Abrupt transition of the northwestern Black Sea shelf ecosystem from a eutrophic to an alternative pristine state

Temel Oguz[1],*, **Violeta Velikova[2]**

[1]**Institute of Marine Sciences, Middle East Technical University, PO Box 28, Erdemli 33731, Mersin, Turkey**
[2]**Permanent Secretariat Commission on the Protection of the Black Sea Against Pollution, Istanbul, Turkey**

ABSTRACT: Long-term (1960–2005) ecological data were used to identify a regime shift in the northwestern Black Sea shelf and to assess whether it has recovered from its former eutrophic state. Following the collapse of fish stocks and the population explosion of the ctenophore *Mnemiopsis leidyi* between 1988 and 1991, anthropogenic P-PO$_4$ loads from the River Danube dropped strongly in 1992–1993. This decline in P-PO$_4$ levels was caused by reductions in fertilizer use and emissions from land-based point sources during the economic recession of former Eastern Bloc countries, as well as by the low discharge rate of the River Danube. Commencing in 1993, the phosphate limitation apparently maintained a low-energy, inefficient food web dominated by the dinoflagellate *Noctiluca scintillans* and jellyfish, and relatively low levels of phytoplankton, bacterioplankton, mesozooplankton and fish. This 'post-eutrophication' regime was markedly different from the classical phytoplankton-mesozooplankton-fish chain of the similarly low nutrient 'pre-eutrophication' regime prior to 1970. Therefore it appears that the food web can attain 2 alternative regimes during periods of low productivity of the ecosystem. The post-eutrophication state cannot be considered as a major improvement or restoration of the northwestern coastal ecosystem.

KEY WORDS: Black Sea · Coastal eutrophication · Nutrient limitation · Alternative community states · Regime shift · Trophic control

INTRODUCTION

The Black Sea has been one of the most polluted and mismanaged semi-enclosed seas in the world. The extensive pollutant loads discharged primarily by the River Danube, together with over-fishing, dumping of toxic wastes, intense shipping, mineral exploitation, introduction of non-native species, damming of inflowing rivers, and climatic variation have led to severe environmental degradation since 1970 (Sapojnikov 1992, Mee 1992, 2006, Vinogradova & Velikova 1992, Zaitsev 1992, Zaitsev & Mamaev 1997, Daskalov 2002, Kideys 2002, Sorokin 2002, Cociasu & Popa 2005, Yunev et al. 2007). Vast amounts of dead plants and animals have often been encountered in the northwest, along the Romanian and Ukrainian coasts. Between 1973 and 1990, despite losses estimated at 60 million

tons of benthic animals including 5 million tons of fish, pollution and eutrophication control measures were not implemented (Mee et al. 2005).

A general consensus of recent assessments of changing environmental conditions of the Black Sea is that the northwestern shelf (NWS) has improved in the last decade due to decreasing nutrient loads from the rivers (Parr et al. 2005, GEF-UNDP 2006, TDA 2007, BSC 2008). There have been fewer algal blooms, lower algal biomass, increasing plankton biodiversity, decreasing opportunistic and gelatinous species, and reappearance of cladocerans and copepods (Shiganova et al. 2008).

Ecological regime shifts denote abrupt changes that result in reorganization of the structure and function of ecosystems from one to another contrasting, persistent state (deYoung et al. 2008). Regime shifts driven syner-

gistically by climate-induced changes, eutrophication, and overfishing have been documented in many marine ecosystems. Concurrent with the apparent regime shift in the Black Sea, other shifts occurred in the Baltic Sea (Möllmann et al. 2009), northwest Atlantic (Choi et al. 2005), northeast Atlantic (Beaugrand et al. 2008), North Sea (Weijerman et al. 2005), and north Pacific (Hare & Mantua 2000). Characteristics of the Black Sea basin-scale regime shift have been studied by Daskalov et al. (2007), Oguz & Gilbert (2007), and Oguz et al. (2008a).

Measures taken at many coastal ecosystems, such as in the Baltic Sea (Hanninen et al. 2000, Lysiak-Pastuszak et al. 2004, Yurkovskis 2004), United States coastal ecosystems (Nixon et al. 1996, Scavia & Bricker 2006), and the Dutch Wadden Sea (Philippart et al. 2007), did not successfully alleviate eutrophication. Even lake and pond ecosystems with a relatively simple food web structure and a faster response to external controls may not achieve a transition to a healthier state after the reduction of nutrient loads or may have a delayed response depending on the internal feedback mechanisms (Genkai-Kato & Carpenter 2005, Ibelings et al. 2007). Here, we offer a novel viewpoint on the post-eutrophication ecological state of the northwestern Black Sea. We document an ecological regime shift that transformed the highly productive and eutrophic coastal ecosystem into a less productive but degraded state during the early 1990s. We assert that it differs considerably from the pristine state and does not truly represent a recovery.

MATERIALS AND METHODS

Study area. The northwestern Black Sea shelf is the triangular region shallower than 100 m between 42.5 and 46.5° N latitude and 28 and 33° E longitude (Fig. 1). It covers roughly 30% of the total Black Sea area and 94% of the overall shelf region around the basin. Its apex is located near Odessa in the north and the base extends along the shelf-break topography (e.g. 100 m depth) from the Bulgarian coast to the southern tip of Crimea (Ukraine). The topographic slope in the southwest makes the shelf progressively narrower towards the Bulgarian coast (Fig. 1). This feature and mesoscale exchanges between the

shelf and deep basin over the broad topographic slope zone (Korotaev et al. 2003, Yankovsky et al. 2004) reduce eutrophication southward. The shelf lying roughly north of ~45° N receives considerable fresh water and nutrient discharges from the Danube, Dniepr, Dniestr and Bug Rivers, and thus offers a more eutrophic and ecologically complex system.

Data sets. The long-term (1960 to 2005) data employed in the current study consists of annual mean concentrations of dissolved inorganic nutrients and biomass of phytoplankton, non-gelatinous and gelatinous zooplankton groups, or species measured at regularly monitored stations of the Ukrainian, Romanian and Bulgarian shelves (Fig. 1) as well as fish catches. This analysis is therefore limited to the
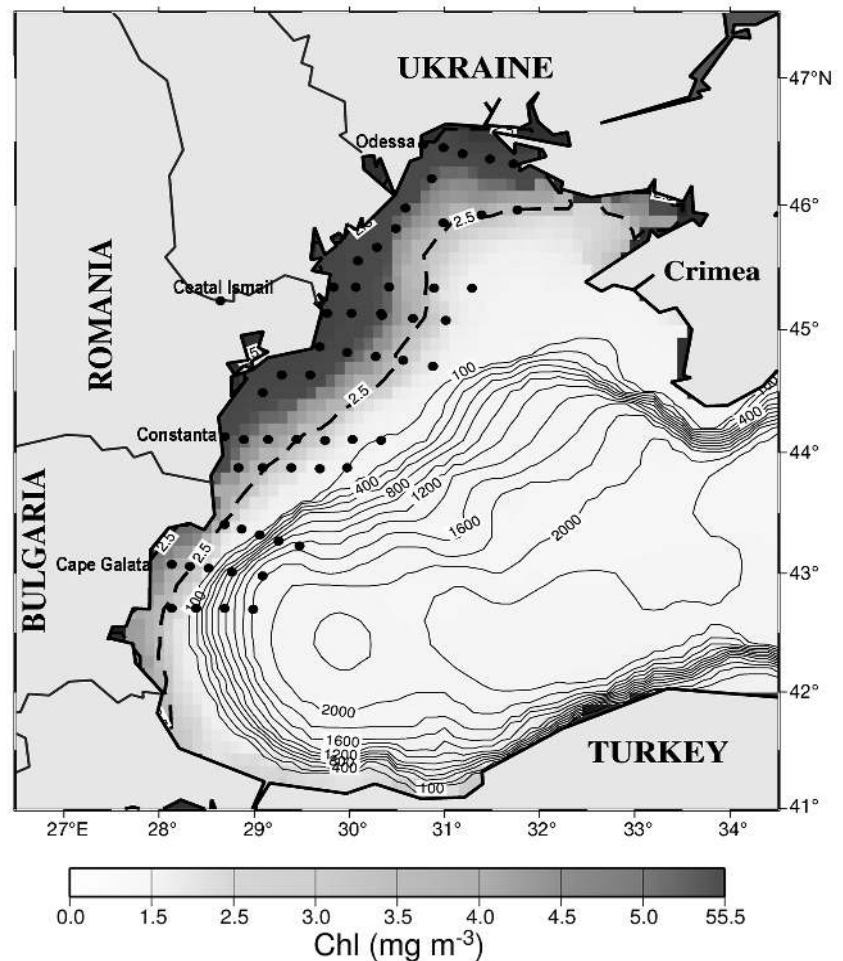

Fig. 1. Main geographic and topographic features of the northwestern Black Sea and the station network of long-term regular measurement sites (●) in the Bulgarian, Romanian and western Ukrainian shelves. Depth contours in m. The black line represents the 2.5 g m^{-3} contour of the 1998–2008 mean surface chlorophyll concentration that separates the more productive inner shelf zone and less productive outer shelf and deep basin (shown in white). The chlorophyll data are retrieved from 9 km monthly Sea-viewing Wide Field-of-view Sensor (SeaWiFS) products provided by http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.seawifs.2.shtml

pelagic ecosystem. Parameters, measurement periods, and data sources are listed in Table 1. The complete data set consists mostly of individual scientific contributions to the assessment of the state of Black Sea environment report (BSC, 2008) for the Secretariat of the Commission on the Protection of the Black Sea against Pollution (the Black Sea Commission, BSC). The individual data sets represent either specific measurements made at a particular station or regional averages of measurements made at several stations. They have been computed from available monthly or seasonal measurements depending on the parameter and institution that performed the measurements. Regional averaging offers a more general representation of the ecological conditions and applies mostly to the Ukrainian time series data (see Table 1). We conclude that a spatially uniform distribution of an 11 yr (1998–2008) average surface chlorophyll concentration (Fig. 1) justifies the use of data from multiple stations for some parameters and a single station for others. A chlorophyll concentration of 2.5 mg m^{-3} (Fig. 1) splits the shelf region into 2 distinct zones in terms of their capacity for biological production. The data sets used in the present study represent the more productive inner zone.

The annual mean sea surface temperature (SST) anomaly data were constructed from monthly measurements made at Odessa from 1950 to 1994 (Belevich & Orlova 1997), and at Constanta from 1980 to 2005 (Cociasu et al. 2008). The River Danube discharge anomaly for 1950 to 2005 was obtained from long-term monthly discharge measurements made at Ceatal Ismail (Cociasu et al. 2008), which is located upstream of the 3 branches of the River Danube (Fig. 1).

The long-term annual mean data sets for the dissolved inorganic nutrient (DIN) and silicate (SiO$_4$) concentrations are limited to measurements at the Romanian coastal monthly monitoring site at 3 nautical miles offshore of Constanta (Cociasu et al. 2008). These offer the only long time series for SiO$_4$ between 1960 and 2005 and for DIN (= NO$_3$ + NO$_2$ + NH$_4$) between 1981 and 2005. The Constanta DIN time series prior to 1981 was estimated by annual mean N-NO$_3$ measurements between the Danube discharge zone and Odessa on the Ukrainian shelf (Zaitsev et al. 2006). The Ukrainian data (see Fig. 2b) provided low N-NO$_3$ values during the pre-eutrophication phase (before 1970) and increasing N-NO$_3$ concentrations during the subsequent transition to the eutrophication phase (the 1970s).

Table 1. Parameters studied, their periods of availability in the Ukrainian, Romanian and Bulgarian shelves, and the data sources. X: no data available

| Parameter | Region | | | Source |
	Ukraine	Romania	Bulgaria	
SST	Odessa 1960–1994	Constanta 1980–2005	X	Belevich & Orlova (1997) Cociasu et al. (2008)
DIN	West coast 1968–1981	Constanta 1980–2005	X	Cociasu et al. (2008) Zaitsev et al. (2006)
P-PO$_4$	West coast 1974–2005	X	X	Loyeva et al. (2006)
SiO$_4$	X	Constanta 1959–2005	X	Cociasu et al. (2008)
Phytoplankton	West coast 1954–2005	Constanta 1983–2005	Galata 1961–2005	Nesterova et al. (2008)
Bacterioplankton	West coast 1979–2008	X	Shelf 1991–2003	Kovalova et al. (2008) Oguz et al. (2008b)
Trophic zooplankton	West coast 1954–2004	Shelf 1984–2007	Shelf 1959–2005	Grishin et al. (2007) Shiganova et al. (2008)
Noctiluca scintillans	West coast 1967–2006	X	Shelf 1967–2006	Shiganova et al. (2008)
Aurelia aurita	Shelf 1965–2001	X	X	Grishin et al. (2007) Shiganova et al. (2008)
Mnemiopsis leidyi	Shelf 1988–2005	X	X	Grishin et al. (2007) Shiganova et al. (2008)
Fish	X	Shelf 1960–2006	X	Navodaru et al. (2001) Maximov and Staicu (2008) Zahaira et al. (2008)

The Constanta phosphorus (P-PO$_4$) time series data were contaminated by the contribution from local waste water treatment plants near the measurement site, and therefore are not representative of typical conditions. An alternative data set provided by seasonal measurements at several stations along the western Ukrainian coastal waters (Loyeva et al. 2006) produced approximately half the concentration of P-PO$_4$ but similar long-term temporal changes.

Long-term annual mean phytoplankton biomass data were available from the Constanta monitoring site (Romania) starting in 1984, and from the Galata monitoring site (Bulgaria) in 1961 (Nesterova et al. 2008). For the Ukrainian shelf, phytoplankton data have been reported as multi-annual averages starting in the early 1970s (Nesterova et al. 2008). Although multi-annual averaging appreciably levels inter-annual variability, the analysis is able to capture transitions between ecological states.

Annual mean trophic zooplankton biomass was available for the Ukrainian and Bulgarian shelves between 1960 and 2005 and the Romanian shelf between 1984 and 2007. Here, trophic zooplankton is referred to as all non-gelatinous and non-opportunistic species groups (e.g. Copepoda, Cladocera, microzooplankton, meroplankton) that serve as the main prey for higher predators. The long-term annual mean jellyfish *Aurelia aurita* and ctenophore *Mnemiopsis leidyi* biomass data were provided as averages of the seasonal measurements only for the Ukrainian shelf at stations shown in Fig. 1.

Noctiluca scintillans has been a dominant species of the food web in the Black Sea. This well-known red tide organism is a voracious predator of phytoplankton, bacteria, detritus, microzooplankton, heterotrophic nanoflagellates, eggs and naupliar stages of copepods (Fock & Greve 2002, Umani et al. 2004). It has almost no predator (except *Sagitta setosa* and a limited number of copepod species) due to its low carbon and high ammonia content. Annual mean *N. scintillans* biomass data were available for the Bulgarian and Ukrainian coasts between 1967 and 2006. Data for the Ukrainian coast were available as multi-annual mean values after 1990. Bulgarian data, which were originally expressed as abundance, were converted to biomass by multiplying the abundance values by the average wet weight of 0.08 g (Fonda Umani et al. 2004).

The lower trophic level food web data were complemented by the long-term total capture production (the sum of fish, molluscs, crustaceans, and aquatic plants harvested or collected for commercial, industrial, and subsistence use excluding aquaculture production), total fish catch of freshwater, migratory and marine species, as well as piscivore catches on the Romanian shelf (Navodaru et al. 2001, Maximov & Staicu 2008).

The Ukrainian and Bulgarian catch data were not included in the analysis because they were not as comprehensive as the Romanian data. However, the data available followed similar temporal changes (Panayotova & Mikhailov 2006, Shlyakhov & Charova 2006).

RESULTS

Long-term variations of major ecosystem properties

Danube discharge rate and SST. The Danube River annual discharge rate and the annual mean SST measured at Odessa and Constanta correlated positively ($r^2 = 0.63$; $p < 0.005$) (Fig. 2a), presumably because they were both regulated by the North Atlantic Oscillation (NAO) (Oguz et al. 2006). They had increasing decadal trends during the 1970s and 1990s but a decreasing trend in the 1980s. These trends were accompanied by strong interannual variation. Their concurrent strong decline in 1993 is of particular importance for the current study.

Dissolved inorganic nutrient concentrations. The most conspicuous feature of SiO$_4$ concentration was a 4-fold decline from 60 µM in 1970–1975 to 15 µM in 1980–1985 (Fig. 2b), which has been explained by its retention in the Iron Gate 1 and 2 reservoirs (Humborg et al. 2000). The latter value remained unchanged during the last 2 decades except for some sub-decadal scale fluctuations. The other inorganic nutrients varied differently; DIN increased from less than 5 to ~15 µM, and P-PO$_4$ from less than 1 to 4 µM before and after the 1970s, respectively. DIN concentration remained around 13 µM in the 1980s and 1990s, whereas P-PO$_4$ concentration decreased abruptly from 4 µM in 1991 to ~0.5 µM in 1992–1993 and remained below 1 µM afterward. Thus the DIN:PO$_4$ ratio changed roughly from less than 10 in the 1980s to greater than 20 in the 1990s, indicating a shift from nitrogen to phosphorus limitation.

We estimated the most limiting nutrient of phytoplankton production by computing the Monod-type nutrient uptake functions, $f_x = X/(K_x + X)$, where X denotes the specific nutrient concentration and K_x refers to the corresponding half saturation constant. In this approach, the lowest f_x represents the most limiting nutrient. For half saturation constants of 3 µM for DIN and SiO$_4$, and 0.2 µM for PO$_4$ (Lancelot et al. 2002, Philippart et al. 2007), DIN was the most limiting nutrient prior to 1990 (Fig. 2c). It imposed a strong limitation (~0.5 to 0.6) during the pristine state, but fluctuated around 0.80 from the mid-1970s to the present. Phosphate limitation was comparable (0.80 to 0.95) with DIN prior to 1991, but decreased abruptly to ~0.5 in 1992–1993, which limited phytoplankton growth. The

phosphorus limitation prevailed with some relaxation (up to ~0.75) during 1995–2002 at times of higher Danube discharge rate and it declined (to ~0.5) during the low Danube discharge period of 2003–2004. The analysis was valid regardless of the exact choices of

half saturation constants. The silicate limitation appeared to be most critical during the 1980s, as suggested by the observation of dinoflagellate-dominated phytoplankton production (Nesterova et al. 2008).

Phytoplankton. Annual mean phytoplankton biomass for the Ukrainian, Romanian and Bulgarian shelves varied similarly (Fig. 3a), consistent with those of nutrient concentrations and nutrient limitation functions. The 2-fold greater biomass in the Ukrainian shelf reflected more intense phytoplankton production on the northern side of the Danube discharge zone. Following an order of magnitude rise during the first half of 1970s, phytoplankton biomass continued to increase
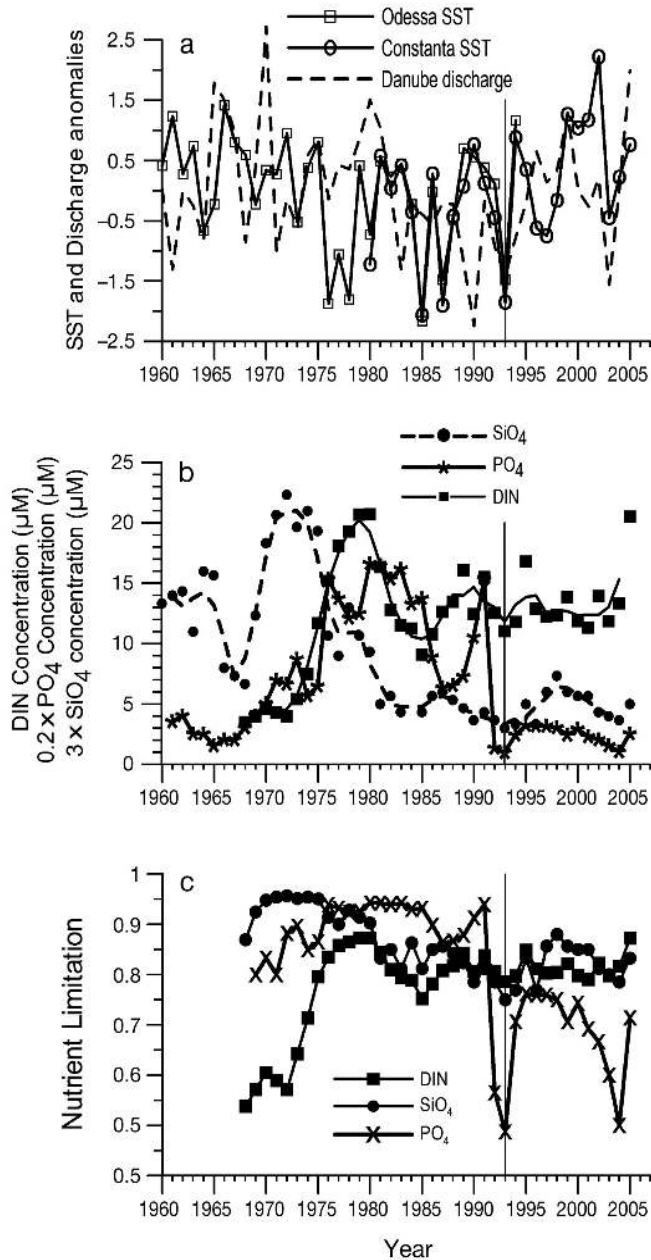

Fig. 2. Time series of annual mean (a) standardized Danube discharge anomaly at Ceatal Ismail (broken line), and standardized sea surface temperature (SST) anomaly measured near Odessa (□) for 1960–1994 and Constanta (O) for 1980–2005; (b) dissolved inorganic nitrogen (DIN) concentration (■), phosphate (P-PO$_4$) concentration (✳) and silicate (SiO$_4$) concentration (●) (symbols denote the original data and lines represent their 3 point moving averages); (c) nutrient limitation functions computed according to the Monod-uptake formula for DIN (■), P-PO$_4$ (**X**) and SiO$_4$ (●)
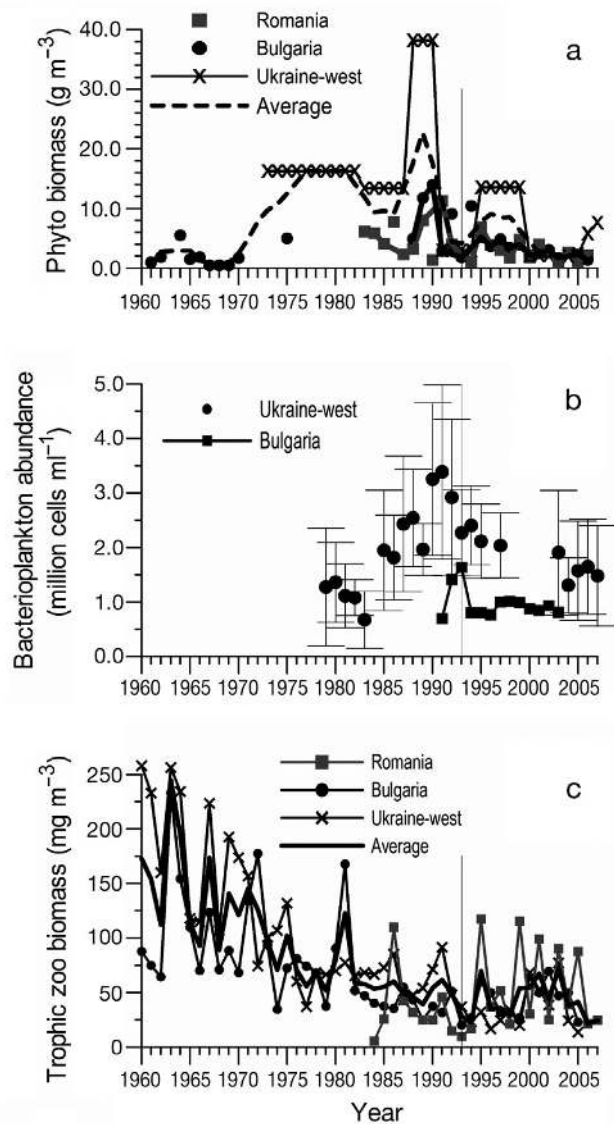

Fig. 3. Time series of the annual mean (a) phytoplankton biomass, (b) bacterioplankton abundance, (c) trophic zooplankton biomass as the averages of all available measurements in Bulgarian, Romanian and Ukrainian shelf areas (smoothed by the 3 point moving average)

at the end of 1980s, but decreased to low values (<3 g m^{-3}) in 1992–1993. Whilst the increase coincided with the population rise of *Mnemiopsis* and its grazing impact on lower trophic levels, the decrease occurred simultaneously with PO$_4$ limitation (Fig. 2c). The biomass in the Ukrainian shelf increased to more than 10 g m^{-3} during the second half of the 1990s, but diminished below 5 g m^{-3} afterwards. However, phytoplankton biomass in the Bulgarian and Romanian shelves remained persistently below 5 g m^{-3} after 1993 because of a substantial decline in the level and frequency of blooms.

The average of these 3 data sets, shown by the bold discontinuous line in Fig. 3a, closely resembled the form of the nutrient limitation function. The transition to the high biomass regime in the 1970s was supported by the 2-fold increase in the DIN limitation function, whereas the transition to the low biomass regime in 1992–1993 coincided with the 2-fold decrease in the P-PO$_4$ limitation function (Fig. 2c).

Bacterioplankton. Bacterioplankton abundance over 10^6 cells ml^{-1} in the Ukrainian shelf indicated an active microbial loop associated with high biological production in the 1980s (Fig. 3b). Its rise to about 3 × 10^6 cells ml^{-1} at the end of 1980s and the subsequent decline to 2 × 10^6 cells ml^{-1} in 1993 were similar to phytoplankton biomass changes and were possibly associated with reduced bottom-up resource supply and weak nutrient recycling. Bacterioplankton abundance also decreased sharply on the Bulgarian shelf (Fig. 3b).

Zooplankton. High interannual variability was characteristic of zooplankton biomass (Fig. 3c), probably due to complex prey-predator interactions and food competition. Nevertheless, 2 decreasing trends were superimposed on these fluctuations. The first one was stronger and encompassed the beginning of 1960s (150 to 250 mg m^{-3}) to the mid-1970s (~50 mg m^{-3}), and was followed by the second one to a minimum (~25 mg m^{-3}) in 1992–1994. During the post-eutrophication period after 1993, biomass also fluctuated annually, but it remained below 50 mg m^{-3} which was indicative of continuing degraded ecosystem conditions as opposed to the high biomass (150 to 250 mg m^{-3}) regime of the pristine state.

Opportunistic species, *Noctiluca scintillans.* Both the Bulgarian and Ukrainian data sets suggested low *Noctiluca* biomass (~100 mg m^{-3}) in the pristine period (Fig. 4a). However, it rapidly increased by an order of magnitude to >1000 mg m^{-3} at times of high phytoplankton biomass in the second half of the 1970s (Fig. 3a). Starting in 1980, relatively high biomass coincided with cold SST years and vice versa for the warm years. Accordingly, 3 specific cold years, 1985, 1993, 2003, had the highest biomass (~1000 mg m^{-3}), whereas warm years (e.g. the mid-1990s) were charac-
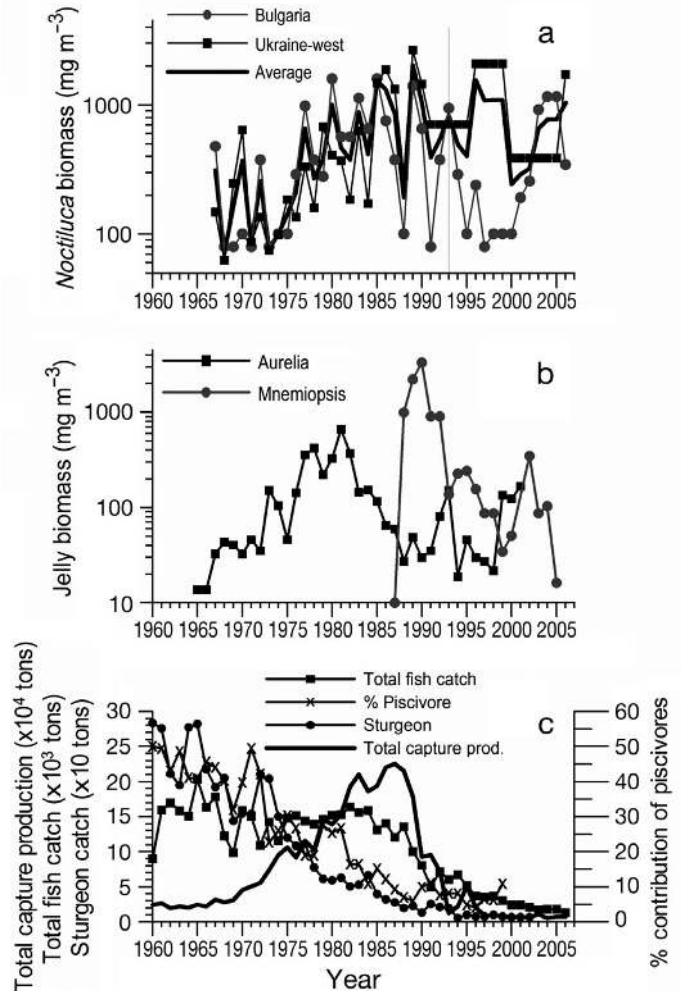

Fig. 4. Time series of the annual mean biomass of (a) *Noctiluca scintillans*, (b) gelatinous zooplankton species *Aurelia aurita* and *Mnemiopsis leidyi*, and (c) total fish catch, sturgeon catch, percent piscivore contribution to the total fish catch, and total capture production in the Romanian sector of NWS taken from http://earthtrends.wri.org/pdf_library/country_profiles/

terized by lower biomass (~100 mg m^{-3}) (except in 1989–1990). Multi-annual averaging of the Ukrainian data masked interannual variability after 1990, though blooms were apparent during the post-eutrophication period.

Gelatinous species, *Aurelia aurita* and *Mnemiopsis leidyi.* *A. aurita* biomass increased from less than 40 mg m^{-3} in the pristine phase to 1000 mg m^{-3} in 1980 (Fig. 4b). This increase tended to follow nutrient enrichment of the system. However, the subsequent declining trend down to ~100 mg m^{-3} in 1988 was coincident with and possibly caused by the prevailing cold climatic conditions of the 1980s (Shiganova et al. 2008). Biomass of the ctenophore *M. leidyi* increased dramatically to 3000 mg m^{-3} in 1989–1990 (Fig. 4b). Its bio-

mass was maintained at ~1000 mg m^{-3} for another 2 yr (1991–1992) and then decreased abruptly to ~100 mg m^{-3} in 1993, when planktonic systems collapsed. *Mnemiopsis* biomass recovered briefly during 1994–1995, but declined during 1996–1998, coincident with the respective warming and cooling phases (Fig. 2a). The subsequent decrease in 1999–2000 was likely related to predation by the new alien species *Beroe ovata* (Kamburska et al. 2006). Moreover, *Aurelia* biomass

decreased considerably at the times of high *Mnemiopsis* biomass. In contrast, when *Mnemiopsis* biomass was low, *Aurelia* increased in biomass to as high as 300 mg m^{-3} (Fig. 4b).

Fish and marine living resources. The total capture production of marine living resources in Romanian coastal waters decreased by an order of magnitude in 1989–1992, and this low production regime prevailed afterward (Fig. 4c). Similarly, the total fish catch de-
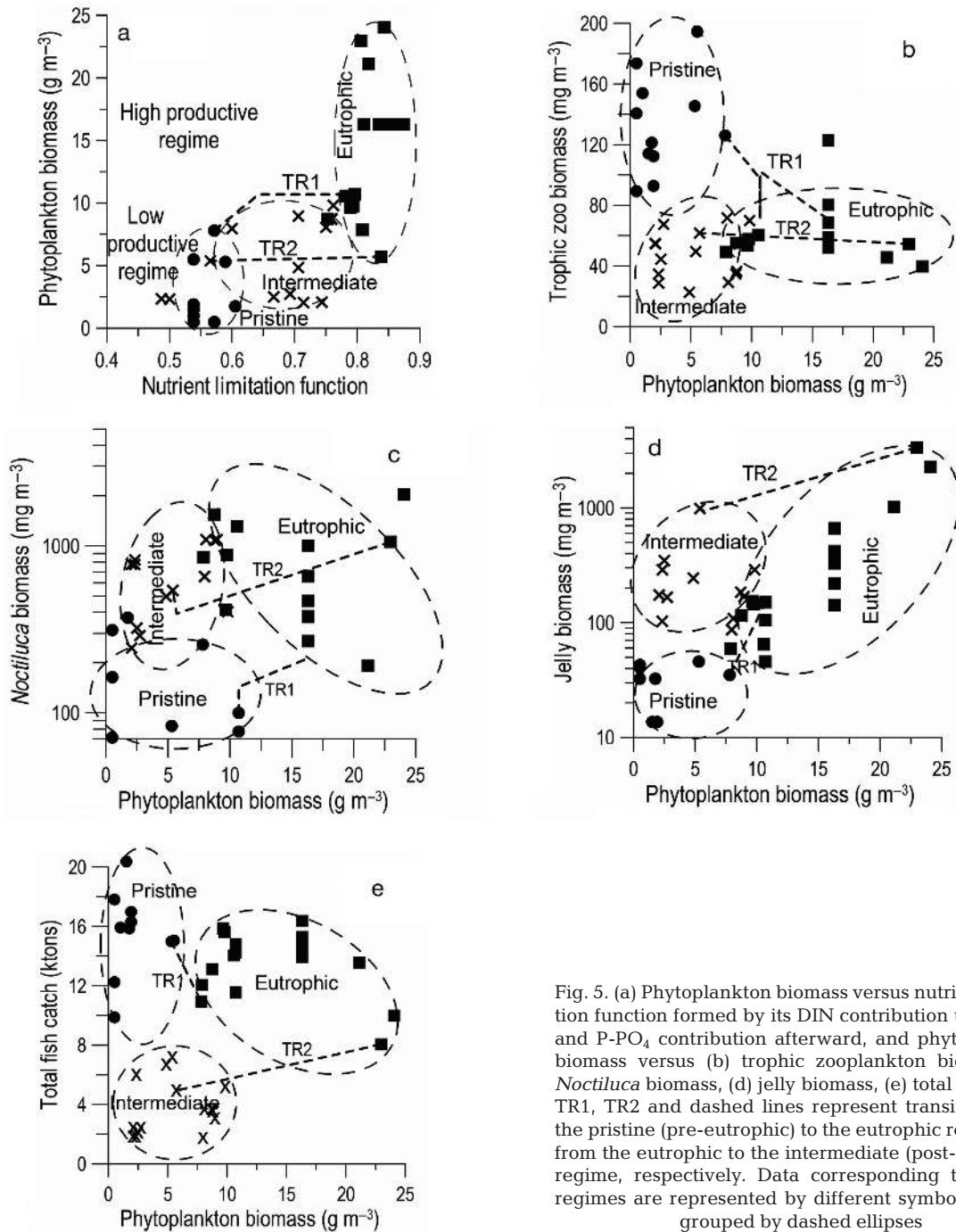

Fig. 5. (a) Phytoplankton biomass versus nutrient limitation function formed by its DIN contribution up to 1992 and P-PO$_4$ contribution afterward, and phytoplankton biomass versus (b) trophic zooplankton biomass, (c) *Noctiluca* biomass, (d) jelly biomass, (e) total fish catch. TR1, TR2 and dashed lines represent transitions from the pristine (pre-eutrophic) to the eutrophic regime and from the eutrophic to the intermediate (post-eutrophic) regime, respectively. Data corresponding to these 3 regimes are represented by different symbols and are grouped by dashed ellipses

clined sharply to less than 6000 tons during 1988–1991 from approximately 15 000 tons during 1960–1985. It then further declined to ~3000 tons during the rest of 1990s. More importantly, piscivorous fish catch of high economical value constituted almost 50 % of the total fish catch prior to 1970, but decreased to 25 % in the early 1980s and even more in the early 1990s due to over-exploitation. These low catch levels persisted during the post-eutrophication phase. The commercial catch of sturgeon also declined without subsequent re-covery. The situation was slightly better in the rest of the Black Sea where the small-pelagic fish catch (mostly anchovy) achieved a partial recovery to its level in the mid-1970s (Shlyakhov & Daskalov 2008).

Alternative states and regime shifts

Fig. 5a displays phytoplankton biomass versus the nutrient limitation function (NLF), which is formed by the contribution of DIN up to 1992 and P-PO$_4$ after-ward (Fig. 2c). The pre-eutrophication phase prior to 1970 and the post-eutrophication phase after 1993 rep-resented the 2 'low nutrient availability and low phyto-plankton biomass' regimes with biomass less than 8 g m^{-3}. In Fig. 5a, these 2 phases are referred to as the 'pristine' and the 'intermediate' states, respectively, and differ from the 'high phytoplankton biomass and high nutrient availability' regime (>10 g m^{-3}) of the eutrophic state.

Phytoplankton biomass is plotted against zooplank-ton biomass in Fig. 5b, *Noctiluca* and jelly biomass in Fig. 5c,d, and total fish catch in Fig. 5e. Phytoplankton biomass was chosen as a state variable representing bottom-up food supply to higher trophic levels. These plots demonstrate 3 different states of the ecosystem: (1) zooplankton- and piscivorous-dominated state prior to 1970 (labeled 'pristine'), (2) phytoplankton, *Noc-tiluca*, jelly and planktivorous-fish dominated state (labeled 'eutrophic'), and (3) *Noctiluca* and jelly-domi-nated state during 1993–2005 (labeled 'intermediate'). TR1 and TR2 link the eutrophic state to the former pris-tine and the latter intermediate states, respectively. All these plots consistently classified the pristine and intermediate states as 2 alternative states of the lower trophic food web system for phytoplankton biomass below an apparent threshold of 10 g m^{-3}.
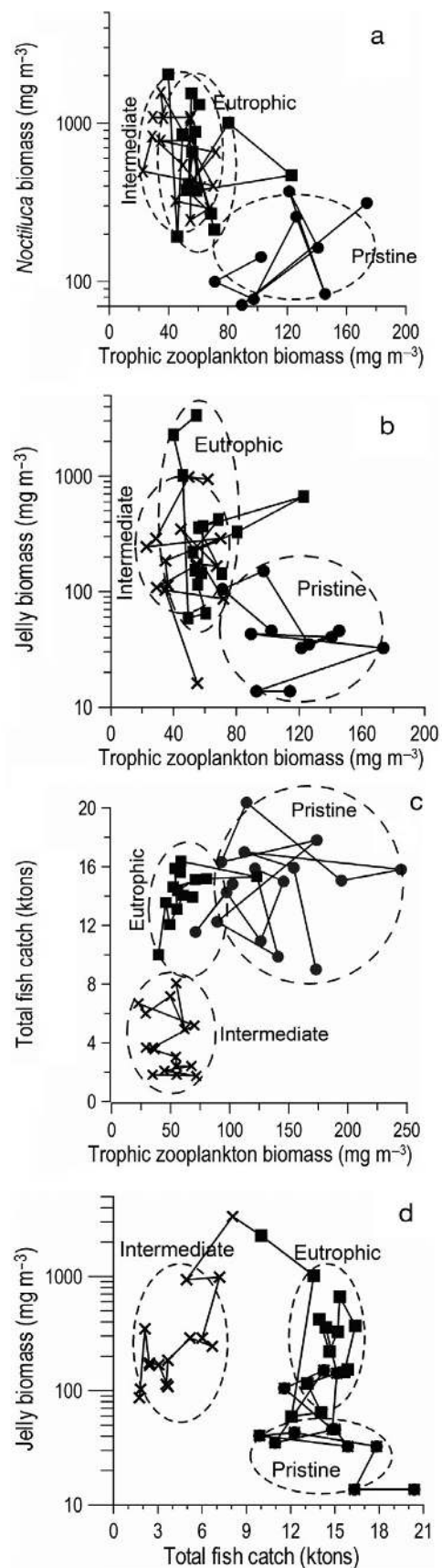

Fig. 6. Trophic zooplankton biomass versus (a) *Noctiluca* biomass, (b) jelly biomass, (c) total fish catch, and (d) jelly biomass versus total fish catch distributions. Lines connect data for consecutive years. Data corresponding to the pristine, eutrophic and intermediate regimes are represented by different sysmbols and are grouped by dashed ellipses

The pristine state was further characterized by high zooplankton biomass and fish catch, and low *Noctiluca* and jelly biomass (Fig. 6a–c). In contrast, the post-eutrophication phase was associated with low zooplankton biomass and fish catch, and moderate *Noctiluca* and jelly biomass. The total fish catch versus jelly biomass plot (Fig. 6d) identified the pristine state as a fish-dominated system and the intermediate state as a jelly-dominated system.

DISCUSSION

A long-term data set was used to elucidate abrupt ecological changes from high to low production along the northwestern Black Sea in the early 1990s. We assessed whether the prevailing low production state could be classified as recovery, or whether it merely reflects a different reorganization of the degraded food web structure at relatively low resource conditions.

Patterns in the long-term data were indicative of 3 alternative states in the NWS ecosystem, comprising a low production system before 1970, a highly productive eutrophic system during the 1980s, and a relatively low production intermediate system after the early 1990s (Fig. 7). The low production system before 1970 was N-limited, and diatom-based phytoplankton production was mainly channeled through mesozoo-
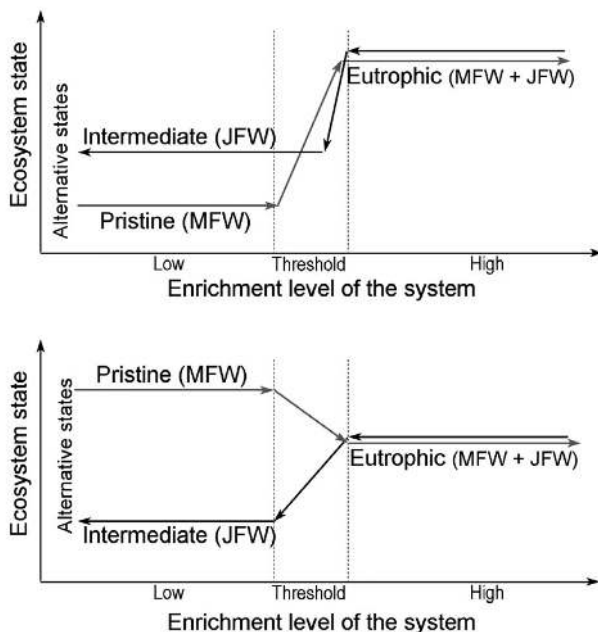

Fig. 7. Schematic representation of the 3 distinct ecosystem states for different properties of the ecosystem with respect to changing nutrient enrichment of the system. MFW and JFW denote the muscular and jelly food webs, respectively. The upper panel applies to *Noctiluca* and *Aurelia*, and the lower panel to trophic zooplankton and total fish catch

plankton (copepods and cladocerans) to planktivorous fish (small pelagics) and finally to piscivores. This system is hereinafter referred to as a 'muscle food web (MFW)' (cf. Sommer et al. 2002) characterized by high ecotrophic efficiency. This state is characterized by high piscivore and zooplankton biomass, and low biomass of small pelagics and phytoplankton biomass, possibly due to a trophic cascade. The heterotrophic dinoflagellate *Noctiluca scintillans* and the jellyfish *Aurelia aurita* were not dominant components of the food web, possibly due to a competitive disadvantage against mesozooplankton and small pelagic fish under low resource availability and to grazing of *Aurelia* by mackerel (Zaitsev & Mamaev 1997).

Following overfishing of the dolphin population between 1950 and 1966, and gradual depletion of bonito, bluefish, mackerel and other piscivores in the mid-1960s and early 1970s (Daskalov et al. 2007), the MFW was simplified into 3 trophic levels. Phosphate and nitrate concentrations increased 10- and 5-fold, respectively, in the first half of the 1970s due to anthropogenic loading. This increase supported an order of magnitude higher phytoplankton biomass, which in turn stimulated greater total capture production, including small pelagics. The growing importance of the microbial loop is inferred by the doubling of the annual mean bacterioplankton abundance. The proportion of autotrophic dinoflagellate blooms increased from 15% prior to 1970 to 60% in the 1980s (Nesterova et al. 2008), and they were accompanied by massive blooms of the heterotrophic dinoflagellate *Noctiluca scintillans* and high biomass of the jellyfish *Aurelia aurita*. This ecotrophically inefficient 'jelly food web' (JFW) structure was presumably facilitated by a strong nanophytoplankton-protozoa link (microbial food web) together with additional food from meroplankton and mesozooplankton nauplii. We hypothesize that the nutrient enrichment and a trophic cascade favored high phytoplankton production, due to grazing pressure upon zooplankton by small pelagic fishes and jellies. In addition, *Noctiluca* would benefit from the high phytoplankton production. This situation constituted the eutrophic state of the ecosystem.

The second transition occurred in the early 1990s due to several concurrent events, including the proliferation of *Mnemiopsis* due to favorable climatic conditions and the collapse of many marine living resources, such as planktivorous fish, due to overfishing (Purcell 2005, Oguz et al. 2008a). *Mnemiopsis* flourished in the food web along the western coastal waters during 1989–1992 (Kamburska et al. 2006), because of its wide prey base (e.g. ciliates, copepods of various sizes, nauplii, larvae of cirripeds, bivalves, eggs and larvae of fish), and its higher growth and reproductive rates relative to *Aurelia* and anchovy larvae during the warmer

Table 2. Approximate ranges of major ecosystem properties during 3 different regimes of the northwestern Black Sea. Bold characters indicate the major differences in the values of ecological properties between the post eutrophication and pristine states. DIN, dissolved inorganic nitrogen; DON, dissolved organic nitrogen

Property	Pristine (<1970)	Intense eutrophication (1975–1992)	Post eutrophication (1993–2005)
DIN (µM)	1	8	7
DON (µM)	10	25	40
SiO_4 (µM)	35–45	20–25	20–25
PO_4 (µM)	<2	3–8	<2
Phytoplankton (g m^{-3})	<3.0	10–20	~5
(predominating group)	(diatom)	(dinoflagellate)	(diatom + dinoflagellate)
Bacteria (million cells ml^{-1})	<1.0	2–3	1–2
Trophic zooplankton (mg m^{-3})	250	75–150	50–100
Noctiluca scintillans (mg m^{-3})	<100	>1000	500–1000
Aurelia+*Mnemiopsis* (mg m^{-3})	50	≤3000	<500
Total capture production (10^3 tons)	30	>200	10
Total fish catch (10^3 tons)	15	5–15	2
% share of piscivores in total fish catch	40–50	30–15	<10

conditions. Increases in phytoplankton biomass and bacterial abundance during the outburst phase (1989–1992) may signify a new top-down trophic cascade immediately after the collapse of planktivorous fish stocks. The early 1990s also corresponded to the collapse of the former Soviet Union and Eastern Bloc countries of the Danube catchment region (Mee et al. 2005), which likely caused a reduction in P-PO$_4$ loadings due to limited fertilizer use and emissions from land-based point sources (Mee et al. 2005). The years 1992 and 1993 were 2 of the coldest of the last century, and were accompanied by some of the lowest Danube discharge rates, which probably drove the severe drop in anthropogenic P-PO$_4$ loadings (Berlinsky et al. 2006, Cociasu et al. 2008) and associated resource availability. In contrast, the decrease in DIN loading was more gradual and spanned the 1990s due to a continuing supply from soil leaching within the Danube catchment basin (Kroiss et al. 2006). As a result, nutrient limitation abruptly shifted from nitrogen to phosphorus, which then severely reduced plankton production. Zooplankton biomass was then apparently not sufficient to maintain the high *Mnemiopsis* abundance that developed immediately after the invasion. In addition, severe winter conditions likely introduced an adverse effect on the overwintering population and, therefore, spring and summer production (Purcell 2005, Oguz et al. 2008a).

Following the switch to a low phytoplankton biomass regime in 1993, the system maintained low biomass of bacterioplankton, zooplankton, and total marine living resources, but moderate *Noctiluca* and gelatinous biomass. As opposed to the diatom-dominated low biomass pristine state and the dinoflagellate-dominated eutrophic state, the recent low biomass state involved mixotrophic composition of all groups that varied interannually and regionally (Nesterova et al. 2008). Population increases of *Beroe* and its predation on *Mnemiopsis* by the end of 1990s suppressed *Mnemiopsis* biomass to some extent, but this was compensated by an increase in *Aurelia* biomass. Noting that conditions in 2005 were not appreciably different from those in 1995, this ecologically-degraded situation seems to be a quasi-stable state with interannual fluctuations. The prevailing low zooplankton biomass, low marine living resources, and moderate *Noctiluca* and jelly biomass are indicative of a degraded ecosystem in the form of an intermediate production state between the low production but healthy pristine state and the highly productive but degraded eutrophic state. The intermediate state is dominated by jellies and opportunistic species as an alternative to the fish-dominated healthy pristine state (Fig. 7). The current state can thus not be interpreted as 'a tendency of improvement and rehabilitation of the northwestern Black Sea shelf' as suggested recently (McQuatters-Gollop et al. 2008).

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