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## **A toolbox to evaluate data reliability for whole-ecosystem models: Application on the Bay of Biscay continental shelf food-web model**

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### **Abstract:**

Ecosystem models are always simplifications of reality and as such their application for ecosystem-based management requires standard validation. Here, the “DataReli” toolbox is proposed to evaluate the quality of the data used during the construction of ecosystem models, their coherence across trophic levels, and whether data limitations prevent the model long-term applications. This toolbox is the combination of three operational and complementary analyses: (i) the pedigree index to determine to what extent a model was calibrated on data of local origin; (ii) the graphical analysis known as PREBAL to assess whether a model respects some basic ecological and fisheries principles; and (iii) a sensitivity analysis to evaluate the robustness of model predictions to small variations in input data. The toolbox is delivered to potential users with main generic recommendations on how interpreting results conjointly and on which decisions to make about parameters’ revisions or model uses’ restrictions. (i) Corrections of parameters should be preferentially envisaged when modelling data-rich environments. (ii) For those models with an overall pedigree index above 0.4, a closer look at the pedigree routine, i.e. values by parameters and compartments, and the PREBAL analysis would help to prioritize parameters needing improvement. (ii) For Ecopath models of no overall acceptable quality (overall pedigree index <0.4), we recommend stopping the DataReli procedure at this point. (iii) In terms of sensitivity analysis, marked responses of model predictions to small variations in the input values must preferentially lead to restrictions in the model applications compared to corrections of parameter estimates. A concrete application of the “DataReli” toolbox to the pre-existing Ecopath model of the Bay of Biscay continental shelf food web is presented. For the present case study, the general level of input data reliability is considered as satisfying with regard to the model applications.

### **Highlights**

► Evaluation of parameter uncertainty in ecosystem models is primordial. ► An operational toolbox composed of three complementary analyses is proposed. ► The toolbox is applied on the Bay of Biscay Ecopath food web model. ► Model evaluation may lead to parameter revisions or model uses’ restrictions.

**Keywords:** Food-web model ; Ecopath ; Model evaluation ; Parameter uncertainty ; Ecosystem-based management ; Bay of Biscay

## 41 1. Introduction

42 To ensure the usability of ecosystem models in the growing context of ecosystem-based  
43 management (Browman et al., 2004), one must know their capabilities and limitations (i.e.  
44 unknowns and caveats). Model limitations are generally divided into uncertainties originating  
45 from the data used during model construction (Gardner and O'Neill, 1983; Lehuta et al.,  
46 2010; Kearney et al., 2013, i.e. their quality generally referring to their origin and their  
47 quantity) and those in relation to the model structure (Gardner et al., 1982; Fulton et al., 2003;  
48 Hill et al., 2007; Johnson et al., 2009, i.e. the number of compartments, the level of taxa  
49 aggregation into compartments and the marine domain targeted in the model (benthos,  
50 pelagos or the entire continuum)).

51 The use of Ecopath to build mass-balance food-web models (Christensen and Walters, 2004;  
52 Christensen et al., 2008) has increased over 20-fold in the last 15 years (Dame and Christian,  
53 2006; Fulton, 2010). While structural uncertainty was rather seldom studied (e.g. Pinnegar et  
54 al., 2005), several methods are now available for this specific modelling software to address  
55 the issue of inherent uncertainties in the input data. Among these methods, some are  
56 implemented in the Ecopath software and used routinely while others are detailed in recent  
57 scientific publications (Kavanagh et al., 2004; Link, 2010; Niiranen et al., 2012). However,  
58 their application has not yet become as an integral part of the modelling process.

59 The more tests a model passes, the more confident modellers become in its predictions  
60 (Rykiel, 1996). In the present paper, we propose an ordered suite of complementary analyses  
61 covering various aspects of data properties related to their use in static ecosystem models such  
62 as Ecopath (Christensen and Walters, 2004; Christensen et al., 2008). We call these analyses  
63 the “DataReli” toolbox for “Data Reliability checking” toolbox. The analyses entering the  
64 DataReli toolbox were selected on three criteria: (i) their ease of implementation; (ii) their  
65 complementarity, i.e. they cover several integration levels (from single ecosystem

66 components to whole ecosystem; and (iii) that they guarantee model long-term applications.  
67 The DataReli toolbox is thus conceptualized in the sense of fulfilling a list of basic  
68 prerequisites with regard to data reliability common to all ecosystem models and some more  
69 specific to the scope for which the model was designed. Three complementary analyses were  
70 chosen: (i) the pedigree index (Pauly et al., 2000), which is designed to evaluate whether a  
71 model is based on extensive field sampling performed within the boundaries of the system  
72 during specific dates; (ii) the “PREBAL” or prebalancing analysis (Link, 2010), which  
73 assesses whether data are coherent to the system level by respecting some basic laws, rules  
74 and principles of ecosystem ecology; (iii) a sensitivity analysis that determines the robustness  
75 of commonly derived model outputs, namely Mixed Trophic Impacts (MTIs) (Ulanowicz and  
76 Puccia, 1990), to small variations in input data values (Rochette et al., 2009). This sensitivity  
77 analysis is useful to strengthen identification of major connections (pairwise interactions  
78 between ecosystem components, and energy pathways) within a steady-state ecosystem.  
79 The present study aims at presenting the DataReli toolbox and ensuring its full transferability  
80 to all future potential users through a concrete application to an existing Ecopath model. Input  
81 data reliability is assessed for the model of the French continental shelf of the Bay of Biscay  
82 food web (Lassalle et al., 2011). The model under study was developed for studying the  
83 ecological roles played by top predators and small pelagics in the continental shelf food web  
84 of the Bay of Biscay (Lassalle et al., 2012) and for ecosystem-based assessment of  
85 anthropogenic effects (Lassalle et al., 2014).

86

## 87 2. Materials and Methods

### 88 2.1 Study area

89 The Bay of Biscay is a large gulf in the Northeast Atlantic located off the western coast of  
90 France and the northern coast of Spain, between 48.5 and 43.5°N and 8 and 3°W (Fig. 1). The

91 ECOPATH model example for the Bay of Biscay was restricted to middle-depth continental  
92 shelf, between the 30-m and 150-m isobaths, in divisions VIIIa and b of the International  
93 Council for the Exploration of the Sea (ICES; [www.ices.dk](http://www.ices.dk)). The surface area represented by  
94 the model was about 102,585 km<sup>2</sup>.

95

## 96 2.2 The Ecopath method and the Bay of Biscay application

97 The mass-balance model of the French Bay of Biscay continental shelf food web was  
98 constructed using Ecopath with Ecosim 6 (EwE; Christensen and Walters, 2004; Christensen  
99 et al., 2008). Successive research programs in this region led to the collection of a significant  
100 amount of local data on various aspects of the ecosystem. Combining this information through  
101 the construction of a EwE model helped to quantify flows between the different elements of  
102 this aquatic exploited ecosystem at a specific point in time. The Ecopath model was originally  
103 proposed by Polovina (1984) and has been combined with routines for network analysis  
104 (Ulanowicz, 1986). The parameterization of an Ecopath model is based on satisfying two  
105 “master” equations. The production equation describes the production term for each  
106 compartment (species or group of species with similar ecotrophic roles) included in the  
107 system:

108  $\text{Production} = \text{fishery catch} + \text{predation mortality} + \text{net migration} + \text{biomass accumulation} +$   
109  $\text{other mortality.}$

110 where “Other mortality” includes natural mortality factors such as mortality due to  
111 senescence, diseases, etc.

112 The consumption equation expresses the principle of conservation of matter within a  
113 compartment:

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

115 The formal expressions of the above equations can be written as follows for a group  $i$  and its  
116 predator  $j$ :

$$117 \quad B_i \times \left(\frac{P}{B}\right)_i = Y_i + \sum_j \left( B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ji} \right) + Ex_i + Bacc_i + B_i(1 - EE_i) \times \left(\frac{P}{B}\right)_i \quad (1)$$

118 and

$$119 \quad B_i \times \left(\frac{Q}{B}\right)_i = B_i \times \left(\frac{P}{B}\right)_i + R_i + U_i \quad (2)$$

120 where the main input parameters are biomass density ( $B$ , here in  $\text{kg C}\cdot\text{km}^{-2}$  or  $\text{tons}\cdot\text{km}^{-2}$ ),  
121 production rate ( $P/B$ ,  $\text{year}^{-1}$ ), consumption rate ( $Q/B$ ,  $\text{year}^{-1}$ ), proportion of  $i$  in the diet of  $j$   
122 ( $DC_{ji}$ ;  $DC$  = diet composition), net migration rate ( $Ex$ ,  $\text{year}^{-1}$ ), biomass accumulation ( $Bacc$ ,  
123  $\text{year}^{-1}$ ), total catch ( $Y$ ;  $\text{kg C}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$  or  $\text{tons}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ; fisheries data are not compulsory  
124 in Ecopath), respiration ( $R$ ;  $\text{kg C}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$  or  $\text{tons}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ), unassimilated food rate ( $U$ )  
125 and ecotrophic efficiency ( $EE$ ; amount of species production used within the system). The  
126 “other mortality” term,  $MO$ , is internally computed from:

$$127 \quad MO_i = B_i(1 - EE_i) \times \left(\frac{P}{B}\right)_i. \quad (3)$$

128 Ecopath requires input of three parameters [biomass ( $B$ ), production/biomass ( $P/B$ ),  
129 consumption/biomass ( $Q/B$ )] for every defined functional group in the system (Christensen et  
130 al., 2005). From these three parameters, one can calculate the fourth main parameter required  
131 for balancing, ecotrophic efficiency ( $EE$ ), which is the most difficult to measure. The final  
132 two input components that must be entered into the model for every functional group are diet  
133 composition and fisheries removals.

134 Thirty-two functional groups were included in the model: two seabird groups, five marine  
135 mammal, nine fish, eight invertebrate (including two cephalopods), three zooplankton, two  
136 primary producer, and one bacteria group, as well as discards from commercial fisheries and  
137 pelagic detritus. The Bay of Biscay supports a multispecies, multifleet fishery with a large  
138 diversity of species caught by a wide range of fishing gears primarily operated from French

139 and Spanish ports (Daurès et al., 2009). As the main purpose of the pre-existing model was to  
140 study general ecosystem properties, fishing activities were included as a single fleet.  
141 Parameter values, diet composition and flow diagram of the Bay of Biscay Ecopath model can  
142 be found in Appendix A. Further information on this model is available in Lassalle et al.  
143 (2011).

144

## 145 2.3 Exploring model uncertainties through a three-step procedure

### 146 2.3.1 Pedigree index

147 For Ecopath results to be meaningful, model parameters need to be based on information  
148 specific to the study area. In Ecopath, the pedigree (Funtowicz and Ravetz, 1990) routine  
149 allows marking/categorizing the data origin of each single input using pre-defined tables (see  
150 Appendix B); the key criterion being that inputs from local data have the best confidence and  
151 the highest level in the scale (Christensen et al., 2005).  
152 When these choices are made for each single input value, an overall pedigree of the model is  
153 calculated as the average of the individual pedigree values (Pauly et al., 2000) and ranges  
154 from 0 (i.e. low precision information) to 1 (i.e. data and parameters fully rooted in local  
155 data). A four-category scale was proposed by Morissette (2007): <0.2, 0.2–0.399, 0.4–0.599,  
156  $\geq 0.6$ ; the last category being termed “very high pedigree”. This overall pedigree  $\tau$  is then very  
157 useful for comparison with other models (Morissette, 2007). It is calculated as follows:

$$158 \tau = \sum_{i=1}^n \frac{\tau_{i,p}}{n} \quad (4)$$

159 where  $\tau_{i,p}$  is the pedigree index value for functional group  $i$  and parameter  $p$  for each of the  $n$   
160 living groups in the ecosystem;  $p$  can represent either  $B$ ,  $P/B$ ,  $Q/B$ ,  $Y$  or the diet composition,  
161  $DC$ .

### 162 2.3.2 PREBAL

163 The pre-balancing (PREBAL) method outlined in Link (2010) was designed to assess the  
164 model structure and data quality before mass balancing and/or dynamic simulations (e.g.  
165 Ecosim module) are performed. From the data perspective, the method allows evaluation of  
166 their ecological cohesiveness despite the natural discrepancies that occur when using myriad  
167 data sources measured across varying scales.

168 Link (2010) provides a set of guidelines/diagnostics to both model developers and reviewers  
169 as a form of a “checklist” that can be tested through graphical representations. These  
170 diagnostics were based on essential laws, rules and principles of ecosystem ecology. (i) The  
171 primary production of an ecosystem forms the basis from which all other productivity, and  
172 hence energy flows, are derived (Lindeman, 1942; Odum, 1956; Pauly, 1980; Ulanowicz,  
173 1986; Pauly and Christensen, 1995). (ii) A decline in biomass from primary producers to top  
174 consumers is expected as it reflects the lower abundance of larger-sized organisms at upper  
175 trophic levels (Sheldon et al., 1972; Thiebaut and Dickie, 1993). There should be more total  
176 biomass of prey in ecosystems than biomass of predators (Lindeman, 1942; Jennings et al.,  
177 2001; Jennings and Mackinson, 2003; Brose et al., 2006). (iii) The relative allocation of  
178 biomasses among habitats, or functional groups, is an appropriate indicator of major pathways  
179 of energy flows within an ecosystem (Lindeman, 1942; Fulton et al., 2005; Link, 2005).

180 Link’s diagnostics of food-web models are divided into five general classes: biomasses across  
181 taxa and trophic levels; biomass ratios; vital rates across taxa and trophic levels ( $P/B$ ,  $Q/B$  and  
182  $R/B$ ); vital rate ratios; and total production and removals (Link, 2010). When checking for  
183 departures from the proposed guidelines, particular attention should be paid to taxa at the two  
184 extremes of the food web: bacteria and primary producers, and homeotherms top predators.  
185 Indeed, the first have lower standing stock biomasses than their terrestrial counterparts  
186 (Steele, 1985; Link et al., 2005). The second tend to have lower production by higher  
187 metabolic and hence consumptive demands per unit body mass (Peters, 1983) than

188 poikilotherms. The maintenance of constant body temperature requires continuous provision  
189 of energy by homeotherms. As such, bacteria, primary producers and homeotherms top  
190 predators could present systematic departures from the expected trends or could not meet the  
191 intended values. Among the set of criteria proposed by Link (2010), the most suitable to the  
192 present model evaluation are retained and detailed in Table 1. If one or several diagnostics are  
193 not met, initial estimates should be revisited before any Ecopath model balancing or tuning is  
194 executed. Link (2010) provided full details of what a departure is symptomatic of. If sufficient  
195 information is not available for revision, modellers or reviewers should carefully  
196 acknowledge of potential model gaps and their consequences when interpreting model  
197 outputs.

### 198 2.3.3 A sensitivity analysis on the mixed trophic impacts

199 The mixed trophic impact (MTI) matrix quantifies the direct and indirect trophic impacts of  
200 each functional group on (the biomass of) all other functional groups (Ulanowicz and Puccia,  
201 1990) at constant trophic structure. MTIs are central in addressing diverse research questions  
202 such as the importance of the competition between fisheries and marine mammals (Morissette  
203 et al., 2013), the identification of keystone species in food webs (Libralato et al., 2006) or the  
204 determination of structural ecosystem changes resulting from exploitation (Cury et al., 2005).  
205 Quantifying the confidence that can be placed on these model outputs would provide valuable  
206 information in the context of the management of living marine resources. Robust MTIs are  
207 defined here as those invariant in their sign, not in their magnitude, indicating potential  
208 direction of changes.

209 Rochette et al. (2009) extended the estimation of uncertainty on qualitative models proposed  
210 by Dambacher et al. (2002) to quantitative ecosystem data. This method was applied on MTI  
211 estimations. The elements of the MTI matrix  $m_{ij}$  are calculated as the product of the net  
212 impacts  $q_{ij}$  of all possible pathways in the food web that link the functional groups  $i$  and  $j$ .



213 Negative  $m_{ij}$  values indicate prevalence of predator effects (top-down effects) while positive  
 214 values indicate prevalence of prey effects (bottom-up effects). The net impact of  $i$  on  $j$ ,  
 215 denoted  $q_{ij}$ , is given by the difference between positive effects  $d_{ji}$  (quantified by the fraction of  
 216 prey  $i$  in the diet of predator  $j$ ; biomass creation), and negative effects  $f_{ij}$  (evaluated as the  
 217 fraction of total consumption of  $j$  used by predator  $i$ ; biomass removal). The compartment  $i$  is  
 218 alternatively a prey then a predator:

$$219 \quad q_{ij} = d_{ji} - f_{ij} \quad . \quad (5)$$

220 To evaluate the sensitivity of the signs of the MTI responses ( $m_{ij}$ ) to small changes in the  
 221 original  $q_{ij}$  values, 5000 Q matrices are created by drawing  $q_{ij}$  values from independent  
 222 uniform distributions defined by original  $q_{ij} \pm 20\%$  (Richardson et al., 2006). The sample of Q  
 223 matrices is then used to calculate  $m_{ij}$  values for each pairwise intersection, record their sign  
 224 and estimate the percentage of  $m_{ij}$  values with the same sign as in the original MTI matrix  
 225 ( $S_{MTI}$ ) (see Fig. 3 in Rochette et al. (2009) and Nelva Pasqual (2014)). Results are  
 226 summarized into one matrix recording the sign of the original  $m_{ij}$  values and the  $S_{MTI}$   
 227 percentages that are categorized into four classes: [0; 50], ]50; 75], ]75; 95] and ]95; 100].  
 228 The original Q matrix on which the sensitivity analysis is performed, then the resulting MTI  
 229 matrix, is slightly different from the one currently implemented in Ecopath (see Appendix C).  
 230 (i) Flows to detritus (i.e. non-assimilated food, natural mortality), as well as fishery, are  
 231 considered in the total mortality fluxes of each component in the calculation of the  
 232 interactions  $d_{ji}$ . Detritus are considered as false predators having kind of a diet ( $d_{det,i}$  = flow to  
 233 detritus), but without having a negative direct impact on its "preys":  $f_{det,i} = 0$ . Fishery and  
 234 discards are considered as true predators. Both matrices D and F are thus built including  
 235 detritus and fishery and prepared so that  $\sum_i d_{ji} = 1$  and  $\sum_j f_{ji} = 1$ . (ii) In the calculation of  
 236 the original MTI matrix, a second difference relates to the diagonal values  $q_{ii}$  of the net impact  
 237 matrix Q that represent intra-effects of a specific compartment. These  $d_{ii}$  values are set to -1.

238 Intra-effects are intra-specific competition for space and resources particularly for primary  
239 producers, intra-component predation, and links with the outside system such as external  
240 recruitment or consumption of species from outside the system (Puccia and Levins, 1985).

241 (iii) The resulting net impact matrix  $Q$  ( $\sim D - F$ ) is inverted according to Dambacher et al.  
242 (2002), the inverted matrix being the original MTI matrix.

243 The calculation of this alternative MTI matrix and the sensitivity analysis performed on it are  
244 not part of the distributed EwE 6 software package. The sensitivity analysis is performed with  
245 the R software and the code is provided in Appendix D. Further technical information can  
246 also be found in Rochette et al. (2009) and on request to the corresponding author of the  
247 present paper.

248

### 249 3. Results

250 Application of the “DataReli” toolbox to the present case study indicates a model based on  
251 data of rather good quality, quantity and coherence at the ecosystem scale.

252 The overall pedigree index for the Bay of Biscay continental shelf food-web model is 0.60;  
253 biomass, diet composition and catches having higher entries on average than  $P/B$  and  $Q/B$   
254 (Table 2). By comparison with other functional groups, cephalopods are noticeably described  
255 with data of globally low confidence and thus appear understudied in the Bay of Biscay  
256 continental shelf food web.

257 PREBAL diagnostics applied to our case study show general coherent decompositions of  
258 parameters with increasing trophic levels (TLs) (Fig. 2). The ecological cohesiveness of the  
259 data is particularly demonstrated for vital rates, and total production and removals.

260 Nevertheless, unexpected punctual departures from rules of thumb are noted (in bold, Table  
261 1). (i) The biomass of surface-feeder seabirds is considerably below the trend line of biomass  
262 allocation across TLs (Fig. 2). This functional group combines a very small biomass with an

263 intermediate TL of 3.71, the maximum TL being 5.18 for dolphins. The biomass estimate of  
264 these marine birds is based on sampling of high precision (maximum pedigree index value of  
265 1). By contrast, their diet compositions correspond to general knowledge about this issue and  
266 are thus far less reliable. (ii) In the biomass ratios diagnostic, the biomass of zooplankton  
267 ( $1652 \text{ kg C km}^{-2} \text{ year}^{-1}$ ) is twice that of benthos ( $730.5 \text{ kg C km}^{-2} \text{ year}^{-1}$ ) and contradicts the  
268 rule of thumb that points to the equitable apportionment of biomass for comparable trophic  
269 level groups in major pathways of trophic flows (Fig. 3). Both biomasses are classified in the  
270 pedigree routine as “sampling-based” but only zooplankton is considered of high resolution  
271 thus indicating lower confidence in the benthos data. Nonetheless, the sensitivity analysis on  
272 the MTI shows a high confidence in the sign of the effect of benthos on other ecosystem  
273 components. More than 85% of their intersections have a  $S_{\text{MTI}}$  superior to 95% (Fig. 4). (iii)  
274 As expected by Link (2010), groups at the two extremes of the Bay of Biscay continental  
275 shelf food web, i.e. primary producers, and marine mammals and seabirds, present out-of-  
276 trend values compared to their trophic position and should be excluded when interpreting  
277 most diagnostics. For example, high-TL homeotherms (groups 1-7) tend to have a lower  
278 production, higher consumption and respiration compared to poikilotherms (Fig. 2).  
279 The sensitivity analysis  $S_{\text{MTI}}$  percentages never reach a homogeneous 100% confidence, but  
280 results show that 87% of the pairwise intersections in the original MTI matrix have a sign  
281 with a confidence percentage superior to 95% (Fig. 4). This means that, for a given  
282 intersection, more than 4750 over 5000 possible configurations of the food web lead to a sign  
283 identical to the one reported in the original MTI matrix. Two intersections have an extremely  
284 undetermined sign ( $S_{\text{MTI}} \sim 35\%$ ): a small increase of long-finned pilot whales and piscivorous  
285 demersal fish (group 6 and 8 respectively) causes an effect on the Harbour porpoises  
286 (*Phocoena phocoena*; group 8) that may be opposed to the original MTI matrix. Most  
287 interactions with a  $S_{\text{MTI}}$  around 50% are related to the upper part of the food web (seabirds,

288 marine mammals, and demersal and pelagic fish), suggesting more uncertain top-down  
289 impacts than bottom-up effects. The Atlantic mackerel (*Scomber scombrus*), when considered  
290 as an impacting group (read along row 12), presents the highest frequency of effects with a  
291  $S_{MTI}$  inferior to 95% (30% of them) and the lowest overall  $S_{MTI}$  value which is equal to 91%.  
292 For cephalopods (groups 17 and 18), uncertain input data revealed by the pedigree routine do  
293 not translate into very uncertain effects in the sensitivity analysis, even when considering  
294 cephalopods as an impacting or an impacted group. As such, improving data precision for this  
295 compartment would not impact our interpretation of ecosystem functioning.

296

#### 297 4. Discussion

298 The “DataReli” toolbox is proposed to modellers to ensure the best congruence between the  
299 reliability of the input data used during model construction and the purposes for which an  
300 ecosystem model, in particular EwE, was intended. From a general perspective, capturing  
301 potential problems in data reliability should prevent the use of this model to address given  
302 research or management questions. Nonetheless, the decision can be taken to correct the  
303 “weak” parameters for improved ecological integrity and validity (e.g. Byron et al., 2011). (i)  
304 Corrections of parameters should be preferentially envisaged when modelling data-rich  
305 environments. A meta-analysis of 50 EwE models showed that few models exhibited a very  
306 high pedigree (10% have a pedigree higher than 0.60, with the maximum value being 0.65)  
307 (Morissette, 2007). As such, an overall pedigree index ( $\tau$ ) in the medium-high range as  
308 defined by Morissette (2007), i.e. between 0.4 and 1, likely testifies to an ecosystem  
309 benefiting from a sufficient amount of data to allow revision of the model. The Bay of Biscay  
310 continental shelf food-web model falls into the highest range of this categorization. This high  
311 comparative pedigree value is even more meaningful when considering that in the present  
312 work the input data should have described a thousand km<sup>2</sup> of a system open to the Atlantic

313 Ocean. (ii) For those models with  $\tau$  above 0.4, a closer look at the pedigree routine, i.e. values  
314 by parameters and compartments, and the PREBAL analysis would help to prioritize  
315 parameters needing improvement. We suggest investing extra effort particularly on  
316 parameters with low pedigree value that lead to noticeable departure from PREBAL  
317 diagnostics. Moreover, their position regarding an expected trend line (threshold) across  
318 trophic levels (pathways) gives the main direction for revisiting those initial estimates. In the  
319 present case study, deviations from the PREBAL trend lines, or threshold values, are more  
320 related to modeller choices or to underlying assumptions of the modelling software than to  
321 poor quality data or ecological incoherencies in the model. As an example, surface-feeder  
322 seabird biomass does not fit with the general biomass allocation pattern in ecosystems  
323 (moderate to sharp decline across TLs) (e.g. Gascuel, 2005; Gascuel et al., 2009). Given the  
324 high quality of the biomass estimate, this below-trend value could be explained by an  
325 underestimation of the TL. Kittiwakes and gulls have a substantial part of their diet coming  
326 from discarded organisms (Arcos and Oro, 2002), which are considered in Ecopath as dead  
327 material with a TL arbitrarily set to unity (Christensen and Pauly, 1992). When calculating the  
328 TL of discards as the weighted average of discarded fish TL, the trophic position of seabirds  
329 markedly increases from 3.72 to 4.49. Including microbial loop in Ecopath models remains a  
330 challenging task (Pavés and González, 2008). Here, the bacterial P/R ratio greater than 1 is  
331 partly related to lack of data regarding the fraction of food not assimilated by bacteria. Higher  
332 biomass of zooplankton compared to benthos is partly driven by differences in data quality.  
333 Benthos biomass was extrapolated from a study covering a small fraction of the Bay of  
334 Biscay continental shelf known as the “Grande Vasière” mudflat while zooplankton biomass  
335 was estimated from large-scale campaigns (Lassalle et al., 2011). (ii)’ For Ecopath models of  
336 no overall acceptable quality ( $\tau < 0.4$ ), we recommend stopping the DataReli procedure at this  
337 point. They should be combined with other modelling approaches before deriving any

338 conclusions (Metcalf, 2010; Gårdmark et al., 2012; Lassalle et al., 2014). (iii) In terms of  
339 sensitivity analysis, marked responses of model predictions (here MTI) to small variations in  
340 the input values must preferentially lead to restrictions in the model applications compared to  
341 corrections of parameter estimates. The Bay of Biscay continental shelf food-web model was  
342 originally designed to provide a holistic understanding of the ecosystem's structure and  
343 functioning with a special emphasis on the ecological roles played by top predators and small  
344 pelagics (Lassalle et al., 2011; Lassalle et al., 2012). Bottom-up processes were demonstrated  
345 to play a significant role in the population dynamics of upper-trophic levels and in the global  
346 structuring of this marine ecosystem (Lassalle et al., 2011). In the context of the marine  
347 strategy framework directive (MSFD; <http://ec.europa.eu>; Directive 2008/56/EC),  
348 mesozooplankton abundance, diversity and/or biomass were identified as reliable indicators  
349 of Bay of Biscay continental shelf changes. Both propositions regarding the functioning and  
350 monitoring of this ecosystem were partly based on the proportion of positive MTI values  
351 when a compartment is considered as an impacting group (Libralato et al., 2006). These  
352 propositions are thus reinforced by the high confidence percentages on the signs of effects  
353 noted in the present sensitivity study.

354

## 355 5. Conclusion

356 In conclusion for the case study, a general level of input data reliability that is satisfying with  
357 regard to the model applications has been achieved. Recently, Essington and Plagányi (2014)  
358 conducted a comparative study on the capacity of 18 ecosystem models for evaluating the  
359 ecosystem effects of forage fish fisheries. The Bay of Biscay Ecopath model was also  
360 positively evaluated in terms of time and spatial matching to stocks and of data  
361 representativeness and availability. However, we believe improvements could be investigated

362 in the future, particularly on the parameterization of pelagic and benthic cephalopods, and  
363 mackerel.

364

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370

371 Figure captions

372 **Fig. 1.** Study area of the Bay of Biscay continental shelf and locations of the main rivers  
373 flowing into it. The shaded area corresponds to the French part of the continental shelf, and  
374 represents the spatial extent of the Ecopath model example.

375

376 **Fig. 2.** Vital rates across taxa and trophic levels for the Bay of Biscay continental shelf food-  
377 web model. Trend lines are also given. *B*: biomass, *Q*: consumption, *P*: production, *R*:  
378 respiration, and ratios accordingly. Homeotherms are marked with an asterisk. Trophic levels  
379 (TL) increase from left to right.

380

381 **Fig. 3.** Biomass ratios across major (A) predator/prey interactions and (B) pathways of  
382 trophic flows for the Bay of Biscay continental shelf food-web model. (A) B.Inv: benthic  
383 invertebrates, D.Pisc: demersal and medium pelagic piscivores, MMB: marine mammals and  
384 birds, Phy: phytoplankton, SP: small pelagics, Z: zooplankton. (B) Ben: benthos, Dem:  
385 demersal, Pel: pelagic, Z: zooplankton.

386

387 **Fig. 4.** Probability of obtaining a sign identical to the one reported in the original MTI matrix  
388 when applying small variations to the original net impact Matrix *Q* for the Bay of Biscay  
389 continental shelf food-web model. The sign is the one of the original MTI matrix. Signs (-)  
390 correspond to negative effects of an increase of the components in rows on the components in  
391 column. Conversely, signs (+) represent positive effects of an increase of the components in  
392 rows on the components in columns. Light grey squares: effects with high confidence  
393 percentage (>95%); medium grey squares: [95–75[; dark grey squares: [75–50[; dark squares:  
394 <50% (this means the average sign from the sensitivity analysis is opposed to the one of the  
395 original MTI matrix).



396 **Table 1.** Food-web model diagnostics used for the evaluation of the Bay of Biscay continental shelf food-web model according to Link (2010).  
 397 Rules of thumb for their appropriate application are presented. Status informs on whether these rules are generally met for the present model.  
 398 Small to moderate departures to these rules are listed in Remarks. Those given in plain text are the discrepancies expected by Link (2010) for  
 399 most ecosystems and those in bold are the discrepancies specific to the present model. *B*: biomass, *Q*: consumption, *P*: production, PP: primary  
 400 producers, *R*: respiration, TL: trophic level.

401	402	403	404	405
Class of diagnostics	Rules of thumb	Status	Remarks	
403	<i>B</i> across taxa and TLs	a range of 5–7 orders of magnitude	OK	/
404	(detritus omitted)	slope ~5–10% decline along increasing TLs	OK	/
405		few taxa notably above or below slope-line	OK	<b><i>B</i> of surface-feeder seabirds too small</b>
406	<i>B</i> ratios	Predator <i>B</i> less than that of their prey	OK	<i>B</i> of phytoplankton less than <i>B</i> of zooplankton
407		Equitable apportionment of <i>B</i> for comparable TL groups in major pathways of trophic flow	~	<b>Higher <i>B</i> of zooplankton compared (~ x2) to benthos</b>
410	Vital rates across taxa and TLs	Decline of <i>Q/B</i> , <i>P/B</i> and <i>R/B</i> along increasing TLs	OK	Exception for homeotherms at upper TLs
411	(detritus omitted)	A few taxa notably above or below slope-line	OK	Exception for homeotherms at upper TLs
412	Vital rate ratios	Predator vital rate less than that of their prey	OK	Exception for homeotherms at upper TLs
413		<i>P/B</i> across taxa less than <i>P/B</i> of PP	OK	/
414		<i>P/Q</i> less than 1 for each taxa	OK	/
415		<i>P/R</i> less than 1 for each taxa	OK	<b>Exception for bacteria</b>
416	Total <i>P</i> and removals	Total, scaled <i>P</i> , <i>Q</i> and <i>R</i> decline along increasing TLs	OK	Exception for homeotherms at upper TLs
417		<i>Q</i> exerted on a taxa less than its own <i>P</i>	OK	/
418		<i>Q</i> by a taxa greater than its own <i>P</i>	OK	/
419		Total human removals less than <i>P</i> of a taxa	OK	/
420		Total human removals less than <i>Q</i> exerted on a taxa	OK	/
421				
422				
423				

424 **Table 2.** Categorizing data origins for major input parameters for the Bay of Biscay continental shelf food-web model. This classification is  
425 based on pre-defined scales, with higher values representing a greater confidence (Christensen et al., 2005) (see Appendix B). \* represents when  
426 the maximum index value is given, i.e. 6 for *B*, diet and catches and 8 for *P/B* and *Q/B*. Blank cells mean that no such input parameter is required  
427 for the functional group, e.g. *P/B* or *Q/B* are not filled for non-living compartments such as detritus and discards, or that the functional group is  
428 not exploited. Default confidence intervals (C.I.) assigned to data based on their origin are given and are expressed as +/- %, with n.a. for missing  
429 parameters.

430	431										
431	Group name	<i>B</i>	C.I. <sub><i>B</i></sub>	<i>P/B</i>	C.I. <sub><i>P/B</i></sub>	<i>Q/B</i>	C.I. <sub><i>Q/B</i></sub>	Diet	C.I. <sub>Diet</sub>	Catches	C.I. <sub>Catches</sub>
432	Plunge and pursuit diver seabirds	6*	10	2	90	4	50	3	80		
433	Surface-feeder seabirds	6*	10	2	90	4	50	3	80		
434	Striped dolphins	6*	10	3	80	4	50	6*	30		
435	Bottlenose dolphins	6*	10	3	80	4	50	6*	30		
436	Common dolphins	6*	10	3	80	4	50	6*	30	5	30
437	Long-finned pilot whales	6*	10	3	80	4	50	6*	30		
438	Harbour porpoises	6*	10	3	80	4	50	6*	30	5	30
439	Piscivorous demersal fish	6*	10	4	50	4	50	5	40	6*	10
440	Pisicvorous and benthivorous demersal fish	6*	10	4	50	4	50	5	40	6*	10
441	Suprabenthivorous demersal fish	6*	10	4	50	4	50	5	40	6*	10
442	Benthivorous demersal fish	6*	10	4	50	4	50	5	40	6*	10
443	Mackerel	4	50-80	4	50	4	50	6*	30	6*	10
444	Horse mackerel	4	50-80	4	50	4	50	6*	30	6*	10
445	Anchovy	6*	10	4	50	4	50	6*	30	6*	10
446	Sardine	6*	10	4	50	4	50	6*	30	6*	10
447	Sprat	6*	10	4	50	4	50	6*	30		
448	Benthic cephalopods	1	n.a.	3	80	3	80	4	50	6*	10
449	Pelagic cephalopods	1	n.a.	3	80	3	80	4	50	6*	10



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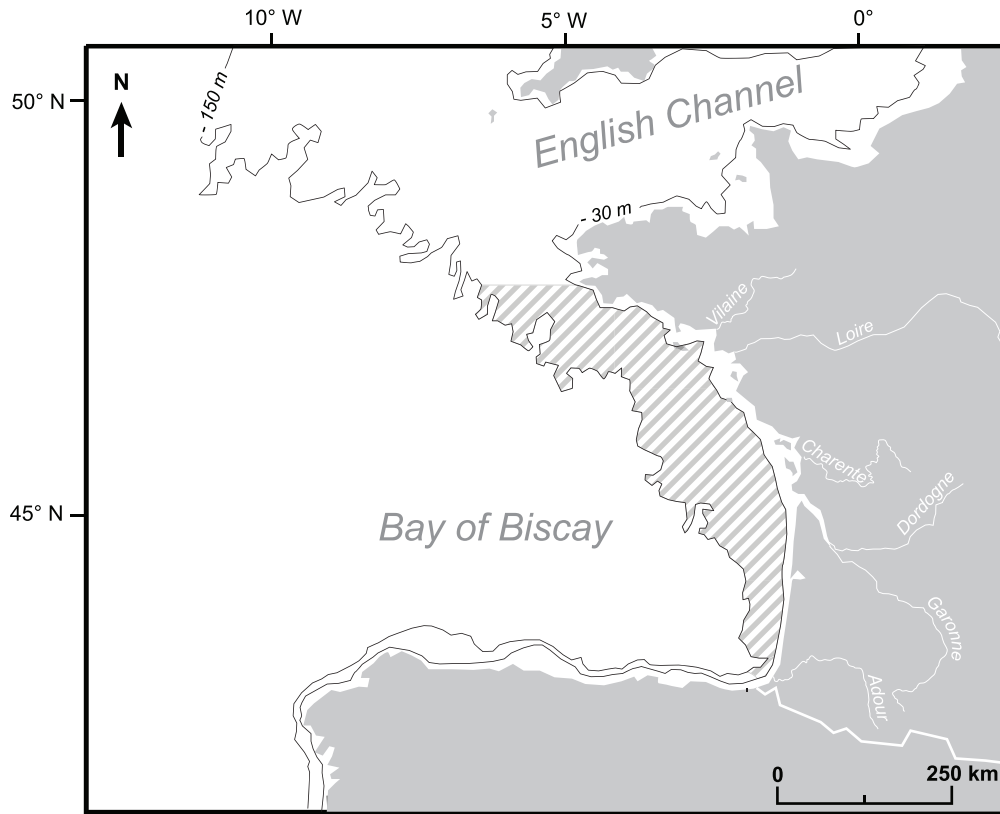
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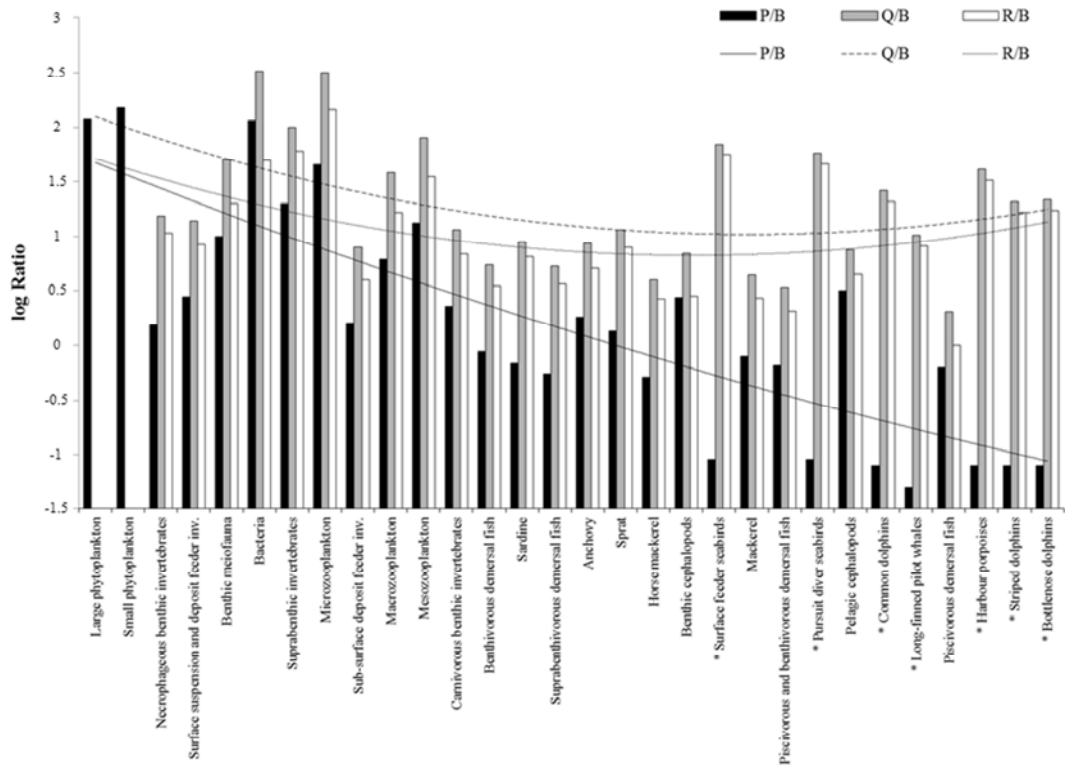
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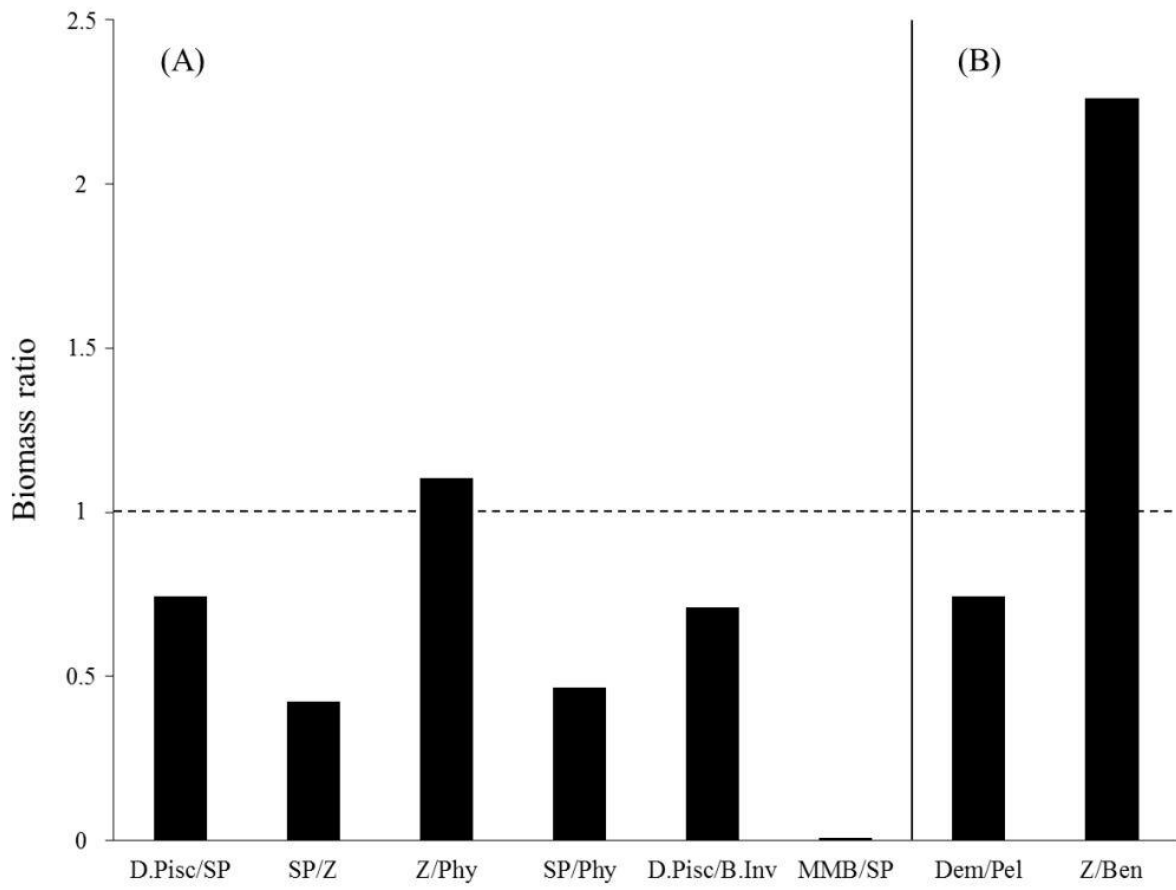
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	Plunge and pursuit diver seabirds	Surface-feeder seabirds	Striped dolphins	Bottlenose dolphins	Common dolphins	Long-finned pilot whales	Harbour porpoises	Piscivorous demersal fish	Piscivorous and benthivorous demersal fish	Suprabenthivorous demersal fish	Benthivorous demersal fish	Mackerel	Horse mackerel	Anchovy	Sardine	Sprat	Benthic cephalopods	Pelagic cephalopods	Carnivorous benthic invertebrates	Necrophageous benthic invertebrates	Sub-surface deposit feeder inv.	Surface suspension and deposit feeder inv.	Benthic meiofauna	Suprabenthic invertebrates	Macrozooplankton	Mesozooplankton	Microzooplankton	Bacteria	Large phytoplankton	Small phytoplankton	Discards	Detritus	Landings	
Plunge and pursuit diver seabirds	+	-	+	-	+	+	+	+	+	+	-	-	-	-	-	+	-	-	-	-	-	+	+	+	+	+	+	+	+	+	-	-		
Surface-feeder seabirds	-	+	+	-	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	-	-	
Striped dolphins	-	-	+	-	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	-	
Bottlenose dolphins	+	+	-	+	+	-	-	+	-	-	-	+	+	+	+	+	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	
Common dolphins	-	-	-	+	-	-	-	-	+	+	+	+	+	+	+	+	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	
Long-finned pilot whales	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	
Harbour porpoises	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
Piscivorous demersal fish	-	-	+	+	-	+	+	+	+	-	-	+	+	+	+	+	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	
Piscivorous and benthivorous demersal fish	-	-	+	+	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	
Suprabenthivorous demersal fish	+	+	+	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	
Benthivorous demersal fish	+	+	+	+	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	
Mackerel	+	-	-	+	+	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	
Horse mackerel	+	-	-	+	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	
Anchovy	+	+	-	+	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Sardine	+	+	-	+	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Sprat	+	+	+	+	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Benthic cephalopods	+	-	+	+	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pelagic cephalopods	-	-	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Carnivorous benthic invertebrates	-	-	-	-	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Necrophageous benthic invertebrates	-	-	+	+	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Sub-surface deposit feeder inv.	-	-	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Surface suspension and deposit feeder inv.	-	-	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Benthic meiofauna	-	-	-	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Suprabenthic invertebrates	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Macrozooplankton	-	+	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Mesozooplankton	+	+	+	+	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Microzooplankton	+	+	-	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Bacteria	+	+	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Large phytoplankton	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Small phytoplankton	+	+	-	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Discards	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Detritus	+	-	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Landings	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

**Appendix A.** Input (regular) and output (bold) parameters for the ecosystem components used in the Bay of Biscay continental shelf model. *TL*: trophic level, *B*: biomass (kg C·km<sup>-2</sup>), *P/B*: production/biomass ratio (year<sup>-1</sup>), *Q/B*: consumption/biomass ratio (year<sup>-1</sup>), *EE*: ecotrophic efficiency, *P/Q*: gross food conversion efficiency, *U/Q*: unassimilated consumption, landings (*Y*) and discards expressed in kg C·km<sup>-2</sup>·year<sup>-1</sup>.

	<i>TL</i>	<i>B</i>	<i>P/B</i>	<i>Q/B</i>	<i>EE</i>	<i>P/Q</i>	<i>U/Q</i>	<i>Y</i>	Discards
1. Plunge and pursuit diver seabirds	<b>4.36</b>	0.27	0.09	57.66	<b>0</b>	<b>0.002</b>	0.2		
2. Surface-feeder seabirds	<b>3.72</b>	0.07	0.09	69.96	<b>0</b>	<b>0.001</b>	0.2		
3. Striped dolphins	<b>4.73</b>	0.59	0.08	20.80	<b>0</b>	<b>0.004</b>	0.2		
4. Bottlenose dolphins	<b>5.18</b>	2.18	0.08	21.67	<b>0</b>	<b>0.004</b>	0.2		
5. Common dolphins	<b>4.61</b>	1.44	0.08	26.11	<b>0.875</b>	<b>0.003</b>	0.2		0.101
6. Long-finned pilot whales	<b>4.64</b>	0.83	0.05	10.34	<b>0</b>	<b>0.005</b>	0.2		
7. Harbour porpoises	<b>4.69</b>	0.12	0.08	40.69	<b>0.833</b>	<b>0.002</b>	0.2		0.0078
8. Piscivorous demersal fish	<b>4.66</b>	48.45	0.63	2.03	<b>0.991</b>	<b>0.311</b>	0.2	10.42	
9. Piscivorous and benthivorous demersal fish	<b>4.01</b>	130	0.66	3.42	<b>0.981</b>	<b>0.192</b>	0.2	10.68	13.82
10. Suprabenthivorous demersal fish	<b>3.49</b>	311.20	0.55	5.30	<b>0.765</b>	<b>0.104</b>	0.2	0.64	26.79
11. Benthivorous demersal fish	<b>3.41</b>	28.97	0.88	5.51	<b>0.949</b>	<b>0.159</b>	0.2	5	0.20
12. Mackerel	<b>3.73</b>	145.93	0.79	4.40	<b>0.978</b>	<b>0.181</b>	0.2	6.24	0.49
13. Horse mackerel	<b>3.69</b>	262.21	0.51	4.00	<b>0.987</b>	<b>0.128</b>	0.2	16.81	1.01
14. Anchovy	<b>3.67</b>	55.75	1.82	8.68	<b>0.825</b>	<b>0.210</b>	0.2	16.80	
15. Sardine	<b>3.44</b>	184.23	0.68	8.97	<b>0.787</b>	<b>0.076</b>	0.2	10.82	
16. Sprat	<b>3.67</b>	49.78	1.34	11.59	<b>0.679</b>	<b>0.116</b>	0.2		
17. Benthic cephalopods	<b>3.70</b>	<b>10.40</b>	2.75	7.00	0.950	<b>0.393</b>	0.2	3.53	
18. Pelagic cephalopods	<b>4.44</b>	<b>14.11</b>	3.20	7.50	0.950	<b>0.427</b>	0.2	1.99	
19. Carnivorous benthic invertebrates	<b>3.23</b>	116.75	2.30	<b>11.50</b>	<b>0.999</b>	0.200	0.2	2.91	1.09
20. Necrophagous benthic invertebrates	<b>2</b>	16.97	1.53	<b>15.30</b>	<b>0.908</b>	0.100	0.2		
21. Sub-surface deposit feeder inv.	<b>2.34</b>	234.83	1.60	<b>8</b>	<b>0.834</b>	0.200	0.3		
22. Surface suspension and deposit feeder inv.	<b>2</b>	223.93	2.80	<b>14</b>	<b>0.891</b>	0.200	0.2		
23. Benthic meiofauna	<b>2</b>	100	10	<b>50</b>	<b>0.921</b>	0.200	0.4		
24. Suprabenthic invertebrates	<b>2.14</b>	38	20	<b>100</b>	<b>0.936</b>	0.200	0.2		
25. Macrozooplankton ( $\geq 2$ mm)	<b>2.57</b>	120	<b>6.13</b>	38	0.950	<b>0.161</b>	0.4		
26. Mesozooplankton (0.2-2 mm)	<b>2.67</b>	638	<b>13.27</b>	80	0.950	<b>0.166</b>	0.4		
27. Microzooplankton ( $\leq 0.2$ mm)	<b>2.18</b>	894	<b>44.91</b>	316	0.950	<b>0.142</b>	0.4		
28. Bacteria	<b>2</b>	394	115	<b>328.57</b>	<b>0.811</b>	0.350	0.5		
29. Large phytoplankton ( $\geq 3$ $\mu$ m)	<b>1</b>	1046	119		<b>0.851</b>				
30. Small phytoplankton ( $< 3$ $\mu$ m)	<b>1</b>	448	151		<b>0.752</b>				
31. Discards	<b>1</b>	46.67			<b>0.731</b>				
32. Detritus	<b>1</b>	2800			<b>0.973</b>				

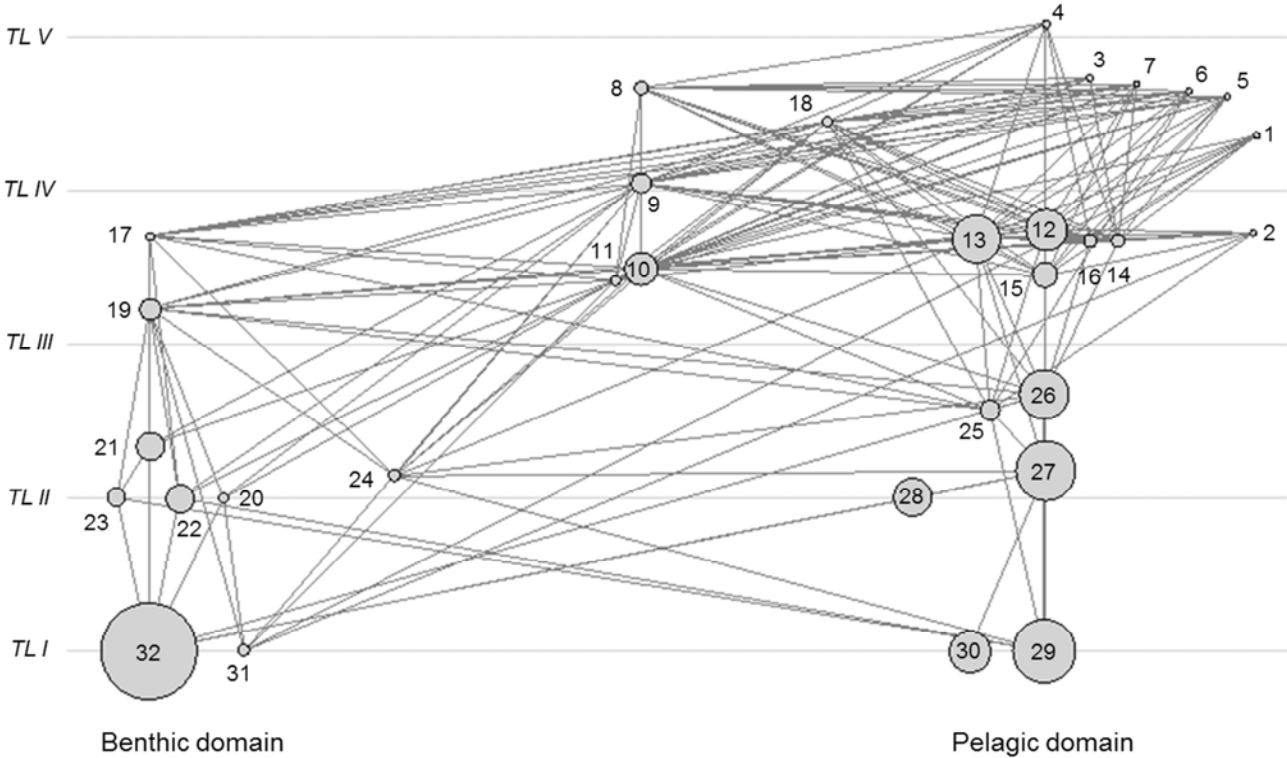
Predator/prey matrix (column/raw). The fraction of one compartment consumed by another is expressed as the fraction of the total diet, the sum of each column being equal to one.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.
1. Plunge and pursuit diver seabirds														
2. Surface-feeder seabirds														
3. Striped dolphins														
4. Bottlenose dolphins														
5. Common dolphins														
6. Long-finned pilot whales														
7. Harbour porpoises														
8. Piscivorous demersal fish			0.014	0.403	0.015	0.002	0.011							
9. Piscivorous and benthivorous demersal fish			0.097	0.200	0.031	0.085	0.240	0.160	0.030		0.010			
10. Suprabenthivorous demersal fish	0.100		0.345	0.007	0.004	0.006	0.216	0.190	0.065	0.005	0.030	0.017	0.010	
11. Benthivorous demersal fish			0.148	0.100	0.032		0.012	0.050	0.010		0.010			
12. Mackerel	0.090	0.070		0.023	0.056	0.004	0.009	0.090	0.09	0.005		0.030	0.005	
13. Horse mackerel	0.140	0.070		0.132	0.050	0.039	0.276	0.200	0.100	0.005	0.020	0.020	0.005	
14. Anchovy	0.070	0.130	0.002	0.002	0.226		0.003	0.135	0.032	0.005		0.011	0.005	
15. Sardine	0.380	0.210		0.031	0.449	0.006	0.213	0.120	0.050	0.005		0.009	0.007	
16. Sprat	0.140	0.110		0.009	0.080			0.055	0.018	0.005		0.007	0.005	
17. Benthic cephalopods			0.006		0.032	0.243	0.009		0.010	0.002	0.003			
18. Pelagic cephalopods			0.122	0.093	0.025	0.006	0.008		0.005	0.003	0.007	0.005	0.010	
19. Carnivorous benthic invertebrates									0.275		0.200		0.020	
20. Necrophagous benthic invertebrates									0.020		0.050			
21. Sub-surface deposit feeders inv.									0.030		0.120			
22. Surface suspension and deposit feeders inv.									0.235		0.540			
23. Benthic meiofauna														
24. Suprabenthic invertebrates									0.010	0.380			0.010	
25. Macrozooplankton ( $\geq 2$ mm)		0.120				0.050				0.175		0.213	0.150	
26. Mesozooplankton (0.2-2 mm)										0.410		0.655	0.723	1
27. Microzooplankton ( $\leq 0.2$ mm)												0.033	0.050	
28. Bacteria														
29. Large phytoplankton ( $\geq 3$ $\mu$ m)														
30. Small phytoplankton ( $< 3$ $\mu$ m)														
31. Discards	0.080	0.290							0.020		0.010			
32. Pelagic detritus														
Import			0.266			0.559	0.003							





Trophic model of the Bay of Biscay continental shelf. Boxes are arranged using trophic-level (TL) as y-axis and benthic/pelagic partitioning as x-axis. The size of each box is proportional to the biomass it represents. Numbers refer to a code for compartments provided in tables above. Benthic and pelagic food chains appeared to be linked mainly in their upper ranges by demersal fishes, particularly suprabenthivorous species. They optimize foraging benefits by feeding from both systems and they are, in turn, consumed by a large panel of pelagic top-predators.



**Appendix B.** Pre-defined tables for each type of input parameters used in Pedigree analysis. A coded statement categorizes the origin a given input. Index refers to the values used to calculate the overall pedigree index of a given model. A confidence interval is suggested for each category.

Parameter	Category	Description	Index	Default confidence interval (+/- %)
Biomass ( <i>B</i> )	1	Missing parameter (estimated by Ecopath)	0.0	n.a.
	2	From other model	0.0	80
	3	Guesstimates	0.0	80
	4	Approximate or indirect method	0.4	50-80
	5	Sampling based, low precision	0.7	40
	6	Sampling based, high precision	1.0	10
<i>P/B</i> and <i>Q/B</i>	1	Missing parameter (estimated by Ecopath)	0.0	n.a.
	2	Guesstimates	0.1	90
	3	From other model	0.2	80
	4	Empirical relationships	0.5	50
	5	Similar group/species, similar system	0.6	40
	6	Similar group/species, same system	0.7	30
	7	Same group/species, similar system	0.8	20
	8	Same group/species, same system	1.0	10
Diets ( <i>DC</i> )	1	General knowledge of related group/species	0.0	80
	2	From other model	0.0	80
	3	General knowledge for same group/species	0.2	80
	4	Qualitative diet composition study	0.5	50
	5	Quantitative but limited diet composition study	0.7	40
	6	Quantitative, detailed, diet composition study	1.0	30
Catches	1	Guesstimates	0.0	>80
	2	From other model	0.0	>80

3	FAO statistics	0.2	80
4	National statistics	0.5	50
5	Local study, low precision/incomplete	0.7	30
6	Local study, high precision/complete	1.0	10

---



(ii)  $F = A / \text{Sum by row}$

The “Flow to the detritus” column was not integrated in the calculation of the sums. In the end,  $f_{det,i}$  values have to be set to zero.

(iii)  $D = A / \text{Sum by column}$

The row corresponding to landings should be zeroes as no compartment “eat” the fishery.

(iv)  $Q = D - \text{the transposed } F$

Diagonal values have to be set to -1 for matrix stability. Transposition means interchanging the rows and columns of a matrix. The matrix Q should be read as the net effect of a compartment in rows on a compartment in column.

(iv)'  $Q = \text{the transposed } D - F$

The exact same matrix Q is obtained except that it is the net effect of a compartment in column on the compartment in rows.

In the present study, the matrix Q was obtained with equation (iv).

**Appendix D.** The R ([www.r-project.org](http://www.r-project.org)) code for the sensitivity analysis. The code is given for data stored in a three-sheet Excel file. The original matrix Q is stored in the “net\_impacts” sheet and is obtained following steps (i) to (iv) described in Appendix C. The original matrix Q minus 20% is in the “Com\_Min” sheet and the original matrix Q plus 20% in the “Com\_Max” sheet. They all three give the net impact of a compartment in rows on the compartment in column.

```

library(RODBC)

#Specify the number of matrix Q to simulate
nb_mat <- 5000

#Connection to the Excel file and importation of the data
db <- "" #File path
channel <- odbcConnectExcel(xls.file = db)
Mini_Mat <- sqlFetch(
  channel = channel,
  ##Name of the Excel source sheet with the original matrix Q minus 20%
  sqtable = "Com_Min",
  rownames = TRUE
)
Mini_Mat <- Mini_Mat[,-1]

Maxi_Mat <- sqlFetch(
  channel = channel,
  ##Name of the Excel source sheet with the original matrix Q plus 20%
  sqtable = "Com_Max",
  rownames = TRUE
)
Maxi_Mat <- Maxi_Mat[,-1]

#Creation of two empty matrices to store the 5000 simulated Q and MTI
matrices
nb_comp <- nrow(Mini_Mat)
streight <- matrix(0,nrow=nb_comp,ncol=nb_comp*nb_mat)
streight_adj <- matrix(0,nrow=nb_comp,ncol=nb_comp*nb_mat)

#Function to invert a matrix Q following Dambacher et al. (2002)
#With the following equation, the CM matrix must be invertible
#No compartment being only an input can be included in the model. Effect of
an input may be regarded after the matrix has been inverted
#Compartment being only an output is allowed since the diagonal has been
set to -1 for auto-regulation
make.adjoint2 <- function(CM,status=FALSE) {
adj2 <- (-1)* solve(CM)*det(- (CM))
adj2}
#The resulting MTI matrix returns the effect of a positive perturbation in
a compartment in rows on a compartment in column

#Simulation of the 5000 Q matrices by drawing  $q_{ij}$  values from independent
uniform distributions. Minimums and maximums for the distributions were
defined according to Mini_Mat and Maxi_Mat
for(t in 1:nb_mat){
col_j <- (nb_comp*t)-nb_comp
for(i in 1:nb_comp){

```

```

for(j in 1:nb_comp){
strenght[i,j+col_j] <- runif(1,Mini_Mat[i,j],Maxi_Mat[i,j])
}}

#Simulation of the 5000 MTI matrices using the make.adijoint2 function to
invert the 5000 Q matrices
begin <- (nb_comp*t)-nb_comp + 1
end <- nb_comp*t
strenght_adj[,begin:end] <- make.adijoint2(strenght[,begin:end])
}

#Transformation of quantitative MTI values, with 1 for positive integers, 0
for nulls and -1 for negative integers
effect <- strenght_adj
for(i in 1:nb_comp){
for(j in 1:(nb_comp*nb_mat)){
if(strenght_adj[i,j]>0){effect[i,j] <- 1
}
else{
if(strenght_adj[i,j]==0){effect[i,j] <- 0
}
else{effect[i,j] <- (-1)
}
}
}}

#Counting for each intersection the number of positive, negative and null
MTI values and storage into three summary matrices (effect_po, effect_neg
and effect_nul, respectively)
effect_pos <- matrix(0,ncol = nb_comp, nrow=nb_comp)
effect_neg <- matrix(0,ncol = nb_comp, nrow=nb_comp)
effect_nul <- matrix(0,ncol = nb_comp, nrow=nb_comp)
for(t in 1:nb_mat){
for(i in 1:nb_comp){
for(j in 1:nb_comp){
if(effect[i,(j+((t*nb_comp)-nb_comp))]==1){effect_pos[i,j] <-
effect_pos[i,j]+1}
else{
if(effect[i,(j+((t*nb_comp)-nb_comp))]==(-1)){effect_neg[i,j] <-
effect_neg[i,j]+1}
else{effect_nul[i,j] <- effect_nul[i,j]+1}
}
}}}}

#For each intersection, sum of the three summary matrices should be equal
to the number of simulations (here 5000). This test must return TRUE.
(sum(effect_neg + effect_pos + effect_nul -
matrix(nb_mat,ncol=nb_comp,nrow=nb_comp)) == 0)

#Importation of the original Q matrix
Reference <- sqlFetch(
channel = channel,
#Name of the Excel source sheet with the original matrix Q
sqtable = "net_impacts",
rownames = TRUE
)
Reference <- as.matrix(Reference[,-1])

#Inversion of the original Q matrix resulting in the original MTI matrix
Reference <- make.adijoint2(Reference)

```



```

#Transformation of the original MTI matrix into three matrices. For a given
intersection, if the original MTI value is positive (negative, null), it
should be specified in the effect_pos_ref (effect_pos_neg, effect_pos_nul)
matrix by putting the number of simulations (here 5000) at the
corresponding intersection
effect_pos_ref <- matrix(0,nrow=nb_comp,ncol=nb_comp)
effect_neg_ref <- matrix(0,nrow=nb_comp,ncol=nb_comp)
effect_nul_ref <- matrix(0,nrow=nb_comp,ncol=nb_comp)

for(i in 1:nb_comp){
for(j in 1:nb_comp){
if(Reference[i,j] > 0){effect_pos_ref[i,j] <- nb_mat}
if(Reference[i,j] < 0){effect_neg_ref[i,j] <- nb_mat}
if(Reference[i,j] == 0){effect_nul_ref[i,j] <- nb_mat}
}}

#For each intersection, calculation of the proportion of simulations with
the same sign as in the original MTI matrix
#Proportion is the final matrix used in the paper to assess sensitivity of
the MTIs to 20% uncertainty in the input data.
proportion <- matrix(0,ncol = nb_comp, nrow=nb_comp)

for(i in 1:nb_comp){
for(j in 1:nb_comp){
if(effect_pos_ref[i,j] == nb_mat){proportion[i,j] <-
(effect_pos[i,j]/nb_mat)*100}
if(effect_neg_ref[i,j] == nb_mat){proportion[i,j] <-
(effect_neg[i,j]/nb_mat)*100}
if(effect_nul_ref[i,j] == nb_mat){proportion[i,j] <-
(effect_nul[i,j]/nb_mat)*100}
}
}

```