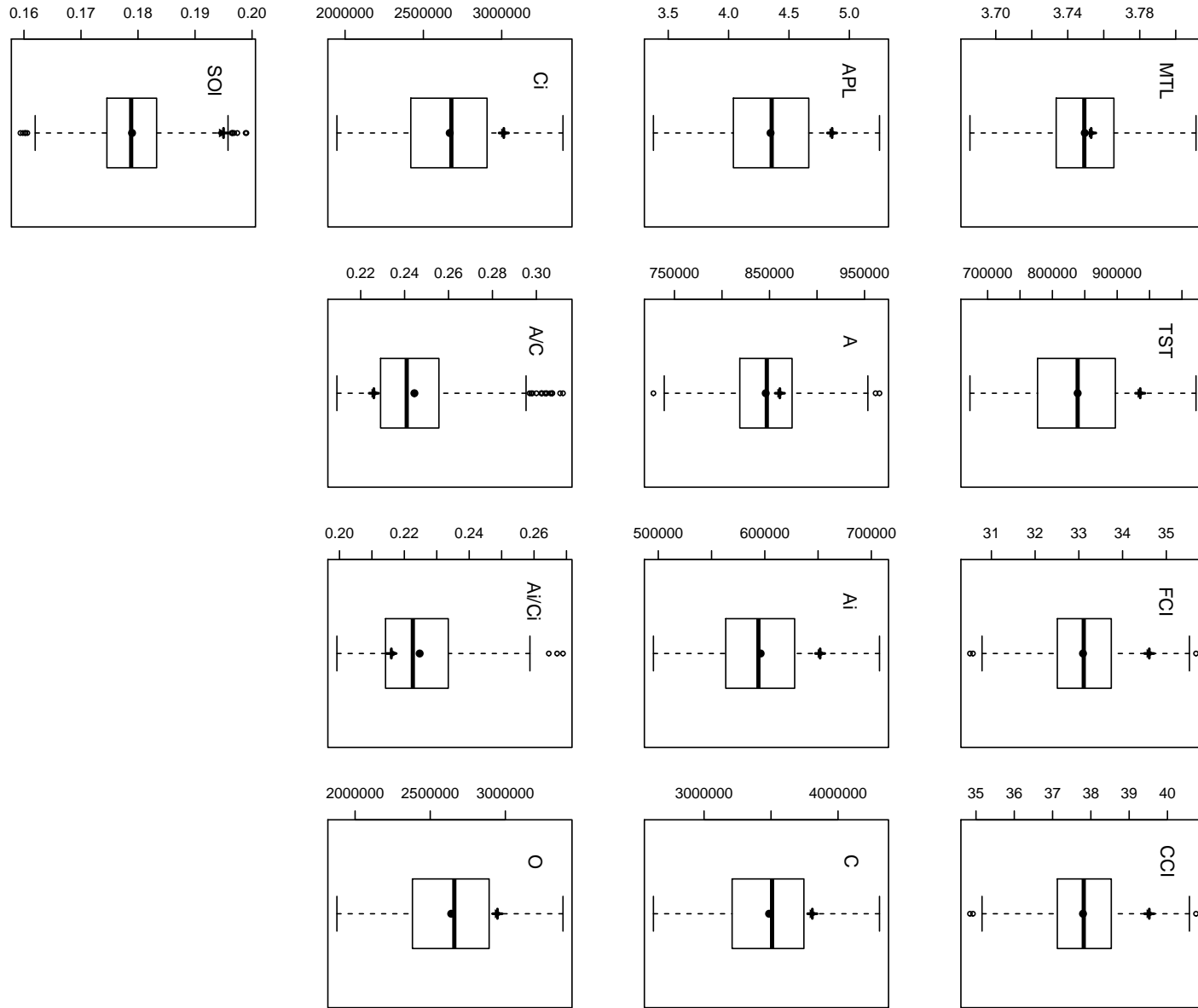




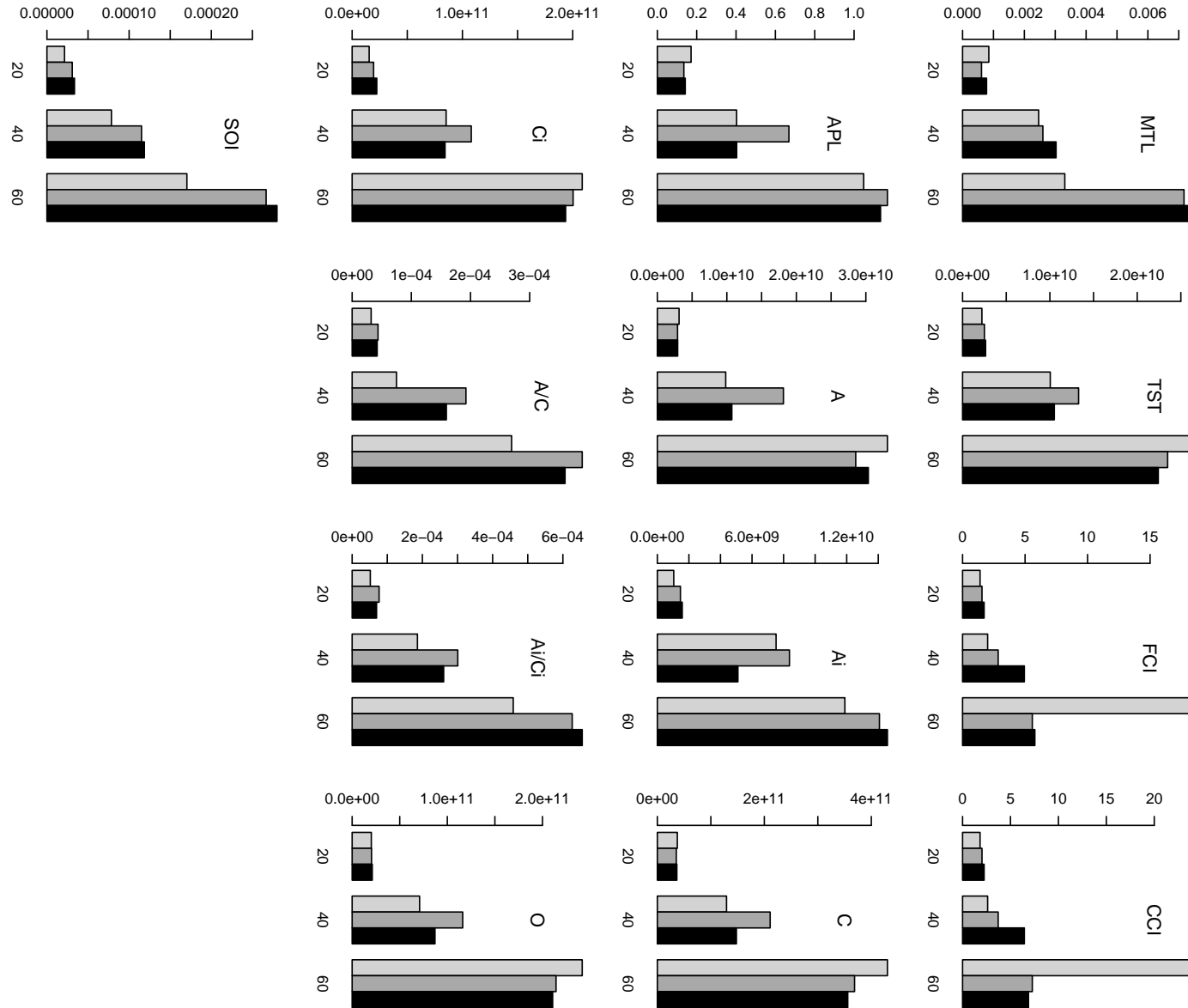
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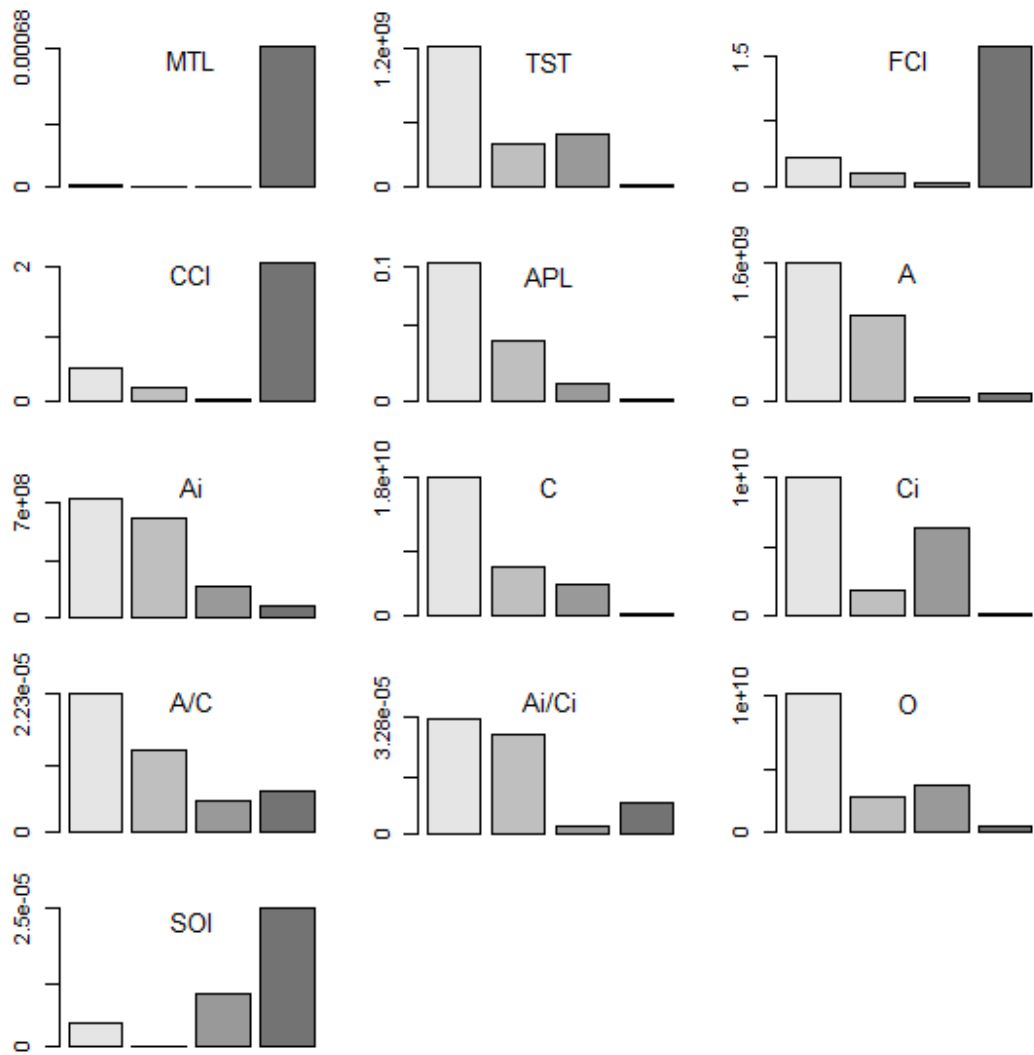


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