

Abrupt transitions of the top-down controlled Black Sea pelagic ecosystem during 1960–2000: Evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations

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Abstract

Functioning of the Black Sea ecosystem has profoundly changed since the early 1970s under cumulative effects of excessive nutrient enrichment, strong cooling/warming, over-exploitation of pelagic fish stocks, and population outbreak of gelatinous carnivores. Applying a set of criteria to the long-term (1960–2000) ecological time-series data, the present study demonstrates that the Black Sea ecosystem was reorganised during this transition phase in different forms of top-down controlled food web structure through successive regime-shifts of distinct ecological properties. The Secchi disc depth, oxic–anoxic interface zone, dissolved oxygen and hydrogen sulphide concentrations also exhibit abrupt transition between their alternate regimes, and indicate tight coupling between the lower trophic food web structure and the biogeochemical pump in terms of regime-shift events.

The first shift, in 1973–1974, marks a switch from large predatory fish to small planktivore fish-controlled system, which persisted until 1989 in the form of increasing small pelagic and phytoplankton biomass and decreasing zooplankton biomass. The increase in phytoplankton biomass is further supported by a bottom-up contribution due to the cumulative response to high anthropogenic nutrient load and the concurrent shift of the physical system to the “cold climate regime” following its ~20-year persistence in the “warm climate regime”. The end of the 1980s signifies the depletion of small planktivores and the transition to a gelatinous carnivore-controlled system. By the end of the 1990s, small planktivore populations take over control of the system again. Concomitantly, their top-down pressure when combined with diminishing anthropogenic nutrient load and more limited nutrient supply into the surface waters due to stabilizing effects of relatively warm winter conditions switched the “high production” regime of phytoplankton to its background “low production” regime.

The Black Sea regime-shifts appear to be sporadic events forced by strong transient decadal perturbations, and therefore differ from the multi-decadal scale cyclical events observed in pelagic ocean ecosystems under low-frequency climatic forcing. The Black Sea observations illustrate that eutrophication and extreme fishery exploitation can indeed induce hysteresis in large marine ecosystems, when they can exert sufficiently strong forcing onto the system. They further

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illustrate the link between the disruption of the top predators, proliferation of new predator stocks, and regime-shift events. Examples of these features have been reported for some aquatic ecosystems, but are extremely limited for large marine ecosystems.

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1. Introduction

Classical ecology is founded on the view that the ecosystem properties change smoothly with varying environmental conditions. By the early 1990s, observations from different types of aquatic and terrestrial ecosystems pointed to a new paradigm. When the ecosystem loses its internal resilience, it becomes vulnerable to some external disturbances and finally responds strongly to environmental conditions at their critical levels (Scheffer et al., 2001; Mayer and Rietkerk, 2004). Such large and sudden transitions between stable states under strong variations of natural climatic and/or human-induced forcing are referred to as “regime-shifts”, although the term is used with slightly varying interpretations (e.g., Scheffer et al., 2001; Steele, 2004; deYoung et al., 2004; Petraitis and Dudgeon, 2004; Duffy-Anderson et al., 2005).

For open-ocean ecosystems, regime-shifts have been reported in the North Pacific, the northwest and northeast Atlantic and large-scale upwelling systems of eastern boundary currents, a concise review of which was given by deYoung et al. (2004). For these ecosystems, the term “regime-shift” has been used to describe a substantial reorganisation of the ecosystem state that persists long enough (e.g., more than a decade) in a new quasi-equilibrium state following changes that were primarily triggered by large-scale climate-induced variations (deYoung et al., 2004). Their two key features are multi-decadal persistence and differing climatic characters of alternate states. Bakun (2005) later re-phrased this definition as “climatic regime-shift events”, implying “apparent transitions between differing average climatic levels over multi-annual to multi-decadal periods”. Bakun (2005) further distinguished “ecosystem regime-shifts” as drastic, large time- and space-scale shifts in the abundances of marine biological communities under some mechanisms other than climate-induced variations.

Coastal, shelf and marginal sea ecosystems, which are heavily subject to human-induced perturbations, experience more complicated regime-shifts under

multiple forcing compared with their oceanic counterparts. Examples are provided for kelp forests, coral reefs, sea grass beds around the world (Jackson et al., 2001), the North Sea (Cook et al., 1997; Reid et al., 2001), around Newfoundland (Myers and Worm, 2003), Georges Bank (Collie and DeLong, 1999), the Yellow and Japan Sea (Zhang et al., 2000), the west coast benthic community of South Africa (Barkai and McQuaid, 1988), and the northern Bering Sea (Grebmeier et al., 2006). Among marginal sea ecosystems, the Black Sea (Fig. 1) is of special interest because of dramatic changes that took place in its ecological properties from the early 1970s to the 1990s. The cause of these changes was the concomitant impacts of eutrophication, overfishing, successive decadal cooling/warming events and successive population outbursts of gelatinous carnivore species *Aurelia aurita*, *Mnemiopsis leidyi* and *Beroe ovata*. The way in which they introduced marked changes in the Black Sea hydro-meteorological and ecological properties have been extensively reported from different

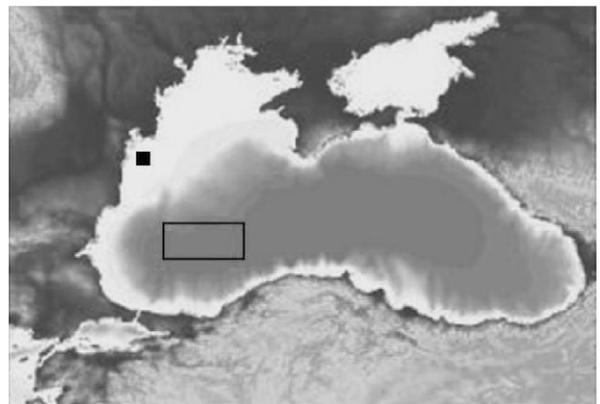


Fig. 1. The geographical setting and bathymetry of the Black Sea. The light grey shaded zone within the northwestern part of the sea is referred to as the Northwestern Shelf (NWS). The interior basin (shown by the dark shaded zone) is separated from the continental shelf around the periphery by the 200m depth contour. The square symbol and the rectangular box along the western coast and within the western interior basin represent the locations of the measurements shown in Fig. 2a and b, respectively.

perspectives (e.g., Kideys, 2002; Daskalov, 2003; Oguz et al., 2003, 2006; Bilio and Niermann, 2004; Oguz, 2005b, c).

Niermann et al. (1999) (see also Bilio and Niermann, 2004) were the first to introduce the regime-shift concept to the Black Sea. They noted a coincidence between the collapse of the anchovy fishery, simultaneous outbreak of *Mnemiopsis* and similar adverse ecosystem changes in the North Sea at the end of the 1980s. They then argued that those events were all related to the concurrent pronounced changes in the North Atlantic Oscillation. Our analysis, on the other hand, suggests over-exploitation of the anchovy stock to be the primary cause of fishery collapse. The North Atlantic Oscillation did however play a substantial role in promoting lower trophic level biological production during the late 1980s and the first half of the 1990s.

The present study constitutes a part of our ongoing efforts towards thorough understanding of long-term ecological changes within the pelagic interior Black Sea ecosystem during its transformation from the pre-eutrophication phase of the 1960s to the post-eutrophication phase of the 1990s. It specifically interprets structural changes that took place in the Black Sea ecosystem in terms of the identification and origin of the regime-shifts and reorganisation of the ecosystem between quasi-stable states under concurrent effects of climatic changes, anthropogenic nutrient enrichment, outbreak of gelatinous species, and over-exploitation of small pelagic stocks. The analysis excludes the northwestern shelf (NWS) (Fig. 1) intentionally, which has its own particular and indeed more complex ecosystem characteristics. The NWS also lacks systematic long-term time series data from different trophic levels in order to provide a clear picture of abrupt ecological transitions encountered during the 1980s and 1990s. As documented in the following sections, the Black Sea ecosystem appears to possess one of the most striking examples of the “ecological regime-shift” events reported so far for large pelagic marine ecosystems.

1.1. An overview of regime-shift concept

A stable state represents various combinations of ecosystem properties and environmental conditions that may persist at a particular spatial extent and temporal scale (Suding et al., 2004). In regime-shift terminology, properties of the ecosystem that are subject to abrupt changes are referred to as response

or state variables, whereas external conditions that induce these changes represent forcing or environmental variables. Stable states are also referred to as “regimes” or “attractors”. The term “quasi-stable” more appropriately describes the stability of states, since they are never strictly stable and often comprise fluctuations and trends depending on the time scales of interest. Regime-shifts represent one form of bifurcation. Other forms are a change in stable equilibrium to a cyclic attractor about which the system oscillates, or limit cycles, etc. The regime-shift analysis (RSA) assists implementation of more efficient management strategies for sustainable utilisation of the resources by quantifying the critical thresholds of the system.

The regime-shift concept applies to all natural, social and economic systems. Because of their nonlinear character, these systems may be exposed to abrupt changes under some strong triggering mechanisms. For natural systems, examples extend from long-time scale events in regional climate of the Earth system (Stocker, 1998; Alley et al., 2003) to those with very short time scales, such as hydraulically controlled flow conditions in straits (e.g., the Bosphorus Strait). Sixteen abrupt climatic cooling/warming shifts, repeated on average every 2000 years, took place during the last glacial period between 25,000 and 60,000 years ago (Stocker, 1998). The switches to the warming phase occurred relatively abruptly, within a decade at most, whereas transition to the cooling was much slower and took place at least over a few centuries. Another example for the climatic regime-shift events is the change from high and low states of the Saharan vegetation cover (Foley et al., 2003). Abrupt transition between the vegetation states, stable at millennial time scales, occurred within about 500 years between 5000 and 6000 years before the present. At the other extreme, the Bosphorus upper layer flow remains at its sub-critical state within the upper half of the strait for about 5–10 h. It then jumps instantaneously to the super-critical state at the constriction section, remains in the super-critical state within the rest of the strait for a few hours, and then reverts instantaneously again to the sub-critical state when it enters into the Sea of Marmara (Oguz, 2005a). On the other hand, in open ocean ecosystems, the states that are stable at multi-decadal time scales may alternate within a few years in response to low frequency changes in large-scale atmospheric systems (deYoung et al., 2004). The major implication of these examples is that,

while quasi-stability of states and abrupt transitions are common to all natural systems, the time scale of events varies broadly.

The type of regime-shift that develops depends on the combination of external forcing (e.g. overfishing, nutrient enrichment, climatic variations, etc.) and internal conditions (e.g. changes in the growth and predation characteristics, physical structure). Depending on the conditions controlling the internal trophic structure, the regime-shift links two different ranges of both forcing and response variables through a linear or nonlinear transition, when the external conditions approach a critical level (see Fig. 3 in Collie et al., 2004). This type of continuous regime-shift is called either “smooth” or “abrupt” depending on the degree of nonlinearity of the transition. The system reverts to its previous conditions along either the same trajectory when the environmental conditions are restored to those before the shift or a different trajectory if the environmental conditions change slightly. A well-known example is the sudden climate-induced oscillations in the Pacific Ocean fishery from a warm “sardine regime” to a cool “anchovy regime” in the early 1950s, back to a warm “sardine regime” at the end of the 1970s, and to an “anchovy regime” again at the beginning of the 1990s (Chavez et al., 2003). These regimes represent two different stable states of the system for two different forms of the climate signal.

Alternatively, under somewhat different conditions of the internal trophic structure, a “discontinuous regime-shift” may occur between two different stable equilibrium states for a particular range of forcing variable. The stable states are linked with each other by catastrophic transitions at the critical thresholds of environmental conditions, when the forcing variable (i.e., environmental condition) changes sufficiently to pass the thresholds. For example, the Georges Bank ecosystem attained two alternate states of high and low haddock stocks for fishing mortalities between 0.21 and 0.36. The haddock stock remained stable at a mean value of 120 kilotonnes for fishing mortalities up to 0.36 from the 1930s to mid-1960 (Collie et al., 2004). Upon further increase of the fishing mortality, the haddock stock collapsed in 1965, and the system moved into its low-stock (about 30 kilotonnes) regime for the next three decades for fishing mortalities greater than 0.21. When sufficiently strong, a perturbation of environmental conditions can force a switch to another stable state before reaching the threshold (Scheffer and Carpenter, 2003). The trajectory connecting the thresholds of

environmental conditions represents an unstable equilibrium that marks the border between the domains of attraction of the alternate stable states. It identifies a combination of a system state and environmental conditions that can persist only at the specified conditions, so that even minor perturbations move the system away from these points to the nearest stable equilibrium state. Scheffer et al. (2000, 2001) and Scheffer and Carpenter (2003) give more details on the theoretical framework of regime-shifts as well as a broad range of observations from different ecosystems.

2. Data description

The data are compiled from all available long-term (1960–2000) measurements carried out within the interior Black Sea deeper than 200 m, which covers approximately 75% of the basin (Fig. 1). They comprise (i) the water-column-integrated phytoplankton biomass (Mikaelyan, 1997) and the surface chlorophyll concentration (Yunev et al., 2002; Vedernikov and Demidov, 2002), both of which were given as averages of the May–November period for the interior basin, (ii) the zooplankton biomass as annual mean of all measurements within the interior basin (Kovelev et al., 1998; Shiganova et al., 2003), (iii) gelatinous carnivore biomass from measurements in the northeastern sector of the Black Sea (Shiganova et al., 2003), (iv) the annual catch and total spawning stock biomass of small pelagic fishes (the sum of anchovy and sprat) provided by Daskalov (2002) and Daskalov et al. (2006), (v) the interior basin-averaged dissolved oxygen and hydrogen sulphide concentrations (Konovalov and Murray, 2001; Konovalov et al., 2005), and the Secchi disc depth (Mankovsky et al., 1998), (vi) the interior basin-averaged winter (December–March) mean sea surface temperature extracted from the site <http://badc.nerc.ac.uk/data/hadisst>, and (vii) the Black Sea climate index time series data (Oguz et al., 2006). They are complemented by nutrient data for the inner northwestern shelf (Sorokin, 2002; Cociasu and Popa, 2002), and for the interior basin taken from the sites <http://sfpl.ims.metu.edu.tr/> and <http://oceanweb.ocean.washington.edu/cruises/>.

3. Background: general characteristics of long-term changes in the ecosystem properties

This section presents long-term changes in major ecosystem properties and asserts likely effects of

various external forces and internal mechanisms that led to different bottom-up and top-down controlled trophic arrangements in the food web structure through distinct regime-shift events.

3.1. Bottom-up regulation of the food web structure

The period up to 1970 represents an oligotrophic, pre-eutrophication regime of the ecosystem with limited anthropogenic nutrient supply (~ 150 kilotonnes yr^{-1}) from the rivers discharging into the northwestern shelf (NWS). The depth-average nitrate and phosphate concentrations, at a 40 m deep station of the inner shelf located approximately 20 miles off Constanta (Romania) (see the location in Fig. 1), were typically of ~ 4.0 and $\sim 0.3 \mu\text{M}$, respectively (Fig. 2a). Within the interior basin, a weak subsurface nitrate peak of $\sim 2.0 \mu\text{M}$ (Fig. 2b) reflects limited contribution of the anthropogenic nitrogen supply into the rest of the sea; nitrate being the most limiting nutrient for the interior basin ecosystem. The maximum phytoplankton biomass of $\sim 2.0 \text{ gm}^{-2}$ (Fig. 3a) and surface chlorophyll concentration around 0.1 mg m^{-3} were other characteristic signatures of the oligotrophic conditions of the interior basin. This period was further subject to relatively warm and mild winters (Oguz, 2005c) with typical winter average temperatures oscillating around $8.5\text{--}9.0^\circ\text{C}$ (Fig. 4c).

Eutrophication was gradually built up by organic and inorganic nutrient input, particularly from the River Danube during the first half of the 1970s (Fig. 4a). The first sign of eutrophication on the shelf is the rapid rise of the depth-averaged phosphate concentration up to $\sim 1.4 \mu\text{M}$ within only a few years, while nitrate was increasing more gradually (Fig. 2a). Accompanying ecosystem changes include enhanced and more widespread episodes of hypoxia and anoxia, increased sedimentation and turbidity, loss of sea grasses, higher frequency and duration of toxic dinoflagellate blooms and losses in benthic primary production (Zaitsev and Mamaev, 1997). For the interior basin, the phytoplankton biomass was still low, around $\sim 3.0\text{--}4.0 \text{ gm}^{-2}$ up to 1973, increased sharply to around $7.0\text{--}8.0 \text{ gm}^{-2}$ in 1974 and fluctuated around these values up to 1983–1984 (Fig. 3a). While no appreciable nitrogen load had yet been introduced during the early 1970s, the abrupt rise in the phytoplankton biomass was likely the response to the change in top-down control of the food web structure (see next section). The warm

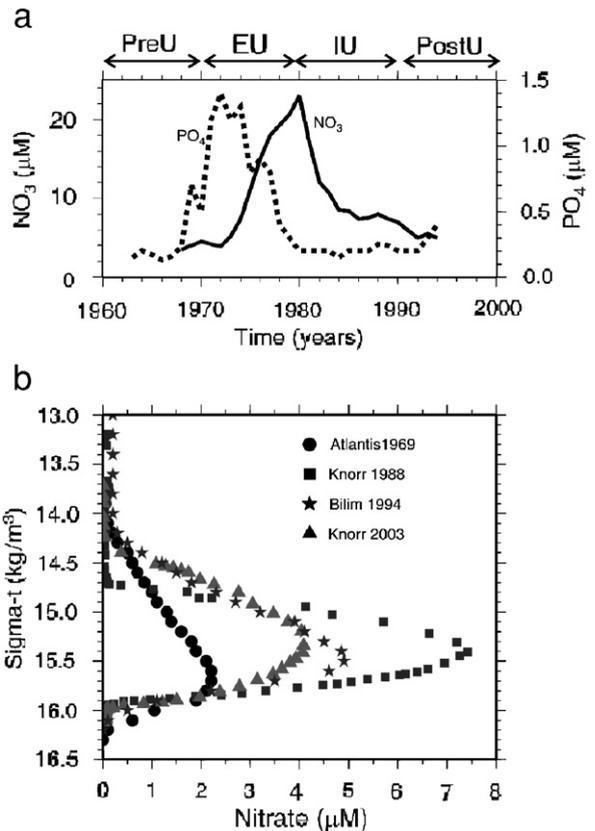


Fig. 2. (a) Long-term changes of 0 to 40 m depth-averaged phosphate (PO_4 , broken line) and nitrate (NO_3 , continuous line) concentrations (in μM) at $44^\circ 10' \text{N}$, $29^\circ 09' \text{W}$ (Fig. 1), which is located approximately 20 nautical miles off Constanta along the Romanian coast of the northwestern Black Sea (after Oguz, 2005a), and (b) nitrate profiles (in μM) versus sigma-t (in kg m^{-3}) measured within the central western gyre during Atlantis 1969 (dots), Knorr 1988 (squares), Bilim 1994 (stars), and Knorr 2003 (triangles) cruises. PreU, EU, IU, and PostU denote, respectively, pre-, early, intense and post-eutrophication phases of the Black Sea ecosystem.

and mild winters continued to persist with some oscillations during this period too (Fig. 4c). The 1970s represent the early-eutrophication phase.

The depth-averaged phosphate concentration at the inner shelf station started declining by the mid-1970s. It is not however clear that this reduction was caused by the construction of the Iron Gate 1 damming system along the River Danube. For example, the depth-averaged nitrate concentration at the same station does not show any reduction. It instead increases rapidly after the dam construction up to its maximum value of $\sim 20 \mu\text{M}$ in 1980 (Fig. 2a). Nitrate concentration then dropped, first sharply in the early 1980s and then more gradually within the second half of the 1980s. The reduction

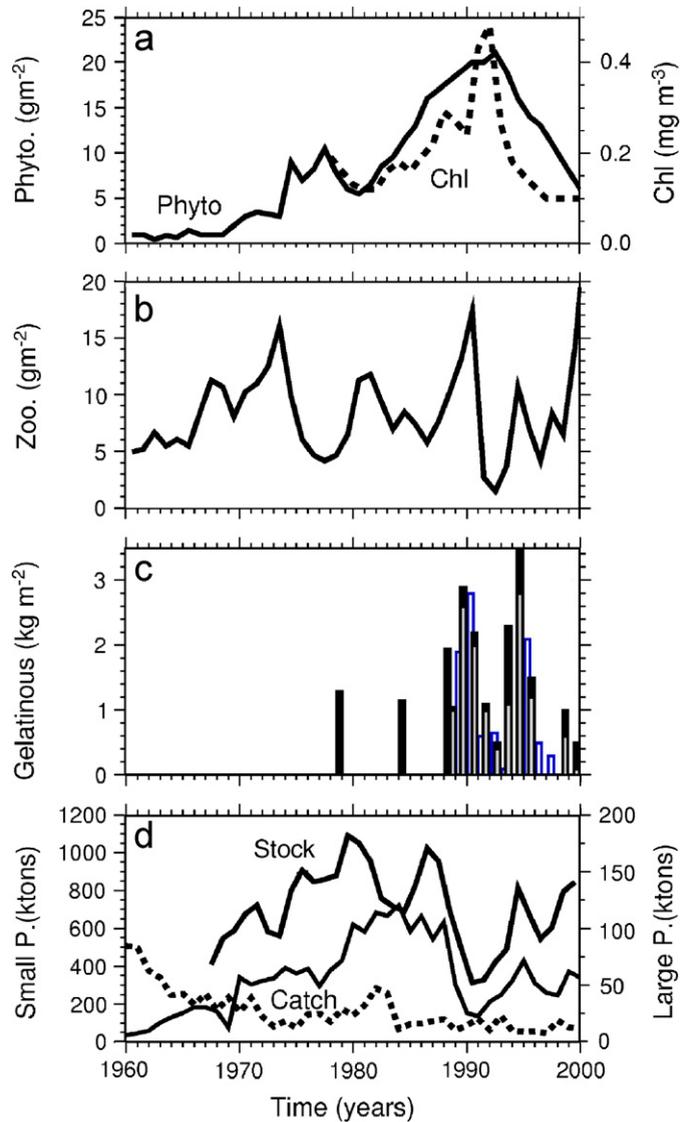


Fig. 3. Long-term changes of the (a) phytoplankton biomass integrated over the upper 50 m of the water column (continuous line) (in g m^{-2}) and surface chlorophyll concentration (broken line) (in mg m^{-3}) during May–November period, (b) annual mean mesozooplankton biomass (in g m^{-2}), (c) gelatinous carnivore biomass (in kg m^{-2}) (*Mnemiopsis leidyi* in black color and *Aurelia aurita* in grey color), (d) annual mean small pelagic fish stock and catch, and large predatory pelagic catch (broken line) (in kilotonnes). They are given as the averages of all measurements within the interior basin. The data sources are indicated in the text.

of nitrate in the NWS follows the construction of the Iron Gate 2 damming system along the River Danube. The organic and inorganic nitrate are distributed horizontally within the basin by the mesoscale-dominated circulation system and vertically by the biological pump (Gregoire and Lacroix, 2003). They eventually accumulate within the chemocline zone at depths of about 50–75 m and give rise to three-to-four-fold increase in the peak nitrate concentration of the interior basin to around $6\text{--}8\ \mu\text{M}$ during the 1980s (Fig. 2b).

Climatically, the mid-1980s and early 1990s were characterized by extremely cold, dry and severe winters (Oguz, 2005b) as suggested by the approximately $1.5\text{--}2.0\ ^\circ\text{C}$ drop in the winter-mean basin-averaged SST (Fig. 4c). The period 1985–1993 in fact had the coldest SSTs of the last century. Physical processes driven by climatic cooling and severe winter conditions (e.g., enhanced vertical mixing and stronger upwelling associated with intensification of the cyclonic basinwide circulation system) promoted favourable conditions for a

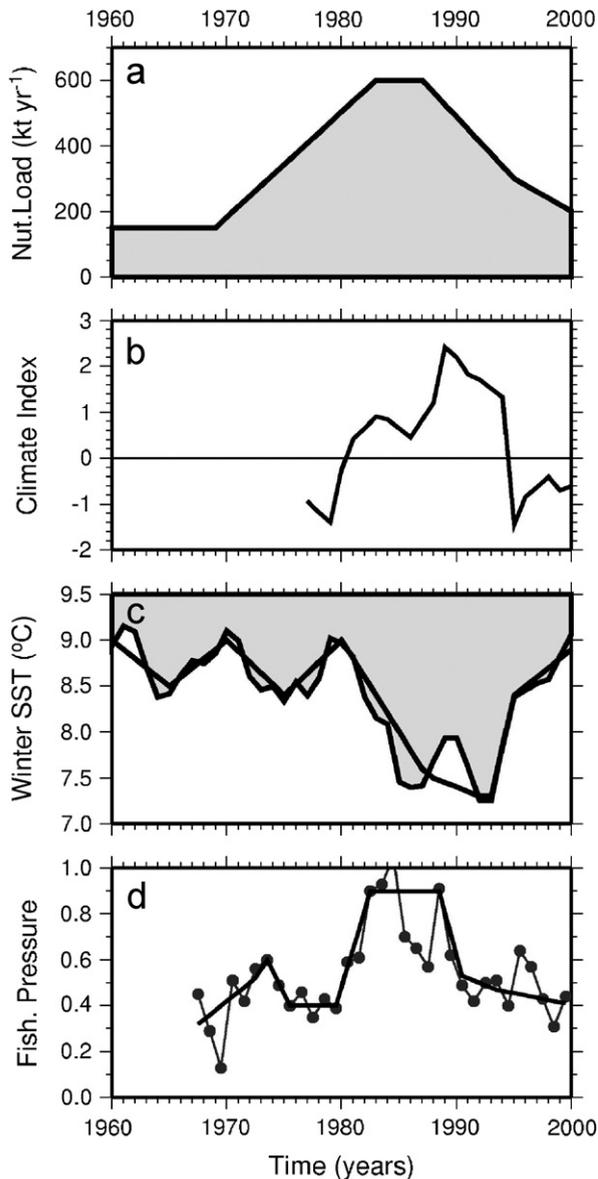


Fig. 4. Long-term changes of the (a) anthropogenic nitrogen load into the sea from the River Danube (in kilotonnes⁻¹), (b) climate index representing the composite effect of atmospheric systems over the North Atlantic and Eurasia, and (c) winter (December–March) mean monthly sea surface temperature (°C) and its smoothed version (straight lines), (d) fishing pressure (catch/stock) on small pelagic fish provided by the original data (dots) and its smoothed version (straight lines). The data sources are indicated in the text.

higher rate of nitrate supply into the surface productive layer from depths below the euphotic zone during winter months of this period. Accumulation of nitrate then initiated successive relatively strong spring and summer phytoplankton blooms,

as supported by model simulations (e.g. Oguz et al., 1999; Tian et al., 2003). Transformation of the ecosystem from its moderate to high productivity state is evident by a continuous increasing trend in May–November euphotic zone integrated phytoplankton biomass from 8.0 to 20.0 g m⁻² and the surface chlorophyll concentration from 0.1 to 0.5 mg m⁻³ (Fig. 3a). The period from the early 1980s to the early 1990s is referred to as the intense-eutrophication phase.

A distinct feature of the post-eutrophication phase after the early 1990s was the diminishing effect of anthropogenic nutrient and pollutant load (Fig. 4a) due to more limited use of fertilizers in agriculture and continuing control measures implemented to prevent anthropogenic pollution. The response in the interior basin ecosystem was the erosion of the subsurface nitrate peak from 6 to 8 μM of the previous decade to its present values of about 4–5 μM (Fig. 2b). Another distinct feature of this phase is an abrupt change from the severe cooling of the previous decade to equally strong warming. After the mid-1990s, the Black Sea maintained warm SSTs similar to those observed prior to 1980. The winter-average SST started increasing from 7.2 °C in 1993 to 9.0 °C in 2000 (Fig. 4c). Once cooling-induced physical processes were no longer effective for promoting enhanced nitrate supply from the internal nitrate pool, the spring phytoplankton bloom was either lost completely or weakened considerably depending on the hydro-meteorological conditions of each particular year after 1995 (Oguz et al., 2003). The loss of the spring phytoplankton bloom adversely affected the intensity of overall summer biological production as indicated by the continuous decrease of phytoplankton biomass and chlorophyll concentration shown in Fig. 3a. In addition, as described in the next section, the annual phytoplankton abundance appears to be regulated by top-down control during the entire transitional phase of the ecosystem as well.

3.2. Top-down regulation of the food web structure

Observations supporting the predominant role of top-down control on weakly exploited or unperturbed marine ecosystems are generally limited (e.g., Shiimoto et al., 1997), and they are recognised as theoretically unlikely (Pace et al., 1999). Its more likely observed form is alteration and destabilization of food webs by over-exploitation of predator

fish stocks. Examples are documented for demersal ecosystems of the northwest Atlantic shelf (Frank et al., 2005), the North Sea (Heath, 2005) and the Baltic Sea (Harvey et al., 2003). For pelagic marine ecosystems, the Black Sea is the best known example and possesses different forms of top-down controlled food web structure under changing top predators during different periods of the last four decades (Daskalov, 2002).

The pristine ecosystem phase of the early 1960s signifies a top-down controlled food web structure. It involves relatively low phytoplankton standing stocks (Fig. 3a), moderate to high zooplankton standing stock (Fig. 3b), low stocks of small pelagic fish (as inferred from the catch data in Fig. 3d) and relatively high stocks of large pelagic predator fish species (as inferred from the catch data in Fig. 3d). The food web appears to experience a new top-down controlled structure immediately after 1973 as evident in the data by the doubling of the phytoplankton and small pelagic standing stocks (Fig. 3a, d) and a similar sharp reciprocal trend in the forage zooplankton abundance (Fig. 3b). In particular, small pelagic (mainly anchovy) stocks increased from less than ~600 kilotonnes at the beginning of the 1970s to their highest documented value of ~1100 kilotonnes at the end of the decade. The changes indicate a weakening predator role of large planktivores on small pelagic stocks due to their continual exploitation (Fig. 3d). The minimal zooplankton–algae models given by Scheffer et al. (2000) and Morozov et al. (2005) provide quantitative support for such a shift at a critical fishing pressure. The models suggest two distinct regimes; one in which zooplankton is relatively unaffected by fish and algae are controlled by zooplankton, and another in which zooplankton is controlled by fish and phytoplankton biomass is relatively high. Switches from one regime to the other occur abruptly at a critical fish density.

The new top-down controlled food web organisation persisted until 1988 with fluctuations in zooplankton biomass and fish stocks. Gelatinous carnivore abundance, dominated mainly by jellyfish *Aurelia aurita*, was less than 1.0 kg wet weight m^{-2} (Fig. 3c) and thus did not yet play a critical role in structuring the food web. However, the opportunistic herbivorous dinoflagellate species *Noctiluca scintillans* became one of the abundant components of the food web structure. In addition to enhanced nutrient availability (i.e., bottom-up control), the new top-down control operating after the depletion

of large pelagics likely contributed to the observed increase in phytoplankton biomass during the 1980s.

According to the data, around 700 kilotonnes of small pelagic fish were harvested each year during 1980–1988 (Fig. 3d). It corresponds to exploitation of more than 70% of the annual stock, reaching ~100% during 1982–1984 (Fig. 3d). This implies that the stock was close to collapsing during 1982–1984 (Fig. 3d). The stock estimate data instead show an elevated stock size at 1985–1987 comparable with that of the late 1970s, before a final collapse in 1989. It in fact reflects the higher stock contribution of sprat, which is an economically less valuable and harvested small pelagic fish as compared to anchovy (Daskalov, 2003). On the contrary, the anchovy stock follows a decreasing trend during 1985–1987. The minimal predation pressure imposed by the already depleted large predatory fish stocks (Fig. 3d) as well as high resource availability from the lowest trophic level might be other factors for sustaining a steady level of small pelagic fish catch during the 1980s.

The period 1988–1990 witnessed the concurrent effects of over-exploitation of pelagic fish stocks and a sudden population explosion of the ctenophore *Mnemiopsis leidyi*. The pelagic fish stocks, which were no longer sustainable under heavy overfishing, diminished rapidly to their low stock regimes of the early 1960s (Fig. 3d). The collapse in 1989 was imminent under unsustainable utilization of stocks, as the catches of immature fishes adversely affected the recruitment stocks (Purcell et al., 2001; Gucu, 2002; Niermann, 2004). Their niche was immediately filled by a large population of gelatinous carnivores, first jellyfish *Aurelia aurita* with a biomass of about 2.0 kg wet weight m^{-2} in 1988 and then its competitor ctenophore *Mnemiopsis leidyi* with a biomass close to 3.0 kg wet weight m^{-2} in 1989 (Fig. 3c). The classical “phytoplankton–zooplankton–pelagic fish” type food chain was then shifted to the one dominated by opportunistic species and gelatinous carnivores, which were a trophic dead-end without fish predators. Heavy *Mnemiopsis* predation on small pelagic fish larvae and food competition on forage zooplankton should have further exacerbated the collapse with large and sudden drop of small pelagic fish stock and catch to ~300 and 150 kilotonnes, respectively, in 1989–1990 (Kideys, 2002; Shiganova et al., 2004). These values are comparable with their levels during the pre-eutrophication phase (Fig. 3d) and suggest

the formation of a gelatinous carnivore controlled food web structure.

The collapse phase of pelagic fish stocks was followed by markedly varying, transient, oscillatory food web organisations during 1991–1996. The oscillations were superimposed on the decadal trends of increasing zooplankton and small pelagic standing stocks and of decreasing phytoplankton and gelatinous carnivore stocks (Fig. 3). Immediately after the population outburst, gelatinous carnivore biomass experienced a marked decline in 1991–1992. This period also coincides with a loss of forage zooplankton biomass and a maximum level of phytoplankton biomass ($> 20 \text{ g m}^{-2}$). The gelatinous carnivore population recovered to its previous high biomass level in 1993–1995 and decreased significantly again to about $0.5 \text{ kg wet weight m}^{-2}$ in 1996. Forage zooplankton and small pelagic stocks underwent similar oscillations as well. Starting by 1997, while the gelatinous population retained its low biomass level, the small pelagic fish stocks showed a sign of recovery, rising to ~ 800 kilotonnes towards the end of the decade (Fig. 3d). The recovery was in response to some control measures introduced to fishery exploitation (Fig. 4d) as well as settlement of *Beroe ovata* into the Black Sea, another gelatinous ctenophore species preying only on *Mnemiopsis* (Kideys, 2002; Shiganova et al., 2004). Small pelagics then started controlling the food web as the main top predator of the system. The ecosystem state developing towards the end of the 1990s reflects healthier conditions with the rise of small pelagic and zooplankton stocks and decline of phytoplankton and gelatinous stocks.

4. Diagnosis of regime-shift events

Various modelling studies (e.g., May et al., 1979; Steele and Henderson, 1984; Spencer and Collie, 1995; Scheffer et al., 2000; Edwards and Yool, 2000; Collie et al., 2004; Morozov et al., 2005) have shown theoretically that marine ecosystems may exhibit regime-shifts under certain ranges of internal and external parameters controlling food web structures. In practice, however, it is not a straightforward matter to display convincingly the existence of regime-shifts from the field data. As stated by Collie et al. (2004), “the existence of multiple equilibrium states is very difficult to demonstrate in marine ecosystems and, indeed, even identifying the variable(s) controlling such changes in biotic constituents of ecosystems can be a formidable challenge”.

This is especially valid if multiple factors are involved in regime-shift events. Commonly used methodology for identifying regime-shifts is to locate sharp changes in long time series either qualitatively or by statistical methods without relating them to the control factors. The qualitative approach relies on the subjective interpretation of large and sudden changes in time series data (e.g., Hughes, 1994; Reid et al., 2001; Chavez et al., 2003; Wooster and Zhang, 2004). The statistical approach (Easterling and Peterson, 1995; Lanzante, 1996; Hare and Mantua, 2000; Percival et al., 2001; Beaugrand, 2004; Rodionov, 2004; Weijerman et al., 2005; Solow and Beet, 2005; Overland et al., 2006) relies on making certain probabilistic statements for detection of sharp changes in the time-series data. Despite their level of sophistication, these statistical tools (i) give a necessary but not sufficient condition to demonstrate firmly their existence (Steele, 2004), (ii) often have limited power and may lead to questionable conclusions, particularly for short and noisy data sets (Scheffer and Carpenter, 2003), (iii) assume a priori the timing of regime-shifts and their detection depends critically on the choice of parameters (e.g., probability level, cut-off length, etc.), (iv) are unable to link abrupt transitions to their external and/or internal drivers, and to identify whether the changes represent abrupt or discontinuous regime shifts. Additional statistical tests are necessary, such as the condition of multimodality of the frequency distribution of the response variable in order to extend statistical power of the regime-shift analyses (Scheffer and Carpenter, 2003).

Rudnick and Davis (2003, 2006) criticised the North Pacific statistical regime-shift detection method of Hare and Mantua (2000) on the ground that the composite time series analysis ensures creation of a step regardless of the frequency content of the time series. They have supported their argument by demonstrating unrealistic abrupt changes generated by red noise. Their criticism has further extended to the unimodality of the probability density function (pdf) of the Pacific Decadal Oscillation, whereas the existence of genuine multiple distinct states requires a multi-modal pdf. Some recent statistical analyses (Overland et al., 2006; Rodionov, 2006) offer more convincing explanations for the North Pacific regime-shifts.

Scheffer and Carpenter (2003) and Collie et al. (2004) proposed a regime-shift diagnosis methodology that is more comprehensive than the approaches

will, therefore, be examined by choosing the phytoplankton biomass as the response variable and the ANL and SST as the forcing variables.

The concurrent changes in phytoplankton biomass and oxygen and hydrogen sulphide concentrations (Oguz, 2005b) support the efficiency of bottom-up control on regulation of the entire biogeochemical pump and a tight coupling between the surface biological production and the biochemical processes at the oxic–anoxic interface. In order to explore this coupling from a regime-shift perspective, dissolved oxygen and hydrogen sulphide concentrations near the oxic–anoxic interface are chosen as the response variables and the ANL as the forcing variable. Similar coupling between biological production and turbidity is examined by looking at Secchi disc depth variations with respect to the ANL.

The top-down control on the food web operates by two mechanisms: (i) the changes in the fishing pressure imposed directly on the small pelagic stocks by their exploitation and (ii) the changes in the predation pressure introduced by varying stocks of large pelagic predatory fish (Fig. 5). As the role of the predation pressure diminishes by the end of the 1960s (Fig. 3d), the examination of anticipated regime-shifts in the small pelagic stock will be based on the fishing pressure effects. The fishing pressure (FP) (i.e., the catch to stock ratio) time series (Fig. 4d) possesses two successive trends of rise and fall. The rise from 1967 to 1973 reflects gradually increasing harvest of low small pelagic stocks. A greater rate of increase in the stock with respect to the harvesting, however, reverses the trend from 1973 to 1979. All these variations occur between the FP values of 0.4 and 0.6. Thereafter, FP first increases sharply because of enhanced stock exploitation, maintains a value around 0.9 until 1988, and then decreases steeply to ~ 0.5 because of lower catchability for comparable fishing effort. A slow reduction in FP characterizes the 1990s.

4.2. Signature of climate-induced regime-shifts in abiotic environment

Recent studies (Daskalov, 2003; Oguz et al., 2006) suggested an apparent link between changes in the Black Sea hydro-meteorological properties and large-scale atmospheric systems over Eurasia. Two particular climate signatures identifying such systems are the North Atlantic Oscillation (NAO) and the East Atlantic-West Russia (EAWR) indices for

the winter season. The winter NAO index explains most of the variability during the 1980s and the first half of the 1990s. The EAWR system, formed by high and low pressure anomaly centres over the Caspian and North Seas, predominantly controls the Black Sea hydro-meteorological properties during the second half of the 1990s. The Black Sea CI (Oguz et al., 2006) involves the composition of these two indices (Fig. 4b). Its major characteristic feature is two sharp transitions between its positive and negative values during the 1980s and 1990s. The trend towards high positive values took place throughout the 1980s. The index remained in its positive mode until 1994 and then changed abruptly to a large negative value in 1995. The negative index prevailed during the rest of the 1990s.

Two particular transition periods shown in the CI coincide with similar sharp changes in the winter SST data (Fig. 4c). Winter SSTs exhibited a relatively warm climate signal during 1950–1980 with some decadal fluctuations in the 8.5–9.0 °C range. By the early 1980s, this state was perturbed markedly by strong changes in the North Atlantic Oscillation and the warm winter SST regime switched to the cold SST regime until 1995. The positive index values are associated with relatively cold winter SSTs, and the negative index values with warm winter SSTs. This close coupling between CI and SST suggests a strong control of large-scale climate forcing on the Black Sea physical properties at interannual-to-decadal time scales. Whether these changes are interpreted as regime-shifts generated by the variations in CI is discussed below.

The RSA, similar to that performed by Hare and Mantua (2000) and Weijerman et al. (2005), reveals two discrete step functions between the cold and warm regimes (Fig. 6a), which satisfies the first requirement of the regime-shift. Both the histogram (Fig. 6b) and the SST versus CI distribution (Fig. 6d) show two distinct modes with the mean SSTs of 8.75 °C and 7.6 °C on either side of the 8.0–8.4 °C bin (Fig. 6b). Two distinct clusters of SST data correspond to the positive and negative values of CI, respectively, and therefore imply an “abrupt” regime-shift. The condition of bimodality is statistically supported as well by a bimodal normal distribution fitted to the data (Fig. 6b). Using Statistica software (<http://www.statsoft.com>), the χ^2 test gives probability of 0.89 for the observed and fitted frequency distributions. Bimodality of the SST distribution is further supported by the bootstrap statistical analysis (Efron and Tibshirani,

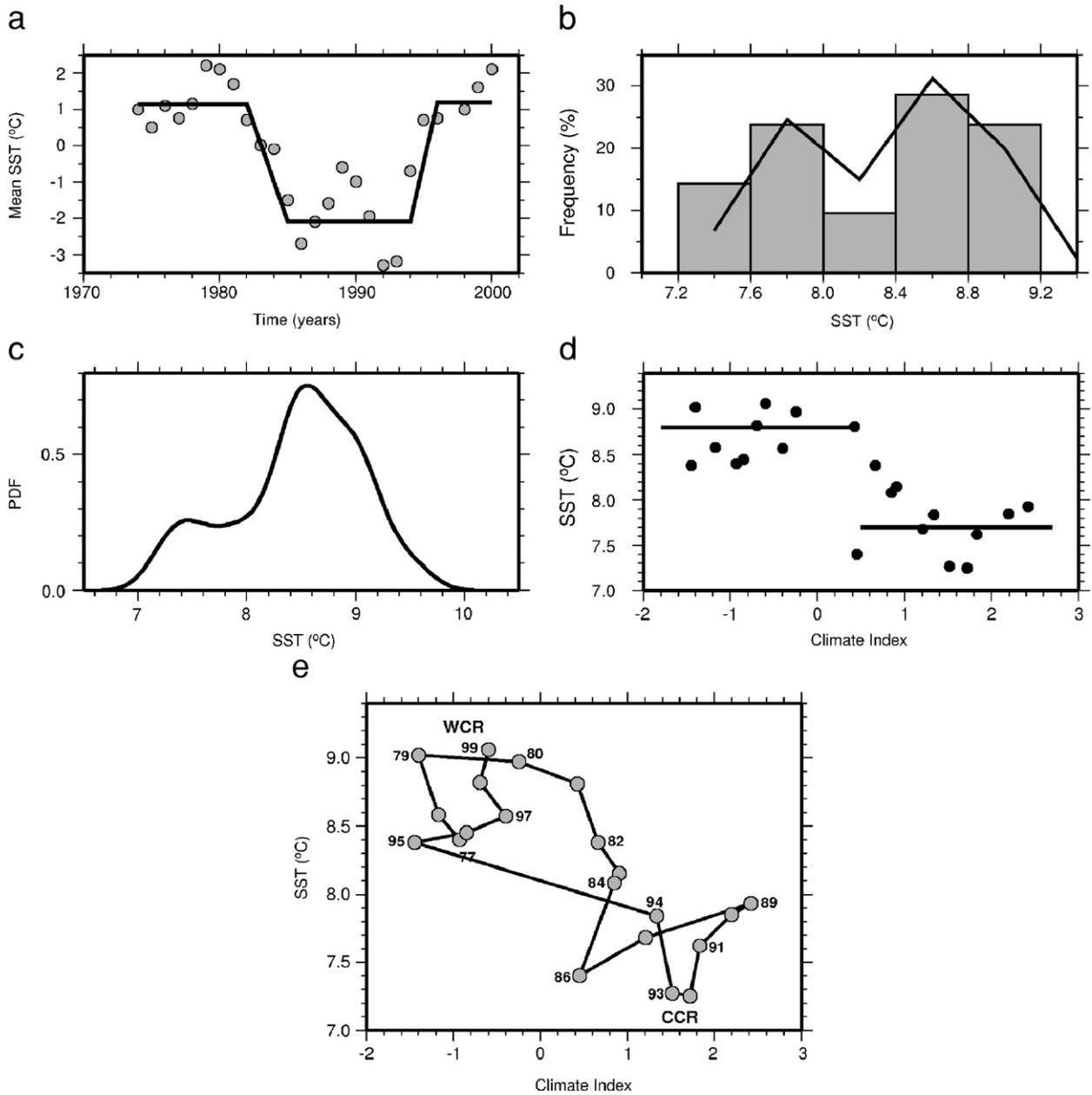


Fig. 6. (a) Long-term change of the standardized SST (dots), the mean quasi-stable states and regime-shifts obtained by the RSA method (straight line), (b) SST frequency distribution showing relative contribution of each 0.4 °C bin and bimodal normal distribution fitted to the observed distribution (continuous line), (c) probability density function obtained by a Gaussian kernel smoothing window size of 0.20 °C, (d) SST distribution with respect to the climate index showing their bimodal functional relationship with the mean states shown by straight lines, (e) the warm and cold climate regimes (WCR, CCR) corresponding to the two different ranges of climate index values, and the transition between them during 1984–1986 and 1994–1995 (numbers near the data points show the last two digits of the years).

1993). Gaussian kernel density estimates indicate the highest probability value of 0.63 for the case of two modes (Table 1). The peaks in the continuous probability density function (pdf) (Fig. 6c) are

consistent with those shown in the binned frequency distribution.

Both the SST frequency and SST-CI distribution (Fig. 6b, d) assist the RSA to define the particular

Table 1

Results of the Efron and Tibshirani (1993) bootstrap calculation of Gaussian kernel density estimates for $n = 1$ –5 modes, with 25000 iterations

Number of modes	Small pelagics	Phytoplankton	SST
1	0.058	0.415	0.348
2	0.928	0.095	0.625
3	0.598	0.853	0.249
4	0.533	0.445	0.058
5	0.172	0.611	0.238

In all cases, the null hypothesis is that we have n modes, and the alternate hypothesis is that we have more than n modes (without specifying how many). We reject the null hypothesis when the probability is less than 0.10. High probability values (in bold numbers) imply strong agreement with the null hypothesis that we have n modes.

years at which the shifts occur. The choice thus has not been made subjectively, as in earlier applications of the method. Moreover, the choice of SST bin width (0.4°C) in the histogram analysis is made according to cluster of the data points in the SST-CI distribution. That choice is critically important to obtain a bimodal distribution. Arbitrarily chosen bins indeed may not show bimodality.

The abrupt transition from the “warm climate regime” (WCR) of the 1960s and 1970s to the “cold climate regime” (CCR) took place during 1982–1983 at values of $\text{CI} \sim 0.5$ (Fig. 6e). The system immediately responded to a sudden change in the CI by shifting back to the warm climate regime in 1995. This demonstrates how a single stochastic event might push the system to its alternate regime through a different trajectory. The data coverage, however, is not yet sufficiently long to refer to it as a persistent climatic state of the Black Sea.

4.3. Signature of regime-shifts at lower trophic level

The RSA supports two sharp changes in the phytoplankton biomass time series (Fig. 7a). They signify transformation of the system’s “low biomass” pristine state (mean $\sim 3.0 \text{ gm}^{-2}$) to the “moderate biomass” state (mean $\sim 7.0 \text{ gm}^{-2}$) in 1973–1974, and to the “high biomass” state (mean $\sim 17.5 \text{ gm}^{-2}$) a decade later in 1984–1985. Further support for the three modes of the phytoplankton biomass is given by the bootstrap analysis (Fig. 7c) with a probability of 0.85 (Table 1). The phytoplankton biomass versus the ANL distribution (Fig. 7e) clearly spots the specific periods of these jumps as well as the respective critical thresholds of

ANL at 300 and 600 kilotonnes y^{-1} . The triple functional relationship between the biomass and the ANL (Fig. 7d) classifies the first shift as an “abrupt” type and the second shift as a “discontinuous” type. The moderate and high stock regimes also emerge as two distinct modes in the observed frequency distribution (Fig. 7b). The normal distributions fitted to the data indeed support the existence of moderate and high stock regimes with a probability of 0.97.

The hysteresis shown in the phytoplankton biomass versus ANL phase diagram (Fig. 7e) possesses an interesting feature of the return trajectory. Once the ANL attained its upper limit of 600 kilotonnes y^{-1} , the moderate biomass state catastrophically moved into the high biomass state. The high biomass state was maintained during the 1987–1995 period of decreasing ANL up to its lower critical threshold of 300 kilotonnes y^{-1} . As the ANL dropped below its lower threshold during the second half of the 1990s, phytoplankton biomass, however, did not show a catastrophic return to the alternate moderate biomass state but gradually converged to the low biomass state of the 1960s. This alternate path was forced by decreasing nutrient availability as well as the adverse effect of the change in top-down control on the phytoplankton biomass, as described in Section 3. The chain of events may be interpreted differently, if the low and moderate biomass states are considered as one composite state. Then, the forward and backward trajectories represent the shifts between this low biomass state and its alternate high biomass state.

We recall our conceptual model of the Black Sea food web (Fig. 5) for the likely role of climatic variations on promoting sharp changes in the phytoplankton biomass. The phytoplankton biomass versus SST phase diagram (Fig. 8a) reveals two distinct modes of biomass (higher than 17.5 gm^{-2} and smaller than 8 gm^{-2}) for two different ranges of SST (lower than 7.8°C and greater than 8.4°C). These modes are linked with two different weakly nonlinear trajectories. After oscillating within the low biomass-warm climate regime (LB-WCR) from 1960 to 1983, the transition to high biomass-cold climate regime (HB-CCR) took place during 1984–1986. This regime remained quasi-stable for eight years, and then a reverse transition to the low biomass-warm climate regime was accomplished in one year, during 1994–1995, as a response to an abrupt switch of the CI to its negative mode. Thereafter, the system gradually

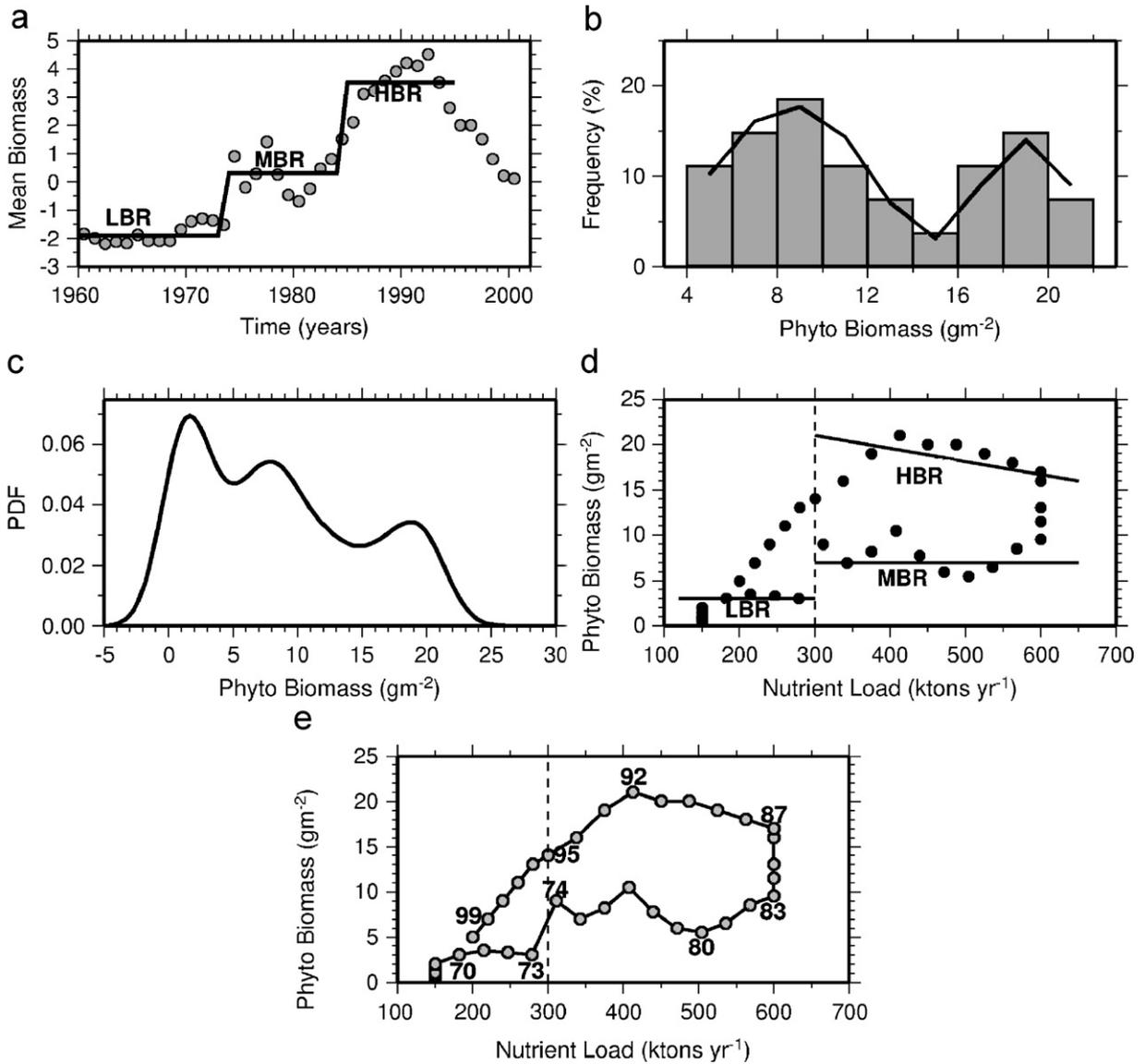


Fig. 7. (a) Long-term change of the standardized phytoplankton biomass (dots) and the mean quasi-stable states and regime-shifts obtained by the RSA method (straight line), (b) phytoplankton biomass frequency distribution showing relative contribution of each 2.0 gm^{-2} bin and bimodal normal distribution fitted to the observed distribution (continuous line), (c) probability density function obtained by a Gaussian kernel smoothing window size of 1.7 gm^{-2} (negative values are an artifact of the kernel smoothing method), (d) phytoplankton biomass distribution with respect to the anthropogenic nutrient load (in kilotonnes yr^{-1}) showing their trimodal functional relationship with the mean states shown by straight lines, (e) trajectories between the low biomass regime (LBR), moderate biomass regime (MBR) and high biomass regime (HBR) with abrupt transition between them during 1973–1974 and 1984–1985 (numbers near the data points show the last two digits of the years).

converged at the end of the 1990s to the conditions of the late 1970s and early 1980s.

Consequently, both the ANL and climate contributed to the abrupt changes in phytoplankton biomass. ANL introduced necessary nutrients (i.e., external conditions) and the climate set the neces-

sary physical mechanisms (i.e., internal conditions), to make them available for production, as pointed out by the conceptual model in Fig. 5. The way in which these multiple control mechanisms operate simultaneously is depicted by the phytoplankton biomass changes versus SST and ANL (Fig. 8b).

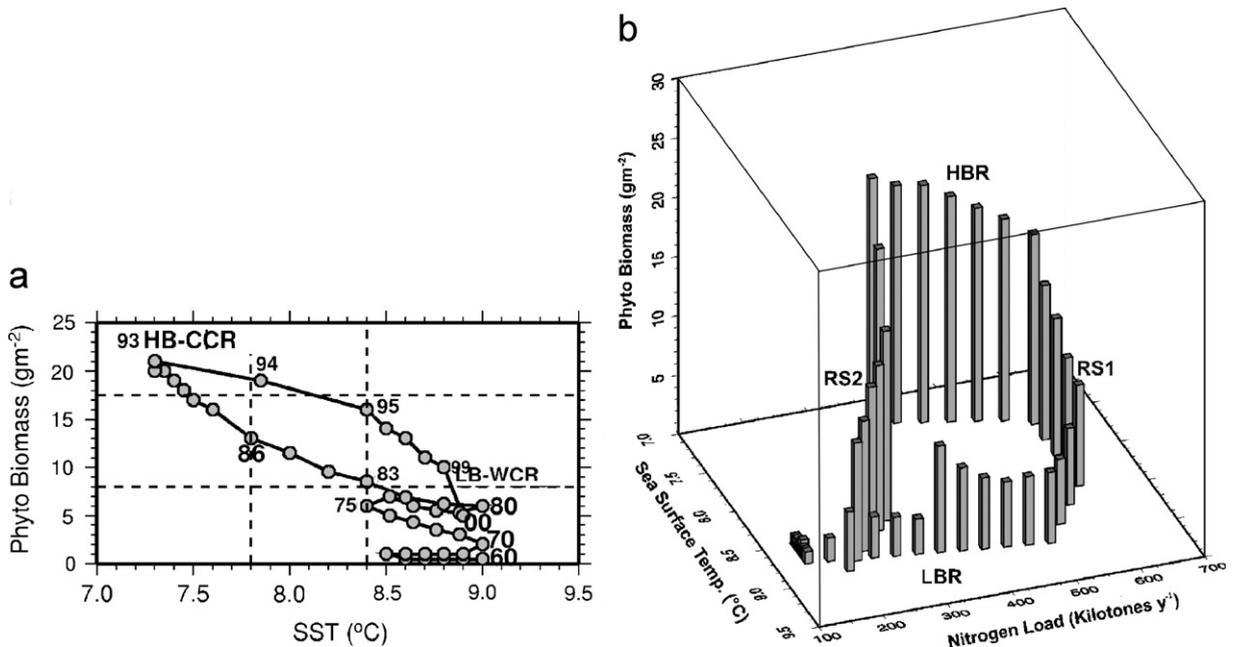


Fig. 8. (a) Phytoplankton biomass distribution with respect to SST showing trajectories along the low biomass-warm climate regime (LB-WCR), and high biomass-cold climate regime (HB-CCR) with abrupt transition between them during 1983–1986 and 1994–1995 (numbers near the data points show the last two digits of the years), and (b) phytoplankton biomass (in g m^{-2}) versus both anthropogenic nitrogen load and SST variations representing two regime-shifts (RS1, RS2) between two alternate states. The system first switches from the low biomass regime (LBR) to the high biomass regime (HBR) during the mid-1980s, and back to the low biomass regime during the mid-1990s.

The system remained poorly productive for the entire range of ANL up to 600 kilotonnes yr^{-1} irrespective of the climatic conditions. Once the system became eutrophic by accommodating sufficiently high nitrogen load (600 kilotonnes yr^{-1}), the phytoplankton biomass started increasing, but the transition (denoted by RS1) to the alternate high biomass quasi-stable state took place only after the SST became less than 7.8 °C (i.e. after cooling led to the necessary physical mechanisms to entrain subsurface nitrate). Thus, the system would not be stabilized in the new high biomass state in the absence of sufficiently strong climatic forcing even if a sufficiently high amount of nutrient load is maintained.

The system preserved its high biomass state for ANL greater than 300 kilotonnes yr^{-1} and SST lower than 7.8 °C. As soon as the ANL dropped below this threshold, the system became unstable again. The biological production declined at an increasing rate as warming developed, and finally the system switched to its poorly productive, low biomass state for SSTs greater than 8.4 °C through the regime-shift RS2 during the second half of the 1990s.

4.4. Signature of regime-shifts in chemical and optical properties

Further support for the existence of “discontinuous” regime-shifts in the Black Sea ecosystem is provided by the biogeochemical data. Particular examples are given for dissolved oxygen and hydrogen sulphide concentrations measured respectively at the 15.4 and 16.4 $\text{kg m}^{-3} \sigma_t$ levels of the oxic–anoxic interface zone, which is a layer of complex oxidation–reduction reactions (Murray et al., 1995; Oguz et al., 2001, Konovalov et al., 2005). These density surfaces roughly correspond, respectively, to 75 and 125 m depths of the interior basin. When plotted against the ANL (Fig. 9a,b), their variations are very similar to that of euphotic zone phytoplankton biomass, which implies close coupling between euphotic zone biological production, material cycling, oxygen consumption, and hydrogen sulphide production through aerobic and anaerobic organic matter remineralization processes further below (as depicted in the conceptual food web structure in Fig. 5). Both dissolved oxygen and hydrogen sulphide concentrations exhibited multiple quasi-stable states for ANL greater than

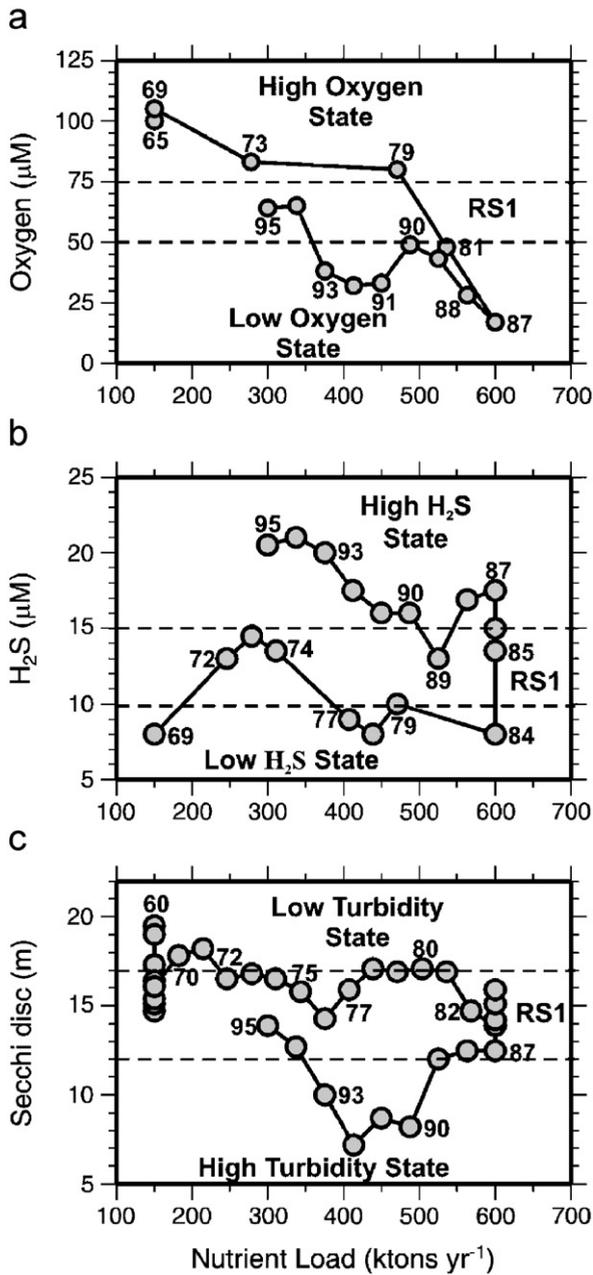


Fig. 9. Distributions of (a) dissolved oxygen concentration (in μM) at the 15.4 kg m^{-3} σ_t level, (b) hydrogen sulphide concentrations (in μM) at the 16.4 kg m^{-3} σ_t level, and (c) Secchi disc depth (in meters) with respect to the anthropogenic nitrogen load (in kilotonnes yr^{-1}). Only one regime-shift (RS1) is shown, and the subsequent regime-shift during the mid-1990s is absent because of the lack of data after 1995. The thresholds for dissolved oxygen, hydrogen sulphide and Secchi disc depth are shown by broken lines. Numbers near the data points denote last two digits of the years.

300 kilotonnes yr^{-1} . Relatively high oxygen concentrations ($>75\ \mu\text{M}$) and low hydrogen sulphide concentrations ($\sim 10\ \mu\text{M}$) shared the same state with low phytoplankton biomass due to relatively poor organic matter recycling prior to the early 1980s. On the other hand, consistent with the abrupt change in phytoplankton biomass to the alternate high biomass state, oxygen abruptly decreased to values less than $50\ \mu\text{M}$, and sulphide abruptly exceeded $15\ \mu\text{M}$ at the threshold of $600\text{ kilotonnes yr}^{-1}$ external nitrogen load. The data, however, are not sufficiently long to show how they shift back to the low productivity state. As in the case of phytoplankton data, the structure of their multiple equilibrium states also depends on the climatic forcing as depicted by [Konovalov et al. \(2005\)](#) for the dissolved oxygen concentration versus SST phase diagram.

The Secchi disc depth (SDD) data also possess multiple equilibrium states, when plotted against the ANL (Fig. 9c). The low biomass state is identified by relatively high SDD values of about $17 \pm 2\text{ m}$ (i.e. low turbidity) for increasing values of the nutrient load. At the threshold $\text{ANL} = 600\text{ kilotonnes yr}^{-1}$, this state switches to a more turbid state identified by SDD values below 12 m . This alternate high turbidity state, coinciding with the high biomass state of phytoplankton biomass, persisted for decreasing values of the nutrient load down to $300\text{ kilotonnes yr}^{-1}$ in 1995. Once again, the likely transition to the low turbidity state can not be identified by the lack of data after 1995.

4.5. Signature of regime-shifts at higher trophic level

The RSA suggests approximately five-fold forward and backward steep changes in the small pelagic stock time series (Fig. 10a). The high stock regime (HSR) persisted during 1974–1987, whereas the low stock regime (LSR) comprised the early eutrophication period (prior to 1974) and the collapse period (1988–1993). The data after 1993 have not been included in the RSA since they do not involve any clear definition of a quasi-stable state. These quasi-stable regimes clearly emerge in the stock frequency histogram as well (Fig. 10b). The entire small pelagic fish stock is equally distributed by 38% above 800 kilotonne and below 600 kilotonne limits. The stocks in the ranges of $500\text{--}600\text{ kilotonnes yr}^{-1}$ and $800\text{--}900\text{ kilotonnes yr}^{-1}$ constitute almost half of the total stock estimates in the respective regimes. The remaining 24% belongs

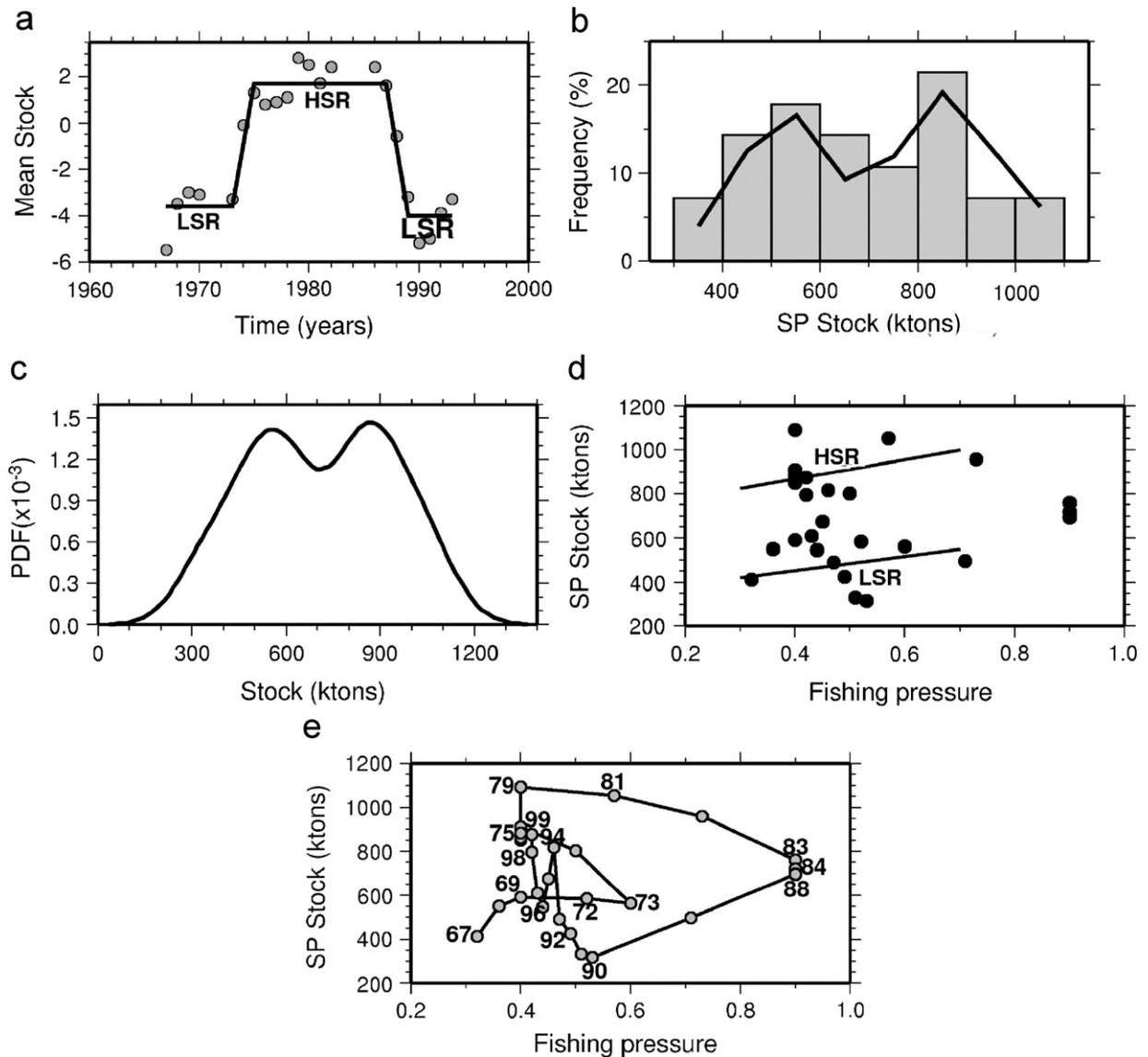


Fig. 10. (a) Long-term change of the standardized small pelagic fish stock abundance (dots) and the mean quasi-stable states and regime-shifts obtained by the RSA method (straight line), (b) small pelagic stock frequency distribution showing the relative contribution of each 200 kilotonne bin and bimodal normal distribution fitted to the observed distribution (continuous line), (c) probability density function distribution obtained by a kernel smoothing window size of 93 kilotonnes, (d) stock versus fishing pressure distribution showing their dual functional relationship with the mean low and high stock regimes (LSR, HSR) represented by straight lines, and (e) trajectories connecting the low and high stock regimes with abrupt transitions between them during 1973–1975 and 1988–1990 (numbers near the data points show the last two digits of the years).

to the transitional range at 600–800 kilotonnes. Two statistically different regression lines for the low and high stock regimes in Fig. 10d point to the existence of a dual functional relationship of the stock for the fishing pressure values between 0.3 and 0.7. Two normal distributions fitted to the histogram (Fig. 10b) with the probability of 0.86 provide further statistical support of the bimodality. More-

over, among the Gaussian kernel density estimates of the first 5 modes, the bimodal pdf distribution (Fig. 10c) attains highest probability of 0.93 (Table 1).

The small pelagic stocks lay within the low stock regime at around 500–600 kilotonnes up to 1973 for increasing fishing pressure from ~ 0.3 to ~ 0.6 (Fig. 10e). The decreasing predation control due to

gradual withdrawal of large pelagics from the system was a likely factor for keeping the stock steady despite an increase in the FP during this period. Further slight reduction in the predation and fishing pressures apparently caused the stock to rise rapidly to 900 kilotonnes in 1975 and 1100 kilotonnes in 1979. We note that, for the FP value around 0.60, the stock almost doubled in 1980 with respect to its value in 1973. Under strong and persistent stock exploitation, the system was, however, unable to maintain its high biomass regime after 1982 and shifted to the low stock regime at 1988–1989.

The low stock regime lasted only for five years, and then the stock increased gradually as it fluctuated simultaneously with the herbivorous zooplankton and gelatinous carnivores during the rest of the 1990s (Fig. 3b–d). In 1999, the small pelagic stock lay at the threshold of the high stock regime. Unless they experience relatively high fishing mortality, the decline of gelatinous carnivore stocks following the settlement of *Beroe ovata* into the Black Sea as a consumer of *Mnemiopsis leidyi* (Shiganova et al., 2004) may weaken the prey–predator oscillations and cause the stock to settle down in the high stock regime.

The relative roles of predation and fishing pressures on small pelagic stock variations are further examined by a simple model. Following Collie et al. (2004), we consider that the temporal variations of small pelagic stock are expressed by the logistic growth equation of the form

$$\frac{dB}{dt} = rB \left(1 - \frac{B}{K} \right) - c \frac{B^2}{d^2 + B^2} - fB,$$

where B defines the yearly stock, and r, f, c denote the growth, fishing mortality, and predation pressure rates, respectively. K is the carrying capacity, and d is the half saturation value for the consumption of small pelagics by their predators. On the basis of available data (Bingel et al., 1993), we set $r = 1 \text{ y}^{-1}$, $K = 2200$ kilotonnes (twice the maximum observed stock), $d = 30$ kilotonnes, and let c vary with time between two extreme values of 180–190 kilotonnes y^{-1} prior to 1970 and 30–50 kilotonnes y^{-1} in the 1980s. f is specified according to Fig. 4d as well as its slight modifications (Fig. 11c). The equation is solved by the fourth-order Runge–Kutta method and, starting from the initial conditions at 1965, integrated ahead in time for 36 years (i.e., until the year 2000).

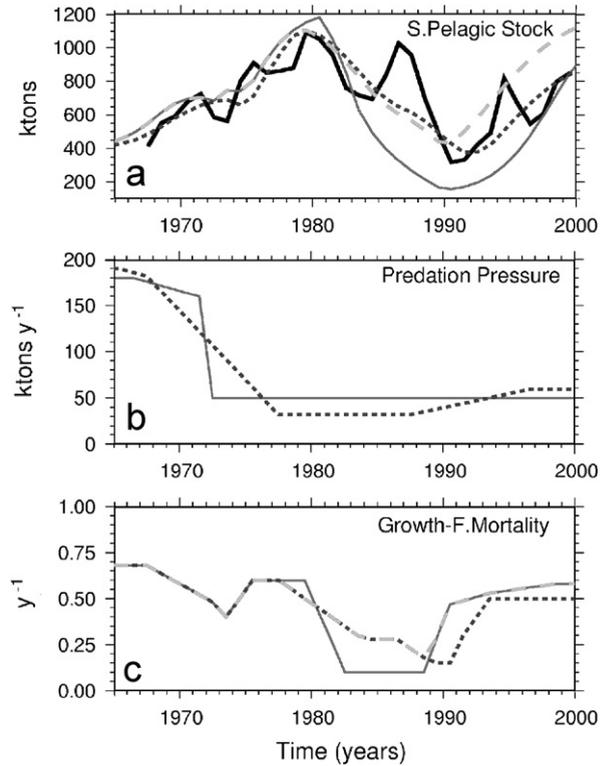


Fig. 11. Long-term changes of (a) observed (thick line) and simulated small pelagic stocks for different combinations of predation pressure and net growth rate variations, (b) predation pressure variations in the form of its abrupt changes during the early 1970s (continuous line) and gradual change during the entire 1970s (dotted line), (c) different forms of growth minus fishing pressure rate using three different fishing pressure variations.

Fig. 11a displays three different stock variations for the combinations of two different forms of the predation pressure rate and three different forms of the growth minus fishing mortality rate (Fig. 11b,c). For all combinations, the model simulates the observed stock reasonably well during 1965–1980. The stock responds to weakening predation pressure of large pelagics by doubling its value during the 1970s as asserted previously in Section 3. The stock variations are not sensitive to the way in which the predation pressure changes, either gradually or abruptly (Fig. 11b); both ways predict comparable stock estimates. A slight increase in the net growth, ($r-f$), during 1974–1980 also contributes to the stock rise. Thereafter, as the role of predation pressure remains minimal, reduction in the net growth rate due to increasing fishing pressure gives rise to a decrease in stocks during the 1980s. The simulation performed with the fishing pressure variations shown

in Fig. 4d (see the continuous line of $r-f$ in Fig. 11c) apparently results in too weak net growth rate and thus underestimates the stock. Slightly weaker fishing pressure variations during the 1980s (dotted line in Fig. 11c) provide a more realistic stock prediction. The third simulation, performed with the net growth rate variation of the second experiment up to 1988 and of the first experiment afterwards (shown by broken lines in Fig. 11c), on the other hand, results in overestimation of the stock during the 1990s. The major implication of the latter experiment is to show how a minor difference in the fishing pressure during the collapse period (1989–1992) was critical for a higher stock development (~ 200 kilotonnes y^{-1}) in the subsequent years. A common feature of all simulations performed with different FP variations is the lack of high small pelagic stock (around 1000 kilotonnes) during 1985–1987. The model is not able to reproduce the observed peak for any type of FP variations under high rates of fishing mortality.

The stock versus FP variations (Fig. 12) plotted using the FP time series shown by dotted lines in Fig. 11c resemble the hysteresis diagram depicted in Fig. 10e for FP values between 0.5 and $0.7 y^{-1}$. In Fig. 12, a slight increase in the stock until 1973 within its LSR reflects an overall response to two opposing contributions: a reduction in the predation pressure and an increase in the fishing mortality. Afterwards a reduction in FP to $0.5 y^{-1}$ triggers a large increase in the stock, which then flips into the HSR when FP is further reduced to $0.4 y^{-1}$. The HSR is maintained up to $0.7 y^{-1}$, at which the stock is prone to shift back to the LSR. The transition, however, takes place between 0.7 and $0.85 y^{-1}$ under ongoing heavy fishing. The stock

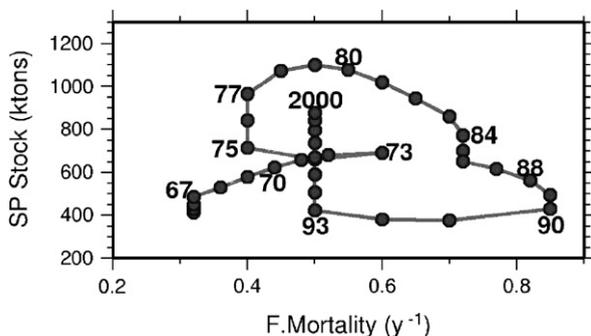


Fig. 12. Stock versus fishing pressure variations obtained by the model computations. This plot resembles closely the one given by the observations in Fig. 10e, shows the alternative low and high stock regimes between the fishing pressure values of 0.5 and $0.7 y^{-1}$.

that lies for several years within the LSR flips again to the HSR at FP threshold value of $0.5 y^{-1}$.

5. Discussion and conclusions

The present study provides an interpretation of the long-term (1960–2000) Black Sea ecological data in terms of regime-shift events. The data amply illustrate the existence of sharp transitions, at multiple trophic levels, between alternate states during the reorganisation of the ecosystem under synchronous forcing of marked nutrient enrichment, overfishing and climatic cooling/warming. The indications, based on a set of regime-shift detection criteria formerly suggested by Scheffer and Carpenter (2003), are convincing, but more conclusive evidence requires model simulations involving all basic ingredients of the food web structure. Our analysis goes beyond the statistical detection methodology of some earlier studies. It relates regime-shifts to successive changes in trophic controls that took place in response to the multiple changes in particular external and internal mechanisms. The analysis therefore introduces some degree of conceptual understanding for the way in which the Black Sea ecosystem responds to the environmental changes. The identification of regime-shifts from the time series data alone, as performed by some statistical regime-shift detection methods, lacks such understanding.

The first major change in the food web is the decline of large predator fish populations and the subsequent rise of small pelagic stocks in the early 1970s. It accompanies similar shifts in the phytoplankton and zooplankton biomasses. These changes together represent a major transformation of the food web structure from high abundance of large pelagics and zooplankton and low abundance of small pelagics and phytoplankton to an alternate regime of high small pelagic fish and phytoplankton abundance and low zooplankton (both herbivorous and carnivorous) abundance. The second regime-shift corresponds to the collapse of small pelagics and the immediate rise of gelatinous stocks in the late 1980s. It alters the previous regime to a low small pelagic fish stock and high zooplankton abundance regime in which gelatinous carnivores act as the top predator. After five years persistence in the low stock regime, small pelagic stocks, together with those of the herbivorous and gelatinous zooplankton, oscillated roughly bi-annually during the 1990s. Thus, it appears that the Black

Sea ecosystem was re-organized from the early 1970s to the end of the 1990s not only in the form of abrupt transitions between alternate quasi-stable states but also through a change in stable equilibrium to a cyclic attractor about which the system oscillates during the 1990s. The modelling work by Morozov et al. (2005) provides theoretical support for the existence of such oscillations in the post-invasion phase of a predator.

A small number of observations from aquatic and terrestrial ecosystems report similar regime-shift events during the disruption of the top predators and the proliferation of new predator stocks (Scheffer et al. 2001; Schmitz, 2004). Nevertheless, examples from large marine ecosystems are limited, and the Black Sea ecological data illustrate such events remarkably well. The Black Sea regime-shifts at the lowest and highest trophic levels as well as in its biogeochemical structure support the assertion by Steele (2004) that eutrophication and extreme over-fishing can indeed induce hysteresis in large marine ecosystems, if they can exert sufficiently strong forcing onto the system. The semi-enclosed character of the Black Sea may also be a factor that reinforces coupling between the response and forcing variables, as compared to open ocean ecosystems.

Volume 60 of “*Progress in Oceanography*” presents a set of regime-shift case studies from open ocean ecosystems. These events are driven by large-scale ocean/atmosphere climatic interactions and fit into the “abrupt regime-shift” category. So far, there is no convincing evidence that climate forcing (e.g., ENSO, Pacific Decadal Oscillation, and North Atlantic Oscillation) induces discontinuous regime-shifts with alternative stable states (Steele, 2004). This is also the case for climate-driven Black Sea regime-shifts observed in the phytoplankton biomass. But contrary to the open ocean ecosystems, the impact of climate forcing is limited to the lowest trophic level in the Black Sea. Higher trophic levels do not seem to be much affected, even though the marked collapse of zooplankton and gelatinous carnivore abundance in 1991–1993 as well as decreasing zooplankton abundance during the second half of the 1970s and the mid-1980s coincides with the cold periods and therefore may arguably be connected to the climatic effects.

The existence of regime-shifts is not sensitive to changes in the shapes of forcing variables within the limits of their uncertainties, as long as they retain an increasing–decreasing temporal trend or vice versa. It is not surprising to witness these regime-shift

events in view of the fact that the Black Sea concurrently experienced its historical high records of atmospheric cooling/warming, anthropogenic nutrient loading and extensive fishing pressure on pelagic fish stocks. These exceptionally strong successive external forcings unavoidably led to a series of step-like changes in different components of the ecosystem within a few years, and the alternate states persisted for about a decade. All these events occurred within four decades, and the system now seems to approach a new state, which resembles the original background conditions.

The RSA described here suggests a sign of rehabilitation of the Black Sea ecosystem within the present decade. The first sign is the current low phytoplankton production state that seems to persist as long as the present conditions of warm winters and low anthropogenic nutrient load do not change abruptly in the near future. The second sign is the increasing stocks of small pelagics. Since the Black Sea is primarily a top-down controlled system, the only way to maintain their high stock regime is to keep fishing pressure less than 0.5. If it is not carefully managed, their stock may easily switch back again to the low stock regime. In general, our RSA identifies the thresholds of some critical ecosystem properties and offers a useful conceptual approach to assist recovery plans and to develop concerted and integrated observational and modelling frameworks that will lead to more efficient management strategies for sustainable utilisation of the Black Sea marine resources.

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References

- Alley, R.B., et al., 2003. Abrupt climate change. *Science* 299, 2005–2010.
- Bakun, A., 2005. Regime-shifts. In: Robinson, A.R., Brink, K.H. (Eds.), *The Global Coastal Ocean Multiscale Interdisciplinary Processes. The Sea: Ideas and Observations on Progress in the*

- Study of Seas, vol. 13. Harvard University Press, Cambridge, p. MA.
- Barkai, A., McQuaid, C., 1988. Predator–prey role reversal in a marine benthic ecosystem. *Science* 242, 62–64.
- Beaugrand, G., 2004. The North Sea regime-shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography* 60, 245–262.
- Bilio, M., Niermann, U., 2004. Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. *Marine Ecology—Progress Series* 269, 173–183.
- Bingel et al., 1993. Stock assessment studies for the Turkish Black Sea coast. NATO-TU Fisheries final report. 108p. and figures.
- Chavez, F.P., Ryan, J., Lluch-Cota, S.E., Niquen, M., 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299, 217–221.
- Cociasu, A., Popa, L., 2002. Significant changes in Danube nutrient loads and their impact on the Romanian Black Sea shelf. Unpublished manuscript.
- Collie, J.S., DeLong, A.K., 1999. Multispecies interactions in the Georges Bank fish community. In: Alaska Sea Grant College Program, Ecosystem Approaches for Fisheries Management. Alaska Sea Grant Publication AK-SG-99-01, pp. 187–210.
- Collie, J.S., Richardson, K., Steele, J.H., 2004. Regime-shifts: can ecological theory illuminate the mechanisms? *Progress in Oceanography* 60, 281–302.
- Cook, R.M., Sinclair, A., Stefansson, G., 1997. Potential collapse of North Sea cod stocks. *Nature* 385, 521–522.
- Daskalov, G.M., 2002. Overfishing drives a trophic cascade in the Black Sea. *Marine Ecology—Progress Series* 225, 53–63.
- Daskalov, G.M., 2003. Long-term changes in fish abundance and environmental indices in the Black Sea. *Marine Ecology—Progress Series* 255, 259–270.
- Daskalov, G., Prodanov, K., Zengin, M., 2006. The Black Sea fisheries and ecosystem change: discriminating between natural variability and human-related effects. In: Proceedings of the Fourth World Fishery Congress, AFS Book.
- deYoung, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N., Shannon, L., 2004. Detecting regime-shifts in the ocean: data considerations. *Progress in Oceanography* 60, 143–164.
- Duffy-Anderson, J.T., Bailey, K., Ciannelli, L., Curry, P., Belgrano, A., Stenseth, N.C., 2005. Phase transitions in marine recruitment processes. *Ecological Complexity* 2, 205–218.
- Easterling, D.A., Peterson, T.C., 1995. A new method for detecting undocumented discontinuities in climatological time series. *International Journal of Climatology* 15, 369–377.
- Edwards, M.A., Yool, A., 2000. The role of higher predation in plankton population models. *Journal of Plankton Research* 22, 1085–1112.
- Efron, B., Tibshirani, R.J., 1993. *An Introduction to the Bootstrap*. Chapman & Hall, London.
- Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308, 1621–1623.
- Foley, J.A., Coe, M.T., Scheffer, M., Wang, G., 2003. Regime shifts in the Sahara and Sahel: interactions between ecological and climatic systems in Northern Africa. *Ecosystems* 6, 524–539.
- Grebmeier, J.M., et al., 2006. A major ecosystem shift in the Northern Bering Sea. *Science* 311, 1461–1464.
- Gregoire, M., Lacroix, G., 2003. Exchange processes and nitrogen cycling on the shelf and continental slope of the Black Sea basin. *Global Biogeochemical Cycles* 17 (2), 1073.
- Gucu, A.C., 2002. Can overfishing be responsible for the successful establishment of *Mnemiopsis leidyi* in the Black Sea? *Estuarine, Coastal and Shelf Science* 54, 439–451.
- Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime-shifts in 1977 and 1989. *Progress in Oceanography* 47, 103–145.
- Harvey, C.J., Cox, S.P., Essington, T.E., Hansson, S., Kitchell, J.F., 2003. An ecosystem model of food web and fisheries interactions in the Baltic Sea. *ICES Journal of Marine Science* 60, 939–950.
- Heath, M.R., 2005. Changes in the structure and function of the North Sea fish food web, 1973–2000, and the impacts of fishing and climate. *ICES Journal of Marine Science* 62, 847–868.
- Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551.
- Jackson, J.B.C., et al., 2001. Historical overfishing and recent collapse of coastal ecosystems. *Science* 293, 629–638.
- Kideys, A.E., 2002. Fall and rise of the Black Sea ecosystem. *Science* 297, 1482–1484.
- Konovalov, S.K., Murray, J.W., 2001. Variations in the chemistry of the Black Sea on a time scale of decades (1960–1995). *Journal of Marine Systems* 31, 217–243.
- Konovalov, S.K., Murray, J.W., Luther III, G.W., 2005. Basic processes of Black Sea biogeochemistry. *Oceanography* 18 (2), 24–35.
- Kovelev, A.V., et al., 1998. Long term changes in the Black Sea zooplankton: the role of natural and anthropogenic factors. In: Ivanov, L., Oguz, T. (Eds.), *Ecosystem Modeling as a Management Tool for the Black Sea*. NATO Science Partnership Sub-ser, 2, 47, vol. 2. Kluwer Academic Publishers, Dordrecht, pp. 221–234.
- Lanzante, J.R., 1996. Resistant, robust and non-parametric techniques for the analysis of climate data: theory and examples, including applications to historical radiosonde station data. *International Journal of Climatology* 16, 1197–1226.
- Mankovsky, V.I., Vladimirov, V.L., Solovov, M.V., Besiktepe, S., 1998. Optical properties of the Black Sea: results of the CoMSBlack and TU-Black Sea Programs. In: Ivanov, L., Oguz, T. (Eds.), *Ecosystem Modeling as a Management Tool for the Black Sea*. NATO Science Partnership Sub-ser, 2, 47, vol. 2. Kluwer Academic Publishers, Dordrecht, pp. 145–162.
- May, R.M., Beddington, J.R., Clark, J.W., Sidney, J.H., Laws, R.M., 1979. Management of multispecies fisheries. *Science* 205, 267–277.
- Mayer, A.L., Rietkerk, M., 2004. The dynamic regime concept for ecosystem management and restoration. *BioScience* 54 (11), 1013–1020.
- Mikaelyan, A.S., 1997. Long-term variability of phytoplankton communities in open Black Sea in relation to environmental changes. In: Ozsoy, E., Mikaelyan, A. (Eds.), *Sensitivity to Change: Black Sea, Baltic Sea and North Sea*. NATO-ASI Series, Environment, vol. 27. Kluwer Academic Publishers, Dordrecht, pp. 105–116.
- Morozov, A.Yu., Nezlin, N.P., Petrovskii, S.V., 2005. Invasion of a top predator into an epipelagic ecosystem can bring a

- paradoxical top-down trophic control. *Biological Invasions* 7, 845–861.
- Murray, J.W., Codispoti, L.A., Friederich, G.E., 1995. Redox environments: the suboxic zone in the Black Sea. In: Huang, C.P., O'Melia, C., Morgan, J.J. (Eds.), *Aquatic Chemistry*. American Chemical Society, pp. 157–176.
- Myers, R.A., Worm, A., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Niermann, U., Kideys, A.E., Kovalev, A.V., Melnikov, V., Belokopytov, V., 1999. Fluctuations of pelagic species of the open Black Sea during 1980–1995 and possible teleconnections. In: Besiktepe, S., et al. (Eds.), *Environmental Degradation of the Black Sea: Challenges and Remedies*, NATO Science Partnership Sub-ser., 2, Vol. 56. Kluwer Academic Publishers, Dordrecht, pp. 147–174pp.
- Oguz, T., 2005a. Hydraulic adjustment of the Bosphorus exchange flow. *Geophysical Research Letters* 32, L06604.
- Oguz, 2005b. Long term impacts of anthropogenic forcing on the reorganisation of the Black Sea ecosystem. *Oceanography* 18 (2), 112–121.
- Oguz, 2005c. Black Sea ecosystem response to climatic variations. *Oceanography* 18 (2), 122–133.
- Oguz, T., Ducklow, H., Malanotte-Rizzoli, P., Rizzoli, J., Vedernikov, J.W.I., Unluata, U., 1999. A physical-biochemical model of plankton productivity and nitrogen cycling in the Black Sea. *Deep-Sea Research I* 46, 597–636.
- Oguz, T., Murray, J.W., Callahan, A., 2001. Modeling redox cycling across the suboxic–anoxic interface zone in the Black Sea. *Deep-Sea Research I* 48, 761–787.
- Oguz, T., Cokacar, T., Malanotte-Rizzoli, P., Ducklow, H.W., 2003. Climatic warming and accompanying changes in the ecological regime of the Black Sea during the 1990s. *Global Biogeochemical Cycles* 17, 1088.
- Oguz, T., Dippner, J.W., Kaymaz, Z., 2006. Climatic regulation of the Black Sea hydro-meteorological and ecological properties at interannual-to-decadal time scales. *Journal of Marine Systems* 60, 235–254.
- Overland, J.E., Percival, D.B., Mofjeld, H.O., 2006. Regime-shifts and red noise in the North Pacific. *Deep-Sea Research I* 53, 582–588.
- Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14, 483–488.
- Percival, D.B., Overland, J.E., Mofjerld, H.O., 2001. Interpretation of North Pacific variability as a short- and long-memory process. *Journal of Climate* 14, 4545–4559.
- Petraitis, P.S., Dudgeon, R.D., 2004. Detection of alternative stable states in marine communities. *Journal of Experimental Marine Biology and Ecology* 300, 343–371.
- Purcell, J.E., Shiganova, T.A., Decker, M.B., Houde, E.D., 2001. The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. *Hydrobiologia* 451, 145–176.
- Reid, P.C., Borges, M.F., Svendsen, E., 2001. A regime-shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fisheries Research* 50, 163–171.
- Rodionov, S.N., 2004. A sequential algorithm for testing climate regime-shifts. *Geophysical Research Letters* 31, L09204.
- Rodionov, S., 2006. Use of prewhitening in climate regime-shift detection. *Geophysical Research Letters* 33, L12707.
- Rudnick, D.L., Davis, R.E., 2003. Red noise and regime-shifts. *Deep-Sea Research I* 50, 691–699.
- Rudnick, D.L., Davis, R.E., 2006. Comments on “red noise and regime-shifts in the North Pacific”. *Deep-Sea Research I* 53, 589–590.
- Schmitz, O.J., 2004. Perturbation and abrupt shift in trophic control of biodiversity and productivity. *Ecology Letters* 7, 403–409.
- Scheffer, M., Carpenter, S., 2003. Regime-shifts in ecosystems: models and evidence. *Trends in Ecology and Evolution* 18, 648–656.
- Scheffer, M., Rinaldi, S., Kuznetsov, Y.A., 2000. Effects of fish on plankton dynamics: a theoretical analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 1208–1219.
- Scheffer, M., Carpenter, S., Folley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Shiganova, T.A., Musaeva, E.I., Bulgakova, Yu.V., Mirzoyan, Z.A., Martynyuk, M.L., 2003. Invaders *Ctenophores Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* Mayer 1912, and their influence on the pelagic ecosystem of north eastern Black Sea. *Oceanology (English Translation)* 30 (2), 180–190.
- Shiganova, T.A., et al., 2004. Interactions between the invading ctenophores *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* Mayer 1912, and their influence on pelagic ecosystem of the Northeastern Black Sea. In: Dumont, H. (Ed.), *Aquatic Invasions in the Black, Caspian and Mediterranean Seas*. Kluwer Academic Publishers, Netherlands, pp. 33–70.
- Shiomoto, A., Tadokoro, K., Nagasawa, K., Ishida, Y., 1997. Trophic relations in the subarctic North Pacific ecosystem: possible feeding effect from pink salmon. *Marine Ecology—Progress Series* 150, 75–85.
- Solow, A.R., Beet, A.R., 2005. A test for a regime-shift. *Fisheries Oceanography* 14, 236–240.
- Sorokin, Y.I., 2002. *The Black Sea Ecology and Oceanography*. Backhuys Publishers, Leiden, 875p.
- Spencer, P.D., Collie, J.S., 1995. A simple predator–prey model of exploited marine fish populations incorporating alternate prey. *ICES Journal of Marine Science* 53, 615–628.
- Steele, J.H., 2004. Regime-shifts in the ocean: reconciling observations and theory. *Progress in Oceanography* 60, 135–141.
- Steele, J.H., Henderson, E.W., 1984. Modeling long-term fluctuations in fish stocks. *Science* 224, 985–986.
- Stocker, T.F., 1998. The seesaw effect. *Science* 282, 61–62.
- Suding, K.N., Gross, K.L., Houseman, G.R., 2004. Alternate states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* 19, 46–53.
- Tian, R.C., Deibel, D., Thompson, R.J., Rivkin, R.B., 2003. Modeling of climate forcing on a cold-ocean ecosystem, Conception Bay, Newfoundland. *Marine Ecology—Progress Series* 262, 1–17.
- Vedernikov, V.I., Demidov, A.B., 2002. Long-term and seasonal variability of chlorophyll and primary production in the eastern regions of the Black Sea. In: Zatzepin, A.G., Flint, M.V. (Eds.), *Multidisciplinary Investigations of the Northeast Part of the Black Sea*. Moscow, Nauka, pp. 212–234.
- Weijerman, M., Lindeboom, H., Zuur, A.F., 2005. Regime-shifts in marine ecosystems of the North Sea and Wadden Sea. *Marine Ecology—Progress Series* 298, 21–39.
- Wooster, W.S., Zhang, C.I., 2004. Regime-shifts in the North Pacific: early indications of the 1976–1977 event. *Progress in Oceanography* 60, 183–200.

- Yunev, O.A., Vedernikov, V.I., Basturk, O., Yilmaz, A., Kideys, A.E., Moncheva, S., Konovalov, S., 2002. Long-term variations of surface chlorophyll-*a* and primary production in the open Black Sea. *Marine Ecology—Progress Series* 230, 11–28.
- Zaitsev, Yu., Mamaev, V., 1997. *Marine Biological Diversity in the Black Sea: A Study of Change and Decline*. GEF Black Sea Environmental Programme, United Nations Publications, 208p.
- Zhang, C.I., Lee, J.B., Kim, S., Oh, J.H., 2000. Climatic regime-shifts and their impacts on marine ecosystems and fisheries resources in Korean waters. *Progress in Oceanography* 47, 171–190.