

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

Daniela Bănaru, Mireille Harmelin-Vivien, Charles F. Boudouresque

▶ To cite this version:

Daniela Bănaru, Mireille Harmelin-Vivien, Charles F. Boudouresque. Man induced change in community control in the north-western Black Sea: the top-down bottom-up balance. Marine Environmental Research, 2010, 69 (4), pp.262. 10.1016/j.marenvres.2009.11.009. hal-00564784

HAL Id: hal-00564784

https://hal.science/hal-00564784

Submitted on 10 Feb 2011

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Accepted Manuscript

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

Daniela Bănaru, Mireille Harmelin-Vivien, Charles F. Boudouresque

PII: S0141-1136(09)00153-6

DOI: 10.1016/j.marenvres.2009.11.009

Reference: MERE 3402

To appear in: Marine Environmental Research



Please cite this article as: Bănaru, D., Harmelin-Vivien, M., Boudouresque, C.F., Man induced change in community control in the north-western Black Sea: the top-down bottom-up balance, *Marine Environmental Research* (2009), doi: 10.1016/j.marenvres.2009.11.009

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

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	
5	Daniela Bănaru ^{a,b*} , Mireille Harmelin-Vivien ^a & Charles F. Boudouresque ^a
6	^a Centre d'Océanologie de Marseille DIMAR UMR CNRS 6540
7	Station Marine d'Endoume rue de la batterie des Lions 13007 Marseille, France
8	^b Ovidius University Constanta, Romania
9	*Corresponding author. Tel.: + 33 491041637; Fax: + 33 491041635. E-mail: <u>Daniela.Bănaru@univmed.fr</u>
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

1. Introduction

1	\neg
1	. /

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

48

49

50

26

Over the last decades, there has been increasing concern about the impact of man on the seas. The marine environment may be affected, both directly and indirectly, by a variety of human activities, including coastal engineering works, pollution, eutrophication, species introduction, fisheries and global warming (Rijnsdorp et al., 1996; Boudouresque et al., 2005). Fishing activities have been proposed as the major human disturbance in coastal areas (Jackson et al., 2001). Increasing human populations and seafood demand as well as the development and improved performance of fisheries techniques have given rise to overfishing (Aldebert, 1997). Nowadays most demersal, benthic and pelagic stocks are fully exploited or overexploited (Pauly et al., 1998; Steneck, 1998; Papaconstantinou and Faruggio, 2000; Pauly et al., 2003). Some authors have predicted "the global collapse of all taxa currently fished" by 2048 (Worm et al., 2006). Branch (2008) and many other scientists disagree with this theory, arguing that the number of fisheries that have not collapsed shows an increasing trend and some fisheries should recover. These intellectual and scientific discussions are nowadays more common than ever in journals. Fisheries scientists often see fish primarily as a resource and try to determine the level at which it can be extracted at a sustainable rate. Marine ecologists regard fish as part of an ecosystem and tend to be more conservative in how much can be taken out without harming the ecosystem. The two scientists representing these opposing camps, Ray Hilborn (Hilborn, 2006) and Boris Worm (Worm et al., 2006), argued for a long time on the fisheries and ecosystems management thematic, as each of them were defending their own expertise area. In July 2009, the Journal "Science" presented the reconciliation between them (Stokstad, 2009). They finally discussed and started to work together and the results and conclusions of their work are complementary and even more valuable. While their methods and 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 at 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; Cociașu and
78	Popa, 2004). This production constitutes an abundant food resource for pelagic and bentho-
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 bentho-
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.

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

2. Methods

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

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

124
$$H' = \sum_{i=1}^{S} (pi * log_2 pi),$$

- where p_i is the percentage of each fish species (i) in the total annual mean fisheries catches
- and S the number of fish species or groups.
- The evenness index of Pielou (J') quantifies how equal the community is numerically. It
- represents the ratio between the diversity (H') and the maximum diversity that could be
- obtained with the same number of species (Frontier and Pichod-Viale, 1995):

$$J' = H'/H'max,$$

- where H' is the index of Shannon, H'max = log_2S .
- 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
- threatened by overexploitation (Pauly et al., 1998). Mean fisheries trophic level (FTL) was
- calculated according to the formula:

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

- where TLi is the trophic level of each species i and p_i is the percentage of species (i) in the
- mean annual catches. Mean fisheries trophic level (FTL) would allow us to analyze the
- change in trophic level between 1965 and 2005.
- Several food web metrics were estimated in this study to provide insight into the dynamics of
- 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)
- and trophic links (L). The linkage density (L/S) (number of interactions per species or groups)
- 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
$$C = L / [S(S-1)/2].$$

- 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
- 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; Cărăuşu, 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 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 bentho-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	became 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 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' pelagic fishes = 1.33 ; H' bentho-demersal fishes = 0.46 ; J' pelagic fishes = 0.55 ; J'
217	bentho-demersal fishes = 0.26) and $2001-2005$ (H' pelagic fishes = 0.31 ; H' bentho-demersal fishes = 0.17 ;
218	$J'_{pelagic fishes} = 0.11$; $J'_{bentho-demersal fishes} = 0.08$). Following the reduction of large predatory fish
219	catches, the mean fisheries trophic level decreased between 1965 and 2005 from 3.21 to 2.96
220	(Table 1).
221	
222	3.2. Past food web

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 bentho-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 bentho-demersal food web. In the bentho-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 bentho-
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

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

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

3.4. Possible future food web

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

298	zoopiankton 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 (Bănaru, 2008) were in bad condition with tumours on their
314	tegument and numerous parasite nematodes in their stomach. Only two bentho-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	up control would be dominant. 4. Discussion
331	
332	This study presents a conceptual model of the structure and functioning of the pelagic and
333	bentho-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 currents trends continue. In this system there is a strong
336	coupling between pelagic and bentho-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 (Bănaru, 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 $378\ 317\ km^2$) compared to its surface (422 $090\ km^2$) 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, Dniper, Dniestr and Bug, which turned the Black Sea into one of
352	the most eutrophicated seas of the world (Cociașu et al., 1996; Zaitev 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 (Zaitev and Mamaev, 1997). Some authors have suggested a recovery of the Black
357	Sea in the late 1990s following the reduction of phytoplankton blooms (Cociașu 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

37	72	indices for fisheries was ever calculated in this area before this study. Commercial pelagic and
37	73	bentho-demersal fish diversity and equitability on the Romanian coast strongly declined
37	74	between 1965-1970 and 2001-2005. In any case, these values are very low $(H' = [0.17-1.33];$
37	75	J' = [0.08-0.55]) compared to the seagrass fish community in the Mediterranean Sea (H' =
37	76	[3.57-4.22] and J' = [0.71-0.81]) (Bell and Harmelin-Vivien, 1982).
37	77	The pelagic biomass production in the Black Sea is 13 times higher than demersal production.
37	78	This ratio is more than 10 times higher than in all the other enclosed seas (except the Sea of
37	79	Azov) (de Leiva Moreno et al., 2000). This explains why the pelagic fisheries dominated in
38	30	the Black Sea in the last decades (83%-93%). Benthic and demersal fish species have a high
38	31	economic value but they represent a small percentage of the Romanian marine total fish
38	32	landings.
38	33	
38	34	4.3. A decreasing mean trophic level
38	35	
38	36	The mean trophic level of the species or groups of species reported in FAO global fisheries
38	37	statistics declined from 3.3 in the early 1950s to less than 3.1 in 1994 (Pauly et al., 1998). Our
38	88	results showed a similar tendency in the Black Sea, where the mean trophic level of the
38	39	commercial fish catches declined from 3.21 in 1965-1970 to 2.96 in 2001-2005. Such a
39	90	decrease reflects a gradual transition in the landings from the long lived, high trophic level,
39	91	piscivorous fishes toward short-lived, low trophic level, planktivorous fishes (Fig. 7).
39	92	Zaitev (1992) showed the same trend in the Black Sea Ukrainian fisheries between 1980 and
39	93	1990 when species number reduced and only small pelagic fish species catches were high.
39	94	Tatara (1991) shows that both a decline in mean trophic level and a linked increase in
39	95	planktivores are responses to the eutrophication of the Seto Inland Sea by nutrient run-off.
39	96	Tang (1993) reported similar findings for the Yellow Sea where, during the 1950s and 1960s,

benthic and demersal species dominated the catches but were gradually replaced by pelagic
planktivorous species such as Pacific herring and mackerel in the 1970s. Some of these effect
can be attributed to "fishing down marine food webs" (Pauly et al., 1998), but in the Black
Sea demersal, benthic and pelagic migratory predators seriously declined in the 1970s and
early 1980 (Zaitev and Mamaev, 1997) before the rise in small pelagic biomass began in the
1980s. The earlier disappearance of predators in the 1980s suggests that subsequent changes
were largely due to the eutrophication processes. Bentho-demersal production has declined
drastically since the 1960s, largely due to hypoxia in the bottom water layer, while anchovy
populations continue to rise. This increase in biomass of small pelagic fish species despite an
increase in harvesting rate of the same species also supports a bottom-up effect of increased
nutrient inputs (de Leiva Moreno et al., 2000).
Many factors interact in the semi-enclosed Black Sea system and are responsible for the
present state of the fisheries. This is also the case of fisheries landings in the Baltic Sea, the
North Sea and the Adriatic Sea, that are nowadays lower than in the past and dominated by
small pelagic fish species of low commercial value (Rijnsdorp et al., 1996; McIntyre, 1999;
Harvey et al., 2003). In the North Sea, Rijnsdorp et al. (1996) compare past and present
changes in abundance of fish species and show a reduction in landings, fish sizes, species
diversity and shifts in the community structure.
4.4. Evidence for a regime-shift
In the Black Sea the decline of large predators because of overfishing gave rise to trophic

In the Black Sea the decline of large predators because of overfishing gave rise to trophic cascades and regime-shifts (Gucu, 2002). Cury and Shannon (2004) consider the regime-shift to be a sudden shift in structure and functioning of a marine ecosystem, affecting several 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 x 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.
504505506	4.7. The future: recovery, stability or growth of the present trends?
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 (Bănaru et al., 2007; Bănaru, 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 <i>Mnemiopsis leidyi</i> by <i>Beroe ovata</i> , 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

the manuscript.

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	
JJ T	
535	Acknowledgements
	Acknowledgements
535	Acknowledgements We are grateful to the captains and crews of the Romanian fishing vessels (Chefalul 10,
535536	
535536537	We are grateful to the captains and crews of the Romanian fishing vessels (Chefalul 10,
535536537538	We are grateful to the captains and crews of the Romanian fishing vessels (Chefalul 10, Meduza II, Meduza IV, Morunul), research vessel (Steaua de Mare) and fishermen (A. Marin,
535536537538539	We are grateful to the captains and crews of the Romanian fishing vessels (Chefalul 10, Meduza II, Meduza IV, Morunul), research vessel (Steaua de Mare) and fishermen (A. Marin, R. M. Boboc, G. Butalchin, P. Braniste, M. Iordan and Stanica C.) for their help in sampling.
535536537538539540	We are grateful to the captains and crews of the Romanian fishing vessels (Chefalul 10, Meduza II, Meduza IV, Morunul), research vessel (Steaua de Mare) and fishermen (A. Marin, R. M. Boboc, G. Butalchin, P. Braniste, M. Iordan and Stanica C.) for their help in sampling. D. Bănaru was financially supported by a grant from the French Government and led a project
535536537538539540541	We are grateful to the captains and crews of the Romanian fishing vessels (Chefalul 10, Meduza II, Meduza IV, Morunul), research vessel (Steaua de Mare) and fishermen (A. Marin, R. M. Boboc, G. Butalchin, P. Braniste, M. Iordan and Stanica C.) for their help in sampling. D. Bănaru was financially supported by a grant from the French Government and led a project funded by the Romanian National Council of Scientific Research in Higher Education
535536537538539540541542	We are grateful to the captains and crews of the Romanian fishing vessels (Chefalul 10, Meduza II, Meduza IV, Morunul), research vessel (Steaua de Mare) and fishermen (A. Marin, R. M. Boboc, G. Butalchin, P. Braniste, M. Iordan and Stanica C.) for their help in sampling. D. Bănaru was financially supported by a grant from the French Government and led a project funded by the Romanian National Council of Scientific Research in Higher Education (CNCSIS). The sampling and work for this study comply with the current laws, collecting and

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	Bănaru, D., Harmelin-Vivien, M., Gomoiu, MT., Onciu, TM., 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	Bănaru, 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	Bănaru, 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	Bănaru, 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 <i>Posidonia</i>
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? <i>Mnemiopsis leidyi</i>
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	Cărăuşu, 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, YJ., 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, MT., 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, MT., 1996. Some remarks concerning actual state of the Danube River – Black Sea
626	ecological system. Geo-Eco-Marina, Constanta 1, 31-33.
627	Gomoiu, MT., 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, JM., 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 ($\delta^{15}N$) 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., Ærtebjerg, G., Nixon, S., 2007.
725	Nutrient and phytoplankton trends on the western lack Sea shelf in reponse to cultural
726	eutrophication and climate changes. Estuarine, Coastal and Shelf Science 74, 63-76.
727	http://europa.eu
728	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 bentho-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 bentho-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	Cărăuşu, 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 bentho-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 bentho-demersal fish species on the Romanian coast
758	in the north-western Black Sea. TL = trophic level, DOM = dissolved organic matter, POM = particulate organic

matter. Fish species are represented in bold characters. Black arrows indicate principal organic matter flows from
prey to predators and grey arrows the secondary ones. The large grey arrow represents the transfer of
sedimentary POM from seawater to sediment. On the left side the arrows indicate bottom-up control by the
primary producers over higher trophic level consumers. Underlined components have become very abundant and
play a key role in the food web. Most of the fish species have disappeared.
Fig. 7. Past, present and future effects of fishing and human induced change on the environmental parameters in
the Black Sea-Danube River commercial fish food web and fisheries.
Fig. 8. Conceptual diagram of the north-western Black Sea coupled pelagic and bentho-demersal food web
structure representing major controls, processes and trophic interactions over the coming decades. The forcing
variables are shown by underlined characters, the response variables are represented by boxes in grey colour and
the processes which link responses and forcing variables by boxes with dotted lines. Large arrows represent
bottom-up control, thin arrows top-down control and dotted arrows indicate controls that have strongly declined
(adapted from Oguz and Gilbert 2007)

774 Table 1

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

Common name	Scientific name	TL	1965- 1970	1971- 1980	1981- 1990	1991- 2000	2001- 2005
Pelagic fish species							
Pontic shad	Alosa immaculata Bennett, 1835	4.1***	939.3	1138.3	104.7	10.0	16.2
Big-scale sand smelt	Atherina boyeri Risso, 1810	3.3*	21.3	30.1	19.6	14.1	13.0
Garpike	Belone belone (Linnaeus, 1761)	4.2***	0.1	0.0	0.2	0.2	0.0
European anchovy	Engraulis encrasicolus (Linnaeus, 1758)	3**	1942.7	2894.1	3091.0	157.9	163.9
Bluefish	Pomatomus saltatrix (Linnaeus, 1766)	4.5***	10.8	2.0	1.5	2.1	3.9
Atlantic bonito	Sarda sarda (Bloch, 1793)	4.5***	3.7	0.0	0.0	0.0	0.0
Atlantic mackerel	Scomber scombrus Linnaeus, 1758	4***	16.0	0.0	0.0	0.2	0.0
European sprat	Sprattus sprattus sprattus (Linnaeus, 1758)	2.8**	2963.0	1904.6	5700.1	2178.8	1999.1
Northern bluefin tuna	Thunnus thynnus (Linnaeus, 1758)	4.3*	< 1	0.0	0.0	0.0	0.0
Horse mackerel	Trachurus mediterraneus (Steindachner, 1868)	3.4**	1829.5	1082.8	1052.8	19.8	12.2
Swordfish	Xiphias gladius Linnaeus, 1758	4.5*	< 1	0.0	0.0	0.0	0.0
Bentho-demersal fish	-						
Whiting	Merlangius merlangus (Linnaeus, 1758)	3.8**	60.5	804.2	1606.8	477.4	281.9
Red mullet	Mullus barbatus ponticus Essipov, 1927	3.4**	1.7	16.4	25.9	4.6	2.9
Flounder	Platichthys flesus (Linnaeus, 1758)	3.5**	138.2	18.6	3.6	0.0	0.0
Turbot	Psetta maeotica (Pallas, 1814)	4**	122.8	33.9	3.2	2.9	14.1
Common sole	Solea solea (Linnaeus, 1758)	2.9**	15.3	1.4	1.1	1.8	6.7
Piked dogfish	Squalus acanthias Linnaeus, 1758	4.4***	7.8	2.6	53.2	9.5	1.5
(1)Mullets	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

⁽¹⁾ Mullets: Golden grey mullet - *Liza aurata* (Risso, 1810), Leaping mullet - *Liza saliens* (Risso, 1810), Flathead mullet - *Mugil cephalus* Linnaeus, 1758.

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

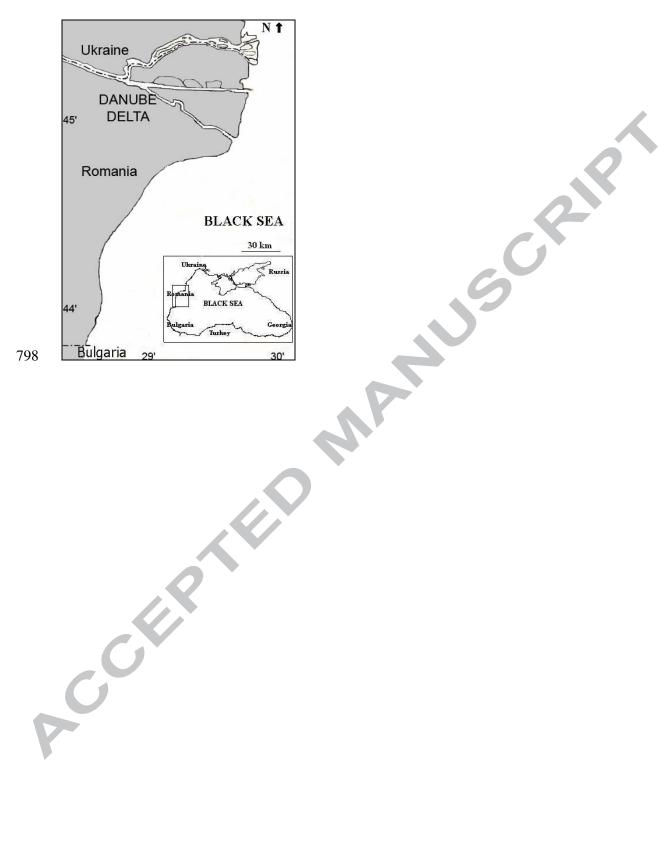
⁽³⁾ Sturgeons: Russian sturgeon - Acipenser gueldenstaedtii Brandt and Ratzeburg, 1833, Starry sturgeon - Acipenser stellatus Pallas, 1771, Beluga - Huso huso (Linnaeus, 1758).

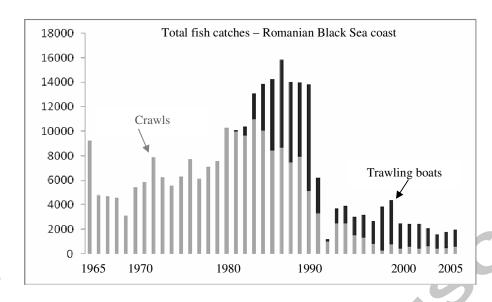
⁽⁴⁾ Rays: Common stingray - Dasyatis pastinaca (Linnaeus, 1758), Thornback ray - Raja clavata Linnaeus, 1758.

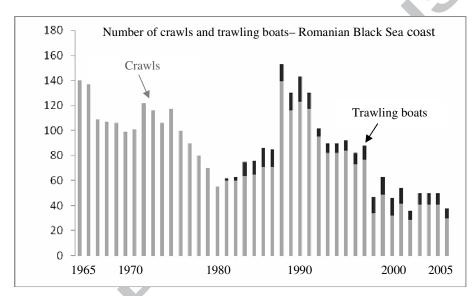
Table 2

Danube mean annual water discharge (*Cociaşu *et al.*, 1996), annual variability of the nutrient concentration in the Black Sea in the zone of the Danube water influence (**Berlinsky *et al.*, 2006), long term changes of phytoplankton variables (***Yunev *et al.*, 2007) and eutrophication phases of the Black Sea (****Oguz and Gilbert, 2007).

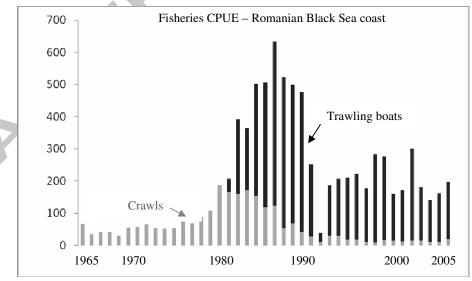
	1960s	1970s	1980s	1990s	
Danube water discharge (km ⁻³)	213,40	223,30	196,00	184,40 *	
Nutrient concentration (mg L ⁻¹)					
$\mathrm{NH_4}^+$	0,025	0,445	0,470	0,081 **	
NO ₂ -	0,003	0,005	0,061	0,006	
NO ₃ -	0,010	0,042	0,619	0,056	
$N_{\rm org}$	0,230	0,441	1,767	0,706 **	
PO ₄ ³⁻	0,014	0,029	0,142	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, Cyanophycea)	0,10	4,10	41,70	**:	*
Multiannual means of surface chlorophyll a (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- ***	**

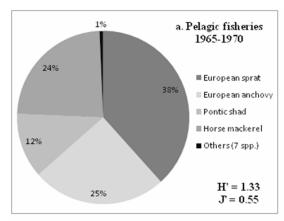


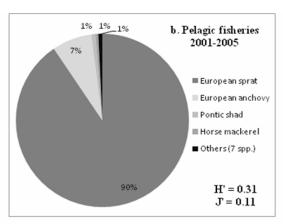


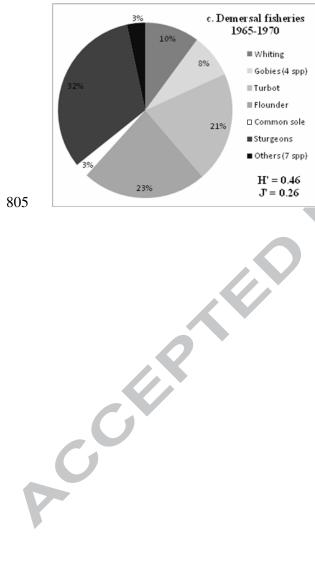


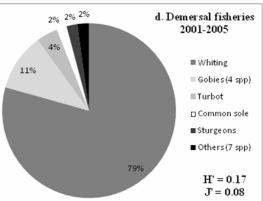
 $\underset{802}{801}$

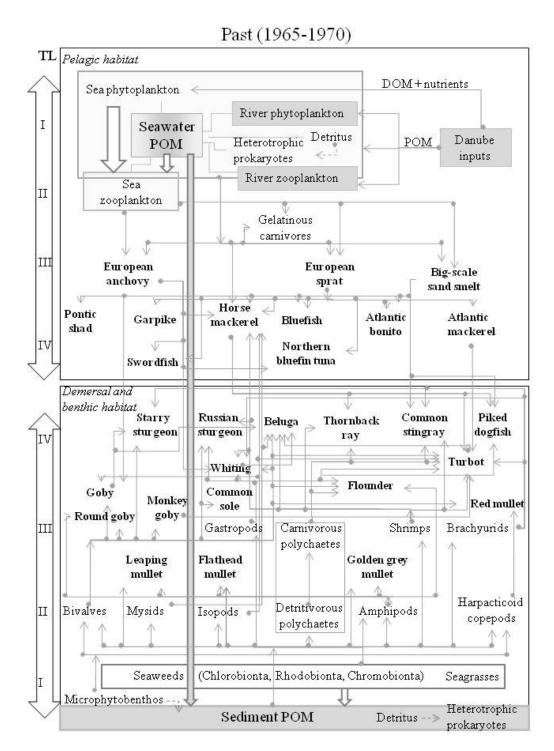




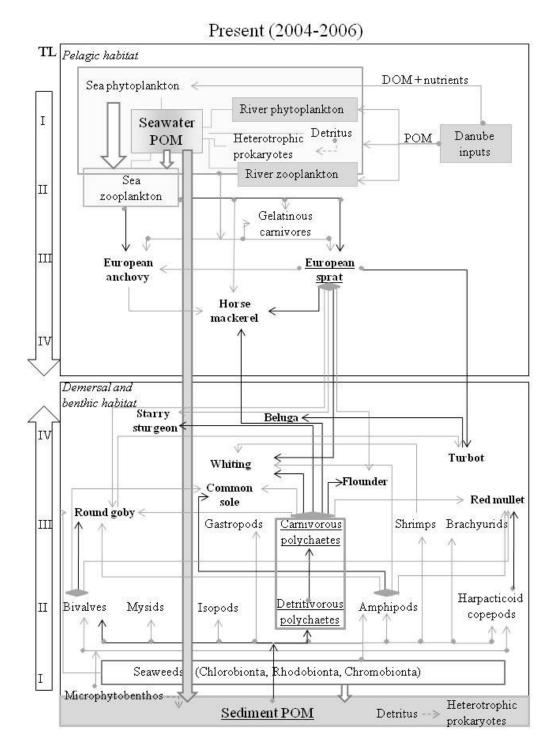






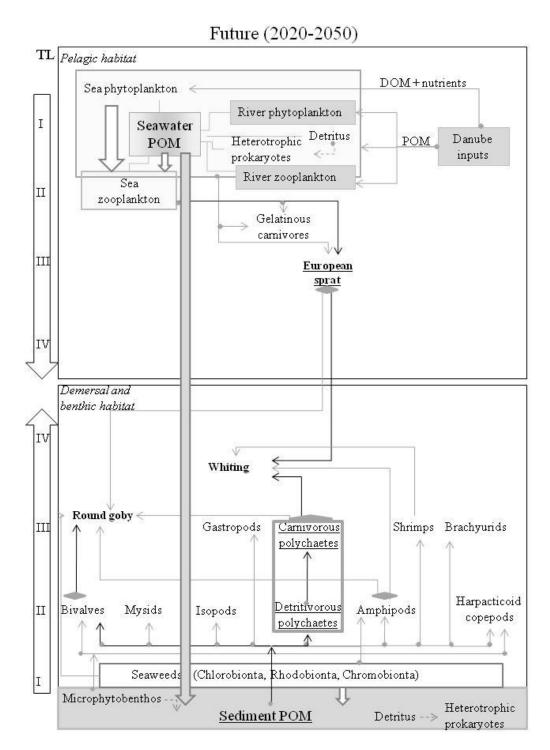


P



P

807



P

808

