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

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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.

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1. Introduction

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

Although the importance of an ecosystem approach is widely accepted, it remains difficult to put these principles into practice (Tallis et al., 2010). In data-rich situations, multi-species/ecosystem models are valuable tools that bring coherence to a large amount of data from a variety of sources (see Plagànyi (2007) for an exhaustive review). They can be useful to provide initially a holistic understanding of the structure and functioning of a particular 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 (Plagànyi 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

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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 VIIId)

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 km^2. There has been long-

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

182   and

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

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

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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 murres *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 g·day^{-1} was calculated according to the

257 following empirical equation (Nilsson and Nilsson, 1976):

258 $Log(R_c) = -0.293 + 0.85 \times log(W)$ (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 $$FMR = 2629 \times W^{0.524} \quad (4)$$

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

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   $Log(Q/B) = 7.964 - 0.204 \times log(W_\infty) - 1.965 \times T' + 0.083 \times A + 0.532 \times h + 0.398 \times$

322   d (6)

323   where W_∞ was the asymptotic weight, *T'* was the mean environmental temperature expressed

324   as 1000/(T (°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   $Z = M + F$ (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   $M = K^{0.65} \times L_\infty^{-0.279} \times T^{0.463}$ (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 °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 < size < 2000 µm) (Whitehead, 1985). However,

364   an ontogenetic dietary shift to smaller prey represented by microzooplankton (< 200 µm) and

365   large phytoplanktonic cells (> 3 µm) was apparent in approximately one year-old pilchards

366   (individuals < 18 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 µm). The last group was composed of the horse mackerel *Trachurus trachurus*, a

371   bentho-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 $P/B = 0.525 \times W^{\wedge}(-0.304)$ (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

estimated by digital image analysis, and the corresponding organic C and N contents of paired

aliquots samples. The semi-automatic method used here allowed estimating individual bio-

volume but not the taxonomic composition of zooplankton. So, gelatinous zooplankton which

has vastly different biological parameters could not be isolated as a specific Ecopath

compartments in the present model. The full procedure was described in Alcaraz et al. (2003).

Annual Q/B ratios were taken from Sanchez and Olaso (2004) for the Cantabrian Sea. An

ecotrophic efficiency of 0.95 was assumed (Table 1 and 2).

2.4.5 Primary producers, bacteria and detritus

These compartments were characterized during 14 IFREMER surveys performed over nine

years from 1994 to 2002, in various seasons, covering the spread of the Gironde and Loire

plumes as well as a larger proportion of the Bay of Biscay continental shelf (see Labry et al.

(2002) for a description of full sampling and sample treatments). Most of the data were

comprised between 1998 and 2002 and as a consequence, matched with the period covered by

data gathered for other compartments (see the second supplementary material).

Total chlorophyll a was determined after size-fractioning filtration between nano- and

microplankton (size > 3 µm) and picoplankton (size < 3 µm) and analysed by fluometric

acidification procedure (Yentsch and Menzel, 1963). A ratio of carbon to chlorophyll a of

50:1 was taken for conversion. Phytoplankton production was determined by the in situ ^{14}C

method (Steeman-Nielsen, 1952).

A significant import of allochthonous material probably derives from large rivers flowing into

the Bay of Biscay. A value of 454 kg C·km^{-2}·year^{-1} was evaluated from Abril et al. (2002) and

the mean discharge value of these systems (www.hydro.eaufrance.fr).

Bacteria were fixed, stained and counted by epifluorescence microscopy (Porter and Feig,

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 VIIIa 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), ascendency (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 ascendency 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    $L = -PPR \times TE^{TL_c - 1} / Pp \times \ln(TE)$ (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 10^3 kg C·km^{-2}·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 respectively874,288,

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 keystoneness 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 keystoneness 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 keystoneness

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 keystoneness. 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 keystoneness, 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 ($> 100,000$ 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

33

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 keystoneness 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.

	TL	OI	B	P/B	Q/B	EE	P/Q	U/Q	Y	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 *Stenella coeruleoalba*	**4.73**	**0.844**	0.59	0.08	20.80	**0**	**0.004**	0.2			
4. Bottlenose dolphins *Tursiops truncatus*	**5.09**	**0.250**	2.18	0.08	21.67	**0**	**0.004**	0.2			
5. Common dolphins *Delphinus delphis*	**4.61**	**0.057**	1.44	0.08	26.11	**0**	**0.003**	0.2			
6. Long-finned pilot whale *Globicephala melas*	**4.65**	**1.914**	0.83	0.05	10.34	**0**	**0.005**	0.2			
7. Harbour porpoise *Phocoena phocoena*	**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 *Scomber scombrus*	**3.75**	**0.124**	450	0.50	4.40	**0.879**	**0.114**	0.2	24.57	BT/PS	0.49
13. Horse mackerel *Trachurus trachurus*	**3.69**	**0.086**	**614.79**	0.36	4.00	0.950	**0.091**	0.2	20.27	BT/PS	1.01
14. Anchovy *Engraulis encrasicolus*	**3.67**		55.75	1.82	8.68	**0.996**	**0.210**	0.2	12.28	PT/PS	
15. Sardine *Sardina pilchardus*	**3.44**	**0.277**	184.20	0.68	8.97	**0.935**	**0.076**	0.2	9.28	PT/PS	
16. Sprat *Sprattus sprattus*	**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 µm)	**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 *Stenella coeruleoalba*														
4. Bottlenose dolphins *Tursiops truncatus*														
5. Common dolphins *Delphinus delphis*														
6. Long-finned pilot whale *Globicephala melas*														
7. Harbour porpoise *Phocoena phocoena*														
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 *Scomber scombrus*	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 *Trachurus trachurus*	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 *Engraulis encrasicolus*	0.070	0.130	0.002	0.002	0.226		0.003	0.130	0.022	0.005		0.011	0.005	
15. Sardine *Sardina pilchardus*	0.380	0.210		0.031	0.449	0.006	0.213	0.115	0.040	0.005		0.009	0.007	
16. Sprat *Sprattus sprattus*	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 µm)														
30. Small phytoplankton (< 3 µm)														
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 *Stenella coeruleoalba*														
4. Bottlenose dolphins *Tursiops truncatus*														
5. Common dolphins *Delphinus delphis*														
6. Long-finned pilot whale *Globicephala melas*														
7. Harbour porpoise *Phocoena phocoena*														
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 *Scomber scombrus*					0.190									
13. Horse mackerel *Trachurus trachurus*					0.085									
14. Anchovy *Engraulis encrasicolus*					0.080									
15. Sardine *Sardina pilchardus*					0.057									
16. Sprat *Sprattus sprattus*					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 ($\geq$ 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 ($\leq$ 0.2 mm)	0.090									0.050	0.200	0.500	0.040	
28. Bacteria													0.130	
29. Large phytoplankton ($\geq$ 3 μm)	0.110							0.600	0.100	0.900	0.600	0.300	0.290	
30. Small phytoplankton (< 3 μm)													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														

40

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)
SOI	0.212	0.164	0.268
CI	0.213	0.340	0.318

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TL V

TL IV

TL III

TL II

TL I

Benthic domain   Pelagic domain

Top row

P: 20,46 — 1494 → 156808

II: 1,021 | 16,70 — 2054 — 71178 → 22834 — 0,146

III: 44,47 | 2,432 — 1521 — 10427 → 3842 — 0,170

IV: 28,92 | 0,409 — 828,8 — 2161 → 552,2 — 0,151

V: 8,027 | 0,0590 — 255,4 — 341,0

Middle flows

35314 — 252791 — 62795 — 120390 — 8520 — 21309 — 1103 — 2863 — 129,0 — 368,0

Bottom row

D: 27,03 — 2847 → 246145

II: 0,553 | 26,21 — 1350 — 72362 → 53392 — 0,217

III: 16,66 | 5,686 — 1086 — 24169 → 7898 — 0,148

IV: 21,03 | 0,841 — 598,2 — 3701 → 1314 — 0,169

V: 11,10 | 0,140 — 189,1 — 748,8

Legend

exports and catches
TST(%)
consumption | TL | predation
| | TE
biomass
flow to detritus — respiration — flow to detritus

Impacted group

																																	Impacting group

● Positive
○ Negative