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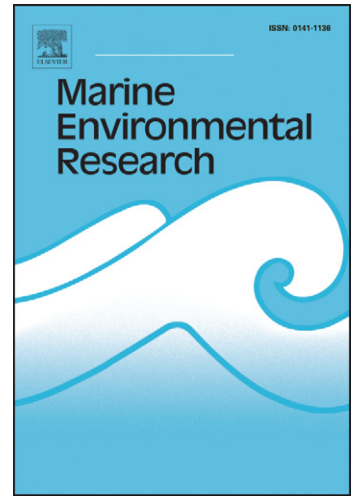

Man induced change in community control in the north-western Black Sea: the top-down bottom-up balance

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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

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

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

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ABSTRACT

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

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

1. Introduction

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 actually right". The recovery of fish stocks depends not only on stopping overfishing but is also strongly conditioned by the state of the ecosystems. Fishing activities have a direct and indirect impact on the ecosystem, where target and non-target species establish complex relationships (Jennings and Kaiser, 1998; Jackson *et al*., 2001). Fishing affects habitat, biodiversity, structure, functioning, stability and productivity of marine ecosystems (Jennings and Kaiser, 1998; Hughes and Petchey, 2001; Worm and Duffy, 2003). It may eliminate key species, cause trophic cascades and shifts in species dominance and change food web functioning from a top-down to a bottom-up pattern of control (Steneck, 1998; Cury *et al*., 2008). A top-down control represents the regulation of ecosystem components at low trophic levels by species at higher trophic level (control by predation). A bottom-up controlled food web is regulated by either primary producers or the input of limited nutrients through changes in the physical environment (controlled by the environment) (Cury *et al*., 2001, 2008). Actually, an ecosystem may be driven by a balance of top-down and bottom-up control rather than by only one type of control (Cury *at al*., 2008). Understanding how fishing activities impact complex food webs is essential for an ecosystem approach to fisheries (FAO, 2003).

The Black Sea-Danube River system is probably the most eloquent example to illustrate the impact of coastal human activities on marine commercial fish food webs. Black Sea species diversity is low compared to that of other seas because of its origin and ecological particularities. Before the Pliocene the Black Sea was a freshwater lake. It became connected temporarily with the Mediterranean Sea during the Mindel-Riss and Riss-Würm interglacial periods and permanently since the end of the Würm glaciation (Lericolais *et al*., 2003). High river freshwater inputs into the semi-enclosed Black Sea induce low salinity and high variation of all ecological parameters. Reduced vertical water circulation creates high stratification and anoxic conditions below 180 m depth (Gomoiu, 1996). High plankton production from the north-western part of the Black Sea is stimulated by the huge Danube

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

In the Black Sea, as in many other seas, overfishing and environmental variability due to increasing human impact have induced the collapse of fisheries (Mee, 1992; Gomoiu, 1996, 2004; Daskalov, 2003; Lotze, 2007). Hilborn (2006) was right in emphasizing that there are some places in the world where fisheries are successful (Iceland, Alaska, USA, Canada and New Zealand) as these fisheries and ecosystems are well managed. But he also says that fish are "a lot less abundant than they were in the past" with strong ecosystem impacts and that "Europe is just a basket case because of the institutional structure, the EU and the need for consensus". "There are a lot of countries that have very little effective governance" and Hilborn says that he "can't be that optimistic about what's going to happen in those places". Thus our study is in agreement with some of Dr Hilborn's ideas. The Romanian fishery in the Black Sea is a typical example of a case where problems due to the lack of fisheries and ecosystems management, along with pollution and overfishing over the last decades, led to the 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):

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

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, $H'max = \log_2 S$.

Trophic level of each fish species was indicated from Stergiou and Karpouzi (2002), Bănaru (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:

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

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). 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 (Briand, 1983; Link, 2002) and was calculated as:

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

Complexity and system persistence or "stability" are related (Briand, 1983). The product S x 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).

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

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

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

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

3. Results

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

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

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

Between 1965 and 1980 the only fishing technique used on the Romanian coast was crawl (stationary net fishing near the coast in shallow waters, about 10 m). Their number was high in the 1960s, decreased in the late 1970s, increased in the 1980s and strongly decreased again after 1987 (Fig. 2b). Since 1980 trawling boats have started to fish in this area. They were more efficient and covered a larger surface, in both shallow and deep waters. Trawling boat catches were higher than those made by crawls (Fig. 2c). Between 1980 and 1988 total catches increased, then decreased drastically after 1990. Probably due to catches and rentability decreases, the number of crawls also stongly decreased. The analysis of CPUE changes by crawls and trawling boats gave a good image of fish catches in this area. After a peak in CPUE in the 1980s, CPUE have decreased for both crawls and trawling boats since 1990 (Fig. 2c).

The specific composition of fish catches also dramatically changed (Fig. 3a-d). In 1965-1970 European sprat, European anchovy, Pontic shad and horse mackerel dominated the pelagic catches, while in 2001-2005 one single species, the European sprat, represented 90% of the pelagic catches. Demersal and benthic catches were dominated in 1965-1970, in order of decreasing percentages, by sturgeons, flounder, turbot, whiting and gobies, while in 2001-2005 only low commercial value fish species, such as whiting and gobies, were frequent.

The species diversity and evenness of commercial fishes on the Romanian Black Sea coast, estimated by the Shannon index (H') and by the Pielou index (J') respectively, decreased between 1965-1970 ($H'_{\text{pelagic fishes}} = 1.33$; $H'_{\text{bentho-demersal fishes}} = 0.46$; $J'_{\text{pelagic fishes}} = 0.55$; $J'_{\text{bentho-demersal fishes}} = 0.26$) and 2001-2005 ($H'_{\text{pelagic fishes}} = 0.31$; $H'_{\text{bentho-demersal fishes}} = 0.17$; $J'_{\text{pelagic fishes}} = 0{,}11$; $J'_{\text{bentho-demersal fishes}} = 0{,}08$). Following the reduction of large predatory fish catches, the mean fisheries trophic level decreased between 1965 and 2005 from 3.21 to 2.96 (Table 1).

3.2. Past food web

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

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

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

Multiple organic matter (OM) sources for food webs existed in this area: Danube POM inputs, marine phytoplankton, multicellular photosynthetic organisms (MPOs) (seaweeds and seagrasses) and microphytobenthos. OM fluxes circulated via many trophic pathways into diverse pelagic, benthic and demersal food webs (Fig 4).

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

3.3. Present food web

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

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

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

4. Discussion

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

4.1 The Black Sea environment and the problem of a baseline

Because of its particularities the Black Sea is probably more vulnerable to human impact than most other seas (Bănaru, 2008). The Black Sea presents the highest enclosure index (99.6) among all the semi-enclosed seas in Europe (de Leiva Moreno *et al*., 2000). Its large catchment area (1 378 317 km^2) compared to its surface (422 090 km^2) has contributed to the increase of nutrients and primary production with the development of human activities. The “low biomass” of phytoplankton in the pristine state of the Black Sea before 1970 was transformed into a "moderate biomass" state in the 1970s and to a "high biomass" state in the 1980s and 1990s (Oguz and Gilbert, 2007). These changes were related to increasing human population and development in agriculture and industrialisation that resulted in the increase in nutrient loads to the Black Sea via major European rivers, particularly the Danube River (Table 2), but also the Don, Dniper, Dniestr and Bug, which turned the Black Sea into one of the most eutrophicated seas of the world (Cociaşu *et al*., 1996; Zaitev and Mamaev, 1997; Berlinsky *et al*., 2006; Yunev *et al*., 2007). Ecosystem changes, particularly in the north-western Black Sea, include enhanced and more widespread episodes of hypoxia and anoxia, increased sedimentation and turbidity, loss of seagrasses and the decline of benthic species diversity (Zaitev and Mamaev, 1997). Some authors have suggested a recovery of the Black Sea in the late 1990s following the reduction of phytoplankton blooms (Cociaşu and Popa, 2004; Dumitrache and Abaza, 2004; Oguz and Gilbert, 2007).

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

4.2. Fisheries trends in the north-western Black Sea

FAO fisheries statistics enabled us to analyse patterns of change in the Romanian fisheries between the past and the present. Fisheries landings strongly decreased between 1965 and 2005 and their specific composition changed. No estimation of Shannon and equitability indices for fisheries was ever calculated in this area before this study. Commercial pelagic and bentho-demersal fish diversity and equitability on the Romanian coast strongly declined between 1965-1970 and 2001-2005. In any case, these values are very low (H' = [0.17-1.33]; J' = [0.08-0.55]) compared to the seagrass fish community in the Mediterranean Sea (H' = [3.57-4.22] and J' = [0.71-0.81]) (Bell and Harmelin-Vivien, 1982).

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

4.3. A decreasing mean trophic level

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

Zaitev (1992) showed the same trend in the Black Sea Ukrainian fisheries between 1980 and 1990 when species number reduced and only small pelagic fish species catches were high. Tatara (1991) shows that both a decline in mean trophic level and a linked increase in planktivores are responses to the eutrophication of the Seto Inland Sea by nutrient run-off. 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 effects 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 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 appears to present one of the most striking examples of "ecological regime-shift" events reported so far for large pelagic marine ecosystems (Oguz and Gilbert, 2007). In the 1980s and 1990s the classical "phytoplankton-zooplankton-pelagic fish" food chain shifted to one dominated by opportunistic species and gelatinous carnivores, which are a trophic dead-end (Oguz and Gilbert, 2007). Some authors argued that these events were related to the North Atlantic Oscillation (NAO) and the East Atlantic-West Russia (EAWR) (Bilio and Niermann, 2004; Oguz and Gilbert, 2007).

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

Analyzing the entire food web we might wonder whether we are really dealing with a "regime-shift" or whether this system has gradually become poorer and more simplified following the loss of species and their trophic links? As it presents most of the consequences of regime-shifts as described by Cury and Shannon (2004), it could be considered as a regime shift.

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

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

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

4.6. The connectivity decline: towards stability or instability?

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

There is disagreement on the relation between the persistence (stability) and effects caused by losing either a low or high trophic level species from a trophic web (Ives *et al.* 1999). The north-western Black Sea food web lost most of its top predators and Duffy (2003) argues that the loss of large consumers has a stronger impact on ecosystem functioning than the loss of primary producers because of their relatively low diversity, low functional redundancy and high interaction strengths. Many ecological studies have dealt with the relation between complexity (connectivity) and stability (persistence) (Briand, 1983). May (1973) argues that an increase in the number of links in a food web decreases the ecosystem's stability. However, there is also disagreement whether higher complexity increases, decreases, or has alternating effects on overall stability (Link, 2002).

The food web analyzed presented in 1965-1970 a connectivity of 21%, a value higher than in the estuary (9.7%) analyzed by Hall and Raffaelli (1991) and lower than on the marine continental shelf (48.2%) analyzed by Link (2002). The C x S Lyapunov stability proxy of the Romanian marine food web presented a value (9.2) similar to that of the cited estuary (9) and much lower than the continental shelf (39.1). The number of species and the connectivity of the Black Sea system in 1965-1970 compared to other systems suggest that, like the marine continental shelf studied by Link (2002), it should be considered as an "unstable" system. After a period of over-exploitation, in 2001-2005 the connectivity of the Black Sea food web has decreased. This new value, similar to the results of Link (2002) after a period of over-exploitation, and compared to the food web connectivity in other systems, should be qualified as "stable". Link (2002) argues that the limits of "stable" and "instable" were mathematically estimated for terrestrial or freshwater ecosystems which are very different from marine ecosystems. In fact, in marine ecosystems, species present mostly a generalist and opportunist feeding behaviour pattern and some characteristics of these systems such as the "cultivation-depensation effects" strongly influence its functioning (Walters and Kitchell, 2001). Finally, we cannot say whether the changing Black Sea commercial fish food web is in the present becoming "stable" or not.

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

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

The reduction of nutrient inputs from the Danube River in the late 1990s, together with the reduction of *Mnemiopsis leidyi* by *Beroe ovata*, induced a decline in gelatinous stocks and an increase in small fish landings (Gucu, 2002; Dumitrache and Abaza, 2004; Oguz and Gilbert, 2007). However, the increase in pelagic fish landings is low compared to the decline of fisheries recorded over the last decades and the recovery effect of the food webs is far from certain, as suggested by our results. A partial recovery of the Black Sea - Danube River system should be possible if nutrient inputs into the Black Sea and all marine fisheries are strongly reduced over the coming decades. However, according to the hypothesis used in this study, Danube inputs and fisheries will maintain the same trends and there will be no recovery or stability but only an increase of the present trends.

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

Acknowledgements

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 ethics permit numbers of the countries (Romania, France and U.K) in which they were performed. Thanks are expressed to M. Paul for improvement of the English and to the editor of Marine Environmental Research and two anonymous reviewers for helping us to improve the manuscript.

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

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

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

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

Fig. 5. Food web of the main commercial pelagic and bentho-demersal fish species on the Romanian coast in the north-western Black Sea in the present (2004-2006) reconstructed from gut content and stable isotope ratio analyses. 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. Seagrasses and most of the top predator fish species present in 1965-1970 have disappeared.

Fig. 6. Future food web of the main commercial pelagic and bentho-demersal fish species on the Romanian coast 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).

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 species							
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).

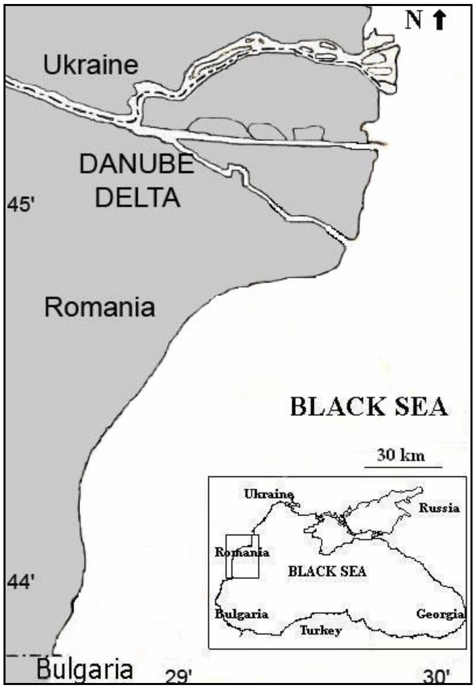
(3)Sturgeons: Russian sturgeon - *Acipenser gueldenstaedtii* Brandt and Ratzeburg, 1833, Starry sturgeon - *Acipenser stellatus* Pallas, 1771, Beluga - *Huso huso* (Linnaeus, 1758).

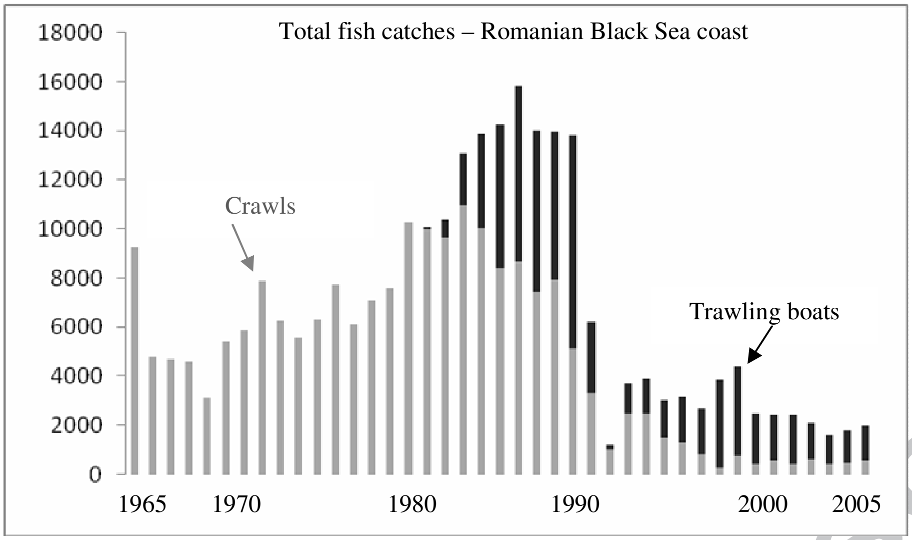
(4)Rays: Common stingray - *Dasyatis pastinaca* (Linnaeus, 1758), Thornback ray - *Raja clavata* Linnaeus, 1758.

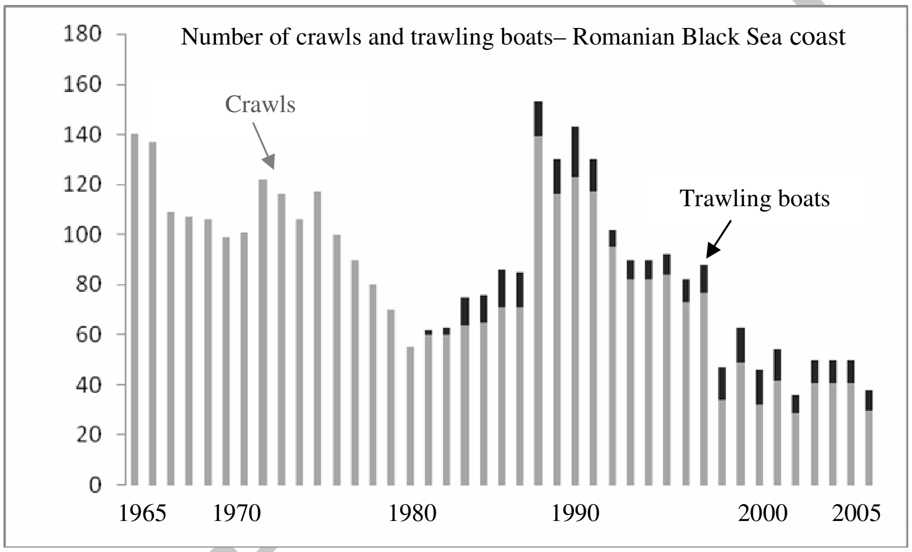
Table 2

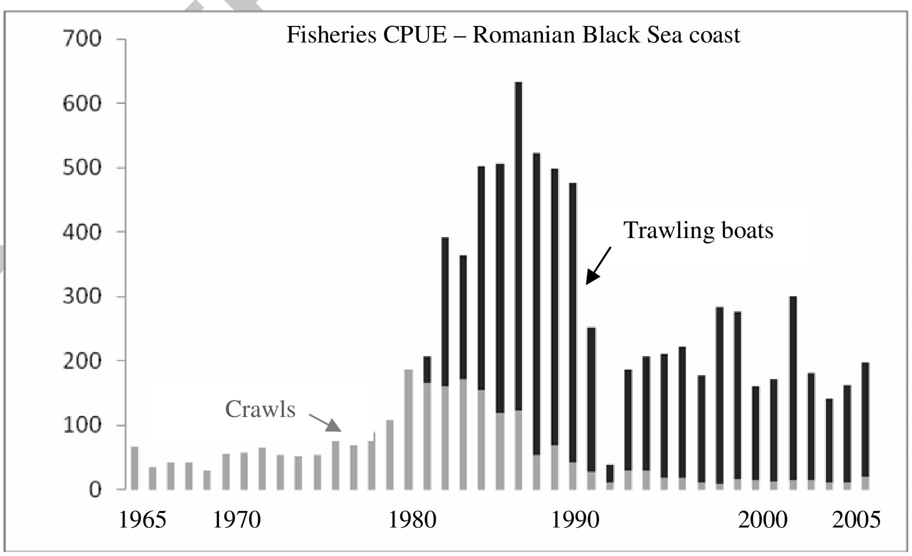
Danube mean annual water discharge (*Cociaşu *et al*., 1996), annual variability of the nutrient concentration in the Black Sea in the zone of the Danube water influence (**Berlinsky *et al*., 2006), long term changes of phytoplankton variables (***Yunev *et al*., 2007) and eutrophication phases of the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

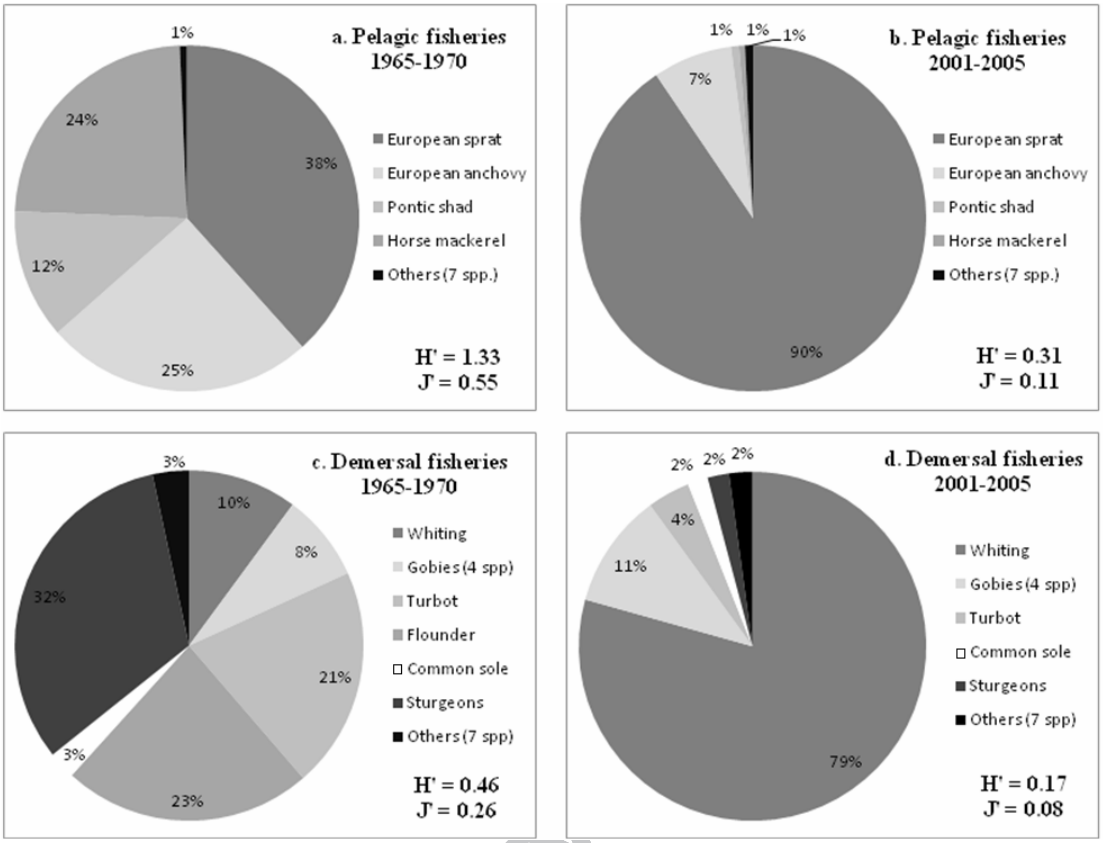
	1960s	1970s	1980s	1990s	
Danube water discharge (km^{-3})	213,40	223,30	196,00	184,40	*
Nutrient concentration ($mg\ L^{-1}$)					
NH_4^+	0,025	0,445	0,470	0,081	**
NO_2^-	0,003	0,005	0,061	0,006	**
NO_3^-	0,010	0,042	0,619	0,056	**
N_{org}	0,230	0,441	1,767	0,706	**
PO_4^{3-}	0,014	0,029	0,142	0,025	**
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, 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-	****


N
Ukraine
DANUBE
DELTA
45'
Romania
BLACK SEA
30 km
Ukraine
Russia
Romania
BLACK SEA
Bulgaria
Georgia
Turkey
44'
Bulgaria
29'
30'

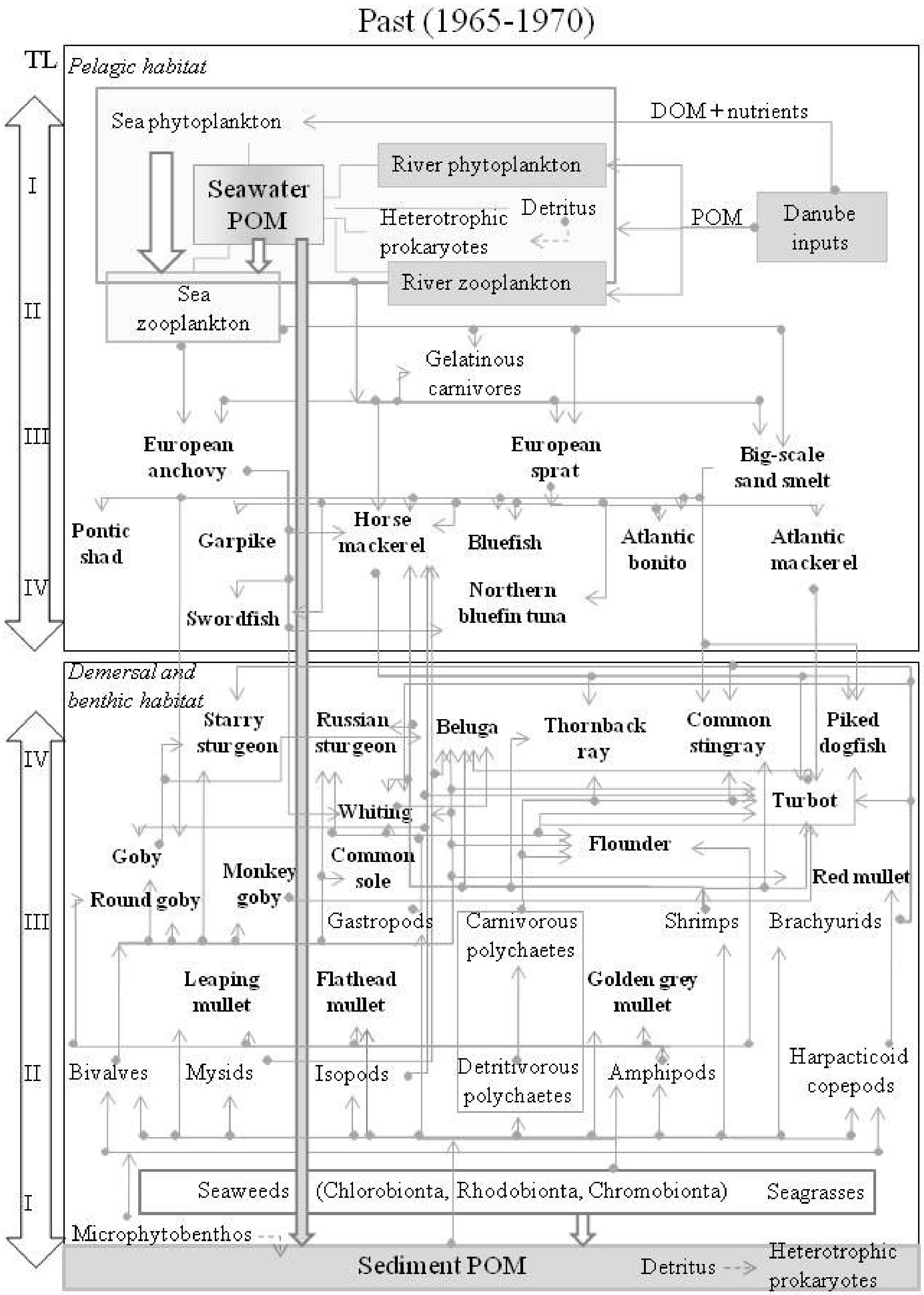

Total fish catches – Romanian Black Sea coast
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
Crawls
Trawling boats
1965
1970
1980
1990
2000
2005


Number of crawls and trawling boats– Romanian Black Sea coast
180
160
140
120
100
80
60
40
20
0
Crawls
Trawling boats
1965
1970
1980
1990
2000
2005

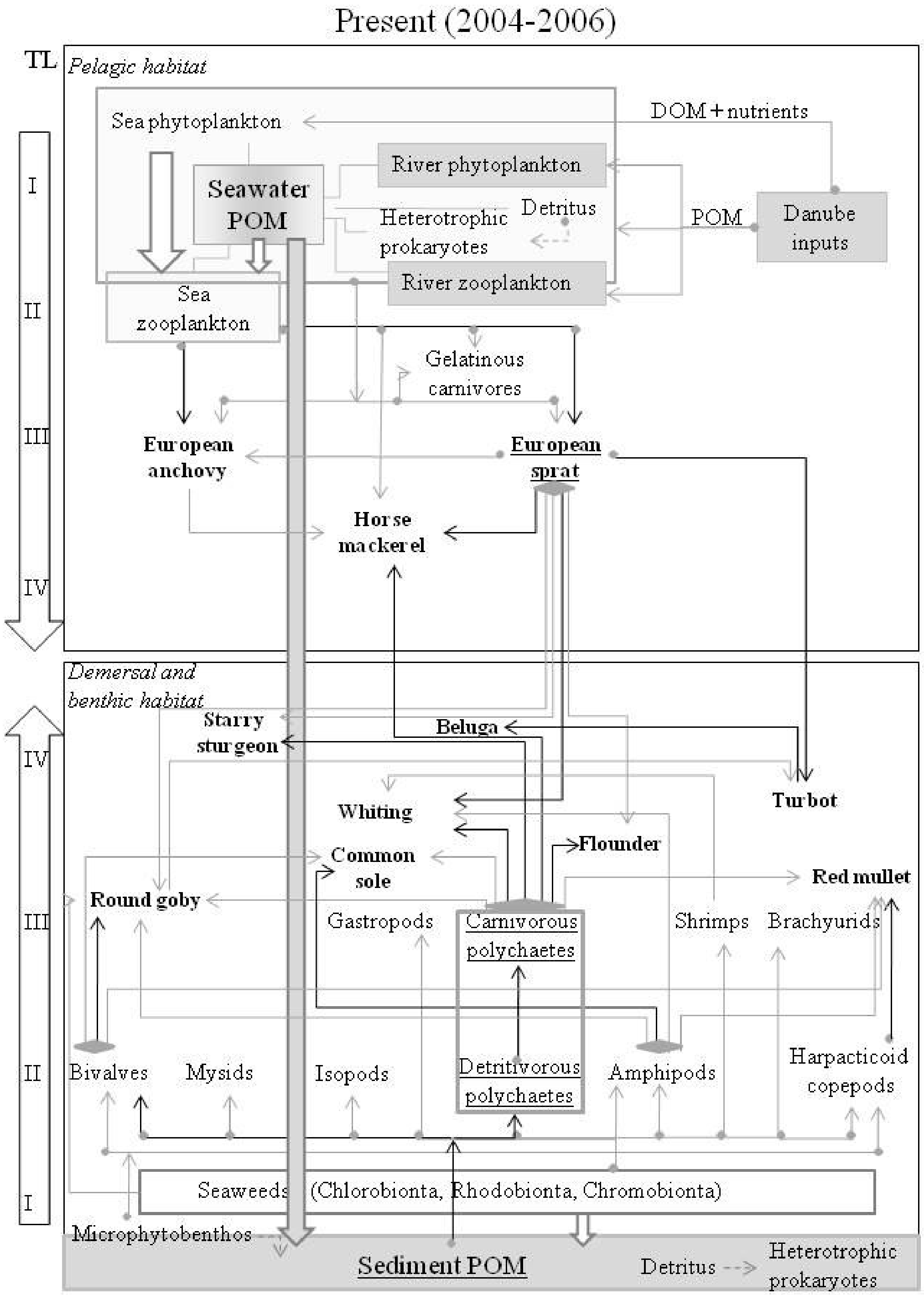

Fisheries CPUE – Romanian Black Sea coast
700
600
500
400
300
200
100
0
Trawling boats
Crawls
1965
1970
1980
1990
2000
2005



a. Pelagic fisheries
1965-1970
1%
24%
38%
12%
25%
European sprat
European anchovy
Pontic shad
Horse mackerel
Others (7 spp.)
H' = 1.33
J' = 0.55
b. Pelagic fisheries
2001-2005
1%
1%
1%
7%
90%
European sprat
European anchovy
Pontic shad
Horse mackerel
Others (7 spp.)
H' = 0.31
J' = 0.11
c. Demersal fisheries
1965-1970
3%
10%
8%
32%
21%
3%
23%
Whiting
Gobies (4 spp)
Turbot
Flounder
Common sole
Sturgeons
Others (7 spp)
H' = 0.46
J' = 0.26
d. Demersal fisheries
2001-2005
2%
2%
2%
4%
11%
79%
Whiting
Gobies (4 spp)
Turbot
Common sole
Sturgeons
Others (7 spp)
H' = 0.17
J' = 0.08

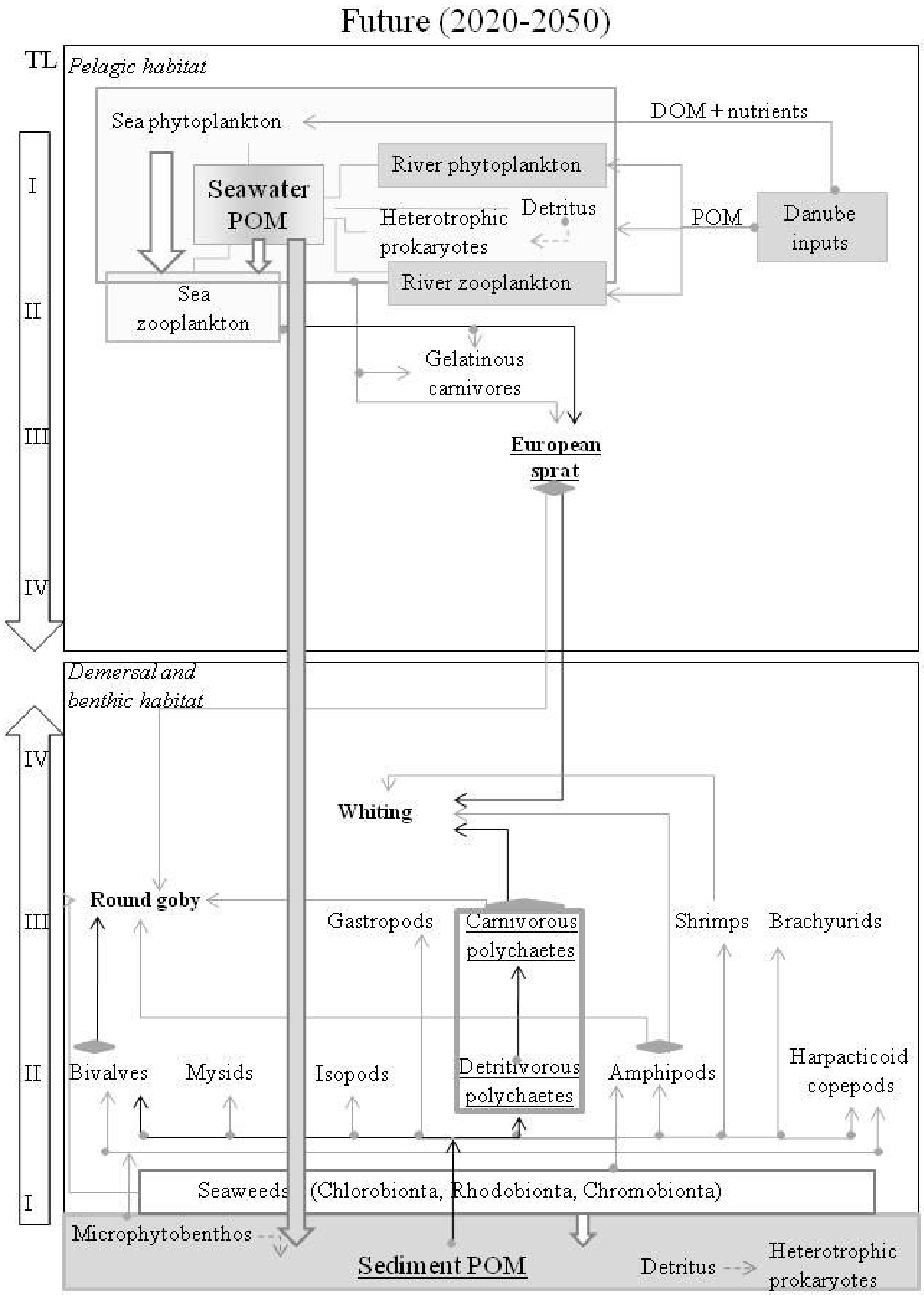

Past (1965-1970)
TL
Pelagic habitat
I
II
III
IV
Sea phytoplankton
DOM+nutrients
River phytoplankton
Seawater POM
Heterotrophic prokaryotes
Detritus
POM
Danube inputs
River zooplankton
Sea zooplankton
Gelatinous carnivores
European anchovy
European sprat
Big-scale sand smelt
Pontic shad
Garpike
Horse mackerel
Bluefish
Atlantic bonito
Atlantic mackerel
Northern bluefin tuna
Swordfish
Demersal and benthic habitat
Starry sturgeon
Russian sturgeon
Beluga
Thornback ray
Common stingray
Piked dogfish
Whiting
Turbot
Flounder
Goby
Monkey goby
Common sole
Red mullet
Round goby
Gastropods
Carnivorous polychaetes
Shrimps
Brachyurids
Leaping mullet
Flathead mullet
Golden grey mullet
Bivalves
Mysids
Isopods
Detritivorous polychaetes
Amphipods
Harpacticoid copepods
Seaweeds
(Chlorobionta, Rhodobionta, Chromobionta)
Seagrasses
Microphytobenthos
Sediment POM
Detritus
Heterotrophic prokaryotes

806



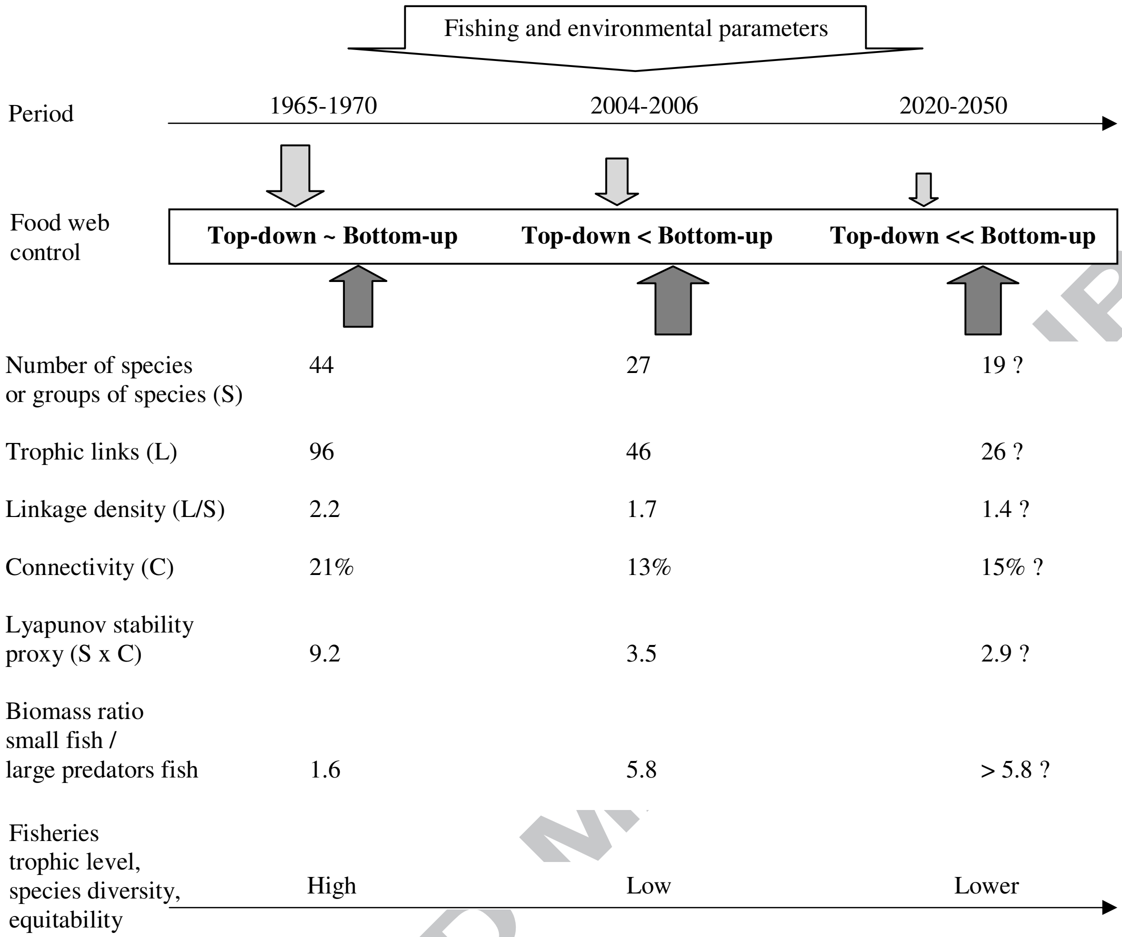
Present (2004-2006)
TL
Pelagic habitat
I
II
III
IV
Sea phytoplankton
DOM + nutrients
River phytoplankton
Seawater POM
Heterotrophic prokaryotes
Detritus
POM
Danube inputs
River zooplankton
Sea zooplankton
Gelatinous carnivores
European anchovy
European sprat
Horse mackerel
Demersal and benthic habitat
IV
III
II
I
Starry sturgeon
Beluga
Turbot
Whiting
Common sole
Flounder
Red mullet
Round goby
Gastropods
Carnivorous polychaetes
Shrimps
Brachyurids
Bivalves
Mysids
Isopods
Detritivorous polychaetes
Amphipods
Harpacticoid copepods
Seaweeds (Chlorobionta, Rhodobionta, Chromobionta)
Microphytobenthos
Sediment POM
Detritus
Heterotrophic prokaryotes

807

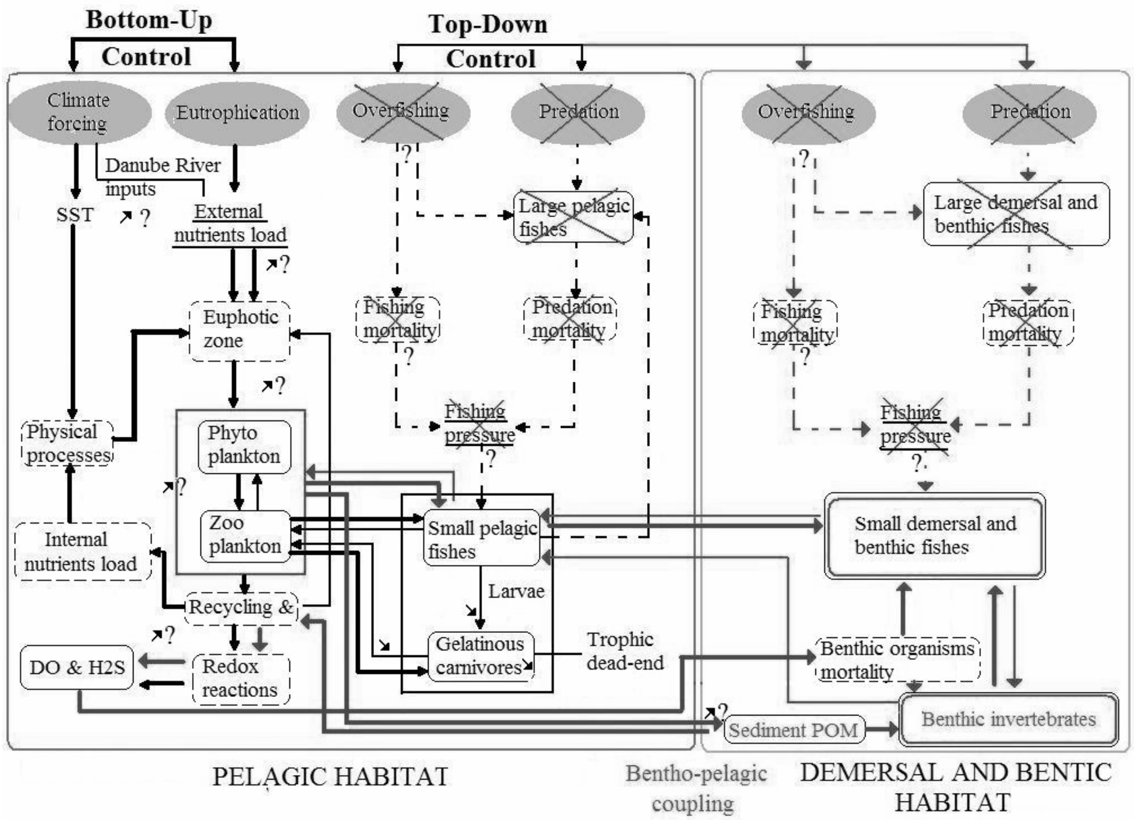


Future (2020-2050)
TL
Pelagic habitat
I
II
III
IV
Sea phytoplankton
DOM+nutrients
River phytoplankton
Seawater POM
Heterotrophic prokaryotes
Detritus
POM
Danube inputs
River zooplankton
Sea zooplankton
Gelatinous carnivores
European sprat
Demersal and benthic habitat
IV
Whiting
III
Round goby
Gastropods
Carnivorous polychaetes
Shrimps
Brachyurids
II
Bivalves
Mysids
Isopods
Detritivorous polychaetes
Amphipods
Harpacticoid copepods
I
Seaweeds (Chlorobionta, Rhodobionta, Chromobionta)
Microphytobenthos
Sediment POM
Detritus
Heterotrophic prokaryotes

808



Fishing and environmental parameters
Period
1965-1970
2004-2006
2020-2050
Food web control
Top-down ~ Bottom-up
Top-down < Bottom-up
Top-down << Bottom-up
Number of species or groups of species (S)
44
27
19 ?
Trophic links (L)
96
46
26 ?
Linkage density (L/S)
2.2
1.7
1.4 ?
Connectivity (C)
21%
13%
15% ?
Lyapunov stability proxy (S x C)
9.2
3.5
2.9 ?
Biomass ratio small fish / large predators fish
1.6
5.8
> 5.8 ?
Fisheries trophic level, species diversity, equitability
High
Low
Lower


Bottom-Up
Control
Top-Down
Control
Climate forcing
Eutrophication
~~Overfishing~~
~~Predation~~
Danube River inputs
SST
External nutrients load
~~Large pelagic fishes~~
~~Large demersal and benthic fishes~~
Euphotic zone
~~Fishing mortality~~
~~Predation mortality~~
~~Fishing pressure~~
Physical processes
Phyto plankton
Zoo plankton
Internal nutrients load
Small pelagic fishes
Small demersal and benthic fishes
Larvae
Recycling &
DO & H2S
Redox reactions
Gelatinous carnivores
Trophic dead-end
Benthic organisms mortality
Sediment POM
Benthic invertebrates
PELAGIC HABITAT
Bentho-pelagic coupling
DEMERSAL AND BENTIC HABITAT

810