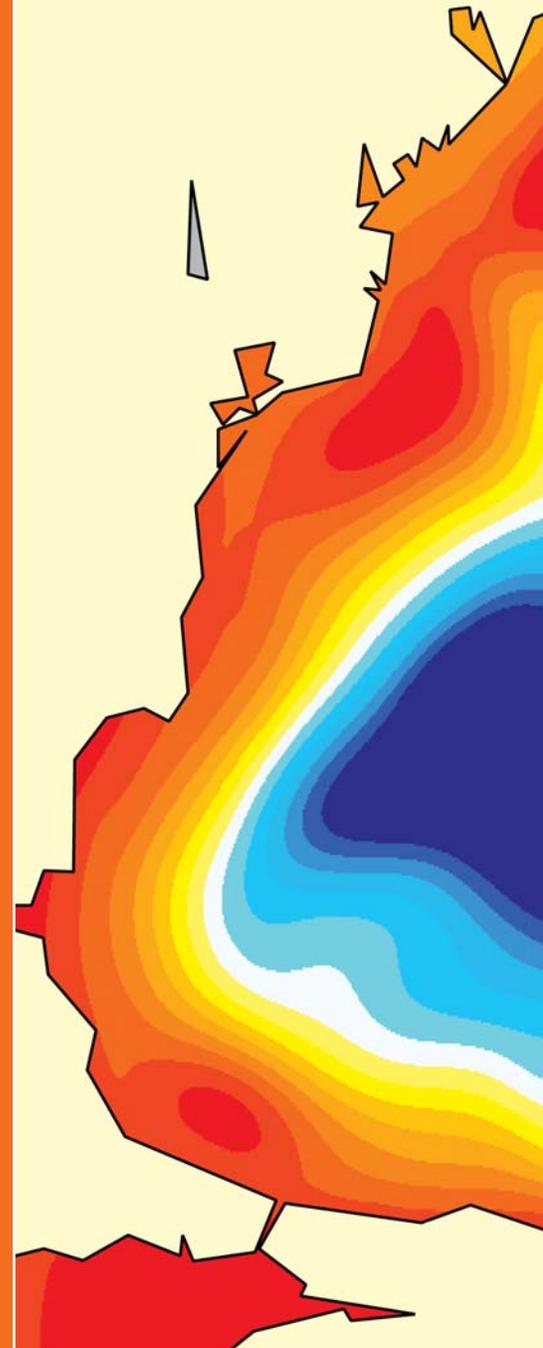
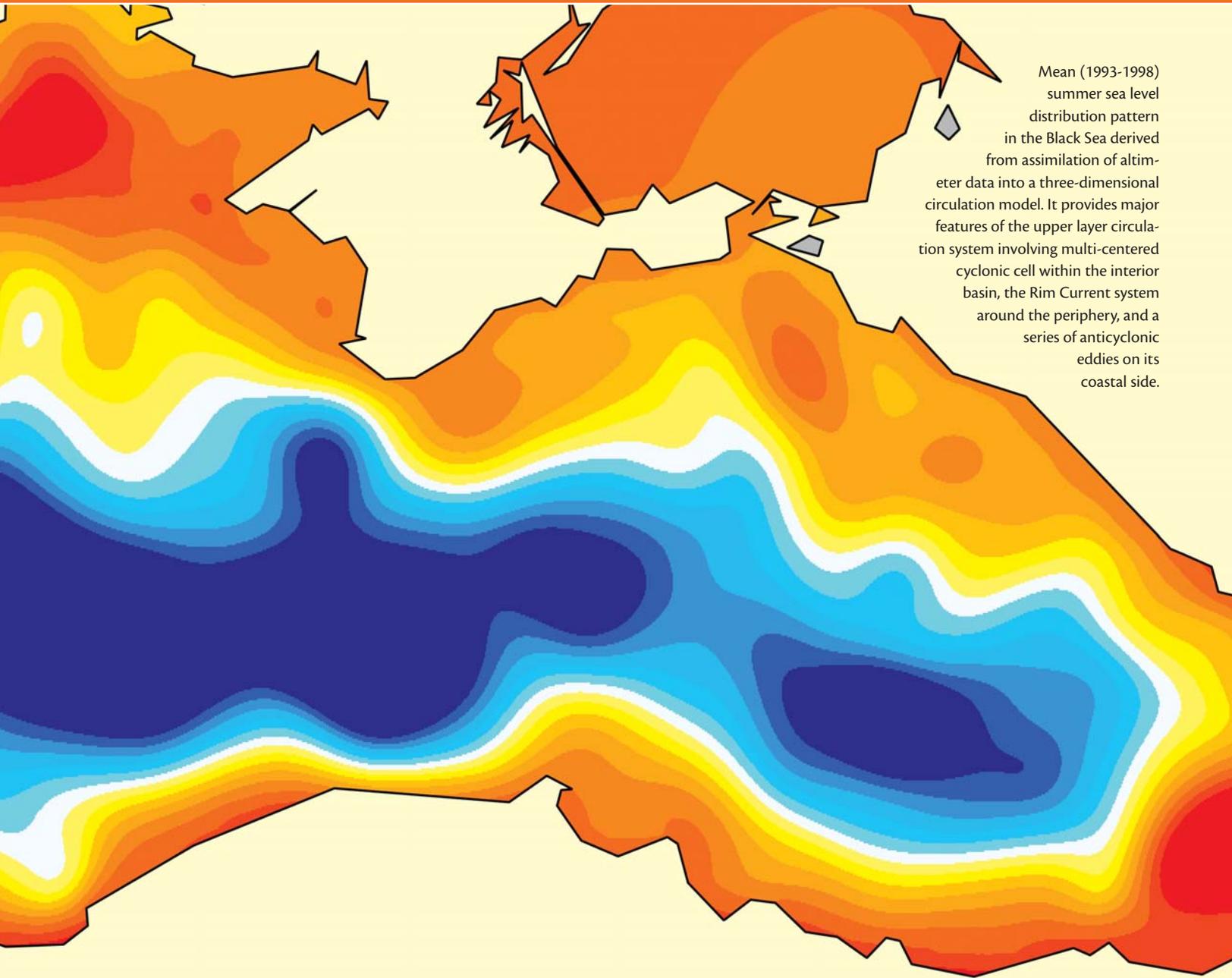


BY TEMEL OGUZ

Black Sea Ecosystem Response to Climatic Teleconnections

Marine ecosystems respond to climate changes at all trophic levels, from primary producers to herbivores to higher predators, in terms of growth, life history traits, and population dynamics (Stensth et al., 2002). Temperature variations directly affect metabolic rates. Anomalies in precipitation, solar radiation, heat flux, and wind stress fields influence circulation, water column stratification, vertical mixing, and upwelling and downwelling characteristics. These physical processes then lead to changes in nutrient cycling, primary production, and predator-prey interactions. For example, unfavorable climate conditions in the northeastern Atlantic due to intensification of the winter circulation observed during the last decades have resulted in a significant decrease in the abundance of the copepod *Calanus finmarchicus* at the expense of an increase in *C. helgolandicus* abundance (Fromentin and Planque, 1996). During El Niño years, weakening upwelling in the central and eastern Pacific, followed by warming of surface waters and increased water-column stratification, inhibited nutrient supply and modified the planktonic food web structure by decreasing primary production, zooplankton abundance, and larval fish productivity. By contrast, the La Niña event gave rise to a more-intense-than-usual upwelling of cold deep waters leading to opposite effects on ecosystem structure. In some cases, climatic effects may be so severe that the resulting anomalous hydrographic events may cause pronounced biological shifts between ecosystem states (e.g., de Young et al., 2004).





Mean (1993-1998) summer sea level distribution pattern in the Black Sea derived from assimilation of altimeter data into a three-dimensional circulation model. It provides major features of the upper layer circulation system involving multi-centered cyclonic cell within the interior basin, the Rim Current system around the periphery, and a series of anticyclonic eddies on its coastal side.

In Oguz (this issue), the 40-year-long record of Black Sea biochemistry has been interpreted in terms of eutrophication, overfishing, and population outburst of the ctenophore *Mnemiopsis*. This interpretation, however, does not completely describe the factors that control long-term variations in ecosystem structure and functioning. There are some critical questions that deserve further explanation: (1) What is the nature of small-amplitude variations superimposed on strong, decadal-scale trends observed in the data? Are these variations simply noise, or do they have any physical significance? If they have some physical significance, are they related to robust climate patterns? (2) How was the Black Sea ecosystem able to support a large fish catch for a decade before it collapsed? (3) Why did the *Mnemiopsis* population explode in 1989, several years after its introduction into the Black Sea

(1982 to 1983)? Was the period in between simply an acclimatization phase, or did some unfavorable conditions cause a delay in their population explosion? (4) Why did *Mnemiopsis* population collapse suddenly during 1992 and 1993, two years after its outburst? (5) Why was the mesozooplankton biomass at its lowest level from 1992 to 1993, although the phytoplankton biomass was at its highest and gelatinous and fish stocks were at their lowest levels? (6) Why did the *Mnemiopsis* biomass increase greatly once again from 1994 to 1995, two years after its collapse? (7) Why did the *Mnemiopsis* population and fish catch start decreasing after 1995?

This paper attempts to answer these questions from the climate perspective and shows how climate changes amplify the effects of anthropogenic inputs. The impact of climate change on ecosystem properties has been pointed out before

by Mikaelyan (1997), Niermann et al. (1999), Konovalov and Murray (2001), Yunev et al. (2002), Lancelot et al. (2002), and others. Daskalov (2003) examined climate's role from a more general perspective, emphasizing the robust signature of low-frequency variability in ecosystem properties. But, none of these studies provided a comprehensive synthesis of the way in which climatic variations played crucial roles in the functioning of the Black Sea ecosystem over the last three decades.

IMPACT OF CLIMATIC VARIATIONS ON ECOSYSTEM FUNCTIONING DURING THE 1980s

The 1980s and 1990s were characterized by dramatic variations in the regional climate (Figure 1). Following a relatively warm cycle from 1960 to 1980, the coldest and most severe winter conditions of the last century prevailed in this region from 1980 to 1995. This cold spell coincided with the strong positive phase of the North Atlantic Oscillation (NAO), and was identified by a total of ~1.8 degree C decrease in the basin-averaged, winter (December to March) mean sea surface temperature (SST) with respect to the long-term trend. In particular, 1985 to 1987 and 1991 to 1993 emerged as the coldest periods of the last century with winter-mean mixed layer temperatures as low as ~7.2 degrees C. A relatively warm cycle existed between these two cold periods with mean winter temperatures of about 8 degrees C. Note that this warmer temperature was even cooler by 0.5 degrees C than the coldest temperature of the previous warm cycle observed around the mid-1970s. Distri-

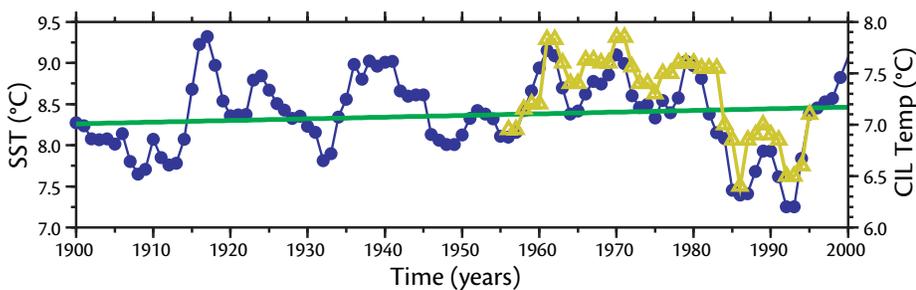


Figure 1. Temporal distribution of winter (December to March) mean sea surface temperature (SST) (°C) averaged over the interior basin with depths greater than 1500 m (dots) (after Rayner et al., 2003), and the mean temperature (°C) of the Cold Intermediate Layer (CIL Temp) for the May to November period (shown by triangles) (after Belokopytov, 1998). The straight line shows the trend of the data. Both the sea surface and CIL temperatures attained their coldest values of the last century from 1980 to 1995. The severe winters associated with cold temperatures induce strong vertical mixing in the upper layer water column, bringing more nutrients into the surface layer and promoting more enhanced primary and secondary productions during spring months. The severity of winters appear to control the intensity of spring *Mnemiopsis* production as well.

bution of the summer to autumn mean cold intermediate layer (CIL) temperature (defined as the cold core layer with a temperature less than 8 degrees C below the seasonal thermocline) indicates persistence of the cold-water signature below the seasonal thermocline during rest of the year (Figure 1). For example, Figure 5 in Oguz et al. (2003) showed the CIL temperature as low as 5.5 degrees C extending to ~50 m depth in April 1993 within the western central basin. This low temperature implies persistence of the link between the NAO and seawater temperature in the summer and autumn as well, even though the NAO is primarily a winter phenomenon and its correlation with hydro-meteorological properties is strongest during winter. More details on the NAO and its connection to the Black Sea properties are provided in the subsequent sections.

The period of pronounced increase in phytoplankton biomass during the 1980s (see Figure 3 in Oguz [this issue]) is well correlated with the sharp drop in winter temperature values. This correlation can be explained by a higher rate of nutrient supply from the chemocline, which leads to higher rate of spring phytoplankton production during cold and severe winters. A coupled physical-ecosystem model provided a quantitative support for very similar process in the Conception Bay, northwest Atlantic Ocean, where the climatic conditions driven by the NAO looked similar to those in the Black Sea during the same period (Tian et al., 2003). Dutkiewicz et al. (2001) showed dependence of this spring bloom formation mechanism on the ratio of mixed-layer depth to Sverdrup critical depth (the depth above which integrated net

daily primary production equals zero) during the spring-bloom period. When the mixed layer is much deeper than the critical depth, for example, in subpolar regions, increased mixing and reduced light levels lead to lower primary production. An example of the latter case has been encountered in northern lati-

...But, none of these studies provided a comprehensive synthesis of the way in which climatic variations played crucial roles in the functioning of the Black Sea ecosystem over the last three decades.

tudes of the North Atlantic during the 1980s (Fromentin and Planque, 1996). In the Black Sea, cold years reinforce the impact of eutrophication; rivers bring additional nutrients into the surface layer, which are deposited in the chemocline throughout the basin. In other words, the impact of eutrophication would have been much weaker in the 1980s if there had been a milder climatic regime as in the previous decade; nutrients would not have been able to recycle efficiently within the water column after they were deposited in the chemocline.

The strong relation between winter temperature and *Mnemiopsis* abundance in the Black Sea has been pointed out by Purcell et al. (2001) and Shiganova et al. (2003), and also suggested for the Narragansett Bay along the Atlantic coast of the United States by Sullivan et al. (2001). Data from the Black Sea and elsewhere showed consistently low spring reproduction and abundance after exceptionally cold winters, which

was reflected in late-summer reproduction and abundance. Thus, the severe winter conditions that prevailed during the 1980s possibly prevented earlier mass development of *Mnemiopsis* immediately after their settlement into the Black Sea from 1982 to 1983. In other words, their growth conditions appear

to become favorable only in the warmer period from 1988 to 1990. Although the change in the CIL temperature was only about 0.5 degrees C with respect to the previous cold years (Figure 1), the warmer CIL was able to cover a broader layer with respect to the earlier cold phase. In particular, the thermocline layer where *Mnemiopsis* resided and reproduced was warmer and deeper (see Figure 5 in Oguz et al. [2003]). Thus, the climatic conditions of the 1980s appear to control timing of the outburst of *Mnemiopsis* population through initiation and intensity of their reproduction. Their food supply was not a limiting factor for the intense *Mnemiopsis* blooms; mesozooplankton prey were abundant as a result of favorable climatic conditions, allowing phytoplankton production (see Figure 4 in Oguz [this issue]).

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Mesozooplankton prey were also mostly available for *Mnemiopsis* because of the collapse of the fishery during this period. Niermann et al. (1999) and Bilio and Niermann (2004) drew attention to the coincidence of the population explosion of *Mnemiopsis* in the Black Sea and regime-shift events in the North Atlantic

In some cases, climatic effects may be so severe that the resulting anomalous hydrographic events may cause pronounced biological shifts between ecosystem states...

and the North Sea during the same period. They suggested that such large-scale atmospheric events might also affect the Black Sea and generate a regime shift, ultimately triggering an explosion of the *Mnemiopsis* population. They did not, however, provide a more-detailed explanation for supporting their hypothesis. As described above, temporal warming of the Black Sea from 1988 to 1990 appears to contribute to population increase of *Mnemiopsis*. But, this event can hardly be called a regime shift.

The fish-catch data (see Figure 6 in Oguz, [this issue]) and the overfishing concept are also worthy of discussion in light of climatic variations. The small pelagic fish catch used to be about 300 to 400 kilotons from 1970 to 1978. During the following two years, the fish catch abruptly increased to around 600 kilotons, and remained at about 600 to 700 kilotons from 1980 to 1988. The sum of the medium and large pelagic catch also increased by 100 percent within approximately five years during the early 1980s.

While overfishing had been continuously depleting fish stocks, climate had been introducing favorable bottom-up ecological conditions to support the higher rate of fish production. This mechanism could be the reason behind the continuation of excessive fishing for nearly a decade-long in the Black Sea. The same

overfishing rate would cause collapse of the Black Sea fishery sooner than the late 1980s if there had been a milder climatic regime as in the previous decade.

IMPACTS OF CLIMATE VARIATIONS ON ECOSYSTEM FUNCTIONING DURING THE 1990s

The abrupt drops observed in the mesozooplankton and *Mnemiopsis* biomass during 1992 and 1993 were closely related to the severity of winters and their response to the subsequent spring and summer months. As in the case of the mid-1980s, these cold years negatively affected the metabolic and reproductive rates and overwintering of the *Mnemiopsis* population. There was no spring production at all right after very strong cooling of the upper-layer water column (see Figure 5 in Oguz [this issue], and Figure 3 in Shiganova et al. [2003]). Consequently, the *Mnemiopsis* biomass decreased abruptly by three to four-fold with respect to its value dur-

ing the 1990. For example, the average *Mnemiopsis* biomass measured within the northeastern Black Sea from 1991 to 1993 was about 0.5-1.0 kg/m² (see Figure 5a in Oguz [this issue]). But, the *Aurelia* biomass increased from its value of 0.3 kg/m² in 1989 to around 1.0 kg/m² in 1993 (Shiganova et al., 2001), which was as high as observed in the mid-1980s. The temporary predominance of *Aurelia* with respect to *Mnemiopsis* from 1991 to 1993 was also evident in the southern Black Sea data (see Figure 5b in Oguz [this issue]).

The period 1991 to 1993, immediately after the fishery collapse, was characterized by low fish stocks (see Figure 6 in Oguz [this issue]). This collapse implies a weak top-down grazing pressure from top predators (i.e., pelagic fishes and gelatinous carnivores) on the mesozooplankton biomass. When combined with the favorable bottom-up conditions, the mesozooplankton biomass was also expected to attain high values comparable to those at the end of 1980s. On the contrary, its biomass was at its minimum level since the 1960s. This low biomass could be related to the adverse effect of cold temperatures on the spring mesozooplankton production, as in the case for *Mnemiopsis* population. This argument is further supported by the increasing trend seen in the mesozooplankton, *Mnemiopsis* biomass, and fish catch and the decreasing trend seen in the phytoplankton biomass from 1994 to 1995, right after the cold climate cycle came to an end. These changes, however, do not necessarily represent a sign of improvement in ecological conditions in response to some protective measures imposed for controlling anthropogenic

nutrient loading and overfishing as argued by Kideys (2002) and others.

Beginning in 1995, the Black Sea physical climate entered a warming cycle. Sea surface temperature increased at a rate of ~0.2 degrees C per year until 2002 (Figure 1), and was accompanied by increases in mean sea level and the net annual mean freshwater flux (Stanev and Peneva, 2000; Oguz et al., 2003). From a fisheries perspective, the positive impacts of the climatic warming were to provide more suitable spawning and overwintering grounds for the anchovy, and to promote more efficient growth of plankton communities by increasing their metabolic processes. Its negative impact was to weaken or remove the major late winter to early spring peak of the classical annual phytoplankton biomass structure (Figure 2). The loss of spring phytoplankton bloom resulted from reduced upward nutrient supply from the chemocline when there is less-efficient vertical turbulent mixing, a lower upwelling rate, and stronger stratification (Oguz et al., 2003). As a result, the total annual phytoplankton biomass was reduced by at least 50 percent after 1996 (see also Figure 3 in Oguz [this issue]). Its effect was reflected at higher trophic levels in terms of reduced stocks of mesozooplankton and gelatinous carnivores (see Figures 4 and 5 in Oguz [this issue]), and pelagic fish (see Figure 6 in Oguz [this issue]). Thus, the prevalent bottom-up control limited *Mnemiopsis* abundance, even though the climatic conditions were favorable for their reproduction. The total fish catch data suggested domination of the stock by small pelagics (less than 30 cm) without any major contribution from other groups with high economic value.

DECADAL OSCILLATIONS

Studying fish-stock ecosystem interactions in the Black Sea, Daskalov (2003) pointed out significant correlations between various ecological and hydro-meteorological properties, suggesting casual links between the physical (abiotic) environment and biological production. Ecosystem properties at different food web trophic levels were found to oscillate quasi-synchronously at periods ranging from interannual (~1 to 5 years) to decadal (10 to 12 years) and interdecadal (~20 to 30 years) (Daskalov 2003). The ~10-year fluctuations in some physical properties have also been pointed out by Polonsky et al. (1997) and Peneva et al. (2000). The interannual-to-decadal variations appear

in the form of small-amplitude oscillations superimposed on the trends introduced by anthropogenic forcing. For relatively short time-series data (around 40 to 50 years), it was not possible to clearly capture interdecadal variations, and the decadal oscillations turned out to be the most dominant signal.

Here, we first show how the both biotic and abiotic data sets tend to oscillate synchronously at a decadal time scale. We then explore the nature of the teleconnection between these regional oscillations and large-scale climatic patterns. Three specific composite indices are constructed from all the available data to represent overall, integrated responses for the Black Sea atmosphere, and the

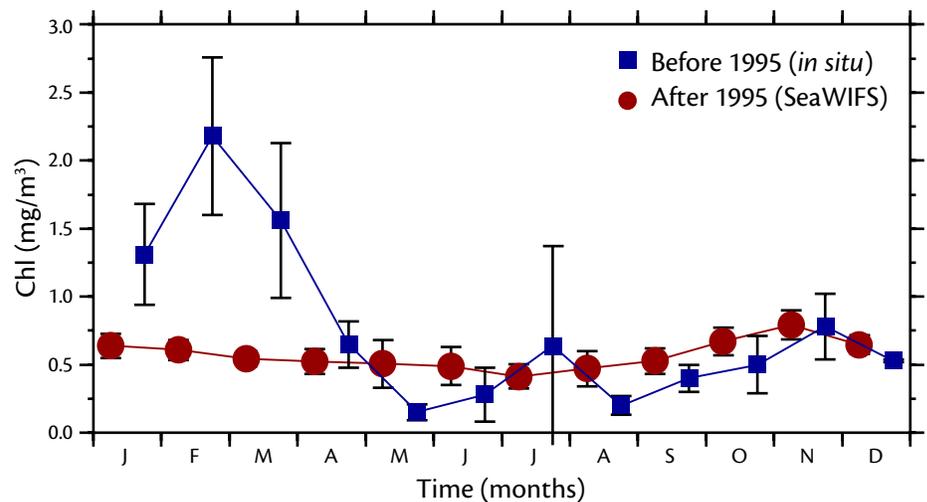


Figure 2. Monthly mean surface chlorophyll (mg/m^3) distributions obtained by averaging all the monthly mean surface chlorophyll concentrations composed from different measurements performed in deep parts of the sea (>200 m depth) prior to the mid-1990s (squares) and from 9-km gridded Sea-viewing Wide-Field-of-view Sensor (SeaWiFS) data for 1997 to 2002 and Ocean Color and Temperature Scanner (OCTS) data for November 1996 to June 1997 (dots) (after Oguz et al., 2003). The loss of the spring phytoplankton bloom is evident after 1995 in response to mild winters with warmer temperatures, as shown in Figure 1, and less-pronounced vertical mixing and subsequently lower rate of nutrient supply into the surface layer.

water column's physical and biochemical structures. These indices are standardized, describing variations of individual basin-averaged data sets within an interval between zero and one. These indices were obtained by subtracting the minimum from each datum value and then dividing by the range. This approach gives rise to a clearer representation of the oscillations even if the trends are not removed from the data. Correlation and linear regression analyses were also performed to support the relationship between these biotic and abiotic data sets.

The atmospheric index, ATI, is formed by averaging the winter (December to March) mean surface air temperature, sea surface atmospheric pressure, and evaporation minus precipitation (E-P). These properties are considered to be the most important relating local climatic response to large-scale atmospheric motions. The latter two data sets are inverted in order to have them vary, in-phase, with the air temperature time series. The ATI (Figure 3) shows a decreasing trend during the first half of each decade in response to decreasing winter air temperatures, increasing surface atmospheric pressure, and E-P. The trend is reversed during the second half of each decade, signifying wetter and milder winter conditions with relatively lower atmospheric pressures prevailing over the Black Sea.

The marine physical climate index, PCI, is calculated similarly from the winter mean SST, summer-to-autumn mean CIL temperature, annual mean sea-level anomaly, and annual mean upper-30-m layer average salinity (inverted) time series. Following quite closely the ATI, the PCI is characterized by colder (warmer) years during the first (second) part of

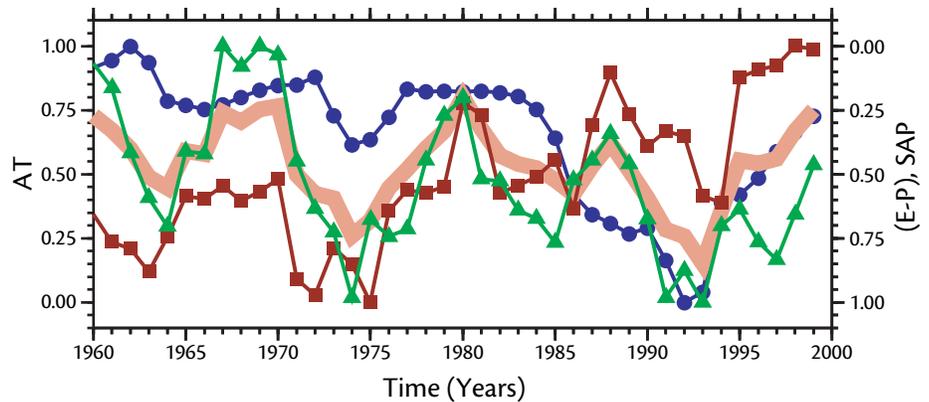


Figure 3. Temporal distributions of winter (December to March) mean atmospheric temperature, AT, (degrees C) (dots) measured at the meteorological station near the Kerch Strait along the north coast of the Black Sea (after Titov, 2000); basin-averaged evaporation minus precipitation, E-P, (triangles); surface atmospheric pressure, SAP, (squares); and the atmospheric index, ATI, (thick line) computed as an average of these three atmospheric time series. The E-P and SAP data are obtained from the European Centre for Mid-Range Weather Forecasts (ECMWF) re-analysis data set in which high-frequency oscillations have been filtered by a three-point moving average. Their axis, on the right hand side of the plot, is inverted to display in-phase variations with that of air temperature and atmospheric index. The data were standardized between zero and one by first subtracting the minimum value from each data set, and then dividing by their range. All the data suggest quasi-periodic oscillations with a period of 10 to 12 years.

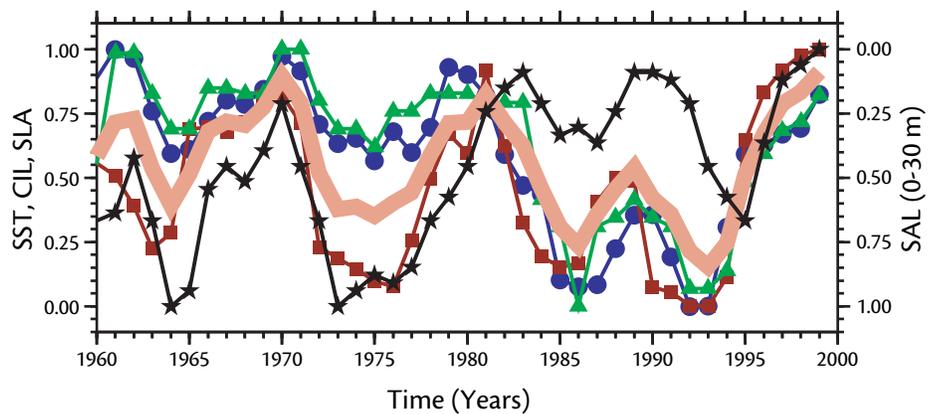


Figure 4. Temporal distributions of the winter (December to March) mean sea surface temperature, SST, (degrees C) (dots) averaged over the interior basin with depths greater than 1500 m (after Rayner et al., 2003); the mean temperature (degrees C) of the Cold Intermediate Layer, CIL, (triangles) for the May to November period (after Belokopytov, 1998); the annual mean salinity anomaly of the upper 200 m layer, SAL, (stars) (after Tsimplis and Rixen, 2003); and the annual-mean detrended sea-level anomaly, SLA, representing an average of all coastal measurements around the periphery of the basin (cm) (squares) (after Reva, 1997). High-frequency oscillations in the data have been filtered by the three point moving average. The SAL axis, on the right hand side of the plot, is inverted to display in phase variations with the others. The data were standardized between zero and one by first subtracting the minimum value from each data set, and then dividing by their range. The distribution of the marine Physical Climate Index (PCI), obtained as an average of these four data sets, is shown by the thick line. Its temporal variations are in phase with those of the SST, CIL, and SLA. All the data suggest quasi-periodic oscillations with a period of 10-12 years.

each decade (Figure 4). The average salinity anomaly of the upper-30-m layer is inversely proportional to both SST and CIL temperatures because of the stronger mixing between surface waters and more-saline subsurface waters, as well as the higher rate of evaporative losses to the atmosphere (Figure 3). Conversely, warm years are characterized by weaker salinity anomalies. The sea-level anomaly (SLA) data, representing an average of the measurements at 20 coastal stations around the sea, essentially reflected changes in the annual mean freshwater flux (runoff plus precipitation minus evaporation). The cold winter cycles were associated with low SLA since cold years were drier with more limited precipitation and river runoff. The contribution of the inverse barometric effect to the SLA is negligible in the Black Sea (Ducet et al., 1999).

The ecological index, ECOI, is formed by including data from different trophic levels of the food web. It included time series of the summer euphotic layer-integrated phytoplankton and mesozooplankton biomass, summer surface chlorophyll concentration, water transparency (Secchi depth), and hydrogen sulfide concentration at 16.4 kg/m³ σ_t surface (Figure 5). The ECOI is made to oscillate in phase with the physical marine climate index by inverting hydrogen sulfide, Secchi depth, and mesozooplankton biomass. The cold cycles covary with increasing phytoplankton biomass, and decreasing mesozooplankton biomass, transparency (Secchi depth), and vice versa for the warm cycles.

All three indices, plotted together in Figure 6, are shown to possess remarkably similar fluctuations with ~10 years

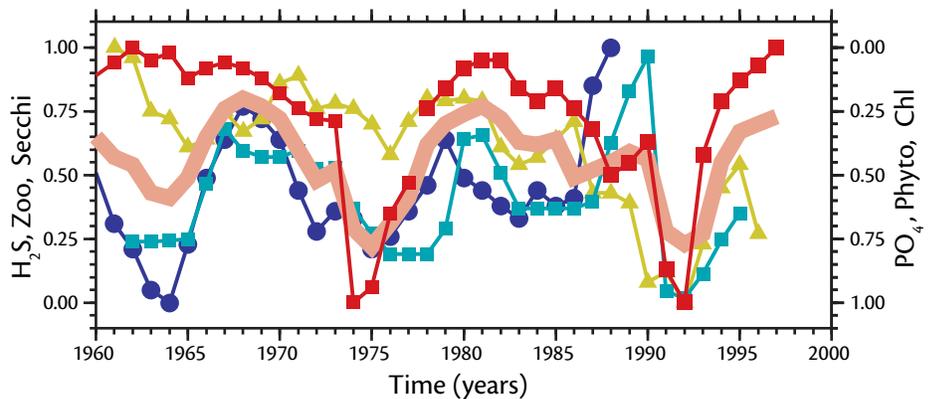


Figure 5. Temporal distributions of the phytoplankton biomass and surface chlorophyll, Chl, (mg/m³) (squares in red) for the May to September period within the interior part of the sea (after Mikaelyan, 1997 and Yunev et al., 2002); the annual mean Secchi depth for the interior basin, Secchi, (in meters) (triangles) (after Mankovsky et al., 1998); annual mean hydrogen sulfide concentration, H₂S, (μ M) at 16.4 kg/m³ σ_t surface (dots) (after Konovalov and Murray, 2001); and annual-mean mesozooplankton biomass (g/m²) within the interior basin (squares in light blue) (after Kovalev et al., 1998). The axis for phytoplankton biomass, chlorophyll concentration on the right-hand side of the plot is inverted to display in phase variations with the others. The data were standardized between zero and one by first subtracting the minimum value from each data set, and then dividing by their range. The distribution of the marine Ecosystem Index (ECOI), obtained as an average of these five data sets, is shown by the thick line. Its temporal variations are in phase with those of chlorophyll concentrations and phytoplankton biomass. All the data suggest quasi-periodic oscillations with a period of 10-12 years.

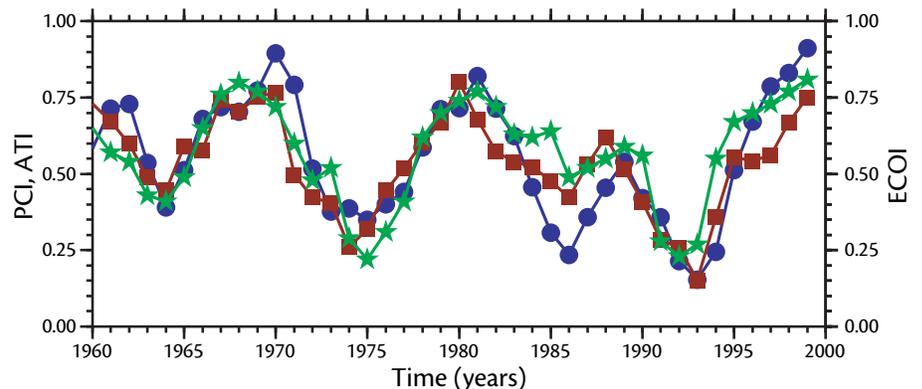


Figure 6. Temporal variations of the atmospheric index (ATI) (squares), marine physical climate index (PCI) (dots), and ecological index (ECOI) (stars) from 1960 to 1999. All three indices possess remarkable synchronous oscillations with a period of 10 to 12 years.

periodicity. As stated before, it was also detected as the most dominant mode of variability (e.g., Daskalov, 2003). The principal component of these three indices described 97 percent of the variability. Highly significant correlation of the PCI with the atmospheric index ($r=0.82$, significant at $p<0.01$) suggests prompt response of the physical climate to atmospheric forcing (Figure 7a). Similarly, the ECOI responds favorably to the PCI (Figure 7b) with correlation coefficient $r=0.78$ ($p<0.01$), indicating that the atmosphere-marine physical and ecosystem structures of the Black Sea respond synchronously to climatic forcing at the decadal time scale. In summary, the major implication of Figures 3 to 5 and their summary in Figure 6 is the robust character of the decadal oscillations, which is traced in the atmospheric and water-column physical and biologi-

cal structures even if the data were composited, and averaged over the basin and over the year. These figures further imply that certain teleconnection patterns must regulate the Black Sea atmosphere, whose response is then ultimately transferred into the water column to exert synchronous oscillatory physical and biogeochemical structuring.

CLIMATIC TELECONNECTIONS

Atmospheric circulation tends to exhibit pronounced low-frequency variability over the globe. This variability is associated with changes in intensity and location of jet streams and storm tracks, and their subsequent impacts at local temperature and precipitation fields. The NAO is known to be the most prominent mode of low-frequency variability controlling atmospheric circulation and climate over the North Atlantic and Eurasia (Mar-

shall et al., 1997). The NAO describes a large-scale meridional oscillation in the atmospheric mass between the subtropical anticyclone near the Azores and the subpolar, low-pressure system near Iceland. The NAO index is a measure of the state of the NAO and is used as a general indicator of the strength of the westerlies and winter climate over the eastern North Atlantic and Eurasia. A positive winter NAO index is associated with the strong pressure gradient between Azores high-pressure and Iceland low-pressure systems, bringing cold and dry air masses with strong westerly winds to southern Europe and the Black Sea region (Hurrell et al., 2003). Conversely, a negative NAO index implies lower surface atmospheric pressure values and milder winters, with warmer air temperatures and less dry/more wet atmospheric conditions over the Black Sea.

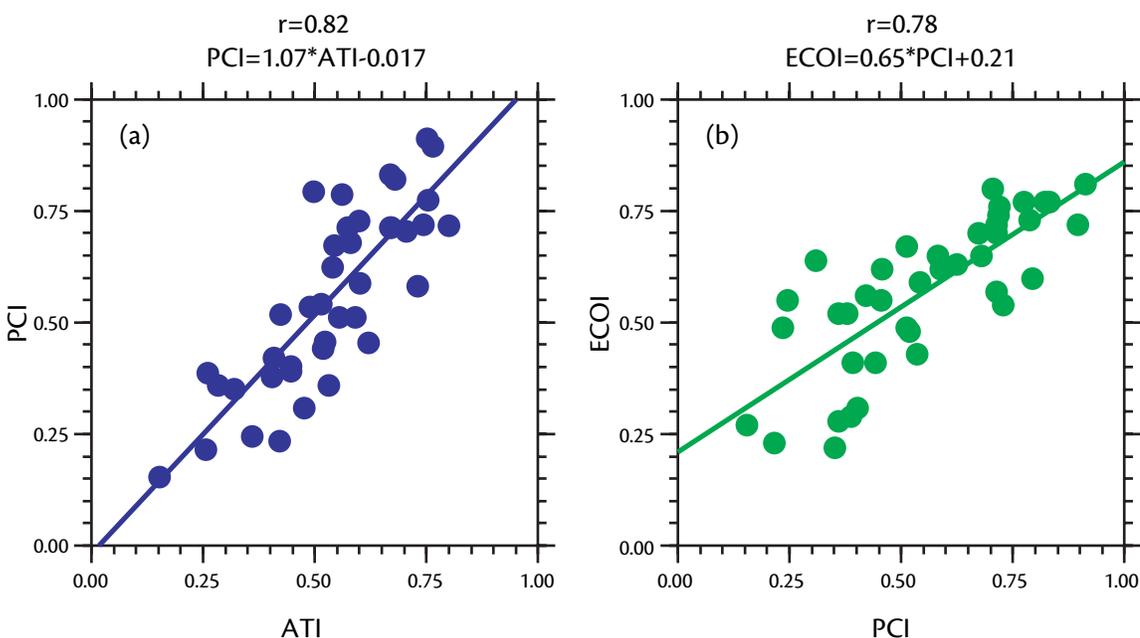


Figure 7. Scatter plots of (a) atmospheric index versus marine climate index, and (b) marine climate index versus ecosystem index. The highly significant strong correlation (around 0.8) of these three indices suggests an integrated, synchronous response of the Black Sea hydrometeorology and ecosystem to large-scale atmospheric circulation systems.

The significant impacts of the NAO on the ecological dynamics of the northern hemisphere marine and terrestrial systems are well documented (e.g., Ottersen et al., 2001; Drinkwater et al., 2003). Time variations of the winter mean NAO index, together with that of the Black Sea ATI, are shown in Figure 8. Two distinct NAO patterns are immediately evident in this plot. The 1950 and 1960s were dominated primarily by its negative phase, while the NAO stagnated in its positive phase (with few short-term exceptions) after the beginning of the 1970s. Within the study period, the NAO and ATI differ at an appreciable rate only during three occasions: 1962 to 1966, 1985 to 1988, and 1997 to 2000 (Figure 8). In general, the correlation coefficient $r=-0.45$ (significant at $p<0.01$) between the NAO index and the Black Sea ATI (Figure 9) suggests fairly robust role of the NAO in controlling the Black Sea's hydro-meteorological and ecological characteristics. Two particular reasons that prevent better correlation: (1) the inadequacy of the station-based character of this index for capturing the spatial variations of the NAO pattern when shifted longitudinally or latitudinally; and (2) the NAO's possible modulation by regional atmospheric patterns, for example, the high/low pressure systems over the Europe and Caspian Sea region, as pointed out by Krichak et al. (2002) for describing variability in precipitation patterns in the Eastern Mediterranean region. These points deserve more detailed analyses.

CONCLUSIONS

The present paper suggests that climate played a crucial role in the fluctuations of the Black Sea ecosystem during the

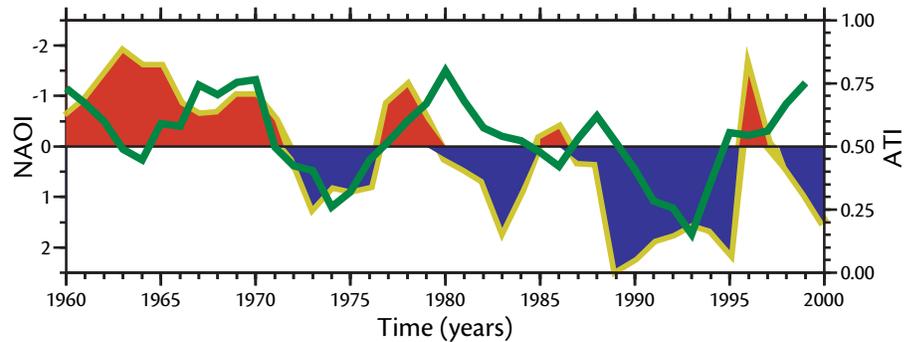


Figure 8. Temporal variations of the atmospheric index (ATI) shown by the continuous line in green, and of the NAO index from 1960 to 2000. The positive values of the NAO index are shown in blue and negative values in red. Both time series were smoothed by a Gaussian filter. The NAO and ATI tend to have quasi-synchronous oscillations over the study period except during 1962-1966, 1985-1988 and 1997-2000. The out of phase oscillations during these three particular periods are due to modulation of the NAO by regional high/low pressure systems over the Europe and Caspian Sea region.

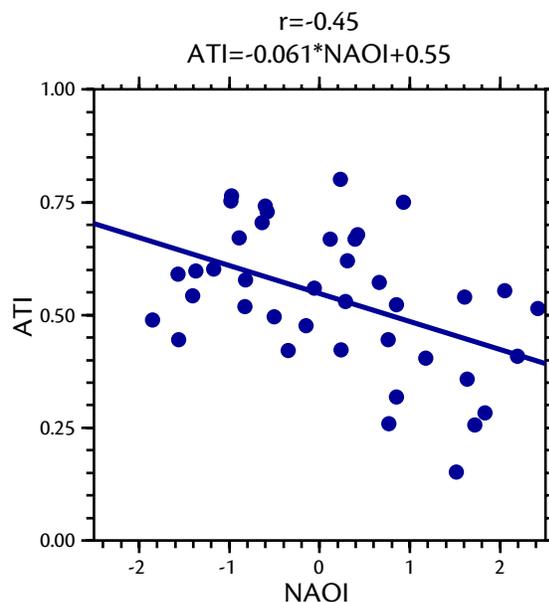


Figure 9. Scatter plot of the Black Sea atmospheric index (ATI) versus NAO index, which indicate teleconnection of the Black Sea atmosphere-marine system to the North Atlantic Oscillation with a correlation coefficient of 0.45 significant at 99 percent confidence level. Both this plot and Figure 8 imply that the Black Sea is principally driven by the atmospheric motions over the North Atlantic with some modulations by regional weather systems.

1980s and 1990s. Atmospheric processes over the North Atlantic and Eurasia were responsible for a large part of the interannual variation of the pelagic food web, enhancing the top-down and bottom-up anthropogenic effects. Strong

vertical mixing, an end-product of the climatic forcing through air-sea surface fluxes, and nutrient accumulation at the subsurface layers due to anthropogenic nutrient supply represented two primary features of ecosystem transforma-

tion during the 1980s and early 1990s. Together they led to enhanced plankton productivity, which then ultimately supported increased jellyfish production and a longer duration of excessive fishing.

Marine ecosystems respond to climate changes at all trophic levels, from primary producers to herbivores to higher predators, in terms of growth, life history traits, and population dynamics (Stensth et al., 2002).

Severe winters with exceptionally low winter temperatures in the 1980s also suppressed reproduction and growth of *Mnemiopsis* in appreciable quantities at the expense of the jellyfish *Aurelia* production until the end of the decade. The effects of strong winters on the ecosystem were felt even more strongly from 1991 to 1993 at which both mesozooplankton and *Mnemiopsis* biomass decreased abruptly. The cold cycle was followed by a warm cycle in the second half of the 1990s. This era was characterized by less-efficient biological productivity. Later, *Beroe ovata*, another gelatinous carnivore, settled into the Black Sea and started consuming *Mnemiopsis* in 1999. Its effect was immediately felt as a major reduction in the *Mnemiopsis* population, some increase in mesozooplankton biomass and fish catch. Although the ecosystem was still poorly productive in terms of phytoplankton, the available resources at higher levels were distributed more efficiently in favor of mesozoo-

plankton and small pelagic fish instead of gelatinous carnivores.

Biochemical data show well-defined, quasi-periodic climate-induced oscillations superimposed on the sharp trends

introduced by anthropogenic perturbations. The primary mode of these oscillations has an approximately 10-year period and is in phase with hydro-meteorological properties. The first half of each decade was characterized by a transition from a warm to a cold regime, and visa versa for the next half. They were found to be generally in phase with the NAO, modulated to some extent by low and high pressure systems prevalent quasi-persistently over the Europe and the Caspian Sea region.

The analysis presented here is only qualitative, based on a unified interpretation of various data sets. A more mechanistic understanding requires a modeling approach. An existing physical and ecosystem modeling infrastructure (e.g., Oguz et al., 1995; Oguz et al., 2000) is readily available to put all the pieces presented in this paper into a quantitative perspective, and to draw more definitive conclusions on the present and future performance of the ecosystem.

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