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1 Lower trophic levels and detrital biomass control the Bay of Biscay continental
2 shelf food web: implications for ecosystem management

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35

36 **Abstract**

37 The Bay of Biscay (North-East Atlantic) has long been subjected to intense direct and indirect
38 human activities that lead to the excessive degradation and sometimes overexploitation of
39 natural resources. Fisheries management is gradually moving away from single-species
40 assessments to more holistic, multi-species approaches that better respond to the reality of
41 ecosystem processes. Quantitative modelling methods such as Ecopath with Ecosim can be
42 useful tools for planning, implementing and evaluating ecosystem-based fisheries
43 management strategies. The aim of this study was therefore to model the energy fluxes within
44 the food web of this highly pressured ecosystem and to extract practical information required
45 in the diagnosis of ecosystem state/health. A well-described model comprising 30 living and
46 two non-living compartments was successfully constructed with data of local origin, for the
47 Bay of Biscay continental shelf. The same level of aggregation was applied to primary
48 producers, mid-trophic-levels and top-predators boxes. The model was even more general as

49 it encompassed the entire continuum of marine habitats, from benthic to pelagic domains.
50 Output values for most ecosystem attributes indicated a relatively mature and stable
51 ecosystem, with a large proportion of its energy flow originating from detritus. Ecological
52 network analysis also provided evidence that bottom-up processes play a significant role in
53 the population dynamics of upper-trophic-levels and in the global structuring of this marine
54 ecosystem. Finally, a novel metric based on ecosystem production depicted an ecosystem not
55 far from being overexploited. This finding being not entirely consistent over indicators,
56 further analyses based on dynamic simulations are required.

57

58 Key words

59 Ecopath; aquatic communities; trophic structure; bottom-up control; multispecies fisheries;
60 ecosystem management; North-East Atlantic, Bay of Biscay, continental shelf.

61

62 **1. Introduction**

63 Impacts of fisheries on target species have been abundantly described and reviewed, e.g.
64 modifications of abundance, spawning potential, growth and maturation, age and size
65 structure, sex ratio, genetics ([Hall, 1999](#)). However, the effect of fishing is not restricted to
66 commercially exploited species but extends to entire ecosystems. In most cases, by targeting
67 and reducing the abundance of high-value consumers, fisheries profoundly modify trophic
68 networks and the flow of biomass (and energy) across the ecosystem, leading sometimes to
69 trophic cascades ([Heithaus et al., 2008](#)) and ultimately to regime shifts ([Daskalov et al.,
70 2007](#)). In addition, fishing practices can durably and substantially damage the living and non-
71 living environment of target and associated resources, e.g. poorly-selective fishing activities
72 generate by-catch and discards and sometimes cause local anoxia ([Diaz et al., 2008](#)), benthic
73 trawls and dredges cause physical changes to the seabed ([Hall-Spencer et al., 2002](#)), and lost
74 fishing gear that preserves its catching abilities leads to temporary “ghost fishing” ([Baeta et
75 al., 2009](#)). Consequently, in the last two decades, a consensus has emerged on the need to
76 move from single species- to ecosystem-based fisheries management (EBFM). The goal is “to
77 rebuild and sustain populations, species, biological communities and marine ecosystems at
78 high levels of productivity and biological diversity so as not to jeopardize a wide range of
79 goods and services from marine ecosystems while providing food, revenues and recreation for
80 humans” ([Browman et al., 2004](#)).

81 Although the importance of an ecosystem approach is widely accepted, it remains difficult to
82 put these principles into practice ([Tallis et al., 2010](#)). In data-rich situations, multi-
83 species/ecosystem models are valuable tools that bring coherence to a large amount of data
84 from a variety of sources (see Plagányi ([2007](#)) for an exhaustive review). They can be useful
85 to provide initially a holistic understanding of the structure and functioning of a particular
86 aquatic system and then supply concrete elements for managing this exploited ecosystem. For

87 example, they have been used to explore marine protected area (MPA) zoning options or to
88 assist the implementation of EBFM through the identification of critical biological indicators
89 and their corresponding threshold values ([Tudela et al., 2005](#); [Coll et al., 2008](#)). Among
90 ecosystem models, Ecopath with Ecosim (EwE) is a well-known and freely-available software
91 package which attempts to represent all trophic groups, in a mass-balanced way ([Polovina,](#)
92 [1984](#); [Christensen and Pauly, 1992](#)). The ecosystem is considered as a unit of biological
93 organization, made up of all the organisms in a given area, interacting with the physical
94 environment, so that a flow of energy leads to characteristic trophic structure and material
95 cycles within the system ([Odum, 1969](#)). Through the development of new components and
96 modules, EwE has become increasingly powerful in providing information on how a system is
97 likely to respond to potential changes in fisheries management practices and, to a lesser
98 extent, to environmental disturbances ([Coll et al., 2007](#); [Shannon et al., 2009](#)). Some of the
99 fundamental strengths of the approach are the achievement of a good trade-off in model
100 structure between simplicity and complexity (i.e. parsimony principle; [Fulton et al. \(2003\)](#))
101 and the use of a common and rigorous analytical framework that make comparisons between
102 various systems possible ([Plagányi and Butterworth, 2004](#)).

103 At the western edge of the Eurasian continent, the Bay of Biscay, opening to the Eastern
104 North Atlantic Ocean, supports a large number of anthropogenic activities including tourism
105 and shellfish farming along the coasts and intensive fisheries for human consumption over the
106 shelf and along the slopes ([Lorance et al., 2009](#)). Fishing activities in the Bay of Biscay
107 involve several European countries and are characterised by the wide variety of fishing
108 vessels, gears and techniques, the large number of landed species (more than a hundred) and
109 the numerous habitats explored ([Léauté, 1998](#)). The major commercially exploited stocks are
110 crustaceans, cephalopods and both pelagic and demersal fish, some of them showing signs of
111 intensive exploitation ([ICES, 2005b](#)). For instance, since 2002, European anchovy recruitment

112 has experienced a severe decline that raises growing concerns from the scientific community
113 and EU member states as to what would be the direct and indirect effects of alternative
114 harvest strategies of forage fish on other ecosystem components ([ICES, 2010](#)).

115 In this context of intense multi-species exploitation, a mass-balanced model of the Bay of
116 Biscay continental shelf food web would be of great interest to stakeholders and decision
117 makers to support the implementation of sustainable fisheries policies and the development of
118 ecosystem-based management in the area. Models already exist for different parts of the Bay
119 of Biscay continental shelf with special hydro-morphological characteristics, i.e. the “Grande
120 Vasière” ([Le Loc'h, 2004](#)), the Cantabrian Sea ([Sanchez and Olaso, 2004](#)). At a broader
121 spatial scale, including the totality of the two ICES sub-divisions VIIIa and b, two models
122 were constructed for the year 1970 and 1998 by Ainsworth et al. ([2001](#)). Little help was
123 provided by local researchers for those two previous models and as a consequence, most
124 biomass data in their initial input matrix were lacking or obtained from similar systems
125 (Sylvie Guénette, pers. comm.). Ainsworth et al. ([2001](#)) paid particular attention to fish
126 species that were divided, according to a length criterion, into 22 distinct functional groups.
127 These models recently served as a strong basis for a Master’s thesis ([Jimeno, 2010](#)), in which
128 the “2007” situation was modelled. Previous models of the Bay of Biscay were lacking of
129 sufficient spatial coverage and amount of local data to be useful. The construction of a new
130 model was made possible by the two successive phases of the French coastal environmental
131 research program (PNEC 1999-2003 and 2004-2007) that both included a specific worksite on
132 the Bay of Biscay and that thus greatly contributed to fill the gaps that existed in the data
133 concerning this area. In the present work, a particular effort was made to combine local
134 information of the same quality, reliability and detail, on both the benthic and pelagic
135 communities, from primary producers to top-predators to better understand the structure,
136 organization and functioning of the Bay of Biscay continental shelf food web. Then, the

137 keystone compartments according to the original definition provided by Power et al. ([1996](#)),
138 i.e. components whose effect is large, and disproportionately large relative to their abundance,
139 were determined. Finally, the ecosystem exploitation status was assessed using a set of
140 metrics, some being based on ecosystem production.

141

142 **2. Material and Methods**

143 2.1 Study area

144 The Bay of Biscay is a large gulf of the Atlantic Ocean located off the western coast of France
145 and the northern coast of Spain, between 48.5 and 43.5 °N and 8 and 3 °W (Fig. 1). The
146 principal rivers in decreasing order of drainage area are: the Loire, Garonne-Dordogne
147 (Gironde complex), Adour, Vilaine and Charente rivers. The continental shelf reaches widths
148 of about 140 km off the coast of Brittany but narrows to less than 15 km off the Spanish
149 shore. The physical and hydrological features of the Bay of Biscay are of great complexity,
150 e.g. coastal upwelling, coastal run-off and river plumes, seasonal currents, eddies, internal
151 waves and tidal fronts ([Planque et al., 2004](#)). These abiotic processes greatly influence the
152 phytoplankton dynamics and as a consequence, the whole food-web composition, structure
153 and functioning ([Varela, 1996](#)).

154 The model was restricted to divisions VIIIa and b of the International Council for the
155 Exploration of the Sea (ICES; www.ices.dk). An ecosystem model has already been built for
156 the Cantabrian Sea, which exhibits particular hydro-morphological characteristics (ICES
157 division VIIIc) ([Sanchez and Olaso, 2004](#)). The deep offshore basin (ICES division VIIIId)
158 was not sufficiently documented to be included into the modelling process. The study site in
159 the Bay of Biscay was limited to the middle-depth continental shelf, between the 30-m and
160 150-m isobaths, and its surface area was considered to be 102,585 km². There has been long-

161 term, consistent and regular monitoring of the benthic, demersal and pelagic biota in this
162 study area.

163

164 2.2 Trophic modelling approach

165 A mass-balance (neglecting year-to-year change in biomass, compared to flows) model of the
166 Bay of Biscay continental shelf was constructed using Ecopath with Ecosim 6 ([Christensen](#)
167 [and Pauly, 1992](#); [Christensen et al., 2008](#)). The model combines biomass, production and
168 consumption estimates to quantify flows between the different elements of aquatic exploited
169 ecosystems at a specific point in time. The parameterisation of the Ecopath model is based on
170 satisfying two “master” equations. The first describes the production term for each
171 compartment (species or group of species with similar ecotrophic roles) included in the
172 system:

173 Production = fishery catch + predation mortality + net migration + biomass accumulation +
174 other mortality.

175 “Other mortality” includes natural mortality factors such as mortality due to senescence,
176 diseases, etc. The second equation expresses the principle of conservation of matter within a
177 compartment:

178 Consumption = production + respiration + unassimilated food.

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

$$181 B_i \times (P/B)_i = Y_i + \sum_j (B_j \times (Q/B)_j \times DC_{ij}) + Ex_i + Bacc_i + B_i(1 - EE_i) \times (P/B)_i \quad (1)$$

182 and

$$183 B_i \times (Q/B)_i = B_i \times (P/B)_i + R_i + U_i \quad (2)$$

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

186 composition), net migration rate (Ex , year⁻¹), biomass accumulation ($Bacc$, year⁻¹), total catch
187 (Y ; kg C·km⁻²), respiration (R ; kg C·km⁻²·year⁻¹), unassimilated food rate (U) and ecotrophic
188 efficiency (EE).

189 Biomass, Q/B and P/B values of multi-species compartments were determined by the
190 weighted average of the relative abundance of each species. There are as many linear
191 equations as groups in the system, so if one of the parameters is unknown for a group, the
192 model computes it by solving the set of linear equations. In particular, EE , which corresponds
193 to the fraction of the production of each group that is used in the food web, is difficult to
194 measure. Hence, it was estimated by the model for most of the groups. The “manual” mass-
195 balanced procedure that includes two major levels of verification was used. First, for those
196 groups with $EE > 1$, the model was modified by adjusting their initial input parameters and
197 the predation intensity exerted by predators on them (slight and gradual increase or decrease
198 in values, within the interval of confidence of the parameter). For this parameter, a value
199 greater than one indicated a demand on the compartment that was too high to be sustainable
200 within the food web. Secondly, the same procedure was applied to the gross food conversion
201 efficiency (GE) estimates, also called P/Q ratio, which must be in the physiologically realistic
202 range of 0.1-0.3 for most consumers and generally higher for small organisms. EE for a
203 detritus group is defined as the ratio between what flows out of that group and what flows into
204 it. Theoretically, under steady-state assumption, this ratio should be equal to one.

205 The Ecopath model was validated using the pre-balance (PREBAL) diagnostics ([Link, 2010](#))
206 to ensure that any potential and major problems are captured before network outputs are used
207 to address research or management questions. PREBAL provides a set of guidelines presented
208 as a form of “checklist”. Diagnostic tests allow evaluation of the cohesiveness of the data
209 despite the natural discrepancies that occur when using myriad data sources measured across
210 varying scales. In brief, each functional group was plotted along the x-axis in order of

211 decreasing trophic level to allow easy visualization of trophic relationships. Byron et al.
212 ([2011](#)) summarized the PREBAL analysis into five simple ecological and physiological
213 “rules” that should be met.

214

215 2.3 Defining the model compartments

216 Functional groups were defined following three criteria: the similarities between the species
217 in terms of size and food preferences, the amount of ecological data available to determine
218 precise parameters and diet compositions and the main research questions to which the model
219 should respond. On this basis, 32 trophic groups were retained (Table 1), two of which were
220 seabirds, five marine mammals, nine fish, eight invertebrates, three zooplankton, two primary
221 producers, one bacteria, discards from commercial fisheries and detritus corresponding to
222 allochthonous imports into the web and autochthonous internal cycling within the web. Data
223 collections for plankton to top-predators (marine birds and small cetaceans) cover a period
224 long enough for sufficient data to be available, but short enough for massive changes in
225 biomass not to have occurred. They encompassed different seasons and years, starting in 1994
226 and ending in 2005. The European anchovy *Engraulis encrasicolus* has been affected by a
227 below average recruitment since 2002, which led to the closure of the fishery in the area from
228 June 2006 to December 2009 ([ICES, 2010](#)). The model presented in this study corresponded
229 to a typical year between 1994 and 2005, before the collapse of the anchovy fishery.
230 Biomasses, diets and species compositions were averaged across seasons.

231

232 2.4 Initial input parameters and diet compositions

233 2.4.1 *Marine mammals and seabirds*

234 Birds were counted visually and identified to species level by aerial surveys on a monthly
235 basis from October 2001 to March 2002, in August 2002, in June 2003 and May 2004

236 (ROMER and ATLANCET surveys). The Bay of Biscay is heavily used as a migration route
237 and as a wintering area for marine birds, so there is a great seasonal variation in their
238 abundance. As this long-distance migratory pattern was included through an annual biomass
239 estimate, imports were not added to their diets. The four most abundant seabird taxa were
240 northern gannets *Sula bassana*, large gulls (i.e. herring gulls *Larus argentatus*, lesser black-
241 backed gulls *Larus fuscus*, great black-backed gulls *Larus maritimus* and yellow-legged gull
242 *Larus michahellis*), kittiwakes *Rissa tridactyla* and auks (i.e. common murre *Uria aalge*,
243 razorbills *Alca torda* and Atlantic puffins *Fratercula arctica*) ([Certain and Bretagnolle, 2008](#))
244 (Table 1). Based on Hunt et al. ([2005](#)), the mean body mass for these taxa was set to 3.2, 1.1,
245 0.4 and 0.9 kg respectively. They were grouped in two categories according to feeding
246 strategies: “surface feeders” for gulls and kittiwakes and “plunge and pursuit divers” for
247 gannets and auks. Wet weights were converted into dry weights and carbon contents based on
248 two conversion factors, i.e. 0.3 and 0.4 respectively. These values were derived from expert’s
249 knowledge on the basis of the carbon to wet mass ratio of 0.1 used by Heymans and Baird
250 ([2000](#)).

251 Their diet regime was assumed to be composed mostly of energy-rich pelagic species and
252 large zooplankton crustaceans ([Hunt et al., 2005](#); [Certain et al., 2011](#)). Some marine birds are
253 also well-known to feed largely on fisheries discards ([Arcos, 2001](#)). This artificial low-quality
254 food source has been shown to be detrimental on a long-term basis for gannets ([Grémillet et](#)
255 [al., 2008](#)) (Table 2).

256 Daily ration for wild piscivorous birds (R_c) in $\text{g}\cdot\text{day}^{-1}$ was calculated according to the
257 following empirical equation ([Nilsson and Nilsson, 1976](#)):

$$258 \text{Log}(R_c) = -0.293 + 0.85 \times \text{log}(W) \quad (3)$$

259 where W is the body mass of birds expressed in g. This value was then multiplied by 365 days
260 and divided by the mean weight of the taxon to provide annual Q/B ratio.

261 The *P/B* ratio for the two functional groups was based on estimates published in Nelson
262 ([1979](#)).

263 Abundance for the small cetacean community (porpoises and dolphins excluding whales) was
264 derived from the combination of results from (i) the SCANS-II project focusing on small
265 cetaceans in the European Atlantic and the North Sea and carried out in July 2005 by ships
266 and aircraft, (ii) the estimated small delphinid abundance in the Bay of Biscay based on
267 repeated extensive aerial surveys (ROMER and ATLANCET campaigns) in different seasons
268 and years (2001–2004) across the Bay of Biscay continental shelf ([Certain et al., 2008](#)), and
269 (iii) the monitoring of marine mammals in the same area based on stranding and spring
270 shipboard observations performed during PELGAS IFREMER cruises (Certain et al. ([2011](#));
271 authors' unpublished data). The five most common species were separated in the model: the
272 common dolphin *Delphinus delphis*, the striped dolphin *Stenella coeruleoalba*, the bottlenose
273 dolphin *Tursiops truncatus*, the long-finned pilot whale *Globicephala melas* and the harbour
274 porpoise *Phocoena phocoena* (Table 1). Following the method developed by Trites and Pauly
275 ([1998](#)), mean body weight was calculated for each species according to its maximum body
276 length. A conversion factor of 0.1 for wet weight to carbon content was used ([Bradford-](#)
277 [Grieve et al., 2003](#)).

278 Diet compositions were obtained from stomach content analysis of stranded animals found
279 along the North-East Atlantic French coast ([Spitz et al., 2006a](#); [Spitz et al., 2006b](#); [Meynier et](#)
280 [al., 2008](#)). Some cetacean species forage both on the shelf and on the oceanic domains of the
281 Bay of Biscay. Consequently, the proportion of oceanic prey in their diet was considered as
282 imports (Table 2).

283 Consumption can be estimated from energy requirements, prey energy densities and prey
284 compositions by percent mass. The daily energy requirement or field metabolic rate (*FMR*) in

285 kJ·day⁻¹ is related to mean body mass (W in kg) according to the model developed by Boyd
286 ([2002](#)), the coefficient used was the one proposed by the author for marine mammals alone:

$$287 \quad FMR = 2629 \times W^{0.524} \quad (4)$$

288 Daily consumption (R_c) in kg·day⁻¹ was calculated by converting energy requirements to food
289 biomass and adjusting by a factor of assimilation efficiency:

$$290 \quad R_c = FMR / (0.8 \times \sum(P_i \times ED_i)) \quad (5)$$

291 where P_i was the proportion by mass of prey species i in the diet and ED_i , the energy density
292 of prey i (kJ·kg⁻¹; Spitz et al. ([2010](#))). Assimilation efficiency was typically estimated at 0.8
293 ([Leaper and Lavigne, 2007](#)). This value was then multiplied by 365 days and divided by the
294 mean weight of the taxon to provide annual Q/B ratio.

295 Values of P/B were taken from Christensen et al. ([2009](#)); they varied from 0.03 for baleen
296 whales to 0.08 for dolphins and porpoises.

297

298 2.4.2 Fish groups

299 Stocks of the common sole *Solea solea*, the European hake *Merluccius merluccius*, two
300 European anglerfish *Lophius budegassa* and *L. piscatorius* and the megrim *Lepidorhombus*
301 *whiffiagonis* were assessed from ICES/ACFM advice report ([ICES, 2004](#)). The biomass of
302 most other benthic and demersal fish species was estimated from bottom-trawl surveys
303 conducted annually in autumn in the Bay of Biscay (EVHOE IFREMER cruises). Data were
304 averaged over six years, between 1998 and 2003 and then multiplied by four to take into
305 account the mean bottom-trawl capture efficiency below 0.3 ([Trenkel and Skaug, 2005](#)). The
306 capture efficiency represents the proportion of individuals in the trawl path being retained by
307 the gear. Wet body weights were converted to dry weights and then to carbon contents using
308 conversion factors of 0.2 and 0.4 respectively ([Brey et al., 2010](#)). The biomass of most pelagic
309 fish species was estimated using data from acoustic surveys conducted each spring in the Bay

310 of Biscay (PELGAS IFREMER cruises). Data were averaged over three years, between 2000
311 and 2003. The distribution range of the horse mackerel *Trachurus trachurus* was not fully
312 encompassed by IFREMER surveys, which resulted in an underestimation of the total
313 biomass. Thus, an ecotrophic efficiency of 0.95 was preferentially entered in the input
314 parameters for this commercially exploited species and the biomass was left to be estimated
315 by the model. Wet body weights were first converted to dry weights with a conversion factor
316 of 0.14 and finally to carbon contents using a conversion factor of 0.45 ([Jorgensen et al.,](#)
317 [1991](#)) (Table 1).

318 The Q/B ratio was determined using Fishbase (Froese and Pauly ([2000](#)); www.fishbase.org).
319 For each species, Q/B was estimated from the empirical relationship proposed by Palomares
320 and Pauly ([1998](#)):

$$321 \quad \text{Log}(Q/B) = 7.964 - 0.204 \times \log(W_{\infty}) - 1.965 \times T' + 0.083 \times A + 0.532 \times h + 0.398 \times$$
$$322 \quad d \quad (6)$$

323 where W_{∞} was the asymptotic weight, T' was the mean environmental temperature expressed
324 as $1000/(T (^{\circ}\text{C}) + 273.15)$, A was the aspect ratio of the caudal fin, h and d were dummy
325 variables indicating herbivores ($h=1, d=0$), detritivores ($h=0, d=1$) and carnivores ($h=0, d=0$).

326 Under steady-state conditions, the P/B ratio is equal to instantaneous coefficient of total
327 mortality (Z) ([Allen, 1971](#)):

$$328 \quad Z = M + F \quad (7)$$

329 with M being natural and F fishing mortality. M was calculated using the Fishbase life-history
330 tool from Pauly's ([1980](#)) empirical equation:

$$331 \quad M = K^{0.65} \times L_{\infty}^{-0.279} \times T^{0.463} \quad (8)$$

332 where K was the curvature parameter of the von Bertalanffy growth function (VBGF), L_{∞} the
333 asymptotic length and T the mean environmental temperature in $^{\circ}\text{C}$. If no estimate of K was
334 available, M was calculated from the preliminary empirical relationship:

335 $M = 10^{(0.566-0.718 \times \log(L_{\infty})+0.02 \times T)}$ (9)

336 Parameters of the VBGF were taken from publications, calculated from survey data or, most
337 often, found on Fishbase.

338 A mean temperature of 11°C for benthic and demersal fish and 14°C for pelagic fish were
339 assumed, considering that former species live on or near the sea bottom. Fishing mortality
340 was set to zero for non-commercial species such as the European sprat *Sprattus Sprattus*.
341 Whenever possible, fishing mortality was taken directly from ICES reports, otherwise, it was
342 estimated from the same sources by dividing catches by biomasses. For the horse mackerel
343 *Trachurus trachurus*, the instantaneous rate of total mortality (Z) was estimated using the
344 Hoenig (1983) empirical equation based on a maximum observed age (t_{max}) of 15 years:

345 $\ln(Z) = 1.44 - 0.984 \times \ln(t_{max})$ (10)

346 For demersal and benthic fish species, knowledge of their diet came from the literature and
347 Fishbase, as well as stomach contents (Le Loc'h, 2004) and carbon and nitrogen stable
348 isotopic analysis performed on specimens captured on a large sedimentary muddy bank
349 known as the “Grande Vasière” and on the external margin of the continental shelf (Le Loc'h
350 et al., 2008) (Table 2). They were consequently grouped into four categories: “Benthivorous
351 demersal fish” comprised 24 species, including the common sole *Solea solea*;
352 “Suprabenthivorous demersal fish” included eight species such as the blue whiting
353 *Micromesistius poutassou* and small European hakes (< 10 cm) *Merluccius merluccius*;
354 “Piscivorous and benthivorous demersal fish” contained, among 41 other species, the
355 European conger *Conger conger*, the pouting *Trisopterus luscus* and the small-spotted
356 catshark *Scyliorhinus canicula*; “Piscivorous demersal fish” included large specimens of the
357 European hake which have a diet consisting of both demersal and pelagic fish (the full list of
358 species is given in the first supplementary material).

359 Based exclusively on experts' knowledge, the pelagic species were divided into five groups,
360 each representing a well-known, valuable and strategic species. Three thoroughly-monitored
361 clupeid species, the European anchovy *Engraulis encrasicolus*, the European sprat *Sprattus*
362 *sprattus* and the European pilchard *Sardina pilchardus*, were taken into account. The first two
363 feed exclusively on mesozooplankton ($200 < \text{size} < 2000 \mu\text{m}$) ([Whitehead, 1985](#)). However,
364 an ontogenetic dietary shift to smaller prey represented by microzooplankton ($< 200 \mu\text{m}$) and
365 large phytoplanktonic cells ($> 3 \mu\text{m}$) was apparent in approximately one year-old pilchards
366 (individuals $< 18 \text{ cm}$) ([Bode et al., 2004](#)). Percentages calculated for the whole pilchard
367 population were weighted averages of those for adults with a weigh of 0.76, and those for
368 juveniles with a weigh of 0.24. The fourth group consisted of the Atlantic mackerel *Scomber*
369 *scombrus*, a zooplankton feeder of which the large individuals prefer macrozooplankton ($>$
370 $2000 \mu\text{m}$). The last group was composed of the horse mackerel *Trachurus trachurus*, a
371 benthic-pelagic species which feeds on both domains (Table 2) ([Cabral and Murta, 2002](#)).

372

373 2.4.3 Invertebrates

374 2.4.3.1 Cephalopods

375 From bottom-trawl surveys conducted annually in autumn in the Bay of Biscay (EVHOE
376 IFREMER cruises), the more abundant pelagic cephalopods in the area appeared to be the
377 broadtail short-finned squid *Illex coindetii*, the European flying squid *Todarodes sagittatus*,
378 and four squid species belonging to the *Loliginidae* family, *Loligo* spp. and *Alloteuthis* spp.
379 The most abundant benthic cephalopods were the horned octopus *Eledone cirrhosa* and the
380 common octopus *Octopus vulgaris*, together with species of the *Sepiidae* family. As there has
381 been little systematic study of catchability and gear selectivity in cephalopods, their biomass
382 was left to be estimated by Ecopath, using an *EE* of 0.95. This value was justified by their
383 commercial exploitation in the ecosystem. For these groups, wet body weights were converted

384 to dry weights then to carbon contents using conversion factors of 0.192 and 0.402
385 respectively ([Brey et al., 2010](#)) (Table 1).
386 The P/B and Q/B ratios corresponded to the values proposed by Sanchez and Olaso ([2004](#)) for
387 the Cantabrian Sea. The P/Q ratio was unusually high for animals of this size, in relation to
388 the special eco-physiological characteristics of cephalopods which allow rapid growth
389 ([Jackson and O'Dor, 2001](#)).
390 In the same way, diet composition was roughly estimated from information gathered for the
391 southern part of the Bay. Part of their diet includes pelagic shrimps, which are considered as
392 macrozooplankton in the present study (Table 2).

393

394 2.4.3.2 *Suprabenthic and benthic invertebrates*

395 Suprabenthic/benthic invertebrates were sampled in 2001 in late spring in the “Grande
396 Vasière” (INTRIGAS II survey). Species were grouped into six compartments according to
397 size, feeding ecology and position regarding the seafloor: “suprabenthic invertebrates”
398 (crustacean suspension feeders mainly members of the Euphausiids family), “metazoan
399 meiofauna” (largely dominated by nematodes), “surface suspension and deposit feeders
400 invertebrates” (various species pertaining to polychaetes, bivalves and crustacean decapods),
401 “sub-surface deposit feeders invertebrates” (eight species of polychaetes, sea urchins and sea
402 cucumbers), “necrophagous benthic invertebrates” (four species of isopods), “carnivorous
403 benthic invertebrates” (polychaetes and crustacean decapods such as the Norwegian lobster
404 *Nephrops norvegicus*). The biomass was obtained from Duchemin et al. ([2008](#)), Le Loc’h
405 ([2004](#)), Le Loc’h et al. ([2008](#)) as ash-free dry weight and converted to carbon content using a
406 factor of 0.4 ([Steele, 1974](#)) (Table 1).

407 The P/B ratio was estimated from Schwinghamer et al. ([1986](#)):

$$408 \quad P/B = 0.525 \times W^{(-0.304)} \quad (11)$$

409 with W , mean body mass converted to an energy equivalent using conversion factor (1 g C =
410 11.4 kcal; Platt and Irwin (1973)).

411 The P/Q ratio, also called the gross food conversion efficiency (GE), was preferentially
412 entered in the model. Indeed, relevant values are available from the literature and typically
413 range from 0.05 to 0.3 (Christensen and Pauly, 1993).

414 Dietary profiles were determined from stable isotope analysis (Le Loc'h et al., 2008) (Table
415 2).

416

417 2.4.4 Zooplankton

418 Microzooplankton includes protozoans < 200 μm , mostly ciliates and heterotrophic
419 flagellates. It was studied in 2004 through four seasonal surveys at three stations located in
420 front of the Gironde River (MICRODYN survey) and three spring surveys in the southern
421 Bay of Biscay in 2003, 2004 and 2005 (PELGAS IFREMER cruises). The cell volume was
422 converted into carbon units using allometric relationships and/or factors (for a complete
423 review of sampling and sample treatments, see Marquis et al. (in press)). Annual Q/B ratio
424 was the intermediate value between the estimate of Sanchez and Olaso (2004) for the
425 Cantabrian Sea and the calculation from phytoplankton grazing experiments on Gironde
426 plume waters (Landry and Hassett, 1982). An ecotrophic efficiency of 0.95 was assumed for
427 this compartment.

428 Mesozooplankton ([200-2000] μm) consists mostly of metazoans with copepods
429 predominating and macrozooplankton (> 2000 μm) consists mainly of metazoans with
430 decapods and jelly plankton (tunicates, cnidarians) predominating. The samples were obtained
431 during BIOMAN surveys covering the South-East of the Bay of Biscay in spring (May and
432 June) for the period 1999-2002 (Irigoien et al., 2009). Achievement of reliable estimates of
433 biomass was based on the statistical relationship between zooplankton sample volume, easily

434 estimated by digital image analysis, and the corresponding organic C and N contents of paired
435 aliquots samples. The semi-automatic method used here allowed estimating individual bio-
436 volume but not the taxonomic composition of zooplankton. So, gelatinous zooplankton which
437 has vastly different biological parameters could not be isolated as a specific Ecopath
438 compartments in the present model. The full procedure was described in Alcaraz et al. (2003).
439 Annual *Q/B* ratios were taken from Sanchez and Olaso (2004) for the Cantabrian Sea. An
440 ecotrophic efficiency of 0.95 was assumed (Table 1 and 2).

441

442 *2.4.5 Primary producers, bacteria and detritus*

443 These compartments were characterized during 14 IFREMER surveys performed over nine
444 years from 1994 to 2002, in various seasons, covering the spread of the Gironde and Loire
445 plumes as well as a larger proportion of the Bay of Biscay continental shelf (see Labry et al.
446 (2002) for a description of full sampling and sample treatments). Most of the data were
447 comprised between 1998 and 2002 and as a consequence, matched with the period covered by
448 data gathered for other compartments (see the second supplementary material).

449 Total chlorophyll *a* was determined after size-fractioning filtration between nano- and
450 microplankton (size > 3 µm) and picoplankton (size < 3 µm) and analysed by fluorometric
451 acidification procedure (Yentsch and Menzel, 1963). A ratio of carbon to chlorophyll *a* of
452 50:1 was taken for conversion. Phytoplankton production was determined by the in situ ¹⁴C
453 method (Steeman-Nielsen, 1952).

454 A significant import of allochthonous material probably derives from large rivers flowing into
455 the Bay of Biscay. A value of 454 kg C·km⁻²·year⁻¹ was evaluated from Abril et al. (2002) and
456 the mean discharge value of these systems (www.hydro.eaufrance.fr).

457 Bacteria were fixed, stained and counted by epifluorescence microscopy (Porter and Feig,
458 1980). Bacterial production was estimated using the method based on the tritiated thymidine

459 incorporation into DNA ([Furhman and Azam, 1982](#)). Values were converted into biomass and
460 bacterial production assuming a cell content of 16 femtogram of carbon. The biomass was
461 multiplied by two to take into account both pelagic and benthic bacteria populations. It is not
462 possible to estimate the Q/B ratio for groups that feed exclusively on detritus. P/Q ratio for
463 bacteria was derived from the paper by Vézina and Platt ([1988](#)) (Table 1 and 2). In Ecopath,
464 detritus is not assumed to respire, although it would if bacteria were considered part of the
465 detritus. This is why it was better to create a separate group for the detritus-feeding bacteria.
466

467 *2.4.6 Placing the fishery into the system: landings and discards*

468 Total French catches from the Bay of Biscay exceeded 90 000 tons in 1997. Anchovy
469 (*Engraulis encrasicolus*) and pilchard (*Sardina pilchardus*) represented over half the pelagic
470 catch, while hake (*Merluccius merluccius*), sole (*Solea solea*) and anglerfish (*Lophius*
471 *piscatorius* and *L. budegassa*) dominated the demersal catch. The major French shellfish
472 fishery is Norway lobster (*Nephrops norvegicus*) and this is located on the “Grande Vasière”
473 in southern Brittany, as well as on the “Vasière” of the Gironde. Prawns and large crustaceans
474 accounted for less of 2500 tons annually from the Bay of Biscay. Catches of cuttlefish (*Sepia*
475 *officinalis*) and squid (*Loligo vulgaris* and *L. forbesii*) vary from year to year depending on
476 their relative abundance; landings exceeded 6000 tons in 1997 ([OSPAR Commission, 2000](#)).
477 Pelagic fish landings were obtained from the relevant working group (WGMHSA; ICES
478 ([2005b](#))). Benthic and demersal fish catches were based on international landings of ICES
479 division VIIa and b averaged over the 1998-2002 period for surveyed stocks ([ICES, 2004](#))
480 and on French landings statistics for the year 2002 for the main other targeted species.
481 Among suprabenthic and benthic invertebrates, the Norwegian lobster has the greatest
482 economic importance. Catches for this species were also available in the above-mentioned
483 reference.

484 Cephalopod landings were taken from the relevant ICES working group (WGCEPH; ICES
485 ([2005a](#))) and were averaged over the 1996-2003 period. Since available landings included
486 captures from division VIIIc as well, 86 % of the total value was considered to take into
487 account the relative VIIIab/VIIIabc surfaces.

488 In pelagic fisheries, discarding occurs in a sporadic way compared to demersal fisheries.

489 Discard estimates are still not available for sardine and anchovy; however, given their high
490 economic value, discard levels are thought to be low. Discard data for cephalopods are still
491 not homogeneously collected by EU member countries. For these compartments, discards
492 were set to zero in the model. Discards for benthic and demersal species were obtained from
493 direct observations on *Nephrops* trawlers operating in the Bay of Biscay, 69 hauls being
494 sampled over the whole 1998 year (Table 1).

495

496 2.5 Trophic structure and ecological network analysis

497 A flow diagram was created to synthesise the main trophic interactions in the ecosystem.

498 Furthermore, to provide a quantitative description of the ecosystem structure, the effective
499 trophic level (*TL*) and the omnivory index (*OI*) were calculated for each functional group,

500 along with the transfer efficiencies (*TE*) between successive aggregated trophic levels along a

501 modified Lindeman spine (Table 1). *OI* is a measure of the variance in trophic level of the

502 prey of a given group. Ecosystem state and functioning were characterized by the total system

503 throughput or activity (*TST*), which quantifies how much matter the system processes, Finn's

504 cycling index (*FCI*), which measures the relative importance of cycling to this total flow, and

505 the total primary production to total respiration ratio (*Pp/R*), which expresses the balance

506 between energy that is fixed and energy that is used for maintenance. The average residence

507 time for energy in the system was estimated as the ratio of total system biomass to the sum of

508 all respiratory flows and all exports ([Herendeen, 1989](#)). It has been assumed that the residence

509 time of particles in a system increases to a maximum during succession, as a result of
510 increasing ecological organisation. The connectance index (CI) and the system omnivory
511 index (SOI) were regarded as two indices reflecting the complexity of the inner linkages
512 within the ecosystem. Taking into account both the size of the ecosystem in terms of flows
513 (TST) and organization (information content), ascendancy (A) has been proposed as an index
514 to characterize the degree of development and maturity of an ecosystem ([Ulanowicz, 1986](#)).
515 Capacity (C) represents the upper limit of A . The relative ascendancy measure (A/C) is the
516 fraction of the potential level of organization that is actually realized ([Ulanowicz, 1986](#)). It is
517 hypothesized that high values of this index are related to low levels of stress in the system and
518 vice-versa. Hence disturbance activities, like fishing, are expected to produce a decrease in A
519 ([Wulff and Ulanowicz, 1989](#)). The complement to A is System Overhead (O), which
520 represents the cost to an ecosystem for circulating matter and energy ([Monaco and](#)
521 [Ulanowicz, 1997](#)). Thus, O effectively represents the degrees of freedom a system has at its
522 disposal to react to perturbations ([Ulanowicz, 1986](#)). Values were compared with those
523 provided by Sanchez and Olaso ([2004](#)) and Jimeno ([2010](#)) and for other comparable shelf
524 ecosystems (summary table in Trites et al. ([1999](#))). Finally, the mixed trophic impact (MTI)
525 routine indicates the effect that a small increase in the biomass of one (impacting) group will
526 have on the biomass of other (impacted) groups ([Ulanowicz and Puccia, 1990](#)). Particular
527 attention was paid to the impacts of fisheries activities on higher trophic-level ecosystem
528 components. Fishing activities were further described using the mean trophic level of the
529 catches (TL_c) and the primary production required to sustain harvest (PPR). TL_c reflects the
530 strategy of a fishery in terms of food-web components selected, and is calculated as the
531 weighted average of TL of harvested species. The PPR required to sustain fisheries has been
532 considered as an ecological footprint that highlights the role of fishing, in channelling marine
533 trophic flows toward human use. To assess the effects of export from the system due to

534 fishing activities, the L index has been applied ([Libralato et al., 2008](#)). It is based on the
535 assumption that the export of secondary production due to fisheries reduces the energy
536 available for upper ecosystem levels, thus resulting in a loss of secondary production. The
537 index that allows quantifying the effects of fishing at an ecosystem level is calculated as:
538
$$L = -PPR \times TE^{TL_c-1} / Pp \times \ln(TE) \quad (12)$$

539 with Pp the primary production of the system. Estimates of PPR and Pp were based on the
540 primary producers' food chain and also by including detrital production. It is possible to
541 associate with each index value a probability of the ecosystem being sustainably fished (P_{sust} ,
542 Libralato et al. ([2008](#)), Coll et al. ([2008](#))). At the same time, the exploitation rates (F/Z ,
543 fishing mortality to total mortality) by ecological group were also taken into account.
544 Libralato et al. ([2006](#)) presented an approach for estimating without bias the
545 “keystoneness” (KS) of living functional groups by combining their overall impact on the
546 system (estimated from the MTI matrix) and their biomass proportion. Keystones are defined
547 as relatively low biomass species with high overall effect. From the positive and negative
548 contribution to the overall effect, it is possible to calculate the bottom-up and top-down
549 effects that contribute to the keystoneness index. The relative importance of top-down or
550 bottom-up trophic controls in continental shelf ecosystems has important implications for how
551 ecosystems respond to perturbations (e.g. Frank et al. ([2007](#))).

552

553 **3. Results**

554 The initial model was not balanced, since they were some ecotrophic efficiencies greater than
555 1. Contrarily, gross food conversion efficiencies were mostly acceptable. Biomass and
556 production estimates of most demersal fish, sardine and anchovy were insufficient to support
557 consumption by mackerel and horse mackerel that constitute the two most abundant fish
558 biomass in the area. More importantly, the biomass of horse mackerel was left to be estimated

559 by the model because of its migratory and bento-pelagic feeding behaviour that renders
560 difficult the estimation of its abundance by scientific surveys. Consequently, proportions of
561 those groups in the diet composition of mackerel and horse mackerel were re-assessed, and
562 when consistent with existing literature, fixed to slightly lower values. In parallel, production
563 terms for piscivorous, piscivorous and benthivorous and benthivorous demersal fish were re-
564 examined to determine higher acceptable values.

565 Among the five ecological and physiological “rules” that should be met, the one concerning
566 the decrease of biomass and vital rates with trophic levels was the more critical in our model.
567 The biomass spectrum has too much biomass in the middle trophic levels, indicating that the
568 model is most likely too focused on fish taxa (Fig. 2a). Twenty-five percent of compartments
569 were fish species or groups. Q/B and R/B across trophic levels did not show the expected
570 decline contrary to the P/B vital rate (Fig. 2b, c and d). This failure was mostly driven by the
571 7 homeotherms’ groups at upper trophic levels which tend to have higher values than the
572 trend line because of a higher consumptive demands per unit body mass than poikilotherms.
573 The normal decomposition pattern was more marked when plotting total or scaled values of P ,
574 Q and R . The unique vital rate ratio approaching 1 concerned zooplankton which had a
575 biomass in the same order of that of phytoplankton. This is the sole reasonable exception to
576 this diagnostic given the high productivity and low standing stock biomass of primary
577 producers.

578 The flow diagram clarified the connections between levels (Fig. 3). Benthic and pelagic food
579 chains appeared to be linked mainly in their upper ranges by demersal fishes, particularly
580 suprabenthivorous species. They optimize foraging benefits by feeding from both systems and
581 they are, in turn, consumed by a large panel of pelagic top-predators. OI in this study ranged
582 between 0.037 and 1.914 and it was lowest for the common dolphin, which feeds almost
583 exclusively on high-value pelagic species, and for the large hake, which preys solely on other

584 fish with *TL* values in the same range (Table 1 and 2). In contrast, other marine top-predators
585 appeared far less specialized, with a significant proportion of their diet coming from imports
586 to the system, assigned by Ecopath to a mid-trophic level position (*TL* II+), or from dead
587 discarded organisms, assigned to a basal trophic level (*TL* I).

588 The ecosystem consisted of five main aggregated trophic levels; biomass values for trophic
589 levels VI to XII were extremely small. Transfer efficiencies between successive discrete
590 trophic levels were regular from lower to higher trophic levels, the mean along this spine
591 being 16.8 %. The primary producers, detritus and discarded organisms in *TL* I took 47.5 % of
592 the throughput of the entire system. *TL* II was mainly bacteria, zooplankton and
593 benthic/suprabenthic invertebrates representing 42.9 % of the total throughput. Thus, most of
594 the activity (90 %) in terms of flow occurred in the lower part of the food web (Fig. 4).

595 The system was estimated to process $939 \cdot 10^3 \text{ kg C} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ (*TST*), with 34.5 % of the total
596 throughput being recycled (*FCI*). The overall residence time was calculated to be 0.046 years
597 equivalent to 17 days. The herbivory to detritivory ratio that quantifies the flow along grazing
598 and detrital food webs is an indication of the importance of detrital components in the system
599 and was equal to 0.76 (Fig. 4). In addition, the *EE* of detritus was estimated to be 0.972,
600 indicating that more or less all the energy entering this compartment is re-used in the system.

601 All these elements suggested a strongly detritus-based trophic organization, with an intensive
602 use of particulate organic matter as a food source. The primary production to respiration ratio
603 (*Pp/R*) was 1.037. Concerning the two proxies for food-chain complexity (Table 3), the global
604 omnivory of 0.212 (*SOI*) is a relatively “intermediate” value when compared with those
605 obtained for other shelf ecosystems in the world and with outputs from previous Bay of
606 Biscay models. The connectance of the trophic compartments of 0.213 (*CI*) was consistent
607 with previous estimates but falls in the lower range. The system showed a relatively low value
608 of *A/C* (22.7 %) and conversely a high value of *O/C*, *A*, *O* and *C* being respectively 874, 288,

609 2,981,572 and 3,856,013 flowbits. These values were close to the ones estimated for the
610 French Atlantic shelf, i.e. 31% and 69 %.

611 The mixed trophic impact routine underlined the fact that marine top-predators had very
612 limited direct or indirect impacts on other trophic groups of the model. Among them, the
613 bottlenose dolphin caused the most pronounced effect (Fig. 5). Fisheries had a direct negative
614 impact on demersal fish stocks, particularly marked for piscivorous species such as large
615 hakes. Fishery wastes, on the other hand, appeared beneficial to surface feeders. Fishing
616 activities could in turn, be positively affected by a small increase in the targeted species, but
617 also by a limited amount of their main food sources, which in the case of forage fish are
618 composed of mesozooplanktonic organisms. In addition, fisheries were characterized by a TL_c
619 of 3.75, a PPR of 14.82 % and a L index of 0.06 calculated using a Pp equal to 445,931 kg
620 $C \cdot km^{-2} \cdot year^{-1}$ and an average transfer efficiency TE across trophic levels of 16.8%. This L
621 value resulted in a probability of having been subjected to a sustainable fishing regime of
622 29.86%. Exploitation rates by ecological group ranged between 0.013 for the carnivorous
623 benthic invertebrates and 0.372 for the piscivorous demersal fish, with a median of 0.117.

624 Another important feature of the MTI matrix concerned the joint favourable effect of sardine,
625 pilchard and sprat on apex predators. The influence of detritus as a structuring compartment
626 highlighted in the previous paragraph was reinforced by its positive effect on various groups,
627 with the exception of primary producers, for which indirect negative influences predominated.

628 Among consumers and producers, the keystone functional groups belonged to the plankton
629 compartments: large phytoplankton, micro- and mesozooplankton (Fig. 6). The bottom-up
630 effect, evaluated through the proportion of positive values contributing to the overall effect
631 was 83, 43 and 70 % respectively.

632 A sensitivity analysis revealed that the main results concerning the functioning of the
633 ecosystem were not affected by lower EE for zooplankton. EE were set to lower values for the

634 three zooplankton compartments, i.e. 0.45, 0.35 and 0.35 for macro-, meso- and
635 microzooplankton respectively, and the model was rerun. The herbivory to detritivory ratio
636 calculated using the Lindeman spine was equal to 0.76 with current setting and to 0.56 with
637 lower values of *EE*. Adding to this, the keystone species identified were the three same
638 compartments (mesozooplankton, large phytoplanktonic cells and microzooplankton), with
639 both sets of *EE*.

640

641 **4. Discussion**

642 Even though our Ecopath model was validated to meet certain standardization requirements
643 on the basis of the PREBAL, gaps exist particularly on model structure that was most likely
644 too focused on fish and that included numerous homeotherms' groups. This particularity of
645 our model was linked to future research questions that would be addressed with the present
646 model on the Bay of Biscay. They necessitate mono-specific boxes for each small pelagics
647 and marine mammals' species frequenting the area. Model structure was recognized in many
648 occasions to greatly influence the effectiveness for a model to capture real ecosystem
649 properties ([Fulton et al., 2003](#)).

650

651 4.1 Late successional position and implications for stability

652 According to Odum ([1969](#)), the “strategy” of long-term evolutionary development of the
653 biosphere is to increase homeostasis with the physical environment, in the sense of achieving
654 maximum protection from its perturbations through a large, diverse and complex organic
655 structure. The author proposed 24 attributes to characterize ecosystem development from
656 “young” to “late” successional stages (the full list of attributes is given in the third
657 supplementary material; Christensen ([1995](#))). A careful analysis of the present system's
658 characteristics revealed that detritus is central to energy flow within the Bay of Biscay

659 continental shelf food web. This finding was confirmed by the Cantabrian Sea model
660 ([Sanchez and Olaso, 2004](#)) that covered a small portion of the Bay presenting distinct hydro-
661 morphological characteristics and the model of Jimeno ([2010](#)) that encompassed the same
662 area as our model but that was built with fewer specific local data. In these two previous
663 attempts, detritus accounted for 19.3 % and 39 % of total consumption and constituted one of
664 the main energy flow inputs as well. In the above-mentioned theory of ecosystem
665 development, this (among other elements) is strongly characteristic of the community
666 energetics of mature stages of ecosystem development. These detritus-based systems were
667 demonstrated to be more likely to support energetically feasible food chains and to be more
668 resilient than ecosystems based solely on primary production. The stabilizing effect of detritus
669 on these systems is the result of constant allochthonous imports and/or a longer residence time
670 of energy linked to internal cycling ([Moore et al., 2004](#)). Odum ([1969](#)) identified an increased
671 degree of cycling as an indicator of more mature communities which tend to internalize flows.
672 The high *FCI* value confirms the strategic position of detritus as a perennial reservoir of
673 energy in the Bay of Biscay. The overall residence time matched with the range already
674 reported for other continental shelves and seas at tropical latitudes ([Christensen and Pauly,](#)
675 [1993](#)) and was thus considered as relatively “long” by the present authors. This high value
676 was associated with ecosystem maturity, notably by selecting species with lower growth
677 potential but stronger competitive performances as succession occurs ([Odum, 1969](#)).
678 In addition to the dominance of detritivory in the food-web functioning, the *Pp/R* ratio
679 indicates most likely that the system is in a state of organic carbon balance. According to
680 Odum’s principles of ecological succession, this feature related to ecosystem bioenergetics is
681 also an excellent index of the relative maturity of the system. *CI* and *SOI* are also correlated
682 with system maturity since the internal ecological organization is expected to increase as the
683 system matures. The relatively moderate values for these outputs suggested a “web-like” food

684 chain with an intermediate level of internal flow complexity, through which energy is
685 transferred efficiently (mean *TE* far above the widely accepted value of 10 %). Comparisons
686 with similar or comparable ecosystems ([Trites et al., 1999](#); [Jimeno, 2010](#)) suggested that the
687 Bay of Biscay continental shelf is relatively immature (ascendency) and has a high resistance
688 to external perturbations (system overhead). This finding qualified the conclusion derived
689 from other holistic metrics regarding the late maturity stage of the system which seems most
690 probably “still developing”.

691 However, the apparent dominance of heterotrophic processes in this food web, mostly based
692 on regenerated production, should be viewed with caution in the light of some methodological
693 choices made during model building. The restriction of the study area to the band between the
694 30-m and 150-m isobaths, corresponding to a zone of relative homogeneity and highly
695 documented, had necessary implications in terms of herbivory to detritivory ratio. First, a
696 large variety of primary producers generally encountered inshore of the 30-m isobath, in the
697 shallowest reaches of the open coast (e.g. seagrasses, macroalgae, and microphytobenthos)
698 were thus partially ignored. Similarly, nutrients and carbon transport between shelves and the
699 open ocean were not taken into account; in the Eastern Biscay, primary production of the
700 shelf has been inferred to depend on oceanic imports ([Huthnance et al., 2009](#)).

701

702 4.2 Bottom-up forcing as a general mechanism of control

703 Cury et al. ([2003](#)) presented a general overview of the different types of energy flow in
704 marine ecosystems that can be elucidated by plotting time series of predator and prey
705 abundances. They illustrated the bottom-up control with a simplified four-level food web,
706 through which the negative impact of the physical factor on the phytoplankton cascades to the
707 zooplankton, the prey fish and the predators. For the South Bay of Biscay, analysis of
708 quantitative long-term estimates of trophic-level abundances indicates that the coastal

709 phytoplankton-mesozooplankton system was mainly bottom-up regulated ([Stenseth et al.,](#)
710 [2006](#)).

711 On the basis of ecosystem models, Libralato et al. ([2006](#)) demonstrated the generally high
712 importance of bottom-up effects in keystone species for shallow coastal ecosystems and semi-
713 enclosed marine environments such as the Chesapeake Bay, Georgia Strait, Prince Williams
714 Sound in the northern hemisphere. Indeed, the lower part of the trophic web (phyto- and
715 zooplankton) appears very important in these ecosystems, even if benthic groups also tend to
716 have a high keystone index (*KS*). This finding contrasts with the traditional and
717 widespread notion that keystone species/groups tend to be high-trophic-status species exerting
718 a high impact by means of top-down effects ([Paine, 1966](#)). Based on the keystone
719 analysis, the middle continental shelf of the Bay of Biscay can be added to the list of
720 ecosystems exhibiting this “non-straightforward” pattern of keystone species. Previous models of
721 the Bay of Biscay (“Biscaya 1970”, “Biscaya 1998” ([Ainsworth et al., 2001](#)) and “Cantabrian
722 Sea 1994” ([Sanchez and Olaso, 2004](#))) were included in the comparative study of Libralato et
723 al. (2006). It was interesting to note that planktonic compartments appeared as well in groups
724 with the highest keystone index, strengthening the conclusion that low trophic levels had a
725 major structuring role in this food web.

726 This result, in conjunction with the trophic aggregation in the Lindeman spine, strongly
727 suggests here a “donor driven” ecosystem, and when associated to direct outputs from the
728 *MTI* matrix, highlighted a marked bottom-up control of small pelagic fish by
729 mesozooplanktonic prey. At upper-trophic-levels, although there is some limited evidence for
730 top-down control of forage fish by predator populations, overall many observations suggest
731 bottom-up control of predator populations by forage fish. Bottom-up control by forage fish is
732 particularly noticeable for seabirds whose feeding strategies are usually less flexible because
733 they are physically constrained to the near-surface layer ([Cury et al., 2000](#)). When looking at

734 the intersection between top-predators and forage fish communities in the present *MTI* matrix,
735 the same conclusion of a dominant ascending regulation was emphasized.
736 The relative importance of top-down and bottom-up mechanisms may be scale-dependent.
737 Considering the large spatial scale of the study ($> 100,000 \text{ km}^2$), the explanation for this
738 strong bottom-up control may lie in part in the species-energy relationship ([Hunt and](#)
739 [McKinnell, 2006](#)). Across temperate to polar biomes, at large geographical scales, there is
740 substantial evidence for a broadly positive monotonic relationship between species richness
741 and energy availability. Global scale patterns of animal distribution most probably reflect
742 natural spatial variability in abundance of prey ([Gaston, 2000](#)). Within the large-scale ($67,000$
743 km^2) fishing areas extending from southern California to western Alaska, a large proportion
744 (87%) of the spatial variation in long-term, averaged, resident fish production was controlled
745 by bottom-up trophic interactions and this linkage extends to regional areas as small as $10,000$
746 km^2 ([Ware and Thomson, 2005](#)). The geographical location of the study area was proposed as
747 a potential factor affecting trophic ecosystem regulation. A comparative study including
748 ecosystems of both sides of the Atlantic showed that warmer, southern areas, which are more
749 species rich, exhibited positive predator-prey associations, suggesting that resources limit
750 predator abundance ([Frank et al., 2007](#)). The Bay of Biscay was considered as a southern
751 locality in the above-mentioned study.

752

753 4.3 Preliminary implications for ecosystem-based fisheries management

754 First, comparison of two models of the Eastern Bering Sea ecosystem, separated by a forty
755 year interval, revealed that fisheries tend to greatly reduce ecosystem maturity ([Trites et al.,](#)
756 [1999](#)). The paper of Christensen ([1995](#)) included several ecosystems for which the maturity
757 state could be compared before and after a disturbance, notably fishing, and the findings were
758 in all cases in agreement with disturbances leading to a reduction in maturity ([Christensen and](#)

759 [Walters, 2004](#)). The relatively late successional stage highlighted by the ecosystem's
760 attributes did not indicate that such a phenomenon was already taking effect in the Bay of
761 Biscay. Secondly, trophodynamic indicators are particularly useful in synthesizing
762 information made available by means of ecosystem models, for use in ecosystem approach to
763 fisheries and in identifying and tracking ecosystem effects of fishing ([Cury et al., 2005](#)). The
764 fairly high percentage of primary production required for harvests in this ecosystem (14.82 %)
765 justifies growing concerns for sustainability and biodiversity. But when compared with
766 previous *PPR* estimates of 24.2 % for tropical and 35.3 % for non-tropical shelves ([Pauly and](#)
767 [Christensen, 1995](#)) and the fisheries of the Cantabrian Sea using 36.6 % of the total primary
768 production ([Sanchez and Olaso, 2004](#)), the present value probably suggests a rate of
769 exploitation that is more respectful of the carrying capacity of the ecosystem and more
770 appropriate to the objective of sustainable fisheries than previously thought. Given the
771 ecosystem-based reference framework relying on %*PPR*/*TL_c* pairs, the Bay of Biscay
772 continental shelf for the period "1994-2005" was classified as an ecosystem that is still
773 "sustainably fished" with a probability around 70 % ([Tudela et al., 2005](#)). However, when
774 using the more complex *L* index, the probability of the ecosystem to be sustainably fished
775 decreased to a considerable lower value (30 %), depicting a much more pessimistic situation
776 regarding the level of system exploitation. This index was different from previous one as it
777 integrates both ecosystem properties and features of fishing activities. This inclusion accounts
778 for differences in ecosystem functioning, thus allowing for meaningful results to be derived
779 for different ecosystem types ([Pranovi and Link, 2009](#)). Adding to this, when considering
780 stock specific exploitation rates, values for small pelagics and hake, when compared to those
781 obtained for the same species in the Cantabrian Sea ([Sanchez and Olaso, 2004](#)) and to those of
782 closely related species in southern coastal upwelling ecosystems ([Coll et al., 2006](#)), pointed
783 towards a moderate exploitation of the resources over the Atlantic French continental shelf.

784 None of them exceeded 0.5, the limit reference point at which stocks should be considered as
785 overexploited ([Rochet and Trenkel, 2003](#)).

786

787 **Conclusions**

788 In the context of other models developed for this area, this was the first attempt to
789 characterize the Bay of Biscay continental shelf functioning with an Ecopath model. The three
790 fundamental characteristics of this system that emerged from the present Ecological Network
791 Analysis were that it was most likely detritus-based, relatively mature and bottom-up
792 controlled, with phytoplanktonic and zooplanktonic keystone species. These conclusions had
793 reinforced partial observations made from previous models of the area about the importance
794 of low trophic levels as drivers of the trophic ecosystem functioning. The model developed
795 here and the findings of the present study provide strong methodological support and relevant
796 scientific basis respectively for addressing additional research questions through Ecosim
797 simulations. Dynamic simulations would help in clarifying the exploitation status of the whole
798 ecosystem and in identifying fishing scenarios that allow the maintenance of forage fish
799 stocks, the conservation of top-predators and the persistence of a stable ecosystem. As a
800 second step, Ecosim would be particularly useful in defining food-web indicator(s) in the light
801 of the Marine Strategy Framework Directive. Based on the ecological properties derived from
802 the model developed here, mesozooplankton abundance, diversity and/or biomass could,
803 along with other factors and especially benthic compartments, be reliable indicators of Bay of
804 Biscay continental shelf changes.

805

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822

823 **Figure Captions**

824 Figure 1: Study area of the Bay of Biscay continental shelf and locations of the main rivers
825 flowing into it. For clarification, ICES divisions VIIIa, b, c and d are also added. Boundaries
826 of the first two are shown with a bold line.

827

828 Figure 2: PREBAL diagnostics depicting values obtained following the manual mass-balance
829 procedure of the model. *TL* increase from right to left. To offer a better visualization, all
830 primary producers' groups (29 and 30 in Table 1) and zooplankton groups (25, 26 and 27 in
831 Table 1) are summed. Abbreviations of vital rates are given in section 2.2. "Trophic
832 modelling approach". Groups depicted in black are primary producers and detritus in figure
833 2a and marine mammals and seabirds in figure 2b, c and d.

834

835 Figure 3: Trophic model of the Bay of Biscay continental shelf. Boxes are arranged using
836 trophic-level (*TL*) as y-axis and benthic/pelagic partitioning as x-axis. The size of each box is
837 proportional to the biomass it represents. Numbers refer to a code for compartments provided
838 in Table 1.

839

840 Figure 4: Biomasses, flows, transfer efficiencies are aggregated into integer trophic levels
841 (*TL*) in the form of Lindeman spine. *P* stands for primary producers, *D* for detritus and *TE* for
842 trophic efficiencies. In the present work, a modified Lindeman Spine is used to demonstrate
843 the contribution of detritus-based and grazing food chains separately.

844

845 Figure 5: Combined direct and indirect trophic impacts. Black circles indicate positive
846 impacts and white circles negative impacts.

847

848 Figure 6: Keystoneness (*KS*) for the functional groups of the Bay of Biscay continental shelf
849 food web. For each functional group, the keystone index (y-axis) is reported against
850 overall effect (x-axis). Overall effects are relative to the maximum effect measured, thus for
851 x-axis the scale is between zero and one. The keystone functional groups are those where the
852 value of the proposed index is close to or greater than zero. Numbers refer to a code for
853 compartments provided in Table 1.
854

Table 1: Input (regular) and output (bold) parameters for the ecosystem components used in the Bay of Biscay continental shelf model. *TL*: trophic level, *OI*: omnivory index, *B*: biomass (kg C·km⁻²), *P/B*: production/biomass ratio (year⁻¹), *Q/B*: consumption/biomass ratio (year⁻¹), *EE*: ecotrophic efficiency, *P/Q*: gross food conversion efficiency, *U/Q*: unassimilated consumption, landings (*Y*) and discards expressed in kg C·km⁻²·year⁻¹, Gear types used to catch each compartment: BT bottom trawler, GN gillnet, LL long-liner, PS purse seiner and PT pelagic trawler.

	<i>TL</i>	<i>OI</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>	Gear type	Discards
1. Plunge and pursuit divers seabirds	4.36	0.499	0.27	0.09	57.66	0	0.002	0.2			
2. Surface feeders seabirds	3.72	1.328	0.07	0.09	69.96	0	0.001	0.2			
3. Striped dolphins <i>Stenella coeruleoalba</i>	4.73	0.844	0.59	0.08	20.80	0	0.004	0.2			
4. Bottlenose dolphins <i>Tursiops truncatus</i>	5.09	0.250	2.18	0.08	21.67	0	0.004	0.2			
5. Common dolphins <i>Delphinus delphis</i>	4.61	0.057	1.44	0.08	26.11	0	0.003	0.2			
6. Long-finned pilot whale <i>Globicephala melas</i>	4.65	1.914	0.83	0.05	10.34	0	0.005	0.2			
7. Harbour porpoise <i>Phocoena phocoena</i>	4.69	0.069	0.06	0.08	40.69	0	0.002	0.2			
8. Piscivorous demersal fish	4.67	0.037	48.45	0.55	2.03	0.996	0.271	0.2	9.90	BT/LL/GN	
9. Piscivorous and benthivorous demersal fish	4.05	0.568	130	0.66	3.42	0.994	0.192	0.2	3.51	BT/GN	13.82
10. Suprabenthivorous demersal fish	3.49	0.114	311.20	0.55	5.30	0.995	0.104	0.2	0.15	BT	26.79
11. Benthivorous demersal fish	3.41	0.394	28.97	0.87	5.51	0.979	0.158	0.2	4.41	BT/GN	0.20
12. Mackerel <i>Scomber scombrus</i>	3.75	0.124	450	0.50	4.40	0.879	0.114	0.2	24.57	BT/PS	0.49
13. Horse mackerel <i>Trachurus trachurus</i>	3.69	0.086	614.79	0.36	4.00	0.950	0.091	0.2	20.27	BT/PS	1.01
14. Anchovy <i>Engraulis encrasicolus</i>	3.67		55.75	1.82	8.68	0.996	0.210	0.2	12.28	PT/PS	
15. Sardine <i>Sardina pilchardus</i>	3.44	0.277	184.20	0.68	8.97	0.935	0.076	0.2	9.28	PT/PS	
16. Sprat <i>Sprattus sprattus</i>	3.67		49.78	1.34	11.59	0.993	0.116	0.2			
17. Benthic cephalopods	3.71	0.321	11.84	2.75	7.00	0.950	0.393	0.2	3.80	BT	
18. Pelagic cephalopods	4.45	0.362	22.45	3.20	7.50	0.950	0.427	0.2	2.27	BT	
19. Carnivorous benthic invertebrates	3.23	0.210	141	2.24	11.20	0.993	0.200	0.2	2.91	BT	1.09
20. Necrophagous benthic invertebrates	2		16.97	1.53	15.30	0.954	0.100	0.2			
21. Sub-surface deposit feeders invertebrates	2.34	0.224	234.80	1.60	8.00	0.966	0.200	0.3			
22. Surface suspension and deposit feeders inv.	2		223.90	2.80	14	0.984	0.200	0.2			
23. Benthic meiofauna	2		100	10	50	0.970	0.200	0.4			
24. Suprabenthic invertebrates	2.14	0.189	38	20	100	0.975	0.200	0.2			
25. Macrozooplankton (≥ 2 mm)	2.57	0.512	120	10.47	38	0.950	0.276	0.4			
26. Mesozooplankton (0.2-2 mm)	2.67	0.381	638	16.44	80	0.950	0.206	0.4			
27. Microzooplankton (≤ 0.2 mm)	2.18	0.154	894	45.05	316	0.950	0.143	0.4			
28. Bacteria	2		394	115	328.57	0.811	0.350	0.5			
29. Large phytoplankton (≥ 3 μ m)	1		1046	119		0.851					

30. Small phytoplankton (< 3 μm)	1		448	151	0.752
31. Discards	1		46.67		0.788
32. Pelagic detritus	1	0.217	2800 ^a		0.972

^a Pelagic detritus biomass was entered preferentially in the model as its estimation was more precise compared to the one of benthic detritus.

Detritus imports to the system were estimated to be 454 kg C·km⁻²·year⁻¹.

Table 2: 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 divers seabirds														
2. Surface feeders seabirds														
3. Striped dolphins <i>Stenella coeruleoalba</i>														
4. Bottlenose dolphins <i>Tursiops truncatus</i>														
5. Common dolphins <i>Delphinus delphis</i>														
6. Long-finned pilot whale <i>Globicephala melas</i>														
7. Harbour porpoise <i>Phocoena phocoena</i>														
8. Piscivorous demersal fish			0.014	0.335	0.015	0.002	0.011							
9. Piscivorous and benthivorous demersal fish			0.097	0.169	0.031	0.085	0.240	0.150	0.040		0.010			
10. Suprabenthivorous demersal fish	0.100		0.345	0.081	0.004	0.006	0.216	0.180	0.055	0.005	0.030	0.017	0.010	
11. Benthivorous demersal fish			0.148	0.125	0.032		0.012	0.050	0.010		0.010			
12. Mackerel <i>Scomber scombrus</i>	0.090	0.070		0.023	0.056	0.004	0.009	0.100	0.09	0.005		0.033	0.005	
13. Horse mackerel <i>Trachurus trachurus</i>	0.140	0.070		0.132	0.050	0.039	0.276	0.220	0.135	0.005	0.020	0.030	0.005	
14. Anchovy <i>Engraulis encrasicolus</i>	0.070	0.130	0.002	0.002	0.226		0.003	0.130	0.022	0.005		0.011	0.005	
15. Sardine <i>Sardina pilchardus</i>	0.380	0.210		0.031	0.449	0.006	0.213	0.115	0.040	0.005		0.009	0.007	
16. Sprat <i>Sprattus sprattus</i>	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 invertebrates									0.030		0.120			
22. Surface suspension and deposit feeders invertebrates									0.220		0.540			
23. Benthic meiofauna														
24. Suprabenthic invertebrates									0.010	0.380			0.010	
25. Macrozooplankton (≥ 2 mm)		0.120				0.050				0.175		0.200	0.150	
26. Mesozooplankton (0.2-2 mm)										0.410		0.655	0.723	1
27. Microzooplankton (≤ 0.2 mm)												0.033	0.050	
28. Bacteria														
29. Large phytoplankton (≥ 3 μ m)														
30. Small phytoplankton (< 3 μ m)														
31. Discards	0.080	0.290							0.020		0.010			
32. Pelagic detritus														
Import			0.266			0.559	0.003							

Table 2: (continued)

	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.	25.	26.	27.	28.
1. Plunge and pursuit divers seabirds														
2. Surface feeders seabirds														
3. Striped dolphins <i>Stenella coeruleoalba</i>														
4. Bottlenose dolphins <i>Tursiops truncatus</i>														
5. Common dolphins <i>Delphinus delphis</i>														
6. Long-finned pilot whale <i>Globicephala melas</i>														
7. Harbour porpoise <i>Phocoena phocoena</i>														
8. Piscivorous demersal fish														
9. Piscivorous and benthivorous demersal fish				0.060	0.100									
10. Suprabenthivorous demersal fish					0.070	0.005								
11. Benthivorous demersal fish				0.002										
12. Mackerel <i>Scomber scombrus</i>					0.190									
13. Horse mackerel <i>Trachurus trachurus</i>					0.085									
14. Anchovy <i>Engraulis encrasicolus</i>					0.080									
15. Sardine <i>Sardina pilchardus</i>					0.057									
16. Sprat <i>Sprattus sprattus</i>					0.073									
17. Benthic cephalopods				0.040	0.035	0.004								
18. Pelagic cephalopods					0.050	0.005								
19. Carnivorous benthic invertebrates				0.210	0.050	0.051								
20. Necrophagous benthic invertebrates						0.005								
21. Sub-surface deposit feeders invertebrates				0.079		0.205								
22. Surface suspension and deposit feeders invertebrates				0.079		0.270								
23. Benthic meiofauna						0.210	0.340							
24. Suprabenthic invertebrates				0.180	0.090	0.035								
25. Macrozooplankton (≥ 2 mm)				0.350	0.090	0.060								
26. Mesozooplankton (0.2-2 mm)	0.800	1			0.030	0.110				0.050	0.200	0.050		
27. Microzooplankton (≤ 0.2 mm)	0.090									0.050	0.200	0.500	0.040	
28. Bacteria														0.130
29. Large phytoplankton (≥ 3 μ m)	0.110							0.600	0.100	0.900	0.600	0.300	0.290	
30. Small phytoplankton (< 3 μ m)														0.180
31. Discards					0.010	0.020								
32. Pelagic detritus					0.030	0.980	0.660	0.400	0.900			0.150	0.360	1
Import														

Table 3: Values taken by indices (*SOI* and *CI*) reflecting the complexity of the inner linkages within the ecosystem for the present model and previous attempts to modelize parts of the Bay of Biscay continental shelf.

	Present model	French Atlantic shelf (Jimeno, 2010)	Cantabrian Sea (Sanchez and Olaso, 2004)
<i>SOI</i>	0.212	0.164	0.268
<i>CI</i>	0.213	0.340	0.318

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