The decline of kilkas, sturgeons and seals in the Caspian Sea: The potential of qualitative loop analysis for the cumulative assessment of multiple drivers of stress

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ABSTRACT

Multiple stressors often act concomitantly on ecosystems but detection of species responses follows the "single species-single driver" strategy, and cumulative impacts are seldom considered. During 1990–2010, multiple perturbations in the Caspian Sea, led to the decline of kilka, sturgeon and Caspian seal populations. Specific causes for their collapse were identified but a cumulative assessment has never been carried out. Using loop analysis, a qualitative modelling technique suitable in poor-data contexts, we show how multiple drivers can be combined to assess their cumulative impact. We confirm that the decline of kilka, sturgeon and Caspian seal populations is compatible with a net effect of the concomitant perturbations. Kilkas collapse was certainly due to the outburst of *M. leidyi* and overfishing. In addition, the excess nutrient might have conspired to reduce these populations. The interplay between concurrent drivers produces trade-offs between opposite effects and ecosystem management must face this challenge.

1. Introduction

In early 2000s the Caspian Sea ecosystem (CSE, henceforth) underwent dramatic changes that culminated in the severe depletion of kilkas (*Clupeonella* spp.), sturgeons (*Acipenser* spp.) and Caspian seals (*Pusa caspica*) (Fazli et al., 2007; UNEP-WCMC, 2010; Harkonen et al., 2012; Tavakoli et al., 2019). The collapse of these populations raised concern because of their economic and conservation values. Scholars explored the causes of such downfall but their effort remained confined in the "single species-single driver" framework (but see Lattuada et al., 2019). Accordingly, recruitment failure observed in anchovy kilka populations in 2001–2004 was attributed to competition and intra-guild predation by the invader *M. leidyi* (Daskalov and Mamedov, 2007); sturgeon decline was associated with poaching (Stone, 2002), and an infection by canine distemper virus was classified as primary cause of mortality for the Caspian seals in 2000–2001 (Kuiken et al., 2006).

These causes occurred in the CSE concomitantly with other drivers, such as unsustainable fish extraction, chemical contamination, stream-flow regulation and eutrophication, (Stolberg et al., 2006; Roohi et al., 2010a; Fazli et al., 2017; Lattuada et al., 2019), but an assessment of their cumulative (net) effect on the decline of kilkas, sturgeons and seals was never carried out. Studies focused on the rapid development of the comb jelly *Mnemiopsis leidyi* led scholars to make the hypothesis that the outbreak of this organism may have played a key role in the decline of those species (Daskalov and Mamedov, 2007; Roohi et al., 2010b). *M. leidyi* is an actively hunting carnivore feeding mainly on zooplankton but also on fish eggs and larvae (Ivanov et al., 2000). Due to its voracious feeding behavior, it might have seriously depleted zooplankton biomass, inducing starvation in planktivorous fish like kilkas (Shiganova and Bulgakova, 2000) and thus leading a cascading collapse of kilka's predators up along the food chain, specifically sturgeons and Caspian seals (Ivanov et al., 2000; Shiganova et al., 2004). Despite this attempt to link species decline to a single cause, a comprehensive understanding of the overall effect of the multiple drivers that occurred in the CSE is still lacking, although this assessment is a pillar of the "ecosystem-based management" approach (Crain et al., 2008; Halpern et al., 2008).

Two are the main objectives of this work: (1) assessing whether the observed decline of kilkas, sturgeons and Caspian seals could be

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compatible with the concomitant action of the multiple, concurrent stress factors that affected the CSE; and (2) making hypotheses about the role that each single source of stress played in the decline of these populations. When a driver targets a population, there is a direct effect on it but the impact may percolate to other species through the connections that form the community web. For example, the comb jelly *M. leidyi* directly affects zooplankton for it feeds on it (Finenko et al., 2006), but it also indirectly influences kilkas (Shiganova et al., 2004) because these latter feed over zooplankton; in turn, the impact may percolate up to the predators of kilkas. To take into account both direct and indirect effects of the drivers of stress in the CSE, we constructed a series of plausible network models, focusing on a parsimonious set of relevant ecological components (species and trophic groups). Next, we identified the press perturbations (Bender et al., 1984; Montoya et al., 2009) that each driver of stress may have induced on specific targets. Finally, through the qualitative Loop Analysis we simulated the response (direction of change in the abundance level) of every and all the model components (Levins, 1974; Puccia and Levins, 1985) to such press perturbations.

Combining these responses, we were able to assess whether the decline of kilkas, sturgeons and Caspian seals could be the net effect of the concurrent drivers of stress. To confirm the plausibility of our results we compared variations predicted for variables other than kilkas, sturgeons and Caspian seals with changes in their levels of abundance in the same period of investigation, as they are documented in the literature.

2. Materials and methods

2.1. Model construction

Central to applying loop analysis is the possibility to diagram the structure of the interactions between system components. First, relevant variables must be identified, and the way they affect each other must be represented in graphical terms according to the loop analysis symbolic language (see "Loop analysis" section). Making these interconnections explicit implies translating an idea about the world into a signed digraph. In ecology, this type of model is generally based on the trophic skeleton, the construction of which requires details about predator-prey relationships. Fendereski et al. (2014) showed that the CSE is highly heterogeneous from this viewpoint. Based on biotic and abiotic features, they partitioned CSE basin into 10 ecoregions. This complexity could not be reproduced here because any modelling effort requires simplifications to achieve an understanding of the system (Levinis, 1966). We then referred to Kosarev and Yablonskaya (1994), who provided a comprehensive synthesis of the Caspian Sea ecology, and used other literature sources to further detail the feeding ecology of the CSE components (Daskalov and Mamedov, 2007; Afraeibandpei et al., 2009; Karpinsky, 2010 and references therein). This information allowed us identifying the parsimonious set of variables and interactions representative of the CSE, with variables defined according to the criterion of trophic quasi-similarity (Supporting information, Appendix A). Species sharing the same prey/resources and predators/consumers were lumped together (tropho-species; Pimm et al., 1991), to lessen the complexity of the web and allow meaningful manipulations without losing realism.

Many fish species in the CSE are of commercial interest, which explains why they have captured the attention of researchers more than other components, a situation that unavoidably biased model construction. The food web we constructed presents in fact a finer partitioning at the level of fish while groups towards the bottom of the trophic hierarchy (i.e., some components of the planktonic food web, and benthic invertebrates) have been condensed in fewer variables. To construct the dietary spectra of fish, we collected information mainly from Kosarev and Yablonskaya (1994). We condensed the feeding strategies of fish in a few categories: (1) zooplankton feeders, (2) species feeding on benthic organisms, (3) predatory fish that exploit mainly other fish species, and (4) omnivores with a mixed diet, mostly

composed of fish and benthic organisms (Supporting information, Table A1). Hence, all alternative models we built display four fish components: (1) zooplankton feeders (K), which are mostly composed of anchovy kilkas (*Clupeonella* spp.); (2) predatory fish (PF), which include Caspian salmon (*Salmo ciscaucasicus*), blackback shad (*Alosa kessleri*), and zander (*Stizostedion lucioperca*); (3) sturgeons (ST), comprising all sturgeon species except for the beluga sturgeon (*Huso huso*), which enters the group of predatory fish; and (4) benthic fish (BF), which include most of the species classified as bony fish (Yazdani et al., 2013). At the top of the food chain stands the Caspian seal (*P. caspica*, CS), a primarily piscivorous endemic species. The model was completed by adding variables at the lower trophic levels of the food web. Primary producers are represented by phytoplankton (A) and phytobenthos (BA) while invertebrate consumers form two trophic groups: zooplankton (Z) and benthic organisms (BO) — molluscs and crustaceans. The models include microbial loop microorganisms – bacteria and protozoa – and detritus from the decomposition of primary producers and excreted material (ML). At the very bottom of the food web, we added the inorganic nutrients (N). From this set of compartments, a suite of signed digraphs has been designed considering alternative feeding preferences of the trophospecies.

2.2. Loop analysis

Loop analysis is a qualitative technique that makes use of signed, directed graphs (i.e., digraphs) to represent and model networks of interacting variables (Levins, 1975; Puccia and Levins, 1985). The signed digraph depicts interactions between variables by only two types of connections: arrows for positive effects (→), and circle-headed links (−●) for negative effects. These links describe the effects of the variables on each other's rate of change. Loop analysis predicts the direction of change in the level (e.g., biomass, number of individuals) of model components (i.e., variables) in response to parameter alterations targeted to one or more of them (i.e., press perturbations; see Bender et al., 1984; Montoya et al., 2009). When a press perturbation increases the rate of change of the target variable, this latter is said to undergo a positive input (Puccia and Levins, 1985). A negative input occurs when the press perturbation reduces the rate of change of the variable. Effects of an input may percolate to the other components, which are connected to the target variable by the interaction network. Their responses can be summarized in a table of predictions that accompanies any model (see Supporting information, Appendix B). These predictions give only the direction of change for the level of the variables: increase (+), decrease (−), or no change (0). Entries in the table of predictions indicate variations expected in the level of column variables in response to positive parameter inputs (i.e., perturbations increasing the rate of change of target variables) affecting any row variable. Predictions on negative inputs can be obtained by simply reversing the sign.

In models with a few components and/or a limited number of connections, expected changes for the variables can be tracked through the digraph anatomy (Bodini, 1998, 2000). However, when the number of variables and connections augments, multiple pathways of interaction emerge and the probability they have opposite effects increases (i.e., some paths exert a positive effect while others have a negative); consequently, predictions may remain ambiguous (Puccia and Levins, 1985). To overcome this problem, we used a routine that performs loop analysis with anumerical simulations (Pereira et al., 2023). The routine exploits the community matrix, that is the numerical counterpart of the graph (in Appendix C below each graph there is its community matrix). The community matrix has three types of coefficients: +1, to design a positive interaction from the row variable to the column variable, which corresponds to an arrow in the graph; −1, to design a negative interaction from the row variable to the column variable, which generates a circle-headed link in the graph; and 0 for no interaction. The simulation operates over the matrix coefficients by generating, for each model, $n \times 1000$ matrices of the same structure (i.s. maintains the interactions). In

each of these matrices, the routine inserts random values extracted within the interval $(0 - 1]$ instead of the $+1$ and -1 coefficients, maintaining the sign. Every simulated matrix yields a table of prediction (see Appendix B for details). Over the $n \times 1000$ tables of predictions obtained, the algorithm returns on a percentage base the direction of change (increase, $+$; decrease, $-$; and no change, 0) for the level of any variable. For example, if more than 50 % of the tables obtained simulating a model yields a positive (negative) sign for a given variable in response to a given press perturbation, then the final table of prediction shows a positive (negative) sign for that prediction. For the cases in which the percentage of matrices yielding a positive (negative) sign is below 50 % but above 20 % the table renders? $+$ (?-), indicating a "tendency of change". When the percentage is below 20 % then the table shows a 0*, indicating a quasi-compensation. That is negative effects and positive effects tend to compensate each other and a null direction of change characterizes the response of the variable to that specific press perturbation.

2.3. Populations' decline, potential drivers and strategy of analysis

Ideally, predictions from models should be tested against long-term field data (Bodini et al., 2018). However, in the case of the CSE, either historical data records pertaining the variables of interest could not be accessed or their scarce availability did not allow organizing a suitable database. This is the reason why we carried out an extensive literature analysis to document observed variations. According to the literature, a strong decline of kilkas, sturgeons and Caspian seals occurred during the period 1990–2010 (Table 1). We then considered this interval as the timeframe for the study. In this section, we summarize the main drivers that were indicated as the causes of the species' decline, and review the most plausible mechanisms that the literature suggested to explain their effect (Lattuada et al., 2019).

Catch and recruit data (Daskalov and Mamedov, 2007; Fazli et al.,

Table 1
Drivers that affected the Caspian Sea in the years 1990–2010. Here a summary of the trophic groups with the drivers influencing them and the type of perturbations generated by the latter. Studies that documented the occurrence of these drivers and discussed their effects on the variables of the CSE are reported.

Target group	Driver	Press type	Reference
Caspian seals	(1) Canine distemper virus	Negative (increased mortality)	Forsyth et al., 1998; Kuiken et al., 2006
	(2) Organochlorine compounds	Negative (increased mortality)	Watanabe et al., 1999; Kajiwara et al., 2002
	(3) Overharvesting	Negative (increased mortality)	Harkonen et al., 2012
Sturgeons	(1) Poaching/ overfishing	Negative (increased mortality)	Pikitch et al., 2005; Mirrasooli et al., 2018
	(2) Destruction of (and reduced access to) spawning grounds	Negative (reduced fecundity)	Ermolin and Svolkinas, 2018; Tavakoli et al., 2019
Kilkas	(1) Overfishing	Negative (increased mortality)	Ivanov et al., 2000; Shiganova and Bulgakova, 2000; Kasymov, 2001; Finenko et al., 2006; Daskalov and Mamedov, 2007
	(2) Alien species (*M. leidyi*)	Negative (increased mortality due to predation on kilkas larvae)	
Zooplankton	(1) Alien species (*M. leidyi*)	Negative (grazing)	Ivanov et al., 2000; Roohi et al., 2010a
Inorganic nutrients	(1) Nutrient load (fertilizers, household wastewaters and *M. leidyi* excretion)	Positive (increase of incoming nutrients flow)	Shiganova et al., 2004; UNEP, 2011

2017) show that kilkas (*Clupeonella* spp., K) decreased steadily from 1999 to 2005. The invader *M. leidyi* was indicated as the major driver responsible for this decline (Kasymov, 2001). The comb jelly was first detected in the CSE in 1995 with a sporadic presence signalled by fishermen, and peaked in 2002 (Bagheri et al., 2014; Roohi et al., 2010a). A stark reduction of kilkas catch occurred in the Caspian Sea during the years that followed the *M. leidyi* detection (Daskalov and Mamedov, 2007). According to literature, the comb jelly competed with kilkas for zooplankton but also exerted a direct pressure on the latter through the consumption of their larvae (Shiganova et al., 2001; Finenko et al., 2006; Daskalov and Mamedov, 2007; Oguz et al., 2008; UNEP, 2011). The outbreak of *M. leidyi* may have caused a negative press perturbation on both kilkas and zooplankton. Although kilkas declined strongly in the post-invasion period, their decrease was already on the way before *M. leidyi* appeared in the CSE (UNEP, 2011). Excessive fish extraction was indicated as mainly responsible for the negative trend that anticipated the effect of the comb jelly. Since 2001, kilkas recruitment was in fact very poor and significant changes in population size, age structure, somatic growth, and condition were reported (Mamedov, 2006). Hence, in the timeframe of the analysis two drivers of stress likely acted directly on kilkas: excessive fishing pressure and predation by the comb jelly. These two sources of mortality are combined in a negative press perturbation over K.

The CSE supports six species of sturgeons (ST). The period 1990–2005 was characterized by a steady decline of all six species (Tavakoli et al., 2019). Overexploitation, poaching and illegal trade as well as habitat destruction (e.g., cut-off access to upper river spawning grounds) and environmental degradation were documented as major causes for sturgeon reduction (Graham and Murphy, 2007; Khodorevskaya et al., 2009; Ivanov et al., 1999). Abundance and biomass of both spawning and total stock collapsed due to the increasing intensity of poaching in sea and rivers foraging areas (Khodorevskaya et al., 2009). Hence, an overall negative press perturbation on sturgeons takes into account the reduced fecundity (i.e., shrinking of spawning grounds) and the increased mortality (overexploitation, environmental degradation).

The Caspian seal (CS) counted over 1 million individuals in the early 20th century and diminished to 100,000 individuals in 2005 (Krylov, 1990; Harkonen et al., 2012; Dmitrieva et al., 2015). Apart from hunting (Harkonen et al., 2012), an unusually high mortality occurred from the spring of 2000 onward due to infection by canine distemper virus (Kennedy et al., 2000; Stone, 2000; Kuiken et al., 2006). Additionally, the high concentration of organochlorine compounds in Caspian seals (Sheikholeslami et al., 2004) increased the susceptibility to viral diseases (Kajiwara et al., 2002). Overall, hunting, chemical contamination and infectious diseases affected negatively the Caspian seal and resulted in the severe decline of its population. These sources of mortality concurred to reduce the growth rate and an overall negative input to CS was considered to take these factors into account.

Nitrogen- and phosphorus-rich compounds from household wastewaters and fertilizers used in agriculture were transported into the Caspian Sea through rivers runoff and drainage systems (Nasrollahzadeh, 2010; Shiganova, 2011). A further input to nutrients (N) came from the massive presence of *M. leidyi*, which increased nutrient recycling through excretion (Shiganova et al., 2004).

According to the literature, the action of the drivers was diffuse and sustained, which justifies why we considered their effects on their target variables as press perturbations (Bender et al., 1984; Giordano and Altafini, 2017). Press perturbations give rise to medium- to long-term effects and loop analysis, in the framework of moving equilibrium (Puccia and Levins, 1985), provides an appropriate apparatus to make predictions about their system-wide consequences. Thus, we simulated the action of these drivers as press perturbations on the specific target variables (Table 1). All but one driver reduced the growth rate of the trophospecies, so they were simulated as negative inputs. The only positive input was the increased inflow of inorganic nutrients. Through

the loop analysis, we predicted the response of the single components as well as of the entire ecosystem to any single driver and then assessed their cumulative effect. Finally, we evaluated whether such predicted effects matched with the observed decline of kilkas, sturgeons and Caspian seals.

3. Results

The trophic network built to describe the ecological community of the CSE is composed of 11 nodes (i.e., trophospecies + inorganic nutrients) and counts 19 predator-prey (resource/consumer) interactions (Fig. 1a). The network was converted into the community matrix (Fig. 1c) from which the corresponding signed digraph was obtained. In the signed digraph, each predator-prey interaction is represented as an arrow-headed (positive) link from the prey/resource to the predator/consumer while the negative impact of the latter is visualized by a circle-headed link pointing towards the prey/resource (Fig. 1b).

When knowledge about interactions is uncertain – because the reports in the literature disagree, information is unavailable, or experts suggest different mechanisms of action – then follow plausible alternatives. Here, we conceived as many as eight alternative graphs; they reflect different hypotheses about the feeding behavior of fish groups. These alternative graphs were obtained imposing variations to the linkage arrangement of the basic scheme (Fig. 1b). Scenarios that account for combinations of interactions (Fig. 1d) were tested for their ability to predict the decline of kilkas, sturgeons and Caspian seals. All graph structures, their tables of predictions and their community matrices are detailed in the Supporting information, Appendix C.

We summarized the outcomes of the simulations in Table 2, in which the type of the input and its target variable appear at the beginning of each row. The predicted directions of change of a variable in response to every single input are ordered along each column. In the last row, one reads the predicted overall directions of change, computed by averaging along every column the percentage values obtained for each single input (Supporting information, Appendix B).

All eight alternative graphs predict a decline in the abundance of CS and ST under the effect of the considered drivers (Table 3). In seven out of eight graphs, also kilkas are expected to decrease; the only exception is the model CSE8 where K is predicted to increase. To assess whether some graphs are more reliable in explaining the dynamics of the CSE, we compared model predictions with the literature that documented changes for variables other than Caspian seals, kilkas and sturgeons in the timeframe of investigation (Table 3).

Roohi et al. (2010b) monitored zooplankton and phytoplankton abundances following *M. leidyi* outburst. Concomitantly with the explosion and persistence of the comb jelly (2001–2006), they found a decline in zooplankton abundance accompanied by an increase of phytoplankton. Nasrollahzadeh et al. (2008) confirmed that phytoplankton abundance in the CSE increased from the years 1996–1998 to 2005. Using remote sensing, Modabberi et al. (2020) found that from 2003 to 2010 the CSE had suffered from an increase of Chl-a. Some models simulated here reproduce these changes; notably, graphs from CSE3 to CSE7 predict the observed changes in the level of A and Z, concurrently with a reduction of K, ST and CS.

Macrobenthos is another variable that changed markedly during the study period, passing from being dominated by crustaceans to the prevalence of annelids and bivalves. The biomass of this group increased in the period 2001–2006 (Roohi et al., 2010a). All models predict an overall effect of the multiple stressors that matches with the observed increase in BO. Roohi et al. (2010b) conjectured that the increase of annelids and bivalves could have raised benthopelagic fish abundance. This hypothesis was partially confirmed by the analysis of landings, which increased for mullet, kutum, carp, bream, and perch in the years 1999–2010 (Fazli et al., 2017; Rabazanov et al., 2019). All models predict concomitant changes for BO and BF that are coherent with trends reported in the literature.

To complete model assessment, we considered the level of inorganic nutrients. Nasrollahzadeh et al. (2008) showed that the long-term mean concentrations of dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) in the southern part of the CSE increased from the period 1994–1999 to the years 2000–2005. Concentrations of DIN and DIP in 2009–2010 resulted more than twofold those recorded during the previous decade (Bagheri et al., 2012). All models but CSE5, CSE7, and CSE8 predicting a nutrient increase. Overall, the graphs that predict correctly the decline of K, ST, and CS and also variations in phytoplankton, zooplankton, macrobenthos, nutrients, and benthic fish, are CSE3, CSE4, and CSE6.

Three out of eight plausible reconstructions of the CSE trophic web (i.e., CSE3, CSE4, and CSE6) make predictions in agreement with the variations reported in the literature regarding eight out of 11 variables (i.e., N, A, Z, BO, K, BF, ST, and CS). Further selection among these three models could not be done because we needed trends for benthic algae (BA) and predatory fish (PF), which were lacking. These models explain variations observed equally well, although the likelihood of mean predictions that render the cumulative effect varies from one model to the other (see the section on "Concurrent inputs" in the Supporting information, Appendix B). When focusing on the contribution of the single stressors to the overall predictions, model CSE4 shows a higher coherence in the results obtained for N, BO, BF, and ST. Model CSE3 performs better for predictions regarding A and Z, whereas model CSE6 shows higher likelihood when the cumulative effect is predicted for K and CS.

4. Discussion

This work illustrates how using loop analysis one can predict the overall effect of multiple perturbations on the abundance of the CSE components, thus overcoming the classical "single species-single driver" approach. Our results show that the decline of kilkas, sturgeons and Caspian seals in the period of investigation, as documented in the literature, is compatible with the combined cumulative action of the multiple drivers that affected the CSE. This action stems from the direct interferences over targeted components and the indirect effects modulated by the structure of the interactions. To assess the possible role that single sources of stress could have played on the decline of the populations, model outcomes suggest some hypotheses.

4.1. Response of kilka, sturgeon and Caspian seal to cumulative stressors

The weak negative coefficient that summarizes the cumulative impact of multiple drivers on kilkas (models CS3, CSE4, CSE6, column K, Table 2) indicates that the various stressors may have had opposite effects. Perturbations on CS and ST (models CSE3, CSE4, CSE6, column K, row ST and Cs, Table 2) counteract the other drivers for they make K increasing. Sturgeon and the Caspian seal are predators of kilkas and their reduced growth rate, due to poaching/overfishing and destruction of spawning habitats (in the case of ST), contamination, overharvesting and infectious diseases (in the case of Cs), reducing their populations (models CS3, CSE4, CSE6, column ST, Cs, row "sign") may have released kilkas from predation.

However, K collapsed in the period of analysis: this means that the bottom-up effects caused by predation by *M. leidyi* on zooplankton and the negative input on K itself due to overfishing and larvae consumption by *M. leidyi* (models CS3, CSE4, CSE6, column K, rows Z and K), must have prevailed over the drivers acting on CS and ST and the net effect was the decline of kilkas. In model CSE4 and CSE6 also nutrient enrichment contributed to kilkas' decline (models CSE4, CSE6, column K, row N), a cause that never was emphasized in the literature and that we present here as a hypothesis for further investigations. This outcome confirms previous conclusions drawn by two of the authors, who discussed the relevance of nutrient enrichment to explain the collapse of anchovy populations in the Black Sea (Bodini et al., 2018). However, in the Black Sea the overfishing of anchovies and nutrient enrichment had
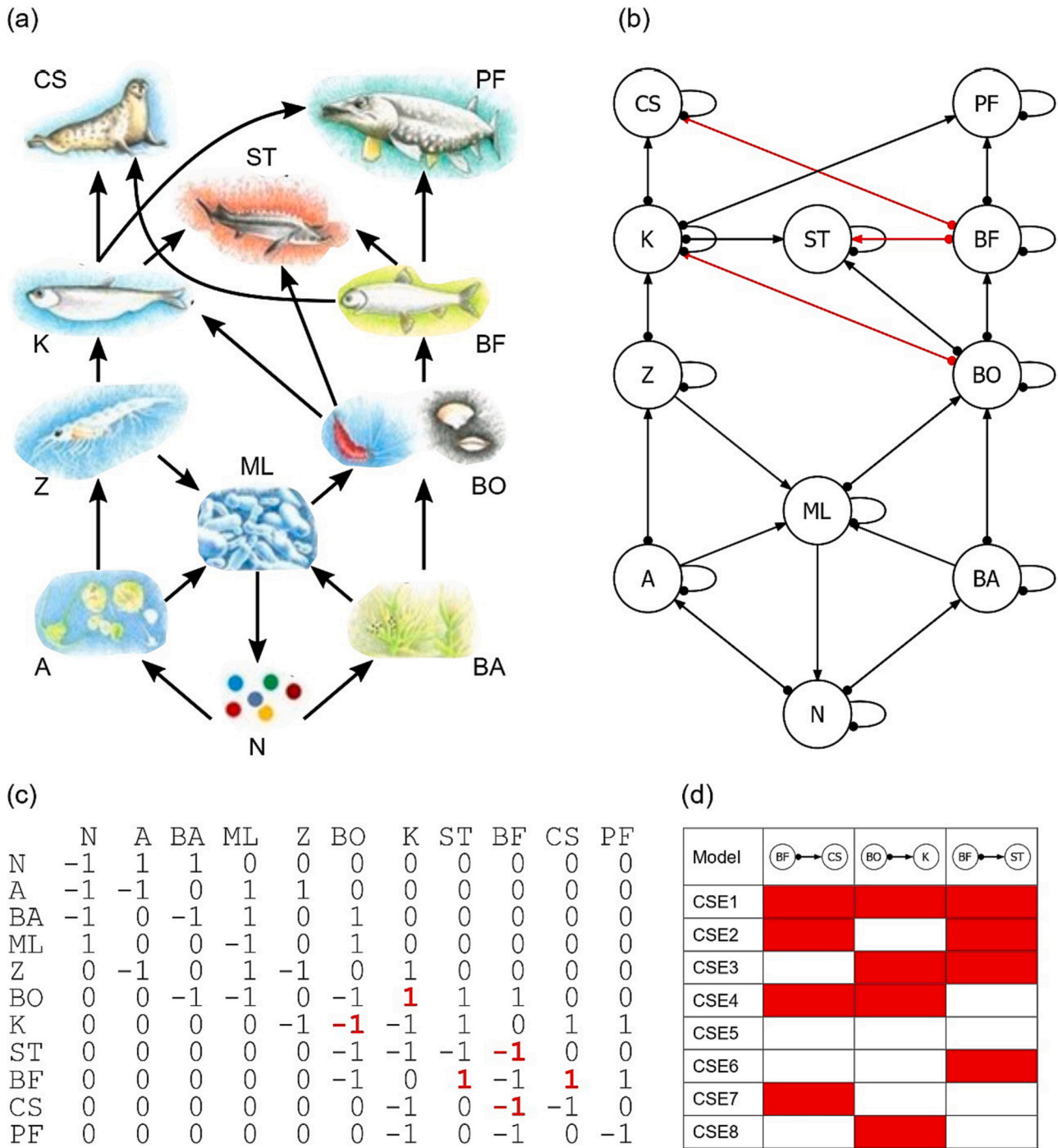
(a)

(b)

(c)

	N	A	BA	ML	Z	BO	K	ST	BF	CS	PF
N	-1	1	1	0	0	0	0	0	0	0	0
A	-1	-1	0	1	1	0	0	0	0	0	0
BA	-1	0	-1	1	0	1	0	0	0	0	0
ML	1	0	0	-1	0	1	0	0	0	0	0
Z	0	-1	0	1	-1	0	1	0	0	0	0
BO	0	0	-1	-1	0	-1	1	1	1	0	0
K	0	0	0	0	-1	-1	-1	1	0	1	1
ST	0	0	0	0	0	-1	-1	-1	-1	0	0
BF	0	0	0	0	0	-1	0	1	-1	1	1
CS	0	0	0	0	0	0	-1	0	-1	-1	0
PF	0	0	0	0	0	0	-1	0	-1	0	-1

(d)

Model	BF ●→ CS	BO ●→ K	BF ●→ ST
CSE1	red	red	red
CSE2	red		red
CSE3		red	red
CSE4	red	red	
CSE5			
CSE6			red
CSE7	red		
CSE8		red	

Fig. 1. Loop analysis model of the Caspian Sea ecosystem. The network depicting trophic interactions among the main variables (a) was converted into a signed digraph (b) and its corresponding community matrix (c). In the digraph, an arrow-headed link indicates a direct positive effect of the variable from which the arrow originates on the growth rate of the component it points to. Such positive effect is shown as a +1 coefficient from the row to the column variable in the community matrix. A negative effect is shown as a circle-headed link in the digraph and a −1 in the community matrix. Absence of any interaction is indicated in the matrix with a 0. Negative self-loops on living components take into account the regulative action of intra-guild interactions (i.e., density dependence); inorganic nutrients are self-damped because of the continuous supply from the outside system (Puccia and Levins, 1985; Bodini, 2000). Presence/absence of interactions involving the variables [CS-BF], [K-BO], and [ST-BF] are signalled in red in the digraph; they determine eight scenarios. Red cells identify, for each model, which of the three interactions are present (d). Digraphs and associated community matrices are in the Supporting information, Appendix C. Compartment codes: N — inorganic nutrients; A — phytoplankton; BA — benthic algae; ML — microbial loop; Z — zooplankton; BO — benthic invertebrates; K — kilkas; BF — benthic fish; PF — predatory fish; ST — sturgeons; and CS — Caspian seals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Cumulative predictions obtained using alternative Caspian Sea ecosystem models. Five press perturbations were considered for each scenario (Table 1), one positive indicating nutrient enrichment (→) and four negative (⊸) on zooplankton (predation by *M. leidyi*), kilkas (overfishing and larvae consumption by *M. leidyi*), sturgeons (poaching/overfishing and spawning habitat destruction), and Caspian seals (canine distemper virus, organochlorine compounds and overharvesting). Cumulative effects are reported for eight plausible models (Fig. 1d) and obtained as the algebraic sum of changes caused by single drivers. Compartment codes: N — inorganic nutrients; A — phytoplankton; BA — benthic algae; ML — microbial loop; Z — zooplankton; BO — benthic invertebrates; K — kilkas; BF — benthic fish; PF — predatory fish; ST — sturgeons; and CS — Caspian seals.

CSE1	N	A	BA	ML	Z	BO	K	BF	ST	PF	CS
→ N	97.768	86.890	61.506	72.664	71.269	91.632	35.844	−54.533	68.759	74.338	−17.992
⊸ Z	−64.854	51.185	−48.954	−35.007	−87.448	−28.870	−74.059	74.616	−34.170	−30.544	−10.739
⊸ K	48.396	−55.649	−7.392	−2.929	78.243	56.485	−91.074	78.522	1.255	3.766	−35.565
⊸ ST	−18.550	7.950	−26.639	−23.291	−23.849	9.623	24.407	43.654	−95.816	72.664	70.432
⊸ CS	7.113	34.449	74.616	71.548	−18.828	−57.880	41.702	44.770	52.859	43.933	−95.258
Mean	13.975	24.965	10.627	16.597	3.877	14.198	−12.636	37.406	−1.423	32.831	−17.824
Sign	+	+	+	+	+	+	−	+	−	+	−

CSE2	N	A	BA	ML	Z	BO	K	BF	ST	PF	CS
→ N	98.345	70.483	62.483	78.207	92.276	95.034	−19.724	−16.138	68.000	67.448	−44.552
⊸ Z	−67.448	60.828	−36.000	−23.310	−86.759	−50.345	−57.241	66.621	−50.069	−43.448	−0.138
⊸ K	64.690	−48.138	37.379	39.862	88.966	32.690	−93.379	85.931	−11.724	−6.207	−31.310
⊸ ST	−10.621	7.586	−24.138	−22.483	−18.621	10.069	15.034	47.034	−95.310	76.828	66.621
⊸ CS	−10.621	39.310	53.931	51.172	−32.138	−55.034	49.241	39.034	53.931	53.655	−95.034
Mean	14.869	26.014	18.731	24.690	8.745	6.483	−21.214	44.496	−7.034	29.655	−20.883
Sign	+	+	+	+	+	+	−	+	−	+	−

CSE3	N	A	BA	ML	Z	BO	K	BF	ST	PF	CS
→ N	98.703	85.214	65.240	72.244	84.695	96.628	22.957	−57.717	68.353	72.503	22.957
⊸ Z	−74.578	56.161	−59.014	−42.931	−91.440	−40.597	−71.984	64.202	−44.488	−45.266	−71.984
⊸ K	46.563	−61.349	−15.953	−10.246	85.214	58.236	−94.034	68.872	0.908	−7.912	−94.034
⊸ ST	−11.543	23.217	2.724	3.502	−29.183	−12.581	38.521	66.018	−95.590	82.620	38.521
⊸ CS	−46.563	61.349	15.953	10.246	−85.214	−58.236	94.034	−68.872	−0.908	7.912	−93.256
Mean	2.516	32.918	1.790	6.563	−7.186	8.690	−2.101	14.501	−14.345	21.971	−39.559
Sign	+	+	+	+	−	+	−	+	−	+	−

CSE4	N	A	BA	ML	Z	BO	K	BF	ST	PF	CS
→ N	98.940	80.132	72.450	86.225	89.404	90.993	−4.371	−5.695	82.252	86.225	−4.636
⊸ Z	−72.450	56.291	−66.887	−49.934	−92.318	−25.298	−58.411	52.583	−70.066	−43.841	−21.325
⊸ K	39.868	−61.325	−20.530	−23.179	74.570	54.172	−92.848	76.689	−60.530	7.815	−40.662
⊸ ST	−51.258	36.159	−65.563	−59.735	−74.834	10.464	81.192	−72.715	−93.113	37.219	30.066
⊸ CS	−0.132	46.755	69.801	66.623	−29.007	−56.821	55.762	63.444	0.132	65.563	−96.291
Mean	2.994	31.602	−2.146	4.000	−6.437	14.702	−3.735	22.861	−28.265	30.596	−26.570
Sign	+	+	−	+	−	+	−	+	−	+	−

CSE5	N	A	BA	ML	Z	BO	K	BF	ST	PF	CS
→ N	100.000	68.267	76.000	84.533	100.000	97.067	−46.667	14.933	79.733	91.200	−46.667
⊸ Z	−76.800	64.800	−67.200	−39.467	−94.133	−43.200	−42.133	32.533	−74.400	−64.000	−42.133
⊸ K	55.733	−66.133	−6.133	−9.333	81.867	61.333	−96.000	78.400	−73.333	−28.267	−96.000
⊸ ST	−40.800	32.533	−90.133	−77.333	−62.933	34.400	73.600	−46.667	−96.800	67.733	73.600
⊸ CS	−55.733	66.133	6.133	9.333	−81.867	−61.333	96.000	−78.400	73.333	28.267	−95.467
Mean	−3.520	33.120	−16.267	−6.453	−11.413	17.653	−3.040	0.160	−18.293	18.987	−41.333
Sign	−	+	−	−	−	+	−	+	−	+	−

CSE6	N	A	BA	ML	Z	BO	K	BF	ST	PF	CS
→ N	99.472	72.559	60.686	68.602	99.208	98.153	−26.121	−38.522	67.546	69.393	−26.121
⊸ Z	−72.559	61.478	−42.216	−29.288	−93.404	−55.673	−50.396	59.631	−48.285	−52.243	−50.396
⊸ K	60.686	−57.784	33.245	29.288	87.335	36.675	−96.306	81.267	−21.108	−26.385	−96.306
⊸ ST	−16.887	20.580	−3.958	−3.166	−33.773	−9.763	40.633	63.061	−95.778	86.280	40.633
⊸ CS	−60.686	57.784	−33.245	−29.288	−87.335	−36.675	96.306	−81.267	21.108	26.385	−94.723
Mean	2.005	30.923	2.902	7.230	−5.594	6.543	−7.177	16.834	−15.303	20.686	−45.383
Sign	+	+	+	+	−	+	−	+	−	+	−

CSE7	N	A	BA	ML	Z	BO	K	BF	ST	PF	CS
→ N	98.128	56.006	83.775	85.647	98.440	80.967	−80.967	51.950	70.671	43.214	−25.741
⊸ Z	−66.927	58.502	−76.911	−51.014	−90.328	−2.340	2.340	0.468	−78.159	−3.276	2.028

(continued on next page)

Table 2 (*continued*)

CSE7	N	A	BA	ML	Z	BO	K	BF	ST	PF	CS
→K	11.076	−53.822	−65.367	−60.686	41.654	68.487	−68.487	49.454	−80.967	35.101	−23.869
→ST	−40.718	33.853	−85.335	−75.663	−61.310	44.462	74.727	−67.551	−91.576	63.807	33.229
→CS	−8.892	47.894	60.062	56.006	−34.477	−59.438	59.438	65.679	14.821	65.055	−95.944
Mean	−1.467	28.487	−16.755	−9.142	−9.204	26.428	−2.590	20.000	−33.042	40.780	−22.059
Sign	−	+	−	−	−	+	−	+	−	+	−

CSE8	N	A	BA	ML	Z	BO	K	BF	ST	PF	CS
→ N	99.737	80.237	72.596	83.399	95.257	95.257	−7.510	−1.186	91.304	96.047	−7.510
→Z	−74.177	51.515	−61.792	−45.982	−93.939	−34.124	−53.096	32.543	−70.224	−57.312	−53.096
→K	41.238	−60.211	−39.657	−32.806	75.231	67.062	−95.257	73.386	−54.941	−6.456	−95.257
→ST	−49.671	28.854	−64.954	−58.366	−75.758	12.516	84.190	−57.049	−98.946	55.731	84.190
→CS	−41.238	60.211	39.657	32.806	−75.231	−67.062	95.257	−73.386	54.941	6.456	−96.047
Mean	−4.822	32.121	−10.830	−4.190	−14.888	14.730	4.717	−5.138	−15.573	18.893	−33.544
Sign	−	+	−	−	−	+	+	−	−	+	−

Table 3

Changes documented for variables of the CSE in the period 1990–2010. Here we summarize literature sources consulted, trends reported, and models that correctly predict such changes under the combined pressure of all five drivers.

Target group	Observed changes in the period 1990–2010	Reference	Models predicting the observed changes
Caspian seals (CS)	Decrease	Kennedy et al., 2000; Stone, 2000; Sheikholeslami et al., 2004; Kuiken et al., 2006; Harkonen et al., 2012; Dmitrieva et al., 2013, 2015	All models
Sturgeons (ST)	Decrease	Graham and Murphy, 2007; Khodorevskaya et al., 2009; IUCN, 2010; Mirrasooli et al., 2018; Pikitch et al., 2005; Ermolin and Svolkinas, 2018; Tavakoli et al., 2019	All models
Kilkas (K)	Decrease	Finenko et al., 2006; Daskalov and Mamedov, 2007; Fazli et al., 2017	All models but CSE8
Benthic fish (BF)	Increase	Fazli et al., 2017; Rabazanov et al., 2019	All models but CSE8
Benthic invertebrates (BO)	Increase	Roohi et al., 2010a	All models
Zooplankton (Z)	Decrease	Roohi et al., 2010b	CSE3, CSE4, CSE5, CSE6, CSE7, CSE8
Phytoplankton (A)	Increase	Nasrollahzadeh et al., 2008; Roohi et al., 2010a; Modabberi et al., 2020	All models
Inorganic nutrients (N)	Increase	UNEP, 2011; Shiganova et al., 2004; Nasrollahzadeh et al., 2008; Bagheri et al., 2012	CSE1, CSE2, CSE3, CSE4, CSE6

antagonistic effects (Bodini et al., 2018) while in the Caspian Sea nutrient excess and kilka over-exploitation act synergistically. In the Black Sea, nutrient enrichment delayed net negative effects of excess harvest, whereas in the Caspian Sea it magnified its consequences. In model CSE3, on the contrary, the input on N tend to increase K.

The different response of K to nutrient enrichment is clearly due to the different structure envisaged in the three graphs. To ascertain the relative role of the alternative configurations all models can be examined. Only two of them (CSE1 and CSE3) indicate that nutrient enrichment brings about a higher level of K (models CSE1, CSE3, column K, row N, Table 2). CSE1 (Fig. 1d) includes all the three predator/prey

interactions ([BF-CS], [BO-K], [BF-ST]), but removing [BO-K] (CSE2) the response of K turns into a negative one. On the other hand, when [BO-K] is the only interaction (model CSE8, Fig. 1d) the response of K remains negative. Thus one can conclude that nutrient enrichment has a positive effect on K when both [BO-K] and [BF-ST] are present in the food web.

Catch data for the CSE indicated that kilkas strongly declined in the period of analysis (UNEP, 2011; Fazli et al., 2017). It is however impossible using loop analysis to assess the response intensity: one can only predict the direction of change for the level of the variables. A low coefficient in Table 2 is not a proxy for the intensity of the net effect of the drivers; it only signals the net direction of change that prevailed in the simulation, after averaging the sign percentages associated to the concurrent inputs (models CSE3, CSE4, CSE6, column K, rows "mean" and "sign", Table 2). Accordingly, a correspondence between the intensity of the observed effects (i.e., reduced catch) and the magnitude of the effect predicted cannot be ascertained. The outcomes presented in Table 2 match with the literature in showing that the impact of *M. leidyi* and the excessive extraction of kilkas must have played a primary role in the decline of this latter component (i.e., K; see Daskalov and Mamedov, 2007; Roohi et al., 2010b), a conclusion that model CSE3 emphasizes as nutrient enrichment in this model does not contribute to kilka decline. The comb jelly *M. leidyi* together with overfishing must have prevailed over the benefit induced by the release of top-down control exerted by Caspian seals and sturgeons.

If the collapse of kilkas emerges from a trade-off between opposite effects of multiple drivers, in the case of Caspian seals such trade-off seems less pronounced. In two models out of the three (CSE4, CSE6), all inputs but that on sturgeons seem to have conspired to reduce the seal population (model CSE4, column CS, Table 2). This result corroborates what Ivanov et al. (2001) posited about the role of *M. leidyi* in the collapse of the Caspian seal, already under stress because of other pressures (i.e., the high levels of organochlorine pesticide residues and viral infections). Still, model CSE3 behaves differently and, in particular, nutrient enrichment tends to increase Cs.

Press perturbations on sturgeons and zooplankton are predicted to reduce sturgeons (CSE3, CSE4, CSE6, column ST, rows Z and ST, Table 2). A negative effect is also associated to the input on kilkas (CSE4, CSE6, column ST, row K, Table 2) but not in CSE3, in which the likelihood of the effect on ST of the input on K is positive but extremely low (0.908). On the other hand, the increased nutrient load would be beneficial for sturgeons in all the three configurations (CSE3, CSE4, CSE6, column ST, row N, Table 2). The positive press perturbation over inorganic nutrients, however, may not have been decisive to avoid the collapse of sturgeons.

4.2. Dynamics of the planktonic food web

Daskalov and Mamedov (2007) documented a reduced level of zooplankton as it was the direct consequence of *M. leidyi* feeding behavior. Models presented here confirm that the increased mortality of zooplankton due to the feeding by the comb jelly would decrease Z (models CSE3, CSE4, CSE6, column Z, row Z, Table 2). However, the voracious behavior of *M. leidyi* is targeted also on kilkas eggs and larvae, and because of this predatory behavior the level of Z is expected to increase (models CSE3, CSE4, CSE6, column Z, row K, Table 2). In addition, the excess of nutrients also increases the level of zooplankton (models CSE3, CSE4, CSE6 column Z, row N, Table 2). These models thus suggest a trade-off between the effect of predation by *M. leidyi* and the increased nutrient enrichment. The combined action of the negative inputs on sturgeons and Caspian seals (models CSE3, CSE4, CSE6, column Z, rows ST and CS, Table 2) must have contributed to the decline of zooplanktonic populations.

Modabberi et al. (2020) using satellite Chl-a concentration data could detect an increase in the abundance of phytoplankton during the years 2003–2010. This evidence is confirmed by our models which reconstruct this dynamic as the combined effects of all the inputs except for the negative press on kilkas (models CSE3, CSE4, CSE6, column A, Table 2). Because K includes the main planktivore populations, according to the cascade trophic interaction model (Carpenter et al., 1985) the negative press on K would increase Z and decrease A and these effects can be visualized in all the three models (models CSE3, CSE4, CSE6, columns A, Z, row K, Table 2). Nevertheless, the concomitant inputs confound the effect of the linear direct trophic cascade.

4.3. Dynamics of the benthic community

The cumulative effect of the drivers on benthic fish is predicted to be positive (model CSE3, CSE4, CSE4, column BF, row "sign", Table 2). Three out of five press perturbations augment BF but target groups of these inputs vary between the models. In CSE3 and CSE6 it is the inputs on Z, K, ST, which make BF increasing, whereas nutrient enrichment and the press over CS tend to reduce BF. In model CSE4, the press over K and Z still contribute to increase BF but now the role of ST and CS changes: the input targeted to the former makes BF decreasing and that on the latter has instead a beneficial effect.

Roohi et al. (2010a) analyzed catch data and found that benthic fish species (i.e., kutum and mullet) augmented in the period 1999–2006. These authors causally linked this increase to the higher abundance of benthic organisms (i.e., anellids and bivalves; bottom-up cascade effect; Roohi et al., 2010a, 2010b), which they associated to the outburst of *M. leidyi*. The models predict that the negative inputs on Z and K, which take into account the effect of the comb jelly, tend to increase BF in the three models (models CSE3, CSE4, CSE6, column BO, rows Z, K, Table 2) thus confirming the hypothesis of those authors. However, the causal interpretation of the concomitant rise of BO and BF proposed by Roohi et al. (2010a) assumes that the prey (i.e., benthic organisms) is the cause and the predator (i.e., benthic fish) and thus it superimposes a preconceived model to the observation. The search for causative mechanisms in ecosystems is based on the correlation between abundance levels of populations; that is the search for shifts in the abundance of a population accompanying the change in the abundance of another. Our analysis suggests that both BO and BF increased because of several causes (i.e., the press perturbations) involving complex bottom-up and top-down mechanisms with multiple interaction pathways. It shows that associating observed patterns of change to interactive mechanisms can be a successful exercise if we link correlations, sources of change (i.e., inputs), and the community structure (Levins and Puccia, 1988; Bodini, 2000; Bodini and Clerici, 2016).

4.4. Assessment of cumulative stressors and management interventions

Results presented in this manuscript suggest that the collapse of kilka, sturgeon and Caspian seal populations in the period 1990–2010 may have been the net effect of multiple, co-occurring stress factors, rather than being caused by single proximal causes (i.e. specific drivers on specific targets). Such a net effect implies trade-offs among opposite effects ignited by the various press perturbations. Not all the inputs, in fact, produce similar variations in the level of a given variable. Recognizing trade-offs is important for management (Halpern et al., 2008; Halpern and Fujita, 2013): the same driver can be responsible for both positive and negative effects (e.g., the increased mortality of the Caspian seals reduced this same population but resulted beneficial for kilkas), a dynamic that may be observed also when interventions are conceived for certain goals (Rodriguez et al., 2021).

This issue points directly to the main limitation of the approach presented in this paper, and that concerns the possibility to assess quantitatively the effects of the various impacts. Through quantitative estimates, one would correctly assess the net effects of opposing factors, but such estimates require details that are difficult to obtain (e.g. the intensity of the press perturbations (Novak et al., 2011), the magnitude of species interactions (Schmitz, 1997)). On the other hand, in several environmental-related questions knowing the expected direction of change can provide valuable inmformation to decision-making (Babcock et al., 2016; Bodini et al., 2018).

In this study, we scrutinized the literature to identify the types of press perturbations that the drivers might have exerted over the CSE in the years 1990–2010 (Tables 1 and 3). For instance, poaching, destruction of spawning grounds and excessive fish extraction all concurred to generate negative press perturbations on sturgeons by reducing the growth rate of this variable but ascertaining their relative contribution is not possible. Analogously, apportioning the overall response of species to any single stress factor is not possible here. Quantitative assessments of links, pathways and press perturbations would contribute to this direction.

Understanding cumulative impacts has become a priority for ecosystem management (Halpern and Fujita, 2013). Lattuada et al. (2019) (but see also Fendereski et al., 2014) addressed the question of cumulative pressures on the CSE by providing a spatial summary of the differential distributions of the risk associated to multiple drivers in different ecoregions. These authors, however, did not estimate the effects of the cumulative pressures over the ecological components, because their goal was not to causally link stressors with potential/observed ecological effects.

Various approaches to explore the consequences of multiple stressors on species or ecosystems have been proposed. Halpern et al. (2008) examined the cumulative impacts of concomitant stressors on marine ecosystems while Maxwell et al. (2013) extended that approach to investigate the cumulative impacts of 24 spatial-explicit anthropogenic stressors and quantified their consequences on individual marine predators. These studies predicted cumulative effects employing impact scores built according to the spatial co-occurrence of stressors (type and intensity) and species (or ecosystems), and that included (i.e., weighted by) species (or ecosystem) vulnerability to human stressors. Vulnerability was estimated using experts' judgment. This assessment determined where important species, habitats and high-risk areas coincided in spatial context, indicating where protection efforts and threats mitigation would be mostly needed. Still, these works did not causally link drivers and species responses in the way we have done it here.

5. Conclusions

Cumulative impacts are the rule rather than the exception in ecosystems. During the period 1990–2010 the CSE was affected by several concomitant stress factors. In the same period kilka, sturgeon and Caspian seal populations collapsed and to find possible causes for their

decline, scholars considered single direct stress factors in isolation, neglecting their interplay. In this work we explored the possibility that the downfall of those population could be the net effects of the multiple drivers that hit the CSE. To this end we constructed the structure of the interactions that make the food web of the CSE and considered the perturbing factors documented in the literature as press perturbations on the indicated target species. Exploiting the algorithm of loop analysis, we predicted the net effect of the various stressors on every species. Predictions obtained from the models reveal that the combined effect of the multiple drivers are compatible with the observed collapse of kilkas, sturgeons and Caspian seals. Furthermore, the responses predicted for other components (i.e., phytoplankton, zooplankton, benthic organisms, and benthic fish) are coherent with the variations that these components exhibited following the same drivers of stress.

Net effects emerged mostly as trade-offs because concomitant press perturbations may affect the same component in opposite ways due to the multiple pathways that carry the impacts. The management of cumulative impacts will become more complex in the near future under the increasing effect of global change because of the uncertainty associated with new and unknown events, and the rapidly changing conditions for which quantitative data are hard to collect. In this new scenario, qualitative models can be helpful. They have the necessary adaptability to be used in changing contexts: when in doubt about critical linkages and dynamic features, alternative models can be developed quickly to find out which difference matters and to reach robust conclusions (Scotti et al., 2020). Loop analysis can be applied to identify synergies/antagonistic effects between stress factors and to cluster together variables according to similarities in their response to disturbance. It is ideal for the integrated modelling of socioecological systems, with the inclusion of economic and governmental variables (Niquil et al., 2021), thus being suitable to develop adaptive management strategies.

CRediT authorship contribution statement

Antonio Bodini: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Daniel Pereira:** Formal analysis, Investigation. **Marco Scotti:** Formal analysis, Investigation, Methodology, Writing – review & editing.

Declaration of competing interest

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

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2024.116091.

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