

Contribution to the Theme Section 'Drivers of dynamics of small pelagic fish resources: biology, management and human factors'

# Who is to blame? Plausible pressures on small pelagic fish population changes in the northwestern Mediterranean Sea

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**ABSTRACT:** Important changes have been observed in recent decades in small pelagic fish (SPF) populations of the NW Mediterranean Sea: declines in biomass and landings of European anchovy and sardine, and a geographical expansion of round sardinella. These changes have been linked to environmental factors directly influencing annual recruitment and growth. The role of climate change in affecting the composition of plankton has also been suggested to explain declines in SPF, while other causes could be the recovery of predators, competition with other pelagic organisms that prey on early life phases of SPF (i.e. gelatinous zooplankton), interspecific competition for food, or impacts from fisheries harvest. To test the role of these potential pressures, we developed qualitative mathematical models of a NW Mediterranean pelagic food web. We used analyses of sign directed graphs and Bayesian belief networks to compare alternative hypotheses about how SPF species may have responded to combinations of different pressures. Data documenting changes in SPF populations were used to test predicted directions of change from signed digraph models. An increase in sea surface temperature (SST) that had either a positive impact on round sardinella or on gelatinous zooplankton abundance was the pressure that alone provided the most plausible insights into observed changes. A combination of various pressures, including an increase in SST, an increase of exploitation and changes to zooplankton also delivered results matching current observations. Predators of SPF were identified as the most informative monitoring variable to discern between likely causes of perturbations to populations of SPF.

**KEY WORDS:** Small pelagic fish · Population change · Food web · Qualitative model · Pressures · Cumulative impacts · Mediterranean Sea

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## 1 INTRODUCTION

Biomass and energy transfer in marine ecosystems from lower (e.g. plankton) to higher (e.g. predators) trophic levels is often modulated by organisms that occur at intermediate trophic levels, such as species of small pelagic fish (SPF) (Cury et al. 2000, Cury et al. 2011, Pikitch et al. 2013). SPF in the Mediterranean Sea are dominant in terms of biomass and are significant components of marine food webs (Palomera et al. 2007, Coll et al. 2008, Van Beveren et al. 2016a). For example, they are a key prey of important demersal and pelagic predators, such as European hake *Merluccius merluccius* (Mellon-Duval et al. 2017), tunas (Navarro et al. 2017), cetaceans (Gómez-Campos et al. 2011) and pelagic seabirds (Navarro et al. 2009). They are involved in essential processes to enhance primary productivity (Tudela & Palomera 1999) and are important in terms of fishery landings (Palomera et al. 2007, Van Beveren et al. 2016a).

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SPF have short life spans, are sensitive to environmental fluctuations and are greatly impacted by climate variation (Cury & Roy 1989, Palomera et al. 2007). Some stocks of SPF are highly exploited or overexploited (Mullon et al. 2009, Pikitch et al. 2013, STECF 2016a). Due to the key role they play in marine ecosystems, changes in SPF populations can impact ecosystem dynamics across entire marine food webs, which can have significant consequences for commercial catch and profit (Cury et al. 2000, Pikitch et al. 2013). Taking into account that marine pelagic fisheries account for 26% of the world's fish and shellfish protein consumption (Tacon & Metian 2009), and that exploitation of SPF stocks is increasing (FAO 2016b), there is an urgent need to understand the ecological and socioeconomic consequences of how SPF will respond to the combined impact of human and environmental pressures.

In general, declines of SPF populations have been observed in the Mediterranean Sea, in parallel with an increase in fishing effort and a decline in primary productivity (Piroddi et al. 2017). Specifically, in recent decades, important changes have been observed in populations of SPF in the NW Mediterranean Sea: a decline in biomass and landings of European anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus*, and an observed spatial expansion of round sardinella *Sardinella aurita* (Sabatés et al. 2006, 2009, Palomera et al. 2007, Van Beveren et al. 2016a).

Although several hypotheses have been formulated to explain changes in SPF, factors that are controlling populations of SPF in the NW Mediterranean Sea are still unclear. Population fluctuations have been linked to environmental changes that can influence annual recruitment, growth and condition of SPF. Several explanatory hypotheses have been formulated (e.g. Palomera et al. 2007, Martín et al. 2008, Van Beveren et al. 2014, Brosset et al. 2017, Saraux et al. 2019), including the impact of higher sea surface temperature (SST) on the distribution of SPF populations that could negatively affect some species, such as sardine, and positively affect others, such as round sardinella (Sabatés et al. 2006, Maynou et al. 2014).

The role of climate change in affecting the composition of plankton has also been suggested to explain observed SPF population changes (Brosset et al. 2015, 2016, Saraux et al. 2019). Other potential causes could be the recent recovery of predators such as Atlantic bluefin tuna (Van Beveren et al. 2017), competition between pelagic organisms that feed on zooplankton and can also prey on early life phases of SPF (e.g. gelatinous zooplankton) (Purcell

et al. 2014, Pascual 2016, Tilves et al. 2016, 2018), interspecific competition for food (e.g. between sardine and the expanding population of round sardinella) (Albo-Puigserver et al. 2017a) and the occurrence of pathogens and disease (Van Beveren et al. 2016b). Historical changes in anchovy and sardine landings have also been attributed to increases in fishing effort and currently high rates of exploitation (Palomera et al. 2007, FAO 2016a, STECF 2016a).

Understanding interspecific interactions in marine food webs and potential impacts of pressures is challenging, and precise quantitative measurements of these effects can be difficult to obtain (Stergiou & Karpouzi 2001). To address this scientific challenge, there is a growing need to develop and use novel methodologies of data integration and modelling that can account for ecological and environmental processes as well as uncertainties in data and knowledge of the system (Christensen et al. 2015, Paravicini et al. 2012). In order to understand the main patterns and trends, it is not always necessary to have precise quantitative measurements, as qualitative analyses of a system may help in predicting its general dynamics (Dambacher et al. 2009, Lassalle et al. 2014). In this context, qualitative mathematical modelling can be used to integrate available knowledge from different disciplines, and also account for complex dynamics driven by feedbacks in ecological systems, which can create counterintuitive results that often confound predictions and effective management. This approach provides a framework to consider alternative hypotheses about the structure and function of ecosystems and produce a general and realistic representation of the causal relationships that drive the system (Levins 1966, 1974). Qualitative mathematical modelling is especially useful when the basic relationships between variables are understood but where precise and detailed data is not available (Dambacher et al. 2009).

In this study, we applied qualitative mathematical modelling to depict a NW Mediterranean pelagic food web based on the available knowledge from the area and assess the likely role of potential pressures on SPF populations during the last 2 decades. We used the methodology of sign directed graphs in combination with an analysis of Bayesian belief networks (BBNs) (Dambacher et al. 2003a,b, Hosack et al. 2008). We considered alternative model structures and looked at the most plausible changes due to different pressures (fisheries, predators, bottom-up causes or temperature) that have been suggested as potential explanations for the decline of sardine *S. pilchardus* and anchovy *E. encrasicolus*, and for the increase of

round sardinella *S. aurita*. The role of pressures to yield consistent results with observations were first investigated individually, and afterwards we considered combinations of multiple pressures (Folt et al. 1999, Crain et al. 2008). Finally, we identified which variables of the pelagic food web models were most information-rich and thus could be monitored in the future to obtain more knowledge about what is happening in the NW Mediterranean pelagic food web to reduce uncertainty from model predictions.

## 2. MATERIALS AND METHODS

### 2.1. Study area

Our study area represents the pelagic marine ecosystem of the NW Mediterranean Sea, with special emphasis on the marine ecosystem of the Ebro River Delta continental shelf in the NW Mediterranean (Fig. 1), from where most of the information included in this study is available (see Table 1). As a consequence of particular oceanographic conditions, such as wind conditions, vertical mixing and river discharges (Salat 1996, Palomera et al. 2007), this area is an important spawning habitat and fishing ground of sardine and anchovy in the Mediterranean Sea (Tugores et al. 2011, Giannoulaki et al. 2013) and has been identified as a priority area for conservation (Coll et al. 2015, Piante & Ody 2015). Important landings of SPF, mainly anchovy and sardine, have been observed in the region since the 1970s, with maximum catch in the early 1990s (Fig. 2). Since then, landings of SPF have declined, and from the mid-2000s, the catch of sardine is lower than that coming from anchovy. While round sardinella is not a primary commercial species, levels of catch have increased in the last few decades, with large fluctuations due to its low commercial value (Fig. 2), highlighting an increase of this species in the NW Mediterranean Sea and a northern expansion of its distribution (Sabatés et al. 2006, 2009). It is important to note that while *Sardina pilchardus* (from hereon referred to as sardine) reproduces in winter, *Sardinella aurita* (from hereon referred to as round sar-

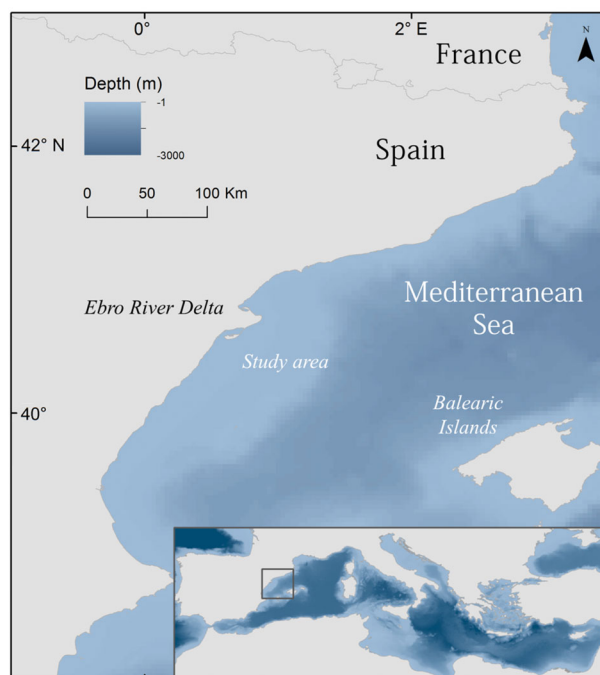


Fig. 1. Study area in the NW Mediterranean Sea (inset: Mediterranean Sea)

dinella) and *Engraulis encrasicolus* (from hereon referred to as anchovy) do this during the summer; therefore, these 3 species are differently affected by environmental conditions (Palomera et al. 2007, Maynou et al. 2014).

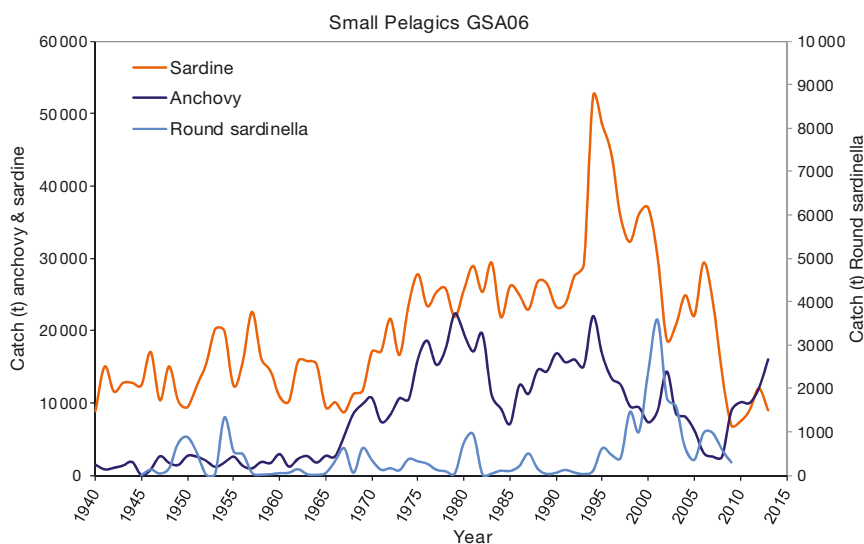


Fig. 2. Anchovy and sardine landings from 1940 to 2014 and round sardinella landings from 1945 to 2009 in the geographical subarea 6 (GSA06; as defined by the General Fisheries Commission for the Mediterranean [GFCM]) region in the Mediterranean Sea. Landings data from 1940 to 1986 are from annual fishing reports of Spanish fishermen organizations. From 1987 onwards, data are from the Spanish Ministry of Agriculture and Fisheries recovered by the Spanish Oceanographic Institute and from Regional Autonomic Fisheries statistics

## 2.2. Sign directed graphs

Qualitative mathematical modelling is based on a general understanding of the relationships that connect ecosystem variables, and can be represented by either equations, matrices or graphs (Puccia & Levins 1985, Dambacher et al. 2009). In this study, we used the modelling methodology of sign directed graphs, or signed digraphs, to assess model stability as an indication of the likelihood of the modelled system to exist and persist in nature, and to predict how the system could possibly respond to an array of possible pressures (Dambacher et al. 2003a,b). Functional groups in signed digraph models and their pressures are depicted as nodes and the signs of the direct effects among them are represented by directed links between the nodes. The graph links contain the signs (+, −, 0) of the direct effects. A signed digraph has an equivalent representation in a community matrix, where each  $a_{ij}$  element represents the direct effect of variable  $j$  on variable  $i$ , and can be used to perform algebraic operations.

From the structure of signed digraphs and the community matrix, the feedback properties of a system can be examined to understand its dynamics and identify processes and interactions that play a key role in maintaining a state of equilibrium. Model stability is assessed to determine whether or not a model is a feasible representation of a real system, such that the model possesses the virtue of persisting despite a shock or perturbation and whether it can exhibit familiar dynamics (Dambacher et al. 2015). The system feedback is calculated by the product of links in the system; while negative feedback (such as a predator–prey relationship) returns the opposite effect to an initial change in a variable and acts to maintain equilibrium, positive feedback can magnify changes in a variable and drives the system away from its previous state through unchecked growth or collapse (Puccia & Levins 1985). Therefore, the qualitative analysis of feedback permits an evaluation of system stability and an understanding of the role of pressures. Analysis of model stability entails an assessment of a system's response to a pulse perturbation, which is an instantaneous and temporary increase or decrease in the abundance or level of 1 or more variables, where stable systems have the ability to return to their former equilibrium levels and unstable systems do not (Dambacher et al. 2003b).

All signed digraph models in this study were obtained using the digraph editor software PowerPlay version 2.0. Stability and perturbation analyses were developed using a Maple software program for

qualitative and symbolic analyses of the community matrix. PowerPlay and the Maple program are available as downloads in Supplement Revisions 1 and 2 from [esapubs.org/archive/ecol/E083/022](http://esapubs.org/archive/ecol/E083/022).

## 2.3. Model formulation of NW Mediterranean pelagic food web

To develop the food web models of the NW Mediterranean pelagic system, we represented a 'relevant subsystem' (Dambacher et al. 2009, 2015) that included the essential dynamics of SPF in the NW Mediterranean Sea, and which tailored the model to the specific problem to be investigated. The goal was to provide a conceptual framework that integrated knowledge of various disciplines, but was constrained to the context of the management problems at hand and the local environment. Therefore, we included those ecological groups that were relevant for sardine, anchovy and round sardinella population dynamics (Palomera et al. 2007, Coll et al. 2008, Albo-Puigserver et al. 2016). The functional groups to depict the food web were chosen based on existing ecological knowledge and literature of the pelagic food web of the NW Mediterranean Sea (see Table 1), with special emphasis on the marine ecosystem of the Ebro River Delta continental shelf in the NW Mediterranean (Fig. 1). We also considered relevant information from adjacent ecosystems when available (such as the Gulf of Lions located in the most northern part of the Mediterranean Sea basin).

Firstly, we developed a core food web model ( $M_0$ ) with 8 variables or nodes (Table 1, Fig. 3).  $M_0$  represented the base configuration of the pelagic food web associated with SPF in the Ebro River Delta (NW Mediterranean) and incorporated the main established knowledge about ecological interactions (Fig. 3). Links between nodes or functional groups and their pressures were based on the available scientific knowledge of the system (Table 1). In Fig. 3, links ending in an arrow represent a positive direct effect, such as births due to consumption of prey, whereas links ending in a filled circle represent negative direct effects, such as mortality due to predation. Self-effects, such as intraspecific resource limitation, are depicted as links that start and end at the same node.  $M_0$  included direct effects between predators and prey, and fisheries. All variables included negative self-effects, thus assuming that they are, to some degree, self-limiting. In our case, this was used to represent intraspecific density-dependent processes. Based on historical evidence from the study

Table 1. Summary of direct effects between variables and factors on the core model. Numbers in the 'From' and 'To' columns and numbers in parentheses in the 'Mechanism' column represent graph nodes in Fig. 3

Sign	Direct effect From	To	Mechanism
+	1;2;3	7	Sardine (1), anchovy (2) and round sardinella (3) are the most important prey for tuna, little tunny and swordfish (7) (Navarro et al. 2017, Van Beveren et al. 2017)
-	1;2;3	5	Sardine (1), anchovy (2) and round sardinella (3) prey on zooplankton (5) (Tudela & Palomera 1997, Plounevez & Champalbert 2000, Lomiri et al. 2008, Costalago et al. 2012, Costalago & Palomera 2014)
-	1	4	Sardine (1) prey also on phytoplankton (4) at adult stages (Lomiri et al. 2008, Costalago & Palomera 2014)
-	3	6	Gelatinous plankton (6) is an important trophic resource for round sardinella (3) (Albo-Puigserver et al. 2017a)
+	4	6	Phytoplankton (4) is preyed on by gelatinous zooplankton (6), but only in high quantities during bloom events. Therefore, gelatinous zooplankton does not have a negative effect on phytoplankton maintained throughout the year (Canepa et al. 2014)
-	6	2;5	Different stages of jellyfish (6) prey on anchovy larvae (2) and zooplankton (5) (Tilves et al. 2016, 2018)
-	8	1;2	Purse-seiners (8) harvest on sardine (1) and anchovy (2) with effort that is independent of amount of catch; thus, no positive links from (1) and (2) back to (8)

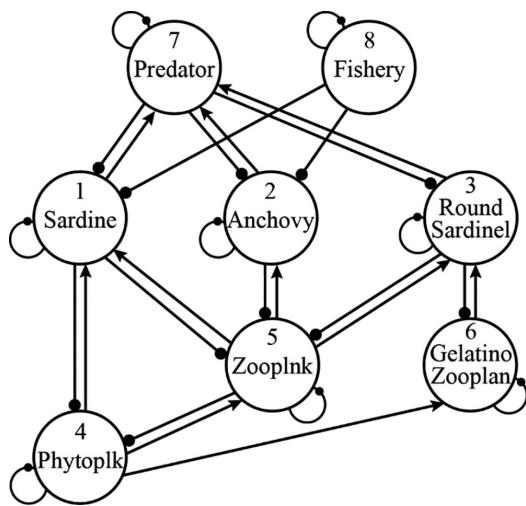


Fig. 3. Signed digraph of the pelagic food web core model  $M_0$  of the NW Mediterranean Sea (Table 1). Positive effects are denoted by links terminating in an arrow, and negative effects by links terminating in a filled circle. 1: sardine, 2: anchovy, 3: round sardinella, 4: phytoplankton, 5: zooplankton, 6: gelatinous zooplankton, 7: predators (tuna), 8: purse-seine fisheries

area (Coll et al. 2008), the role of SPF in the core model was represented as having the role of wasp-waist control (Cury et al. 2000), impacting both on their prey and their predators (e.g. large demersal and pelagic fish, seabirds and marine mammals).

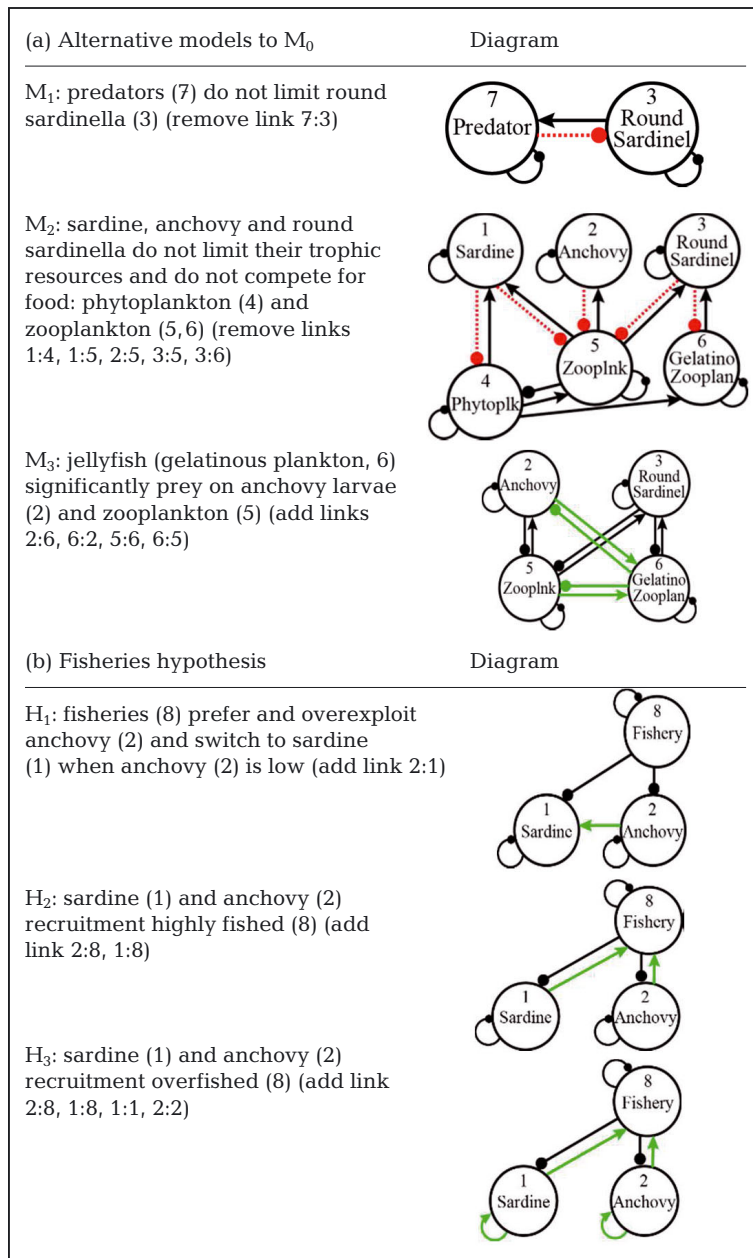
Secondly, to address the uncertainties in some relationships between model variables, we compared alternative model structures to  $M_0$  by building 4 alternative food web models ( $M_1$ ,  $M_2$ ,  $M_3$  and  $M_4$ ;

Table 2a, Fig. 4). These alternative models included relationships that had scarce information or ambiguity in the response, thus alternative links of the core model were proposed: Model  $M_1$  was modified to represent that predators do not limit round sardinella due to its recent expansion (Sabatés et al. 2006, 2009); Model  $M_2$  incorporated the modification of SPF not limiting their trophic resources and therefore not competing for food due to partial difference in their diets (Albo-Puigserver et al. 2016); Model  $M_3$  incorporated significant predation of gelatinous plankton on anchovy larvae and zooplankton, as has been recently described to occur in the study area (Tilves et al. 2016, 2018); and  $M_4$  incorporated all additional links of  $M_1$ ,  $M_2$  and  $M_3$  to the core model  $M_0$ .

Thirdly, 3 hypotheses regarding how fisheries interact with SPF were tested ( $H_1$  to  $H_3$ , Table 2b) (Palomera et al. 2007, SAC-GFCM 2015):  $H_1$ : Overall fishing effort is unresponsive to stock abundance; thus, there is no positive link from fish stocks to fishery, but fisheries preferably target anchovy and switch to sardine when anchovy is low (observed from M. Coll's personal experience interacting with the fishery's operations); here, anchovy abundance effectively suppresses the intensity of fishing effort on sardine, which constitutes a modified interaction (Dambacher & Ramos-Jiliberto 2007) and is represented in the signed digraph by a positive link from anchovy to sardine;  $H_2$ : Sardine and anchovy are both highly fished, such that the level of fishing effort on both stocks increases as a function of combined stock abundance, which is represented by a positive link from both the sardine and anchovy populations back



Table 2. (a) Alternative models to the core model  $M_0$  (Table 1, Fig. 3) showing the structural changes to the core model configuration. (b) Hypotheses regarding how fisheries interact with small pelagic fish. Numbers in parentheses represent graph nodes in Fig. 3. Links deleted from the core model ( $M_0$ ) are in red, those added are in green



to fisheries; and  $H_3$ : Sardine and anchovy recruitment is overfished, which destabilizes the stock's population dynamics and imposes a positive self-effect on sardine and anchovy population (Dambacher et al. 2015). Finally, combinations of  $H_1$  with the 2 other fisheries hypotheses was tested ( $H_1$  &  $H_2$  and  $H_1$  &  $H_3$ ).

## 2.4. Structural stability of food web models

Assessing the potential for a signed digraph model to be stable is important because it indicates whether the model is a feasible representation of a real system that can persist despite everyday disturbances, and also whether such a system could exhibit predictable dynamics. Model stability is based on the system's feedback cycles, both in terms of the balance of positive and negative cycles, and the balance of short versus long feedback cycles (Dambacher et al. 2003b). System feedback is defined at different levels of the system depending on the number of interactions that form a feedback cycle (level 1, or self-effects; level 2 resulting from pairwise interactions such as predator–prey interactions; and higher levels involving any number  $n - 1$  of links with  $n$  variables). There are 2 criteria for stability: (i) feedback at any level of the system is not dominated by positive feedback, and (ii) the system is not dominated by higher-level feedback or cycles with long path lengths. Based on their structural characteristics, signed digraph models can be assessed *a priori* to determine their potential to be stable and if they are prone to failing stability Criterion (i) or (ii) (Dambacher et al. 2003b).

The potential for a signed digraph model to pass or fail Criterion (i) is determined by its maximum weighted feedback,  $wF_n$ , which follows from an accounting of all feedback cycles (positive and negative) at the highest level of the system and calculating the ratio of the net to absolute sums (or prediction weight) (Dambacher et al. 2003b). Values of  $wF_n$  close to  $-1.0$  imply a limited amount of positive feedback and thus a relatively high potential for stability, values of  $wF_n$  close to  $+1.0$  imply a relatively

large amount of positive feedback and an unstable system, while a value of  $wF_n$  near zero indicates a roughly equal chance for the system to be stable or unstable (Dambacher et al. 2003b). When a system is destabilized due to excessive positive feedback, a pulse-type disturbance to the system kicks off exponential growth or decay in 1 or more variables, and

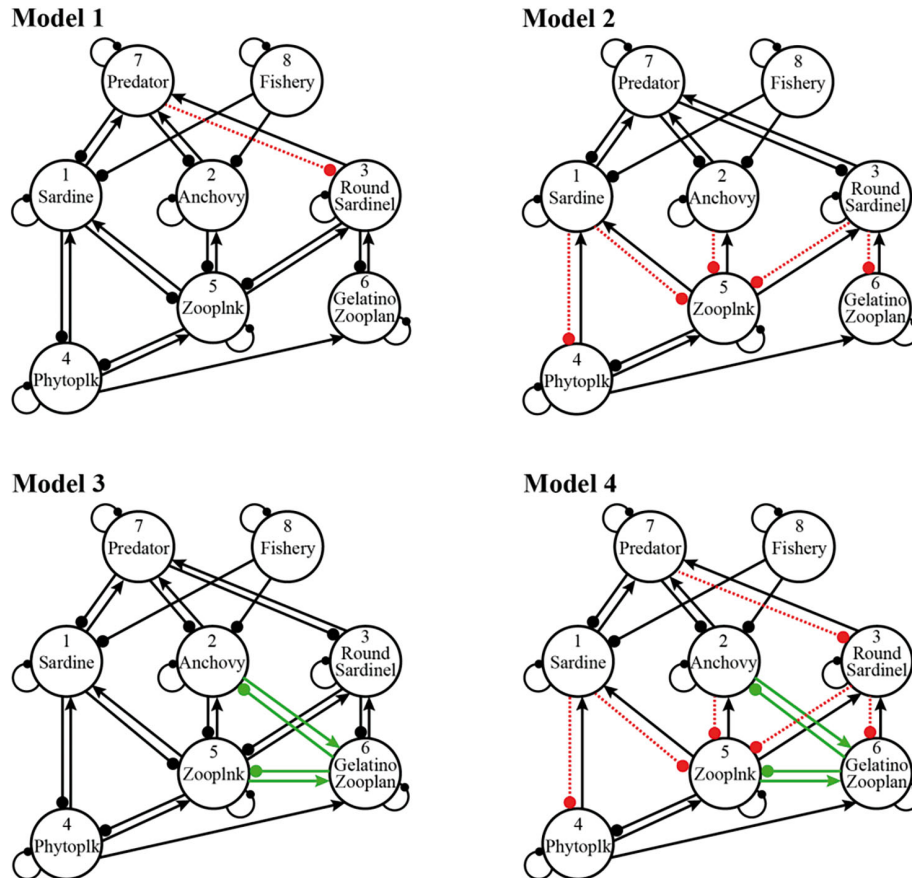


Fig. 4. Signed digraphs of the alternative food web models  $M_1$  to  $M_4$  of the NW Mediterranean Sea (Table 2a). Positive effects are denoted by links terminating in an arrow, and negative effects by links terminating in a filled circle. Node numbers are the same as in Fig. 3. Links deleted from the core model ( $M_0$ ; Fig. 3) are in red, those added are in green

thereafter it is unable to return to the former equilibrium by its own internal dynamics or processes.

Models that fail Criterion (ii) are destabilized by systemic overcompensation, which is due to feedback at higher levels in the system overwhelming feedback at lower levels, leading to undamped oscillations (Dambacher et al. 2003b). The potential for a model to pass or fail stability criterion (ii) is assessed by the relative balance of feedback at higher versus lower levels of the system through a weighted determinant ( $wD$ ). Positive values of  $wD$  imply a high potential for stability, while those close to, or less than, zero imply a low potential for stability. The degree to which a weighted determinant is 'close' to zero is complicated by the fact that values of  $wD$  naturally decrease as the size, or number of variables, in a system increases. Determination of the relative value of a weighted determinant for a given signed digraph model or community matrix is made possible by comparison to a standard 'model c-type system' (i.e. model with the same number of variables constructed as a strain-chain system with predator-prey

interactions between each successive trophic level, Dambacher et al. 2003b). For a given signed digraph model, a value of  $wD$  that is less than that for a corresponding model c-type system indicates that it has a high potential for failing stability Criterion (ii). A useful stability metric can thus be the ratio of a model's value for  $wD$  with respect to that of a model c-type system, with a ratio less (greater) than 1 indicating a high (low) potential for failing Criterion (ii).

Dambacher et al. (2003b) tested the utility of the above 2 stability metrics through quantitative simulations in a random and evenly distributed parameter space. These metrics proved a robust means to assess potential stability of signed digraph models of any size or level of complexity. Here, we apply their results to assess the potential stability of the 5 models ( $M_0$ ,  $M_1$ ,  $M_2$ ,  $M_3$  and  $M_4$ ) and their combinations with the 3 hypotheses ( $H_1$ ,  $H_2$  and  $H_3$ ). Accordingly, we apply a threshold value of  $wF_n \geq 0$  and a  $wD$  ratio to model c < 1 to distinguish model structures with a low potential for stability from those with a moderate to high potential.

## 2.5. Perturbation scenarios

Prior to undertaking an analysis of a system's expected response to a permanent shift in its equilibrium (i.e., a press perturbation), one must first determine if it has the potential to be stable during the shift from the old to the new equilibrium state. Once this condition is established, then predicting the direction of change for the system variables proceeds from an analysis of all the direct and indirect effects formed by the pathways of interaction that lead from the input variable to each response variable. When there are both positive and negative effects influencing the response of a variable, then its prediction is qualitatively ambiguous. To resolve this ambiguity, knowledge of the relative strength of interactions involved in the pathways can be used to determine whether the positive or negative effects will prevail (Puccia & Levins 1985). Alternatively, the relative balance of positive versus negative effects in a response prediction can be used to assign a probability of sign determinacy to response predictions (Dambacher et al. 2015).

Previous work tested the sign determinacy of qualitative response predictions across a wide array of signed digraph models (Dambacher et al. 2003a, Hosack et al. 2008). Numerical simulations were previously used to randomly allocate interaction strengths within signed digraph models and examined the frequency with which qualitative predictions of perturbation response matched the sign of responses in quantitatively specified systems. For example, if there are 4 pathways of interaction leading from an input variable to a response variable, with 2 positive and 2 negative in the sign of their effect, then in numerical simulations that randomly assign interaction strengths, the probability of either a positive or negative shift in the response variable will be 50% either way, with probability of sign determinacy being no better than a coin toss. If, however, there are 3 pathways with a positive effect and 1 with a negative effect, then the frequency of a positive response will exceed 90%, with the probability that the 1 single negative effect could overwhelm the other 3 positive effects being less than 10%.

Hosack et al. (2008) developed the means to incorporate probabilities of sign determinacy for qualitative model predictions within BBNs as conditional probabilities, and we used this method in our study (i.e. Eqs. 5 and 6 of Hosack et al. 2008). These conditional probabilities were derived directly from the sign directed graphs based on the number of positive and negative effects that make up any given

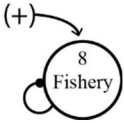
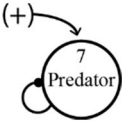
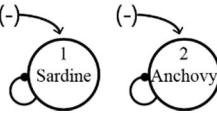
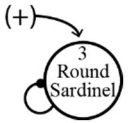
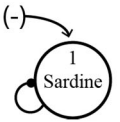

response prediction. Representing qualitative models within a BBN has a number of advantages, including (1) a probabilistic representation of qualitative model predictions, including the means to assess multiple perturbations simultaneously, (2) the ability to validate a qualitative model against observed perturbation responses, (3) diagnosis of most likely source of a perturbation, and (4) a sensitivity analysis that can identify the most informative monitoring variables for diagnosis of perturbation sources or for model validation. The first 3 of these functions (i.e. prediction, validation, diagnosis) are reported in the BBN as probabilities, while the 4th (i.e. sensitivity analysis) is reported as mutual information, which is a measure of the mutual dependence between 2 variables.

In this study, we used only those models with a moderate to high potential for stability to develop BBNs to analyse the outputs of perturbation scenarios. Since there are various possible explanations for the decline of SPF in the study area, we calculated the probability of sign determinacy of each model's predictions when applying different pressures to input variables of the pelagic food web of the NW Mediterranean Sea (Figs. 3 & 4), and selected models with predictions that were most consistent with field observations.

Specifically, we applied 6 pressures scenarios to each model based on existing hypothesis of change. Individual perturbations were developed to reproduce sustained changes in main pressures on SPF, mainly related to sustained changes in fisheries, predators, zooplankton composition and climate conditions (i.e. SST). Pressures were developed by considering inputs to the following variables and pressures (Table 3):  $P_1$ : an increase of purse-seine fishery, the main fisheries for SPF (thus increasing fishing mortality) (Palomera et al. 2007);  $P_2$ : a recovery of SPF predators that could have a negative impact on the abundance of SPF (thus increasing predation mortality) (Navarro et al. 2009, 2017, Gómez-Campos et al. 2011, Mellon-Duval et al. 2017);  $P_3$ : a change in zooplankton that affects its composition (thus resulting in lower quality of food for sardine and anchovy, with the ultimate consequence of a reduction of sardine and anchovy abundance) (Brosset et al. 2015, 2016, Saraux et al. 2019);  $P_4$ : an increase of SST that increases the abundance of round sardinella (thus resulting in a spatial expansion and higher abundance) (Sabatés et al. 2006, 2009);  $P_5$ : an increase of SST that reduces the reproduction rate of sardine (thus increasing natural mortality) (Palomera et al. 2007); and  $P_6$ : an increase of SST that increases the abundance of gelatinous zooplankton



Table 3. Pressures  $P_1$  to  $P_6$  applied in perturbation scenarios analysed in Bayesian belief networks. Numbers in parentheses represent graph nodes in Fig. 3

Pressure		Input variables
<b>Fisheries</b> $P_1$ : increase of purse-seine fishery effort (8)		Positive input to fisheries
<b>Predator</b> $P_2$ : recovery and increase in the abundance of predators (7)		Positive input to predators
<b>Bottom-up</b> $P_3$ : changes in zooplankton (5) composition with lower quality of food for sardine (1) and anchovy (2)		Negative input to sardine and anchovy
<b>Temperature</b> $P_4$ : increase in temperature increases the abundance of round sardinella (3)		Positive input to round sardinella
$P_5$ : increase in temperature reduces reproduction rate of sardine (1)		Negative input to sardine
$P_6$ : increase in temperature increases abundance of gelatinous zooplankton (6)		Positive input to gelatinous zooplankton

## 2.6. Sensitivity analyses

Perturbation scenarios that provided predictions that were highly consistent (i.e. >90% probability) with observations (Table 4) were retained for sensitivity analyses (Hosack et al. 2008). A sensitivity analysis within the BBN shows how the probabilities of observing 1 node are affected by changes in another node, and can be used to identify which variables of a model are most informative. Specifically, sensitivity analyses use the change in mutual information between 2 nodes due to the reduction of entropy in node X because of a finding at node Y, where the expected reduction in entropy of X due to a finding at Y is zero if X is independent of Y (Hosack et al. 2008). For our purpose, variables identified as being most informative were highlighted as interesting to be monitored in order to detect the most likely source of input to the food web and most plausible pressure(s) on SPF. BBN analyses were performed using the software NETICA v.4.08 following Hosack et al. (2008).

## 3. RESULTS

### 3.1. Structure stability

(thus resulting in a benefit on its growth and persistence in the water column) (Licandro et al. 2010).

A total of 280 perturbation scenarios were developed by applying the individual or multiple perturbations ( $P_1$  to  $P_6$ ) with the different alternative models ( $M_0$  to  $M_4$ ) and structural hypotheses ( $H_1$  and  $H_2$ ). Results of perturbation scenarios were analysed considering available observations that describe a decline in sardine *S. pilchardus* and anchovy *E. encrasicolus*, and an increase in round sardinella *S. aurita* in the study area (Table 4). Predictions for each perturbation scenario were classified as being highly sign-determined when the probability of decline or increase for a variables was  $\geq 90\%$ , moderately sign-determined with a probability between 80 and 90%, or ambiguous with a probability  $< 80\%$ .

The stability analyses revealed a moderate to high potential for stability for the core model and most of the alternative model structures analysed (Table 5). The exception was model structures that included recruitment overfishing of anchovy and sardine by purse-seine fisheries (structural hypothesis  $H_3$ ), all of which had a low potential for stability. Ten models that were formulated with  $H_3$  alone or combining  $H_3$  with  $H_1$  had values of  $wF_n \geq 0$  or  $wD$  ratio to model  $c < 1$ . These models were judged to have little to no potential for stability, and thus unlikely to represent viable responses for press perturbations, and were subsequently excluded from BBN analyses.

Table 4. Available knowledge documenting small pelagic fish population changes in the NW Mediterranean Sea. GSA06: geographical subarea 6 (as defined by the General Fisheries Commission for the Mediterranean [GFCM])

Node in Fig. 3	Variable name	Observation	Narratives and references
1	Sardine <i>Sardina pilchardus</i>	Decrease of biomass	Decrease in body size and condition during last decade maintaining the same high recruitment with disappearance of the older age classes (Palomera et al. 2007, Van Beveren et al. 2014)
		Decrease of abundance	Decline in abundance in GSA06 between 2003 and 2006 by acoustic survey data, consistent with the decrease in stock sizes in the area since the 1990s (Tugores et al. 2010)
		Decrease of landings	Stock status depleted (SAC-GFCM 2015) and decrease in landings (this study)
2	Anchovy <i>Engraulis encrasicolus</i>	Decrease of biomass	Decrease in body size and condition during last decade maintaining the same high recruitment (Palomera et al. 2007, Van Beveren et al. 2014, Brosset et al. 2017)
		Decrease of abundance	Decline in abundance in GSA06 between 2003 and 2006 by acoustic survey data, consistent with the decrease in stock sizes in the area since the 1990s (Tugores et al. 2010)
		Decrease of landings	Since 2001, landings decreased to the lowest levels of the time series available, with a slight recovery since 2010 (Martin et al. 2012, STECF 2016b)
3	Round sardinella <i>Sardinella aurita</i>	Expansion of distribution	Expansion to more northern areas of the Mediterranean Sea and higher abundance (Aegean Sea: Tsiakras 2008; Adriatic Sea: Sinovčić et al. 2004; NW Mediterranean Sea: Sabatés et al. 2006, 2009)
		Increase of landings	Overall increase in landings was observed over the period 1950–2010 in the western Mediterranean Sea, with a maximum in 2003 (Sabatés et al. 2006, Alheit et al. 2014, Stergiou et al. 2016)

Table 5. Stability properties of core and alternative models (Figs. 3 & 4); models with low potential for stability in *italics* (i.e.  $wF_n \geq 0$  or  $wD$  ratio to model c < 1). See 'Materials and methods' for explanations of model c-type system, Models  $M_0$  to  $M_4$ , Hypotheses  $H_1$  to  $H_3$ , and Criteria (i) and (ii). BBN: Bayesian belief network,  $wD$ : weighted determinant,  $wF_n$ : maximum weighted feedback

Model and hypothesis	Criterion (i) $wF_n$	Criterion (ii) $wD$	$wD$ ratio to model c	Included in BBN
$M_0$	-0.32	0.000021	8800	Yes
$M_1$	-0.32	0.000024	10000	Yes
$M_2$	-1.0	0.000026	100000	Yes
$M_3$	-0.27	$0.53 \times 10^{-5}$	2200	Yes
$M_4$	-0.57	0.000053	22000	Yes
$M_0-H_1$	-0.33	0.000017	7200	Yes
$M_0-H_2$	-0.25	0.000011	4600	Yes
$M_0-H_3$	<i>0.074</i>	<i><math>0.49 \times 10^{-11}</math></i>	<i>0.002</i>	No
$M_0-H_1$ & $H_2$	-0.28	$0.99 \times 10^{-5}$	41000	Yes
$M_0-H_1$ & $H_3$	<i>0</i>	<i><math>0.11 \times 10^{-10}</math></i>	<i>0.0046</i>	No
$M_1-H_1$	-0.32	0.00002	8300	Yes
$M_1-H_2$	-0.24	0.000013	5300	Yes
$M_1-H_3$	<i>0.069</i>	<i><math>0.25 \times 10^{-11}</math></i>	<i>0.001</i>	No
$M_1-H_1$ & $H_2$	-0.26	0.000012	4900	Yes
$M_1-H_1$ & $H_3$	<i>0</i>	<i><math>-0.45 \times 10^{-11}</math></i>	<i>-0.0018</i>	No
$M_2-H_1$	-1	0.0002	82000	Yes
$M_2-H_2$	-0.67	0.000088	36000	Yes
$M_2-H_3$	<i>0.33</i>	<i>0</i>	<i>0</i>	No
$M_2-H_1$ & $H_2$	-0.73	0.000069	28000	Yes
$M_2-H_1$ & $H_3$	0.67	$-0.14 \times 10^{-10}$	-0.0058	No
$M_3-H_1$	-0.23	$0.39 \times 10^{-5}$	1600	Yes
$M_3-H_2$	-0.22	$0.31 \times 10^{-5}$	1300	Yes
$M_3-H_3$	<i>-0.016</i>	<i><math>-0.29 \times 10^{-11}</math></i>	<i>-0.0012</i>	No
$M_3-H_1$ & $H_2$	-0.21	$0.26 \times 10^{-5}$	1100	Yes
$M_3-H_1$ & $H_3$	<i>-0.035</i>	<i><math>0.42 \times 10^{-11}</math></i>	<i>0.0017</i>	No
$M_4-H_1$	-0.56	0.000045	19000	Yes
$M_4-H_2$	-0.34	0.000025	10000	Yes
$M_4-H_3$	<i>0.069</i>	<i><math>0.23 \times 10^{-12}</math></i>	<i>0.000096</i>	No
$M_4-H_1$ & $H_2$	-0.36	0.000023	9500	Yes
$M_4-H_1$ & $H_3$	<i>0</i>	<i><math>-0.30 \times 10^{-10}</math></i>	<i>-0.012</i>	No

### 3.2. Perturbation scenarios with single pressures

Perturbation scenarios that combined alternative model  $M_2$  with either  $P_4$  or  $P_6$  as single pressures were highly consistent with observed changes in populations of sardine, anchovy and round sardinella, with all predictions having a high ( $\geq 90\%$ ) probability of sign determinacy (Table 6). All these models included 4 perturbation scenarios that incorporated the modification of SPF not limiting their trophic resources, and therefore not competing for food due to partial difference in SPF diets, in combination with 2 structural hypothesis:  $H_1$  (fisheries preferably target anchovy and switch to sardine when anchovy is low) or the core hypothesis (fish-

eries target anchovy and sardine independently of their abundance).  $P_4$ , which is a positive input to round sardinella, and  $P_6$ , which is a positive input to gelatinous zooplankton, both resulted from an increase in SST. Five scenarios with predictions that had a moderate (80–90 %) probability of sign determinacy included pressures based on an increase in the purse-seine fishery ( $P_1$ ) or a decrease in the composition of zooplankton ( $P_3$ ). These scenarios included alternative model  $M_2$  in combination with structural hypotheses  $H_1$ ,  $H_1$  &  $H_2$ , or the core model.

### 3.3 Perturbation scenarios with multiple pressures

Results from the perturbation scenarios including multiple pressures yielding predictions that were highly consistent with observations were also based on alternative model  $M_2$  in combination with structural hypothesis  $H_1$  or the core model (Table 7). These included scenarios that considered 5 or 3 simultaneous pressures.

Considering predictions with a moderate (80–90 %) probability of sign determinacy, model configuration  $M_3$ , which incorporated significant predation of gelatinous zooplankton on anchovy larvae and zooplankton, was included in 3 scenarios (Table 7). In these 3 scenarios, model  $M_3$  was combined with structural hypotheses  $H_1$ ,  $H_1$  &  $H_2$ , or the core model.

In perturbation scenarios with multiple pressures, it was always the same combination of pressures that gave prediction probabilities with a moderate to high level of sign determinacy (>80 %) (Table 7). The greatest number of combined pressures, 5, included the same 5 pressures in each perturbation scenario (i.e.  $P_1$ ,  $P_2$ ,  $P_3$ ,  $P_4$  and  $P_6$ ). Scenarios with 4 pressures always included  $P_2$ ,  $P_4$ ,  $P_5$  and  $P_6$ , those with 3 pressures always included  $P_3$ ,  $P_4$  and  $P_6$ , while a combination with 2 pressures,  $P_1$  and  $P_3$ , occurred in only 1 perturbation scenario.

### 3.4. Most informative indicators

A sensitivity analysis on model configuration  $M_2$  within the BBNs was used to further discriminate between which inputs, and thus which source of a perturbation, were most likely to provide high probabilities of predicting field observations (i.e. a decline in anchovy and sardine and increase in round sardinella).

Sensitivity analysis under the core model hypothesis (fisheries target anchovy and sardine independ-

Table 6. Predictions of Bayesian belief networks from perturbation scenarios considering a single pressure at a time ( $P_1$  to  $P_6$ ; see Table 3) for alternative model  $M_2$  in combination with structural hypotheses  $H_1$ ,  $H_1$  &  $H_2$ , or the core model. Only predictions of decline or increase of  $\geq 80\%$  probability of sign determinacy (classified as moderate) are shown; scenarios where prediction probabilities exceed 90 % (classified as high) are in **bold**; ✓ indicates inclusion of a pressure within a perturbation scenario. Sard: sardine; preds: predators

Structural hypothesis	Pressure					Prediction probability			
	$P_1$ : increase in purse-seine	$P_2$ : increase in preds	$P_3$ : decrease in zooplankton composition	$P_4$ : increase in round sardinella	$P_5$ : decrease in sard	$P_6$ : increase in gelatinous zooplankton	Decrease in sardine	Decrease in anchovy	Increase in round sardinella
$H_1$				✓			<b>High</b>	<b>High</b>	<b>High</b>
$H_1$				✓		✓	<b>High</b>	<b>High</b>	<b>High</b>
<b>Core</b>						✓	<b>High</b>	<b>High</b>	<b>High</b>
<b>Core</b>						✓	<b>High</b>	<b>High</b>	<b>High</b>
$H_1$							High	Moderate	High
$H_1$							High	Moderate	High
$H_1$ & $H_2$	✓						High	Moderate	High
Core	✓						Moderate	Moderate	High
Core	✓						Moderate	Moderate	High

Table 7. Predictions of Bayesian belief networks from perturbation scenarios considering combinations of multiple pressures (P<sub>1</sub> to P<sub>6</sub>; see Table 3), for alternative model M<sub>2</sub> in combination with structural hypothesis H<sub>1</sub> or the core model, or alternative model M<sub>3</sub> in combination with structural hypotheses H<sub>1</sub>, H<sub>1</sub> & H<sub>2</sub>, or the core model. Only predictions of decline or increase with ≥80% probability of sign determinacy (classified as moderate) are shown; scenarios where all prediction probabilities exceed 90% (classified as high) are in **bold**; ✓ indicates inclusion of pressure within a perturbation scenario

Alternative model	Structural hypothesis	Pressure						Prediction probability		
		P <sub>1</sub> : increase in purse-seine	P <sub>2</sub> : increase in predators	P <sub>3</sub> : decrease in zooplankton composition	P <sub>4</sub> : increase in round sardinella	P <sub>5</sub> : decrease in sardine	P <sub>6</sub> : increase in gelatinous zooplankton	Decrease in sardine	Decrease in anchovy	Increase in round sardinella
M <sub>2</sub>	H <sub>1</sub>	✓	✓	✓	✓	✓	✓	<b>High</b>	<b>High</b>	<b>High</b>
M <sub>3</sub>	H <sub>1</sub>	✓	✓	✓	✓	✓	✓	High	Moderate	High
M <sub>3</sub>	H <sub>1</sub> & H <sub>2</sub>	✓	✓	✓	✓	✓	✓	High	Moderate	High
M <sub>2</sub>	<b>Core</b>	✓	✓	✓	✓	✓	✓	<b>High</b>	<b>High</b>	<b>High</b>
M <sub>3</sub>	Core	✓	✓	✓	✓	✓	✓	High	Moderate	High
M <sub>2</sub>	H <sub>1</sub>	✓	✓	✓	✓	✓	✓	High	Moderate	High
M <sub>2</sub>	Core	✓	✓	✓	✓	✓	✓	High	Moderate	High
M <sub>2</sub>	H <sub>1</sub>	✓	✓	✓	✓	✓	✓	<b>High</b>	<b>High</b>	<b>High</b>
M <sub>2</sub>	<b>Core</b>	✓	✓	✓	✓	✓	✓	<b>High</b>	<b>High</b>	<b>High</b>
M <sub>2</sub>	H <sub>1</sub>	✓	✓	✓	✓	✓	✓	High	Moderate	High

ently of their abundance), structural hypothesis H<sub>1</sub> (fisheries preferably target anchovy and switch to sardine when anchovy is low), or a combination of both of them (core and H<sub>1</sub>, where both were given the same weight of 50% probability of occurrence) yielded similar results (Table 8). To distinguish between likely inputs to sardine, anchovy, and round sardinella, the most informative model variable, after excluding their own input variable, was, in all but 1 instance, the variable ‘predators’. Therefore, information about predators in the ecosystem (e.g. if they have declined or increased) would allow in the future to further decrease the uncertainty in the results of the perturbation scenarios performed in this study.

The one exception to these results was observed under the structural hypothesis H<sub>1</sub>. In this case, the most informative variable in the model to distinguish which is the likely perturbation source to round sardinella was ‘sardine’ (Table 8). Therefore, further information on sardine dynamics would allow in the future decreasing the uncertainty in those perturbation scenarios performed in relation to round sardinella.

#### 4. DISCUSSION

##### 4.1. Structure of NW Mediterranean pelagic food web

This study provides insights about plausible causes of change in the NW Mediterranean pelagic food web, highlights some uncertainties and identifies guidance for future research. Testing of the alternative model structures found the configuration most frequently selected was model M<sub>2</sub>, which represents the modification of SPF not limiting their trophic resources and therefore not competing for food (for phytoplankton and zooplankton) due to partial difference in their trophic niche (Costalago et al. 2012, Costalago & Palomera 2014, Albo-Puigserver et al. 2016). This suggests an ecosystem structure where there is no wasp-waist control of SPF (as previously suggested in true upwelling systems, Cury et al. 2000), but only control to the predators and not to the prey, which is in agreement with findings in other regions (Koehn et al. 2016). These results would suggest that population changes of SPF could have an impact on their predators. On the contrary, in previous studies in the study area covering the 1970s to the early 2000s, we described sardine as an important species exerting wasp-waist control in the system (Coll et al. 2008), thus also exerting control on its prey. These new results may indicate a loss of wasp-

Table 8. Sensitivity analysis results from Bayesian belief networks, for model configuration  $M_2$  under the core model hypothesis, structural hypothesis  $H_1$ , or a combination of both of core and  $H_1$ , given an input to small pelagic fish, with probability of occurrence attributed to each model hypothesis. For each input variable (horizontal row), the 2 variables with the largest mutual information are in **bold**. Preds: predators

Model and hypothesis	Input to	Mutual information			
		Sardine (%)	Anchovy (%)	Round sardinella (%)	Preds (%)
$M_2$ 50% Core; 50% $H_1$	Sardine	<b>16.1</b>	2.31	1.01	<b>4.5</b>
$M_2$ 50% Core; 50% $H_1$	Anchovy	0.1	<b>21.7</b>	2.0	<b>9.7</b>
$M_2$ 50% Core; 50% $H_1$	Round sardinella	3.4	2.3	<b>12.0</b>	<b>4.5</b>
$M_2$ Core (100%)	Sardine	<b>21.7</b>	2.3	1.3	<b>5.8</b>
$M_2$ Core (100%)	Anchovy	2.3	<b>21.7</b>	1.3	<b>5.8</b>
$M_2$ Core (100%)	Round sardinella	2.3	2.3	<b>12.3</b>	<b>5.8</b>
$M_2$ $H_1$ (100%)	Sardine	<b>11.5</b>	2.3	0.8	<b>3.5</b>
$M_2$ $H_1$ (100%)	Anchovy	1.1	<b>21.7</b>	2.8	<b>14.8</b>
$M_2$ $H_1$ (100%)	Round sardinella	<b>4.9</b>	2.3	<b>11.8</b>	3.5

waist control of SPF due to a decline of their biomass and the current low levels of the stock (Table 4). They also highlight that a further development of this work should focus on testing individually the role of sardine as a wasp-waist organism.

The rest of the other model structures, models  $M_1$ ,  $M_3$  and  $M_4$ , did not produce predictions that were as highly consistent with observations as model  $M_2$  for either single or multiple pressures, and thus are considered to be less likely to represent observed dynamics of the system. This suggests that the hypothesis that predators do not limit round sardinella due to its larger abundance and recent expansion (Sabatés et al. 2006) ( $M_1$ ), the significant predation of gelatinous plankton on anchovy larvae and zooplankton (Tilves et al. 2016) ( $M_3$ ), and a combination of all the alternative hypotheses are less able to lead to model predictions consistent with observed changes in SPF.

Our results also demonstrate that to understand the structure of the pelagic marine food web, it is important to consider how fisheries affect SPF populations. In our analyses, the structural hypothesis  $H_1$  gave predictions that were highly consistent with observations several times. Hence, our results support the possibility that fisheries preferably target anchovy and switch to sardine when anchovy is low as a plausible mechanism governing purse-seine fisheries (as has been already observed when interacting with fishermen in the study area). This mechanism, however, is ruled by market and price behaviours, which highlights the need to consider fisheries dynamics within the ecosystem dynamics. Future development of this work should include a socioeconomic model linked with the biological processes modelled in this

study, as has been done elsewhere (Dambacher et al. 2009, 2015). Our results also showed that the structural hypothesis considering that sardine and anchovy recruitment is highly fished (Palomera et al. 2007) ( $H_2$ ) in combination with  $H_1$  could be potentially viable. An explicit socioeconomic model of the fishery could help distinguish between these plausible options.

Models that included the structural hypothesis that sardine and anchovy recruitment was overfished ( $H_3$ )

had a high potential to be unstable, and hence we did not incorporate these models into our analyses to predict change in equilibrium. The dynamics of these models are dominated by excessive amounts of higher-level feedback and thus are prone to exhibit undamped oscillations. Since both stocks of sardine and anchovy have been, or are, highly fished and could be overfished (Palomera et al. 2007, STECF 2016a), these ecosystems could be near to or at an unstable state, and the system could shift to another equilibrium or become highly oscillatory if recruitment overfishing were to persist. Modelling the dynamics of unstable systems exceeds the scope of traditional approaches to ecosystem modelling (qualitative or quantitative) and requires precise knowledge of system thresholds and extra caution in interpretation and application of modelling results.

#### 4.2. Plausible pressures on SPF change

Perturbation scenarios with only a single pressure yielded results that were consistent with observations. An increase in SST that produces a positive impact on round sardinella or on gelatinous zooplankton was selected as a pressure that could alone describe field observations, i.e. a decline in anchovy and sardine, and an increase in round sardinella. In fact, there is strong evidence of an overall increase of SST in the area, and biological impacts on several organisms spanning different habitats have already been documented (Calvo et al. 2011), which includes impacts on anchovy and sardine (Checkley et al. 2017). These results complement previous knowledge highlighting that an increase in SST has proba-



bly already impacted the ecosystem functioning of the pelagic food web of the NW Mediterranean Sea. Therefore, the geographic expansion of round sardinella and the increase in gelatinous zooplankton (Sabatés et al. 2006, 2009, Maynou et al. 2014, Tilves et al. 2016), which are linked to changes in SST, may have had important effects on other compartments of the pelagic system, such as the abundance of sardine and anchovy through, for example, mechanisms of competition for food between SPF. These results are in line with a previous study where the analysis of long time series of SPF landings from the Atlantic and Pacific Oceans highlighted that the hypothesis with broadest support regarding SPF changes was process noise dependence (Hosack et al. 2013). This hypothesis states that environmental parameters may cause one species to predominate over the other due to changes in environmental conditions, such as temperature, acting directly on SPF, or acting through their food abundance or quality.

An increase of fisheries impacts alone could also have led to important changes in the pelagic food web, but considering our results, the probability that this is the main driver of change is lower than an increase of SST. This is in line with previous consideration in the Gulf of Lions pelagic ecosystem (Van Beveren 2015, Saraux et al. 2019). Fisheries statistics and stock assessment models, however, suggest that sardine and anchovy have been highly fished in the study area (SAC-GFCM 2015, STECF 2016b,c). Therefore, our results could also reflect the fact that the role of fisheries has been important in the past, but once the stock is relatively low, as in the current case, then environmental factors such as SST can dominate SPF dynamics (Planque et al. 2010, Essington et al. 2015).

Bottom-up changes of the food web could also be part of the drivers of SPF changes, due to changes in zooplankton abundance, composition or quality, and could have strong effects on the reproduction, growth and mortality of SPF, as has been proposed by Brosset et al. (2015, 2016). These changes could explain the low body condition that sardine and anchovy have shown in the Mediterranean Sea in recent years (Albo-Puigserver et al. 2017b, Brosset et al. 2017). Changes in plankton composition and quality need to be further analysed (Saraux et al. 2019), and if confirmed, new results could be tested in our models.

The increase of predators as a potential explanation for the decline in SPF did not yield predictions that were consistent with observations. This suggests that it is unlikely that the recovery of predators of

SPF will have an effect on SPF populations under current food web structure. Previous studies have already suggested that predation mortality of Atlantic bluefin tuna *Thunnus thynnus* on SPF populations has a very low impact on their abundance (Van Beveren et al. 2017), and that SPF species are not the only prey or dominant source of food for pelagic predators (Navarro et al. 2017).

With respect to cumulative impacts, it is important to highlight that perturbation scenarios combining multiple pressures showed several combination sets of pressures that had moderate to high probabilities of producing observed results, though in general they all had lower probabilities of occurrence than a single pressure alone. Interestingly, the same sets of multiple pressures gave predictions with moderate to high levels of sign determinacy in combination with various alternative models and structural hypotheses, suggesting perhaps that idiosyncratic sets of pressures can produce similar results across different model structures. Even though a more parsimonious response is preferred, a combination of drivers that yield a decline of sardine and anchovy and an increase of round sardinella cannot be disregarded, as multiple pressures often spatially overlap in the ocean worldwide (Halpern et al. 2015), and in the Mediterranean Sea in particular (Coll et al. 2012, Micheli et al. 2013). The most frequent set of multiple pressures considered included an increase of SST positively affecting round sardinella and gelatinous zooplankton, a decrease of zooplankton quality, an increase of fishing impact and an increase of predators. Therefore, we cannot falsify the possibility that cumulative impacts of pressures and their synergistic effects may be important when trying to understand the causes of change of SPF populations in the NW Mediterranean Sea.

Our study provides a first means to compare different hypotheses that have been proposed to explain SPF changes in the region but have not been previously tested together, and can be the basis for future work. Quantitative dynamic modelling approaches could help further evaluate these alternative hypotheses (e.g. Fulton 2010, Fulton et al. 2015). Another promising approach will be to test some of the key aspects of our more plausible model structures using analysis of time series data by state-space modelling (Hosack et al. 2013). Furthermore, as more information is collected, additional models based on refined or new hypotheses can be considered and current models can be modified to address aspects of the problem not considered so far (Dambacher et al. 2015).

### 4.3. Complementing monitoring strategies

Even though several combinations of drivers and structural hypotheses were considered in this study, further work needs to be done to reduce uncertainty in modelling predictions and consider new hypotheses. Sensitivity analyses allowed us to identify key monitoring variables to reduce model structural uncertainty. One important monitoring variable identified in our models was 'predators'. The importance of this variable can be linked to the large bottom-up control that SPF play in the ecosystem and the dependency of predators on their populations (Cury et al. 2011). This suggests that it is important to distinguish which predators base their diet on anchovy and sardine and could be monitored in order to indirectly observe any effects of change in populations of SPF. The breeding success and fitness of predators can be highly affected by the quantity (food availability) and quality (energy intake per unit) of their prey (Österblom et al. 2008). Thus, predators that rely mainly on SPF would be highly sensitive to changes in SPF populations, as has been previously reported for seabirds such as Audouin's gull *Larus audouinii* of the Ebro Delta (Arcos & Oro 2002, Payo-Payo et al. 2016), Steller sea lions *Eumetopias jubatus* in the Gulf of Alaska (Rosen & Trites 2000) or African penguin *Spheniscus demersus* in South Africa (Robinson et al. 2015).

To increase the knowledge of which pressures are driving round sardinella, our analyses suggest that sardine populations are a good monitoring target and research investment. The importance of this variable is probably related to the divergent trends that both species have shown in the ecosystem historically, with a decline of sardines and an increase of round sardinella (Palomera et al. 2007). This result is relevant since there is a lack of information about sardine biology and ecology in the Mediterranean Sea (Palomera et al. 2007), and further studies could be beneficial.

### 4.4. Complexity when predicting and managing change

While there were 19 perturbation scenarios that gave predictions moderately or highly consistent with observations, the vast majority of the 285 scenarios considered yielded low levels of sign determinacy. This highlights the challenge of predicting complex systems such as marine food webs and the need to use complementary modelling techniques

that quantify the strength of the interactions (Fulton 2010, Fulton et al. 2015). Results from this study provide insight into model structure that can inform future quantitative modelling endeavours in the study area such as the ones developed for SPF in other marine ecosystems (e.g. Shannon et al. 2004, Koehn et al. 2016, Punt et al. 2016, Kaplan et al. 2017).

Of all the pressures that were tested, managing for pressures such as SST or changes in plankton abundance is difficult at local or regional scales. Here, we can only aim to manage fisheries in a sustainable and adaptive way, with all the challenges implied in the process. Future work should focus on testing which management alternatives can ensure the sustainability of the marine ecosystems of the NW Mediterranean and are also robust to a changing climate.

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