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Uncovering ecological regime shifts in the Sea of Marmara and reconsidering management strategies

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ABSTRACT

Ecosystem regime shifts can alter ecosystem services, affect human well-being, and trigger policy conflicts due to economic losses and reductions in societal and environmental benefits. Intensive anthropogenic activities make the Sea of Marmara ecosystem suffer from nearly all existing available types of ecosystem pressures such as biological degradation, exposure to hydrological processes, nutrient and organic matter enrichment, plastic pollution, ocean warming, resulting in deterioration of habitats. In this study, using an integrated ecosystem assessment, we investigated for the first time the historical development and ecosystem state of the Sea of Marmara. Multivariate analyses were applied to the most comprehensive and unique long-term data sets of 9 biotic and 15 abiotic variables for ecosystem state and drivers respectively, from 1986 to 2020. Observed changes were confirmed by detecting shifts in the datasets. The Sea of Marmara ecosystem was classified into three regimes: i) an early initial state regime under the top-down control of predatory medium pelagic fish and fisheries exploitation until mid-1990s, ii) a transitional regime between mid-1990s and mid-2010s as from ecosystem restructuring, and iii) an alternate state late regime with prevailing impacts of climate change from mid-2010s until 2020. During the 20 years transitional regime, three different phases were also characterized; i) the 1st phase between mid-1990s and early 2000s with its gradual change in ecosystem state from a decrease in predators and significant shift in physical drivers of the ecosystem, ii) the 2nd phase between 2000 and mid-2000s with a strong shift in ecosystem state, an ongoing increase in climate indices and fishing mortality, and a gradual decrease in water quality; and iii) the 3rd phase between mid-2000s and mid-2010s with the reorganization of the ecosystem dominated by small pelagic fish and ameliorated water quality. During late regime, we observed that most of the biotic variables, mainly fish biomass, and climate variables did not return to their initial state despite the improvement in some abiotic variables such as water quality. We identify these observed changes in the SoM ecosystem as a non-linear regime shift. Finally, we also developed concrete suggestions for improved regional management.

1. Introduction

Our planet is currently facing a biodiversity crisis with an unprecedented threat, one million species currently at risk of going extinct (Díaz et al., 2019). Overfishing is one of the biggest threats to marine biodiversity. Currently, one third of globally assessed fish stocks are being overfished, and the remaining two thirds are fished at their maximum sustainable yield, with just 6% of stocks underfished (Díaz et al., 2019). The Mediterranean and Black Sea ecosystems are suffering the most from overfishing with 62% of its stocks fished beyond their maximum sustainable yield as of 2017 (FAO, 2020). Fish had long been assumed to be an endless, infinite resource, where more effort leads to more catches, similar to agricultural production. However, this led to overcapacity and overfishing across the globe since the 1980s, heavily impacting the

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marine ecosystem health and its biodiversity, which serves as a buffer against climate change impacts, such as ocean acidification, increasing dead zones, and massive influxes of invasive species.

Regime shifts in the marine environment that indicate transitions between alternate ecosystem states have only become apparent since the 2000s through studies focusing on distinct ecosystem components (Conversi et al., 2010). The proposed criteria to define a regime shift are based on its classified dynamics through the relationship characteristics between forcing (usually abiotic) and response variables (usually biotic) in the ecosystem (Lees et al., 2006). If their relationship is non-linear, it is characterized as a sudden or abrupt shift from one dynamic regime to another or discontinuous regime shifts (Lees et al., 2006; Litzow and Hunsicker, 2016). The synergistic effects of overfishing, eutrophication and climate change are recognized as the main drivers of regime shifts in marine ecosystems (Alheit et al., 2005; Kirby et al., 2009; Möllmann et al., 2009; Oguz and Velikova, 2010).

Since the onset of industrial fishing in the mid-20th century, fishers have been targeting the most commercially valuable (generally the largest-sized) fish species. When one such stock of a fish species was depleted, industrial fisheries would simply switch to targeting the next most valuable stock, a process now named 'Fishing Down Marine Food Webs' (Pauly et al., 1998). The consequences of these actions (not noticed at the time) was the complete removal of higher trophic levels, which are essential for healthy ecosystem functioning. With the trophic web now out-of-sync, new relationships are forced to form, such as a switch in some cases from a top-down to bottom-up control of the ecosystem. During this process, species that became locally extinct were not documented in any formal type of records, aside from catch statistics, and did not attract any attention. Another social aspect contributing to the masking of such drastic ecosystem changes has been termed 'shifting baselines' (Pauly, 1995); this is when each fisher uses the state of the environment when they begin their career to be the accepted 'norm' to which they will compare future changes, so if the prior state of the ecosystem has not been taught to newer generations, the baseline continually resets itself to an accepted more degraded state as the norm. Shifting baselines are now considered to be common not only for fisheries, but also for many disciplines whenever the historical perspective being communicated to younger generations is lacking, and must accompany sequential noticeable changes.

Regime shifts in ecosystems can affect ecosystem services, economic well-being, and human health, often triggering policy conflicts (Lynham et al., 2017). For example, changes in pelagic fish stock structure whether resultant from overfishing or climate forcing lead to significant changes in trophic control in the marine food web. The dynamic nature of the life-history characteristics of small pelagics is considered an indicator of the impact of climate variability on marine ecosystems (Cury et al., 2000; Daskalov, 2002; Palomera et al., 2007; Albo-Puigserver et al., 2021). Further, small pelagics are very important both for maintaining the integrity of the marine ecosystem and its economic stability (Cury and Shannon, 2004; Coll and Libralato, 2012). One of the notable abrupt transitions in a marine ecosystem occurred in the Black Sea due to overfishing and eutrophication, culminating with the collapse of small pelagic fish stocks, namely, anchovy during the 1990s (Gucu, 2002; Oguz and Gilbert, 2007). The collapse was attributed to a population outbreak of the invasive ctenophore species, *Mnemiopsis leidyi,* which consumed pelagic eggs of small pelagic fish species and also competed against small pelagics for zooplankton. Resulting from this collapse in the Black Sea, the fisheries economy based on anchovy, equivalent to 17 million USD annually, declined to 300 thousand USD during the early 1990s, and this loss was remarkable especially for Turkey, until the ecosystem recovered around 1997 (Knowler and Barbier, 2005; Oguz et al., 2008). Thus, changes in ecosystem states may also trigger polarization amongst stakeholders affecting the ability to meet on common ground towards establishing adaptive governance (Österblom et al., 2010).

The Sea of Marmara (SoM) is a nearly enclosed marine basin solely under Turkish jurisdiction. This sea contains highly important biological corridors connecting the Mediterranean and the Black Seas via the Bosphorus and Dardanelles Straits. It is surrounded by the Marmara region, which contains the metropolitan city of Istanbul with an official population of 15.6 million as of early 2022 (www.worldpopulationreview.com) located in the northeast of the Marmara region, and Izmit Bay in the east of the region with heavy industrial development. Due to these intensive anthropogenic and industrial activity pressures, the SoM suffers from a wide range of ecosystem pressures such as biodiversity loss, overfishing, pollution and habitat deterioration. Spatial and temporal characteristics of nutrient composition in the SoM are strongly related to its hydrodynamic conditions in terms of water exchange, possessing a structure of two water layers, and climatic conditions. The euphotic zone is fed with continuous nutrient inputs by three main sources: i) the Black Sea via the Bosphorus Strait; ii) the bottom layer by vertical mixing and; iii) anthropogenic discharges (Ediger et al., 2016). The main proportion of those inputs is consumed by the process of photosynthesis to produce particulate organic matter (POM). Therefore, the main nutrient concentrations (NO_3 and PO_4) in surface waters are generally lower throughout the year. In addition, as the POM sinks to the intermediate and bottom layers it is decomposed by heterotrophs (Polat and Tugrul, 1995). During this process oxygen is consumed and hence decreased by consumption in the lower layers, while inorganic matter is released. Aside from these natural processes, anthropogenic inputs provide other notable sources of organic matter which further contribute to depleted oxygen conditions and rich nutrient composition in the lower layers of the SoM. Overall, in the last 25 years, environmental pollution has also led to an increase in nitrate (NO_3) and phosphate (PO_4) concentrations in the lower layer, along with the reduction of dissolved oxygen (DO) concentrations (Ediger et al., 2016).

Fisheries in the SoM were highly abundant and became highly important to the economy after the 1970s. The presence of extensive pelagic resources (Atlantic bonito *Sarda sarda*, bluefish *Pomatomus salatatrix*, European anchovy *Engraulis encrasicolis*, Mediterranean horse mackerel *Trachurus mediterraneus*), along with some important demersal resources led to the development of different types of fishing techniques. SoM's fisheries are mostly based on the purse seine fisheries targeting seasonally-migratory pelagic fishes and to a lesser extent coastal fisheries targeting demersal and some migratory stocks. Despite the large numbers of vessels, the small scale fleet lands only about 10% of the total catch (Ulman et al., 2013; Ertör-Akyazi and Ertör, 2022).

Enclosed and semi-enclosed seas provide a unique opportunity for evaluating human impacts on marine ecosystems, which can demonstrate localized impacts before similar changes are detectable in oceanic systems (Caddy, 1993). As a nearly enclosed sea with a permanent stratification due to its nature, the SoM ecosystem can also provide important insights on the impact of extended or stable stratification in the water column which is a high risk due to climate change (Li et al., 2020). In the present study, we investigate for the first time, using an integrated ecosystem assessment (IEA), the historical development and ecosystem state of the SoM. We applied multivariate analyses to the most comprehensive and unique long-term data sets from 1986 to 2020. The main objectives were to: (1) assess the changes in the SoM over the last three decades; (2) identify the common ecosystem trends; (3) test for the occurrence of regime shifts; and (4) assess the potential drivers for the ecosystem changes. In the last section, we also discussed how management strategies could be restructured to promote sustainable governance for improving long-term marine ecosystem health.

2. Materials and methods

2.1. The Sea of Marmara (SoM)

The SoM is a nearly enclosed basin with an 11,500 km^2 surface area and 400 m average depth (Fig. 1). It is connected to the Black Sea via Istanbul Strait (Bosphorus) and to the Mediterranean Sea via Çanakkale

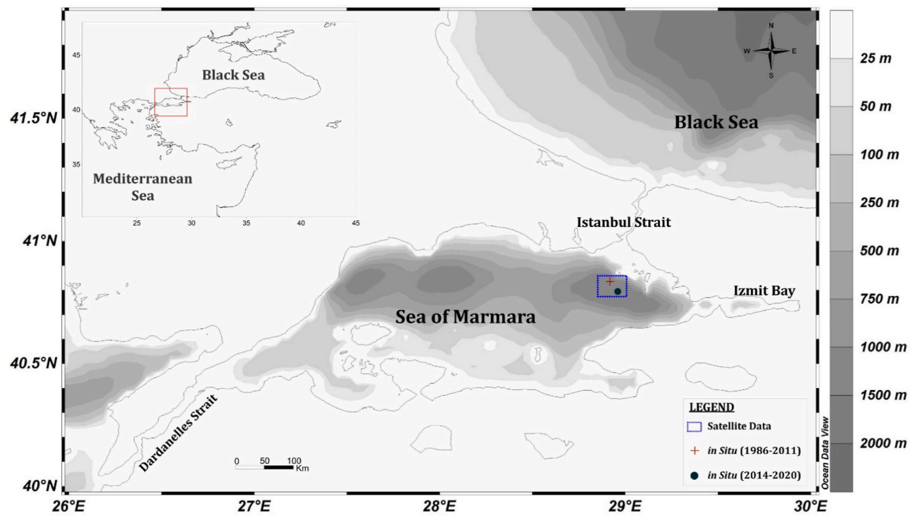

Fig. 1. Bathymetric map of the Sea of Marmara showing the geographical locations of data sources.

Strait (Dardanelles), together which are called the Turkish Strait System (TSS). Due to water exchanges by the straits, the Marmara Sea has density-dependent permanent layers separated by a sharp interface at depth. The upper layer is comprised of low salinity (~18 psμ) waters originating from the Black Sea via the Bosphorus, while its counter current-the lower layer is comprised of high salinity (~38psμ) waters originating from the Mediterranean Sea via the Dardanelles Strait (Beşiktepe et al., 1994; Altıok et al., 2014).

Structure of the upper layer current is shaped by the prevailing winds, atmospheric pressure and water level changes, as well as the current speed of the water flowing from the Bosphorus to the SoM. When the water enters from the strait to the sea, it forms a thin jet stream which increases to its highest speed (Beşiktepe et al., 1994). As this stream enters the SoM, the upper layer current flows southwards first, then westward, and finally northwestward along the southern continental slope. Although the upper layer is permanent throughout the year, its structure in terms of density and thickness by depth varies according to hydrogeographic conditions. Additionally, the water temperature has seasonal variations depending on meteorological conditions, and salinity ranges between 21 and 25 psμ, reaching the highest values during winter months due to vertical mixing of strong winds and decreased water transport from the Black Sea (Beşiktepe et al., 1994). The movement of the lower layer current after it passes through the Dardanelles Strait follows a canyon formed which extends from the Strait; then the lower layer current moves towards the west trench first and then towards the east and is also shaped by seasonality. Specifically, the higher saline and warmer waters are unable to mix with the deeper layer during summer and move towards the north (Beşiktepe et al., 1994). Also, water temperature and salinity of the bottom layer remain constant at 14.5 °C and 38.5 psμ throughout the year. The top layer temperature varies according to air temperature and its salinity varies between 21 and 25 psμ, reaching higher values due to the mixture created by winds and a reduction in the water volume stemming from the Black Sea during winter (Beşiktepe et al., 1994).

2.2. Data set

First, an intensive search was undertaken to seek out the available data sets on the abiotic and biotic variables featuring the SoM ecosystem. Then, variables were selected based on their continuity in time-series and low cross-correlations (<0.8). Finally, 24 variables were chosen according to their best representativeness of the i) ecosystem state by different trophic groups as *biotic variables*-small pelagics (anchovy, sardine and Mediterranean horse mackerel), medium pelagics (bonito and bluefish), total zooplankton, *Noctiluca scintillans* abundance, net primary productivity and chlorophyll-a concentrations; and ii) drivers of key environmental parameters as *abiotic variables*: dissolved oxygen, nutrients, fishing mortality and hydroclimatic parameters. The time-series' were compiled for the 1986–2020 period (Table 1).

Biomass (B, in tonnes) and fishing mortality (F, y^{-1}) time-series of small and medium pelagics were obtained from the only stock assessment study based on catch-based analysis (Demirel et al., 2020). The most continuous available other biotic and environmental data set for the SoM was available between 1986 and 2020 for the northeastern part (Fig. 1) which included two measurements per year; one in winter (January–February) and one in summer (July–August). Therefore, winter and summer values of total zooplankton and *Noctiluca scintillans* abundance, *in situ* sea surface temperature (SST, ∘C), sea surface salinity (SSS, psu), dissolved oxygen (DO, mg L^{-1}), nutrient concentrations (PO_4, NO_3+NO_2: NO_x, and SiO_2, μM), Chlorophyll-a (Chl-a, μg L^{-1}) and net primary productivity (NPP, gC m^{-2} y^{-1}) were collected for the northeast part of the SoM. Abiotic data sets from 1986 to 1996 were obtained from open access national project reports and scientific publications (Ergin et al., 1993; Polat and Tugrul, 1995; Ediger et al., 2016). Data sets including zooplankton, *N. scintillans* abundances and abiotic variables from 1996 to 2011 were obtained from long term monitoring projects by the General Directorate of Istanbul Water and Sewerage Administration (ISKI), and their related scientific publications (Yılmaz et al., 2005; Yilmaz, 2015; Ediger et al., 2016; Tas et al., 2020). The data sets for 2014–2020 were obtained from the Turkish Ministry of Environment, Urbanization and Climate Change's ongoing monitoring project with special permission. In situ SST and Chl-a data set were compared with satellite-derived data, and were found to be a great match. *In situ* NPP data was only available from 1986 to 1995, thus the data set was completed using satellite-derived data from 1997 to 2020 using GlobColour monthly reprocessed NPP (also Chl-a) data products provided by ACRI-ST, which were obtained from Copernicus Marine Environmental Monitoring Service (CMEMS). The products had a 4-km spatial resolution and were space-time interpolated. The North Atlantic Oscillation (NAO for 1986–2020; http://www.esrl.noaa.gov/psd/data/climateindices/list/) provided by the NOAA Climate Prediction Center, College Park, Maryland, USA, and the unsmoothed Atlantic Multidecadal Oscillation (AMO for 1986–2020 provided by the NOAA Physical Sciences Laboratory, Boulder, Colorado, USA), and the sea level anomaly (SLA, m with a 0.125° × 0.125° spatial resolution for 1993–2020 provided by ACRI-ST, was obtained from Copernicus Marine Environmental Monitoring Service) were included as climate indices. No data for zooplankton, *N. scintillans*, water quality indicators and SSS

Table 1
List of 24 variables used in the ecosystem assessment of the Sea of Marmara.

Indicators	Definition	Abbreviation	Period	Unit
BIOTIC				
Fish (biomass)	Anchovy	BAnch	Annual	tonnes
	Sardine	BSar		
	Mediterranean horse mackerel	BMhm		
	Atlantic bonito	BBon		
	Bluefish	BBlu		
Zooplankton	Total zooplankton	Zoo	Annual average	ind. m^{-2}
Phytoplankton	*Noctiluca scintillans*	Noc		
	Primary productivity	PP		gC m^{-2} y^{-1}
	Chlorophyll-a	Chl		μg L^{-1}
ABIOTIC				
Climatic	Sea surface temperature	SST	Annual average	°C
	Atlantic Multidecadal Oscillation	AMO	Winter (December–February)	–
	North Atlantic Oscillation in winter	Wi_NAO		–
	Sea level height in winter	Wi_SL		m
	Sea surface salinity in winter	Wi_SSS		psu
Water Quality	Dissolved oxygen	DO	Annual average	mg L^{-1}
	Ortho phosphate	PO_4		μM
	Nitrite + Nitrate	NO_x		
	Silicate	SiO_2		
Fisheries	Anchovy fishing mortality (F)	FAnch	Annual	y^{-1}
	Sardine F	FSar		
	Mediterranean horse mackerel F	FMhm		
	Atlantic bonito F	FBon		
	Bluefish F	FBlu		
	Population growth	PopG		%

Table 2
Results of the regime shift analysis (STARS) and chronological clustering (CC) on three separate principal component analysis (PCAs) outputs: regime shift years identified in time-series of PC1 and PC2 scores and Regime Shift Index (RSI) (Rodionov, 2004).

Group	STARS			CC	
	PC1	PC2	RSI	α = 0.01	α = 0.05
PCA_all	1993↑		−0.80		
		1995↓	−2.00	1995	1995
	2001↓		−1.30	2007	2004
	2012↓		−0.77	2016	2019
		2016↑	1.55		
PCA_bio	1991↑		−0.26		1993
		1993↓	−2.47	1993	2002
	2002→		−1.82	2002	2005
	2007↓		−1.11	2009	2012
	2014↓		−0.42		2017
		2017↑	1.02		
PCA_abio	1995↑		0.77		1995
	2002↑		0.33	1995	2004
		2016↑	0.85		2016

were available in 2012 and 2013; thus, four-year averages were used for each variable to present continuity.

2.3. Data analysis

We applied common methods of Integrated Ecosystem Assessment (see IEA, Diekmann and Möllmann, 2010) to investigate the state of the Sea of Marmara ecosystem along with its historical development. First, Principal Component Analysis (PCA) was used to explore the major modes of variability in time-series data on an ordination plot (Legendre and Legendre, 1998). Prior to further analyses with PCA results, we first applied Kaiser-Meyer-Olkin (KMO) test to determine how the factors explain each other and Bartlett's test of Sphericity to check if there are interrelationship among variables. The results of both test show if data set is plausible to further conduct PCA analysis. From our results, we had a KMO value of 0.723 which indicates the presence of a strong partial correlation (Field, 2000). In addition, Bartlett's test of sphericity was significant ($p < 0.01$) which indicates interrelationship among variables (Pett et al., 2003). Hence, our data set is ideal for applying PCA. PCA was performed using all data sets (PCA_all), then using biomass and abundance of biological components as biotic variables (PCA_bio), and using climatic, water quality and fisheries data as abiotic variables (PCA_abio) separately. PCA retrieves the eigenvalue and eigenvectors from the covariance matrix of original variables. The eigenvectors account for principal components (PCs), and the eigenvalues indicate the difference explained by the PCs. Thus, PCs are weighted linear combinations of the original variables, and factor loadings represent the contribution of each variable. Year scores of PC1 and PC2 were plotted over time to display temporal PC trends and ecosystem shifts (Diekmann and Möllmann, 2010). Finally, a time trajectory is visualized using a scatter plot of PC1 (x-axis) and PC2 (y-axis) (Diekmann and Möllmann, 2010). A traffic light plot (TLP) was used to visualize systematic patterns in the time-series matrix containing the quintile values for each variable. TLP is a simple and useful tool to check ecosystem development in time. Following Diekmann et al. (2012), raw values of each variable were categorized into quintiles using a specific color for each. The variables were sorted according to their loadings along the first PC_all axis (PC1_all). Sequential *t*-test analysis of regime shifts (STARS) detection method (Rodionov, 2004, 2006) was used to detect the occurrence of regime shifts in the Sea of Marmara. STARS was applied to the first two PCs obtained from the previous PCAs (PCA_all, PCA_bio, and PCA_abio) protocol. Since the determination of the regimes is influenced by the selection of the cut-off length (l) and the significance level *p* of the *t*-test, prior to analysis, we applied a $l = 5$ categorization using $p < 0.05$. We also set a prewhitening procedure to remove the red noise component from the time-series using least-squares estimation for serial correlation (Rodionov, 2006). Cumulative Regime Shift Indices (RSI) were then estimated representing a cumulative sum of normalized deviations, which were used to detect the time of an abrupt change. Variables indicating ecosystem state and drivers were also applied in STARS to detect potential regime shifts. Chronological clustering (CC), another ordination technique, was used to identify the occurrence of the most significant shifts as abrupt changes in the time-series. The CC was applied to annual scores of PC1 and PC2 of PCAs (PCA_all, PCA_bio and PCA_abio). Prior to CC analysis, Euclidean distance matrix was applied. Following the recommendation by Diekmann and Möllmann (2010), a significance level ($\alpha = 0.01$) and a connectedness level (0.5) were set. A posterior test was also used to check whether identified first and last groups were similar. We also used Min/Max Autocorrelation Factor Analysis (MAFA) to extract trends and analyze relationships between fish biomass and forcing variables (Zuur et al., 2007). MAFA is a technique related to PCA which extracts trends from a time-series data set. The MAF1 was used to identify the most important trends in the time-series, and to extract the time-series components that are the most continuous in time (Zuur et al., 2007). The loadings determine the relationship of individual response variables to particular MAFA axes. Cross-correlations between MAFA axes and response variables are also known as canonical correlations. Significant negative or positive correlations of variables with MAFA axes allow for the identification of significant relationships between trends and explanatory variables. Finally, cross-correlation analyses (using Pearson's product-moment correlation coefficients) between time series indices were performed to determine the most significant time lags (at time lags of zero, one and two years) between biotic and abiotic variables.

PCA, CC and MAFA were performed using the BRODGAR 2.5.6 program (www.brodgar.com). The STARS software is available freely as an MS EXCEL add-in and can downloaded at https://sites.google.com/view/regime-shift-test.

3. Results

3.1. Ecosystem changes

The first two principal components (PC1 and PC2) of PCA_all explained 43.3% and 14.6%, respectively. Of the dataset variability, and the annual scores of the first factorial plane can be interpreted as indicators displaying the main trends in the ecosystem and its biotic environment (Fig. 2). According to loadings of biotic and abiotic variables, PC1 of PCA_all represented mainly fish biomass and pressures of fish mortality and SST. In contrast, PC2 represented the biotic factors of PP and Chl-a and abiotic factors of water quality, nutrients and climatic indices.

The temporal development of the SoM was visualized using a traffic light plot (Fig. 3). Variables were sorted according to their loadings along PC1, and values of each variable were drawn from the lowest (green) to the highest quintile (red). TLP showed a shift from variables placed at the upper left with high values during the mid-1980s until the late 1990s, to variables at the bottom right with high values in the last ten years. A different state was clearly observed before the mid-1990s characterized by high pelagic fish biomass (Fig. 4a–e) and oxygen level (Fig. 4p), but low primary productivity (Fig. 4h), climatic variables (Fig. 4l-o), nutrients and fishing mortality (Fig. 4q–y). After the mid-1990s, high nutrient concentrations and PP values suggested eutrophication and gradual increases in fishing mortality and temperature, along with decreasing fish biomasses, especially for medium pelagics. The

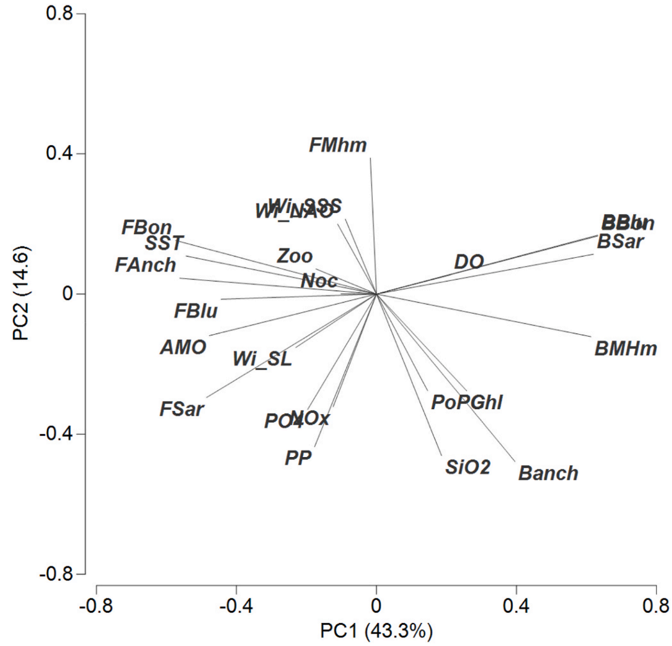

Fig. 2. Principal Component Analysis for whole data set (PCA_all) and factor loadings of each variable.

decrease in medium pelagics resulted in an instant increase in small pelagics, especially anchovy, until the mid-2000s. During the 2010s, nutrient concentrations and PP were relatively low but higher than their initial states, and SST remained high. Fish biomass was lowest as fishing intensity reached its peak (Figs. 3 and 4).

The trajectory of PC1 scores was characterized by a sharp decrease in the mid-1990s and then a gradual shift from positive to negative values beginning in the 2000s. PC1 remained negative with a continuous gradual decrease until the end of the period (Fig. 5a and b). PC2 displayed a more-less stable structure until the mid-1990s, then a sharp decrease to a negative trend until the mid-2000s, and gradually increasing to a positive trend until the end of the time series. Plotting time scores of PC1 vs PC2 visualized the overall changes in the SoM ecosystem as well as in its biotic and abiotic components. In order to distinguish the temporal trends of biotic variables and the environmental and anthropogenic drivers, two additional PCAs (PCA_bio, PCA_abio) were performed. The trajectories of the first two biotic PCs (explaining 51.7% and 20.8% of the variability) revealed similar patterns compared with those derived by PCA_all (Fig. 5a,c). On the other hand, the first two abiotic PCs (explaining 26.9% and 22.0% of the variability) showed different trends compared with those of PCA_all and PCA_bio (Fig. 5e). Using the PCA_all output, the period from 1986 to 2000 was concentrated on the right-hand side of the plot (Fig. 5b), and the period from 1994 to 2000 was grouped in the lower quadrant. Over time, the scores moved to the left part of the plot in 2001 and moved to the upper quadrant in 2012, where they remained concentrated for the remaining series. The transitional period in the mid-1990s until the mid-2010s was distinguishable; later biotic conditions of PP, Chl-a, and abiotic water quality indicators returned to a relatively similar state by the end of the period (Fig. 5a and b). We also found a similar pattern with two separate regimes and a transition period in PCA_bio output (Fig. 5c and d). PCA_abio output, on the other hand, was different (Fig. 5e and f). The transition period from the mid-1990s and mid-2010s

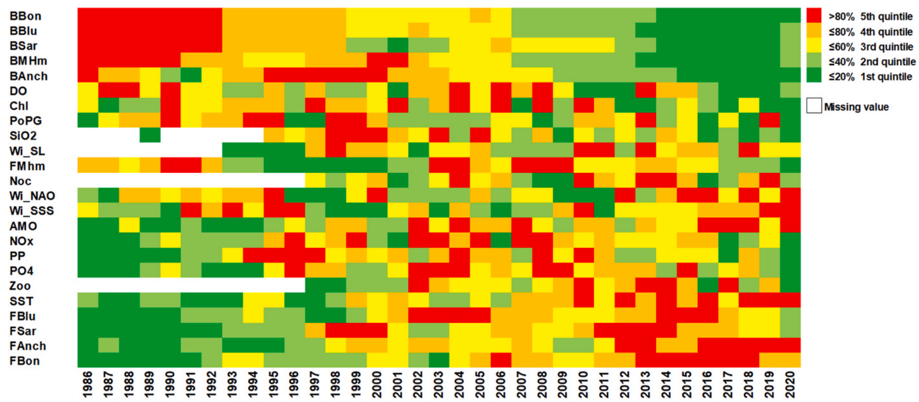

Fig. 3. Traffic-light plot representing the development of the Sea of Marmara ecosystem; raw time-series data transformed into quintiles and sorted according to PC1 of PCA_all loadings; red represents high values while yellow represents mid-values and green represents low values of the respective variable; abbreviations see Table 1.

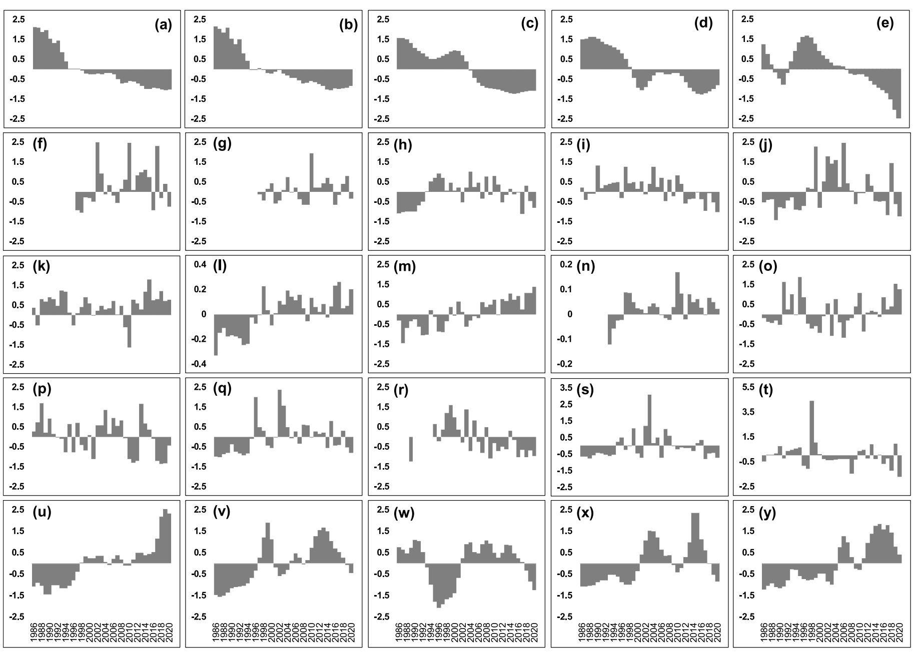

Fig. 4. Times-series development based on anomalies of the entire data sets and additional total pelagic fish catch of the SoM pelagic ecosystem. Biotic variables: fish biomass (tonnes) for (a) Atlantic bonito; (b) bluefish; (c) Mediterranean horse mackerel; (d) sardine; (e) anchovy; (f) total zooplankton abundance (ind. m^{-2}) and phytoplankton indicators; (g) *Noctiluca scintillans* abundance (ind.m^{-2}); (h) annual net primary productivity (PP, gC m^{-2} y^{-1}); (i) chlorophyll-a concentration (Chl, μg L^{-1}); (j) total pelagic fish catch (tonnes) in the SoM; (k) climatic variable in the winter season North Atlantic Oscillation (NAO) index; and (l) winter season Atlantic Multidecadal Oscillation (AMO) index; (m) annual sea surface temperature (SST, °C); (n) winter season sea level height (SL; m); (o) winter season sea surface salinity (SSS, psu); (p) water quality indicators of dissolved oxygen (DO, mg L^{-1}); (q) ortho phosphate (PO_4, μM); (r) silicate (SiO_2, μM); (s) nitrate + nitrite concentrations (NO_x, μM); (t) pressure indicators of annual Istanbul city population growth (%); (u) fishing mortality (F, y^{-1}) for anchovy, (v) sardine, (w) Mediterranean horse mackerel, (x) bluefish, and (y) bonito.

was visible, but abiotic conditions returned to a similar state by the end of the period.

3.2. Regime shifts

We applied the sequential regime shift analysis to the time series PC1 and PC2 scores of PCAs (PCA_all, PCA_bio, and PCA_abio) to verify the observations in the dataset and to detect the timing of potential regime shifts. We found 1993, 2001 and 2012 to be strong regime shift years (displayed by the Regime Shift Index) in PC1 of PCA_all data (Table 3), indicating the early and late regimes with a transitional period between the two regimes. We further detected strong regime shifts of PC1 from the biological data (PCA_bio) in 2007, indicating the beginning of a new regime. Regime shifts were further observed on PC2 of PCA_all in 1995, and the weaker one in 2016 indicating the beginning and end of the transition period. Further, another strong shift in PC2 of PCA_bio was also detected in 1993, and a weaker one in 2017. Chronological clustering analysis of the entire normalized data set identified three major breakpoints in 1995, 2007, and 2016 using an alpha value of 0.01 (Table 2). Another alpha value (0.05) was also considered to provide more information and more breaks in the time-series; thus, the years 1995, 2004, and 2019 also highlighted key differences. A posterior test was also applied to check for similarities within breakpoints indicating a change in the ecosystem beginning with its original state. All major breaks were significantly different from each other ($H < 0.01$). As a notable result, CC found the year 2020 as "singletons" indicating it did not belong to the cluster immediately before or after. CC for PCA_bio and PCA_abio data sets also identified three major breakpoints in mid-1990s, mid-2000s and mid-2010s.

Next, the automatic sequential method was applied to detect regime shifts in ecosystem state and drivers in the time-series as an indicative of overall changes in the ecosystem. Major shifts were detected using a cut-off period of five years in the mid-1990s and mid-2010s (Table 3). A decrease in medium pelagics resulted in an increase in small pelagics (Fig. 3a–e) during the 1990s. But as a further response to environmental fluctuations, an increase in fishing pressure resulted in discernible regime shifts, notably the reduction of fish biomass during mid-1990s followed by the decrease in water quality from nutrient level increases (Table 3).

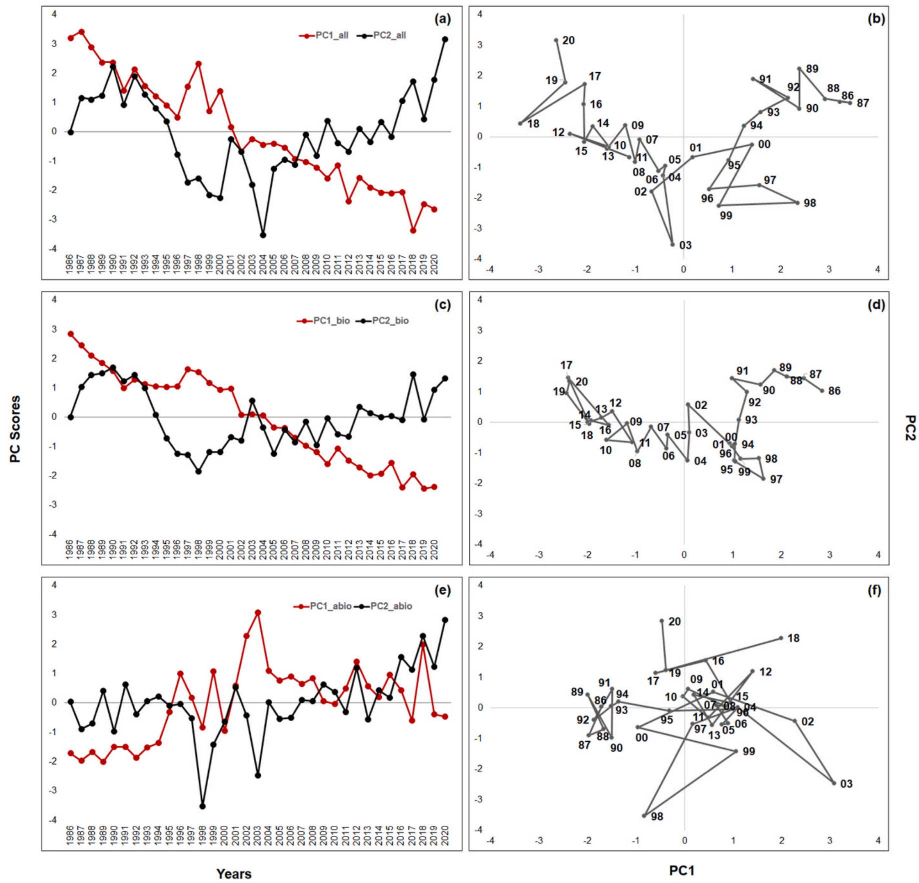

Fig. 5. Temporal trends of PC1 (red line) and PC2 (black line) scores of (a) PCA_all for whole data set, (c) PCA_bio for biotic variables as indicators of ecosystem state, and (e) PCA_abio for ecosystem drivers; (b,d,f) Time trajectory of PCAs biplot (PC1 and PC2) from 1986 (86) to 2020 (20). For abbreviations see Table 1.

Table 3
Results of the regime shift analysis (STARS) on ecosystem state and drivers presented as a decadal time-series. Years and their calculated RSI values are provided in parentheses. Significant RSI values were marked bold. (**$p < 0.01$, *$p < 0.05$). Blank rows indicate no shift in variables for respective period. For abbreviations see Table 1.

Variable	1990s	2000s	2010s
Biotic - State			
BBlu	1993 (**-2.92****)		2012 (**-0.59****)
BBon	1993 (**-4.19****)/1999 (**-0.39****)	2008 (**-0.21****)	
BMHm		2003 (**-2.53****)	2016 (0.26)
BSar	1997 (**-1.92***)	2002 (1.67)	2011 (**-0.95***)
Banch	1992 (2.87)/1998 (**-1.54***)		
Zoo			
Noc			
PP	1993 (**1.62****)		
Chl			2017 (**-0.30****)
Abiotic - Driver			
Wi_NAO			
AMO	1997 (**0.71****)		
SST	1999 (**0.27****)		2018 (**0.56****)
Wi_SL			2010 (**0.02***)
Wi_SSS			
DO			2017 (**-0.11****)
PO4		2002 (**0.31***)	
SiO2			
NOx		2002 (**0.05***)	
FAnch	1997 (**1.65****)		2017 (**3.18****)
FSar		2000 (−0.03)	
FMhm	1992 (**-1.27***)	2001 (**1.16***)	2018 (**-0.69***)
FBlu		2001 (**0.08***)	2016 (−0.40)
FBon		2005 (**0.64****)	2013 (**0.34***)
PoPG			

3.3. Key ecosystem components

The autocorrelations were high (0.98 and 0.95) and significant ($p < 0.001$) for the first and second MAFA axes (Table 4). According to the canonical correlations illustrating the relationships between biotic variables, Chl-a concentration, small and medium pelagic fish biomasses, and the first axis were significantly positively correlated with the trends of decreasing values (Table 4). In addition, primary productivity and anchovy biomass were significantly ($p < 0.05$) negatively correlated with the secondary axis. The majority of the fifteen cross-correlations were negative, and ten were significantly different from 0 at the 5% α level. Correlations between the MAF1 and the explanatory variables, i.e., AMO, SST and fishing mortalities of all fish species except from Mediterranean horse mackerel, were significantly negative (Table 4). This indicates the presence of a negative relationship between fish biomass and Chl-a. Additionally, correlations between the MAF2 and the water quality indicators, i.e., nutrients, were significant and negative, indicating their impact on PP and anchovy biomass with a similar negative relationship (Table 4). Significant explanatory variables were considered as key drivers for ecosystem state changes.

The correlations between time-series of biotic variables and significant abiotic variables at time lags of zero, one and two years showed that medium pelagic fish biomasses were significantly positively correlated with small pelagic fish biomasses with either one-year lags or from the same year, but were negatively correlated with SST and with fishing mortality of anchovy from the preceding year (Table 5). The medium pelagic fish biomasses were also negatively correlated with AMO in the same year and fishing mortality the following year. Climatic variables, i.e., SST and AMO, were negatively correlated with fish biomass, subsequent and same year respectively. Small pelagic fish biomasses were

Table 4
Correlations between explanatory variables and the first two significant MAFA axes. Significant correlations are presented in bold (significance level for correlations: r2 > ±0.34).

Response Variables		MAF1	MAF2
Fish	BBon	**0.93**	0.33
	BBlu	**0.93**	0.30
	BMhm	**0.96**	−0.16
	BSar	**0.88**	0.30
	BAnch	**0.66**	**−0.65**
Zooplankton	Zoo	−0.28	0.08
	Noc	−0.17	0.12
Phytoplankton	PP	−0.23	**−0.59**
	Chl	**0.39**	−0.26
Explanatory Variables			
Climatic	Wi_NAO	−0.13	0.20
	AMO	**−0.72**	−0.26
	SST	**−0.82**	0.01
Water Quality	Wi_SL	−0.24	−0.04
	Wi_SSS	−0.18	0.25
	DO	0.32	0.09
	PO_4	−0.25	**−0.51**
	SiO_2	**0.36**	**−0.58**
	NO_x	−0.14	**−0.44**
Fisheries	FAnch	**−0.83**	−0.08
	FSar	**−0.68**	**−0.42**
	FMhm	−0.09	**0.60**
	FBlu	**−0.62**	−0.15
	FBon	**−0.86**	0.14
	PoPG	0.23	−0.19

negatively correlated with SST in the same year and the fishing mortality of the following year. PP was significantly positive correlated with nutrients, with PO_4 in the same year and with NO_x and SiO_2 of the subsequent year. An assumed general pattern emerges in the variability of primary productivity as a proxy of phytoplankton biomass that was related to the small pelagic fish biomass negatively in the subsequent year. The changes in small pelagic fish biomass, especially sardine and Mediterranean horse mackerel, were significantly correlated with overall fishing mortality. Changes in water quality indicators were correlated with the changes in phytoplankton in the same year. The AMO index was correlated with the PP and small pelagic fish biomass of the subsequent year and the medium pelagic fish biomass of the preceding year (Table 5).

4. Discussion

Our study provides the first comprehensive ecosystem assessment to understand the factors behind the changes observed in the SoM pelagic ecosystem over the last three decades (Fig. 6). Ecosystem changes were assessed using a large dataset that included information on ecosystem drivers and its states. Observed changes were confirmed by the detection of significant shifts in all used datasets. We classified the SoM ecosystem into three regimes, i) an early regime as an initial state under the top-down control of medium pelagic predators, Atlantic bonito and bluefish, and fisheries exploitation until mid-1990s, ii) a transitional regime as the SoM ecosystem reorganized between mid-1990s and mid-2010s, and iii) a late regime as an alternate state from mid-2010s until 2020 with prevailing impacts of climate change (Fig. 6). During the transitional regime, three different phases were characterized i) the first phase from mid-1990s to early 2000s with a gradual change in ecosystem state and decrease in top predators, but with a strong shift in ecosystem drivers, ii) the second phase between early and mid-2000s with a strong shift in ecosystem state, an ongoing increase in climate indices and fishing mortality, and a gradual decrease in water quality, and iii) the third phase from mid-2000s to mid-2010s with the reorganization of the ecosystem state towards a small pelagic fish dominated fish community and ameliorated water quality. The observation that most of the biotic variables, mainly fish biomass, did not return to their initial states despite an improvement in some abiotic variables indicates the Sea of Marmara ecosystem has shifted to an alternative state with a reorganized system, and hence with reduced buffers that would protect it from climate change impacts, thus, its potential to experience further abrupt shifts has increased (Conversi et al., 2010; Litzow and Hunsicker, 2016) over the very recent period.

Prior to the period modeled in this study, there were significant stressors imposed on the SoM ecosystem that need mentioning. A study on the number of commercially extinct species in the SoM showed that nine medium and large pelagic species have become locally extirpated and a further 11 medium and large pelagics have become commercially extinct, suffering >90% catch losses over a 50-year period from 1967 to 2016 (Ulman et al., 2020). As a result, the SoM ecosystem was simplified, ceasing to be top-down controlled by large predators. Loss of predatory fish and its propagating consequences through trophic cascade mechanisms were severely highlighted in many marine ecosystems, including the North Sea (Kenny et al., 2009), the Baltic Sea (Möllmann et al., 2009; Lindegren et al., 2010), and the Black Sea (Oguz

Table 5
Cross-correlation analyses (Pearson correlation coefficients, r^2) between time-series indices of biotic variables and key drivers in lagged relationship (*t*) at significance level (at $p < 0.05$). For abbreviations see Table 1.

	BBlu		BBon		BMhm		BSar		BAnch		PP		Chl	
	t	r^2	*t*	r^2	*t*	r^2	*t*	r^2	*t*	r^2	*t*	r^2	*t*	r^2
BMHm	**−1**	**0.86**	**−1**	**0.85**										
BSar	**1**	**0.91**	**1**	**0.92**	**−1**	**0.73**								
Banch	**0**	**0.38**	**0**	**0.39**	**0**	**0.68**	**1**	**0.48**						
PP	**1**	**−0.54**	**1**	**−0.52**	1	−0.27	**1**	**−0.35**	**1**	**0.37**				
Chl	−1	0.28	−1	0.28	**−1**	**0.40**	−1	0.34	**0**	**0.49**	**0**	**0.52**		
AMO	**0**	**−0.76**	**0**	**−0.76**	**0**	**−0.65**	**−1**	**−0.75**	1	−0.32	**−1**	**0.4**	1	−0.21
SST	**−1**	**−0.75**	**−1**	**−0.76**	**−1**	**−0.77**	**0**	**−0.75**	**0**	**−0.62**	−1	0.13	**1**	**−0.46**
PO4	**1**	**−0.43**	**1**	**−0.42**	1	−0.25	**1**	**−0.38**	−1	0.25	**0**	**0.45**	−2	0.25
SiO2	−1	0.14	−1	0.12	**0**	**0.46**	−1	0.14	**−1**	**0.71**	**1**	**0.37**	**0**	**0.46**
NOx	2	−0.31	2	−0.28	1	−0.15	1	−0.27	−2	0.26	**1**	**0.50**	**1**	**0.36**
FAnch	**−1**	**−0.79**	**−1**	**−0.81**	**−1**	**−0.71**	**−1**	**−0.85**	**1**	**−0.64**	−2	0.16	**0**	**−0.46**
FSar	**1**	**−0.79**	**1**	**−0.79**	**−1**	**−0.63**	**1**	**−0.87**	2	−0.21	**−1**	**0.50**	1	−0.26
FMhm	0	0.16	0	0.18	1	−0.33	2	0.12	**1**	**−0.51**	**−1**	**−0.42**	−1	−0.09
FBlu	**1**	**−0.64**	**1**	**−0.61**	**1**	**−0.68**	**−1**	**−0.7**	**1**	**−0.38**	0	0.24	−1	−0.16
FBon	**1**	**−0.75**	**1**	**−0.75**	**0**	**−0.87**	**0**	**−0.71**	**1**	**−0.64**	−1	0.16	**1**	**−0.51**

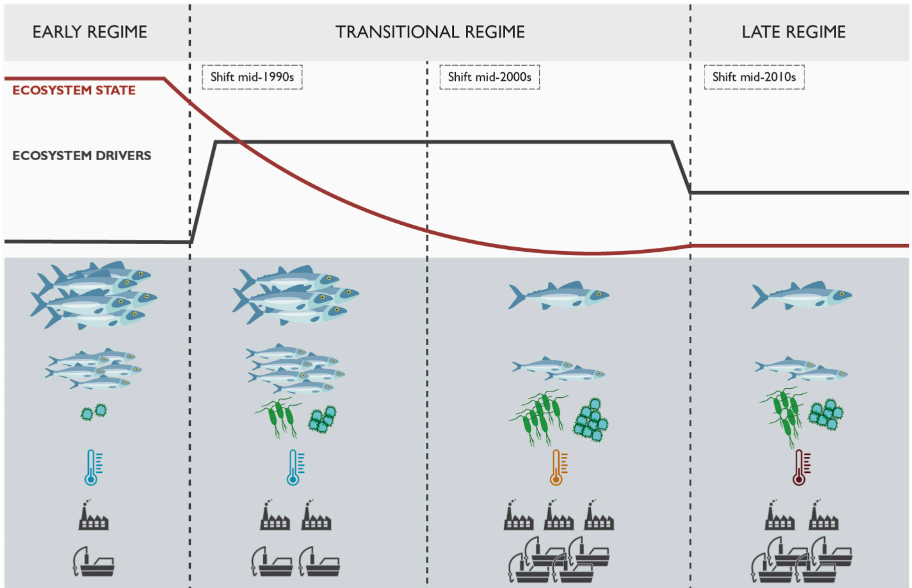

Fig. 6. A conceptual diagram displaying the changes in the Sea of Marmara (SoM) ecosystem between 1986 and 2020. Dashed vertical black lines indicate regime shifts and icons illustrate respective status of biotic variables of medium and small pelagics, zooplankton, phytoplankton, and abiotic variables of climate, water quality and pressure.

and Gilbert 2007; Daskalov et al., 2007; Llope et al., 2011). The Black Sea ecosystem experience showed that reorganization of the ecosystem led to a bottom-up control of the ecosystem resulting in a population explosion of small pelagics (Bănaru et al., 2010). This explosion reduced the grazing pressure on the phytoplankton and led to eutrophication that made the system susceptible to further enrichment by a succession of cold winters from 1985 to 1987 (Oguz et al., 2008). Therefore, the SoM should be considered highly similar to the Black Sea case as they are intricately connected and directly influence each other. Our analyses showed that, similar to the changes in the Black Sea, a series of transformations occurred in the SoM commencing around the mid-1980s.

4.1. Early regime and shift in mid-1990s

High biomasses of medium pelagics, bonito and bluefish, characterized the early regime. In addition, Mediterranean horse mackerel and sardine were also found in high biomasses, but a significant decrease in anchovy biomass was observed from 1989 to 1992 (Fig. 4e). Those years coincided with the infamous anchovy-invasive comb jelly shift in the Black Sea when *Mnemiopsis leidyi* proliferated in great numbers, and consequently the Black Sea anchovy stocks collapsed (Kideys, 2002). According to very limited available research, the *M. leidyi* invasion was also observed in the SoM pelagic ecosystem (Shiganova et al., 1995). We hypothesize that this could be the reason for the biomass decrease in the same period. During this early regime period, water quality was good with low nutrient loadings and high dissolved oxygen, and primary productivity and chlorophyll-a values were low (Figs. 3, Fig. 4p–t).

The 1980s were a pivotal period for Turkey's development to modernity, as these years marked the beginning of the integration of the country into the global economy (Adaman and Arsel, 2005; Knudsen, 2009). Istanbul, the biggest city of both the Marmara region and Turkey in terms of its economic output and population, was transforming as the new megalopolis of the country, enhanced by the accelerating industrialization at the peripheries of the city in the 1980s. The impacts of urbanization and industrialization on the SoM marine ecosystem were not yet visible during this period (Fig. 6). The 1980s were also the beginning of a period when large-scale industrial fisheries in the SoM and the Black Sea started receiving government subsidies to modernize and increase the capacities of the commercial fleet tremendously (Knudsen 2009). Subsidies were also provided to privately-owned fishmeal factories, where especially under-sized fish species were processed. This led to a "spiral of growth" for the large-scale fishing vessels operating in both the Black Sea and the SoM (Knudsen, 2009), and became the driving force for the declining commercial catches over the subsequent period from the mid-1990s to mid-2010s (Figs. 3, 4a-e).

4.2. Transitional regime and regime shift in mid-2000s

The first regime shift occurred in mid-1990s, as the SoM ecosystem entered its transition regime. Considering the ecosystem state, there were declines in bonito and bluefish biomasses that resulted in increases in anchovy and sardine biomasses, which caused a decrease in ecosystem resilience. The increases in small pelagic biomasses along with reduced zooplankton biomass (Fig. 4f) resulted in increases in PP and Chl-a. For ecosystem drivers, around 1995, AMO entered a warm phase, and since then, the yearly average SST in the SoM has been gradually increasing. Until mid-2000s, a decrease in water quality from increasing nutrient loadings and decreasing DO in surface water along with ongoing industrialization in the region were evident. The regime shift in the SoM was driven by the combined and synergistic effects of overfishing, climate variability and eutrophication. In 1999, the ecosystem state was reorganized (Fig. 5d, PC1 of PCA_bio); bluefish and bonito biomasses further decreased; and anchovy and Mediterranean horse mackerel catches became more prominent. The changes in the fishing mortality of anchovy, bluefish and bonito (Figs. 3 and 5e and f) exerted a top-down pressure on the ecosystem, resulting in a significant decline in fish stocks. Most of the variables relating to fisheries exploitation were significantly correlated with the first MAFA axis (Table 3). In addition, the regime change in the primary productivity, which was enhanced by the changes in the nutrient concentrations (Figs. 3 and 4) and coupled with the significant changes in SST and AMO (Table 4, Fig. 5e and f), exerted bottom-up pressure leading to ecosystem degradation. This degradation is inferred from the increased nutrient availability detected by the regime shift analysis. The period also fostered a new turning point from the first mucilage outbreak event in 2007, which should be considered a first warning sign for the shift in the SoM from a healthy to a compromised or degraded state of health.

One of the key missing links in assessing the pelagic ecosystem of the SoM is the analysis of its jellyfish dynamics. Unfortunately, a lack of jellyfish biomass data in time-series format prevented us from including this important factor in the quantification of the shift in trophic energy to gelatinous biomass, which we understand is occurring. We suggest that stressors to the ecosystem from overfishing and other anthropogenic impacts influenced this gelatinous increase. Nevertheless, some jellyfish species, such as the ctenophore *Mnemiopsis leidyi* in the 1980s and the Trachymedusa *Liriope tetraphylla* in the mid-to late-2000s, caused dramatic impacts to pelagic food web functioning (Yılmaz and İşinibilir Okyar, 2016). The 2007 mucilage phenomenon commenced after the decimation of the dominant summer zooplankton species, *Penilia avirostris* during the *L. tetraphylla* blooms (Yilmaz, 2015). The zooplankton composition of the SoM was already differentiated from the neighboring basins through the dominance of cladocerans over copepods and minimal vertical migrations due to the permanent thermohaline stratification. However, this confined layer was also susceptible to changes in predator densities and other trophic constraints. This environment also provided the optimum conditions for the heterotrophic dinoflagellate *Noctiluca scintillans* which competed for the same food resources as zooplankton (Yılmaz et al., 2005). The years with highly elevated primary productivity supported prolonged *N. scintillans* red-tides, which were witnessed for a shocking six months in 2004. Harmful algal blooms (HABs) in coastal waters of the SoM have been increasingly reported particularly after 2000 (Tas et al., 2020).

Based on these observations, it is evident that the SoM faced a similar ecosystem transition temporal regime shift as that of the Black Sea. While it took just a few decades for the Black Sea first to transition from a top-down controlled oligotrophic ecosystem structure to an overfished, eutrophic structure (Oguz and Velikova, 2010), the SoM experienced a similar transition within two decades due to a shift towards industrialization, overcapacity of the fishing fleet, high urbanization, and its consequent pollution, much of it from neighboring agricultural inputs. Overfishing significantly decreased the stocks of small and predatory medium pelagic fish species by the mid-1990s (Fig. 4a–e). This decrease was followed by a substantial increase in the already intensive nutrient input after the onset of the 2000s (Fig. 4j,l). We suggest that the depletion of the Black Sea fish stocks by the 1990s similarly contributed to the slightly later overexploitation of the fish resources in the SoM in late 1990s, as the migratory stocks are shared between the two basins. As the SoM fisheries catches peaked in 1999 at 80,000 t, the medium pelagics, which are the commercially more valuable species, had already suffered from overfishing demonstrated by a strong decline in CPUE of about 90% since the 1970s (Ulman and Pauly, 2016; Demirel et al., 2020; Ulman et al., 2020). Overcapacity and overfishing had been serious factors since the 2000s in the SoM and the Black Sea, and marine capture fisheries had been stagnating from the 2000s onwards (Fisheries Acquis Centre, 2007; Tokaç et al., 2014; Turkstat, 2022). As a result, economic growth initiatives of the central government were restructured towards a heavy emphasis on export-oriented aquaculture sector during this period, heavily draining the SoM and the Black Sea from small pelagic fish required for fish meal production used in aquaculture (Ertör and Ortega-Cerdà, 2019). The removal first of top predators, and then subsequently the medium pelagic predators (fishing down marine food webs or FDMFW) went unnoticed by Turkish citizens. This was likely related with increased urbanization and rising disconnect of urban citizens from nature. In addition, most people drawn to a growing metropolis like Istanbul lacked a historical connection to the sea, as a result, they had no baseline related with marine environments. Yet, the shifting baselines syndrome was prevalent in fisheries as younger generations were found to perceive its state as acceptable, in the absence of an understanding of its prior riches (Ulman and Pauly, 2016): Often, elderly fishers state that they rarely speak about the incredible amount of biodiversity that they had observed in the past, as younger generations cannot relate this to the present. Consequently, current generations consider the present state of biodiversity as normal due to a lack of historical ecological knowledge passed down about the incredible assortment and abundances of fisheries that existed in these ecosystems just half a century ago.

In Turkey, the modern governing policies have been highly focused and reliant on large-scale urban development investments, and construction and energy projects to sustain economic growth (Adaman et al., 2014). This substantially limits the public space for political deliberation and contestation about the damage of marine and terrestrial environments. Rather, consecutive central governments have been long promoting the idea that environmental problems can only be addressed via economic growth (Turhan and Gündoğan, 2017). An inevitable consequence of these policies for the SoM was, therefore, heavily loaded pollution sources from industrial facilities, urban municipal waste and ship building industries that accelerated the increase of nutrients and reduction of dissolved oxygen from the surface water. Lack of waste treatment facilities, as well as a lack of monitoring and enforcement of waste discharges into the SoM further impacted the ecosystem. However, more recently, particularly after 2005, investments into wastewater treatment have been initiated and are improving (Öztürk et al., 2021).

4.3. Late regime and regime shift in mid-2010s

Ecosystem restructuring triggered by human-induced changes; namely, synergistic effects of overfishing, climate change and eutrophication, have been relatively common in many basins such as the North Atlantic, alike to the regime shifts reported in the Black Sea (Daskalov et al., 2007; Llope et al., 2011), the Baltic Sea (Möllmann et al., 2009; Lindegren et al., 2010; Blenckner et al., 2015), the Gulf of Cadiz (de Carvalho-Souza et al., 2021), and the Portuguese continental shelf (Szalaj et al., 2021). In the SoM, the strongest regime shift was detected commencing in mid010s onwards with the lowest fish biomass, the highest anchovy fishing mortality, and increasing climate related variables until the end of our study period of 2020 (Figs. 4 and 5). Thus, due to heavy fishing capacity and the focus narrowly targeting small pelagics, the state of the marine ecosystem has shifted once again. Although a decrease in PP and chlorophyll levels were noticed due to improvements in water quality which began in 2014 from the national marine monitoring programme for the SoM supported by the Ministry of Environment, many studies reported harmful effects of HABs for short periods in different parts of the SoM, such as water discoloration, light limitation, hypoxia and mucilage formations (Tüfekçi et al., 2010; Balkis and Taş, 2016; Tas et al., 2020). Still, marine pollution and waste treatment mitigation measures gained more attention from the public and scientific organizations from the 2010s onwards, which have demonstrated success in reducing the inflow of nutrients to the SoM. However, the climatic effects were strong, worsening the ecological health in this period. During the mid-2010s, a change in winter NAO (that entered its high phase) resulted in an increase in SST (Fig. 4). A very recent study on small pelagic fish distribution under global change scenarios reported that a northwards shift is expected for small pelagics such as anchovy and Mediterranean horse mackerel seeking to maintain their preferred ecological niches in warming seas (Schickele et al., 2021). Among the small and medium pelagic fish species, bluefish shows the largest thermal tolerance (thermal amplitude-bioclimatic envelope) while Mediterranean horse mackerels have the lowest (Cheung et al., 2013). Therefore, a continuous increase in SST, which is expected, may benefit bluefish over the short term, but over the long-term, the small pelagics such as anchovy and Mediterranean horse mackerel may alter their life cycles to spend more time in the slightly cooler Black Sea. Regardless, climate induced shifts and trajectories should be modeled to predict and advise short-term and long-term fisheries scenarios so that they can be optimized.

The time-series development and ecosystem changes in the SoM showed similar trends to the Black Sea ecosystem. A recent Black Sea study on its regime shift stated that after 2005 both fish biomass and water quality showed improved conditions (Daskalov et al., 2017), but this improvement in fish biomass was observed for only anchovy and sprat, the small pelagics. Daskalov et al. (2017) emphasized that the predatory bonito and bluefish stocks were not considered as their stocks had already collapsed, leaving only small pelagics as viable commercial fisheries in the Black Sea (Daskalov et al., 2020). Similarly, in the SoM, the alternate state of the restructured ecosystem had a much reduced resilience and was dominated by anchovy; however, its biomass continued to decrease in this case (Fig. 4e). Medium pelagics of bonito and bluefish comprised approximately 40% percent of total catches in SoM in 1970s, but have steadily decreased, ending up comprising only 10% of total catches in 2020. Overall, the decrease in total catches was not sharply pronounced for last five years, owing to annual variabilities in anchovy catches. According to official statistics, the number of purse seine vessels operating in the SoM decreased by 1/4 in the last ten years (Turkstat, 2022), but still this fleet has incredibly high capacities and technological sophistication, which somewhat offsets the fleet reduction (Ertör-Akyazi, 2020).

4.4. Methodological evaluation

Global change, including human activities and climate variation, has caused many ecosystem regime shifts leading to a loss of ecosystem services. The study of tipping points is a useful tool in different types of ecosystems, and it has become a research hotspot in the last decade. However, implementing an integrated ecosystem approach requires a wide spectrum of variables with time-series data sets without data gaps. Many countries such as Turkey lack detailed long-term data sets for fish stocks which are needed for the evaluation of proper stock assessment practice, and the SoM stocks are defined in the “data poor stocks” category (FAO, 2020). Existing data are mostly limited to two to three-year data sets which themselves are neither planned nor organized properly to provide what is needed to easily understand trends. Here, we used time-series of biomass of pelagic fishes (B, tonnes) and their fishing mortality (F, y^{-}) values from the only stock assessment study based on catch-based analysis in the SoM (Demirel et al., 2020), and therefore showed that the use of this type of data can be beneficial for efforts in understanding regime shifts. However, we are aware that our results are affected by the assumptions of the catch-based stock assessment model. A second limitation is related with the spatial representativeness of the SoM: the time-series of zooplankton and phytoplankton abundance data, as well as nutrient and dissolved oxygen concentrations were only available for the northeastern part of the SoM. In order to be consistent, we collected and used satellite data from the same locations. Thus, our results are also affected by the limited spatial coverage. Present study also highlighted the data needs and the necessity to extend assessment efforts for a better understanding of the changes in the SoM considering its multiple myriad of current stressors such as climate change, deoxygenation, invasive species and fisheries.

4.5. Implications for management

The current state of the SoM ecosystem demonstrates that sustainable governance of marine ecosystems requires collaboration between local and central government authorities, which is currently not the case for the SoM. Sustainable governance processes also necessitate specific spaces and opportunities for participation of different stakeholders in decision-making processes to be able to provide a long-term solution incorporating the diverse set of climate change impacts, fisheries regulations, and urban and industrial stressors.

During late 2020, a wide-scale and highly intense mucilage outbreak in the SoM attracted a lot of media attention. According to our analyses, it is evident that the mucilage outbreak was an unsurprising result of gradual shifts in the ecosystem state and trophic cascades caused by overfishing, climate change impacts, and marine pollution. Improving the health of the Sea of Marmara ecosystem should be undertaken by a multidisciplinary team of scientists, under a participatory approach involving different stakeholders such as fishers, the private sector, and local and central governmental authorities to improve its current and long-term environmental status. On June 6, 2021, the Ministry of Environment, Urbanization and Climate launched the Sea of Marmara Action Plan. This action plan put forth 22 targets, including establishing the entire SoM as a protected area, increased enforcement, and monitoring for wastewater discharges, with an increased number of advanced biological treatment facilities, with the aim of ensuring ecosystem-based management for the fisheries (Marmara Sea Action Plan, 2022).

From a fishery management point of view, it is clear that the SoM fishery is declining in many aspects such as catch amounts, total fishery income, number of target species, and average fish sizes. Here, our results also showed that fisheries both affect and are affected by ecological conditions. Although there are indirect management measures (e.g. minimum landing sizes, a cap on new commercial licenses issued, and a seasonal fishing ban for industrial fisheries), there are no restrictions for fishing effort, and total catches. As a result, since the fishery of the SoM is not well managed in line with stock assessment results and the changing conditions of climate change and human-induced pressures, its ecosystem resilience is weakened, gradually reducing and even blocking ecosystem services with time. Hence, concrete suggestions should be developed for fisheries management, considering its effects on ecosystem functioning. Here we propose a few immediate action plans for better management: 1) Fishing pressure on all fish stocks of the Sea of Marmara needs to be reduced; approximately 60% reduction in fishing pressure may improve its current “poor” stock status to “medium” stock status within 10 years (Demirel et al., 2020), which would improve ecosystem benefits substantially including fisheries incomes in medium to long term; 2) The fishing effort of large-scale industrial fisheries should be limited and an individual non-shared and non-transferable quota or Total Allowable Catch (TAC) system should be introduced to fishing vessels for the main commercial species of the SoM in consultation with stakeholders such as marine scientists and fishing organizations in the region to achieve successful implementation and prevent unintended consequences of such systems and polarization between stakeholders; 3) Minimum landing size regulations should be improved in many cases based on science, and then regulated in relation to the selectivity of fishing gear and fishing area in order to both control and deter catching of fish under the legal size; effective monitoring and enforcement of these regulations should be ensured (Yıldız and Ulman, 2020); 4) One of the most important effects of climate change is the increasing sea water temperature which also affects the SoM. Considering that temperature change will affect all biological processes of marine species, namely, reproduction, migration, feeding and distribution characteristics, as well as the carrying capacity of the ecosystem by exerting constraints on the primary productivity, the shifts in fishing seasons need to be constantly reevaluated to limit the catches of juveniles. An effective response to these impacts of climate change would require the establishment of legal and institutional structures to enable adaptive management of fisheries, and more specifically, co-management in the case of the SoM, as co-management entails opportunities in terms of benefiting marine ecosystems, participation of stakeholders and effective implementation of existing fishing policies (d'Armengol et al., 2018; Galappaththi et al., 2022; Tokaç et al., 2014).

5. Conclusion

The pelagic ecosystem of the SoM has undergone significant changes and transformations in the last 35 years. The present study contributes to the field a first comprehensive assessment for the SoM regarding the changes that occurred in its pelagic ecosystem between the years 1986 and 2020. The changes in the ecosystem status and the relationship with the human-induced environmental factors that triggered these changes were found to be significant shifts in all biotic and abiotic datasets of the

SoM pelagic ecosystem. The results imply that the SoM ecosystem can be classified into three periods: the early regime as the initial state under the top-down control of medium pelagic predators, Atlantic bonito and bluefish, and fisheries exploitation until mid-1990s, the transitional regime between mid-1990s and mid-2010s during which the ecosystem was reorganized, and the late regime as an alternative ecosystem occurring from mid-2015 until the end of the period to 2020. During this late regime, most of the biotic variables, especially fish biomass, did not return to their initial state, contrary to the trends observed in abiotic variables due to concomitant impacts of climate change and fisheries exploitation. We identify these observed changes in the SoM ecosystem as a non-linear regime shift.

Author contributions

ND: Supervision, Conceptualization, Formal analysis, Visualization, Writing- Original draft preparation. EA, TY, GG, DB, NY: Data curation, Investigation. ND, EA, AU, PEA: Writing- Reviewing and Editing.

Data statement

The data that support the findings of this study are available from the corresponding author, ND, upon reasonable request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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