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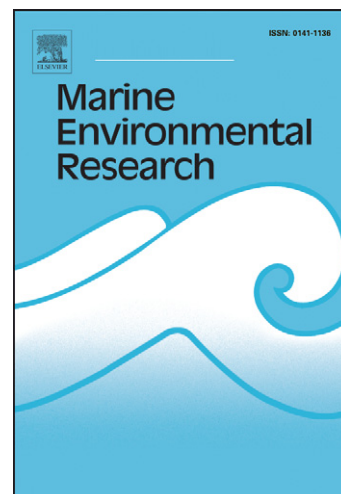
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1 **Man induced change in community control in the north-western Black Sea:**
2 **the top-down bottom-up balance**

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). Fishing
32 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, 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 x
 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).

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 km²) compared to its surface (422 090 km²) 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 (Bănar, 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; Bănar,
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 (Bănar *et al.*, 2007; Bănar, 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).

534

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536

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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
Pelagic fish species							
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
Benthic-demersal fish species							
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
⁽¹⁾ Mullet	3 spp	3***	8.8	2.1	2.7	0.0	3.4
⁽²⁾ Gobies	4 spp	3.1**	48.5	46.0	24.6	13.0	37.9
⁽³⁾ Sturgeons	3 spp	4.2**	194.0	114.3	34.0	6.4	7.0
⁽⁴⁾ 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 ⁽¹⁾Mullet: Golden grey mullet - *Liza aurata* (Risso, 1810), Leaping mullet - *Liza saliens* (Risso, 1810), Flathead
 783 mullet - *Mugil cephalus* Linnaeus, 1758.

784

⁽²⁾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

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

788

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

789

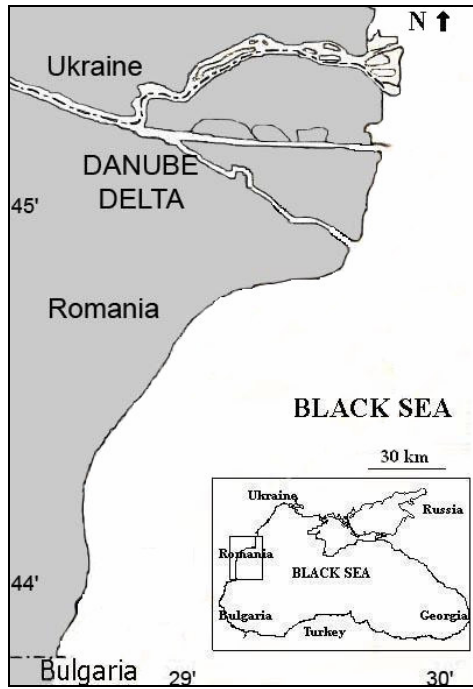
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791 **Table 2**

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).
 796

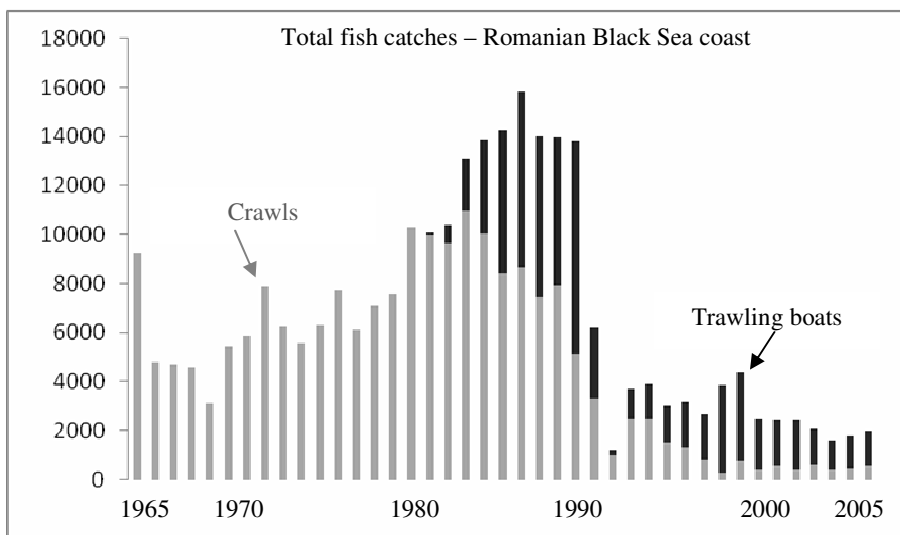
	1960s	1970s	1980s	1990s	
Danube water discharge (km ³)	213,40	223,30	196,00	184,40	*
Nutrient concentration (mg L ⁻¹)					
NH ₄ ⁺	0,025	0,445	0,470	0,081	**
NO ₂ ⁻	0,003	0,005	0,061	0,006	**
NO ₃ ⁻	0,010	0,042	0,619	0,056	**
N _{org}	0,230	0,441	1,767	0,706	**
PO ₄ ³⁻	0,014	0,029	0,142	0,025	**
P _{org}	0,016	0,025	0,066	0,022	**
SiO ₃ ²⁻	2,980	2,367	1,965	0,795	**
Contribution % of algal groups in phytoplankton density					
Diatoms (cells L ⁻¹)	92,30	84,10	38,30		***
Dinoflagellates (cells L ⁻¹)	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 ⁻³)	0,66	1,67	9,00	1,70	***
O ₂	high	high	low	low	****
Eutrophication phases of the Black Sea	Pre-	Early-	Intense-	Post-	****

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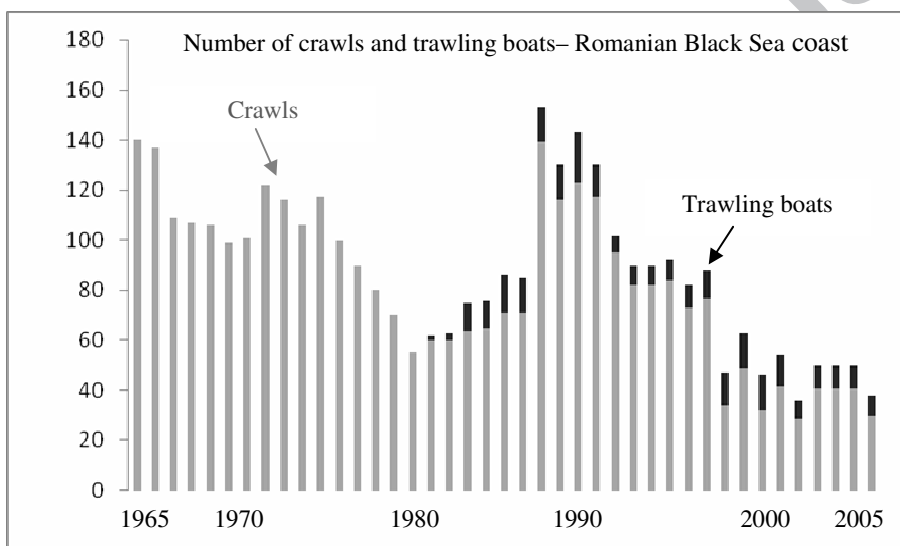


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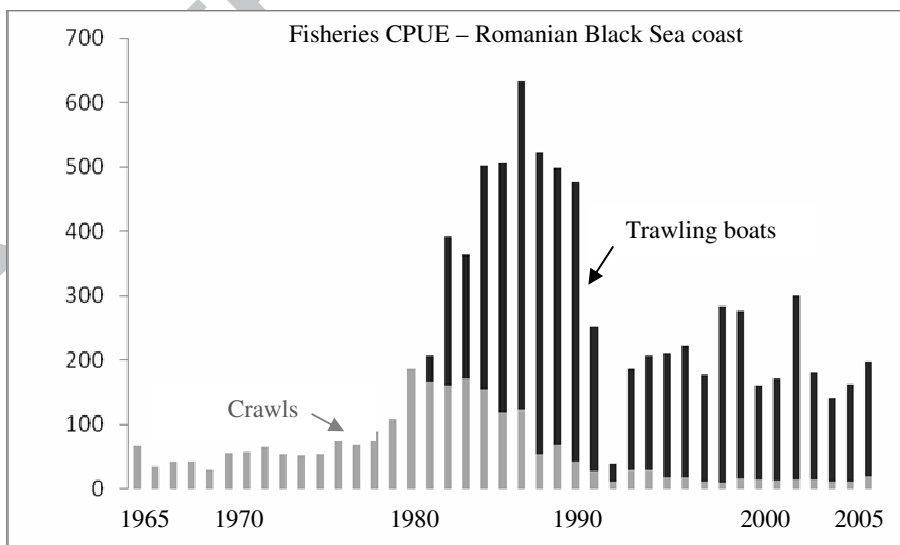
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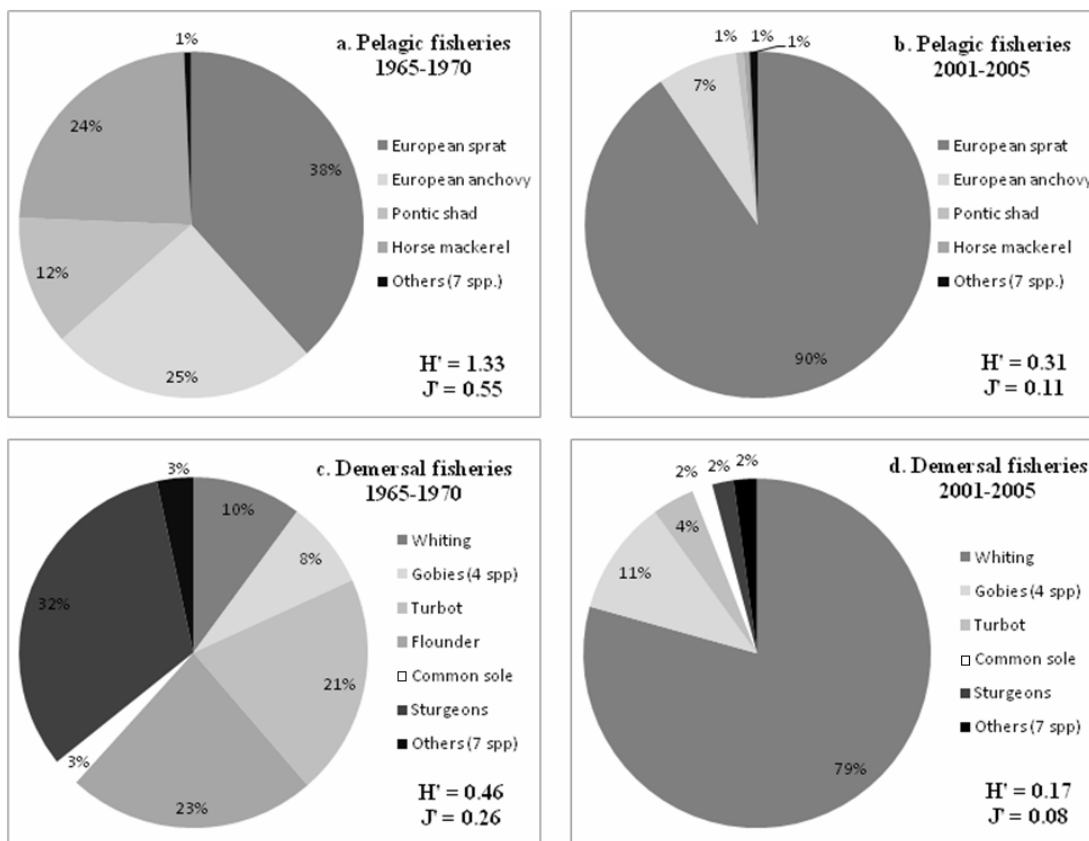
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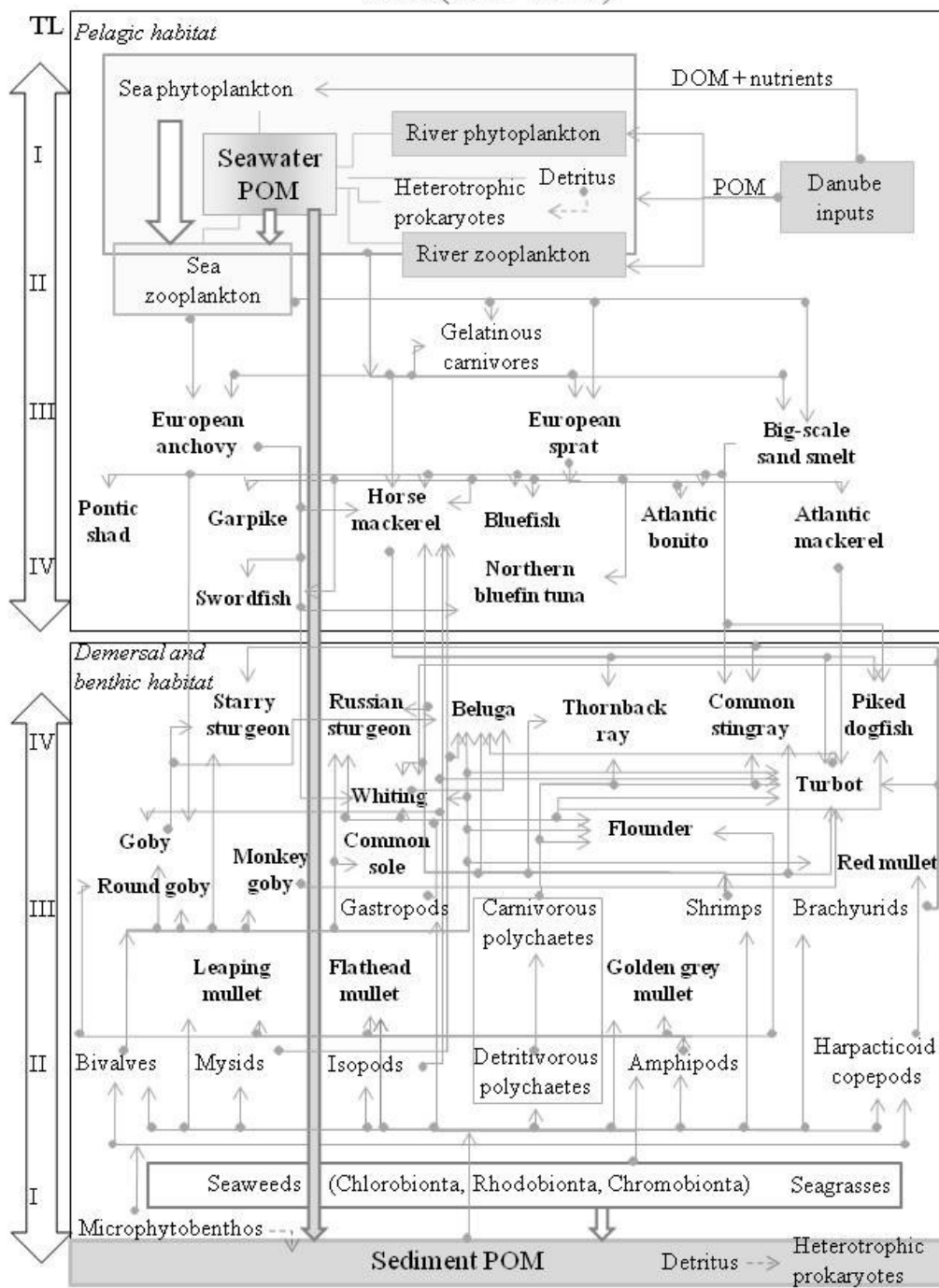
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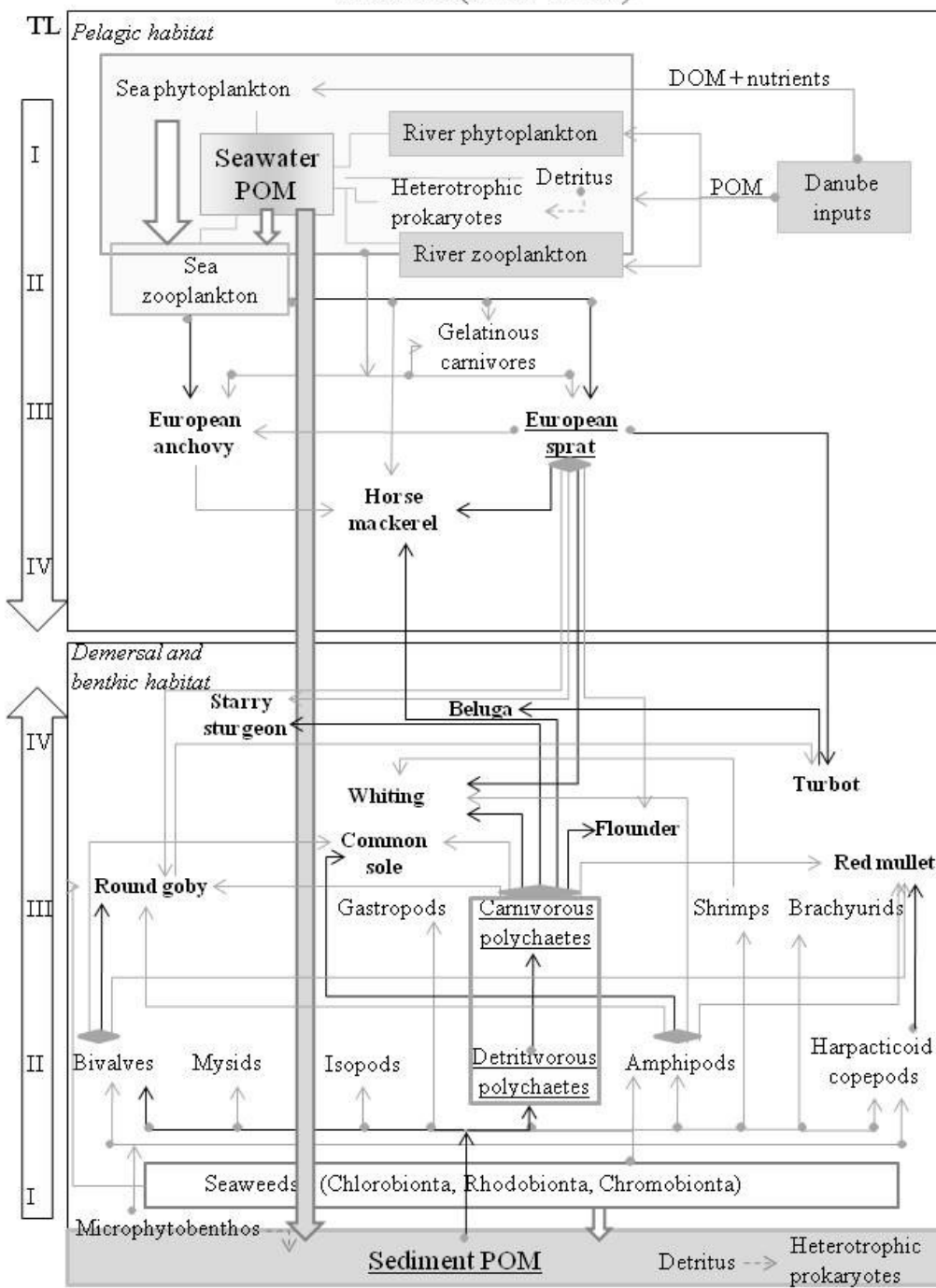
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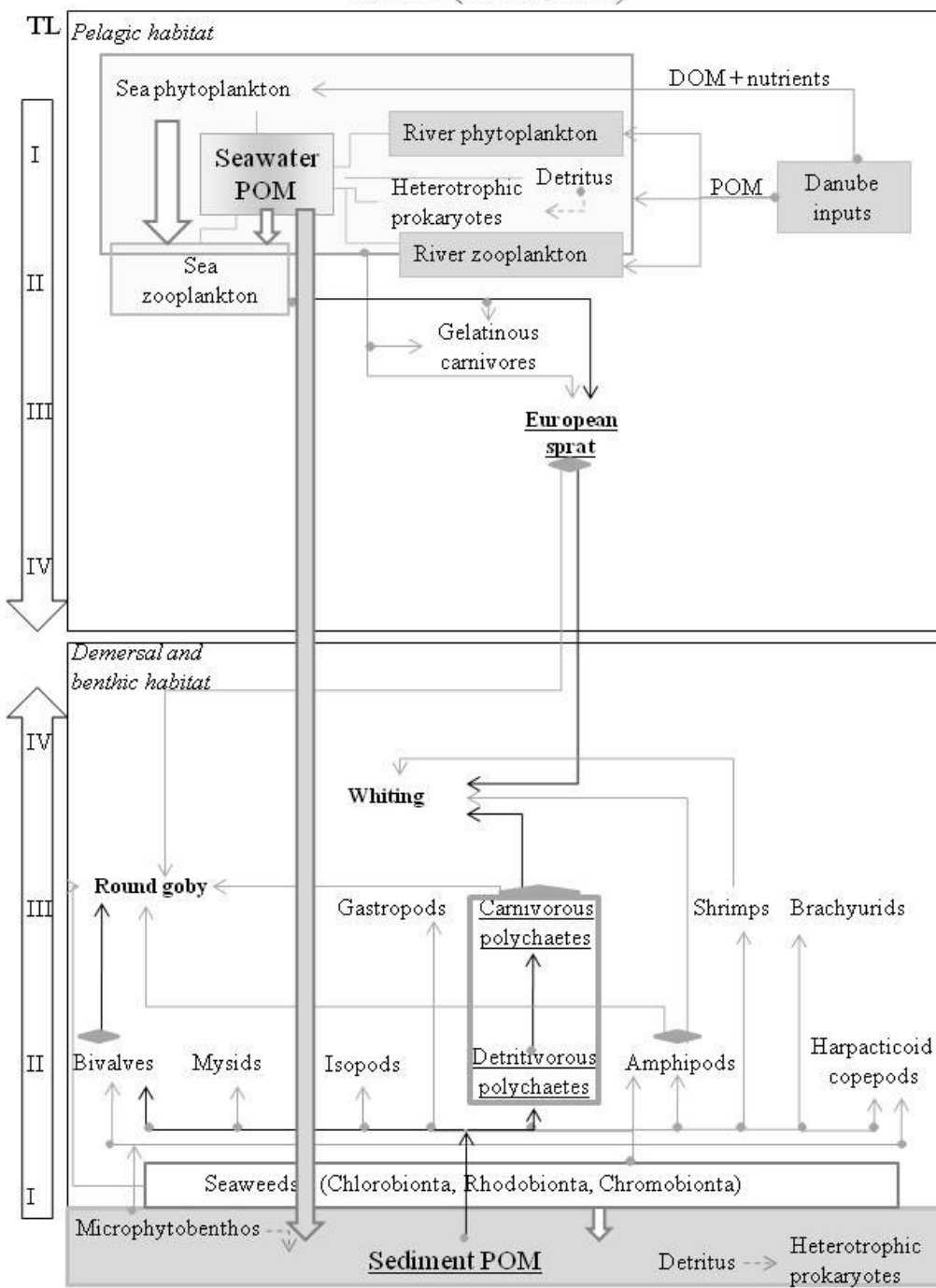


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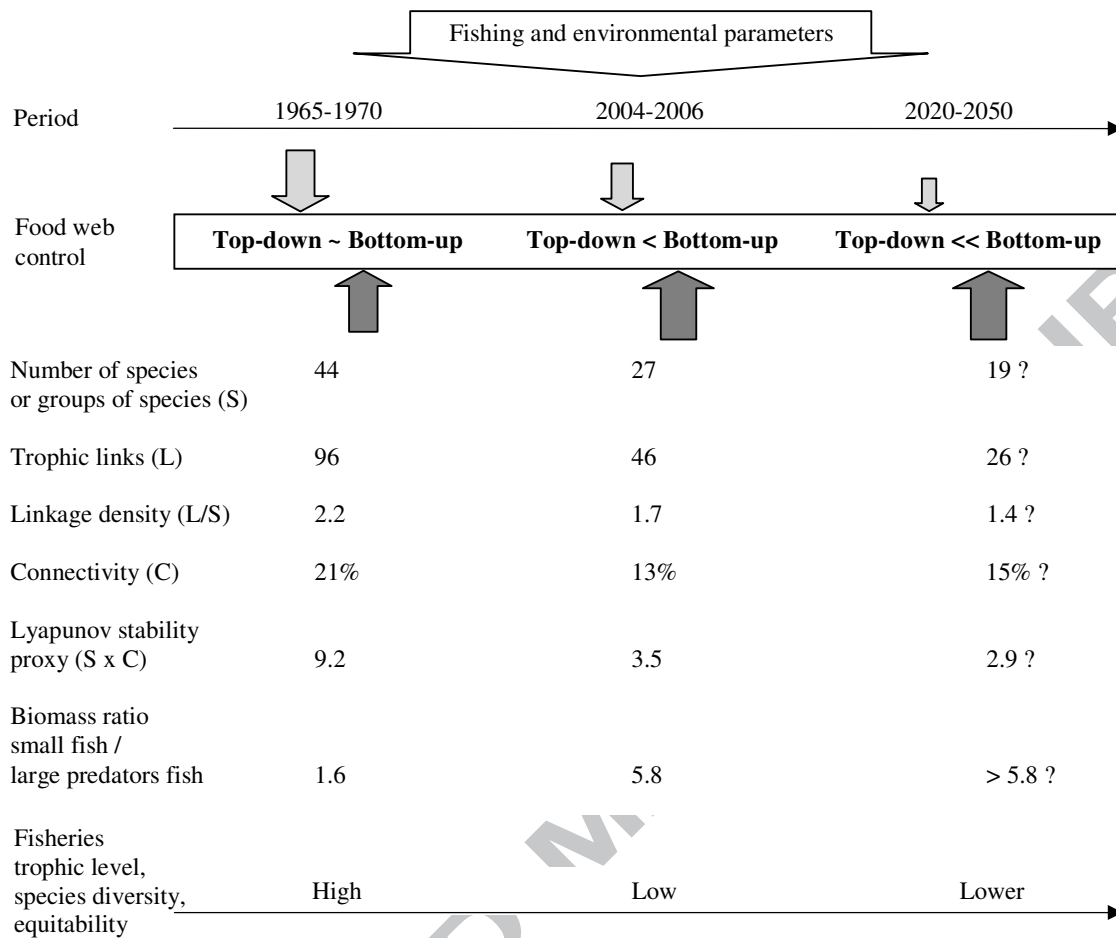
Present (2004-2006)

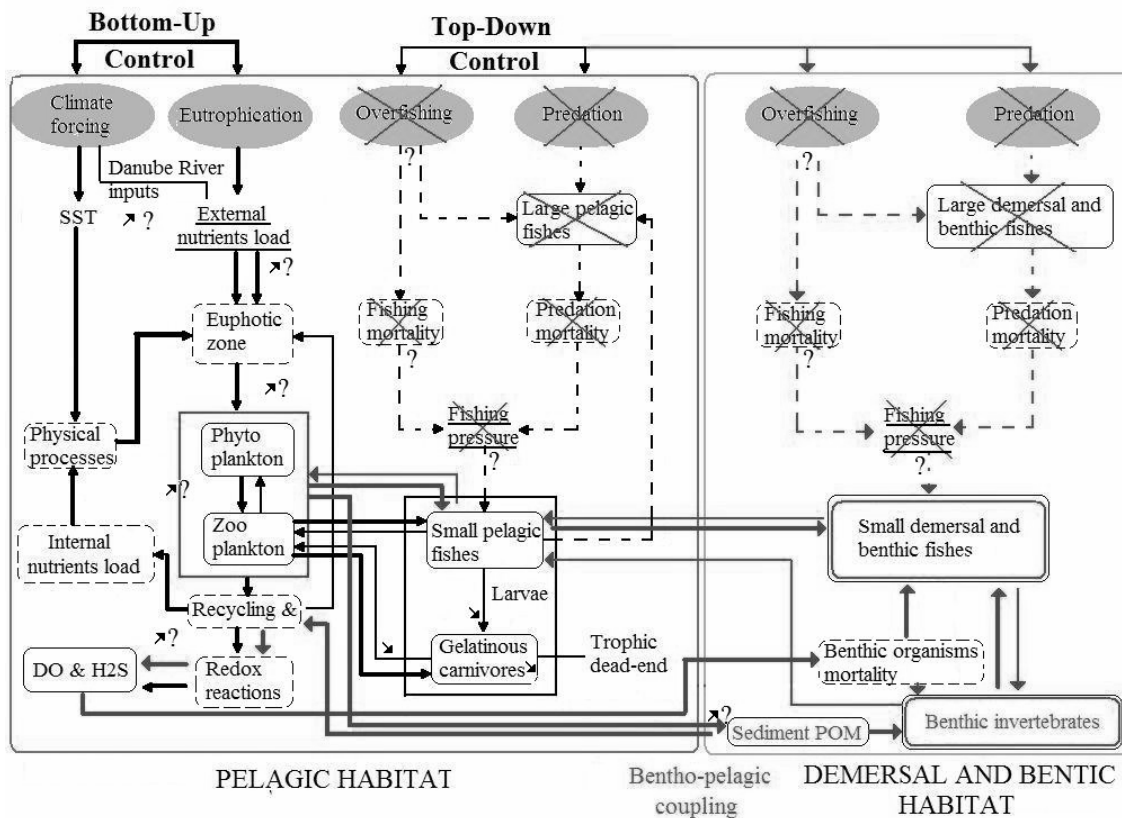


Future (2020-2050)



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