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1 **Man induced change in community control in the north-western Black Sea:**  
2 **the top-down bottom-up balance**

3 Running title: **Community control in Black Sea food webs**

4  
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10  
11 **ABSTRACT**

12  
13 The present study shows how marine commercial fish food webs dramatically changed in the  
14 north-western Black Sea on both pelagic and benthic environments. Fisheries landings,  
15 diversity and equitability strongly decreased between 1965-1970 and 2001-2005. Fishes  
16 adapted their feeding behaviour to the increasingly low species diversity of the Black Sea  
17 communities. Their food web became poor and simplified following the loss of many top  
18 predator species and their trophic links. Linkage density, connectivity and Lyapunov stability  
19 proxy strongly decreased. The north-western Black Sea system switched from a complex top-  
20 down and bottom-up functioning pattern to a dominantly bottom-up functioning pattern. This  
21 study contributes to a better understanding of these transformations within the Danube –  
22 Black Sea system in the last decades. An attempt is made to relate these changes with river  
23 inputs, fisheries and coastal pollution.

24  
25 **Keywords:** marine food webs, commercial fish species, overfishing, Danube River inputs

26 **1. Introduction**

27

28 Over the last decades, there has been increasing concern about the impact of man on the seas.

29 The marine environment may be affected, both directly and indirectly, by a variety of human  
30 activities, including coastal engineering works, pollution, eutrophication, species introduction,31 fisheries and global warming (Rijnsdorp *et al.*, 1996; Boudouresque *et al.*, 2005). Fishing32 activities have been proposed as the major human disturbance in coastal areas (Jackson *et al.*,

33 2001). Increasing human populations and seafood demand as well as the development and

34 improved performance of fisheries techniques have given rise to overfishing (Aldebert, 1997).

35 Nowadays most demersal, benthic and pelagic stocks are fully exploited or overexploited

36 (Pauly *et al.*, 1998; Steneck, 1998; Papaconstantinou and Faruggio, 2000; Pauly *et al.*, 2003).

37 Some authors have predicted “the global collapse of all taxa currently fished” by 2048 (Worm

38 *et al.*, 2006). Branch (2008) and many other scientists disagree with this theory, arguing that

39 the number of fisheries that have not collapsed shows an increasing trend and some fisheries

40 should recover. These intellectual and scientific discussions are nowadays more common than

41 ever in journals. Fisheries scientists often see fish primarily as a resource and try to determine

42 the level at which it can be extracted at a sustainable rate. Marine ecologists regard fish as

43 part of an ecosystem and tend to be more conservative in how much can be taken out without

44 harming the ecosystem. The two scientists representing these opposing camps, Ray Hilborn

45 (Hilborn, 2006) and Boris Worm (Worm *et al.*, 2006), argued for a long time on the fisheries

46 and ecosystems management thematic, as each of them were defending their own expertise

47 area. In July 2009, the Journal “Science” presented the reconciliation between them (Stokstad,

48 2009). They finally discussed and started to work together and the results and conclusions of

49 their work are complementary and even more valuable. While their methods and

50 interpretations differed, the collaboration unearthed one important discovery “both sides were

51 actually right". The recovery of fish stocks depends not only on stopping overfishing but is  
52 also strongly conditioned by the state of the ecosystems. Fishing activities have a direct and  
53 indirect impact on the ecosystem, where target and non-target species establish complex  
54 relationships (Jennings and Kaiser, 1998; Jackson *et al.*, 2001). Fishing affects habitat,  
55 biodiversity, structure, functioning, stability and productivity of marine ecosystems (Jennings  
56 and Kaiser, 1998; Hughes and Petchey, 2001; Worm and Duffy, 2003). It may eliminate key  
57 species, cause trophic cascades and shifts in species dominance and change food web  
58 functioning from a top-down to a bottom-up pattern of control (Steneck, 1998; Cury *et al.*,  
59 2008). A top-down control represents the regulation of ecosystem components at low trophic  
60 levels by species at higher trophic level (control by predation). A bottom-up controlled food  
61 web is regulated by either primary producers or the input of limited nutrients through changes  
62 in the physical environment (controlled by the environment) (Cury *et al.*, 2001, 2008).  
63 Actually, an ecosystem may be driven by a balance of top-down and bottom-up control rather  
64 than by only one type of control (Cury *et al.*, 2008). Understanding how fishing activities  
65 impact complex food webs is essential for an ecosystem approach to fisheries (FAO, 2003).  
66 The Black Sea-Danube River system is probably the most eloquent example to illustrate the  
67 impact of coastal human activities on marine commercial fish food webs. Black Sea species  
68 diversity is low compared to that of other seas because of its origin and ecological  
69 particularities. Before the Pliocene the Black Sea was a freshwater lake. It became connected  
70 temporarily with the Mediterranean Sea during the Mindel-Riss and Riss-Würm interglacial  
71 periods and permanently since the end of the Würm glaciation (Lericolais *et al.*, 2003). High  
72 river freshwater inputs into the semi-enclosed Black Sea induce low salinity and high  
73 variation of all ecological parameters. Reduced vertical water circulation creates high  
74 stratification and anoxic conditions below 180 m depth (Gomoiu, 1996). High plankton  
75 production from the north-western part of the Black Sea is stimulated by the huge Danube

76 River inputs of nutrients, dissolved organic matter (DOM) and particulate organic matter  
77 (POM) along with the existence of a large continental shelf (Humborg, 1997; Cociaşu and  
78 Popa, 2004). This production constitutes an abundant food resource for pelagic and benthic-  
79 demersal fishes which were in the past very abundant in this area (FAO, 2003). Many studies  
80 have focused on the Black Sea pelagic ecosystems. Following the introduction of new  
81 gelatinous carnivores into the Black Sea, some authors have analysed their relation to the  
82 pelagic food webs (Gomoiu, 1996, 2004; Zaitsev and Mamaev, 1997; Shiganova *et al.*, 2003).  
83 Others have analysed the role of the Danube River inputs on pelagic ecosystems (Ivanov *et*  
84 *al.*, 2000; Lancelot *et al.*, 2002; Grégoire *et al.*, 2008) and the impact of overfishing on  
85 pelagic fisheries (Gucu, 2002; Oguz and Gilbert, 2007). However, no study to date has dealt  
86 with demersal and benthic fish food webs or the relationships between pelagic and benthic-  
87 demersal fish food webs.

88 In the Black Sea, as in many other seas, overfishing and environmental variability due to  
89 increasing human impact have induced the collapse of fisheries (Mee, 1992; Gomoiu, 1996,  
90 2004; Daskalov, 2003; Lotze, 2007). Hilborn (2006) was right in emphasizing that there are  
91 some places in the world where fisheries are successful (Iceland, Alaska, USA, Canada and  
92 New Zealand) as these fisheries and ecosystems are well managed. But he also says that fish  
93 are “a lot less abundant than they were in the past” with strong ecosystem impacts and that  
94 “Europe is just a basket case because of the institutional structure, the EU and the need for  
95 consensus”. “There are a lot of countries that have very little effective governance” and  
96 Hilborn says that he “can’t be that optimistic about what’s going to happen in those places”.

97 Thus our study is in agreement with some of Dr Hilborn’s ideas. The Romanian fishery in the  
98 Black Sea is a typical example of a case where problems due to the lack of fisheries and  
99 ecosystems management, along with pollution and overfishing over the last decades, led to the  
100 situation described in this present study.

101 Was the fisheries collapse simply followed by diversity losses and food web truncation or  
102 does it generate a reorganisation of food webs and controls? Our hypothesis is that both  
103 phenomena occurred in benthic-demersal and pelagic habitats. In order to demonstrate these  
104 changes, we compare past and present food webs of the commercial pelagic and benthic-  
105 demersal fish species in the north-western Black Sea. According to the state of the present  
106 ecosystems and current fisheries trends, a possible change of fish food web structure in this  
107 area over the next decades is presented. We also discuss the decrease in mean trophic level of  
108 commercial fish catches, the possible occurrence of a regime-shift, changes in food web  
109 controls and connectivity, and attempt to analyse the future of the system.

110

## 111 **2. Methods**

112

113 Fisheries statistics for the Romanian Black Sea coast (Fig. 1) are presented in this study on the  
114 basis of FAO statistics (FAO 1976, 1983, 1993, 1999, 2005). Annual mean catch values were  
115 calculated for 1965-1970, 1971-1980, 1981-1990, 1991-2000 and 2001-2005. As fish catches  
116 fluctuate widely from year to year, the comparison of the mean annual values for these  
117 periods enabled us to better exhibit fisheries trends and specific composition. The percentage  
118 of small pelagic fish species was also calculated for all these periods. The ratio between the  
119 annual mean biomass of all small fish and large predator fish species was estimated for 1965-  
120 1970 and 2001-2005 in order to show the relative importance of top-down and bottom-up  
121 effects on fish catches.

122 Shannon index ( $H'$ ) was used to measure diversity. It was calculated on mean annual values  
123 of fisheries catches according to the following formula (Frontier and Pichod-Viale, 1995):

124

$$H' = \sum_{i=1}^S (p_i * \log_2 p_i),$$



125 where  $p_i$  is the percentage of each fish species (i) in the total annual mean fisheries catches  
 126 and S the number of fish species or groups.

127 The evenness index of Pielou ( $J'$ ) quantifies how equal the community is numerically. It  
 128 represents the ratio between the diversity ( $H'$ ) and the maximum diversity that could be  
 129 obtained with the same number of species (Frontier and Pichod-Viale, 1995):

$$130 \quad J' = H'/H'_{\max},$$

131 where  $H'$  is the index of Shannon,  $H'_{\max} = \log_2 S$ .

132 Trophic level of each fish species was indicated from Stergiou and Karpouzi (2002), Bănaru  
 133 (2008) and [www.fishbase.org](http://www.fishbase.org), because it represents an important metric for commercial fishes  
 134 threatened by overexploitation (Pauly *et al.*, 1998). Mean fisheries trophic level (FTL) was  
 135 calculated according to the formula:

$$136 \quad FTL = \sum_{i=1}^S ((TL_i * p_i) / 100),$$

137 where  $TL_i$  is the trophic level of each species i and  $p_i$  is the percentage of species (i) in the  
 138 mean annual catches. Mean fisheries trophic level (FTL) would allow us to analyze the  
 139 change in trophic level between 1965 and 2005.

140 Several food web metrics were estimated in this study to provide insight into the dynamics of  
 141 biomass partitioning and production in this ecosystem (May, 1973; Pimm, 1982; Link, 2002).

142 Central among these parameters are species richness (S) (the number of species or groups)  
 143 and trophic links (L). The linkage density (L/S) (number of interactions per species or groups)  
 144 was also calculated. The connectivity (C) is a good index to estimate food web complexity  
 145 (Briand, 1983; Link, 2002) and was calculated as:

$$146 \quad C = L / [S(S-1)/2].$$

147 Complexity and system persistence or “stability” are related (Briand, 1983). The product  $S \times$   
 148  $C$ , also named Lyapunov stability proxy, was estimated in this study as it can give an  
 149 assessment of the overall mathematical “stability” for a system (Link, 2002).

150 The structure of marine commercial fish species food webs and the links between prey and  
151 predators existing between 1965 and 1970 on the Romanian coast were reconstructed on the  
152 basis of literature data (Bănărescu, 1964; Gomoiu, 1996, 2004). Older data were also used  
153 (Borcea, 1933; Cărăușu, 1952). No quantitative data on prey consumption by fishes were  
154 available at that time and this is a connection food web only (which underlines the trophic  
155 links and not their degree of importance).

156 A food web conceptual model based on past (1965-1970) commercial fishes was compared  
157 with the present one (2004-2006) established from a coupled analysis of gut contents and  
158 stable isotopes giving qualitative and quantitative relationships between fish and their prey in  
159 the same region (Bănaru, 2008; Bănaru and Harmelin-Vivien, 2009a, 2009b). This is a  
160 connection and energetic food web which shows all the trophic links but also underlines the  
161 main prey of fishes. Combined stable isotope and gut content analyses in estuarine fish diet  
162 studies offer interesting and complementary insights into fish trophic relationships. Gut  
163 contents provide information on recently consumed prey, whereas stable isotope signatures of  
164 fish muscle offer integrated information on food ingested over weeks or months (Vander  
165 Zanden *et al.*, 1997).

166 The expected future fish food web (2020-2050) was constructed on the basis of the present  
167 fisheries, food web and state of the Danube-Black Sea system. Two main human influence  
168 vectors were considered in this area: river inputs and fisheries. We based our future model on  
169 the hypothesis that in the future these vectors will maintain the same trends and impact as in  
170 the present. Danube River discharge and nutrient inputs strongly increased between 1970 and  
171 1990. Subsequently, the nutrient inputs decreased though their values are still obviously  
172 higher than in the 1960s (Cociașu and Popa, 2004). Romania and Bulgaria, situated in the  
173 north-western Black Sea, as new members of the European Union both received in 2008 their  
174 first fisheries quotas: 15 000 t of European sprat and 90 t of turbot (<http://europa.eu>).

175 According to our results, these quotas overestimate the regional fishery resources and the  
176 potential of marine ecosystems to support them. So we expect that the mean annual catches  
177 will continue to decline over the next decades and more fish species may disappear or become  
178 very rare.

179

### 180 **3. Results**

181

#### 182 3.1. Fisheries' trends between 1965 and 2005 on the Romanian coast

183

184 In 1965-1970, 29 fish species were commercially exploited on the Romanian Black Sea coast  
185 (Table 1). During that period 7 species were caught in large quantities ( $> 100 \text{ t yr}^{-1}$ ). They  
186 were pelagic fish species such as Pontic shad, European anchovy, European sprat and horse  
187 mackerel, but also high value benthic-demersal fish species such as flounder, turbot and  
188 sturgeons. By 2001-2005, many fish species had disappeared (Atlantic bonito, Atlantic  
189 mackerel, Northern bluefin tuna, swordfish, common stingray, thornback ray), others had  
190 become rare (bluefish, garpike, red mullet, flounder, common sole, piked dogfish, golden grey  
191 mullet, leaping mullet, flathead mullet, some gobies, Russian sturgeon, starry sturgeon and  
192 beluga). Only 3 species are still (2001-2005) caught in large quantities: European anchovy,  
193 European sprat and whiting ( $> 100 \text{ t yr}^{-1}$ ) (Table 1).

194 Since 2006, the Romanian Government has prohibited fishing of flounder, common sole and  
195 sturgeons, considered as endangered species. Mean annual catches of commercial fish  
196 drastically declined by 69% between 1965-1970 and 2001-2005 (Table 1, Fig. 2a).

197 Between 1965 and 1980 the only fishing technique used on the Romanian coast was crawl  
198 (stationary net fishing near the coast in shallow waters, about 10 m). Their number was high  
199 in the 1960s, decreased in the late 1970s, increased in the 1980s and strongly decreased again

200 after 1987 (Fig. 2b). Since 1980 trawling boats have started to fish in this area. They were  
201 more efficient and covered a larger surface, in both shallow and deep waters. Trawling boat  
202 catches were higher than those made by crawls (Fig. 2c). Between 1980 and 1988 total  
203 catches increased, then decreased drastically after 1990. Probably due to catches and  
204 rentability decreases, the number of crawls also stongly decreased. The analysis of CPUE  
205 changes by crawls and trawling boats gave a good image of fish catches in this area. After a  
206 peak in CPUE in the 1980s, CPUE have decreased for both crawls and trawling boats since  
207 1990 (Fig. 2c).

208 The specific composition of fish catches also dramatically changed (Fig. 3a-d). In 1965-1970  
209 European sprat, European anchovy, Pontic shad and horse mackerel dominated the pelagic  
210 catches, while in 2001-2005 one single species, the European sprat, represented 90% of the  
211 pelagic catches. Demersal and benthic catches were dominated in 1965-1970, in order of  
212 decreasing percentages, by sturgeons, flounder, turbot, whiting and gobies, while in 2001-  
213 2005 only low commercial value fish species, such as whiting and gobies, were frequent.  
214 The species diversity and evenness of commercial fishes on the Romanian Black Sea coast,  
215 estimated by the Shannon index ( $H'$ ) and by the Pielou index ( $J'$ ) respectively, decreased  
216 between 1965-1970 ( $H'_{\text{pelagic fishes}} = 1.33$  ;  $H'_{\text{benthic-demersal fishes}} = 0.46$  ;  $J'_{\text{pelagic fishes}} = 0.55$  ;  $J'_{\text{benthic-demersal fishes}} = 0.26$ ) and 2001-2005 ( $H'_{\text{pelagic fishes}} = 0.31$  ;  $H'_{\text{benthic-demersal fishes}} = 0.17$  ;  
217  $J'_{\text{pelagic fishes}} = 0.11$  ;  $J'_{\text{benthic-demersal fishes}} = 0.08$ ). Following the reduction of large predatory fish  
218 catches, the mean fisheries trophic level decreased between 1965 and 2005 from 3.21 to 2.96  
219 (Table 1).

220  
221

222 3.2. Past food web

223

224 A conceptual model of past (1965-1970) food web structure focused on commercial fish  
225 species was reconstructed on the basis of literature data (Fig. 4). This food web was related to  
226 two habitats: pelagic and benthic-demersal in which the different compartments were  
227 organised according to their trophic level. In the pelagic habitat, organic matter sources and  
228 primary producers with trophic level I were positioned in the upper part of the box and  
229 consumers were located below according to increasing trophic levels (Fig. 4).

230 River inputs of nutrients and dissolved organic matter (DOM) enhanced the development of  
231 marine phytoplankton (including species with mixotrophic and/or occasional heterotrophic  
232 nutrition) (Lavrentyev *et al.* 2004). Seawater particulate organic matter (POM) represented a  
233 complex of marine and freshwater phytoplankton, zooplankton, detritus and heterotrophic  
234 prokaryotes. This POM was consumed by large sea zooplankton and gelatinous carnivores.  
235 Sea zooplankton was consumed by small fishes which were in turn preyed on by larger  
236 predators. Arrows indicate that organic matter flows from prey to predators or from one  
237 compartment to another. As no quantitative data on fish prey existed for this period, arrows of  
238 equal thickness were used to indicate all feeding relationships mentioned in the literature  
239 without any weighting difference between them (Fig. 4).

240 A large part of the seawater POM (represented by the large grey arrow) settled on the bottom  
241 and entered the benthic-demersal food web. In the benthic-demersal habitat, the different  
242 compartments were also organised according to their trophic level, but organic matter sources  
243 and primary producers with trophic level I were located in the lower part of the benthic-  
244 demersal box, while consumers with higher trophic levels were positioned in the upper part  
245 (Fig. 4).

246 Multiple organic matter (OM) sources for food webs existed in this area: Danube POM inputs,  
247 marine phytoplankton, multicellular photosynthetic organisms (MPOs) (seaweeds and

248 seagrasses) and microphytobenthos. OM fluxes circulated via many trophic pathways into  
249 diverse pelagic, benthic and demersal food webs (Fig 4).  
250 In the pelagic food web, small pelagic fish species dominated in biomass but larger predators  
251 were also abundant at that time (Table 1). In the benthic and demersal food webs large  
252 predators, such as sturgeons and turbot, dominated in biomass, but the biomass of smaller fish  
253 species was also high (Table 1). Sedimentary POM, settled from the surface or produced by  
254 seaweeds and seagrasses (MPOs), maintained a high biomass of benthic invertebrates which  
255 sustained complex benthic and demersal fish food webs (bottom-up control) (Fig. 4). In both  
256 habitats trophic relationships between fishes and their prey were diverse and complex. The 44  
257 species or groups of species established 96 trophic links with a linkage of 2.2, a connectivity  
258 of 21%, and a Lyapunov stability proxy of 9.2. In the entire food web small fish dominated in  
259 biomass, as the ratio between the annual mean catches of small fish and large predators fish  
260 species was 1.6. However, large predatory fishes exerted an important top-down control on  
261 the other components of the food web.

262

### 263 3.3. Present food web

264

265 A similar conceptual model of the present food web structure was constructed focusing on  
266 commercial fish species (Fig. 5), on the basis of a study carried out in 2004-2006 on the  
267 Romanian Black Sea coast. Gut content and stable isotope analyses were used as a basis to  
268 describe qualitative and quantitative feeding behaviour to be compared with the previous one.  
269 Black arrows indicate the main organic matter flows from prey to predators and grey arrows  
270 secondary ones.

271 In this food web, seawater POM was more abundant than in the previous period because of  
272 the high phytoplankton development enhanced by the higher nutrient input brought by the

273 Danube River to the sea. Over time the quantity of sedimentary POM has also increased and  
274 accumulated. Water turbidity has increased, seagrasses have disappeared and seaweeds have  
275 strongly declined. POM degradation induced seasonally hypoxic and anoxic phenomena  
276 which affected mainly benthic organisms. Only a few of them such as detritivorous and  
277 carnivorous polychaetes have strongly benefited from the large quantities of POM settled on  
278 the sediment. Underlined components, represented by European sprat and detritivorous and  
279 carnivorous polychaetes, play a key role in food web structure and functioning (Fig. 5). In  
280 both habitats, there was a severe reduction of the food web complexity due to overfishing of  
281 the top predators. In pelagic habitat, only horse mackerel, which was becoming a rare species,  
282 preyed on small pelagic fish species (European sprat and European anchovy). In benthic-  
283 demersal habitat, turbot and whiting both preyed on European sprat, but only whiting was  
284 abundant and could exert significant top-down control. A strong coupling between pelagic  
285 and benthic-demersal food webs occurred as most fishes preyed on European sprat and  
286 polychaetes which were the most abundant prey. Organic matter fluxes were channelled  
287 through these two key prey types, strongly influenced by the Danube River inputs (Fig. 5).  
288 The food web relationships have nowadays become simpler and the number of species (27),  
289 trophic links (46), linkage density (1.7), connectivity (13%) and Lyapunov stability proxy  
290 (3.5) have strongly declined compared to the past model. In this food web, bottom-up control  
291 by phytoplankton was dominant and the biomass ratio between the annual mean catches of  
292 small and large fish species increased to 5.8.

293

#### 294 3.4. Possible future food web

295

296 Marine phytoplankton is likely to continue to produce a high biomass due to the still high  
297 Danube River nutrient and MOD inputs (Fig. 6). In the pelagic habitat this will sustain

298 zooplankton production and assure feeding resources for the European sprat, but also for  
299 gelatinous carnivores which may continue to develop even if they strongly decline compared  
300 to the 1980s and 1990s. Phytoplankton blooms may continue to enhance the sedimentation of  
301 large quantities of POM, inducing further degradation and anoxic phenomena in the benthic  
302 environment. This may reduce the species diversity and the biomass of seaweeds and benthic  
303 invertebrates. However, polychaete populations may continue to be favoured by this  
304 sedimentary POM and develop high biomasses (Fig. 6). The round goby will continue to prey  
305 on bivalves which may benefit from sedimentary POM, and whiting will probably continue to  
306 prey on European sprat and polychaetes. Thus, European sprat and polychaetes are likely to  
307 become even more abundant than they currently are and continue to dominate this future  
308 system. This system would probably be characterised by a few opportunistic fish species of  
309 low commercial value. In the north-western Black Sea, European anchovy, horse mackerel  
310 and red mullet represent today rare species. Flounder, common sole, starry sturgeon and  
311 beluga are considered as endangered species and fishing of them has been banned since 2006.  
312 Turbot stocks are considerably reduced by overfishing and pollution, and over 90% of the  
313 individuals studied in 2004-2006 (Bănar, 2008) were in bad condition with tumours on their  
314 tegument and numerous parasite nematodes in their stomach. Only two benthic-demersal  
315 species are still frequent in this area: round goby and whiting. Round goby is nowadays fished  
316 by local fishermen using artisanal techniques and whiting is only used to make fishfood. For  
317 all these reasons, on the Romanian coast, only the European sprat will probably be of value to  
318 commercial fishing in the future period. This species, in a reasonable fisheries management  
319 context (i.e. lower quotas than those attributed by the European Union), may hold out as it  
320 disposes of optimum feeding conditions and presents a fast growth and high reproduction rate  
321 ([www.fishbase.org](http://www.fishbase.org)).



322 In this context, the fish food web would be extremely simple and connectivity (15%) would  
323 continue to be low compared to the past food web model because most of the predatory fishes  
324 will probably have almost or completely disappeared. The food web would probably  
325 encompass 19 species or groups of species only, 26 trophic links, a linkage density of 1.4 and  
326 a Lyapunov stability proxy of 2.9. Fisheries trophic level, species diversity and equitability  
327 would probably be lower than in the present. In the future commercial fish food web, bottom-  
328 up control would be dominant.

329

#### 330 **4. Discussion**

331

332 This study presents a conceptual model of the structure and functioning of the pelagic and  
333 benthic-demersal commercial fish food web of the north-western Black Sea, the patterns of  
334 change between past (1965-1970) and present (2001-2005) and the further changes which  
335 may be expected in the future if the current trends continue. In this system there is a strong  
336 coupling between pelagic and benthic-demersal fish food webs, and to better understand  
337 ecosystem processes these two compartments should be analysed together.

338

##### 339 4.1 The Black Sea environment and the problem of a baseline

340

341 Because of its particularities the Black Sea is probably more vulnerable to human impact than  
342 most other seas (Bănar, 2008). The Black Sea presents the highest enclosure index (99.6)  
343 among all the semi-enclosed seas in Europe (de Leiva Moreno *et al.*, 2000). Its large  
344 catchment area (1 378 317 km<sup>2</sup>) compared to its surface (422 090 km<sup>2</sup>) has contributed to the  
345 increase of nutrients and primary production with the development of human activities. The  
346 “low biomass” of phytoplankton in the pristine state of the Black Sea before 1970 was

347 transformed into a “moderate biomass” state in the 1970s and to a “high biomass” state in the  
348 1980s and 1990s (Oguz and Gilbert, 2007). These changes were related to increasing human  
349 population and development in agriculture and industrialisation that resulted in the increase in  
350 nutrient loads to the Black Sea via major European rivers, particularly the Danube River  
351 (Table 2), but also the Don, Dniiper, Dniestr and Bug, which turned the Black Sea into one of  
352 the most eutrophicated seas of the world (Cociaşu *et al.*, 1996; Zaitsev and Mamaev, 1997;  
353 Berlinsky *et al.*, 2006; Yunev *et al.*, 2007). Ecosystem changes, particularly in the north-  
354 western Black Sea, include enhanced and more widespread episodes of hypoxia and anoxia,  
355 increased sedimentation and turbidity, loss of seagrasses and the decline of benthic species  
356 diversity (Zaitsev and Mamaev, 1997). Some authors have suggested a recovery of the Black  
357 Sea in the late 1990s following the reduction of phytoplankton blooms (Cociaşu and Popa,  
358 2004; Dumitrache and Abaza, 2004; Oguz and Gilbert, 2007).

359 The high natural variation of all ecological parameters in the Black Sea-Danube River system  
360 resulted in the selection of a few fish species during its geological times. We might wonder  
361 what would be the natural diversity of the fish food web in the north-western Black Sea in the  
362 absence of human influence. We do not possess a real baseline to analyse the evolution of this  
363 system’s species diversity under natural conditions. The fish ecology was first described in  
364 this region by Borcea (1933). We considered the period 1965-1970 as a “relative baseline” for  
365 comparison of the present fish food web results.

366

367 4.2. Fisheries trends in the north-western Black Sea

368

369 FAO fisheries statistics enabled us to analyse patterns of change in the Romanian fisheries  
370 between the past and the present. Fisheries landings strongly decreased between 1965 and  
371 2005 and their specific composition changed. No estimation of Shannon and equitability

372 indices for fisheries was ever calculated in this area before this study. Commercial pelagic and  
373 benthic-demersal fish diversity and equitability on the Romanian coast strongly declined  
374 between 1965-1970 and 2001-2005. In any case, these values are very low ( $H' = [0.17-1.33]$ ;  
375  $J' = [0.08-0.55]$ ) compared to the seagrass fish community in the Mediterranean Sea ( $H' =$   
376  $[3.57-4.22]$  and  $J' = [0.71-0.81]$ ) (Bell and Harmelin-Vivien, 1982).

377 The pelagic biomass production in the Black Sea is 13 times higher than demersal production.  
378 This ratio is more than 10 times higher than in all the other enclosed seas (except the Sea of  
379 Azov) (de Leiva Moreno *et al.*, 2000). This explains why the pelagic fisheries dominated in  
380 the Black Sea in the last decades (83%-93%). Benthic and demersal fish species have a high  
381 economic value but they represent a small percentage of the Romanian marine total fish  
382 landings.

383

#### 384 4.3. A decreasing mean trophic level

385

386 The mean trophic level of the species or groups of species reported in FAO global fisheries  
387 statistics declined from 3.3 in the early 1950s to less than 3.1 in 1994 (Pauly *et al.*, 1998). Our  
388 results showed a similar tendency in the Black Sea, where the mean trophic level of the  
389 commercial fish catches declined from 3.21 in 1965-1970 to 2.96 in 2001-2005. Such a  
390 decrease reflects a gradual transition in the landings from the long lived, high trophic level,  
391 piscivorous fishes toward short-lived, low trophic level, planktivorous fishes (Fig. 7).

392 Zaitsev (1992) showed the same trend in the Black Sea Ukrainian fisheries between 1980 and  
393 1990 when species number reduced and only small pelagic fish species catches were high.

394 Tatara (1991) shows that both a decline in mean trophic level and a linked increase in  
395 planktivores are responses to the eutrophication of the Seto Inland Sea by nutrient run-off.

396 Tang (1993) reported similar findings for the Yellow Sea where, during the 1950s and 1960s,

397 benthic and demersal species dominated the catches but were gradually replaced by pelagic  
398 planktivorous species such as Pacific herring and mackerel in the 1970s. Some of these effects  
399 can be attributed to “fishing down marine food webs” (Pauly *et al.*, 1998), but in the Black  
400 Sea demersal, benthic and pelagic migratory predators seriously declined in the 1970s and  
401 early 1980 (Zaitsev and Mamaev, 1997) before the rise in small pelagic biomass began in the  
402 1980s. The earlier disappearance of predators in the 1980s suggests that subsequent changes  
403 were largely due to the eutrophication processes. Benthic-demersal production has declined  
404 drastically since the 1960s, largely due to hypoxia in the bottom water layer, while anchovy  
405 populations continue to rise. This increase in biomass of small pelagic fish species despite an  
406 increase in harvesting rate of the same species also supports a bottom-up effect of increased  
407 nutrient inputs (de Leiva Moreno *et al.*, 2000).

408 Many factors interact in the semi-enclosed Black Sea system and are responsible for the  
409 present state of the fisheries. This is also the case of fisheries landings in the Baltic Sea, the  
410 North Sea and the Adriatic Sea, that are nowadays lower than in the past and dominated by  
411 small pelagic fish species of low commercial value (Rijnsdorp *et al.*, 1996; McIntyre, 1999;  
412 Harvey *et al.*, 2003). In the North Sea, Rijnsdorp *et al.* (1996) compare past and present  
413 changes in abundance of fish species and show a reduction in landings, fish sizes, species  
414 diversity and shifts in the community structure.

415

#### 416 4.4. Evidence for a regime-shift

417

418 In the Black Sea the decline of large predators because of overfishing gave rise to trophic  
419 cascades and regime-shifts (Gucu, 2002). Cury and Shannon (2004) consider the regime-shift  
420 to be a sudden shift in structure and functioning of a marine ecosystem, affecting several  
421 living components and resulting in an alternate state. The Black Sea pelagic ecosystem

422 appears to present one of the most striking examples of “ecological regime-shift” events  
423 reported so far for large pelagic marine ecosystems (Oguz and Gilbert, 2007). In the 1980s  
424 and 1990s the classical “phytoplankton-zooplankton-pelagic fish” food chain shifted to one  
425 dominated by opportunistic species and gelatinous carnivores, which are a trophic dead-end  
426 (Oguz and Gilbert, 2007). Some authors argued that these events were related to the North  
427 Atlantic Oscillation (NAO) and the East Atlantic-West Russia (EAWR) (Bilio and Niermann,  
428 2004; Oguz and Gilbert, 2007).

429 Many studies have focused on trophic interaction between gelatinous carnivores and small  
430 pelagic fish species. But what happens to the rest of the food web, particularly demersal and  
431 benthic fishes and how will these events affect the entire food web? Regime-shift in the  
432 benthic and demersal species dominance in the north-western Black Sea is more difficult to  
433 assess because of the lack of long term data on the species diversity and biomass of these  
434 communities. Comparing past (1965-1970) and present (2004-2006) food webs of commercial  
435 fish species offers a basis for analyzing changes in their feeding behaviour and the subsequent  
436 change in food web structure and functioning. Most fish species have modified their diet  
437 compared to past studies from the same area (Bănaru, 2008). They have adapted their feeding  
438 behaviour to the increasingly low species diversity of the Black Sea communities. At present,  
439 the importance of polychaetes and European sprat in fish diets has increased compared to  
440 forty years ago. This may be explained by the dominance of polychaetes in benthic  
441 biocenoses and European sprat in the pelagic compartment (Friedrich *et al.*, 2002; Bănaru,  
442 2008). These two prey types are among the organisms which benefit the most from the  
443 Danube inputs that contribute along with fisheries to inducing a drastic decrease in  
444 complexity of the food webs (Bănaru *et al.*, 2007; Bănaru, 2008).

445 Analyzing the entire food web we might wonder whether we are really dealing with a  
446 “regime-shift” or whether this system has gradually become poorer and more simplified

447 following the loss of species and their trophic links? As it presents most of the consequences  
448 of regime-shifts as described by Cury and Shannon (2004), it could be considered as a regime  
449 shift.

450

451 4.5. The change in the top-down bottom-up balance

452

453 Our results showed that in the Black Sea, as all over the world (Pauly *et al.*, 1998; Cury *et al.*,  
454 2001), overfishing has induced shifts in ecosystems from a complex top-down and bottom-up  
455 functioning system to a dominant bottom-up functioning pattern (Fig. 7). The biomass ratio  
456 between small fishes and large predator species catches was 3.6 higher in 2001-2005 than in  
457 1965-1970 in the north-western Black Sea. This underlines the effects of the increase in  
458 bottom-up control in this system. However, an ecosystem is not driven entirely by only one  
459 type of control, but by a subtle and changing combination of control types that might depend  
460 on its state, diversity and integrity (Cury *et al.*, 2001).

461 Oguz and Gilbert (2007) described a system controlled top-down by fisheries and gelatinous  
462 carnivores in the western-central Black Sea between 1970s and 1990s. As indicated in Fig. 8,  
463 in the present, on the Romanian coast, the two top-down control forcing factors: overfishing  
464 and gelatinous carnivores have strongly decreased and the system is mainly dominated by the  
465 bottom-up control. If our hypothesis is correct this trend would probably continue over the  
466 next decades. Overfishing of large predator fish species has induced their loss and the  
467 reduction of predation on small fish. The collapse of almost all fisheries has strongly reduced  
468 the fishing effort but overfishing may persist because the European quotas for Romania and  
469 Bulgaria are overestimated.

470

471 4.6. The connectivity decline: towards stability or instability?

472

473 Over the last decades, fishery yields have continually decreased in the north-western Black  
474 Sea with no recovery. This influences fish food webs and, as shown here, species number,  
475 trophic links, linkage density, connectivity and Lyapunov stability proxy which strongly  
476 declined between 1965-1970 and 2001-2005.

477 There is disagreement on the relation between the persistence (stability) and effects caused by  
478 losing either a low or high trophic level species from a trophic web (Ives *et al.* 1999). The  
479 north-western Black Sea food web lost most of its top predators and Duffy (2003) argues that  
480 the loss of large consumers has a stronger impact on ecosystem functioning than the loss of  
481 primary producers because of their relatively low diversity, low functional redundancy and  
482 high interaction strengths. Many ecological studies have dealt with the relation between  
483 complexity (connectivity) and stability (persistence) (Briand, 1983). May (1973) argues that  
484 an increase in the number of links in a food web decreases the ecosystem's stability.

485 However, there is also disagreement whether higher complexity increases, decreases, or has  
486 alternating effects on overall stability (Link, 2002).

487 The food web analyzed presented in 1965-1970 a connectivity of 21%, a value higher than in  
488 the estuary (9.7%) analyzed by Hall and Raffaelli (1991) and lower than on the marine  
489 continental shelf (48.2%) analyzed by Link (2002). The  $C \times S$  Lyapunov stability proxy of the  
490 Romanian marine food web presented a value (9.2) similar to that of the cited estuary (9) and  
491 much lower than the continental shelf (39.1). The number of species and the connectivity of  
492 the Black Sea system in 1965-1970 compared to other systems suggest that, like the marine  
493 continental shelf studied by Link (2002), it should be considered as an "unstable" system.

494 After a period of over-exploitation, in 2001-2005 the connectivity of the Black Sea food web  
495 has decreased. This new value, similar to the results of Link (2002) after a period of over-  
496 exploitation, and compared to the food web connectivity in other systems, should be qualified

497 as “stable”. Link (2002) argues that the limits of “stable” and “instable” were mathematically  
498 estimated for terrestrial or freshwater ecosystems which are very different from marine  
499 ecosystems. In fact, in marine ecosystems, species present mostly a generalist and opportunist  
500 feeding behaviour pattern and some characteristics of these systems such as the “cultivation-  
501 depensation effects” strongly influence its functioning (Walters and Kitchell, 2001). Finally,  
502 we cannot say whether the changing Black Sea commercial fish food web is in the present  
503 becoming “stable” or not.

504

505 4.7. The future: recovery, stability or growth of the present trends?

506

507 The Danube River plays an essential role in the functioning and future of the north-western  
508 Black Sea, being at the same time a natural enrichment factor for this marine area and a major  
509 human influence vector (Bănanu *et al.*, 2007; Bănanu, 2008). In the north-western  
510 Mediterranean Sea (Gulf of Lions) the Rhone River inputs increase the primary production of  
511 the oligotrophic waters and increase fisheries landings (Darnaude *et al.*, 2004; Ferraton *et al.*,  
512 2007). For a long time this was also the case for the Black Sea - Danube River system.  
513 However, the high degree of enclosure of this sea has resulted in an accumulation of primary  
514 production and eutrophication (de Leiva Moreno *et al.*, 2000). Excessively high Danube River  
515 inputs finally induce hypoxia and the decline of fishery landings. It is thus difficult to separate  
516 the respective roles Danube River inputs and overfishing play in the decline of fisheries and  
517 changes in fish food webs.

518 The reduction of nutrient inputs from the Danube River in the late 1990s, together with the  
519 reduction of *Mnemiopsis leidyi* by *Beroe ovata*, induced a decline in gelatinous stocks and an  
520 increase in small fish landings (Gucu, 2002; Dumitrache and Abaza, 2004; Oguz and Gilbert,  
521 2007). However, the increase in pelagic fish landings is low compared to the decline of



522 fisheries recorded over the last decades and the recovery effect of the food webs is far from  
523 certain, as suggested by our results. A partial recovery of the Black Sea - Danube River  
524 system should be possible if nutrient inputs into the Black Sea and all marine fisheries are  
525 strongly reduced over the coming decades. However, according to the hypothesis used in this  
526 study, Danube inputs and fisheries will maintain the same trends and there will be no recovery  
527 or stability but only an increase of the present trends.

528 This study has demonstrated that the Black Sea, considered as a “poor pocket of the  
529 Mediterranean Sea”, also presents reduced trophic relationships. The success of the fisheries  
530 management in this area in the future will depend on research focused on the mechanisms  
531 underlying ecosystem dynamics and fisheries interactions. In the present environmental and  
532 economic context in Europe, the proper understanding of these aspects is essential for  
533 ecosystem-based fisheries management (Cury *et al.*, 2008).

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547 **References**

548

549 Aldebert, Y., 1997. Demersal resources of the Gulf of Lions (NW Mediterranean): impact of  
550 exploitation on fish diversity. *Vie Milieu* 47(4), 275-284.

551 Bănar, D., Harmelin-Vivien, M., Gomoiu, M.-T., Onciu, T.-M., 2007. Influence of the  
552 Danube River inputs on C and N stable isotope ratios of the Romanian coastal waters  
553 and sediment (Black Sea). *Marine Pollution Bulletin* 54, 1385-1394.

554 Bănar, D., 2008. Influence des apports du Danube sur les réseaux trophiques des poissons de  
555 la côte roumaine (mer Noire). Thèse de Doctorat (PhD), Université de la Méditerranée  
556 309 pp. (in French).

557 Bănar, D., Harmelin-Vivien, M., 2009a. Trophic links and riverine effects on food webs of  
558 pelagic fish of the north-western Black Sea. *Marine and Freshwater Research* 60, 529-  
559 540.

560 Bănar, D., Harmelin-Vivien, M., 2009b. Feeding behaviour of Black Sea bottom fishes: Did  
561 it change over time? *Acta Oecologica* 35(6), 769-777.

562 Bănărescu, P., 1964. Fauna Republicii Populare Romîne. Pisces - Osteichthyes (pesti ganoizi  
563 si ososi). Eds. Academiei RPR, Bucuresti, Vol. XIII., 962 pp. (in Romanian).

564 Bell, J.D., Harmelin-Vivien, M.L., 1982. Fish fauna of French Mediterranean *Posidonia*  
565 *oceanica* seagrass meadows. 1. Community structure. *Thethys* 10,337-347.

566 Berlinsky, N., Bogatova, Y., Garkavaya, G., 2006. Estuary of the Danube. Handbook of  
567 Environmental Chemistry 5, 233-264.

568 Bilio, M., Niermann, U., 2004. Is the comb jelly really to blame for it all? *Mnemiopsis leidyi*  
569 and the ecological concerns about the Caspian Sea. *Marine Ecology Progress Series*  
570 269, 173-183.

- 571 Borcea, I., 1933. Nouvelles observations sur les migrations et sur la période de ponte des  
572 espèces de poissons migrateurs de la mer Noire. Annales Scientifique de l'Université de  
573 Jassy 17(3-4), 503-564 (in French).
- 574 Boudouresque, C.F., Ruitton, S., Verlaque, M., 2005. Large-scale disturbances, regime shifts  
575 and recovery in littoral systems subject to biological invasions. In: Velikova, V. Chipev,  
576 N. eds. Unesco-Roste / BAS Workshop en regime shifts, Varna, Bulgaria, pp. 85-101.
- 577 Branch, T.A., 2008. Not all fisheries will be collapsed in 2048. *Marine Policy* 32, 38-39.
- 578 Briand, F., 1983. Environmental control of food web structure. *Ecology* 64, 253-263.
- 579 Cărăușu, S., 1952. *Tratat de ihtiologie*. Eds. Acad. RPR Bucuresti, 800 pp. (in Romanian).
- 580 Cociașu, A., Dorogan, L., Humborg, C., Popa, L., 1996. Long term ecological changes in  
581 Romanian coastal waters of the Black Sea. *Marine Pollution Bulletin* 23(1), 32-38.
- 582 Cociașu, A., Popa, L., 2004. Significant changes in Danube nutrient loads and their impact on  
583 the Romanian Black Sea coastal waters. *Recherches marines, INCDM, Constanta* 35,  
584 25-37.
- 585 Cury, P., Shannon, L., Shin, Y.-J., 2001. The functioning of marine ecosystems. Reykjavik  
586 Conference on Responsible Fisheries in the Marine Ecosystems, Reykjavik, Iceland, 1-4  
587 October 2001, 22 pp.
- 588 Cury, P., Shannon, L., 2004. Regime shifts in upwelling ecosystems: observed changes and  
589 possible mechanisms in the northern and southern Benguela. *Progress in Oceanography*  
590 60, 223-243.
- 591 Cury, P.M., Shin, Y.J., Planque, B., Durant, J.M., Fromentin, J.M., Kramer-Schadt, S.,  
592 Stenseth, N.C., Travers, M., Grimm, V., 2008. Ecosystem oceanography for global  
593 change in fisheries. *Trends in Ecology and Evolution* 23(6), 338-346.

- 594 Darnaude, A.M., Salen-Picard, C., Polunin, N.V.C., Harmelin-Vivien, M.L., 2004.  
595 Trophodynamic linkage between river run-off and coastal fishery yield elucidated by  
596 stable isotope data in the Gulf of Lions (NW Mediterranean). *Oecologia* 138, 325-332.
- 597 Daskalov, G.M., 2003. Long-term changes in fish abundance and environmental indices in the  
598 Black Sea. *Marine Ecology Progress Series* 255, 259-270.
- 599 de Leiva Moreno, J.I., Agostini, N.V., Caddy, J.F., Carocci, F., 2000. Is the pelagic-demersal  
600 ratio from fishery landings a useful proxy for nutrient availability? A preliminary data  
601 exploration for the semi-enclosed seas around Europe. *ICES Journal of Marine Science*  
602 57, 1091-1102.
- 603 Duffy, J.E., 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*  
604 6, 680-687.
- 605 Dumitrache, C., Abaza, V., 2004. The present state of benthic communities in the Romanian  
606 coastal waters. *Recherches marines, INCDM, Constanta* 35, 61-75.
- 607 FAO, 1976. Statistical bulletin no.1: nominal catches 1964-1974. General Fisheries Council  
608 for the Mediterranean, 115 pp.
- 609 FAO, 1983. Statistical bulletin no.4: nominal catches 1970-1980. General Fisheries Council  
610 for the Mediterranean, 118 pp.
- 611 FAO, 1993. Statistical bulletin no.9: nominal catches 1964-1974. General Fisheries Council  
612 for the Mediterranean, 237 pp.
- 613 FAO, 1999. Fishery statistics. Capture production. Yearbook 88/1, 752 pp.
- 614 FAO, 2003. The ecosystem approach to fisheries. FAO Technical Guidelines for Responsible  
615 Fisheries 4(2), 1-112.
- 616 FAO, 2005. Fishery statistics. Capture production. Yearbook 100/1, 539 pp.

- 617 Ferraton, F., Harmelin-Vivien, M., Mellon-Duval, C., Souplet, A., 2007. Spatio-temporal  
618 variation in diet may affect condition and abundance of juvenile European hake in the  
619 Gulf of Lions (NW Mediterranean). *Marine Ecology Progress Series* 337, 197-208.
- 620 Friedrich, J., Dinkel, C., Friedl, G., Pimenov, N., Wijsman, J., Gomoiu, M.-T., Cociașu, A.,  
621 Popa, L., Wehrli, B., 2002. Benthic nutrient cycling and diagenetic pathways in the  
622 north-western Black Sea. *Estuarine, Coastal and Shelf Science* 54, 369-383.
- 623 Frontier, S., Pichod-Viale, D., 1995. *Ecosystèmes - structure fonctionnement évolution*.  
624 Collection d'écologie 21, Eds. Masson, 447 pp.
- 625 Gomoiu, M.-T., 1996. Some remarks concerning actual state of the Danube River – Black Sea  
626 ecological system. *Geo-Eco-Marina, Constanta* 1, 31-33.
- 627 Gomoiu, M.-T., 2004. Introduction to Topic 2.1 part Black Sea: Ecological changes in the  
628 Black Sea. In: *The Southern and Eastern Mediterranean Sea and the Black Sea: new  
629 challenges for marine biodiversity research and monitoring: summary of discussions*.  
630 Magni, P. et al. (Eds.) Electronic conference, 6-24 September 2004, pp. 22-27.
- 631 Grégoire, M., Raick, C., Soetaert, K., 2008. Numerical modeling of the central Black Sea  
632 ecosystem functioning during the eutrophication phase. *Progress in Oceanography* 76,  
633 286-333.
- 634 Gucu, A.C., 2002. Can overfishing be responsible for the successful establishment of  
635 *Mnemiopsis leidyi* in the Black Sea? *Estuarine, Coastal and Shelf Science* 54, 439-451.
- 636 Hall, S.J., Raffaelli, D.G., 1991. Food-web patterns: lessons from a species-rich web. *Journal*  
637 *of Animal Ecology* 60, 823-842.
- 638 Harvey, C.J., Cox, S.P., Essington, T.E., Hansson, S., Kitchell, J.F., 2003. An ecosystem  
639 model of food web and fisheries interactions in the Baltic Sea. *ICES Journal of Marine*  
640 *Science* 60, 939-950.
- 641 Hilborn, R., 2006. Reinterpreting the Fisheries Crisis. Public lecture, May 9, 2006.

- 642 Hughes, J.B., Petchey, O.L., 2001. Merging perspectives on biodiversity and ecosystem  
643 functioning. *Trends in Ecology and Evolution* 16(5), 222-223.
- 644 Humborg, C., 1997. Primary productivity regime and nutrient removal in the Danube Estuary.  
645 *Estuarine, Coastal and Shelf Science* 45, 579-589.
- 646 Ivanov, V.A., Lyubartseva, S.P., Mikhailova, N., Shapiro, N.B., 2000. Mathematical  
647 modelling of marine systems - Modelling of the ecosystem of the Black-Sea shelf zone  
648 near the estuary of the Danube. *Physical Oceanography* 1(6), 509-524.
- 649 Ives, A.R., Gross, K., Klug J.L., 1999. Stability and variability in competitive communities.  
650 *Science* 286, 542-544.
- 651 Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J.,  
652 Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange,  
653 C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J.,  
654 Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal  
655 ecosystems. *Science* 293, 629-638.
- 656 Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. *Advances in*  
657 *Marine Biology* 34, 201-351.
- 658 Lancelot, C., Martin, J.-M., Panin, N., Zaitsev, Y., 2002. The North-Western Black Sea: A  
659 pilot site to understand the complex interactions between human activities and the  
660 coastal environment. *Coastal and Shelf Science* 54, 279-284.
- 661 Lavrentyev, P.J., McCarthy, M.J., Klarer, D.M., Jochem, F., Gardner, W.S., 2004. Estuarine  
662 Microbial Food Web Patterns in a Lake Erie Coastal Wetland. *Microbial Ecology* 48,  
663 567-577.
- 664 Lericolais, G., Popescu, I., Panin, N., Guichard, F., Popescu, S., Manolakakis, L., 2003.  
665 Evidence from recent oceanographic surveys of a last rapid sea level rise of the Black  
666 Sea. Human records of recent geological evolution in the Mediterranean basin –

- 667 historical and archaeological evidence. CIESM publ., Monaco, CIESM Workshop  
668 monographs 24, 109-117.
- 669 Link, J., 2002. Does food web theory work for marine ecosystems? Marine Ecology Progress  
670 Series 230, 1-9.
- 671 Lotze, H.K. 2007. Rise and fall of fishing and marine resource use in the Wadden Sea,  
672 southern North Sea. Fisheries Research 87, 208–218.
- 673 May, R.M., 1973. Stability and complexity in model ecosystems. Princetown University  
674 Press, Princetown.
- 675 McIntyre, A.D., 1999. Introductory remarks on threats to commercial fish stocks. Acta  
676 Adriatica 40(Suppl.), 35-38.
- 677 Mee, L.D., 1992. The Black Sea in crisis: a need for concerted international action. Ambio 21,  
678 278-286.
- 679 Oguz, T., Gilbert, D., 2007. Abrupt transitions of the top-down controlled Black Sea pelagic  
680 ecosystem during 1960-2000: Evidence for regime-shifts under strong fishery  
681 exploitation and nutrient enrichment modulated by climate-induced variations. Deep-  
682 Sea Research I 54, 220-242.
- 683 Papaconstantinou, C., Faruggio, H., 2000. Fisheries in the Mediterranean. Mediterranean  
684 Marine Science 1(1), 5-18.
- 685 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F.J., 1998. Fishing down marine  
686 food webs. Science 279, 860-863.
- 687 Pauly, D., Alder, J., Bennett, E., Christensen, V., Tyedmers, P., Watson, R., 2003. The future  
688 for fisheries. Science 302, 1359-1361.
- 689 Pimm, S.L., 1982. Food webs. Chapman and Hall, London.

- 690 Rijnsdorp, A.D., Van Leeuwen, P.I., Daan, N., Heessen, H.J.L., 1996. Changes in abundance  
691 of demersal fish species in the North Sea between 1906-1909 and 1990-1995. ICES-  
692 Journal of marine Science 53, 1054-1062.
- 693 Shiganova, T.A., Musaeva, E.I., Bulgakova, Yu.V., Mirzoyan, Z.A., Martynyuk, M.L., 2003.  
694 Invaders Ctenophores *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* (Mayer, 1912)  
695 and their influence on the pelagic ecosystem of north eastern Black Sea. Oceanology  
696 30(2), 180-190 (English Translation).
- 697 Steneck, R.S., 1998. Human influences on coastal ecosystems: does overfishing create trophic  
698 cascade? Trends in Ecology and Evolution 13(11), 429-430.
- 699 Stergiou, K.I., Karpouzi, V.S., 2002. Feeding habits and trophic levels of Mediterranean fish.  
700 Reviews in Fish Biology and Fisheries 11, 217-254.
- 701 Stokstad, E., 2009. Détente in the Fisheries War. Science 324, 170-171.
- 702 Tang, Q., 1993. Effects of long term physical and biological perturbations on the  
703 contemporary biomass yields of the Yellow Sea ecosystem. In: Large Marine  
704 Ecosystems, Eds. Sherman, K. Alexander, L.B. and Gold, B.D. AAAS Press,  
705 Washington DC.
- 706 Tatara, K., 1991. Utilisation of the biological production in eutrophicated sea areas by  
707 commercial fisheries, and the environmental quality standard for fishing ground.  
708 International Conference on the Environmental Management of Enclosed Seas, Kobe,  
709 Japan, July-August 1990.
- 710 Vander Zanden, M.J., Cabana, G., Rasmussen, J.B., 1997. Comparing trophic position of  
711 freshwater fish calculated using stable nitrogen isotope ratios ( $\delta^{15}\text{N}$ ) and literature  
712 dietary data. Canadian Journal of Fisheries and Aquatic Sciences 54, 1142-1158.
- 713 Walters, C.J., Kitchell, J.F., 2001. Cultivation/depensation effects on juvenile survival and  
714 recruitment. Canadian Journal of Fisheries and Aquatic Sciences 58, 39-50.



- 715 Worm, B., Duffy, J.E., 2003. Biodiversity, productivity and stability in real food webs. Trends  
716 in Ecology and Evolution 18(12), 628-632.
- 717 Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., et al., 2006.  
718 Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787-790.
- 719 Zaitsev, Y.P., 1992. Recent changes in the trophic structure of the Black Sea. Fisheries  
720 Oceanography 1(2), 180-189.
- 721 Zaitsev, Yu., Mamaev, V., 1997. Marine Biological Diversity in the Black Sea: A study of  
722 Change and Decline. GEF Black Sea Environmental Programme, United Nations  
723 Publication, 208 pp.
- 724 Yunev, O.A., Carstensen, J., Moncheva, S., Khaliulin, A., Ertbjerg, G., Nixon, S., 2007.  
725 Nutrient and phytoplankton trends on the western Black Sea shelf in response to cultural  
726 eutrophication and climate changes. Estuarine, Coastal and Shelf Science 74, 63-76.
- 727 <http://europa.eu>
- 728 [www.fishbase.org](http://www.fishbase.org)

729 **Fig. 1.** Map of the area studied on the Romanian Black Sea coast, seawards of the Danube River.

730

731 **Fig. 2 a.** Total Romanian Black Sea fish catches (tonnes  $y^{-1}$ ) reported by FAO between 1965 and 2005 and  
732 detailed catches by crawls and by trawling boats (data from G. Radu, pers. comm.). **b.** Number of Romanian  
733 Black Sea crawls and trawling boats between 1965 and 2005 (data from G. Radu, pers. comm.). **c.** CPUE  
734 calculated for the Romanian Black Sea crawls and trawling boats between 1965 and 2005.

735

736 **Fig. 3 a-d.** Percentages of species in pelagic and benthic-demersal fisheries catches on the Romanian Black Sea  
737 coast; comparison between 1965-1970 and 2001-2005.  $H'$  = diversity index of Shannon;  $J'$  = evenness index of  
738 Pielou.

739

740 **Fig. 4.** Food web of the main commercial pelagic and benthic-demersal fish species on the Romanian coast in the  
741 north-western Black Sea in the past (1965-1970), reconstructed on the basis of literature data (Borcea 1933;  
742 Cărăușu, 1952; Bănărescu 1964; Gomoiu 1996, 2004) TL = trophic level, DOM = dissolved organic matter,  
743 POM = particulate organic matter. Fish species are represented in bold characters. Grey arrows indicate all  
744 trophic links (organic matter flows from prey to predators). The large grey arrow represents the transfer of  
745 sedimentary POM from seawater to sediment. On the left side the arrows indicate the top-down control by the  
746 large predatory fishes over the lower trophic level prey.

747

748 **Fig. 5.** Food web of the main commercial pelagic and benthic-demersal fish species on the Romanian coast in the  
749 north-western Black Sea in the present (2004-2006) reconstructed from gut content and stable isotope ratio  
750 analyses. TL = trophic level, DOM = dissolved organic matter, POM = particulate organic matter. Fish species  
751 are represented in bold characters. Black arrows indicate principal organic matter flows from prey to predators  
752 and grey arrows the secondary ones. The large grey arrow represents the transfer of sedimentary POM from  
753 seawater to sediment. On the left side the arrows indicate bottom-up control by the primary producers over  
754 higher trophic level consumers. Underlined components have become very abundant and play a key role in the  
755 food web. Seagrasses and most of the top predator fish species present in 1965-1970 have disappeared.

756

757 **Fig. 6.** Future food web of the main commercial pelagic and benthic-demersal fish species on the Romanian coast  
758 in the north-western Black Sea. TL = trophic level, DOM = dissolved organic matter, POM = particulate organic

759 matter. Fish species are represented in bold characters. Black arrows indicate principal organic matter flows from  
760 prey to predators and grey arrows the secondary ones. The large grey arrow represents the transfer of  
761 sedimentary POM from seawater to sediment. On the left side the arrows indicate bottom-up control by the  
762 primary producers over higher trophic level consumers. Underlined components have become very abundant and  
763 play a key role in the food web. Most of the fish species have disappeared.

764

765 **Fig. 7.** Past, present and future effects of fishing and human induced change on the environmental parameters in  
766 the Black Sea-Danube River commercial fish food web and fisheries.

767

768 **Fig. 8.** Conceptual diagram of the north-western Black Sea coupled pelagic and benthic-demersal food web  
769 structure representing major controls, processes and trophic interactions over the coming decades. The forcing  
770 variables are shown by underlined characters, the response variables are represented by boxes in grey colour and  
771 the processes which link responses and forcing variables by boxes with dotted lines. Large arrows represent  
772 bottom-up control, thin arrows top-down control and dotted arrows indicate controls that have strongly declined  
773 (adapted from Oguz and Gilbert 2007).

774 **Table 1**

775 List of common and scientific names of commercial fish species from the Romanian Black Sea coast and their  
 776 calculated mean annual catches (in tonnes) between 1965 and 2005 according to FAO data. For mullets, gobies,  
 777 sturgeons and rays FAO data were available only for groups and not for individual species. The list presents first  
 778 the pelagic and then the benthic-demersal fish species in alphabetic order of their scientific names. spp = species,  
 779 TL = trophic level data from \*Stergiou and Karpouzi 2002, \*\*Bănaru 2008, \*\*\*www.fishbase.org.

780

Common name	Scientific name	TL	1965- 1970	1971- 1980	1981- 1990	1991- 2000	2001- 2005
<b>Pelagic fish species</b>							
Pontic shad	<i>Alosa immaculata</i> Bennett, 1835	4.1***	939.3	1138.3	104.7	10.0	16.2
Big-scale sand smelt	<i>Atherina boyeri</i> Risso, 1810	3.3*	21.3	30.1	19.6	14.1	13.0
Garpike	<i>Belone belone</i> (Linnaeus, 1761)	4.2***	0.1	0.0	0.2	0.2	0.0
European anchovy	<i>Engraulis encrasicolus</i> (Linnaeus, 1758)	3**	1942.7	2894.1	3091.0	157.9	163.9
Bluefish	<i>Pomatomus saltatrix</i> (Linnaeus, 1766)	4.5***	10.8	2.0	1.5	2.1	3.9
Atlantic bonito	<i>Sarda sarda</i> (Bloch, 1793)	4.5***	3.7	0.0	0.0	0.0	0.0
Atlantic mackerel	<i>Scomber scombrus</i> Linnaeus, 1758	4***	16.0	0.0	0.0	0.2	0.0
European sprat	<i>Sprattus sprattus sprattus</i> (Linnaeus, 1758)	2.8**	2963.0	1904.6	5700.1	2178.8	1999.1
Northern bluefin tuna	<i>Thunnus thynnus</i> (Linnaeus, 1758)	4.3*	< 1	0.0	0.0	0.0	0.0
Horse mackerel	<i>Trachurus mediterraneus</i> (Steindachner, 1868)	3.4**	1829.5	1082.8	1052.8	19.8	12.2
Swordfish	<i>Xiphias gladius</i> Linnaeus, 1758	4.5*	< 1	0.0	0.0	0.0	0.0
<b>Benthic-demersal fish species</b>							
Whiting	<i>Merlangius merlangus</i> (Linnaeus, 1758)	3.8**	60.5	804.2	1606.8	477.4	281.9
Red mullet	<i>Mullus barbatus ponticus</i> Essipov, 1927	3.4**	1.7	16.4	25.9	4.6	2.9
Flounder	<i>Platichthys flesus</i> (Linnaeus, 1758)	3.5**	138.2	18.6	3.6	0.0	0.0
Turbot	<i>Psetta maeotica</i> (Pallas, 1814)	4**	122.8	33.9	3.2	2.9	14.1
Common sole	<i>Solea solea</i> (Linnaeus, 1758)	2.9**	15.3	1.4	1.1	1.8	6.7
Piked dogfish	<i>Squalus acanthias</i> Linnaeus, 1758	4.4***	7.8	2.6	53.2	9.5	1.5
<sup>(1)</sup> Mulletts	3 spp	3***	8.8	2.1	2.7	0.0	3.4
<sup>(2)</sup> Gobies	4 spp	3.1**	48.5	46.0	24.6	13.0	37.9
<sup>(3)</sup> Sturgeons	3 spp	4.2**	194.0	114.3	34.0	6.4	7.0
<sup>(4)</sup> Rays	2 spp	3.7*	1.8	0.0	0.0	0.0	0.0
Total mean annual catches			8325.8	8091.4	11725.0	2898.7	2563.7
Percentage of pelagic fish species catches			92.9%	87.2%	85.4%	82.5%	86.2%
Mean fisheries trophic level (FTL)			3.21	3.27	3.07	3.00	2.96

781

782 <sup>(1)</sup>Mulletts: Golden grey mullet - *Liza aurata* (Risso, 1810), Leaping mullet - *Liza saliens* (Risso, 1810), Flathead  
 783 mullet - *Mugil cephalus* Linnaeus, 1758.

784

<sup>(2)</sup>Gobies: Monkey goby - *Apollonia fluviatilis* (Pallas, 1814), Round goby - *Apollonia melanostomus* (Pallas,  
 785 1814), Goby - *Gobius cephalarges* (Pallas, 1814), Goby - *Mesogobius batrachocephalus* (Pallas, 1814).

786

<sup>(3)</sup>Sturgeons: Russian sturgeon - *Acipenser gueldenstaedtii* Brandt and Ratzeburg, 1833, Starry sturgeon -  
 787 *Acipenser stellatus* Pallas, 1771, Beluga - *Huso huso* (Linnaeus, 1758).

788

<sup>(4)</sup>Rays: Common stingray - *Dasyatis pastinaca* (Linnaeus, 1758), Thornback ray - *Raja clavata* Linnaeus, 1758.

789

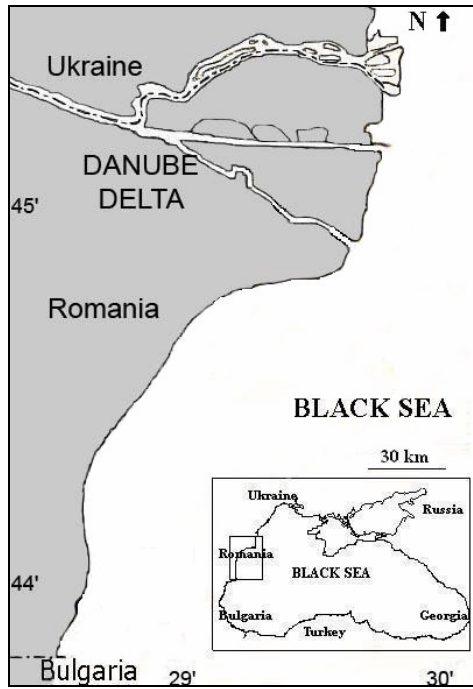
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791 **Table 2**

792 Danube mean annual water discharge (\*Cociașu *et al.*, 1996), annual variability of the nutrient concentration  
 793 in the Black Sea in the zone of the Danube water influence (\*\*Berlinsky *et al.*, 2006), long term changes of  
 794 phytoplankton variables (\*\*Yunev *et al.*, 2007) and eutrophication phases of the Black Sea (\*\*\*\*Oguz and  
 795 Gilbert, 2007).  
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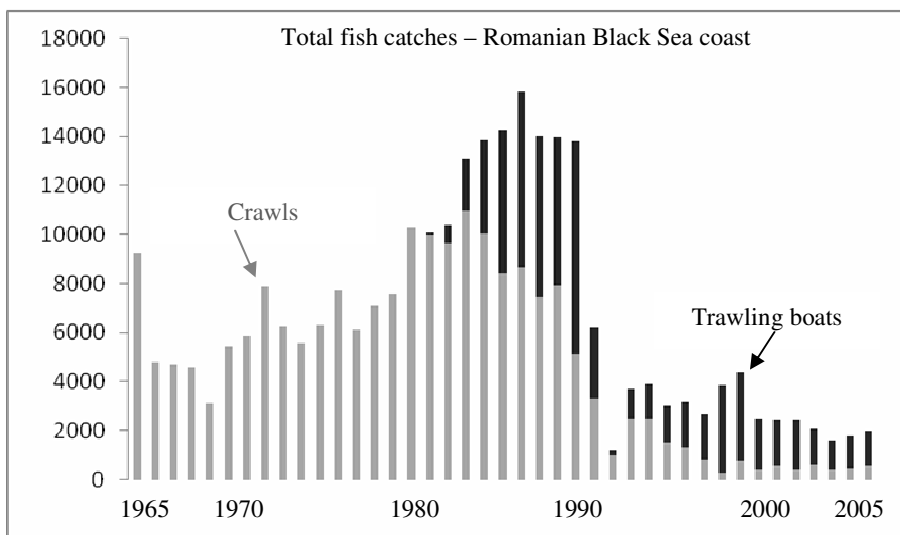
	1960s	1970s	1980s	1990s	
Danube water discharge (km <sup>3</sup> )	213,40	223,30	196,00	184,40	*
Nutrient concentration (mg L <sup>-1</sup> )					
NH <sub>4</sub> <sup>+</sup>	0,025	0,445	0,470	0,081	**
NO <sub>2</sub> <sup>-</sup>	0,003	0,005	0,061	0,006	**
NO <sub>3</sub> <sup>-</sup>	0,010	0,042	0,619	0,056	**
N <sub>org</sub>	0,230	0,441	1,767	0,706	**
PO <sub>4</sub> <sup>3-</sup>	0,014	0,029	0,142	0,025	**
P <sub>org</sub>	0,016	0,025	0,066	0,022	**
SiO <sub>3</sub> <sup>2-</sup>	2,980	2,367	1,965	0,795	**
Contribution % of algal groups in phytoplankton density					
Diatoms (cells L <sup>-1</sup> )	92,30	84,10	38,30		***
Dinoflagellates (cells L <sup>-1</sup> )	7,60	11,80	20,00		***
Others (Cryptophyceae, Chrysophyceae, Cyanophyceae)	0,10	4,10	41,70		***
Multiannual means of surface chlorophyll <i>a</i> (mg m <sup>-3</sup> )	0,66	1,67	9,00	1,70	***
O <sub>2</sub>	high	high	low	low	****
Eutrophication phases of the Black Sea	Pre-	Early-	Intense-	Post-	****

797

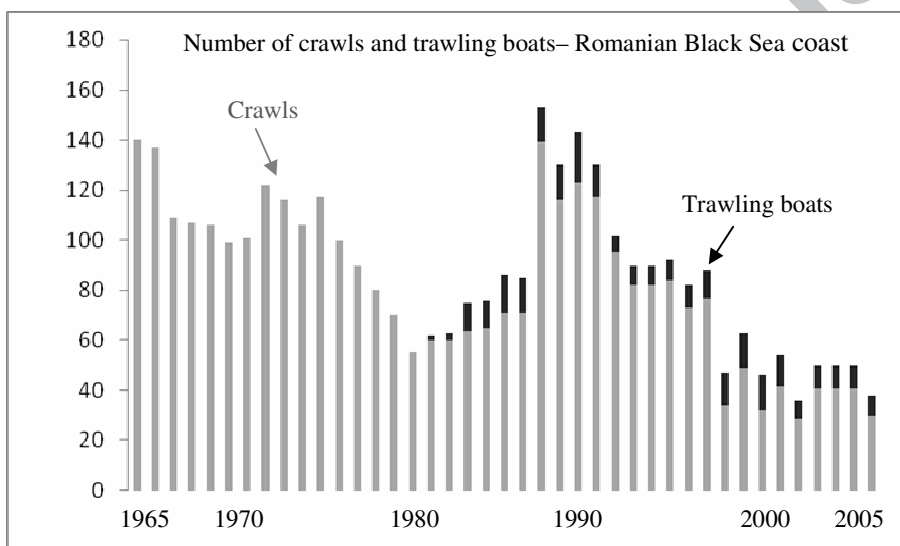


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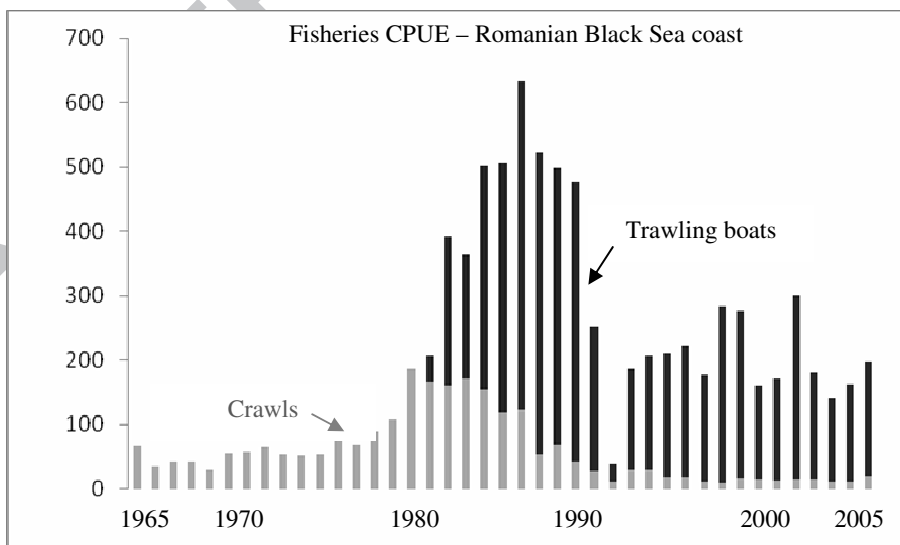
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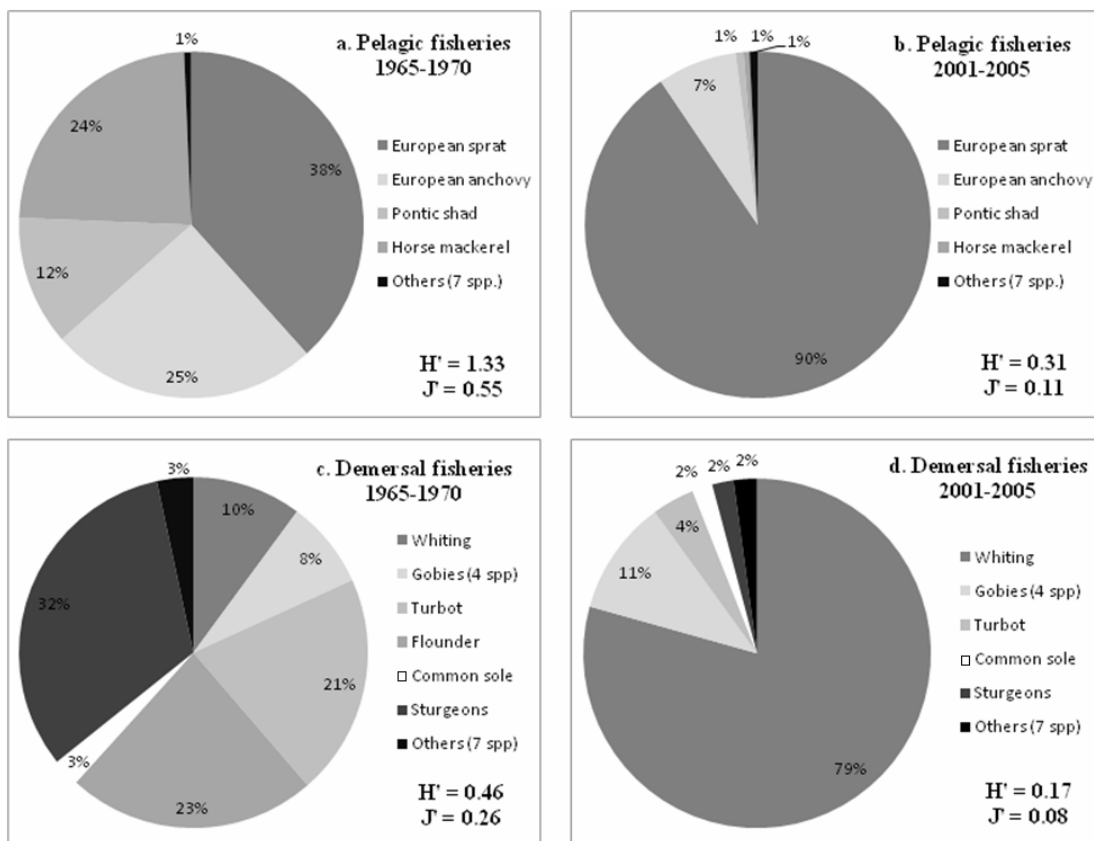
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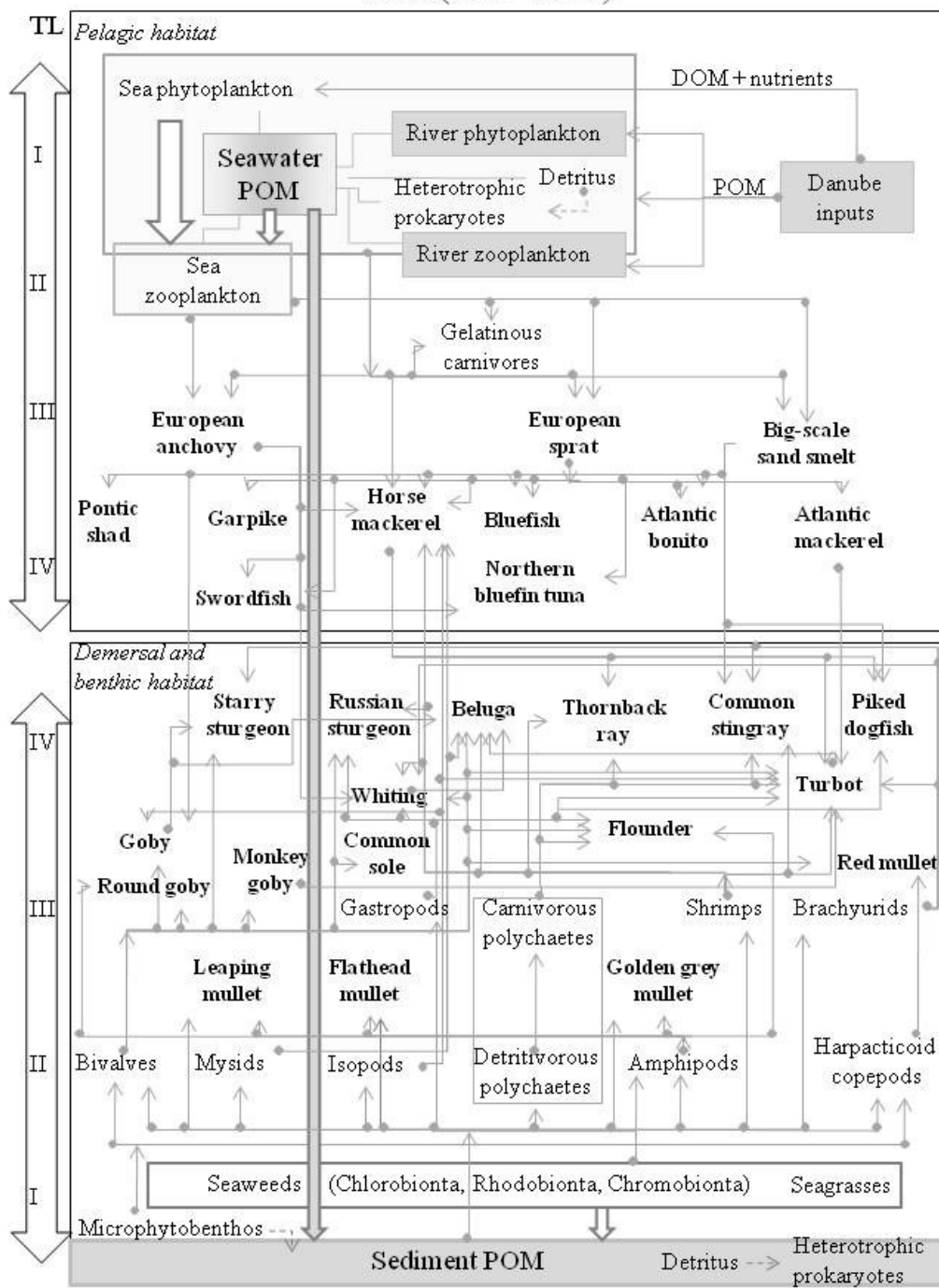


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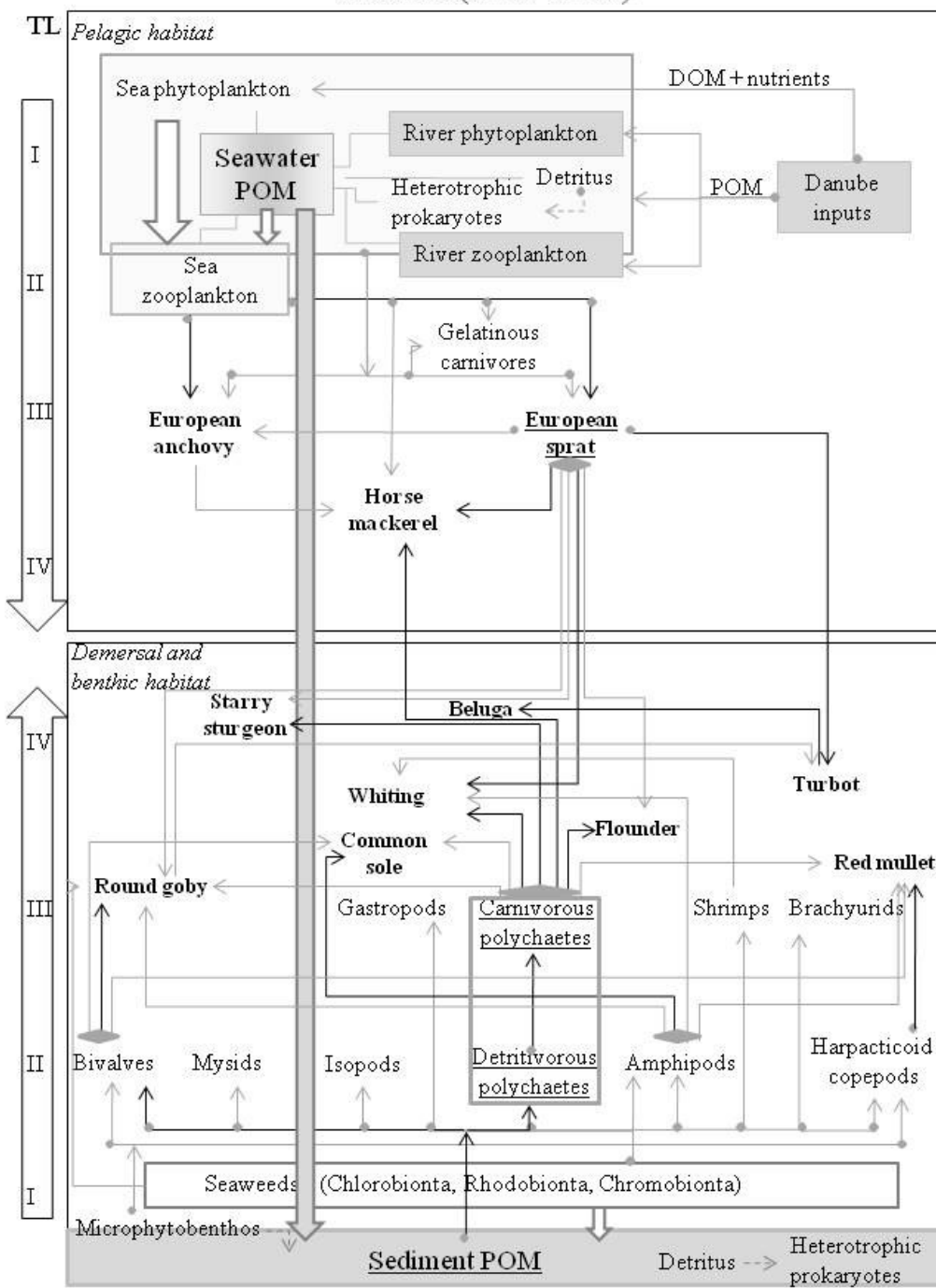


Past (1965-1970)



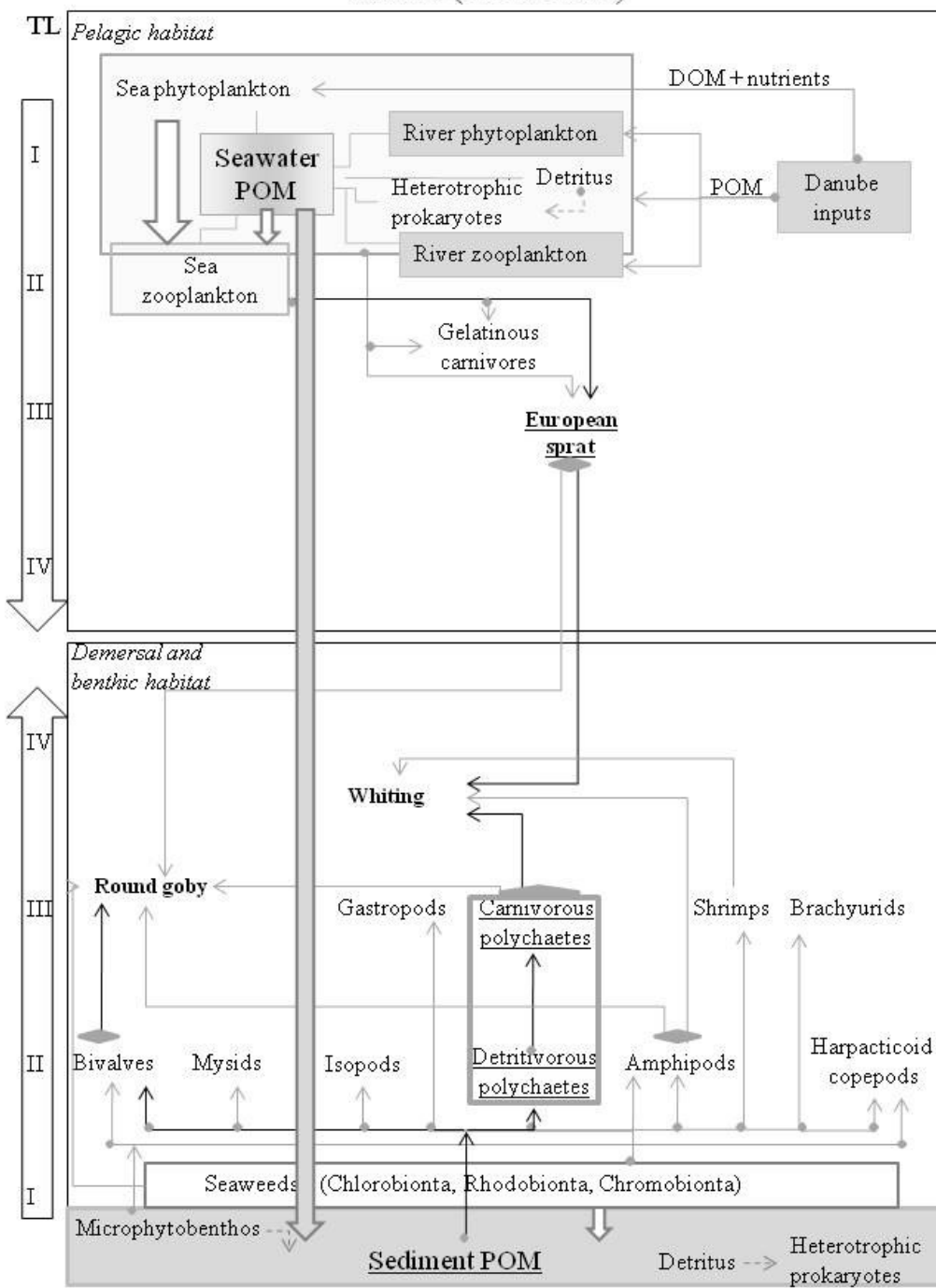
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Present (2004-2006)

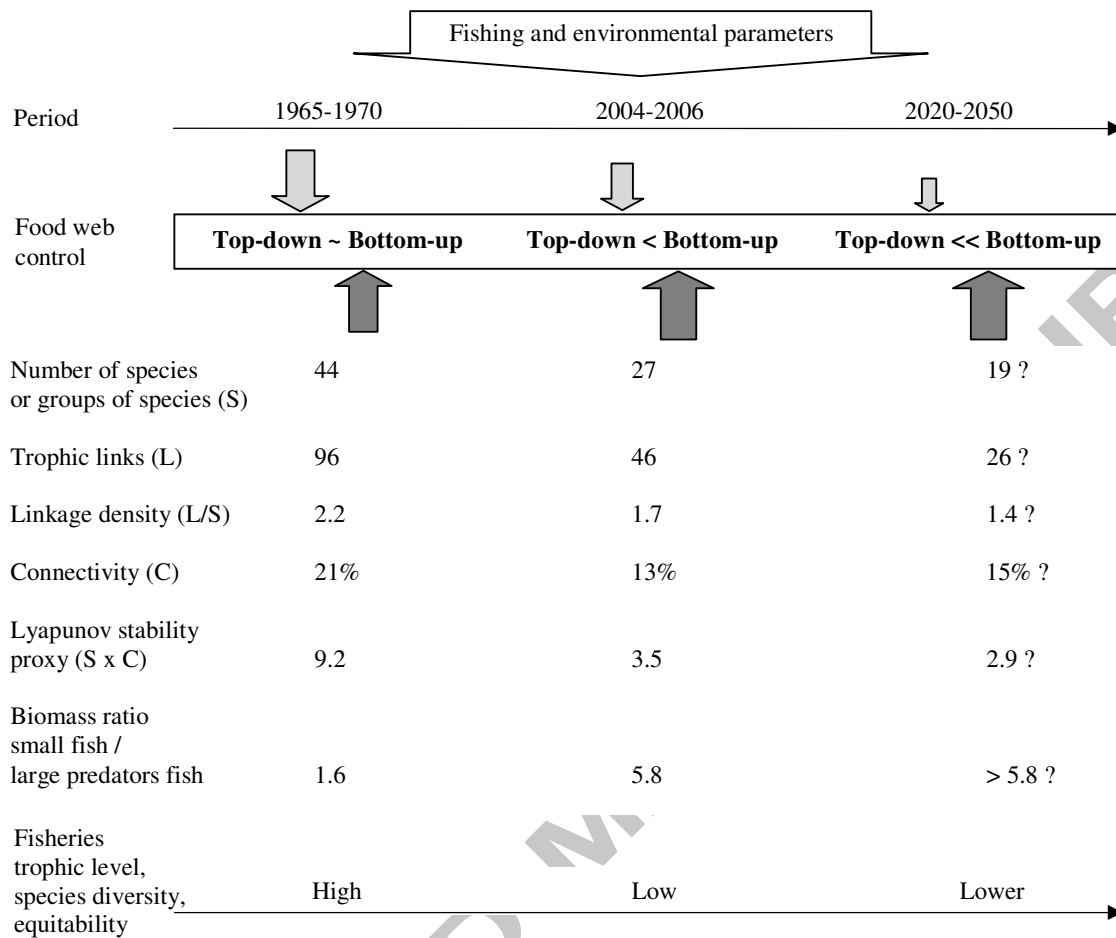


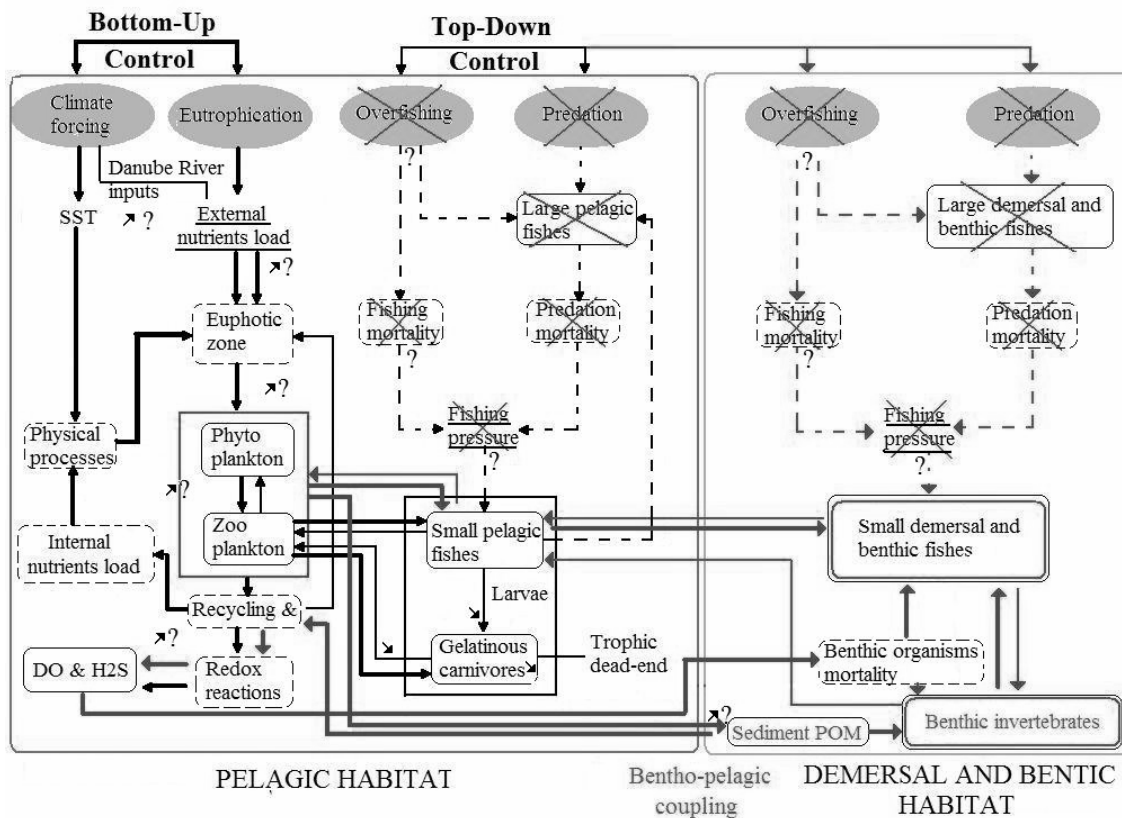
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Future (2020-2050)



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