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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 , year^{-1}), consumption rate (Q/B , year^{-1}), proportion of i in the diet of j (DC_{ij} ; DC = diet

151 composition), net migration rate (Ex , year⁻¹), biomass accumulation ($Bacc$, year⁻¹), total catch (Y ;
152 kg C·km⁻² year⁻¹), respiration (R ; kg C·km⁻²·year⁻¹), amount of consumed food that is
153 unassimilated (U ; kg C·km⁻²·year⁻¹) 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 km² (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 1st (25%) and the 3rd (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^{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 ⁻² ·year ⁻¹	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	~	

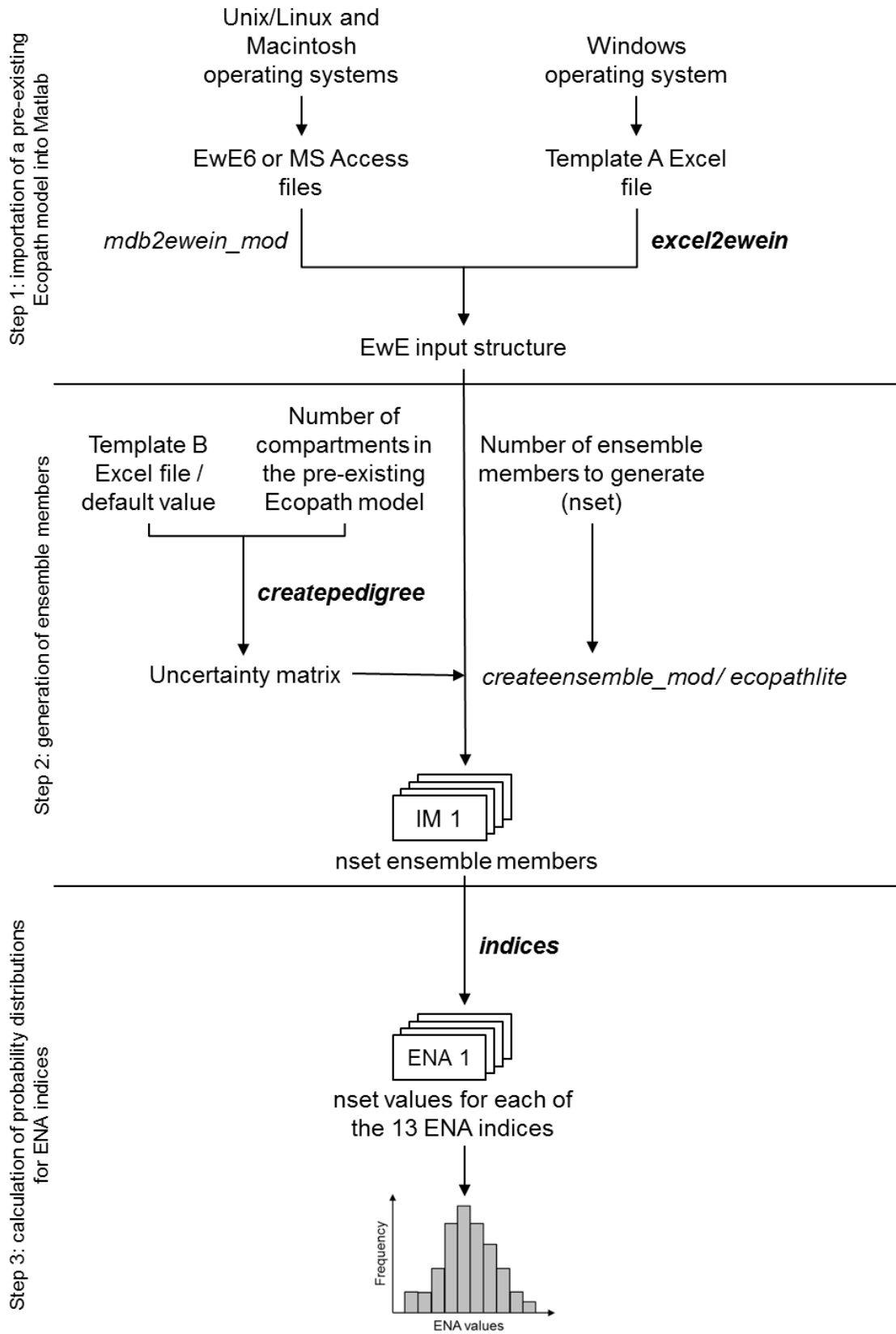
Comprehensive cycling index (CCI) / no units	Proportion of all flows in a system that is recycled	$1.142 \times FCI$	Allesina and Ulanowicz (2004)	39.53	~	
Averaged path length (APL) / no units	Average number of functional groups that an atom of carbon passes through between its entry into the system 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	~	

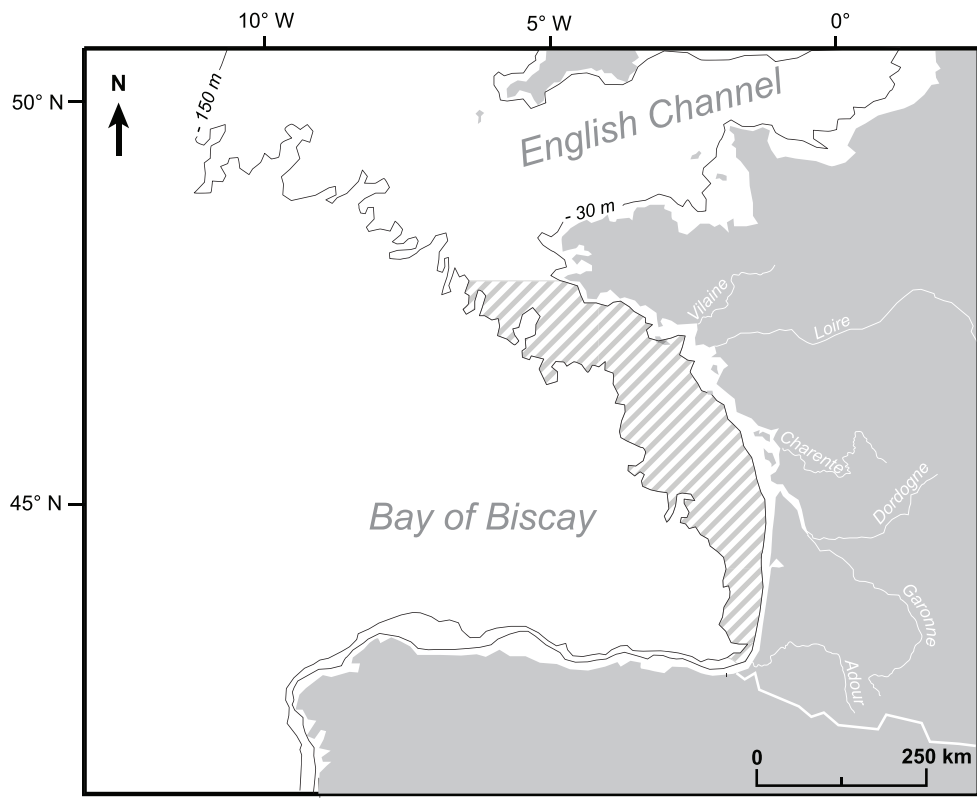
(A/C) / no units	that is organized					
Overheads (O) / flowbits	Unorganized part of the system	$C - A$	Ulanowicz (1986)	29473 25	~	
System Omnivory Index (SOI) / no units *	Omnivory	$\left\{ \begin{array}{l} \frac{\sum_i \log \left[\frac{Q_i}{\min(Q)} \right] \times BQB_i}{s} \quad \text{if } s > 0 \\ \sum_i \log \left[\frac{Q_i}{\min(Q)} \right] \times BQB_i \end{array} \right.$	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

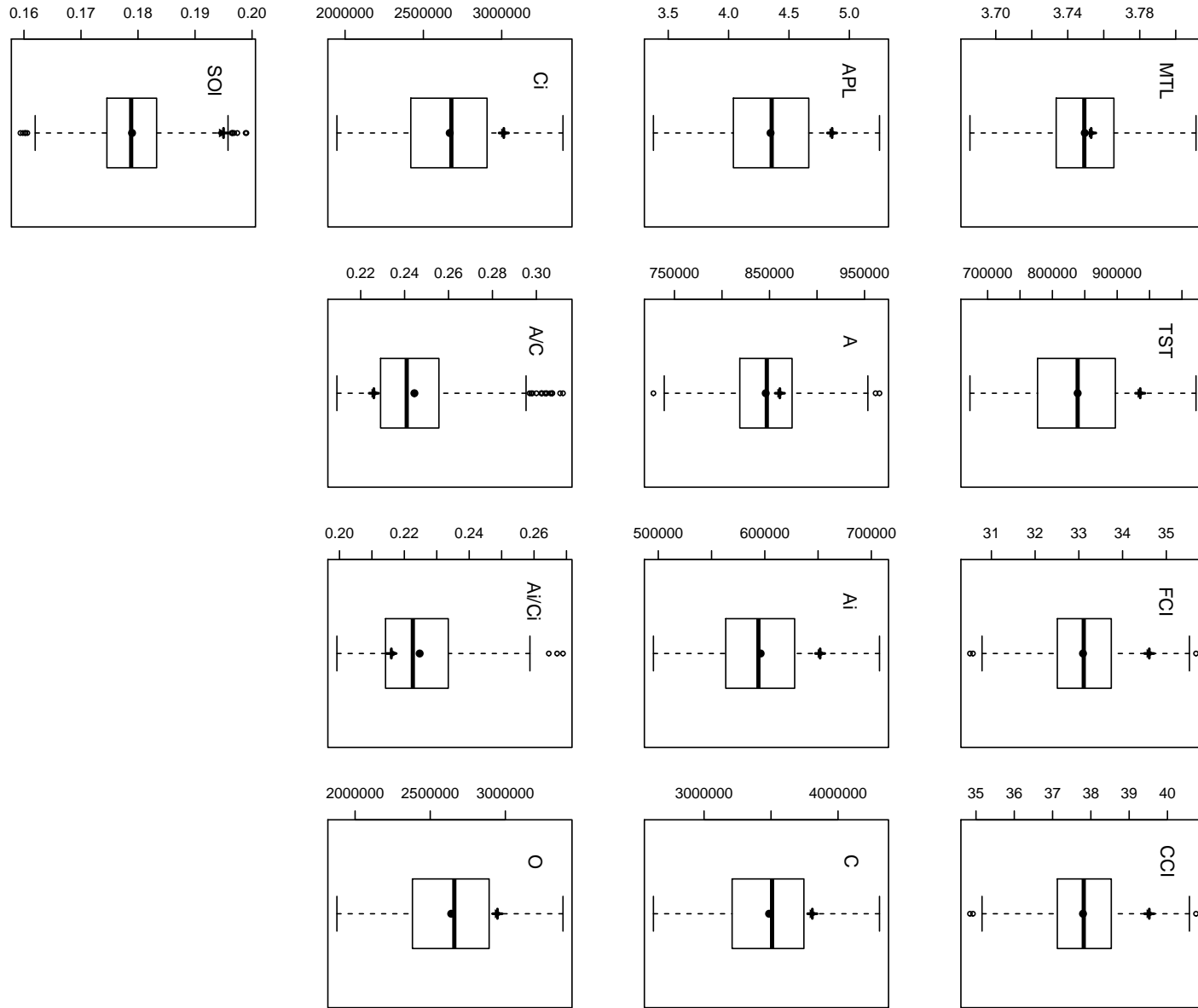
Application of the ENAtool routine (<i>nset</i> of 1000 and levels of uncertainty based on pedigrees)	Preliminary sensitivity analyses Global / All combinations of <i>nset</i> (10, 100, 1000) and levels of uncertainty (20, 40, 60%) Local / <i>nset</i> of 1000 and level of uncertainty of 20%	
<ul style="list-style-type: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



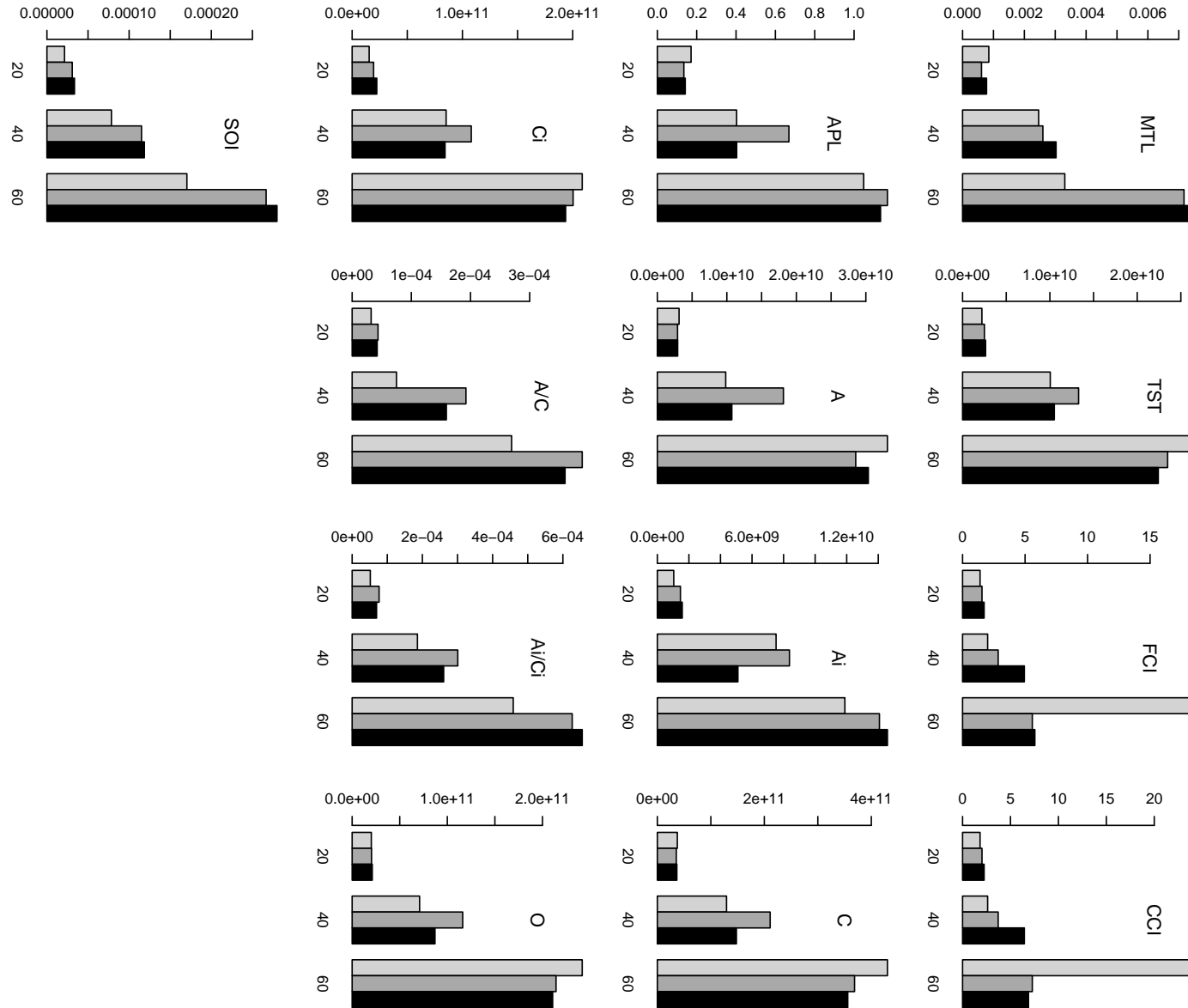


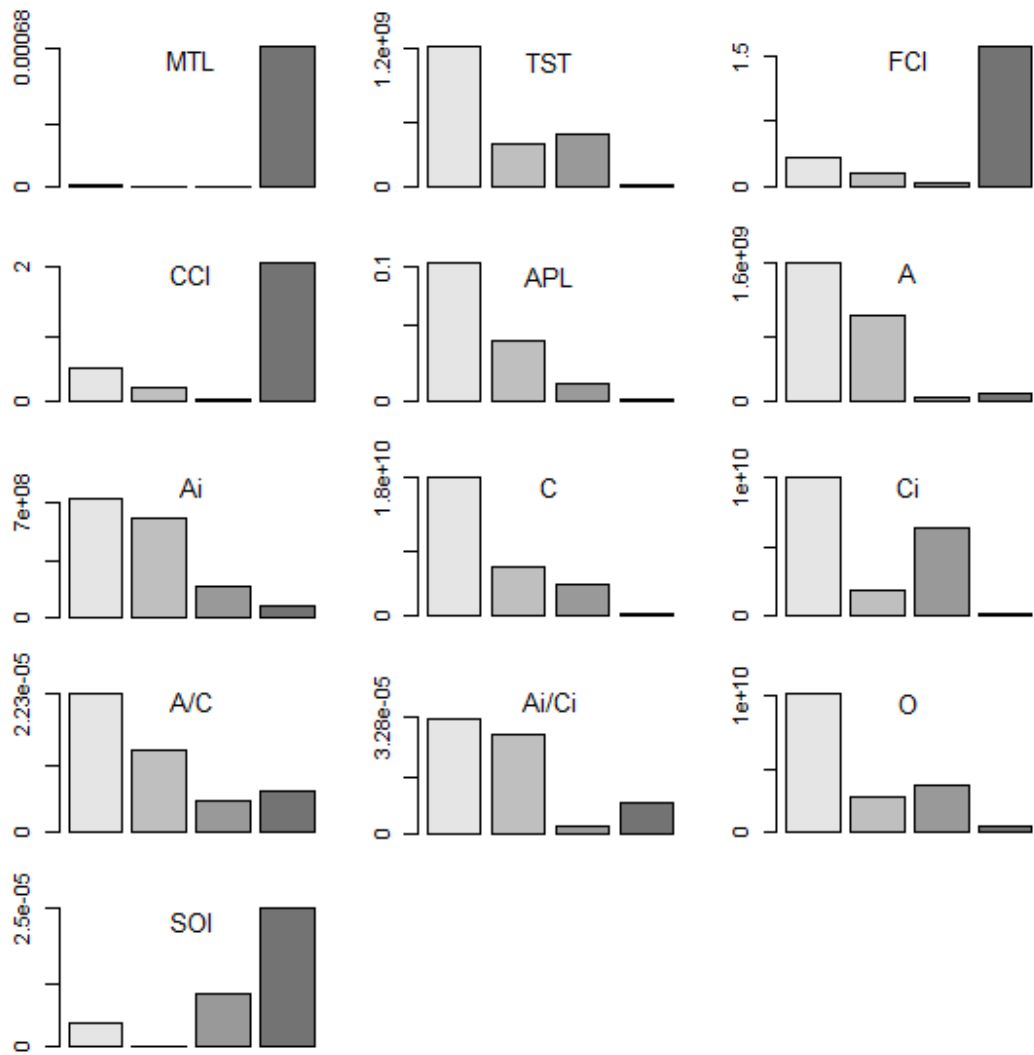
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556 References

- 557 Allesina, S., Ulanowicz, R.E., 2004. Cycling in ecological networks: Finn's index revisited.
558 Computational Biology and Chemistry 28, 227-233.
- 559 Aydin, K.Y., Gaichas, S.K., Ortiz, I., Kinzey, D., Friday, N., 2007. A comparison of the Bering
560 Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling.
561 NOAA Technical Memorandum. 298 pp.
- 562 Baeta, A., Niquil, N., Marques, J.C., Patrício, J., 2011. Modelling the effects of eutrophication,
563 mitigation measures and an extreme flood event on estuarine benthic food webs. Ecological
564 Modelling 222, 1209-1221.
- 565 Baird, D., McGlade, J.M., Ulanowicz, R.E., 1991. The comparative ecology of six marine
566 ecosystems. Philosophical Transactions of the Royal Society of London. Series B: Biological
567 Sciences 333, 15-29.
- 568 Beaugrand, G., 2004. The North Sea regime shift: Evidence, causes, mechanisms and
569 consequences. Progress In Oceanography 60, 245-262.
- 570 Borja, Á., Elliott, M., Carstensen, J., Heiskanen, A.-S., van de Bund, W., 2010. Marine
571 management – Towards an integrated implementation of the European Marine Strategy
572 Framework and the Water Framework Directives. Marine Pollution Bulletin 60, 2175-2186.
- 573 Borrett, S.R., Lau, M.K., 2014. enaR: An r package for Ecosystem Network Analysis. Methods in
574 Ecology and Evolution 5, 1206-1213.
- 575 Christensen, V., 1995. Ecosystem maturity - towards quantification. Ecological Modelling 77, 3-
576 32.
- 577 Christensen, V., Pauly, D., 1992. ECOPATH II - a software for balancing steady-state ecosystem
578 models and calculating network characteristics. Ecological Modelling 61, 169-185.

- 579 Christensen, V., Pauly, D. (ed.). 1993. Trophic models of aquatic ecosystems. International
580 Center for Living Aquatic Resources Management; The International Council for the Exploration
581 of the Sea; The Danish International Development Agency, Manila, Philippines. 390 pp.
- 582 Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations.
583 Ecological Modelling 172, 109-139.
- 584 Christensen, V., Walters, C.J., Pauly, D., 2005. Ecopath with Ecosim: A user's guide. Fisheries
585 Centre, University of British Columbia, Vancouver, Canada. 154 pp.
- 586 Christensen, V., Walters, C.J., Pauly, D., Forrest, R., 2008. Ecopath with Ecosim version 6. User
587 guide - November 2008. Lenfest Ocean Futures Project 2008. Fisheries Centre, The University of
588 British Columbia, Vancouver, Canada. 235 pp.
- 589 Coll, M., Libralato, S., 2012. Contributions of foodweb modelling to the ecosystem approach to
590 marine resource management in the Mediterranean Sea. Fish and Fisheries 13, 60-88.
- 591 Colléter, M., Guitton, J., Gascuel, D., 2013a. An introduction to the EcoTroph R package:
592 Analyzing aquatic ecosystem trophic networks. R Journal 5, 98-107.
- 593 Colléter, M., Valls, A., Guitton, J., Morissette, L., Arreguín-Sánchez, F., Christensen, V.,
594 Gascuel, D., Pauly, D., 2013b. EcoBase: A repository solution to gather and communicate
595 information from EwE models. Fisheries Centre, University of British Columbia, Canada. 60 pp.
- 596 Dame, J.K., Christian, R.R., 2006. Uncertainty and the use of network analysis for ecosystem-
597 based fisheries management. Fisheries 31, 331-341.
- 598 Finn, J.T., 1980. Flow-analysis of models of the Hubbard Brook ecosystem. Ecology 61, 562-
599 571.
- 600 Fulton, A.E., 2010. Approaches to end-to-end ecosystem models. Journal of Marine Systems 81,
601 171-183.

- 602 Funtowicz, S.O., Ravetz, J.R., 1990. Uncertainty and quality in science for policy. Kluwer
603 Academic Publishers. 229 pp.
- 604 Gårdmark, A., Lindegren, M., Neuenfeldt, S., Blenckner, T., Heikinheimo, O., Müller-Karulis,
605 B., Niiranen, S., Tomczak, M., Aro, E., Wikström, A., Möllmann, C., 2012. Biological ensemble
606 modelling to evaluate potential futures of living marine resources. *Ecological Applications* 23,
607 742-754.
- 608 Heymans, J.J., Baird, D., 2000. Network analysis of the northern Benguela ecosystem by means
609 of NETWRK and ECOPATH. *Ecological Modelling* 131, 97-119.
- 610 Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine
611 ecosystems. *Science* 328, 1523-1528.
- 612 Johnson, G.A., Niquil, N., Asmus, H., Bacher, C., Asmus, R., Baird, D., 2009. The effects of
613 aggregation on the performance of the inverse method and indicators of network analysis.
614 *Ecological Modelling* 220, 3448-3464.
- 615 Kay, J.J., Graham, L.A., Ulanowicz, R.E., 1989. A detailed guide to network analysis. *In*: F.
616 Wulff, J.G. Field, K.H. Mann (ed.). *Network Analysis in Marine Ecology*, Springer-Verlag,
617 Berlin, Germany. pp. 15-61.
- 618 Kearney, K.A., 2012. An analysis of marine ecosystem dynamics through development of a
619 coupled physical-biogeochemical-fisheries food web model. PhD thesis, Princeton University.
620 179 pp.
- 621 Kearney, K.A., 2015. A Matlab implementation of Ecopath: v0.1: Guesnet et al. 2015 snapshot.
622 Zenodo. [10.5281/zenodo.17837](https://doi.org/10.5281/zenodo.17837).
- 623 Kearney, K.A., Stock, C., Aydin, K.Y., Sarmiento, J.L., 2012. Coupling planktonic ecosystem
624 and fisheries food web models for a pelagic ecosystem: Description and validation for the
625 subarctic Pacific. *Ecological Modelling* 237–238, 43-62.

- 626 Kones, J.K., Soetaert, K., van Oevelen, D., Owino, J.O., 2009. Are network indices robust
627 indicators of food web functioning? A Monte Carlo approach. *Ecological Modelling* 220, 370-
628 382.
- 629 Kones, J.K., Soetaert, K., van Oevelen, D., Owino, J.O., Mavuti, K., 2006. Gaining insight into
630 food webs reconstructed by the inverse method. *Journal of Marine Systems* 60, 153-166.
- 631 Lassalle, G., Bourdaud, P., Saint-Béat, B., Rochette, S., Niquil, N., 2014. A toolbox to evaluate
632 data reliability for whole-ecosystem models: Application on the Bay of Biscay continental shelf
633 food-web model. *Ecological Modelling* 285, 13-21.
- 634 Lassalle, G., Lobry, J., Le Loc'h, F., Bustamante, P., Certain, G., Delmas, D., Dupuy, C., Hily,
635 C., Labry, C., Le Pape, O., Marquis, E., Petitgas, P., Pusineri, C., Ridoux, V., Spitz, J., Niquil,
636 N., 2011. Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf
637 food web: implications for ecosystem management. *Progress In Oceanography* 91, 61-75.
- 638 Leguerrier, D., Degré, D., Niquil, N., 2007. Network analysis and inter-ecosystem comparison of
639 two intertidal mudflat food webs (Brouage mudflat and Aiguillon Cove, SW France). *Estuarine,
640 Coastal and Shelf Science* 74, 403-418.
- 641 Libralato, S., 2008. System Omnivory Index. *In: S.E. Jorgensen, B. Fath (ed.). Encyclopedia of
642 Ecology*, Academic Press, Oxford. pp. 3472-3477.
- 643 Lobry, J., David, V., Pasquaud, S., Lepage, M., Sautour, B., Rochard, E., 2008. Diversity and
644 stability of an estuarine trophic network. *Marine Ecology Progress Series* 358, 13-25.
- 645 Lucey, S.M., Aydin, K.Y., Gaichas, S.K., Fogarty, M.J., Hyun, S.-Y., Cadrin, S.X., 2014.
646 Improving the EBFM toolbox with an open source mass balance model. *In: J. Steenbeek, C.
647 Piroddi, M. Coll, J.J. Heymans, S. Villasante, V. Christensen (ed.) Ecopath 30 years conference
648 proceedings: Extended abstracts*, Fisheries Centre, University of British Columbia, Canada. pp.
649 204-205.

- 650 Niiranen, S., Blenckner, T., Hjerne, O., Tomczak, M., 2012. Uncertainties in a Baltic Sea food-
651 web model reveal challenges for future projections. *Ambio* 41, 613-625.
- 652 Niquil, N., Kagami, M., Urabe, J., Christaki, U., Viscogliosi, E., Sime-Ngando, T., 2011.
653 Potential role of fungi in plankton food web functioning and stability: a simulation analysis based
654 on Lake Biwa inverse model. *Hydrobiologia* 659, 65-79.
- 655 Niquil, N., Le Loc'h, F., Tecchio, S., Chaalali, A., Vouriot, P., Mialet, B., Fizzala, X., Féral, J.-
656 P., Lamare, S., Dauvin, J.-C., Safi, G., 2014. Ongoing research on ecosystem health indicators for
657 food webs in the MSFD context. *In*: E. Evariste, J.-C. Dauvin, P. Claquin, A. Auber, A. Winder,
658 B. Thenail, S. Fletcher, J.-P. Robin (ed.) Trans-Channel forum proceedings "Science and
659 Governance of the Channel Marine Ecosystem", INTERREG IV A Programme, Université de
660 Caen Basse-Normandie, Caen, France. pp. 160.
- 661 Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262-270.
- 662 Patricio, J., Ulanowicz, R., Pardal, M.A., Marques, J.C., 2006. Ascendency as ecological
663 indicator for environmental quality assessment at the ecosystem level: A case study. *In*: K.
664 Martens, H. Queiroga, M.R. Cunha, A. Cunha, M.H. Moreira, V. Quintino, A.M. Rodrigues, J.
665 Seroôdio, R.M. Warwick (ed.). *Marine Biodiversity*, Springer Netherlands. pp. 19-30.
- 666 Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim, and Ecospace as tools for
667 evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science* 57, 697-706.
- 668 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food
669 webs. *Science* 279, 860-863.
- 670 Pérez-España, H., Arreguín-Sánchez, F., 2001. An inverse relationship between stability and
671 maturity in models of aquatic ecosystems. *Ecological Modelling* 145, 189-196.
- 672 Plagányi, E.E., 2007. *Models for an ecosystem approach to fisheries*. FAO, Rome, Italy. 107 pp.

- 673 Polovina, J.J., 1984. Model of coral reef ecosystem I. The Ecopath model and its application to
674 French Frigate Shoals. *Coral Reefs* 3, 1-11.
- 675 Reyjol, Y., Argillier, C., Bonne, W., Borja, A., Buijse, A.D., Cardoso, A.C., Daufresne, M.,
676 Kernan, M., Ferreira, M.T., Poikane, S., Prat, N., Solheim, A.-L., Stroffek, S., Usseglio-Polatera,
677 P., Villeneuve, B., van de Bund, W., 2014. Assessing the ecological status in the context of the
678 European Water Framework Directive: Where do we go now? *Science of The Total Environment*
679 497–498, 332-344.
- 680 Richardson, T.L., Jackson, G.A., Ducklow, H.W., Roman, M.R., 2006. Spatial and seasonal
681 patterns of carbon cycling through planktonic food webs of the Arabian Sea determined by
682 inverse analysis. *Deep Sea Research Part II: Topical Studies in Oceanography* 53, 555-575.
- 683 Rombouts, I., Beaugrand, G., Fizzala, X., Gaill, F., Greenstreet, S., Lamare, S., Le Loc'h, F.,
684 McQuatters-Gollop, A., Mialet, B., Niquil, N., Percelay, J., Renaud, F., Rossberg, A., Féral, J.-P.,
685 2013. Food web indicators under the Marine Strategy Framework Directive: From complexity to
686 simplicity? *Ecological Indicators* 29, 246-254.
- 687 Saint-Béat, B., Baird, D., Asmus, H., Asmus, R., Bacher, C., Pacella, S.R., Johnson, G.A., David,
688 V., Vézina, A.F., Niquil, N., 2015. Trophic networks: How do theories link ecosystem structure
689 and functioning to stability properties? A review. *Ecological Indicators* 52, 458-471.
- 690 Saint-Béat, B., Dupuy, C., Bocher, P., Chalumeau, J., De Crignis, M., Fontaine, C., Guizien, K.,
691 Lavaud, J., Lefebvre, S., Montanié, H., Mouget, J.-L., Orvain, F., Pascal, P.-Y., Quaintenne, G.,
692 Radenac, G., Richard, P., Robin, F., Vézina, A.F., Niquil, N., 2013. Key features of intertidal
693 food webs that support migratory shorebirds. *PLoS ONE* 8, e76739.
- 694 Selleslagh, J., Lobry, J., Amara, R., Brylinski, J.M., Boët, P., 2012. Trophic functioning of
695 coastal ecosystems along an anthropogenic pressure gradient: A French case study with emphasis
696 on a small and low impacted estuary. *Estuarine, Coastal and Shelf Science* 112, 73-85.

- 697 Tomczak, M.T., Heymans, J.J., Yletyinen, J., Niiranen, S., Otto, S.A., Blenckner, T., 2013.
698 Ecological network indicators of ecosystem status and change in the Baltic sea. PLoS ONE 8,
699 e75439.
- 700 Ulanowicz, R.E., 1986. Growth and development: Ecosystem phenomenology. Springer-Verlag,
701 New-York, USA. 203 pp.
- 702 Ulanowicz, R.E., 2004. Quantitative methods for ecological network analysis. Computational
703 Biology and Chemistry 28, 321-339.
- 704 Ulanowicz, R.E., Wulff, F., 1991. Comparing ecosystem structures: The Chesapeake Bay and the
705 Baltic Sea. *In*: J. Cole, G. Lovett, S. Findlay (ed.). Comparative Analysis of Ecosystems -
706 Patterns, Mechanisms and Theories, Springer-Verlag, New-York, USA. pp. 140-166.
- 707 Ulanowicz, R.E., Jørgensen, S.E., Fath, B.D., 2006. Exergy, information and aggradation: An
708 ecosystems reconciliation. Ecological Modelling 198, 520-524.
- 709 Vézina, A.F., Platt, T., 1988. Food web dynamics in the oceans. 1. Best-estimates of flow
710 networks using inverse methods. Marine Ecology Progress Series 42, 269-287.

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