

Insights into the ecology of the Black Sea through the qualitative loop analysis of the community structure

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Abstract

Overfishing, excess nutrient load, and invasion of *Mnemiopsis leidyi* acted on the Black Sea from 1960s to 1990s. Under the effect of these drivers, the ecosystem underwent several transformations that culminated in the shift from a planktonic food chain to a network with most of the energy diverted to jellyfish. The interplay between multiple stressors and the intricate web of trophic interactions make it difficult to understand which causative mechanisms linked the sources of change to the observed variations. To study such interplay, we focused on the structure of the trophic interactions and applied loop analysis to qualitatively predict the response of variables to stressors. Significant variations in biomass trends were identified with statistical analysis and considered as benchmark to validate loop analysis predictions. The results of the comparisons were used to select the most influential trophic interactions that explain the changes observed between 1960 and 1990. The models were applied to test (1) the importance of various environmental drivers and (2) the mechanisms that produced the observed changes. The results suggested that the changes observed before *M. leidyi* invasion were strongly influenced by the excess nutrient addition, an outcome that challenges the relevance of the trophic cascade as described in literature. The concurrent effect of overfishing, climate, and nutrient enrichment likely triggered the outburst of *M. leidyi* in the late 1980s. Our work shows the potential of loop analysis to grasp the causal relationships between the drivers, the structure of the interactions, and the responses of the variables.

During the period 1960–2000, the Black Sea ecosystem underwent extensive modifications. Overfishing (Prodanov et al. 1997; Daskalov 2002; Gucu 2002), excess nutrient loading (Mee 1992; Zaitsev 1992), and the presence of invasive species (Shiganova 1998; Kideys and Romanova 2001; Kideys 2002) have been indicated as major drivers for community reorganization. They triggered a series of processes that culminated in the shift from a planktonic food chain, whose backbone was the zooplankton-planktivores-piscivores grazing chain, to a web in which the main flow of energy was diverted to jellyfish (Shushkina and Musayeva 1990; Mills 1995). In particular, such transition has been highlighted by the outburst of the comb jellyfish *Mnemiopsis leidyi* and the contemporary collapse of the planktivorous (mainly anchovy) stock (Oguz et al. 2008a,b). Ecologists directed their efforts toward disentangling causative mechanisms of these transformations with emphasis on the relative

importance and balancing of bottom-up forcing and top-down cascades (Bănară et al. 2010). The bulk of the investigations converged to indicate overfishing as the main driver of community reorganization (Daskalov 2002; Oguz and Gilbert 2007; Llope et al. 2011). Alternative drivers suggested include climate, eutrophication, and invasive species as possible causes of change (Shiganova et al. 2001; Kideys 2002; Oguz and Gilbert 2007). One question of interest is how the interplay between these drivers determined the observed changes in the Black Sea (Daskalov 2002; Oguz and Gilbert 2007). Such interplay complicates analysis and interpretation of causality, particularly given the reticulate structure of food webs. Most research conducted on the regime shift in the Black Sea ecosystem relied on the information contained in the time series of species biomasses (Daskalov et al. 2007; Oguz and Velikova 2010). To explore the causality behind the changes in consumer/resource populations, the relationships between adjacent trophic levels were investigated (Daskalov et al. 2007). Annual averages of each trophic level biomass were used as the response variable and regressed against other trophic levels and environmental variables (Daskalov et al. 2007). Data were handled in the framework

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Additional Supporting Information may be found in the online version of this article.

of bottom-up vs. top-down control as a reference scheme for interpretation. Models have been also introduced in support of these analyses. Mass-balance models (Daskalov 2002; Akoglu et al. 2014), energy flow networks (Gucu 2002; Vasas et al. 2007), and dynamical models (Oguz et al. 2001; Oguz et al. 2008b; Llope et al. 2011) were developed to substantiate the interaction mechanisms derived from the statistical models.

The major aim of this article is to contribute to the wider understanding of the mechanisms responsible for changes in the Black Sea ecosystem and so we focused on the community's interactive structure as a possible locus of explanation. The impact of drivers in fact may percolate from target variables to the rest of the community through pathways of interactions that emerge from the linkage structure of the community. We analyzed the interactive web of the Black Sea by applying the qualitative algorithm of loop analysis (Levins 1974; Puccia and Levins 1985). We used loop analysis to explain the relationship that connects the sources of change (i.e., the drivers), the structure of the linkages between the variables, and the variation in the level of the variables (Dambacher and Ramos-Jiliberto 2007). To disentangle this relationship, we mapped out the structure of the interactions between the components of the community. Predictions of biomass variability were obtained by identifying the variables which were subjected to press perturbations. The model predictions were compared to the observed patterns of biomass variation for the period 1960–1990. This allowed for: (1) the selection of a reliable scheme for the Black Sea community structure, (2) the identification of the patterns of variation in response to the different drivers, and (3) additional hypotheses on the role of drivers in respect to the changes that Black Sea underwent in the considered period. We show how loop analysis can be applied for testing sets of interactions responsible for the spreading of press perturbations and possible mechanisms of ecosystem response.

Methods

Loop analysis

Loop analysis is a qualitative technique that uses signed digraphs to represent networks of interacting variables (Levins 1974; Puccia and Levins 1985). Variables may represent a single species (e.g., *Noctiluca scintillans* or *M. leidy*) as well as groups of species (e.g., edible zooplankton or demersal fish). Loop analysis allows the prediction of the direction of change in the biomass of system variables in response to parameter alteration targeted to specific variables (i.e., press perturbations; see Bender et al. 1984; Bodini 2000). For example, a stressor that increases the mortality rate of a species. This increased mortality reduces the growth rate of the target species: a negative input on it. The species responds to this input by changing its biomass level. Furthermore, the

input may propagate its effects to the other species that are connected by the network to the target variable. Variable responses can be calculated by a routine that summarizes in a matrix implementation the algorithm of loop analysis. Main features of the loop analysis algorithm are provided in the Supporting Information, Appendix A. The predictions obtained with loop analysis indicate only the direction of change for the level of the variables: increase (+), decrease (−), or no change (0). Predictions can be arranged in a table of predictions (Supporting Information, Appendix A). One example of such table is given in Fig. 1b and summarizes all possible outcomes for the model of Fig. 1a. The entries of the table denote variations expected in the level (e.g., biomass) of all column variables in response to positive parameter inputs (i.e., perturbations that increase the rate of change of target variables) affecting any row variable. Conventionally, the calculation considers positive inputs; consequences of negative inputs can be obtained by simply reversing the signs in the table. In models with few variables and/or a limited number of connections, expected changes for the variables can be tracked through the graph anatomy (Bodini 1998, 2000). However, when variables and connections increase, multiple pathways of interactions emerge and the probability that pathways have opposite effects increases. In these cases, the model yields ambiguous predictions (i.e., some positive and some negative paths that produce opposite effects). To overcome this problem, we implemented a numerical simulation based on a routine that randomly assigns (from a uniform distribution) numerical values in the interval (0,1] to the coefficients of the community matrix (i.e., the coefficients of the links in the signed digraph). This procedure and the code for the R statistical environment (R Core Team 2014) are described in the Supporting Information, Appendix A.

Model construction

Signed digraphs were built upon knowledge concerning main trophic interactions (i.e., who eats whom) that characterized the pelagic community of the Black Sea. This knowledge was provided by the vast literature about the ecology of the system. Particular attention was given to what presented in modeling exercises, which included conceptual models (Daskalov et al. 2007; Oguz and Gilbert 2007; Oguz et al. 2008a), dynamic models (Oguz et al. 2001; Oguz et al. 2008b), and mass-balance models (Daskalov 2002; Gucu 2002; Vasas et al. 2007; Akoglu et al. 2014). The presence/absence of certain players led us to identify two phases as for community structure and models: (1) the pre-invasion phase in which *M. leidy* was not present; (2) the post-invasion phase in which *M. leidy* became established as local population after invasion. The structure of the community changed from one period to the next. Also, we could not identify a unique representation of the system within each period. Therefore, alternative graphs (built upon a core model) were

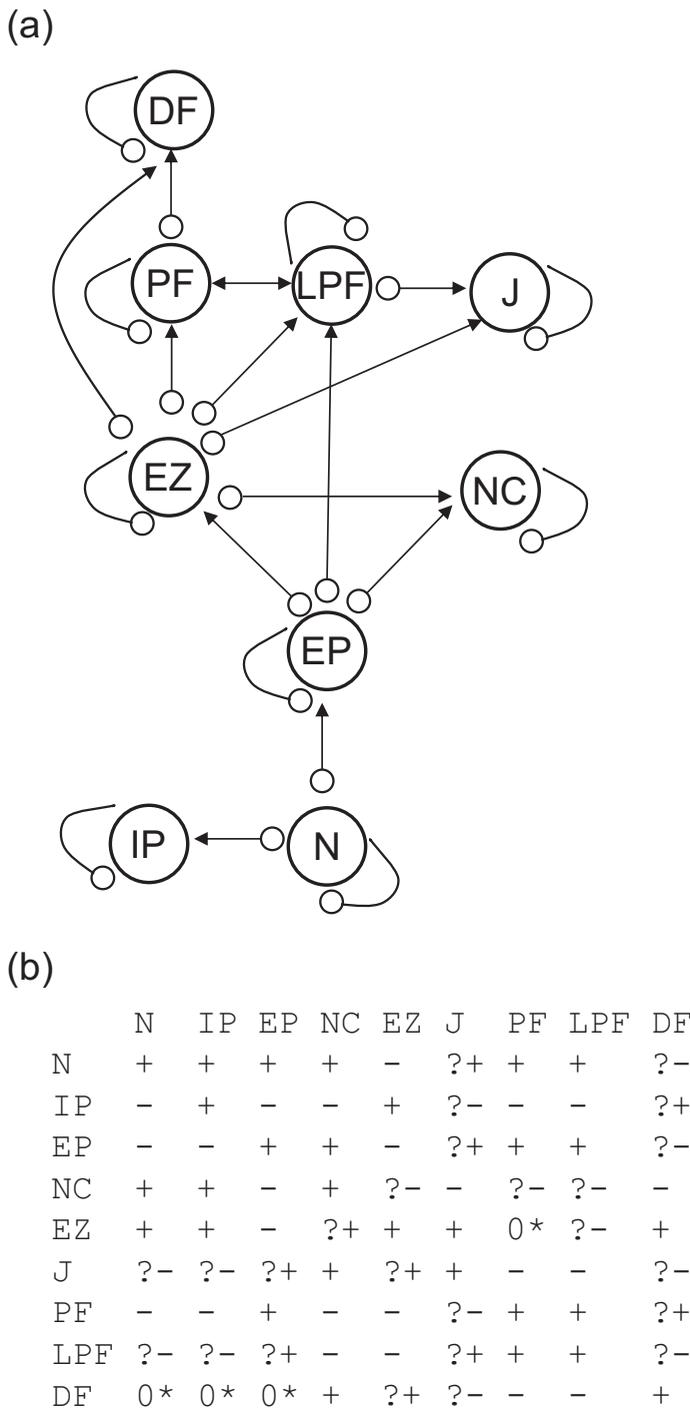


Fig. 1. Signed-digraph describing the community structure for the pre-invasion period (a) and its table of predictions (b). All interactions refer to trophic relationships or consumption of resources (i.e., see the connection from nutrients to phytoplankton) except for the mutual (positive) connection between small and medium pelagic fish and their larvae (i.e., such connection describes reproduction and ontogenetic development). Keys for nodes are: inorganic nutrients (N), inedible phytoplankton (IP), edible phytoplankton (EP), *N. scintillans* (NC), edible zooplankton (EZ), jellyfish (J), small and medium pelagic fish (PF), larvae of small and medium pelagic fish (LPF), and demersal fish (DF).

constructed for the different phases (the whole array of alternative graphs is shown in the Supporting Information, Appendix B). All the graphs are equally plausible, on the basis of the ecological information at our disposal. In the models, some variables represent single species (i.e., *N. scintillans* or *M. leidy*), while others lump together many populations (e.g., edible phytoplankton or small and medium pelagic fish). This uneven resolution is justified by the structure of the database. For several groups, data were aggregated and considering resolution at the species level could not be possible. Hence, the architecture of the various models came out as a reasonable compromise between the need to describe the system in its complexity and the possibility to use field data to verify model predictions.

Data series and statistical analysis

Oguz and Gilbert (2007) divided the ecological history of the Black Sea in four periods called pre-eutrophication (1960–1970), eutrophication (1970–1980), iper-eutrophication (1980–1990), and post-eutrophication (1990–2000). This partitioning reflected the succession of events that occurred in the ecosystem with reference to its trophic state. Considering the data at our disposal, we focused on the 1960–1990 as main period of investigation. We used annual time series of the groups that entered as variables in our models. Time series for phytoplankton and zooplankton biomasses were collected from Prodanov et al. (1997). The periods covered are: 1960–1989 for phytoplankton and 1964–1992 for zooplankton. Biomasses of *N. scintillans* (1960–1988) and jellyfish (1960–1988) were obtained from Simonov et al. (1992); in the case of jellyfish, the data refer to ctenophores. More details on these trophic groups (i.e., phytoplankton, zooplankton, *N. scintillans*, and jellyfish) and their biomasses are available in the Supporting Information, Appendix C (Tables C1, C3). Data on stock and catch of fish species were obtained from Prodanov et al. (1997) and using the website of the Sea Around Us research initiative (Pauly and Zeller 2015). An accurate analysis of the literature (Oguz et al. 2012; Akoglu et al. 2014 and references therein) allowed to identify two main fish groups: small and medium pelagic fish and demersal fish. The time series of the stock for the former group spans from 1967 to 1993, while catch data cover a longer period (i.e., from 1950 to 1992). Stock data for demersal fish cover the period from 1971 to 1988 and catch data the period 1967–1992. Details on the composition (i.e., species included), stock, and catch data used for these two compartments are in the Supporting Information, Appendix C (Tables C2, C3). The data used in this manuscript refer to periods that encompass the main transformations that occurred in the Black Sea, from eutrophication (early 1970s) to the bloom of *M. leidy* in late 1980s (although complete information is lacking for what concerns the 1950s, a crucial period for the decline of large pelagic fish).

In the literature, it has been shown that a convenient partitioning of the time series to catch significant variations in

Table 1. Changes in the biomass of planktonic groups in the period 1960–1992. Results of the Mann–Whitney *U*-test applied to biomass data of phytoplankton, zooplankton, *N. scintillans*, and jellyfish. Differences refer to periods of either 5 or 10 yr. Significant differences in bold.

Group	Dataset	10 yr			5 yr		
		Period	<i>W</i>	<i>p</i>	Period	<i>W</i>	<i>p</i>
Phytoplankton	1960–1989	1960–1969 < 1970–1979	16	0.004	1960–1964 > 1965–1969	14	0.421
					1965–1969 < 1970–1974	10	0.214
					1970–1974 < 1975–1979	5	0.041
		1970–1979 > 1980–1989	49	0.544	1975–1979 < 1980–1984	11	0.421
Zooplankton	1964–1992	1964–1969 > 1970–1979	46	0.047	1980–1984 > 1985–1989	22	0.028
					1965–1969 > 1970–1974	13	0.500
					1970–1974 > 1975–1979	25	0.004
		1970–1979 > 1980–1989	50	0.515	1975–1979 < 1980–1984	6	0.111
<i>N. scintillans</i>	1960–1988	1960–1969 > 1970–1979	55	0.370	1980–1984 > 1985–1989	11	0.655
					1960–1964 > 1965–1969	18	0.155
					1965–1969 < 1970–1974	11	0.421
					1970–1974 > 1975–1979	12	0.579
		1970–1979 < 1980–1988	16	0.009	1975–1979 < 1980–1984	6	0.111
Jellyfish	1960–1988	1960–1969 < 1970–1979	4	<0.001	1980–1984 < 1985–1988	2	0.032
					1960–1964 > 1965–1969	19	0.104
					1965–1969 < 1970–1974	1	0.008
					1970–1974 < 1975–1979	11	0.421
		1970–1979 > 1980–1988	62	0.089	1975–1979 > 1980–1984	19	0.111
					1980–1984 < 1985–1988	7.5	0.311

Table 2. Changes in stock and catch of fish groups in the period 1950–1993. Results of the Mann–Whitney *U*-test applied to data about small and medium pelagic fish and demersal fish. Both stocks and catches are measured in terms of biomass. Differences refer to periods of either 5 yr or 10 yr. Significant differences in bold.

Group	Dataset	10 yr			5 yr		
		Period	<i>W</i>	<i>p</i>	Period	<i>W</i>	<i>p</i>
Small and medium pelagic fish (stock)	1967–1993	1970–1979 < 1980–1989	23	0.022	1970–1974 < 1975–1979	4	0.048
					1975–1979 < 1980–1984	6	0.111
					1980–1984 > 1985–1989	14	0.421
					1985–1989 > 1990–1993	20	0.008
Small and medium pelagic fish (catch)	1950–1992	1950–1959 > 1960–1969	65	0.140	1950–1954 > 1955–1959	25	0.004
					1955–1959 > 1960–1964	16	0.274
					1960–1964 < 1965–1969	2	0.016
					1965–1969 < 1970–1974	0	0.004
		1960–1969 < 1970–1979	0	<0.001	1970–1974 < 1975–1979	7	0.155
		1970–1979 < 1980–1989	1	<0.001	1975–1979 < 1980–1984	0	0.004
					1980–1984 > 1985–1989	14	0.421
					1985–1989 > 1990–1992	15	0.018
Demersal fish (stock)	1971–1988	1971–1979 < 1980–1988	32.5	0.254	1971–1974 < 1975–1979	0	0.010
					1975–1979 < 1980–1984	4	0.095
Demersal fish (catch)	1967–1992	1970–1979 < 1980–1989	13	0.002	1980–1984 > 1985–1988	20	0.008
					1967–1969 < 1970–1974	5	0.286
					1970–1974 < 1975–1979	8	0.210
					1975–1979 < 1980–1984	8	0.210
					1980–1984 < 1985–1989	3	0.028

Table 3. Comparisons between the predictions of loop analysis and the trends determined with statistical analysis of empirical data. The comparisons refer to the pre-invasion period (1960–1979) and to the post-invasion period with low *M. leidyi* biomass (1980–1989). This is because for those years the construction of the dataset concerning the main trophic groups was possible. Expected changes triggered in column compartments by either positive (e.g., +N) or negative (e.g., –PF) inputs on row variables are summarized. The row “All” indicates the cumulative impact generated by the concurrent effect of multiple inputs, while the trends identified with statistical analysis are in the row “Test”. Cells with gray background in the row “All” highlight the match between statistical analysis results and cumulative impacts predicted with loop analysis. Keys for the codes: N, inorganic nutrients; EP, edible phytoplankton; NC, *N. scintillans*; EZ, edible zooplankton; J, jellyfish; PF, small and medium pelagic fish; DF, demersal fish.

	EP	NC	EZ	J	PF	DF
1960–1979						
+N	+	+	–	?+	+	?–
+PF	+	–	–	?–	+	?+
+DF	0*	+	?+	?–	–	+
All	+	+	–	?–	+	+
Test	+	0	–	+	+	+
1980–1989						
+N	+	+	–	?+	+	?–
–PF	–	+	+	?+	–	?–
All	0*	+	0*	+	0*	–
Test	–	+	0	0	0	–

the biomass of trophic groups should consider decadal periods (Gucu 2002; Daskalov et al. 2007; Oguz and Gilbert 2007; Oguz et al. 2012). This is corroborated by the observation that pelagic fish stocks showed marked decadal-scale fluctuations (Daskalov 2003; Oguz et al. 2006; Daskalov et al. 2007). Moreover, the use of decadal periods perfectly matches the main subdivision operated by Oguz and Gilbert (2007) to distinguish different phases determined by the trophic status of the waterbody. To use our dataset proficiently, we considered decadal periods but we further partitioned the time series into periods of 5 yr. This helped to grasp significant variations in fish stock time series from 1971 to 1988. Also the biomass of components such as phytoplankton and zooplankton showed variations that follow decadal trends (Daskalov 2003; Oguz 2007; Oguz and Gilbert 2007). Therefore, periods of 5 yr and 10 yr are a reliable time to identify the long term biomass variations required for applying loop analysis (Bodini 1998, 2000). For each and every group of pelagic population, we compared biomass data between consecutive periods in search for significant differences from one period to the next. All statistical comparisons were based on empirical data and performed using the Mann–Whitney

U-test in the R statistical environment (R Core Team 2014). Differences along the time series were expected to confirm the classification proposed by Oguz and Gilbert (2007). The outcomes of these comparisons were used as benchmark for model predictions.

Biomass trends and model predictions

Model predictions were examined in respect to biomass variations between successive periods as detected by the statistical analysis. The statistical analysis helped to identify the significant variations in the biomass trends of the empirical dataset. Such variations were compared with the expected direction of change for the variables as predicted by the models (i.e., response to parameter change). In ecology, it is often the case that the entry point of a parameter change is not known. In the case of the Black Sea, however, several literature sources agree in identifying certain types of perturbations that affected the system and the period in which they occurred (e.g., see Oguz and Gilbert 2007). Therefore, we simulated these perturbations as inputs to specific variables to obtain the expected variations in the biomass levels of the main trophic groups. Reliable predictions are those that meet statistically significant variations observed in the time series. A null prediction (i.e., no variation expected for a variable in response to a certain input) corresponds to a nonsignificant difference in the biomass levels of a variable between successive periods (Puccia and Levins 1985). Thus, our approach consists of two steps: (1) using loop analysis to predict the variation expected in the level of the main variables (i.e., trophic groups) following inputs affecting specific target variables; (2) examining the soundness of model predictions with respect to statistically significant variations in the time series data.

Null models

To further validate the food web models used in this manuscript, we compared their predictions with the ones of null models. First, we investigated the uniqueness of the predictions generated by the realistic food webs. Second, we tested the presence of nonrandom matching between the predictions of the realistic food webs and the significant changes in the biomass trends. For each food web, we generated 1000 random networks (i.e., null models) using the Erdős–Rényi algorithm (Erdős and Rényi 1959). Number of nodes and interactions of the null models were the same as in the realistic food webs, but with link arrangements defined according to random topology. We imposed negative self-loops on all variables to ensure the generation of stable matrices. We excluded from the analysis the random networks composed of more than one component (i.e., with two or more disconnected subnetworks), and also those with no primary producers and top predators. The comparison between food webs and null models was carried out for the concurrent effect of all perturbations studied in each scenario (i.e., using all inputs analyzed for each period). Food webs and null

models were considered to be equivalent in case of complete match between the predictions of the main trophic groups (i.e., edible phytoplankton, edible zooplankton, *N. scintillans*, jellyfish, small and medium pelagic fish, and demersal fish). In the Appendix B of Supporting Information, we investigated the specific match for predictions generated by single inputs, also taking into account all realistic models that were not selected for the manuscript. Finally, we tested whether realistic models outperformed random models in predicting biomass changes of main trophic groups (i.e., same groups considered to prove the uniqueness of the food web predictions). Significant differences were assumed if less than 50 random models (out of 1000) predicted the same number (or more) of biomass changes than the realistic models for the period between 1960 and 1989 (i.e., one-tail test).

Results

Pre-invasion period (1960–1979)

The signed digraph in Fig. 1a depicts the structure of the trophic interactions of the Black Sea in the pre-invasion period (i.e., before *M. leidy* settled in the Black Sea). This model was selected from a suite of community structure graphs that were investigated for their capability to qualitatively predict changes observed in the biomass trends of the trophic groups. The entire suite of models is reported in the Appendix B of the Supporting Information. The graph in Fig. 1a corresponds to model V of the pre-invasion period in the Supporting Information, Appendix B. The trophic interactions that make up the community were selected on the base of the literature at disposal. With the exception of *N. scintillans*, all variables represent trophic groups. The reason for this choice is that previous research on the Black Sea exploited datasets that were organized around groups of pelagic populations (Daskalov et al. 2007; Oguz and Gilbert 2007). *N. scintillans* was reported as a significant component of the trophic web so that data for this single species were collected and made available (Simonov et al. 1992). The fundamental backbone around which the model of Fig. 1a was constructed is the grazing chain from inorganic nutrients to demersal fish. Inorganic nutrients (N) constitute the very bottom of the web. They are exploited by phytoplankton, which was divided in two variables: edible phytoplankton (EP) and inedible phytoplankton (IP). Edible phytoplankton (EP), in turn, is the main resource for edible zooplankton (EZ), *N. scintillans* (NC) and the larvae of small and medium pelagic fish (LPF). *N. scintillans* feeds also on EZ; this latter is exploited by the jellyfish (J; e.g., *Aurelia aurita*), and by small and medium pelagic fish (PF) and their larvae (LPF). LPF have a mutually positive interaction with the adult component (PF) and are consumed by jellyfish (J). Finally, demersal fish (DF) prey upon small and medium pelagic fish (PF) as well as on edible zooplankton (EZ). The relevance of the predatory pressure of demersal fish (DF) on small and

medium pelagic fish (PF) is corroborated by data on feeding preferences of *Merlangius merlangus* on *Engraulis encrasicolus* and *Sprattus sprattus* (Mazlum and Bilgin 2014), and of *Squalus acanthias* on *E. encrasicolus* (Demirhan et al. 2007). The choice of having larvae and adults for small and medium pelagic fish (PF) responds to the need of exploring the role of LPF in sustaining the outburst of the invader *M. leidy* in the post-invasion period (Oguz et al. 2008a,b). The alternative models that describe the community in the pre-invasion period (and without large pelagic fish) consider as major structural variations the following links in various combinations (see the Fig. B1 in the Appendix B of Supporting Information): no predation by demersal fish (DF) on edible zooplankton (EZ; models I, VI, and VII); no exploitation of edible zooplankton (EZ) by *N. scintillans* (NC; models III–IV and VI–X); exploitation of fish larvae (LPF) by demersal fish (DF; models II–III and VII), no exploitation of edible phytoplankton (EP) by fish larvae (LPF; models IX–X); exploitation of *N. scintillans* (NC) by the jellyfish (J; models VIII–IX). It is not clear from the literature whether these interactions are stable component of the structure of the interactions so we did not consider them as pillars in the community structure of the Black Sea. They were however useful to set up alternative schemes.

In the period 1950–1960, also top predators as dolphins and large pelagic fish (e.g., tuna and sharks) were part of the Black Sea community. They were heavily fished so they disappeared by late 1960s (Oguz et al. 2012; Akoglu et al. 2014). In the food web of Fig. 1a, there are no dolphins and large pelagic fish because we focused on the Black Sea dynamics after their decline, due to the absence of comprehensive data regarding the main trophic groups prior the 1960s. Such lack of data impaired the possibility of comparing loop analysis predictions with empirical trends prior the 1960s, one of the premises of our study. For this reason, the main models presented in the manuscript do not include dolphins and large pelagic fish. However, because their decline played an important role in the dynamics of the Black Sea, we constructed alternative models (presented in the Supporting Information, Appendix B) in which this component (TP, top predators) was included. We defined trophic connections for TP according to Akoglu et al. (2014). Given the negligible importance of the trophic interaction between top predators (TP; i.e., dolphins and large pelagic fish) and demersal fish (DF) we considered for the top predators (TP) first a unique trophic interaction (i.e., predation on small and medium pelagic fish, PF). Nevertheless, we also considered an alternative model that includes predation on both small and medium pelagic fish (PF) and demersal fish (DF; see the Fig. B2 in the Appendix B of Supporting Information).

Figures 2, 3 illustrate biomass trends for the main trophic groups that we included as variables in the models. Data availability limited the number of components that could be represented in the dataset. Figure 2 describes the biomass

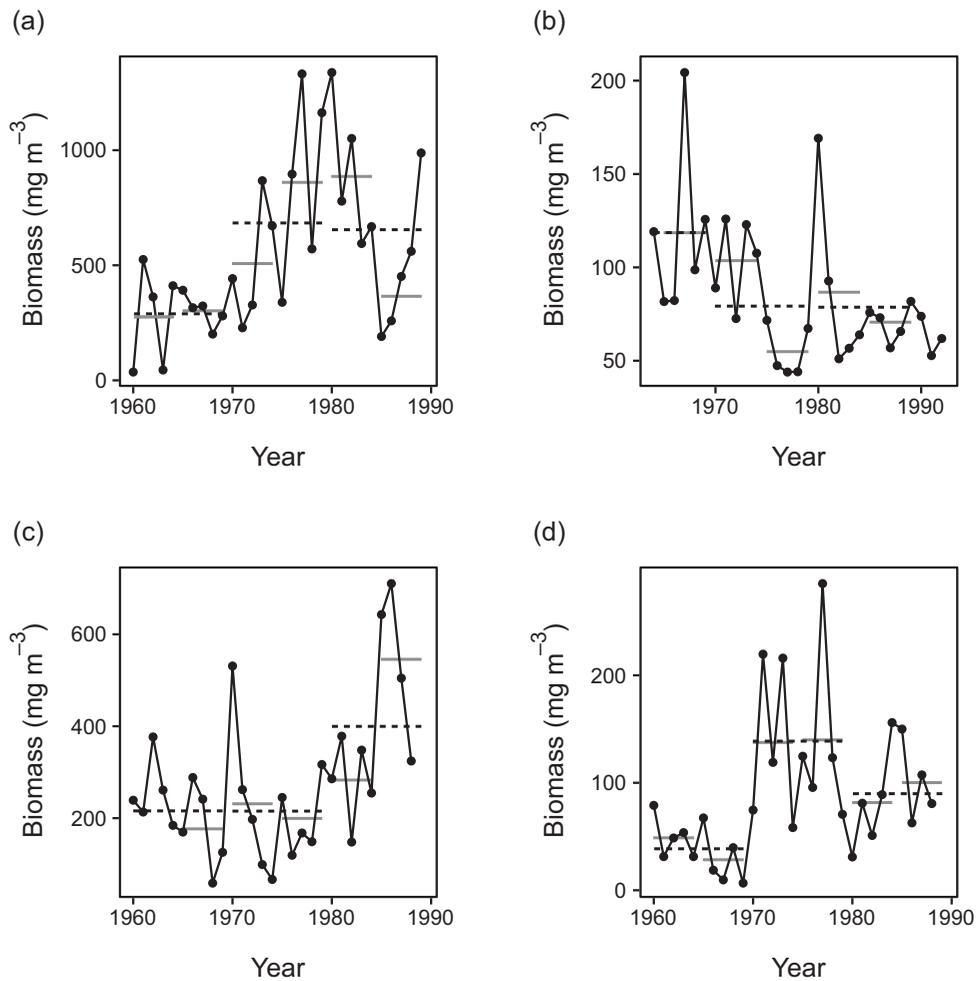


Fig. 2. Biomass time series of phytoplankton (a), zooplankton (b), *N. scintillans* (c), and jellyfish (d). Source data are available in the Supporting Information, Appendix C (Table C3). Average biomass over periods of 5 yr and 10 yr is visualized with solid gray lines and dotted black lines, respectively.

trends for phytoplankton, zooplankton, *N. scintillans*, and jellyfish. The charts in Fig. 3 show the trends for stock and catch of small and medium pelagic fish and demersal fish. Solid gray lines and dotted black lines in the charts identify average values calculated over periods of 5 yr and 10 yr, respectively. The whole dataset is reported in the Supporting Information, Appendix C (Table C3).

Biomasses (which refer to stocks and catches in the case of fish groups) in successive periods were compared with the Mann–Whitney *U*-test. Results are reported in Table 1 (plankton groups) and Table 2 (fish).

Figure 1b shows the table of predictions obtained for the graph of the community structure represented in Fig. 1a. This table provides expectations about the direction of change for the level of the column variables (i.e., the biomass) following positive parameter inputs on the row variables. Predictions were obtained with a simulation routine based on quantification of interaction coefficients (i.e., link

intensities). Values of link intensities were assigned randomly in the uniform interval (0,1]. The results of the simulations and the predictions for the complete set of models are given in the Supporting Information, Appendix B. The direction of change predicted by the models for each variable following specific input was contrasted with variations in biomass trends in the period 1960–1979.

According to the literature, two main drivers affected the Black Sea between 1960s and 1970s: overfishing of top predators (i.e., dolphins and large pelagic fish) and increased nutrient loading. Overfishing started in the 1950s and continued during the 1960s until the stock of top predators resulted severely depleted (Oguz et al. 2012). Massive addition of nutrients began in late 1960s and continued during the following two decades (Oguz and Gilbert 2007). The dynamics of the entire community during the 1970s must have been conditioned by these events. The two events generated press perturbations (inputs) that affected the system

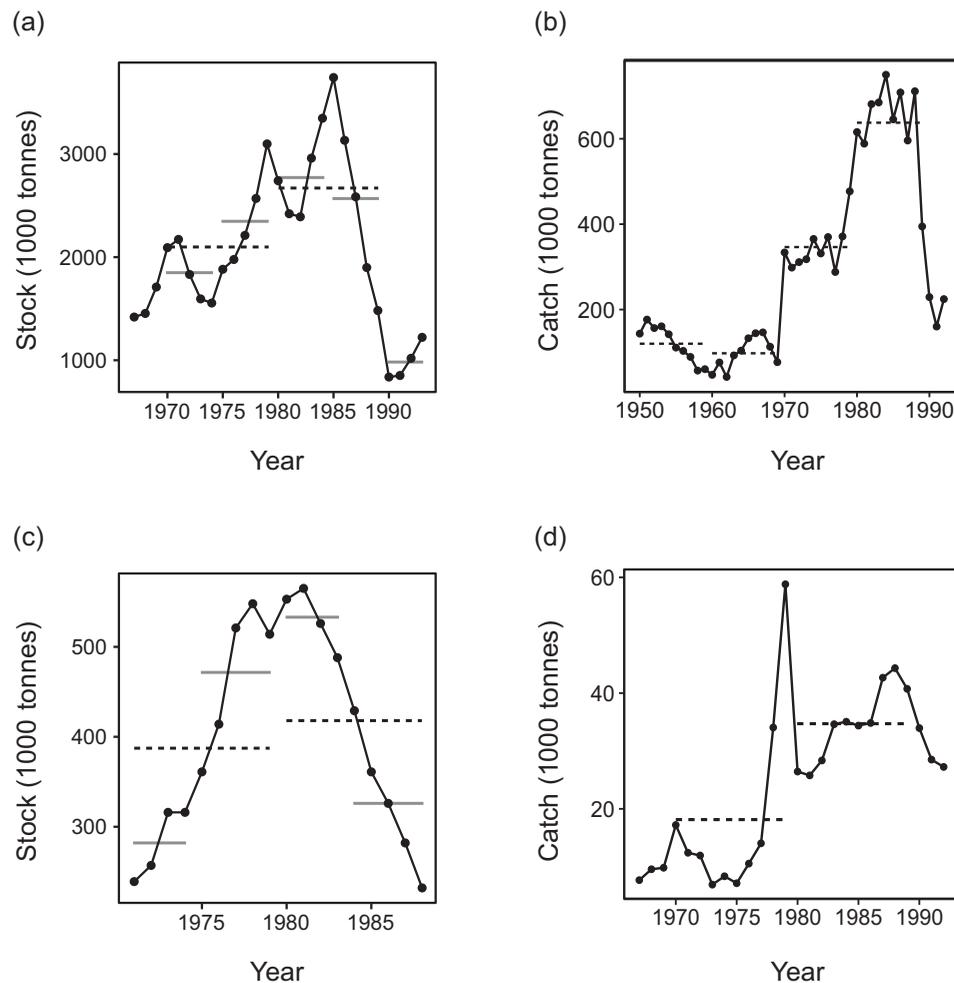


Fig. 3. Stock and catch time series of small and medium pelagic fish (**a**, stock; **b**, catch) and demersal fish (**c**, stock; **d**, catch). Stocks and catches are expressed as 1000 tons. Source data are in the Supporting Information, Appendix C (Table C3). Average biomass over periods of 5 yr and 10 yr is visualized with solid gray lines and dotted black lines, respectively. In the case of catches, for the sake of clarity, only average values over periods of 10 yr are shown.

through inorganic nutrients (N, increased flux of nutrients), small and medium pelagic fish (PF, reduced mortality), and demersal fish (DF, reduced mortality). All these perturbations acted so as to increase the rate of change of the target variables. Accordingly, we considered that three positive inputs entered the system. Predictions generated by these inputs were obtained from the table of predictions in Fig. 1b. To compare model outcomes with variations in the biomass trends of the variables, we pooled the effects of the three inputs. Variations in the trends were detected using statistical analysis (Tables 1, 2), whose results are summarized in Table 3 under the header 1960–1979.

Demersal fish (DF)

Although our dataset was far from complete, we observed that after 1970 the stock of this group increased (Fig. 3c): the biomass in the period 1975–1979 was significantly higher than in 1971–1974 ($W=0$, $p=0.010$; Table 2). This

increment is likely to be a consequence of the lack of predatory control on the group. Since DF and PF benefited from this reduced predation, the observed increase in DF stock must be considered as the combined effect of both inputs. The model shows that both these inputs are predicted to increase the level of DF (Table 3 in the period 1960–1979, entries corresponding to the intersections between rows +PF and +DF, and column DF). The positive input on N is expected to decrease DF (Table 3, entry at the intersection between row +N and column DF). Overall, because two inputs against one are in favor of an increase we can reasonably assume (Puccia and Levins 1985) that this component is predicted to increase, in agreement with the observed increase in its biomass during the 1970s (Table 2).

Small and medium pelagic fish (PF)

The stock of small and medium pelagic fish augmented significantly from the period 1970–1974 to 1975–1979

($W = 4$, $p = 0.048$; Table 2—see also Fig. 3a). The positive input to this component is expected to increase its biomass (Table 3, row +PF and column PF). Nevertheless, the positive input on DF is expected to decrease this component (Table 3, row +DF and column PF). Finally, the input on N is predicted to increase PF (Table 3, row +N and column PF). Overall, the predictive scenario corresponds to the observed variation in the stock of PF. These results suggest that nutrient loading must have been decisive to drive the increase in the biomass of PF.

Jellyfish (J)

The biomass of jellyfish increased significantly between late 1960s and early 1970s ($W = 1$, $p = 0.008$; Table 1). In particular, this increase occurred between 1969 and 1971, when the biomass of jellyfish peaked (despite fluctuations, the biomass of jellyfish remained high for all the 1970s; see Fig. 2d). Press perturbations on PF and DF contrast the positive effect that the input on N produces on this variable (Table 3, rows +N, +PF, and +DF, and column J) and there is no match between predictions and observation.

***N. scintillans* (NC)**

The biomass of this component fluctuated widely. Averages taken over periods of 5 yr and 10 yr between 1960 and 1979 (see Fig. 2c and Table 1) did not show any significant variation. The predictive scenario differs from the indication provided by the statistical analysis conducted on the biomass trend for this variable. In fact, the input on PF tends to reduce this component, while the inputs on N and DF positively affect its biomass (Table 3, rows +N, +PF, +DF, and column NC). As in the case of jellyfish, a quantitative assessment would be necessary to ascertain whether the contrasting pathways can yield results that match with the observed trends. In the case of jellyfish, the input on nutrients should overcome that on fish groups whereas in the case of *N. scintillans*, the top-down and bottom-up effects must compensate for each other.

Edible zooplankton (EZ)

The biomass of this group declined during the 1970s (Fig. 2b). Its decrease began in late 1960s and continued for the successive 10 yr. In particular, we observed a significant decrease in zooplankton biomass from the period 1970–1974 to 1975–1979 ($W = 25$, $p = 0.004$; Table 1), to reach the lowest biomass in 1978. The positive input to N is predicted to decrease the level of EZ (Table 3, row +N and column EZ), and so is that on variable PF (Table 3, row +PF and column EZ). A tendency to increase is instead associated to the positive input on DF (Table 3, row +DF and column EZ). The overall prediction for variable EZ is that of a decrease, thus matching with the biomass trend.

Edible phytoplankton (EP)

The biomass of phytoplankton increased during the 1970s (Fig. 2a). Its levels in the period 1970–1974 were lower than

the levels measured in 1975–1979 ($W = 5$, $p = 0.041$; Table 1). The analysis conducted over decadal periods (1960–1969 vs. 1970–1979) also reveals a significant increase for this component ($W = 16$, $p = 0.004$; Table 1). This might confirm that eutrophication began in late 1960s and continued in the following decade, during which phytoplankton biomass increased continuously (Oguz and Gilbert 2007). Model predictions are compatible with these trends. Both inputs on N and PF (Table 3, rows +N and +PF with response on column EP) are predicted to increase the level of phytoplankton whereas no change is expected for this component due to the positive input on DF (Table 3, row +DF and column EP: 0* prediction).

Post-invasion period, with low *M. leidyi* biomass (1980–1989)

A second period characterized by strong changes began in the 1980s when the presence of *M. leidyi* was detected. Its abundance remained low until the end of the decade (Oguz et al. 2008a). Only in 1989, the noticeable increase of this population was reported in the Black Sea (Gucu 2002; Oguz et al. 2008a). The concomitant collapse of small and medium pelagic fish (mainly anchovies) was detected (Oguz et al. 2008a). Since in the first part of the 1980s the presence of *M. leidyi* was negligible, we used the community structure of Fig. 1a to analyze the events that took place in the Black Sea during that period. We compared the changes predicted by the model with the differences in biomass tested over the period 1980–1989. Two main drivers were documented in the literature for this period: an increased mortality for small and medium pelagic fish and a further nutrient enrichment. They correspond to a negative input to PF and a positive input to N, respectively. The section related to the period 1980–1989 in Table 3 summarizes the predictions of loop analysis and compares them with the results of tests applied to time series data.

Small and medium pelagic fish (PF)

The catch of this component increased further between the end of 1970s and early 1980s ($W = 0$, $p = 0.004$; Table 2). This was accompanied by an increased mortality for the group (Daskalov 2011). This input would bring about a reduced biomass for PF (Table 3, row –PF and column PF). The stock trend reveals that no significant variations affected this component between 1980–1984 and 1985–1989 (Table 2 and Fig. 3a). In the period 1980–1985, nutrient enrichment of anthropogenic origin reached its highest levels (Daskalov 2003; Oguz and Gilbert 2007). Also, strong nitrate supply into the surface productive layer occurred; it was caused by the enhanced vertical mixing that was induced by lower winter temperatures (Oguz and Gilbert 2007). This suggests an additional positive input on N. The model predicts that PF would increase (Table 3, row +N and column PF). Increased mortality and higher resource availability might have exerted opposite effects on this group. The observed

lack of variation in the stock may come about from the compensation of these effects.

Demersal fish (DF)

The stock of this group (Fig. 3c) decreased significantly between 1980–1984 and 1985–1988 ($W = 20$, $p = 0.008$; Table 2). This variation is also predicted by the two inputs that were considered as main drivers in the period (Table 3, rows +N and –PF, and column DF). The model thus explains correctly the observed behavior of DF.

***N. scintillans* (NC) and jellyfish (J)**

N. scintillans increased in biomass between the 1970s and the 1980s ($W = 16$, $p = 0.009$; Table 1). This difference is due to the strong increase observed between 1980–1984 and 1985–1988 ($W = 2$, $p = 0.032$; Table 1). Fishing pressure on small and medium pelagic fish and nutrient overload that occurred during the 1980s must have favored the growth of this organism. The predictive framework confirms the role of these two drivers as both inputs are predicted to augment the level of *N. scintillans* (Table 3, rows +N and –PF, and column NC). Discrepancies between model predictions and biomass trends can be observed for jellyfish. This group did not change significantly between early 1980s and late 1980s (Table 1; Fig. 2d), whereas expectations from the model are that both inputs increase jellyfish biomass (Table 3, rows +N and –PF, and column J).

Edible zooplankton (EZ)

This group did not change significantly neither between decades (1970s vs. 1980s) nor within the 1980s (Table 1; Fig. 2b). The two inputs (positive on N and negative on PF) are predicted to change the level of this variable in opposite directions (Table 3, rows +N and –PF, and column EZ); compensation of effects becomes the hypothesis that explains the lack of significant variations in the level of zooplankton biomass.

Edible phytoplankton (EP)

Our dataset indicates that phytoplankton increased most noticeably in the 1970s and its biomass remained high until early 1980s, then it started to decline (Fig. 2a). Table 1 shows that a significant decrease characterized this component in the 1980s: biomass in 1980–1984 was significantly higher than in 1985–1989 ($W = 22$, $p = 0.028$). This contradicts previous evidence of literature that indicated the 1980s as the period of maximum eutrophication, a period in which phytoplankton biomass should have increased markedly (intense eutrophication period; Oguz and Gilbert 2007). Although discrepancies between predictions and observation emerge when all the components of phytoplankton are considered, in the case of EP an increase associated to the positive input to N can be overcompensated for by the negative input on PF (Table 3, rows +N and –PF, and column EP); the possibility that this latter effect predominates over the positive

effect of nutrient addition may explain the observed outcome, a conclusion presented with skepticism.

Post-invasion period, with high *M. leidyi* biomass (1989–1994)

To further investigate the ecosystem response to perturbations in the post-invasion period, we included the comb jelly *M. leidyi* (MN) as an additional variable. We considered the predatory activity of *M. leidyi* as mainly directed to zooplankton (EZ) and fish larvae (LPF) (Gucu 2002; Oguz et al. 2008a,b). In Fig. 4, we present three graphs that reproduce the structure of the community with *M. leidyi*. They essentially add this invader to the community represented in Fig. 1a. Three different scenarios are presented: (1) *M. leidyi* that feeds upon both fish larvae and zooplankton (Fig. 4a); (2) the invader that preys upon zooplankton only (Fig. 4b); (3) the comb jelly that consumes fish larvae only (Fig. 4c). These alternatives envisage extreme “all or nothing” conditions that help assessing the importance of the various interactions in affecting system response to the drivers of change. This approach is necessary because loop analysis does not allow modulating the intensity of interactions, being a qualitative method.

According to the literature, *M. leidyi* markedly increased from 1989 to 1993 (Shiganova 1998; Oguz and Gilbert 2007; Oguz et al. 2008a). Our biomass database does not cover that period except for small and medium pelagic fish. The stock of this group declined in the period 1986–1993 (Fig. 3a; see Oguz and Gilbert 2007; Oguz et al. 2008a; Daskalov 2011) and a significant decrease occurred between 1985–1989 and 1990–1993 ($W = 20$, $p = 0.008$; Table 2). The literature causally connects the outburst of *M. leidyi* and the decline of small and medium pelagic fish (mainly anchovies) identifying overfishing as the main cause for both these phenomena (Prodanov et al. 1997; Gucu 2002; Daskalov 2011). However, climate change and nutrient enrichment have also been documented as active drivers in the period (Shiganova et al. 2001; Oguz et al. 2008a,b). Considering overfishing first, the three graphs of Fig. 4 predict that an increased mortality for small and medium pelagic fish (negative input on variable PF) reduces the level of the component itself. But the response of *M. leidyi* may be different in relation to its feeding habits (Table 4).

***M. leidyi* (MN) feeding on both fish larvae (LPF) and zooplankton (EZ)**

Model 4a predicts no change for the comb jelly population: increased mortality for PF would not affect the biomass level of *M. leidyi*. However, this prediction stems from the compensation between opposite effects that spread via the multiple pathways connecting PF to *M. leidyi*. Models 4b and 4c help clarifying how the preponderance of either feeding behaviors of *M. leidyi* may relate its outburst with overfishing.

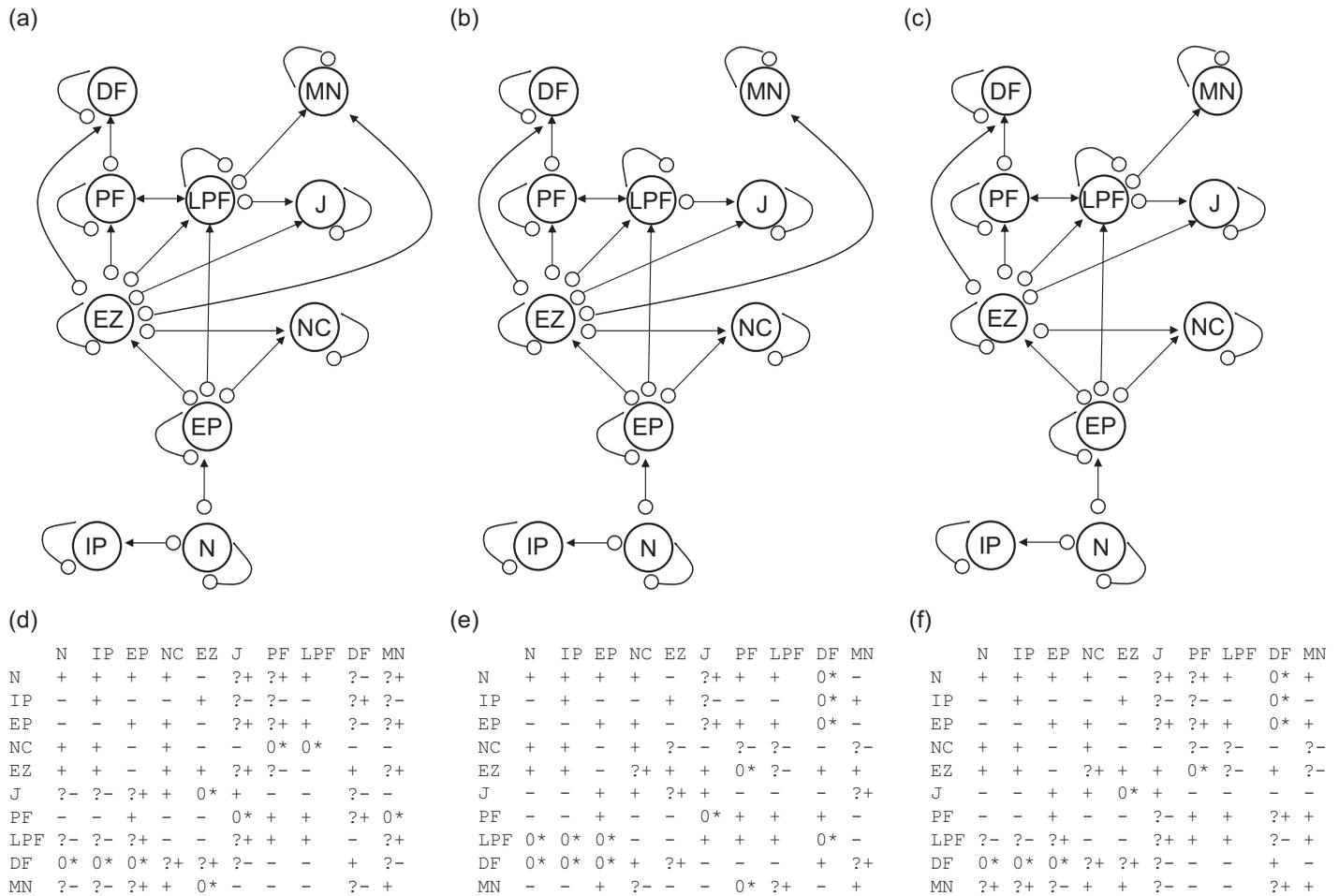


Fig. 4. Signed-digraphs describing the community structure of the post-invasion period and their tables of predictions. Post-invasion refers to the period after the establishment and the outburst of *M. leidy* (1989–1994). Keys for nodes are the same as in Fig. 1 and MN indicates *M. leidy*. The three graphs describe different scenarios for the feeding preferences of *M. leidy*: (a) the invader preys upon both zooplankton and fish larvae; (b) the comb jelly feeds preferentially on zooplankton; (c) the invader consumes mainly fish larvae. The tables of predictions obtained for the three scenarios are visualized below the corresponding graphs (d–f).

***M. leidy* (MN) feeding on zooplankton (EZ) only**

In model 4b, a negative input on PF is expected to increase the biomass of *M. leidy*. This is in agreement with the hypothesis that overfishing might have triggered the bloom of the comb jelly.

***M. leidy* (MN) feeding upon fish larvae (LPF) only**

Model 4c predicts that the biomass of the invader decreases following overfishing of PF.

According to the outcomes of the models in Fig. 4, the outburst of *M. leidy* could have been facilitated by overfishing if *M. leidy* fed preferentially on zooplankton rather than on fish larvae.

Oguz and Gilbert (2007) and Oguz et al. (2008a) proposed that climate played a key role in the bloom of the invader. The literature supports this hypothesis (Shiganova et al. 2001). The abundance of the comb jelly remained negligible

in the 1980s; according to the climate hypothesis *M. leidy* was constrained by low winter temperatures. An abrupt explosion was observed when winter temperatures in late 1980s and early 1990s increased (Oguz and Gilbert 2007; Oguz et al. 2008a). Thus, the climatic conditions of late 1980s must have favored the growth of this species, which began to interfere with small and medium pelagic fish through competition and predation. To simulate the effects of warmer winter temperatures that positively affected the growth rate of *M. leidy*, we assumed a positive input on MN. The models of Fig. 4 all predict an increase in the level of *M. leidy*. In model 4b, where the invader feeds on zooplankton only, the positive input due to warmer temperatures maintains the level of PF unchanged, while that of their larvae is expected to increase. Predictions from model 4c, where the feeding preference of *M. leidy* is on fish larvae, indicate that the positive input on *M. leidy* decreases both small and

Table 4. Predicted changes in the post-invasion period, with high *M. leidyi* biomass (1989–1994). The consequences generated by the three inputs (see the rows: nutrient enrichment, +N; overfishing of small and medium pelagic fish, –PF; climate change, +MN) are summarized. The responses of small and medium pelagic fish (PF) and *M. leidyi* (MN) depend on the architecture of the food web (i.e., as a function of *M. leidyi* feeding habits) and are listed in the columns. Keys for the three feeding habit scenarios in the header (see also Fig. 4): EZ, edible zooplankton; LPF, fish larvae.

	MN feeding on:					
	EZ and LPF		EZ		LPF	
	Consequences on:					
	PF	MN	PF	MN	PF	MN
+N	?+	?+	+	–	?+	+
–PF	–	0*	–	+	–	–
+MN	–	+	0*	+	–	+

medium pelagic fish and their larvae. If *M. leidyi* gets its food mainly from fish larvae, then the hypothesis that climate change favored the comb jelly growth but also contributed to reduce the population of anchovies is supported. This hypothesis offers a mechanism through which the predation of *M. leidyi* over fish larvae might have contributed to further reduce the stock of small and medium pelagic fish (Oguz and Gilbert 2007; Oguz et al. 2008a,b).

The complete picture of the post-invasion period must account for a further nutrient enrichment that took place in the years of *M. leidyi* outburst. Oguz et al. (2008a,b) documented a peak in the nitrate concentration in the chemocline (the layer below the euphotic zone and whose upper part makes nitrate available to the euphotic zone) during late 1980s. These authors included in their simulations the condition of progressively increasing nitrate flux from the subsurface layer due to a varying entrainment rate. They posited that nutrient enrichment and overfishing almost equally contributed to the anchovy-*Mnemiopsis* shift. They also hypothesized that enrichment mechanisms alone could produce the shift, irrespective of the fishing pressure. In fact, nutrient concentrations above a certain threshold initiated a switch in the system which supported *M. leidyi* while causing a decline in the anchovy stock (Oguz et al. 2008b). To investigate the effects of further nutrient enrichment, a positive input to variable N in the models of Fig. 4 was assumed, resulting in different responses. In model 4a, both PF and the comb jelly show a tendency to increase. In model 4b, PF is expected to increase but MN is predicted to decline. Finally, in model 4c, a tendency to augment characterizes PF and an increase is expected for the comb jelly. The effect of nutrient enrichment seems to be mediated by the relative importance of predation vs. competition between the comb

jelly and small and medium pelagic fish. If the competition for the zooplankton prevails (model 4b) the predictions for PF and MN diverge from what Oguz et al. (2008b) found in their simulation exercise. Small and medium pelagic fish are expected to increase and the comb jelly should decline. In model 4c, in which predation over fish larvae prevails in the *M. leidyi* feeding habits, predicted changes can be in agreement with the outcomes of the above cited study: *M. leidyi* is expected to increase, and the level of small and medium pelagic fish tends to increase as well, but with a 25% probability (see Supporting Information, Appendix B—model III in the models for the post-invasion period, with high *M. leidyi* biomass) that the opposite effect occurs. Particular combinations of the link values can make this possible: for example, when the suppressive effects of *N. scintillans* and jellyfish on zooplankton are very strong. These two links in fact form the negative pathways $N \rightarrow EP \rightarrow NC \rightarrow EZ \rightarrow PF$ and $N \rightarrow EP \rightarrow LPF \rightarrow J \rightarrow EZ \rightarrow PF$ that spread the input on N to PF with negative consequences. In particular, the role of *N. scintillans* might have been decisive because in the 1980s this organism attained high abundance. Overall, if *M. leidyi* feeds preferentially on zooplankton, the hypothesis that an increased nutrient availability could have contributed to the outburst of this species is not supported by our model.

Null models

Null models were used to test if the realistic food webs in Figs. 1, 4 generated unique sets of predictions. We compared the predictions made by (realistic) literature-based food webs with those obtained from random networks with equivalent structural properties (i.e., same number of nodes and links as in the realistic food webs). Comparisons were carried out for the predictions generated on the main trophic groups (i.e., EP, EZ, NC, J, PF, and DF) in response to the combination of all inputs specific to each period (e.g., eutrophication and reduced mortality of both fish groups in the pre-invasion phase). In all cases, realistic models significantly deviate from their random counterparts ($p < 0.001$). Significant differences persist even when comparing single inputs, for all realistic food webs studied in this work (see the Table B2 in the Appendix B of Supporting Information). To prove the nonrandom matching between predictions from realistic food webs and biomass changes, we compared the responses of realistic models with those of random models. The comparison was restricted to the responses of the main trophic groups (i.e., EP, EZ, NC, J, PF, and DF) following inputs that occurred in the years 1960–1979 and 1980–1989 (see Table 3). The model in Fig. 1 represents the backbone for all analyses and its performance (i.e., ability to predict real biomass trends) is significantly better than the one of random networks ($p = 0.048$). All other realistic models display nonsignificant deviations from random networks (see the Table B3 in the Appendix B of Supporting Information).

Discussion

Several pieces of the literature converged to the hypothesis that overfishing of top predators ignited a trophic cascade in the Black Sea (Daskalov et al. 2007; Daskalov 2011). What emerges from our investigation is that this mechanism cannot fully explain what occurred in the decade 1970–1980. The overexploitation of top predators created favorable conditions for the growth of small and medium pelagic fish and demersal fish. The decline of top predators was simulated with positive inputs on PF and DF. In this scenario, model predictions become coherent with the biomass trend of small and medium pelagic fish only if nutrient enrichment is also simulated (i.e., positive input on N; Table 3). Whenever the inputs associated to overfishing create a contrast or uncertainty between model predictions and biomass trends (as in the case for jellyfish and edible zooplankton), the contribution of the input on inorganic nutrients goes in the direction of the agreement between model outcomes and observed biomass trends. The interesting conclusion from these results is that nutrient load must have played a decisive role in driving ecosystem dynamics in the pre-invasion period. This finding challenges the dominant role assigned to the trophic cascade associated to the overfishing of top predators, a perspective commonly accepted in the literature (Prodanov et al. 1997; Gucu 2002; Daskalov et al. 2007; Oguz 2007; Daskalov 2011). Another evidence that attenuates the role of the top-down cascade is the inertia that phytoplankton shows to input on DF. Although this outcome requires further corroborating evidence, it is in agreement with previous finding based on experimental research (Micheli 1999): the spreading of effects attenuates through marine pelagic food webs, resulting in a weak coupling between phytoplankton and consumers at the top of the food chain.

Model predictions about *N. scintillans* in the pre-invasion period are inconsistent with its biomass trend which showed no significant variations. None of the models that we tested (Supporting Information, Appendix B) predict changes that match with the biomass trend for this component. This lack of agreement indicates that further refinement of the food web structure might be needed. *N. scintillans* increased in abundance in the period 1980–1989 (Oguz and Velikova 2010). Our analysis of biomass trends confirms this evidence ($W = 2$, $p = 0.032$; Table 1). Oguz and Velikova (2010) hypothesized that nutrient enrichment and the trophic cascade associated with the increased mortality of small and medium pelagics were major drivers for the increased biomass of *N. scintillans*. Moreover, Oguz (2017) pointed out that during the 1980s the competitive advantage of *N. scintillans* in consuming prey might have suppressed zooplankton. The predictions from the model of Fig. 1a show that both inputs increase *N. scintillans* (Table 3, 1980–1989 section). This matches the observed biomass trend and confirms

the hypotheses of these authors. However, the assumption that *N. scintillans* might have played a role in suppressing zooplankton must be framed in the context of the constancy of the level of zooplankton, as shown by the biomass trend of this component (Table 1; Fig. 2b). Our models predict a null variation of zooplankton in the 1980s which can be explained by the concomitant opposite effects of the negative input on PF and the positive input on N. The positive input on nutrients is predicted to increase *N. scintillans* and decrease the zooplankton, so the question of zooplankton suppression by *N. scintillans* through competition needs to be discussed within the predictive framework of the positive input on nutrients. The decline predicted for zooplankton is caused, among others, by the chain of effects that pertains the pathway $N \rightarrow EP \rightarrow NC \rightarrow EZ$, which includes the efficiency at which *N. scintillans* exploits phytoplankton and the direct suppressing effect over zooplankton through predation (this latter mechanism corresponds to an intraguild predation; see Moustaka-Gouni et al. 2016). Thus, the efficiency of exploitation of phytoplankton (the link $EP \rightarrow NC$) and the capability to directly suppress zooplankton (the link $NC \rightarrow EZ$) act synergistically by propagating negative effects on zooplankton following the input on nutrients. The input of nutrients, on the other hand, tends to increase zooplankton via the pathway $N \rightarrow EP \rightarrow EZ$, which includes the efficiency at which this latter component exploits the primary producers. The stronger the capability of *N. scintillans* to exploit phytoplankton, the greater the negative effect carried by the pathway $N \rightarrow EP \rightarrow NC \rightarrow EZ$ which contrasts the positive effect associated to the path $N \rightarrow EP \rightarrow EZ$.

Due to the lack of data during the post-invasion period, model predictions can only be used to discuss hypotheses about the mechanisms responsible for the outburst of *M. leidyi* and the concomitant crash of small and medium pelagic fish (Table 4). According to Prodanov et al. (1997), Gucu (2002), and Daskalov et al. (2007), the shift in dominance from fish to *M. leidyi* could be due to “two major and contrasting hypotheses”: (1) overfishing (Prodanov et al. 1997; Gucu 2002; Daskalov et al. 2007); (2) excessive food competition and predation by *M. leidyi* on fish larvae (Vinogradov et al. 1989; Kideys et al. 2000; Purcell et al. 2001; Shiganova et al. 2001). Climatic conditions could have also favored the outburst of the invader (Shiganova et al. 2001). Oguz et al. (2008a,b) posited that even nutrient enrichment contributed to the shift and that the enrichment alone could have produced the anchovy-gelatinous shift irrespective of fishing pressure (i.e., in case of high levels of food availability for the comb jelly). The graphs in Fig. 4 portray three scenarios associated with the feeding behavior of *M. leidyi* and can help to shape causative hypotheses for the outburst of the invader and the collapse of the pelagic fish. The hypothesis that overfishing caused the decline of small and medium pelagic fish and the resultant outburst of the gelatinous invader holds in the case of *M. leidyi* feeding only (or

preferentially) on zooplankton (competition prevails, model 4b). A negative input on PF in fact reduces this variable and increases the comb jelly (Table 4). However, the role of the other drivers may not be neglected. Nutrient enrichment is predicted to increase the biomass of small and medium pelagic fish, and reduce that of *M. leidyi* when this latter preferentially feeds on zooplankton. In this scenario, fish collapse depends on the fishing pressure because it is only the negative input on PF that decreases this component. Nevertheless, the effect of this input must be strong enough to counteract that of nutrient enrichment, which tends to increase the biomass of small and medium pelagic fish and reduce that of the invader. The predation-competition hypothesis is based on the concomitant action of the more efficient exploitation of zooplankton and of the strong pressure that the comb jelly exerted over fish larvae (Vinogradov et al. 1989; Kideys et al. 2000; Purcell et al. 2001; Shiganova et al. 2001). According to this hypothesis, the outburst of the comb jelly due to favorable climatic conditions could have contributed to the collapse of small and medium pelagic fish (Shiganova et al. 2001). Models 4a and 4c, which incorporate the feeding of the comb jelly upon fish larvae, predict that higher winter temperatures (simulated through the positive input on MN) would reduce the biomass of small and medium pelagic fish (Table 4). This does not occur in model 4b in which the comb jelly only exploits zooplankton. In models 4a and 4c, nutrient enrichment complicates the scenario. The concomitant increase of *M. leidyi* and the collapse of small and medium pelagic fish can occur only if the positive input on MN overcomes the effect of the positive input on N. Moreover, in model 4c, overfishing (negative input on PF) tends to reduce *M. leidyi* and conditions become less favorable for the outburst of this species. According to these results, we suggest that no single event can be responsible for the changes that occurred in the post-invasion period. Multiple drivers are predicted to cause contrasting effects on the same variables and this makes unlikely that a single factor prevailed in driving the dynamics of the Black Sea. The hypothesis that nutrient enrichment alone may have induced the shift in dominance from small and medium pelagic fish to *M. leidyi* (Oguz et al. 2008b) holds only for model 4c, that is when the predation of *M. leidyi* over fish larvae prevails in respect to the feeding pressure on zooplankton. The suppressive effect of jellyfish and *N. scintillans* on zooplankton is crucial for the nutrient-induced anchovy-gelatinous shift and the high abundance that *N. scintillans* attained in late 1980s makes this hypothesis possible. Overall, what emerges from this analysis is that a concurrent effect of the three drivers can be more plausible (Oguz et al. 2008a,b). Likely the three static configurations in Fig. 4 represent different phases in a dynamic picture of the whole ecosystem, a conclusion that we present with circumspection.

Outcomes of this study also offer an interpretation for the catch data. The catch of small and medium pelagic fish

increased from 1960s to 1970s ($W=0$, $p<0.001$; Table 2). The lack of predatory control due to the depletion of top predators (Supporting Information, Appendix B for models studying the consequences of the decline in the biomass of dolphins and large pelagic fish) and nutrient enrichment favored the growth of small and medium pelagic fish, a trend corroborated by the increase of their catch. Fishing pressures shifted from the depleted large pelagic stock to target the increasing small and medium pelagic stock. Catch augmented further because of the continuous fishing pressure that was ignited by the changes in late 1960s and early 1970s. The augmented catch between 1970s and 1980s (see Table 2: 1970–1979 < 1980–1989, $W=1$, $p<0.001$; 1975–1979 < 1980–1984, $W=0$, $p=0.004$) increased the mortality of this group and acted as a press perturbation itself. The press perturbation did not affect the biomass of this group because of the positive contribution of nutrient enrichment. The high pressure on this group continued throughout the 1980s and depleted this component whose stock collapsed between 1985–1989 and 1990–1993 ($W=20$, $p=0.008$; Table 2). The catch data for demersal fish do not allow making the same kind of speculations. However, one can observe that between 1980–1984 and 1985–1989 a significant increase in catch ($W=3$, $p=0.028$; Table 2) corresponded to a reduced stock ($W=20$, $p=0.008$; Table 2). But it is difficult to find a cause and effect explanation because of the structure of the catch data for this component.

Our conclusions were drawn from the simple structural analysis of paths and feedbacks. Nonlinear relationships like those used by Oguz et al. (2008a,b) to represent the response of anchovy stock to nutrient enrichment cannot be considered in the framework of loop analysis. In qualitative modeling, the functional form of the relationships is not specified and nonlinearity remains hidden in the composition of pathways and complementary feedbacks. Loop analysis does not offer interpretation for tipping point dynamics. In the absence of any quantitative analysis, model results help to identify whether the predicted direction of change for the variables can be compatible with the observed phenomena (e.g., outburst of *M. leidyi* and collapse of anchovies) and generate hypotheses about potential causative mechanisms affecting the dynamics of the ecosystem. Our database covers the period from late 1960s to late 1980s. A comparison between model predictions and biomass trends (tested with statistical analysis) was thus possible for the pre-invasion period only (i.e., with reference to *M. leidyi* invasion). This allowed us to validate a basic scheme for the community structure that we used also in the post-invasion period. Scholars who focused on the Black Sea worked with data from different regions (i.e., western coast and interior basin, Oguz and Gilbert 2007; northwestern part, Oguz and Velikova 2010). Other studies targeted the whole basin by combining data from various regions that were presented in different studies (Daskalov 2002; Daskalov et al. 2007).

Difficulties associated to the use of Black Sea data were highlighted by Myroshnychenko et al. (2014). The heterogeneity of the data makes difficult to compare results in a meaningful way. Here, we followed the whole basin approach and combined data from different regions to obtain average values for the biomass of the main pelagic groups.

Conclusions

In this article, we focused on the transformations that occurred in the Black Sea during the period 1960–1990. We used qualitative analysis of the community structure to grasp the main mechanisms responsible for the observed changes. We are aware that the structure of the trophic interactions does not fully explain ecosystem dynamics. Important factors such as physiological responses to changing conditions, complex life cycles, and seasonality play a key role. Our analysis shows how the trophic structure may propagate the effects of changing conditions within the community. It helps to ascertain whether the resulting effects (i.e., predicted changes in the level of variables) are compatible with observed patterns of biomass change, possibly suggesting interpretation in terms of ecological mechanisms.

Other issues deserve to be discussed to frame our analysis in a correct perspective. (1) According to the methodology of loop analysis, we translated varying conditions into inputs to the growth rate of variables. Then, we simulated the response of the variables and compared predictions with variations in their real biomass trends. One difficulty is to establish the timing between the input occurrence and the response of the variables. We considered that intervals of 5 yr and 10 yr were adequate time periods in which to measure the response of the variables, as proposed by the literature (Daskalov 2002; Daskalov et al. 2007; Oguz and Gilbert 2007). As for the timing of changing conditions, the literature provided indications but this information is quite heterogeneous. The exact period in which an input occurred could be defined only with a certain approximation (Gucu 2002; Oguz and Gilbert 2007; Llope et al. 2011). (2) We considered that changing conditions were targeted to specific components. However, it is clear that increasing fishing pressure acts on fish groups only, while climate variations can concurrently affect multiple species in the community. It is acknowledged that higher winter temperatures boosted the growth of *M. leidyi*, but it is not certain whether and how climate affected the growth of other variables such as phytoplankton or zooplankton. Addressing this issue would require the consideration of additional inputs whose nature, however, is not presently known. (3) Identifying signs of regime shifts was not among our aims. A regime shift is defined as the significant change in abundance in relation to a trend. Understanding such patterns is partially precluded with qualitative predictions, although qualitative analysis was already applied to investigate regime shift

phenomena (Marzloff et al. 2009). Here, we used qualitative models to understand how the structure of the interactions can explain variations in the biomass of the variables and to test which drivers and mechanisms could be responsible for the observed changes.

Loop analysis can be used to explore which backbone of trophic interactions reproduces cause-effect mechanisms compatible with observed trends of empirical data. This is because community-level responses can be assigned to changing parameters of target variables (e.g., overfishing that reduces the growth rate of fish) rather than being explained only as a function of variable fluctuations (e.g., environmental stochasticity). Therefore, it is important that changing conditions can be assigned to specific inputs on the variables. This article shows that the locus of control in the ecological community of the Black Sea is diffuse and that the behavior of the system depends on the structure of its interaction network. It highlights how combining modeling analysis with field data offers a unique opportunity to proficiently exploit the potential of mathematical models to shed light on ecosystem dynamics. In particular, we show that predictions obtained with loop analysis under the hypothesis of moving equilibrium are long term predictions. Accordingly, the way they can be validated by field data requires that long term trends are analyzed.

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Conflict of Interest

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