SHORT COMMUNICATION

Regional peculiarities of community-wide trophic cascades in strongly degraded Black Sea food web

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The community-wide trophic cascade due to collapsed fish stocks and population outburst of invasive predators after the early 1990s resulted in different pelagic and benthic food web structures in the Black Sea. The northeastern region assumed their most simplified forms characterized by increasing mesozooplankton and polychaete biomass. The ecological degradation is more severe in the northwestern part, whereas the southern basin maintains an anchovy fishery under relatively weak gelatinous predation.

KEYWORDS: Black Sea; benthic and pelagic food webs; fishery collapse; invasive species; trophic cascade

Coastal, marginal and semi-enclosed seas providing important economic resources are threatened at an increasing rate by acute human-induced pressures and subsequent severe degradation of food webs. Weakening of their resilience against external stresses makes them more vulnerable to overexploitation, nutrient enrichment and recycling, non-native species invasion and climatic variations. One of the well-marked signatures of their impacts is degradation of the food web structure by the development of an additional jelly-dominated food chain that may further be modified by changes in climate. This generally involves extensive summer blooms of harmful algae and red tide species (e.g. *Noctiluca scintillans*) and of jellyfish consumers. They complement the classical pelagic food chain that typically ends with large predatory fish consumers (Sommer *et al.*, 2002). A further marked change in food webs may arise due to community-level trophic cascades developed following heavy exploitation of higher trophic level fish stocks (Baum and Worm, 2009).

The Black Sea ecosystem is known to have complex pelagic and benthic food web organizations during different phases of its evolution. On the basis of composite data sets for the entire sea, the pelagic ecosystem was shown to experience two cascade mechanisms; first due to the collapse of large-bodied predatory fishes prior to the early-1970s and then collapse of the forage fishes at 1989−1991 (Daskalov *et al.*, 2007). These trophic cascades might have not acted in isolation but be

supported by the nutrient enrichment, climatic effects and population explosion of the invasive ctenophore, *Mnemiopsis leidyi* (Oguz and Gilbert, 2007; Oguz *et al.*, 2008; Oguz and Velikova, 2010). Benthic community structure, on the other hand, was heavily impacted by the opportunistic carnivorous gastropod species *Rapana venosa* in addition to *M. leidyi* (Shiganova *et al.*, 2008).

The present work points to regional differences in the Black Sea food web structure during the last two decades due to regional peculiarities of the community-wide trophic cascade mechanism. A distinct and common feature of this period is the abrupt decline of anthropogenic nutrient loads from the River Danube following disintegration of the former Soviet Union and shift of the nutrient limitation from dissolved inorganic nitrogen to phosphate in western coastal waters (Oguz and Velikova, 2010). Using an end-to-end ecosystem approach, the changes in pelagic and benthic food webs of the northeastern Black Sea will be first documented in terms of modifications in the trophic structures, and shifts in biomass and productivity towards lower trophic levels. They are then compared with those of the northwestern and southern regions. The degradation of the northeastern food web started with moderate level eutrophication commencing in the early 1970s in response to heavy fertilizer consumption in the Krasnodar region of the former Soviet Union.

The available data are compiled from the report of the Black Sea Commission, BSC (BSC, 2008) and comprise five trophic levels; primary producers (phytoplankton), primary, secondary and tertiary consumers (zooplankton, fish and jellyfish) and macrozoobenthos. *Mnemiopsis* and *Beroe* abundances are collected in offshore waters of the northeastern Black Sea during August and September, respectively, representing their peak production periods (Shiganova *et al.*, 2008). The annual mean non-gelatinous zooplankton biomass data comprise those reported originally by Kovalev *et al.* (Kovalev *et al.*, 1998) for the interior region of the central and eastern basins for 1960–1998 and Arashkevich *et al.* (Arashkevich *et al.*, 2008) for offshore waters of the northeastern Black Sea during 1999–2008 (see also Shiganova *et al.*, 2008). The phytoplankton biomass data represent the summer–autumn (May–November) mean integrated values over the euphotic zone for the interior region of the eastern basin (Nesterova *et al.*, 2008). The zoobenthos data are provided in terms of the annually mean biomass on the basis of the available measurements performed along the northeastern Black Sea coastal waters (Chikina and Kucheruk, 2005; Revkov *et al.*, 2008). The total annual fish landings for the Russian Federation exclusive economic zone (i.e. the northeastern Black Sea) are

retrieved from the Global Fisheries Mapping database of the Sea around Us project (http://www.seaaroundus.org). They are further complemented by the basin-average winter mean sea surface temperature compiled from different sources (BSC, 2008).

The fish landing (Fig. 1a) shows a severe decline from ~100 ktons in 1986 to less than 25 ktons in 1990. Thereafter, it remained at ~10 ktons level during the 1990s followed by a slight increase to 25 ktons after 2000. The catch data therefore infer relatively weak grazing pressure of planktivores on the lower trophic levels following the collapse at 1989–1990. The collapse coincided with the *Mnemiopsis* population outburst with a mean value of 1000 individual per m^2 (Fig. 1b), reaching at a maximum value of 7600 ind. m^{-2} ($\approx$ 4.6 kg m^{-2}) (Vinogradov *et al.*, 1999). According to model simulations (Oguz *et al.*, 2008), the collapse was initiated by the fishery overexploitation but then reinforced in response to the predation by and food completion with the *Mnemiopsis* population. Concurrently, the zooplankton biomass decreased and phytoplankton biomass increased considerably in 1991 and 1992 under heavy *Mnemiopsis* predation (Fig. 1a and d).

Starting during the exceptionally cold year 1993, zooplankton biomass experienced a decadal increasing trend (Fig. 1a), whereas *Mnemiopsis* abundance fluctuated interannualy superimposed on a generally decreasing trend (Fig. 1b). A similar decreasing trend of the phytoplankton biomass from more than 20 to less than 5 g m^{-2} during 1993–2002 (Fig. 1d) may be associated with strong predation pressure due to increasing non-gelationous zooplankton biomass. In addition, it is consistent with the warming trend of winter mean sea surface temperature giving rise to unfavorable physical conditions for promoting phytoplankton production (Fig. 1d). Thus, in the absence of fish stocks, *Mnemiopsis* constituted an effective top predator species in the system and introduced a trophic cascade that was further supported by the climatic warming trend during the 1990s. A similar system with much higher abundance of *M. leidyi* also prevailed in the western region (Kamburska *et al.*, 2006; Oguz and Velikova, 2010), whereas the southern region maintained the small pelagic fishery together with a relatively low *Mnemiopsis* abundance (Oguz *et al.*, 2012). Exploring the causes of such peculiar regional differences in the Black Sea food web structure requires additional data and model-based analyses.

More noticeable increase in non-gelationous zooplankton biomass occurred after 1999 up to more than 25 g m^{-2} at 2005–2008 in the northeastern region (Fig. 1a). This apparently coincided with low *Mnemiopsis* abundance below 200 ind. m^{-2} (Fig. 1b), implying
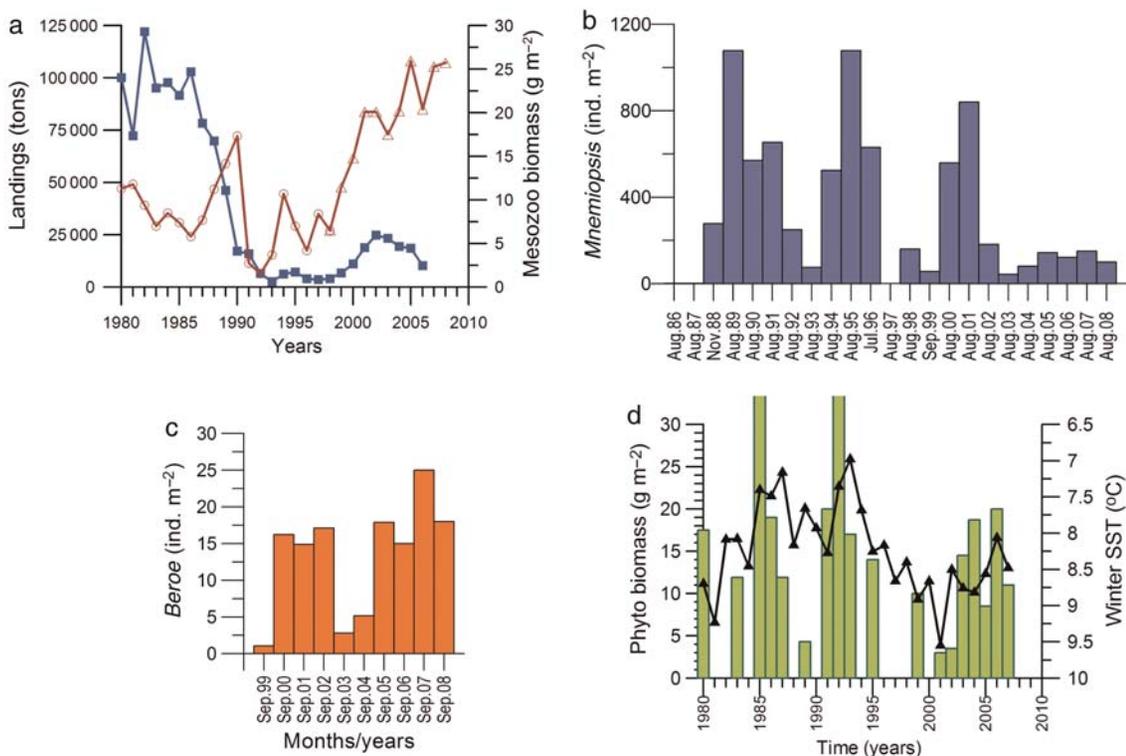
Fig. 1. Variations of (**a**) total fish landings (closed square) and mesozooplankton biomass provided by Kovalev *et al.* (Kovalev *et al.*, 1998) (open circle) and Arashkevich *et al.* (Arashkevich *et al.*, 2008) (open triangle), (**b**) *Mnemiopsis* abundance (ind.m^{-2}) in August, (**c**) *Beroe* abundance (ind.m^{-2}) in September, (**d**) summer-autumn mean phytoplankton biomass integrated over the euphotic zone (g m^{-2}) (vertical bars) and the winter mean sea surface temperature (closed triangle). "Aug" and "Sep" in (b) and (c) refer to August and September, and the subsequent two digit numbers to the last two digits of the years, respectively.

weakening of top-down predator control of *Mnemiopsis* as a result of their extensive predation following the population outburst of the predatory ctenophore *Beroe ovata* (Fig. 1c) (Shiganova *et al.*, 2008). Relatively cold climatic conditions during 2003–2005 may also have contributed to the low *Mnemiopsis* abundance (Vinogradov *et al.*, 2005). On the other hand, contrary to even stronger grazing pressure by zooplankton, there was an increasing trend in phytoplankton biomass after 2002. This may be explained by the positive correlation with the cooling cycle of winter mean sea surface temperature (Fig. 1d) that indicates favorable winter vertical mixing conditions for the subsequent stronger spring and summer phytoplankton production. As in the case of the warming trend in the 1990s, the cooling phase after 2001 thus appears to exert a considerable modifying effect on the pelagic food web structure. The total catch and, possibly, the total fish stock increased to some extent after 2001 once their competitor and predator *Mnemiopsis* population was reduced. Nevertheless, forage fishes appear to exert weak grazing pressure on the lower trophic levels. The biomass of the jellyfish *Aurelia aurita,* as a competitor of *Mnemiopsis,*

increased during this period (Arashkevich *et al.*, 2008). Its maximum value of about 600 g m^{-2} was, however, half of the observed biomass during the intense eutrophication period of the 1980s prior to the outburst of the *Mnemiopsis* population (Shiganova *et al.*, 1998).

The trophic cascade structure inferred from the data shown in Fig. 1 may also be supported quantitatively by correlation analysis. For example, considering the data set for 1993–2006, *Mnemiopsis* abundance shows a negative correlation with zooplankton biomass ($r = -0.41$, $P < 0.05$) and fish catch ($r = -0.27$, $P < 0.05$), and a positive correlation with phytoplankton ($r = 0.5$, $P < 0.05$). The correlation of phytoplankton with other members of the food web is, however, not statistically significant due to the combination of decreasing and increasing trends in the data. When the former period (1992–2001) is considered alone, its correlation with zooplankton biomass and SST becomes very high; $r = -1.0$ and $r = -0.9$ ($P < 0.05$), respectively.

The *Mnemiopsis* population outburst also exerted a strong impact on the zoobenthic community starting in the early 1990s. An increase in the organic material sedimentation rate reinforced oxygen deficiency in

deeper water and thus the lower boundary of the phytal zone became shallower along the northeastern coast of the Black Sea (Alekseev and Sinegub, 1992). Heavy *Mnemiopsis* predation on bivalve larvae restricted the settlement of young bivalves, whereas adult bivalves were consumed by the predatory gastropod species *Rapana*. As a result, the native bivalve communities *Chamelea gallina* at the depth range of $20-30$ m and *Mythilus galloprovincialis* at the depth range of $30-50$ m disappeared completely leading to a serious degradation of macrozoobenthic communities during the 1990s. In 1999, only a few specimens of *C. gallina* were recorded along the northeastern coast. The dominant species in the $10-30$ m depth range became the opportunistic bivalve species *Anadara inequivalvis* (Chikina and Kucheruk, 2005). This is a non-native species introduced into the Black Sea from the Indo-Pacific region around 1970, and competes for food (filter-feeder) and space with native species.

The reduction in the *Mnemiopsis* population by its predator *B. ovata* introduced a new transient cascade mechanism that resulted in replacement of macrozoobenthos with the opportunistic polychaete species after 1999 (Fig. 2). Reduction in *Mnemiopsis* predation strength allowed for temporally an order of magnitude increase in settlement (on the order of thousands) of *C. gallina*

Fig. 2. Time versus relative abundance of the predators (upper) and major elements of the benthic food web (lower) illustrating a conceptual model of the benthic trophic cascade and development of a new alternate state following the shift in predation pressure from the ctenophore *Mnemiopsis leidyi* to *Beroe ovata*. The numbers refer to the relative abundances of benthic fish (1), *Mnemiopsis* (2), *Beroe* (3), bivalve (4), *Rapana* (5), polychaete (6).

larvae and juveniles at in the $10-20$ m depth range and of *A. inaequivalvis* at $20-25$ m in 2000. A consequence of such a very dense young bivalve community of ~ 400 g m^{-2} (*Chamelea, Anadara, Pitar rudis*) during $2000-2002$ was their very slow growth rate due to the limited food availability to support their large population (Chikina and Kucheruk, 2005). At the same time, they have been exposed to heavy predation by the predatory gastropod *Rapana*, and their biomass reduced to ~ 100 g m^{-2} in 2003. Subsequently, the population density of *Rapana* increased from its background value of 1 ind. per 10 m^2 to 8 ind. m^{-2} in 2001 and 100 ind. m^{-2} in $2002-2003$ due to their intense predation pressure on bivalve populations. Subsequently, bivalve biomass and abundance decreased abruptly from 470 g m^{-2} and 1292 ind. m^{-2} in 2002 to $35-45$ g m^{-2} and $29-61$ ind. m^{-2} in $2003-2004$. The abrupt loss of bivalves resulted in the macrozoobethos community structure changing to an opportunistic deposit-feeding polychaete-dominated system as encountered in the northwestern Black Sea during the 1980s. Polychaete abundance increased from 300 to 1500 ind. m^{-2} and biomass from 2.5 to 7.5 g m^{-2} in $2003-2004$ (Chikina and Kucheruk, 2005). The lack of sufficient food for high *Rapana* population then caused a decline of their population to a background level in $2004-2005$.

The lack of recovery of forage fish stocks in the presence of high food availability and relatively weak gelatinous competition during the last decade is an interesting feature of the ecosystem evolution in the northeastern Black Sea. One explanation is the impact of ongoing heavy fishery exploitation. An alternative and more likely explanation may be the resilience of the ecosystem to recovery due to complex internal dynamical processes in the case of alternative stable states. Comparison of the ecosystem properties during the 1980s and 2000s (see fourth and fifth columns in Table I) clearly documents the presence of two alternate states before and after the community-wide trophic cascade introduced by *Mnemiopsis*. If this is really the case, then the recovery of fish stocks may delay until another community-level regime shift brings the system back to a new fish-dominated state.

Table I documents differences between the main elements of the recent ecosystem structure of the northeastern, western and southern regions. For example, in the western shelf ecosystem, the pelagic food web structure continued to be influenced by stronger predation controls by gelatinous ctenophore *M. leidyi* and the opportunistic heterotrophic dinoflagellate species *N. scintillans*, respectively, even after the introduction of *Beroe* and in the absence of forage fish stocks (Oguz and
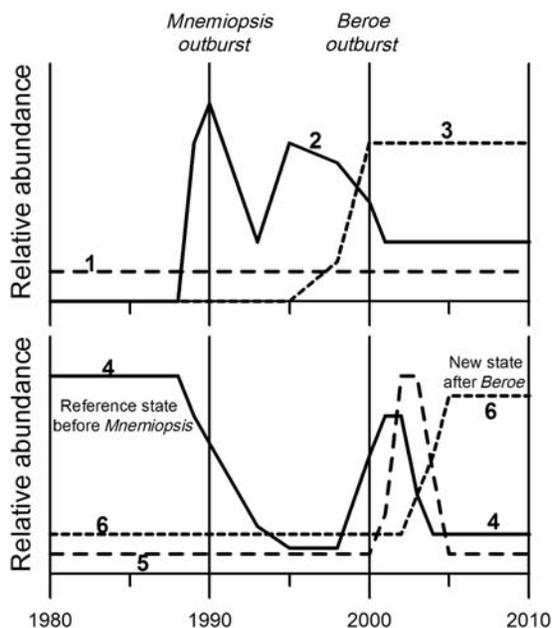
Table I: Approximate ranges of major ecosystem properties for three regions of the Black Sea during the last decade following the introduction of the gelatinous ctenophore species Beroe ovata *into the Black Sea*

Property	Northwestern region	Southern region	Northeastern region	Northeastern region (before 1990s)	Unit
Fish landing	0.04–0.1	1.5–2.3	0.15–0.3 (L)	~1.3 (H)	tons km^{-2}
Aurelia + Mnemiopsis	>500	<100	<200 (L)	>600 (H)	ind. m^{-2}
Noctiluca scintillans	<15000	<1000	<1000 (L)	>1000 (H)	ind. m^{-2}
Zooplankton	5–10	<3	25 (H)	<10 (L)	g m^{-2}
Phytoplankton	3–6	<0.5	<0.5 (L)	>1.0 (H)	g m^{-3}
Polychaete	~ 5500	~ 500	~ 1500 (H)	~ 300 (L)	ind. m^{-2}

The fifth column compares the alternate state of northeastern region during the 1980s with the recent one shown at fourth column. The values show approximate ranges and may involve some uncertainty due to conversion of the original data to common units for all regions. They allow for a gross comparison of ecological properties among the regions. The data are compiled from BSC (BSC, 2008). The bold letters L and H within parantheses refer to the "Low" and "High" abundance/biomass, respectively.

Velikova, 2010). The average *Mnemiopsis* abundance along the western shelf during 1998–2004 was roughly an order of magnitude higher than the northeastern region, even though the abundance became comparable for the open waters of the western basin (Kamburska *et al.*, 2006). They were complemented by the non-gelatinous mesozooplankton biomass of ~ 5 g m^{-2} depending on the warm/cold winter climatic conditions and the size of the *Mnemiopsis* population. The benthic food web was dominated by polychaetes as in the case of the northeastern region (Vorobyova and Bondarenko, 2009). On the other hand, the southern Black Sea was characterized by a relatively healthy structure (Table I) in which the impact of opportunistic and gelatinous species is less critical. The *Rapana* stocks reduced considerably along the western and southern coastal waters due to their over-harvesting and commercial export to east Asia. The southern region is able to provide roughly 85% of the total fish catch of the Black Sea that is, however, limited to the low commercial valued anchovy (Oguz *et al.*, 2012). Even this regional ecosystem structure, representing best of the Black Sea conditions, may be easily categorized as one of the worst observed cases at the global scale due to the complete depletion of higher trophic level fish catches except anchovy. The level of degradation of the northwestern and northeastern food webs in terms of fish biomass/landings, jellyfish/mesozooplankton abundance ratio, pelagic and benthic communities alternations may be considered rather exceptional cases among large marine ecosystems.

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