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

Vanessa Guesnet, Géraldine Lassalle, Aurélie Chaalali, Kelly Kearney,
Blanche Saint-Béat, Battle Karimi, Boutheina Grami, Samuele Tecchio,
Nathalie Niquil, Jérémy Lobry

HAL Id: hal-01186765
https://hal.science/hal-01186765

Submitted on 16 May 2020

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

7   Incorporating food-web parameter uncertainty into Ecopath-derived ecological

8   network indicators

9

10   Guesnet Vanessa [a], Lassalle Géraldine [a,1], Chaalali Aurélie [b,2], Kearney Kelly [c], Saint-Béat

11   Blanche [d], Karimi Battle [e], Grami Boutheina [f], Tecchio Samuele [b], Niquil Nathalie [b], and Lobry

12   Jérémy [a]

13

14   [a] IRSTEA, UR EABX, Aquatic Ecosystems and Global Changes, 50 avenue de Verdun, 33612

15   Cestas cedex, France; vanessa.guesnet@yahoo.fr; geraldine.lassalle@irstea.fr;

16   jeremy.lobry@irstea.fr

17   [b] CNRS, UMR 7208 BOREA, Université de Caen Basse-Normandie, Esplanade de la Paix, CS

18   14032, 14032 Caen cedex 5; France; aurelie.chaalali@gmail.com; samuele.tecchio@unicaen.fr;

19   nathalie.niquil@unicaen.fr

20   [c] Cooperative Institute for Marine and Atmospheric Studies, University of Miami Rosenstiel

21   School of Marine and Atmospheric Science, NOAA Atlantic Oceanographic and Meteorological

22   Laboratory, 4301 Rickenbacker Causeway, Miami, FL 33149, United States;

23   kkearney@rsmas.miami.edu

24   [d] Littoral Environnement et Sociétés, UMR 7266 CNRS-Université de La Rochelle, 2 rue

25   Olympe de Gouges, 17042 La Rochelle cedex, France; blanche.saintbeat@gmail.com

26   [e] UMR 6249 Laboratoire Chrono-Environnement, Pôle Universitaire du Pays de Montbéliard, 4

27   place Tharradin, BP 71427, 25211 Montbeliard cedex, France; karimi.battle@gmail.com

[1] Corresponding author. Tel.: +33 5 57 89 08 02.
E-mail addresses: geraldine.lassalle@irstea.fr; geraldinelassalle2@hotmail.com (G. Lassalle).
[2] Present address: IFREMER, Unité Écologie et Modèles pour l'Halieutique, Route de l'Ile d'Yeu, BP 21105, 44311
Nantes Cedex 03, France.

28   [f] Laboratoire de Cytologie Végétale et Phytoplanctonologie, Département des Sciences de la Vie,

29   Faculté des Sciences de Bizerte, Université de Carthage, Zarzouna, Bizerte, Tunisia;

30   grami.boutheina@gmail.com

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 (Plagànyi, 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).

6

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    $$B_i \times (P/B)_i = Y_i + \sum_j \left(B_j \times (Q/B)_j \times DC_{ij} \right) + Ex_i + Bacc_i + B_i (1 - EE_i) \times (P/B)_i \ (1)$$

147   and

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

149   where the main input parameters are biomass density (B, here in kg C·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

11

199   default level of uncertainty expressed as ±%. 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

12

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

13

247   the 30-m and 150-m isobaths with a surface area of 102,585 km^2 (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

14

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

19

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

21

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

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 ±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.

503

	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 Detritus				

537

25

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 ith

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 ascendency A_i, internal capacity C_i and internal relative ascendency

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	$\dfrac{\sum_i TL_i \times Y_i}{\sum_i Y_i}$	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	$\dfrac{TST_c}{TST} = \sum_j \dfrac{\sum_i T_{ij} + Imports_j}{TST}$	Finn (1980)	34.61	~	

26

|						
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	$\dfrac{TST}{\sum_i Exports + \sum_i Respiration}$	Finn (1980)	4.857	$\dfrac{TST - \sum_i Imports}{\sum_i Imports}$	Kay et al. (1989); Baird et al. (1991)
Ascendency (A) / flowbits	Quantification of the system activity in association with the degree of flows specialization	$\sum_i \sum_j T_{ij} \times log\left[\dfrac{TST \times T_{ij}}{\sum_j T_{ij} \times \sum_i T_{ij}}\right]$	Ulanowicz (1986)	860882	~	
Capacity (C) / flowbits	Maximum potential ascendency	$-\sum_i \sum_j T_{ij} \times log\left[\dfrac{T_{ij}}{TST}\right]$	Patricio et al. (2006)	3808206	$-TST \times \sum_i \dfrac{\sum_j T_{ij}}{TST} \times log\left[\dfrac{1}{7}\right]$	Ulanowicz (1986)
Relative ascendency	Fraction of the system	$\dfrac{A}{C}$	Ulanowicz (1986)	0.226	~	

27

(A/C) / no units	that is organized				
Overheads (O) / flowbits	Unorganized part of the system	$C - A$	Ulanowicz (1986)	2947325	~
System Omnivory Index (SOI) / no units [*]	Omnivory	$$\begin{cases} \dfrac{\sum_i log\left[\dfrac{Q_i}{min(Q)}\right] \times BQB_i}{S} & si\ s > 0 \\ \sum_i log\left[\dfrac{Q_i}{min(Q)}\right] \times BQB_i \end{cases}$$ with $s = \sum_i log\left[\dfrac{Q_i}{min(Q)}\right]$ and $BQB_i = OI_i = \sum_j \left(TL_j - \left(\sum_j TL_j \times DC_{ji}\right)\right)$	Villy Christensen, pers. comm.	0.195	$\dfrac{\sum_i OI_i \times log[Q_i]}{\sum_i log[Q_i]}$	Christensen and Pauly (1993)

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 (*nset* of 1000 and levels of uncertainty based on pedigrees)	Preliminary sensitivity analyses	
	Global / All combinations of *nset* (10, 100, 1000) and levels of uncertainty (20, 40, 60%)	Local / *nset* of 1000 and level of uncertainty of 20%
• The single ENA indices values obtained from the pre-existing Ecopath model using the EwE software all felt 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).	• No influence of *nset* on the variance of ENA indices distributions. • The variance of ENA indices distributions systematically increased with the level of uncertainty.	• The variance of ENA indices distributions changed the most when variations were applied to *B* and *DC*.

29

551

552

553

32

554

33
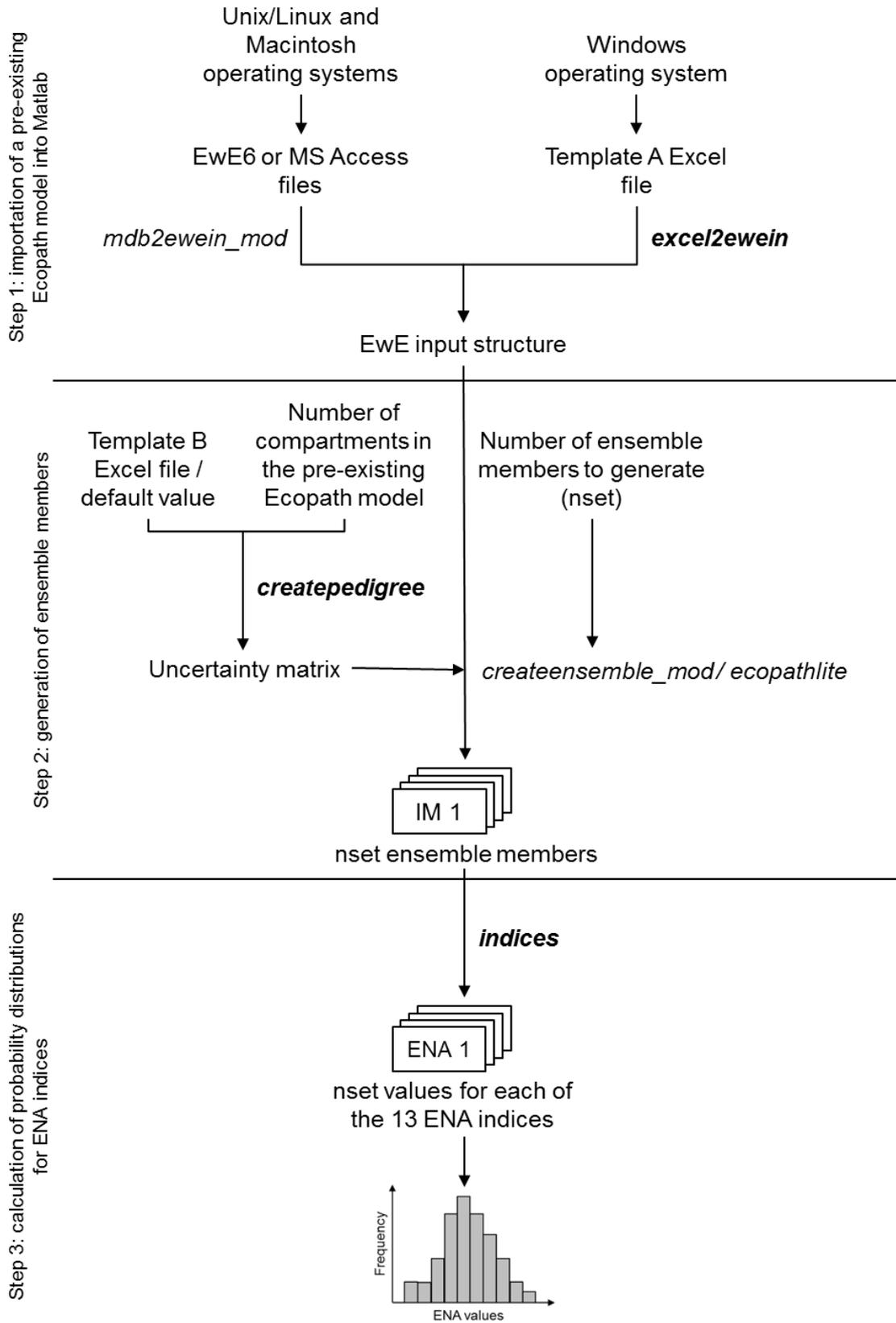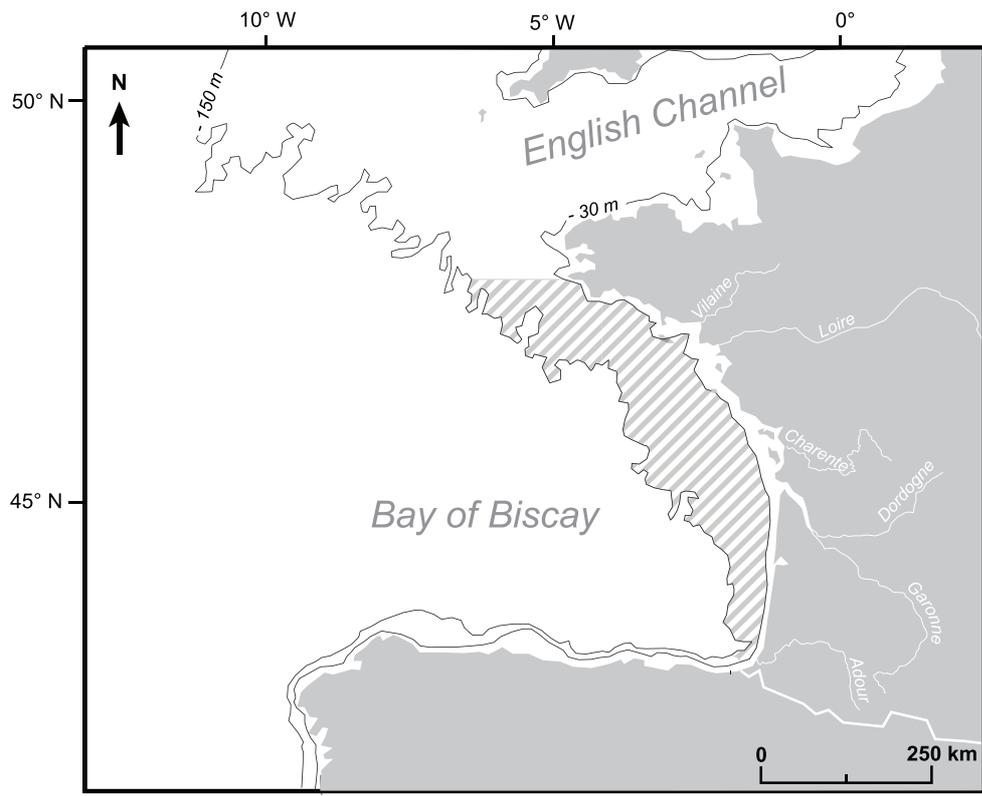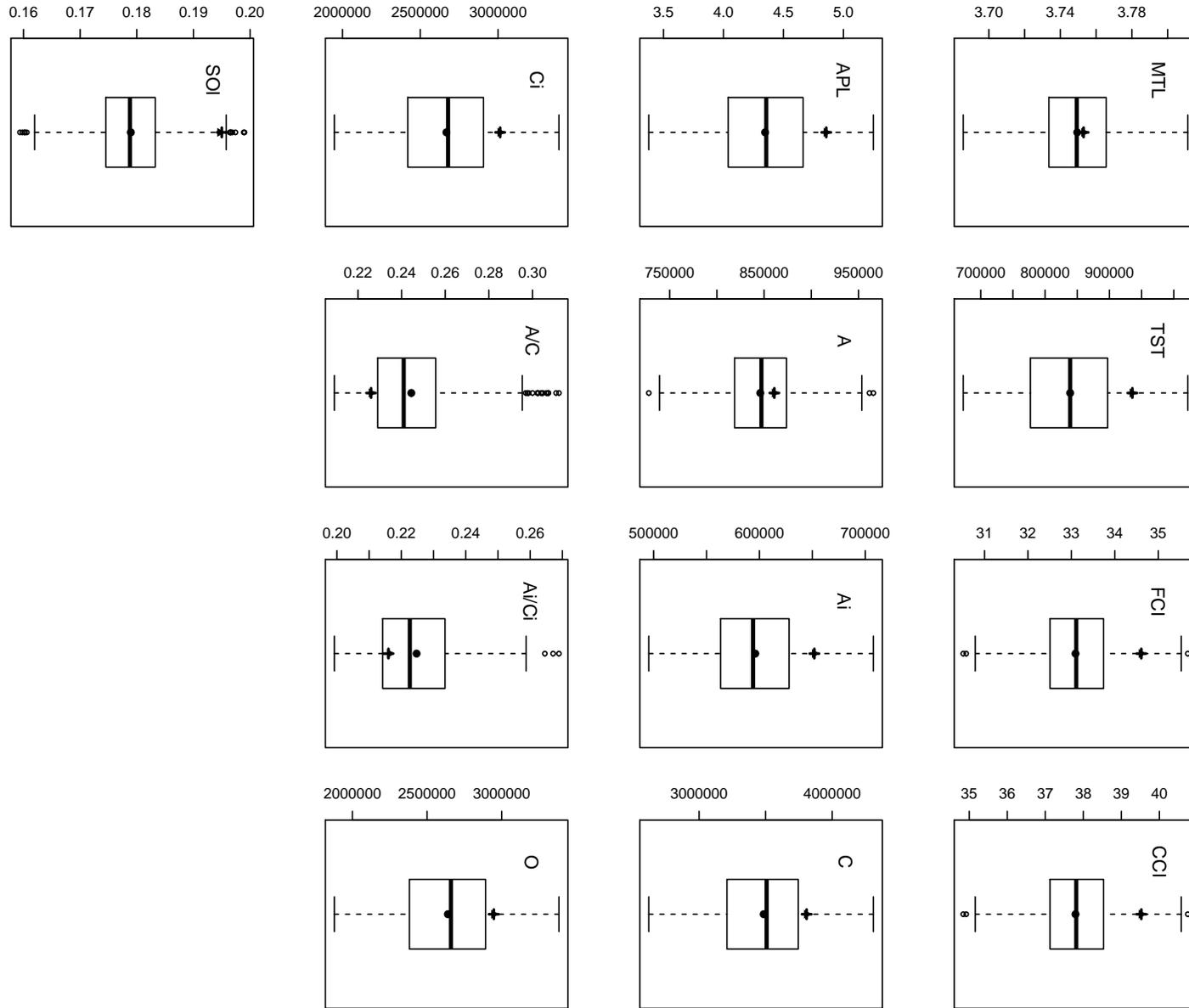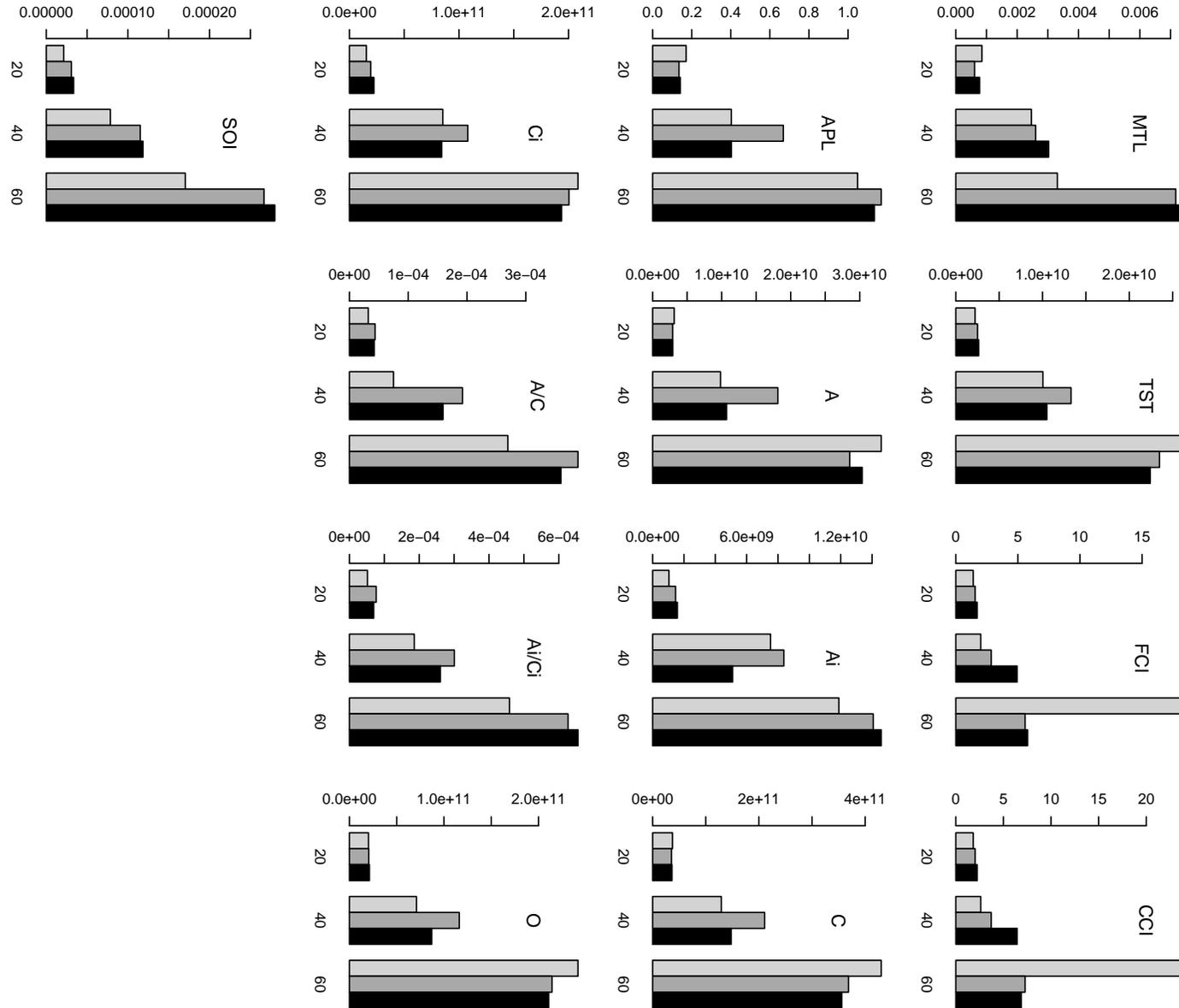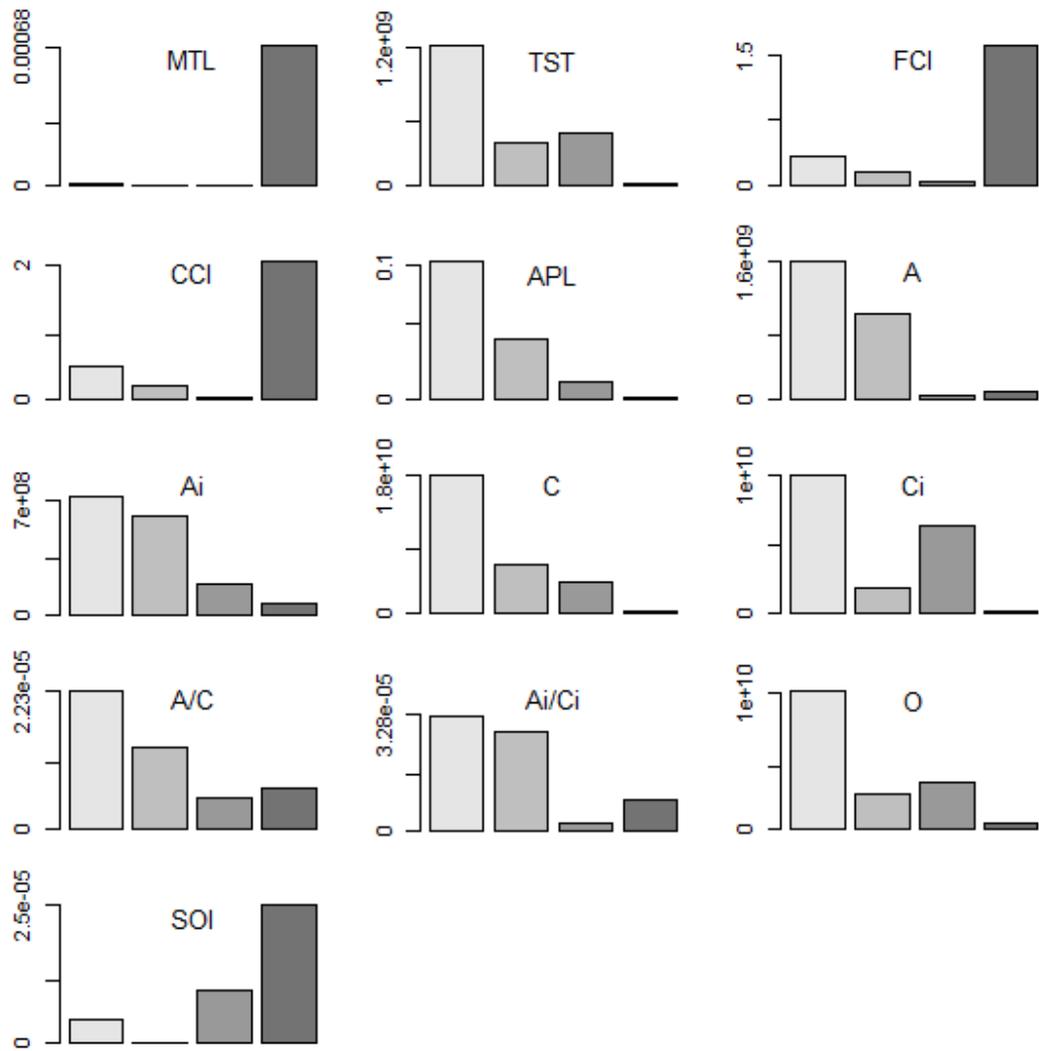
555

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., Ulanowizc, 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.

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   Plagànyi, 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.

711

712