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Decadal changes in the Sea of Marmara indicate degraded ecosystem conditions and unsustainable fisheries

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Globally, all marine ecosystems are under pressure by anthropogenic stressors. However, semi-enclosed seas are at a greater risk of degradation due to their limited connectivity to open seas. This leads to a greater accumulation of pollutants and abrupt regime shifts triggered by unsustainable exploitation of living resources, as ecosystems exhibit low degrees of redundancy and more frequent large-scale episodic events such as harmful algal blooms. The Sea of Marmara is a semi-enclosed marine region that has been subjected to various anthropogenic stressors since the 1990s. Recently, local and governmental authorities have employed basin-wide ecosystem management plans to control and manage point and nonpoint (diffuse) sources of pollutants. However, the management of fisheries in relation to the dynamics of the Sea of Marmara food web has attracted less attention from policymakers, even though fisheries exploitation is one of the most significant anthropogenic pressures. In this study, we capitalized on a previous static ecosystem model of the Sea of Marmara by revising and extending it to simulate the changes between 1990 and 2020. We delineated the temporal dynamics and regime shifts in the food web in terms of ecosystem structure and function by using ecological indicators and developed quantitative management advice for its fisheries. The results showed that the ecosystem has experienced three regimes since 1990, with regime shifts occurring with the onset of the 2000s and the mid 2010s. The first regime exhibited high diversity and material cycling, the second regime was characterized by low diversity and increased impact of fisheries, and the third regime culminated in a fished-down food web state. The analysis of fishery dynamics showed that the majority of harvested species were overexploited. We suggest that the implementation of quotas for exploited species should be considered an immediate solution to the unsustainable exploitation of fish stocks and can help restore ecosystem conditions.

KEYWORDS

Ecopath with Ecosim, Sea of Marmara, regime shifts, fisheries, food web, ecosystem-based fisheries management

1 Introduction

Climate change, pollution, and fishing are the three major stressors jeopardizing the global well-being of marine ecosystems (Pauly and Zeller, 2019). Compared with semi-open (e.g., North Sea) and open (e.g., Philippine Sea) seas, semi-enclosed seas, such as the Mediterranean Sea, are more exposed to anthropogenic stressors that negatively affect biodiversity, increase the susceptibility of marine ecosystems to fishing and deteriorate marine habitats (Caddy, 2000; Hidalgo et al., 2018; Ramirez et al., 2018). These ecosystems are characterized by their limited connectivity to the open sea, which predisposes them to accumulation of pollutants, overexploitation of resources, and occurrence of large-scale episodic events such as harmful algal blooms (Oguz and Su, 2004). Furthermore, stressors can exert cascading effects on marine food webs and initiate abrupt regime shifts, i.e., rapid changes in the structure and function of ecosystems, with catastrophic consequences (Möllmann et al., 2011). When multiple stressors act concomitantly and/or sequentially, the extent of cascading effects can culminate in regime shifts, such as the infamous anchovy collapse in the Black Sea in 1989 (Daskalov, 2002; 2003; Oguz and Gilbert, 2007; Oguz et al., 2008). These phenomena highlight the urgent need for effective management and conservation strategies, particularly for semi-enclosed seas.

Ecosystem-based management (EBM) emphasizes holistic planning of human activities to preserve ecosystem integrity, ensure the sustainable delivery of ecosystem services and maintain biodiversity (Haugen et al., 2024). This approach is necessitated by the escalating impacts of human actions on ecosystems, challenging the resilience of natural systems and their capacity to support human needs (Folke et al., 2016). Within the context of EBM, modeling tools are invaluable for simulating ecosystem dynamics, assessing the implications of various management decisions and predicting responses to environmental changes and anthropogenic pressures (Fulford et al., 2020). Furthermore, ecological indicators, which are important proxies of ecosystems because they combine multiple aspects of the structure and function of food webs, are considered easily interpretable metrics of complicated ecosystem-level data (Smit et al., 2021) and can delineate changes in marine ecosystems under the influence of ecosystem-wide stressors and regime shifts. Therefore, indicator-based ecosystem assessment is the suggested method for achieving EBM and ecosystem-based fisheries management (EBFM; Pikitch et al., 2004). Ecopath with Ecosim (EwE; Christensen et al., 2005) is one of the most widely used ecosystem models for analyzing and simulating energy flows in ecosystems under different scenarios. EwE aids in understanding the effects of fishing, changes in trophic interactions in the food web, and the impacts of anthropogenic activities on ecosystem structure and function (e.g., Piroddi et al., 2017; Akoglu, 2023). In addition, EwE facilitates the computation of various ecological indicators for modeled ecosystems (e.g., Craig and Link, 2023 and references therein). Therefore, EwE can help stakeholders make informed decisions to achieve sustainable resource use and conserve ecosystem health by providing insights into the potential outcomes of management strategies (Keramidas et al., 2023).

The Sea of Marmara (SoM), located in the Northeastern Mediterranean, is an important ecological passage connecting the Aegean and Black Seas. Thus, the rich biodiversity and productive waters of the SoM are characterized by a wide variety of marine species, positioning it as an economically important area (Ulman et al., 2020). For centuries, it has served as a critical nexus for the development of civilizations, most notably evidenced by the establishment of Istanbul along its shores. Today, SoM lies at the heart of Turkey's most densely populated region and serves as a fulcrum for industrial and commercial activities. Thus, SoM experiences pollution from domestic and industrial effluents (Burak et al., 2009), eutrophication due to nutrient enrichment from agricultural activities (Albay, 2023), and overfishing (Gul and Demirel, 2016; Demirel et al., 2020; Ulman et al., 2020). Furthermore, climate change-related global warming has increased the average sea surface temperatures in the SoM since 1970 and has facilitated the increased establishment of Indo-Pacific species (Turan and Gürlek, 2016), which has changed food web dynamics, a phenomenon known as the Mediterraneanization of the Marmara and Black Seas (Oguz and Öztürk, 2011). Consequently, regime shifts were also observed in the SoM (Demirel et al., 2023a). The SoM region is densely populated, and urban and industrial wastes cause intensive pollution (Burak et al., 2009). This basin-wide pollution causes significant deoxygenation and leads to habitat contraction in the water column, driving demersal species to deeper areas where the impact of the more oxygenated Mediterranean waters is pronounced (Kabasakal et al., 2023) and confining pelagic species to the narrow oxygen-saturated upper layer.

SoM fish stocks are at risk of overexploitation (Tsikliras et al., 2015), similar to 80% of fish stocks in the Mediterranean Sea (Froese et al., 2018). Recent stock assessments have found that almost all commercially exploited fish species in the SoM were overexploited, and sardine and horse mackerel were fished at their maximally sustainable levels (Demirel et al., 2020). Studies that applied indirect methods to calculate fishing mortalities also found that whiting and bluefish had high exploitation rates at levels of overexploitation (Akyol and Ceyhan, 2007; Karadurmuş, 2022). Hake, an iconic fish species in the SoM that was once abundant in catches, had almost disappeared as of 2017 (Demirel et al., 2022). Considering the status of the SoM fish species, the need for immediate action for their sustainable utilization is undisputed.

To date, fisheries, ecosystem dynamics, and historical regime shifts in SoM have been studied using statistical stock assessment models and time series of environmental parameters (Demirel et al., 2020; 2023a), traditional knowledge and anecdotal information (Ulman et al., 2020), and a mass balance food web model (Saygu et al., 2023). As precautionary measures against regime shifts and stock collapse, various fishing and environmental management policy options have been proposed (Demirel et al., 2023b), such as reducing fishing effort (Koyun et al., 2022; Yildiz et al., 2023), decreasing the fishing mortality of stocks (Demirel et al., 2020), increasing the selectivity of fishing gear (Yildiz et al., 2020; Gül and Demirel, 2021), revising minimum landing sizes (Yildiz and Ulman, 2020), establishing temporal fishing bans (Yildiz et al., 2020), and shifting the fishing season (Demirel et al., 2023a). However, management advice based on an ecosystem-wide assessment that

capitalizes on a time series of ecological indicators using a temporal food web model is lacking. Therefore, in this study, we aimed to i) develop the first temporal food web model of the SoM; ii) determine historical regime shifts by investigating the changes in the structure and function of the SoM ecosystem and its fisheries using ecological indicators derived from ecological network analysis; iii) develop quantitative fisheries management advice considering prey-predator interactions in the food web in addition to fisheries dynamics to aid in the sustainability of the entire SoM ecosystem; and iv) test the viability of the suggested fishing policy measures using the temporal model.

2 Materials and methods

The Sea of Marmara is a semi-enclosed sea with narrow connections to the Mediterranean and Black Seas through two narrow straits (Figure 1). The SoM has a stratified two-layer water structure separated by a strong halocline at 20–25 m (Uysal, 2006). The sub-halocline layer consists of oxygen-rich Mediterranean Sea waters that enter the SoM through the Dardanelles Strait and travel to the Black Sea at the bottom, whereas the supra-halocline layer consists of Black Sea waters that enter the SoM through the Bosphorus Strait and travel to the Mediterranean Sea at the surface (Beşiktepe et al., 1994). This two-layer structure facilitates the cooccurrence of both the Mediterranean and Black Sea species in the SoM and also makes it a pathway for introductions and geographical expansions of alien and indigenous species. The SoM covers an area of 11,500 km², featuring three deep basins (greater than 1,000 m) in the north and a broad shelf region (less than 100 m deep) in the southern half of the basin.

Fishing practices in the SoM are predominantly inshore, targeting benthic and demersal species with beam trawls. A significant seasonal pelagic fishery using purse-seines, in line with the migration of Atlantic bonito and bluefish between the Black Sea and the Aegean Sea (Zengin and Güngör, 2017), marks a period of increased fishing activity (Koyun et al., 2022). Of the 64 commercially targeted fish and invertebrate species, a significant proportion of the catch, occasionally up to 90%, is dominated by European anchovy, Mediterranean horse mackerel, deep-water rose shrimp, European pilchard, bluefish, Atlantic bonito, whiting, and European hake (Saygu et al., 2023).

2.1 The model

The trophodynamic model Ecopath with Ecosim (Christensen et al., 2005) version 6.6.8 was used to simulate the changes in the SoM ecosystem from 1990 to 2020. Ecopath with Ecosim (EwE) is a modelling package that consists of three modules: i) Ecopath, the static module that provides a mass-balanced snapshot of the ecosystem's food web in a given period; ii) Ecosim, the dynamic module for temporal simulations; and iii) Ecospace, the two-dimensional spatiotemporal module for spatially explicit temporal simulations. In this study, we used the Ecopath module to establish a model of the SoM ecosystem for the early 1990s (1990–1992). Subsequently, a temporal Ecosim simulation was conducted and validated against time-series data. The equations of the Ecopath with Ecosim model used in this study are provided in the [Supplementary Material](#).

In this study, we updated and used a previously published Ecopath model of SoM (Saygu et al., 2023) to establish a basis for

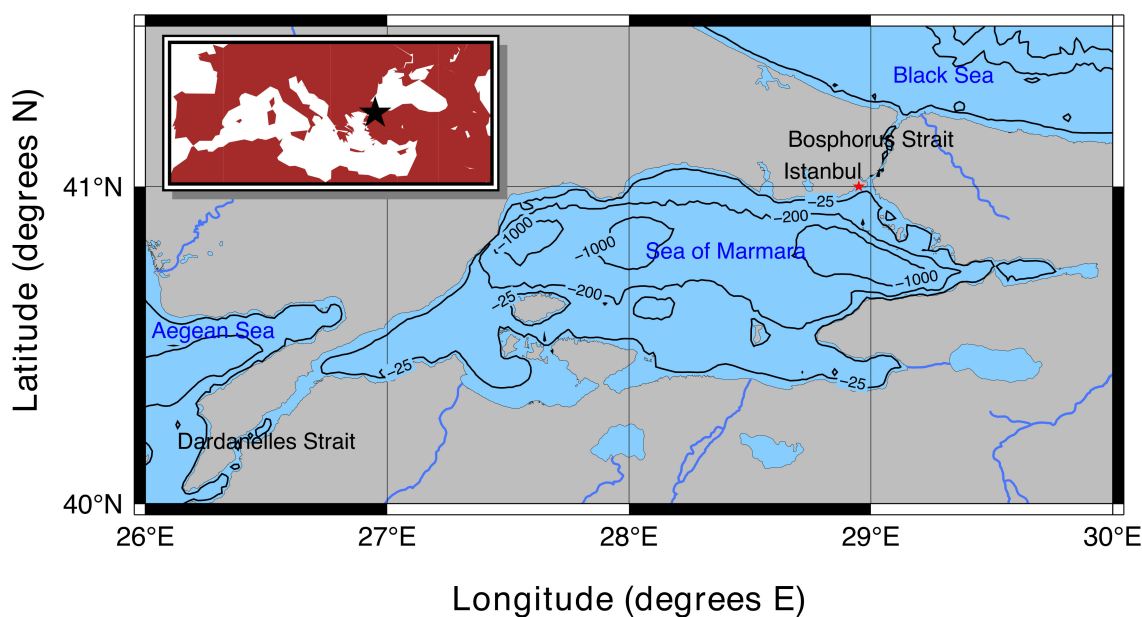


FIGURE 1

Map of the Sea of Marmara and its location in the Mediterranean Basin with respect to the European and Asian continents (denoted by a black star, top-left inset map).

the temporal SoM Ecosim model. The model consisted of 17 functional groups; phytoplankton as primary producers, mesozooplankton, benthic invertebrates (polychaetes, amphipods, isopods and cumaceans), deep-water rose shrimp (*Parapenaeus longirostris* Lucas, 1846), European anchovy (*Engraulis encrasicolus* Linnaeus, 1758), European pilchard (*Sardina pilchardus* Walbaum, 1792), Mediterranean horse mackerel (*Trachurus mediterraneus* Steindachner, 1868), mullets (*Mullus barbatus* Linnaeus 1758 and *Mullus surmuletus* Linnaeus 1758), turbot (*Scophthalmus maximus* Linnaeus, 1758), whiting (*Merlangius merlangus* Linnaeus, 1758), European hake (*Merluccius merluccius* Linnaeus, 1758), bluefish (*Pomatomus saltatrix* Linnaeus, 1766), Atlantic bonito (*Sarda sarda* Bloch, 1793), thornback ray (*Raja clavata* Linnaeus, 1758), spiny dogfish (*Squalus acanthias* Linnaeus, 1758), dolphins (*Tursiops truncatus* Montagu, 1821 and *Delphinus delphis* Linnaeus, 1758) and detritus. The Ecopath model by Saygu et al. (2023) represented the mid-90s (1993-1997); therefore, it was updated and reparameterized to represent the conditions of the early 1990s between 1990-1992 capitalizing on the work by Demirel et al. (2020). First, the biomass values were updated to represent the conditions of the early 1990s. Fishing mortalities show significant annual variations; therefore, as a second step, the P/B values were updated as they were the sum of fishing mortalities (F) and natural mortalities (M) since P/B is assumed to be equal to Z, which is equal to the sum of F and M, under steady state conditions (Allen, 1971). Finally, after the reparameterization of the P/B values, certain Q/B values were increased, considering the P/Q (gross growth efficiency) values, which usually range between 0.1 and 0.3, according to the best practices in Ecopath modelling (Heymans et al., 2016). The original SoM Ecopath model included three fishing fleets commonly used in the SoM, but due to the lack of time-series effort data and gear-specific fishing mortality estimates, we had to combine the three fleets into a single fleet. The revised SoM Ecopath model was evaluated using the pedigree routine, which assigns uncertainty ranges between 0 and 1 depending on the uncertainty of the data used, and the pre-balance diagnostics (PREBAL) analysis (Link, 2010). The specifics of the SoM Ecopath model are already available in the literature; therefore, we have avoided a detailed description and only provided information regarding the modifications. The initial conditions and parameters of the updated SoM Ecopath model for the early 1990s are listed in [Supplementary Table 1](#).

Time series of fishing mortalities or effort, and primary production anomalies are required to drive an Ecosim simulation, and time series of reference biomass and catch values are required for model validation. Here, we capitalized on the time series of absolute statistical catches (Turkstat, 2023) and absolute biomass values from statistical stock assessments to validate the catches and biomasses of fish groups/species simulated by the model. We used a time series of fishing mortalities obtained from stock assessments to drive the dynamics of fished groups in the temporal simulation (Demirel et al., 2020). The basin-averaged time series of zooplankton and phytoplankton absolute biomass values were obtained from the Inter-Sectoral Impact Model Comparison Project (ISIMIP) products by capitalizing on the physical

Geophysical Fluid Dynamics Laboratory Modular Ocean Model and biogeochemical COBALT2 model (GFDL-MOM6-COBALT2) simulations for observation-based climate oceanic conditions (Liu et al., 2022) and were used to validate and parameterize mesozooplankton and phytoplankton groups. GFDL-MOM6-COBALT2 zooplankton and phytoplankton outputs had a 15-arcminute resolution and were available until 2010. First, zooplankton and phytoplankton biomasses were interpolated onto a 4 × 4 km grid in SoM with Climate Data Operators (CDO; Schulzweida, 2023) using an inverse distance-weighted interpolation algorithm, and the basin-averaged annual zooplankton and phytoplankton biomasses were calculated for the SoM Ecosim model period. Remote-sensing primary productivity measurements obtained from the Copernicus Marine Environmental Monitoring Service (CMEMS) were used to drive the primary production of phytoplankton group in the SoM Ecosim model relatively. The CMEMS primary productivity product is a multisensor product with a resolution of 4 × 4 km and is interpolated both in space and in time. Basin-wide annual primary productivity anomalies were calculated for the simulation period in SoM. The CMEMS primary productivity product dates back to September 1997, and does not cover the period back to 1990. Therefore, time series of monthly primary productivities were hindcasted to 1990 using “forecast” package (Hyndman and Khandakar, 2008) in R (R Core Team, 2023) before basin- and annual-averaged anomalies were calculated.

Stepwise fitting approach was used to calibrate the SoM Ecosim model (Scott et al., 2016), capitalizing on the automated time series fitting routine of Ecosim. The model with the lowest adjusted Akaike Information Criterion value for small sample sizes (AIC_c; Akaike, 1974) was selected as the optimized model. The time series of biomasses and catches simulated by the model was compared with the reference biomass and catch values to assess the model skill. Finally, the simulated biomass and catch data were compared with the reference biomass and catch data using Taylor diagrams (Taylor, 2001). Taylor diagrams combine three important metrics of model performance with respect to reference data and show correlations between the simulated and reference values, the root mean square errors/distances (RMSD) of the simulated values with respect to reference data, and their normalized standard deviations. In addition, we included the model bias in the Taylor diagrams to show the cumulative error of the simulated biomasses and catches normalized by the reference biomass and catch values.

2.2 Ecological network analysis and regime shifts

The time series of ecological indicators were calculated from the dynamic Ecosim simulation outputs using the Ecological Network Analysis routine of EwE. The time series of the total system throughput (TST), which is the sum of all flows in the food web, relative ascendancy (A/C), and relative overhead (O/C), indicating the organizational status and resistance of the ecosystem against perturbations, respectively, were analyzed as macro-ecosystem indicators. A/C and O/C are relative indicators that complement

each other and indicate the trade-off between the recovery capacity of an ecosystem (i.e., ascendancy) and its strength against perturbations (i.e., resilience). In a healthy ecosystem, a balance between A/C and O/C is desirable (Costanza and Mageau, 1999). The changes in the primary production (PP) were also investigated. Considering recycled flows in the food web, Finn's cycling index (FCI), which shows the recycled part of the TST (Finn, 1976); the predatory cycling index (PCI), which shows the recycled part of the TST excluding the detrital compartments; the path length (PL), which shows the average number of groups a unit of flow travels in the food web (Finn, 1976); and the proportion of flows going to detritus (PFD), which shows the flows that were diverted back to detritus by means of mortality and defecation fluxes, were calculated. In a healthy ecosystem, the values of FCI, PCI, and PL are expected to be high, whereas the value of PFD is expected to be low (Odum, 1969).

Shannon's diversity index was used to assess diversity changes in the food web (Shannon, 1948). The time series of the mean trophic level of the catch (mTL_c) was calculated to demonstrate the impact of fisheries on the ecosystem. Fisheries prioritize the exploitation of high trophic level (HTL) species at first; however, as the stocks of these species deplete over time, low trophic level (LTL) species become dominant in the catch, a phenomenon known as "fishing down the food web" (Pauly et al., 1998). Therefore, a decrease in mTL_c may indicate unsustainability of fisheries. Furthermore, the time series of the Fishing in Balance (FiB) index, which shows the changes in fishing capacity and catches and indicates the ecological impact of fisheries considering the trophic level spectrum of the exploited species, was also used (Pauly and Watson, 2005). FiB can increase when an increase in technological development or geographical expansion of fisheries occurs or when new HTL species are included in the catches. However, the value of FiB can decrease when stocks collapse or fisheries increasingly target LTL, as HTL species become depleted over time. If a decrease in mTL_c is matched with an increase in catch, or vice versa, FiB does not change. The relative primary production required to sustain catches (%PPR_c) was also calculated to assess the footprint of fisheries in the ecosystem (Pauly and Christensen, 1995). %PPR_c shows how much of the ecosystem's primary productivity is required to produce the harvest by the fisheries. Furthermore, the biomass ratios of predatory fish to forage fish, demersal and cartilaginous fish to other fish, predatory and cartilaginous fish to pelagic fish, and fish to invertebrates were calculated because these ratios indicate proportional levels of organisms in the food web and are expected to be high in well-functioning, diverse, and sustainably exploited ecosystems (Shannon et al., 2009).

A sequential t-test analysis for the detection of regime shifts (STARS) was conducted on the anomalies of the time series of the ecological indicators to detect historical regime shifts (Rodionov, 2004). Time-series outputs from model simulations are generally hampered by autocorrelation; therefore, a prewhitening procedure using ordinary least squares was used before shift detection. Considering the decadal changes in SoM, a 9-year cut-off length with a significance level of 0.05

was used to detect ecosystem shifts. Furthermore, the time series of the ecological indicator anomalies were analyzed using principal component analysis (PCA) (Abdi and Williams, 2010). PCA is a dimensional reduction method used to investigate the variables that explain most of the variability in a given dataset and correlate them. The number of principal components to be retained was determined based on the empirical Kaiser criterion (Braeken and Van Assen, 2017).

2.3 Equilibrium analysis and fishing policy assessment

Maximum sustainable yield (MSY) values and their corresponding fishing mortalities (F_{MSY}) for fished groups/species in the model were calculated by conducting an "equilibrium analysis" with EwE's " F_{MSY} " routine under a full compensation ecosystem scenario, that is, considering the prey-predator interactions in the food web as well as the consequences of fisheries exploitation by capitalizing on a long-term Ecosim simulation (Walters et al., 2005). The " F_{MSY} " routine calculates MSY values for exploited species/groups by running simulations without time-series data and applying increasing levels of fishing mortalities on exploited species/groups sequentially, while other exploited groups are fished at their base fishing mortality rates in Ecopath, and trophic interactions between the groups/species are allowed. The analysis identifies a calculated MSY value for a group/species as valid if other fished groups/species and prey-predator interactions are maintained in the ecosystem. Finally, we tested the effect of the calculated F_{MSY} values using a long-term equilibrium simulation with Ecosim by applying the calculated F_{MSY} values to their respective fish stocks, and evaluated the stock-level responses of fishing policy by assessing the biomass and catch values when all the biomasses and catches of all the groups/species in the model reached equilibrium.

3 Results

3.1 Model skill

The pedigree of the revised Ecopath SoM model was 0.41 and equal to that reported by Saygu et al. (2023). The PREBAL diagnostics showed that the biomasses of demersal fishes could be underestimated, whereas the biomasses of plankton groups and European hake could be overestimated (Supplementary Figure 1). PREBAL diagnostics of P/B values indicated possible overestimation for plankton groups. Considering Q/B values, dolphins and mesoplankton could be overestimated, whereas demersal groups could be underestimated.

The results of the calibration procedure are given in Supplementary Table 2. Incorporating fishing mortalities to drive fishery dynamics improved the model fit by almost 100% compared with the baseline model. Incorporating trophic effects increased model fit by an additional 50%. Finally, the model fit improved by

6% when primary productivity anomalies were included. The lowest AIC_c score was -738.4 and belonged to the model with time series of primary production anomalies, fishing mortalities, and trophic interactions; therefore, it was selected as the best model. Comparisons of simulated biomasses and catches with reference time-series data are shown in [Supplementary Figures 2, 3](#), respectively. Simulated biomasses of European pilchard, mullets, turbot, whiting, spiny dogfish, and thornback ray, and the simulated catches of European pilchard, Mediterranean horse mackerel, mullets, turbot, whiting, spiny dogfish, and thornback ray aligned with the stock assessment predicted biomasses and statistical catch data.

Taylor diagrams showed that RMSD values were lower than or close to 1.0 for biomasses except European anchovy and mesozooplankton and were close to or lower than 1.0 for catches ([Figure 2](#)). The RMSD values of the simulated biomasses of deep-water rose shrimp, European pilchard, Mediterranean horse mackerel, mullets, turbot, whiting, and spiny dogfish, and the RMSD values of the simulated catches of mullets, spiny dogfish, and thornback ray were close to or lower than 0.5, indicating good performance of the model specifically for these species/groups. The correlations of simulated biomasses and catches with reference data were above 0.8 and 0.6, respectively, for the majority of the groups/species.

3.2 Ecological network analysis and regime shifts

The STARS analysis detected regime shifts in the majority of the ecological indicators ([Figure 3](#)), with two or three regimes in the SoM since 1990. The macroecosystem indicators TST and PP showed three regimes, separated by upward and downward shifts in 2002 and 2016, respectively. A/C and O/C experienced two

contrasting shifts in 2003 and 2016, respectively. The cycling indicators FCI and PL showed decreasing shifts in 2002 and 2003, respectively, and did not show any shifts afterwards, whereas PCI showed an increasing shift in 2002 and a downward shift in 2016. STARS did not detect any regime shift in the PFD. The catch and biomass indicators showed positive shifts in 2002 and 2003, respectively, while both indicators showed a final negative shift in 2016. In 1999, a downward shift was detected in the Shannon diversity index. Among the fishery-related indicators, the mTL_c showed a decreasing shift in 2016, and the FiB showed an increasing shift in 1998 and a decreasing shift in 2016, which coincided with the decreasing shifts in catch and biomass in 2016. %PPR_c showed one upward shift in 1998. Considering community-related indicators, i.e., biomass ratios of functional groups in the ecosystem, STARS analysis detected downward shifts in the biomass ratios of predatory fish to forage fish, predatory and cartilaginous fish to other fish, and fish to invertebrates in 2000 and demersal and cartilaginous fish to pelagic fish in 1999. In 2016, STARS detected an additional upward shift in the ratio of demersal and cartilaginous fish to pelagic fish.

According to the empirical Kaiser criterion, only two principal components were retained. The first two principal components explained 82% of the variability in the data. PCA of the indicator anomalies showed a temporal separation of the indicators before the 2000s and after the 2000s in the SoM ([Figure 4](#)). The 1990s were characterized by high values of A/C, FCI, PL, Shannon's diversity index, and biomass ratios of predatory and cartilaginous fish to other fish, predatory fish to forage fish, and demersal and cartilaginous fish to pelagic fish. The 2000s and the 2010s were grouped closer together, mostly on the opposite side of the 1990s, and were characterized by higher values of TST, O/C, PP, PCI as well as biomass, catch, and FiB indicators. The 2000s spread between the 1990s and the 2010s but were more closely aligned with the 2010s.

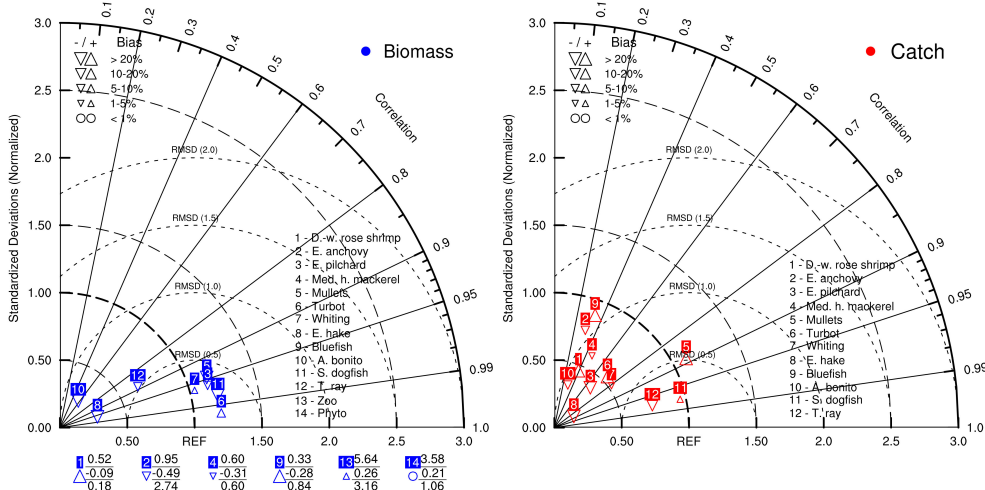


FIGURE 2 Taylor diagrams showing the model skill considering simulated biomasses (left) and catches (right) with respect to stock assessment predicted biomasses and statistical catch data. Numbers below the Taylor diagram of biomasses indicate groups with either standard deviations greater than three (top) or negative correlations with reference data (middle); root mean square errors/distances (RMSD) values (bottom).

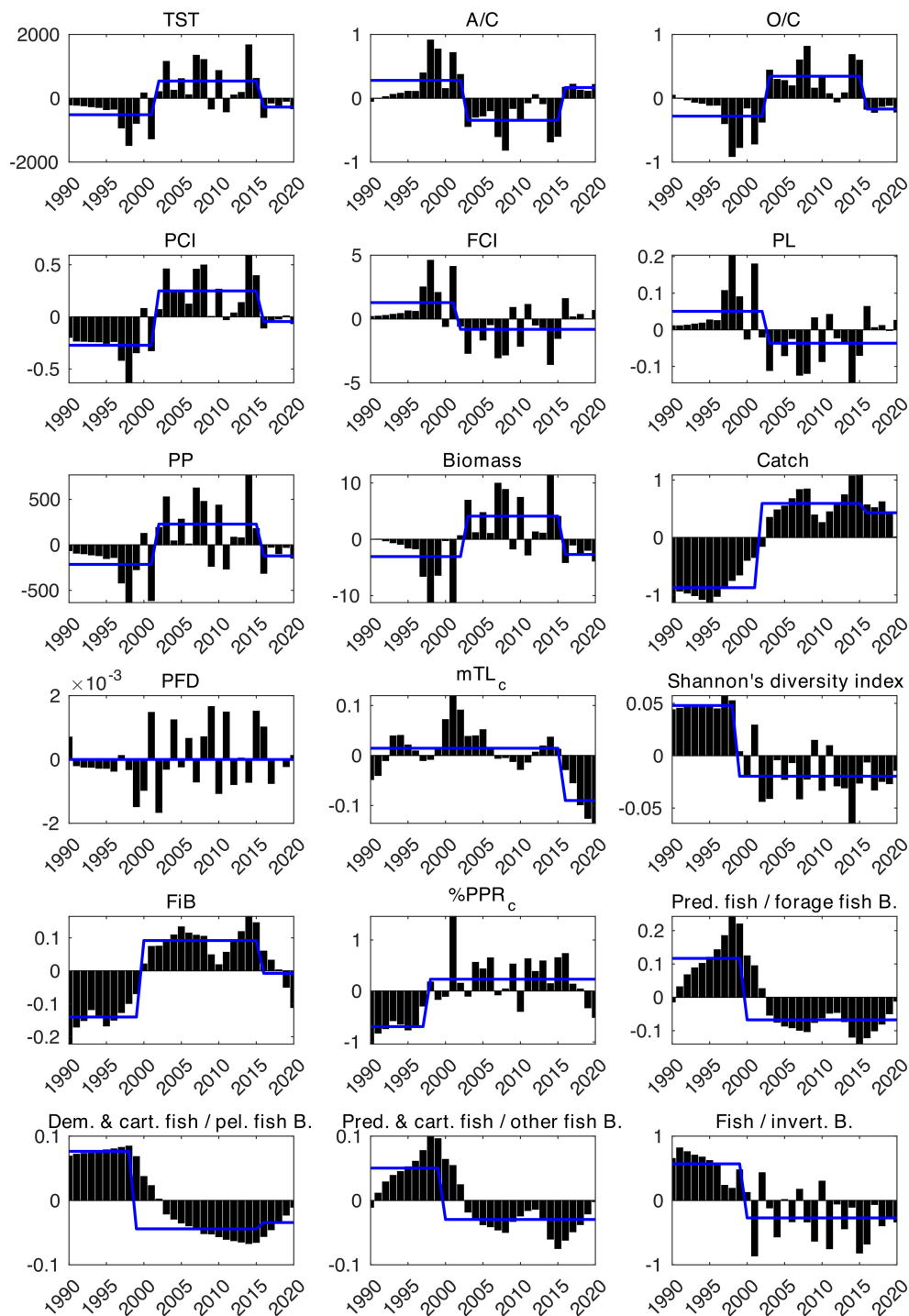


FIGURE 3

Results of STARS analysis of time-series anomalies of ecological indicators. The bars represent anomaly values, and the blue lines show different regimes.

3.3 Equilibrium analysis and fishing policy assessment

The EwE equilibrium analysis suggested overexploitation of European anchovy, European pilchard, Mediterranean horse mackerel, European hake, thornback ray, and spiny dogfish by comparing the calculated MSY values with the average statistical

catches over the modelling period, 1990–2020 (Table 1). The time series of catches and F_{MSY} values from Demirel et al. (2020) with respect to the model-calculated MSY and F_{MSY} values are shown in Figure 5. In line with Table 1, European anchovy, European pilchard, Mediterranean horse mackerel, European hake, thornback ray, and spiny dogfish were overexploited, considering their corresponding MSY values. The catches of Atlantic bonito,

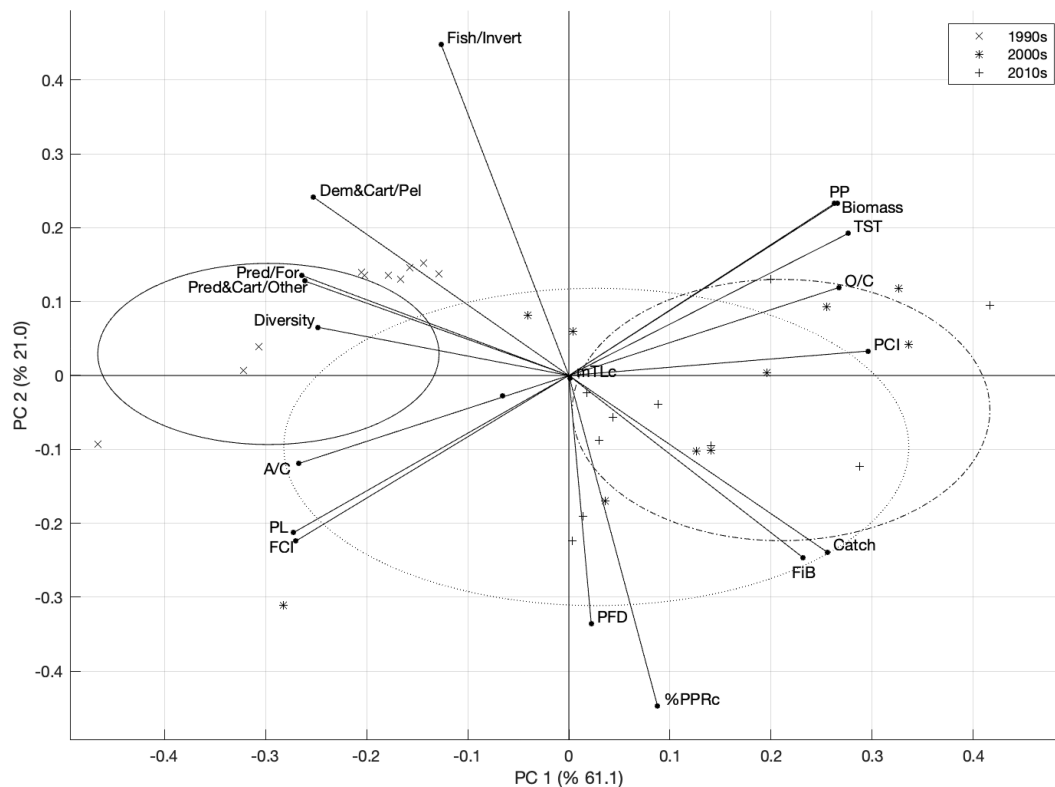


FIGURE 4

PCA analysis of time series of indicator anomalies in SoM. Fish/Invertebrate: biomass ratio of fish to invertebrates, Pred&Cart/Other: biomass ratio of predatory and cartilaginous fish to other fish, Pred/Forage: biomass ratio of predatory fish to forage fish, Dem&Cart/Pelagic: biomass ratio of demersal and cartilaginous fish to pelagic fish. Circles represent groups of decades, i.e., 1990s (solid line), 2000s (dotted line), 2010s (dash-dotted line).

bluefish, whiting, and turbot occasionally exceeded the calculated MSY values during the 1990s and the 2000s.

When the F_{MSY} values calculated by equilibrium analysis were tested, the long-term equilibrium simulation results showed that the calculated stock-specific MSY values could be achieved at a level of 80% or higher for the majority of the species, except for European pilchard, turbot, whiting, European hake, and Atlantic bonito (Table 1). The catches of European anchovy, deep-water rose shrimp, Mediterranean horse mackerel, and bluefish were calculated to reach values higher than the calculated MSY values, and the catches of turbot, whiting, European hake, and Atlantic bonito were lower than 80% of the predicted MSY values.

4 Discussion

This study presents the first temporal food web model for the Sea of Marmara and enables us to assess its ecosystem-wide changes using time series of ecological indicators. Our results indicated that the SoM ecosystem has experienced three regime shifts since 1990. The first “high biodiversity” regime extended from the early 1990s to the end/onset of the 1990s/2000s and was characterized by high biodiversity and material cycling, as well as relatively higher proportions of predatory, cartilaginous and demersal fish to other fish, indicating low impact of fisheries on the ecosystem and a

healthier ecosystem status *sensu* Odum (1969). At the end of the 1990s and in the early 2000s, the SoM ecosystem shifted to a second regime with decreased biodiversity and material cycling but high biomass and catches supported by increased primary productivity, indicating degraded ecosystem conditions. The footprint of SoM fisheries in the ecosystem increased. The higher fisheries impact during the 2000s culminated in a third regime shift in the second half of the 2010s. This third regime was characterized by lower catches and biomass, indicating a “fishing down the food web” impact. The relative resilience of the system decreased and a higher level of relative ascendancy was observed.

4.1 Model skill

The PREBAL analysis of the SoM Ecopath model was considered acceptable as the P/Q values were consistent with the ecological theory, and the P/B and Q/B values mostly followed the increasing trend line from high to low trophic levels with occasional under- and over-estimated groups. Although the individual pedigree values slightly increased considering the reparameterization of the phytoplankton and zooplankton groups using CMEMS data products, the overall pedigree value of the model did not change.

In the SoM Ecosim model, incorporating fishing mortalities and primary productivity anomalies, in addition to trophic effects,

TABLE 1 Model predictions of maximum sustainable yield (MSY) and their corresponding fishing mortality (F_{MSY}) rates for exploited species/groups and their comparison with average catches over the modelling period (1990-2020) compared with the values reported by Demirel et al. (2020) and the biomass and catch results from the equilibrium analysis (EA) of the long-term Ecosim simulation.

Species/Group	F_{MSY} (y^{-1}) (This study)	MSY (tonnes) (This study)	Average catch (tonnes, 1990-2020)	# of years catch > MSY (1990-2020)	F_{MSY} (y^{-1}) (Demirel et al., 2020)	MSY (tonnes) (Demirel et al., 2020)	EA Biomass (tonnes)	EA Catches (tonnes y^{-1})
Deep-water rose shrimp	0.58	2595	1732	7	0.60	2784	4766	2764
European anchovy	0.36	16874	17828	17	0.34	15566	75465	27167
European pilchard	0.19	5092	5357	12	0.34	5315	18787	3570
Mediterranean horse mackerel	0.39	3772	6397	11	0.25	4098	12876	5022
Mullets	0.27	1137	517	1	0.44*	821*	3557	960
Turbot	0.18	104	69	5	0.26	139	267	48
Whiting	0.27	1745	1102	7	0.29	1366	3401	578
European hake	0.28	2055	2921	11	0.24	4816	3130	876
Bluefish	0.22	3237	2555	9	0.33	3514	16221	3569
Atlantic bonito	0.19	2038	1811	8	0.24	2183	7438	1413
Thornback ray	0.08	116	165	15	0.06	196	1389	111
Spiny dogfish	0.08	100	99	9	0.10	39	1003	80

Gray shaded rows indicate overexploited species/groups according to the model-calculated MSY values. The star symbols (*) denote the values calculated by combining mullet species (*Mullus barbatus* and *Mullus surmuletus*).

significantly improved the model's fit to reference data, despite the limitations and uncertainties of the available data. However, primary productivity anomalies provided marginal improvement compared to fishing mortalities and trophic effects. All simulated catches and biomasses had low RMSD values, and the majority of the groups had high correlations with the reference biomasses and statistical catches (Figure 2). The model exhibited higher skill in simulating the catch and biomass dynamics of nine out of 12 groups/species (Supplementary Figures 2, 3). The poor representation of the remaining three species was due to the adjustment of initial conditions; i.e., biomasses, to balance the revised Ecopath model. Considering all of these factors, the model successfully reproduced the dynamics of the SoM ecosystem.

4.2 Ecological network analysis and regime shifts

The STARS analysis showed that three main regimes prevailed in the SoM (Figure 3). The first "high biodiversity" regime exhibited lower levels of %PPR_c, catches, and FiB, although these indicators increased towards the end of this period. This era was marked by a relatively small footprint of fisheries exploitation in the ecosystem and a top-down control on the food web by piscivorous fish. In the early 2000s, the second "low biodiversity" regime with increased primary productivity and biomass emerged. This first regime shift

indicated a reduction in the complexity of the ecosystem and a dominance of small- and medium-sized pelagic fishes, suggesting enhanced fisheries exploitation, as evidenced by increased catch, % PPR_c, and FiB values. Furthermore, the decreasing shift in the predatory fish biomass to forage fish biomass ratio indicated a shift from a top-down control to a more bottom-up influence on the food web dynamics. Low values of FCI and PL during this period indicated limited material cycling and shorter pathways for material/energy transfers in the food web, restricting high trophic levels from the ecosystem's increased primary production. By the mid-2010s, the third "fished down" regime commenced, denoted by the diminishing levels of FiB and mTL_c. This period reflected the consequences of over a decade of intensive fishing that started in the 1990s, leading to a significant decrease in pelagic fish biomass. Concurrently, a slight increase in the ratios of demersal and cartilaginous fish to other fish species was observed, indicating a regime shift in catch composition rather than the recovery of demersal fish populations. In addition, PCA confirmed the regime shift analysis, showing distinct clusters for the 1990s with low biomass, high FCI, PL, and high biomass ratios of predatory, cartilaginous and demersal fish to other fish, and the 2010s with low biomass, catches, FiB, and mTL_c, and the 2000s bridging them but leaning towards the 2010s (Figure 4). Similar to our findings, Demirel et al. (2023b) also found that the SoM ecosystem has experienced three regimes since 1986, based on an analysis of the time series of environmental and biological parameters. Our

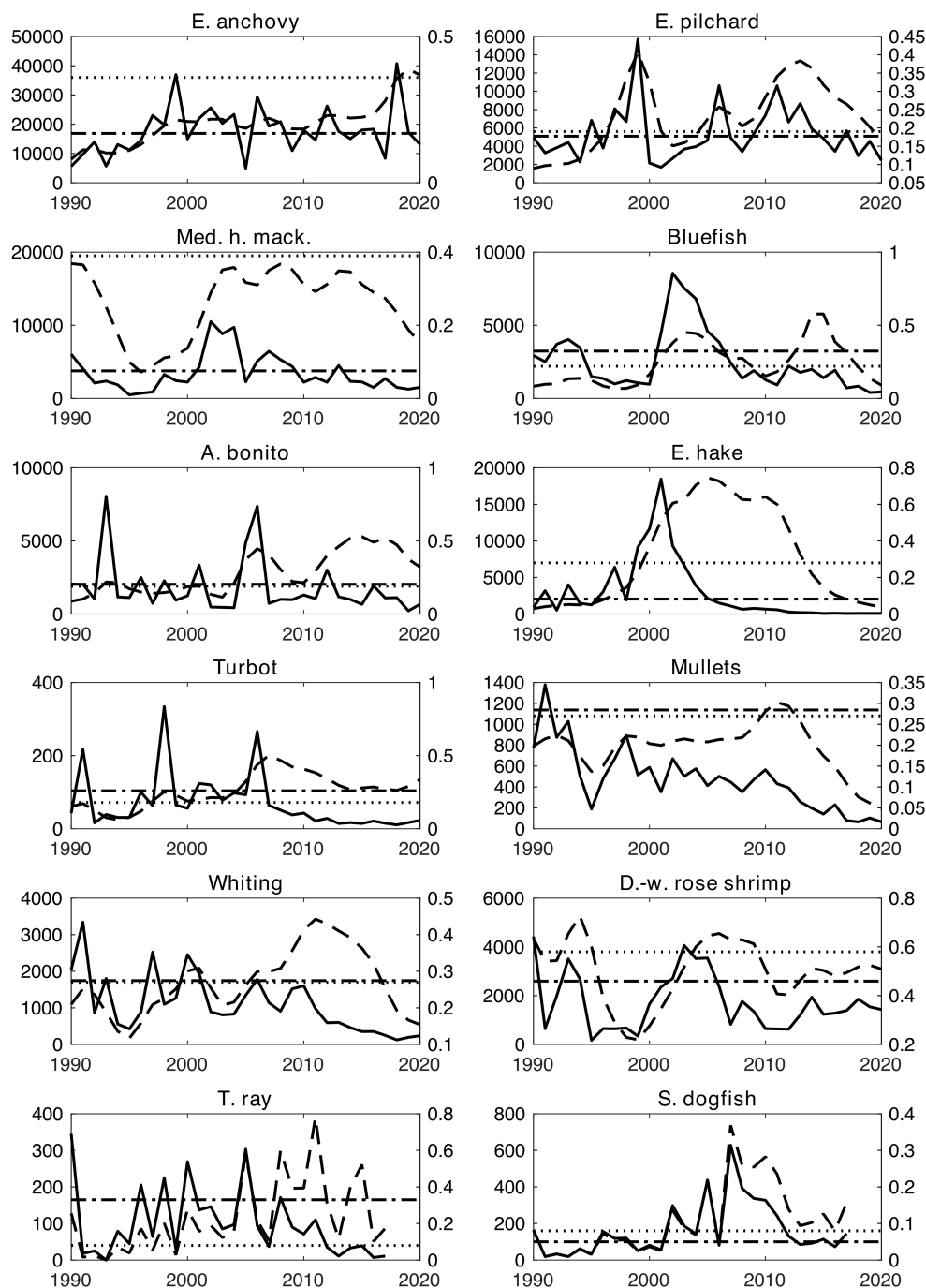


FIGURE 5

Time series of catches (solid lines) and EwE-calculated MSY values (dash-dotted vertical lines) in tonnes on the left Y-axes, as well as their corresponding time series of fishing mortalities (dashed lines, from Demirel et al. (2020)) and EwE-calculated F_{MSY} values (dotted lines) per year on the right Y-axes. X-axes show simulation years.

analysis enriched the results of the integrated ecosystem assessment by Demirel et al. (2023b) as we based our analysis on a comprehensive time-series dataset of ecological indicators that combined multiple aspects of the SoM ecosystem, allowing us to delineate the structural and functional changes in the food web and examine the ecological transitions of the SoM.

Using three Ecopath mass balance models parameterized for the mid 1990s, mid 2000s and the mid 2010s, Saygu et al. (2023) found

that the total biomass in the SoM ecosystem decreased by 13% from the mid 1990s to the mid 2000s, but catches increased by 50%. In our study, considering the decadal scales in our simulation, the total biomass in the SoM ecosystem increased from the 1990s to the 2000s, in line with the increase in statistical catches from the 1990s to the 2000s, and decreased in the third regime. The discrepancies between the two studies may be due to differences in modelling methodologies. The SoM mass balance models were parameterized

using the average productivity values over the respective model periods. However, in this study, we utilized the time series of a merged multisensor remote sensing product to drive primary production in the model, allowing the temporal model to capture the dynamics of the SoM ecosystem more accurately. Furthermore, our study revealed a significant increase in PCI during the 2000s, despite lower FCI and PL values, suggesting enhanced prey-predator interactions due to increased biomasses in the food web amidst reduced overall ecosystem cycling. Thus, as reflected in most ecological indicators, our results highlighted the complex response of the SoM marine ecosystem to anthropogenic pressures.

Pollution and overfishing can lead to a decline in biodiversity and the dominance of pelagic species (Caddy, 2000). A subsequent decline in fish stocks due to continuous overfishing, a pattern also observed in SoM, is inevitable in semi-enclosed seas (Williams et al., 2024). The transition from a high to a low biodiversity regime in the SoM was consistent with global observations in semi-enclosed marine systems, including the Mediterranean (Vasilakopoulos et al., 2014) and Red Seas (Spaet et al., 2016), where overexploitation altered community structures, shrank fish stock sizes, and decreased biodiversity. Similar to SoM, ecosystem overfishing deteriorated the fish stocks in the Baltic Sea and resulted in a series of regime shifts (Tomczak et al., 2013; 2022). In the western Mediterranean, overfishing and environmental drivers drove the historical changes in the ecosystem, climate being responsible for the change in the distribution of organisms latitudinally and overfishing being responsible for the declines in stocks (Coll et al., 2024). However, the changes in the SoM closely resembled the degradation of the Black Sea ecosystem in the late 20th century (Kideys, 2002; Llope et al., 2011; Daskalov et al., 2017; Oguz, 2017). Fishing decreased the Black Sea's biodiversity in the 1960s by first overexploiting predatory larger fish species (Llope et al., 2011; Daskalov et al., 2017), and eutrophication contributed further to this biodiversity decrease by promoting small-sized, opportunistic *r*-strategist species (Oguz, 2017), culminating in a catastrophic fish stock collapse and a regime shift in the late 1980s (Kideys, 2002). Since then, a low biodiversity and biomass regime have continued in the Black Sea. In this study, we demonstrated that similar changes, with comparable intensities to the Black Sea, have also occurred in the SoM since the 1990s, and the SoM ecosystem has shifted to an overexploited, low diversity, and low biomass regime with degraded food web conditions *sensu* Odum (1969).

4.3 Equilibrium analysis and fishing policy assessment

The equilibrium analysis showed that European anchovy, European pilchard, Mediterranean horse mackerel, European hake, thornback ray, and spiny dogfish were overexploited during the 2000s. Atlantic bonito, bluefish, whiting, and turbot were also possibly overexploited in the 1990s, 2000s, and the 2010s, as their catches exhibited occasional sharp declines and peaks that exceeded the respective MSY values in their catches (Table 1; Figure 5), indicating unsustainable fishing. This suggested a mechanism

realized by episodes of a few years of overexploitation followed by respective stock collapses and gradual recovery over the decades.

The long-term Ecosim simulation with F_{MSY} values applied to their respective stocks showed that all catches and biomasses of the species were maintained at equilibrium levels without any collapse or perturbation, indicating fisheries' sustainability. The catch levels for most stocks corresponded to the levels of their calculated MSY values or higher. However, the catches of turbot, whiting, and European hake were lower than their respective MSYs. For turbot and whiting, the calculated MSY values in this study and by Demirel et al. (2020) were higher than their long-term average catch levels. According to our long-term equilibrium simulation, the catches of these stocks could not be restored to the levels of their calculated MSYs or long-term average catches. Furthermore, considering European hake, although the calculated MSY value was lower than its average long-term catch in the equilibrium analysis, the catches also stabilized at approximately 43% of the hake's long-term average catch and 30% of the hake's calculated MSY value (Table 1). Therefore, we concluded that the sustainable levels of catches for turbot, whiting, and European hake should be much lower than the MSY values calculated in this study or in the literature. However, the equilibrium analysis was carried out using the early 1990s mass balance Ecopath model, and the life history parameters, such as total mortality of the stocks, were assumed not to change significantly over time, and prey-predator dynamics remained stable in the ecosystem. Furthermore, bottom-up effects that can affect the carrying capacity of the ecosystem, such as primary production, could have also played a role in the sustained catches in the long-term equilibrium simulation, as average primary productivity levels were projected to the future due to the unavailability of regional primary production projections. Therefore, the equilibrium analysis may have exhibited a shortcoming in representing the dynamics of these fish stocks compared to other examined stocks because of possible changes in their life history traits that were not represented dynamically in the model or changes in the bottom-up effects that could not be represented in the long-term equilibrium analysis simulation.

Demirel et al. (2020) observed similar trends in their catch-based stock assessment model. However, all calculated MSY values in our study, except for European anchovy, mullets, whiting, and spiny dogfish, were lower than those reported by Demirel et al. (2020). The differences in the calculated F_{MSY} and MSY values between this study and those of Demirel et al. (2020) highlighted methodological variations and emphasized the importance of incorporating prey-predator interactions in MSY calculations, which are not explicitly considered in catch-based stock assessments contrary to the Ecosim equilibrium analysis. Furthermore, the equilibrium analysis ensures that food web dynamics are not disrupted when calculating fisheries exploitation levels, in line with EBFM, so that the ecosystem's long-term structure and function are not affected. Therefore, supporting stock assessment models with parallel applications of mechanistic models, as well as increasing the adoption of whole-of-ecosystem models to develop management advice for fisheries as a step forward in the implementation of EBFM in marine ecosystems, is necessary.

Individual catch quotas in fisheries management have been successfully implemented in marine ecosystems worldwide (Marchal et al., 2016) and have been proven to improve fisheries economics (Arnason, 2023), as well as the well-being of marine ecosystems and the sustainability of harvested stocks (Chu, 2009; Hoshino et al., 2020). Therefore, we suggest that MSY values should be employed as quotas for species-specific fisheries in the SoM. In a given fishing season, fisheries for the species should halt as soon as the respective quota is reached, regardless of the duration of the fishing season.

4.4 Limitations of the approach

Models are bound by the quality of the data used to initialize and parametrize their variables. SoM is a data-poor marine region, and systematic survey data for fish stocks and plankton with large spatial and temporal coverage are lacking (Saygu et al., 2023). Thus, the degree of uncertainty in our model results should not be overruled. The reference biomass time series used in this study were the products of a catch-based stock assessment model developed for data-poor marine regions (Demirel et al., 2020). Furthermore, the statistical catches used to validate the simulated catches were impaired by methodological discrepancies, such as the questionnaire-based approach used to collect fishery statistics (Turkstat, 2018). Therefore, the skill of the SoM Ecosim model should be tentatively evaluated by considering the uncertainties in the reference data sources.

The SoM is affected by increasing sea surface temperatures (SST) over the modelling period (Akoğlu, 2021). SST anomalies have increased by $\sim 0.5^{\circ}\text{C}$ since the 1990s (Demirel et al., 2023a). However, we did not incorporate the environmental responses of functional groups to changes in ocean temperature in this study as information on the temperature responses of species in the SoM is limited, and global databases do not contain such data that are statistically representative of the species in the basin, as it is quite small. This may also have limited the ability of our model to capture the dynamics of the SoM ecosystem. Future work should consider including the environmental responses of organisms, e.g., to SST and especially to O_2 , as more such studies are being conducted considering the recent mucilage events and deoxygenation in the SoM (Yalçın et al., 2017).

Aggregation of species into functional groups is also an important consideration in food web modelling and may have an impact on key species of ecosystems, concealing their roles in the food web, and altering the resulting food web representations. However, aggregation helps reduce the ecological complexity while maintaining the important structural properties of the food webs; thus, facilitating evaluation of models against observations and delineating complex phenomena (Olivier and Planque, 2017; Giacomuzzo and Jordán, 2021). In this study, we capitalized on the model of Saygu et al. (2023) and did not modify the species and functional groups in the model. We aimed to represent all economically important fish species in the model to the greatest extent possible, unless constrained by the data. Therefore, the model included 11 separate commercially important fish species, and the functional group of “mulletts” included two commercially exploited Mullidae species because their

registration in the statistical data was dubious. For the remaining groups, i.e., planktonic, benthic, and mammalian groups, representation at the functional level was inevitable due to data constraints and their functional role in the ecosystem. This may have created a drawback for the assessment of mullet fisheries; however, because the focus of our study was on the commercially prevalent organisms in the food web, the aggregation level and representation of state variables in our model were fit for our purpose.

The use of global earth system model products for parameterizing plankton groups could have impaired the lower-trophic-level dynamics simulated by the SoM Ecosim model. Global models are optimized for larger spatial scales and lack the skill to capture mesoscale and sub-mesoscale dynamics in marginal seas and small semi-enclosed marine basins such as SoM. Therefore, plankton and other lower-trophic-level dynamics simulated by the SoM Ecosim model could have been adversely affected by the use of coarse global products, although they were re-interpolated to a higher spatial resolution in our study.

5 Conclusion

Our study showed notable decadal changes in the SoM ecosystem with an indicator-based approach using a temporal food web model for the first time. Our findings delineate three distinct ecological regimes, characterized by their unique characteristics and responses to anthropogenic pressures, particularly fisheries exploitation and environmental degradation. Initially, the SoM ecosystem exhibited attributes of high biodiversity, efficient material cycling, and a balanced trophic structure, which were progressively compromised by increased fishing activities and environmental stressors. The transition from a regime of high ecological complexity and biodiversity to a state characterized by hampered trophic interactions, reduced biodiversity, and a “fished down” marine food web signals a critical need for urgent and comprehensive management strategies. These shifts highlight the pressing challenges of overfishing, habitat degradation, and the broader implications of anthropogenic influences on semi-enclosed marine ecosystems.

The identification of overexploited species and the recommendation for EBFM practices, including the implementation of species-specific MSY values as quotas, offer a pathway towards mitigating biodiversity loss and promoting the resilience of the SoM ecosystem. The application of global earth system models and reliance on data-poor methodologies underscored the critical need for enhanced regional data collection, model validation, and integration of mechanistic models with conventional stock assessments. Future research should prioritize the refinement of input data, the adoption of regional model outputs, and the exploration of novel management strategies that incorporate the complex interplay between species dynamics, environmental variability, and human impacts. Such endeavors are essential for advancing our understanding of the SoM ecosystem and developing more effective conservation and management strategies, ensuring the long-term sustainability of this fragile marine environment and its invaluable resources.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author.

Author contributions

EA: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. İS: Conceptualization, Data curation, Investigation, Writing – review & editing. ND: Conceptualization, Data curation, Investigation, Writing – review & editing.

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Conflict of interest

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1412656/full#supplementary-material>

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