Identifying Statistical Interaction Networks (SINs) in a fish community using multivariate time series analysis: an application to the Gulf of Lions

Authors: C.M. Bensebaini[1*], G. Certain[1], S. Gourguet[2], O. Thebaud[2], T. Hattab[1], N. Billet[1], A. Jadaud[1], JM. Fromentin[1].

[1] MARBEC, University of Montpellier, IRD, Ifremer, CNRS, Sète France

[2] Ifremer, Univ Brest, CNRS, UMR 6308 AMURE, Unité d'Economie Maritime, IUEM, F-29280 Plouzané, France

*Corresponding author: tel: +33 767162285; e-mail: cmbenseb@ifremer.fr

Abstract

The need for ecosystem-based approach to fisheries management is widely recognized. Designing ecosystem models for management purpose requires the identification of key interactions and forcings driving the dynamics of fish stocks, which can be a very challenging task given the complexity of interactions that determine the evolution of marine ecosystems. To overcome this difficulty, this study proposes a statistical approach based on multivariate time series analysis to identify the main biotic interactions and abiotic factors using as a case study a complex and exploited marine ecosystem, the Gulf of Lions (GOL) in the Mediterranean Sea. To do so, first, pairwise Granger causality tests were performed to detect and select the strongest interactions and drivers, then Multivariate Auto-Regressive (MAR) models were run to check the relevance of the selected causal relationships in a multivariate system. The results led us to identify three statistical interaction networks (SINs) of moderated complexity. The first one showed statistical interactions between blackbellied angler (*Lophius budegassa*), hake (*Merluccius merluccius*), grey gurnard (*Eutrigla gurnardus*), and John dory (*Zeus faber*), and the effect of nitrate concentration. The second focused on blackbellied angler, red mullet (*Mullus barbatus*), anchovy (*Engraulis encrasicolus*), under the combined influence of demersal trawlers, SST and nitrate concentration. The third one included horned octopus (*Eledone cirrhosa*), capelan (*Trisopterus capelanus*), sardine (*Sardina pilchardus*), and the effect of nitrate concentration. These SINs can serve as a basis to build models of intermediate complexities to describe the dynamics of the main fish stocks of the GOL.

Keywords: Granger causality, Multivariate Auto-Regressive (MAR) models, Statistical interaction networks, environmental effects, fishing effects, Gulf of Lions.

1. Introduction

The collapse of several stocks worldwide in the late 1980s (Crespo and Dunn, 2017; Hilborn *et al.*, 2020), and the increasing threat of climate change on marine resources (Barange and Perry, 2009) has led to the recommendation of implementing an ecosystem-based approach to fisheries management (FAO, 1995; Cury *et al.*, 2008). EBFM is a multi-factorial approach for fisheries management, ideally accounting for as many drivers as possible, such as interspecific interactions, environmental changes, pollution and other constraints on habitat and water quality. This led to different perspectives on how to implement ecosystem models, depending on the region, the purpose, and the accessible level of complexity (Plaganyi, 2007; Trochta *et al.*, 2018).

In many areas though, fisheries management (when it exists) is still based on classical, single-species stock assessment models, where fishing mortality is the main driver of the fish stock dynamics. For example, in the Mediterranean region, where an ambitious management plan is ongoing since 2020 (the “Westmed” plan, see Sola *et al.*, 2020 for details), most of the stock assessment models routinely used to provide advice regarding fisheries management are based on classical single-species assessment approaches (statistical catch at age or surplus production models, see STECF, 2023). Furthermore, the spatial and/or bio-economic models currently used to inform the Westmed plan do not consider interactions between species (see the example of the IAM model, the BEMTOOL model, or the ISIS-Fish model in STECF, 2022). The need to develop ecosystem models tailored for operational management in the Mediterranean region is clear, and some steps have already been taken in this direction, for example in the Adriatic Sea (Angelini *et al.*, 2016). However, most areas of the Mediterranean Sea still lack such approaches.

This is the case for the Gulf of Lions (GOL), which is a continental shelf bordering the French coast whose northern location in the Mediterranean basin makes it a potential refuge from climate change (Pennino *et al.*, 2020). The GOL ecosystem has been under strong fishing pressure since many decades (Aldebert, 1997). Today, the ecological status of the GOL ecosystem is of great concern (FAO, 2023). Several ecosystem models have already been proposed for the GOL (Banaru *et al.*, 2013, 2019; Corrales *et al.*, 2015; Diaz *et al.*, 2019; Cresson *et al.*, 2020; Vilas *et al.*, 2021; Seyer *et al.*, 2023). However, none are currently used for decision making and fisheries management, most likely because these highly complex models are not well tailored to produce reliable diagnostics regarding fishing mortality or management strategies.

Ecosystem models are most often structured by trophic interactions, in the sense that they try to represent what we know about the numerous trophic relationships possibly existing in the system. However, the focus of fisheries management is not on modeling exhaustively the food web, but rather on explaining the joint dynamics of the most important harvested stocks. If evidence on food web structure can be obtained through diet or isotope analysis, it is more challenging to gather evidence that the consumption of a given predator affects the population dynamics of its preys and *vice versa*. Some well-studied systems provide examples of studies deciphering the effects of trophic interactions on fish dynamics can be found. These include Lindegren *et al.* (2009) who studied cod-herring-sprat (*Gadus morhua; Clupea harengus; Sprattus sprattus*) interactions in the Baltic sea; Or Durant *et al.* (2019) who showed a strong dependence on synchrony with zooplankton prey in the Arcto-boreal small pelagic fish population (the Barents sea) in contrast to the temperate fish population (Bay of Biscay); Or Shears *et al*. (2003) who addressed the trophic cascade effects of increased predator abundance in the Leigh marine reserve (northeastern New Zealand). These studies are usually restricted to a few interacting species, usually 2-4 predominant ones, rather than the entire food web. Furthermore, modeling species interactions within a given ecosystem is a challenge for several other reasons. First, whatever the environment, most trophic interactions within a food web are not strong enough to significantly drive the dynamics of the species composing it (Mutshinda *et al.*, 2009; Kawatsu *et al.*, 2021). In addition to key prey-predator relationships, other non-trophic interspecific interactions – such as competition, commensalism, or mutualism – can also drive community dynamics (Rockwood, 2015), even though they may be more challenging to identify in marine systems. Lastly, external drivers can also exert a strong control on stock dynamics, through recruitment success (Cury and Roy, 1989) or fishing pressure (Kuparinen *et al.*, 2016).

All these driving forces and interactions, when combined with intrinsic population dynamic processes (*i.e.* density dependence) can quickly lead to complex and data-intensive models (Smit *et al.*, 2021). Unfortunately, a high level of information is not always available, and information on the biology or ecology of marine species, or environmental factors, is primarily supplied through monitoring programs, rarely available before the 1960s (Lotze and Worm, 2009). In the Mediterranean, routine surveys were initiated in the 1990s (Fortibuoni *et al.*, 2017). Both the Mediterranean international bottom trawl survey (MEDITS; Jadaud and Certain 1994) and its pelagic counterpart (PELMED; Bourdeix and Hattab 1985) are carried out on a yearly basis, providing relatively short time series of ~30 points.

To build ecosystem models for management purposes, it is therefore relevant to take a parsimonious approach. This requires clear identification of (1) the stocks under focus and (2) the main factors driving their dynamics, whether they are trophic, non-trophic, or exogenous drivers; as well as (3) possibly selecting the most influential among these factors to avoid the pitfall of fitting overly complex models to limited time series (Plaganyi *et al.*, 2014). To achieve this, one can use prior knowledge on the ecosystem under focus. But in certain cases, such knowledge may be limited to a few components, with the risk of missing unknown but important interactions. To solve this, we propose in this study an extensive analysis of ecosystem monitoring data tailored to identify key interactions. To do so, we apply a relatively simple statistical approach to identify key variables and interactions through the multivariate analysis of time series. The approach builds on the Granger causality (GC) concept, which measures the ability of one variable to improve the prediction of another (Granger, 1969). Notably GC can be measured using Multivariate Auto-Regressive (MAR) models (see Barraquand *et al.*, 2021), which are a particularly efficient technique to detect biotic and abiotic interactions within a community dynamics (Certain *et al.*, 2018). GC has been extensively used in the field of economics (Masih and Masih, 1996; Foresti, 2006). In ecology, it has proven to be very effective in evidencing interspecific relationships (Parker *et al.*, 2020) and stock-recruitment relationships (Ye, 2000); as well as assessing the influence of an environmental driver on population dynamics (McLean *et al.*, 2018; Rincón *et al.*, 2019; Chivers *et al.*, 2020; Hays *et al.*, 2021). The objective of this study is thus to reduce the complexity of the GOL ecosystem by identifying the most significant biotic interactions and abiotic effects through multivariate analysis of available time series using GC tests. Although this approach is applied to the GOL ecosystem, its ease of implementation makes it reproducible for other ecosystem with similar data sets.

2. Materials and methods

2.1. Case study: Gulf of Lions (GOL) fisheries

Like most Mediterranean fisheries, the GOL fisheries are mixed fisheries characterized by many fleets with relatively small vessels exploiting several dozens of species. The rapid development of the fishing fleet in the 1960s exerted a strong fishing pressure on the exploited stocks and the first signs of over-exploitation were reported as early as the late 1980s (Aldebert, 1997; Van Beveren *et al.*, 2016). To support the regulation of these fisheries under the EU common fisheries policy, annual monitoring surveys (MEDITS survey, demersal trawl, (Jadaud and Certain, 1994), and PELMED survey, acoustic survey, (Bourdeix and Hattab, 1985, Fig. 1) were launched in the early 1990s (Bertrand *et al.*, 1997; Spedicato *et al.*, 2019). They extensively cover the GOL continental shelf and provides standardized time series of abundances for the most important pelagic and demersal species in the area.

In the mid-2000s, an environmental shift in the GOL, probably mediated through the planktonic food web, caused rapid and abrupt changes in abundance and body condition of several species (Saraux *et al.*, 2019; Feuilloley *et al.*, 2020; Bensebaini *et al.*, 2022; Garcia *et al.*, 2023) and resulted in a massive transfer of fishing effort from pelagic to demersal stocks which later on resulted in an increased fishing pressure on demersal stocks (Saraux *et al.*, 2019), which later led to the implementation of a restructuring plan decreasing the fishing effort of demersal trawlers operating in the area (EU, 2019). However, despite the reduction in fishing effort, landings by demersal trawlers remain the most important. Data on landings in recent years (2018-2020) showed that 47 species account for 90% of total landings, and of which around 50% are landed by trawlers (Certain *et al.*, 2022). For many reasons such as a lack of data throughout the whole time series (see e.g. Morfin *et al.*, 2012), we restricted our analysis to 25 species that were regularly caught (i.e. there were no missing values in the time series). Because envisioning multispecies models for management purpose requires to focus on key species and their interactions (Plaganyi *et al.*, 2014), it was necessary to select some species of key importance to the fishery. Therefore, from these 25 species we identified 6 "target species" for our analysis: hake (*Merluccius merluccius*), red mullet (*Mullus barbatus*), horned octopus (*Eledone cirrhosa*), blackbellied angler (*Lophius budegassa*), sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*). The species were selected based on the possibility of stock assessments, the availability of routine sampling by MEDITS and PELMED surveys (Morfin *et al.*, 2012; Saraux *et al.*, 2014), as well as their significance in terms of landings and economic value (Table 1).

2.2. Data processing

Our focus is to identify any biotic and abiotic interactions possibly affecting the 6 target species mentioned above. Data were extracted from two monitoring campaigns, set up in the early 1990s, which take place once a year, one for demersal stocks, from mid-May to the end of June (MEDITS), and the other for pelagic stocks, during the month of July (PELMED). The standardized densities (log-transformed and centered) of 25 species have been considered for this analysis (Fig. 1). For 11 species, the large data s*et al*lowed to split the series into juveniles and adults with the exception of red mullet, where only adults have been retained as juveniles are poorly sampled. For the remaining 15 species, division into two life stages was not possible due to the lack of data for some years (i.e. there are missing values in the time series when it is split), resulting in a total of 36 time series (Table 2). In addition, data on 9 abiotic drivers have been chosen and extracted based on the work of Feuilloley *et al* (2020). Six of them are environmental descriptors: Sea Surface Temperature (SST), Western Mediterranean oscillation index (WeMOI), mixed layer depth (MLD), Rhône River flow, nitrate and phosphate concentration in the Rhône River, and the three remaining relates to the fishing effort of either demersal trawlers, pelagic trawlers, and seiners. Environmental data covered the whole period from the early 1990s to 2020, while fishing effort data covered from 2001 to 2020 (Table 2).

The data were collected on a monthly or daily scale, then an annual average was calculated over a one-year period from July 1st to June 30th to better match the dates of the MEDITS and PELMED surveys. These data have been standardized (scaled and centered) before analysis. The details on biotic and abiotic time series used for this study are provided in Appendix A.

2.3. Granger causality and Multivariate Auto-Regressive (MAR) Models

We propose here a statistical approach to identify key variables and interactions through multivariate time series analysis. Our dataset is comprised of 45 time series, 36 corresponding to species and 9 to covariates describing the environment and the fishing effort. Fitting a full Multivariate Auto-Regressive MAR model to such high number of series is quite impractical and would require much longer time series than the one at hand (between 20 to 28 points). For example, simulations made by Certain *et al.* (2018) suggested that a nonlinear and stochastic ecological system of dimension 10 would require time series with at least 500 to 800 points to be correctly fitted. To overcome this problem, we focused on pairwise interactions, sequentially performing pairwise GC tests with one time lag to select the most important interactions. Then, MAR models with one time lag were built with the selected interactions to check their consistence in a multivariate system; *i.e.* the robustness of coefficient estimates when the effect of other variables and covariates was taken into account. The analytical process is summarized in Fig. 2, and details regarding GC tests and MAR modeling are provided in the following sections.

2.4. Pairwise Granger causality test

The GC test posed by Granger (1969), is a statistical hypothesis test to determine whether one time series is useful in forecasting another. More specifically, x Granger causes y if y is better predicted with x than without. This translates into the implementation of two auto-regressive models predicting y values, one taking into account only past y values (the univariate model; Eq. 1), and the other both past y and x values (the bivariate model; Eq. 2).

$$y_t = \sum_{p=1}^{n} a_p y_{t-p} + \eta_t,\ \ \eta_t \sim N(0,\sigma_\eta^2)\ldots\ldots\ldots\ldots\ldots\ldots\text{(Eq.1)}$$

$$y_t = \sum_{p=1}^{n} b_{1,p} x_{t-p} + \sum_{p=1}^{n} b_{2,p} y_{t-p} + \epsilon_t,\ \ \epsilon_t \sim N(0,\sigma_\epsilon^2)\ldots\ldots\ldots\ldots\ldots\text{(Eq. 2)}$$

Where subscript p is indicating time lags. a_p and $b_{2,p}$ are the autocorrelation coefficients while $b_{1,p}$ is the coefficients outlining the effect of x_{t-p} on y_t. η_t and ϵ_t are the associated errors, which follow a normal distribution with a mean of 0 and variances of σ_η^2 and σ_ϵ^2 respectively. GC is deduced when predictions regarding future values of y issued from the bivariate model (Eq. 2) outperforms the univariate one (Eq. 1). The effect size (G) of the interaction is defined as the ratio between the residual variance of the bivariate model and the univariate model (Eq. 5).

$$G = \ln\left(\frac{\sigma_\eta^2}{\sigma_\epsilon^2}\right)\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{(Eq. 3)}$$

If there is no interaction between x and y, x does not improve the prediction of y, so $\sigma_\eta^2 \approx \sigma_\epsilon^2$ and $G \approx 0$. In the opposite case where x affects y, $\sigma_\epsilon^2 < \sigma_\eta^2$, and hence $G > 0$ (Detto *et al.*, 2012; Barraquand *et al.*, 2021).

The approach involved the following steps. To test whether time series x “Granger causes” time series y, both a univariate autoregressive model for x (Eq. 1) and a bivariate model (Eq. 2) were fitted. Then, effect size (G) was calculated following Eq. 3, and p-values were computed by a Wald test (see “grangertest” function within R package vars; Pfaff and Stigler, 2023).To search for potential biotic interactions driving the dynamics of our 6 target species, we performed a succession of pairwise GC tests, using the 36 biotic time series extracted. As the aim was to reveal which species potentially drives the dynamics of the 6 target species, the tests involving two non-target species were not conducted. In total, 315 tests were performed. We only considered a simple time lag of one year (p=1), because of the shortness of the available time series. Performing many sequential pairwise tests using short time series has several shortcomings. First, the large number of tests theoretically would require multiple-testing corrections, such as Bonferroni correction (Moran, 2003) or Holm's test (Holm, 1979). However, there is a growing body of literature explaining that large non-significant effects should not be discarded, especially when samples are small as in our case (Amrhein *et al.*, 2019). Conversely, even if "statistically significant", an interaction may have a weak effect size and thus may not be useful for the purpose of describing the dynamics of the target series.

Because of these statistical issues and because our focus is primarily on identifying interactions strong enough to be of importance for the dynamics of the system (e.g. with large effect size), we set a subjective threshold for effect sizes (thereafter noted G_{th}) to distinguish "potentially strong" interactions. We assumed that only interactions able to explain at least 25% of the variance in the response variable were of interest, which corresponds to causal effect size greater than 0.28 ($G_{th} \geq \ln(1/0.75) \approx 0.28$). In a second step, we computed *p*-values with the Wald test to further classify these "potentially strong" interactions, and we retained those for which *p*-value≤0.1. This 10% threshold was derived from a power analysis (detailed in Appendix B) that demonstrated that with short series around 20 points, the GC test was not very powerful in detecting weak interaction coefficients, but remained efficient in detecting high ones (>0.3), provided that the assumed α risk was a bit higher than the classical 5%. Finally, we decided to only retain interactions satisfying both criteria ($G \geq G_{th}$ and *p*-value≤0.1).

After this series of pairwise interaction tests, a number of non-target species potentially affecting the dynamics of the target species were identified. Once this was done, the effects of abiotic drivers were then tested on this selected pool of biotic time series. For each selected biotic time series, 7 pairwise GC tests were conducted: 6 for environmental series, and one for fishing effort, as we only tested the effort of the fleet presenting the highest proportion of catches of the species under consideration.

2.5. Multivariate Auto-Regressive (MAR) Models

After these two sequences of biotic and abiotic pairwise GC tests, a number of relevant interactions potentially driving the dynamics of six target stocks were identified. The variables connected through these interactions form a "Statistically Interacting Network" (SIN). In this last part, we checked the relevance of these SINs using Multivariate Auto-Regressive (MAR) modeling. A MAR model is a system of *m* linear equations describing the variation of each variable (here fish densities) and their interactions, and *l* linear equations describing the effect of each exogenous variable or covariates (here environmental factors and fishing pressures). In matrix form, it is written as follows (Holmes *et al.*, 2018):

$$MAR(1){:}x_t = Bx_{t-1} + a + Cu_t + w_t,\ w_t \sim N(0{,}Q_t)\ldots\ldots\ldots\ldots\ldots\text{(Eq. 4)}$$

with x_t a vector whose elements corresponds to the *m* response variables of the model. B is the $m*m$ interaction matrix, with b_{ij} the effect of variable j on variable i. The diagonal of the matrix B represents the effect of the variables on themselves. u_t is a vector of *l* covariates and C is the $m*l$ matrix of covariates effects, with c_{ij} the effect of covariate j on variable i. w_t is a multivariate normally distributed error vector with mean 0 and variance-covariance matrix Q. Matrix B and C parameters were estimated by a maximum likelihood estimation using a Kalman filter (Harvey, 1989).

We therefore modeled each SIN identified by the pairwise GC test with a MAR(1) model. In these models, only the auto-correlation coefficients and coefficients of interactions identified previously with the pairwise GC test were estimated, while all other possible interactions, discarded by the pairwise test, were set to zero. Because all the interactions are modeled at once, some interaction coefficients may differ from the values obtained through the pairwise GC test. For instance, this may occur when the detected interaction was actually attributable to a confounding or a mediating variable not accounted for in the pairwise test, but recovered in the MAR(1) model. In a nutshell, a "confounder" is a third variable that has an effect on both *x* and *y*, and is the cause of the interaction between *x* and *y*, while a "mediator" is a third variable that is impacted by *x* and has an effect on *y*, and is the cause of the interaction between *x* and *y* (Lederer *et al.*, 2019). Therefore, comparing the interaction coefficients derived from the pairwise GC test and the MAR(1) model is another way of evaluating the robustness of the detected interactions: if a given interaction, recovered by the pairwise GC test, remains relevant in the MAR(1) model, our confidence in this interaction is strengthened.

As noted above, the major environmental shift that occurred in the GOL (Feuilloley *et al.*, 2020) has had a considerable impact on densities and body condition of many fish species (Saraux *et al.*, 2019; Bensebaini *et al.*, 2022). Such a drastic environemental event may act as a hidden confounding factor in a multivariate statistical analysis, leading to spurious interactions. In order to investigate this, the effect of a simple covariate describing the three phases of this major environmental shift was included in the SINs previously highlighted. The "Shift" covariate, based on Bensebaini *et al*. (2022), was taken into account in MAR models with effects on species whose interactions could not be explained (for more details of the analysis see Appendix C). The coefficients obtained from the different models (with and without the "Shift" covariate) were compared to each other to assess their relevance (see Appendix C).

3. Results

3.1. Pairwise test: biotic interactions

Regarding the biotic interactions, out of 315 tested links, 10 were retained by our procedure (i.e. about 3.2%, Fig. 3, Table 3) with $G \geq 0.28$ and p-value≤ 0.1, 39 were "weak" with $G < 0.28$ and p-values≤ 0.1 (i.e. about 12.4%, Appendix D: Table D.2), and 266 were deemed irrelevant (weak effect size and large p-value). The 10 retained interactions were rather strong since their associated effect sizes varied between 0.28 and 0.38.

Fig. 4 (the top of the figure) shows an example of a biotic interaction with on the left the two series tested and on the right the scatter-plot of the two time series. Time series show a positive relationship between adult red mullet and juvenile blackbellied angler, and the scatter-plot shows that there is a positive correlation between the two variables. The graphics of the other interactions could be seen in Appendix D: Fig. D.1, and D.2.

The selected biotic interactions were compared to a table of trophic links that may exist between the studied species (Appendix D: Table D.1). This table has been prepared from bibliographic references on the diet studies of the different investigated species in the Mediterranean in general and in the western basin in particular. Finally, an ecological hypothesis has been proposed to the 10 detected links (Table 3), to categorize them into "growth", "stock-recruitment relationship", "predation", and "unknown" when no biotic relationship was documented. Intraspecific interactions were expressed through two sorts of mechanisms controlling the population dynamics; the "growth", for the positive effect of juvenile hake on adult hakes (+0.35), and "stock-recruitment relationship", for the positive effect of adults on juveniles of hake (+0.8), and for the negative effect of juveniles on adults of Horned octopus (-0.42). Among interspecific interactions, "predation" is usually one of the easiest links to identify, such as the positive effect of adult grey gurnard on adult hake (+0.38), adult red mullet on juvenile blackbellied angler (+0.64). The 5 remaining links, i.e., the positive effects of adult blackbellied angler on juvenile hake (+0.77), John dory on juvenile hake (+0.48), sardine on juvenile horned octopus (+0.52), the negative effect of juvenile capelan on sardine (-0.43), anchovy on adult red mullet (-0.51) could not be identified, so they are noted "unknown" in Table 3, as no main hypothesis from literature could be retained to explain them.

3.2. Pairwise test: abiotic drivers

Each biotic time series selected previously is submitted to some exogenous forcings (environmental and fishing pressure). Out of the 84 tests carried out, 6 effects were retained as strong (Fig. 3, Table 4) with $G \geq 0.28$ and p-value≤ 0.1, 13 were "weak" ($0<G<0.28$) but still associated to low p-values (i.e. about 15.5%, Appendix D: Table D.3) and 65 were deemed irrelevant (weak effect size and large *p*-value). The results showed that the selected abiotic effects were not negligible since G_{obs} (observed value of G) varied between 0.28 and 0.84. There was a positive effect of the SST on adult red mullet (+0.34), and phosphate concentration on adult grey gurnard (+0.30); a negative effect of nitrate concentration on sardine (-0.34) and juvenile blackbellied angler (-0.46); a negative effect of demersal trawlers on adult red mullet (-0.46), and juvenile blackbellied angler (-0.44).

The Fig. 4 (the bottom of the figure) shows an example of the effect of an abiotic driver on the density of a species. Time series show a negative relationship between demersal trawlers and adult red mullet, and the scatter-plot shows that there is a clear negative correlation between the two variables. The effects of the other drivers could be consulted in Appendix D: Fig. D.3, and D.4.

3.3. Network characterization and Multivariate Auto-Regressive (MAR) Model

The final step of our analysis was to fit MAR(1) models to the three identified SINs (Fig. 5), in order to investigate whether interactions detected by the pairwise GC tests would still be relevant in a multivariate context. The first MAR model represented a network of statistical interactions between adult blackbellied angler, juvenile and adult hake, adult grey gurnard, John dory, and the effect of nitrate concentration. The second focused on juvenile blackbellied angler, adult red mullet, anchovy, under the combined influence of demersal trawlers, SST and nitrate concentration. The third one included juvenile and adult horned octopus, juvenile capelan, sardine, and the effect of nitrate concentration. Our results show that all interactions but one detected by the pairwise test were also recovered by the MAR(1) model. Most coefficients obtained by the MAR models showed the same sign, but tended to have lower values than with the pairwise GC test. The one interaction that disappeared was the effect of fishing effort of demersal trawlers on juveniles blackbellied angler (the coefficient value changed from -0.44 to -0.06, see Fig. 4). The dominant pattern, though, is that interactions identified by the pairwise procedure still hold in a multivariate context. By adding the effect of the "shift" covariate (Appendix C), the results showed that the values of two interaction coefficients slightly changed in value, i.e., the effect of adult blackbellied angler on juvenile hake, and the effect of juvenile capelin on sardines. In the first interaction, the value went from 0.38 to 0.14, in the second, it went from -0.27 to -0.38. Regarding the autocorrelation coefficients, they were correctly estimated (≠0), except for juvenile hake (-0.05) and juvenile horned octopus (-0.06), whose values were nearly close to zero.

4. Discussion

The aim of this study was to identify the most relevant interactions driving the dynamics of an exploited marine system, using a relatively simple and effective statistical approach. The method was applied to the time series available in the GOL, resulting in the identification of three statistical interactions networks (SINs), which provides basic information to implement an Ecosystem model of intermediate complexity (MICE; Plaganyi *et al.*, 2014) in this area in further studies.

4.1. Effect of environmental drivers

Each of the SINs identified in this study were affected by at least one driver. The importance of nutrient concentration supplied by the Rhône River has already been discussed for the dynamics of pelagic fishes (Feuilloley *et al.*, 2020; Many *et al.*, 2021). Our findings strengthen these conclusions and identify further taxons to which this enrichment matters most (e.g. juvenile blackbellied angler, and adult grey gurnard). The positive effect of temperature on red mullet is consistent with previous studies that indicated a preference for warmer waters by this species (Maravelias *et al.*, 2007; Tserpes *et al.*, 2019), especially regarding recruitment success that may be favored by warmer SST (Levi *et al.*, 2003). This result is further in agreement with stock assessment outputs that tends to document that red mullet recruitment has substantially increased since 2010 in the GOL (STECF, 2023).

4.2. Fishing effects

Concerning the effect of fishing effort, only the effect on adults red mullet has been retained with the MAR, although the fish community of the GOL is known to be under intense fishing pressure since the 1970s (MEDITS, 2007). Still, over the time period studied, time series of fishing effort did not have a strong effect on species dynamics. This apparent lack of fishing effect may be attributed to the fact that the MEDITS time series started in the mid-1990s, so two to three decades after the strong increase in fishing pressure in the GOL (Van Beveren *et al.*, 2016). During the period of growth and development of the fisheries, an increase in fishing effort and catches is usually observed, often followed by a decrease in the abundance of the exploited populations (King, 2007). In the GOL, this period was between the 1960s and 1980s (see also Maurin and Meglio, 1961; Meuriot *et al.*, 1987), and the first signs of overexploitation appeared at the end of the 1980s with a decline in abundance of the most vulnerable species, such as rays and small sharks, and then of the most important commercial species in the 1990s, such as seabass, sole or hake (Aldebert *et al.*, 1993; Alaya, 1996). In other word, all the effect of increase of fishing effort on species density had been already achieved by the time MEDITS started, leading to community dynamics being driven more strongly by environmental drivers and species interactions, with the effects of fluctuations in fishing effort observed during the survey time period being too weak to weigh into the dynamics of species composition.

The fact that environmental factors have had more effect than fishing tend to support that the GOL has been overexploited since decades, as populations that are already overexploited are often more vulnerable to environmental variations (Planque *et al.*, 2010), especially when these variations all occur at the same time. Communities already weakened by overfishing can suffer serious and irreversible ecological following an environmental upheaval, as was the case with the small pelagic community in the in the mid-2000s (Saraux *et al.*, 2019; Feuilloley *et al.*, 2020).

4.3. Statistic versus trophic interactions

Aquatic, and especially marine systems are known to have particularly complex food webs (Link, 2002) composed of hundreds of interacting species. Most of these trophic interactions are weak and do not always lead to detectable effects in terms of predator-prey dynamics. In fact, restricting ourselves to the taxons studied here, the literature review revealed at least 23 trophic links between the studied species (see Fig. 6, Appendix D: Table D.1). Among these links, only 3 have been highlighted by our approach, while 7 interactions would not correspond to documented feeding. This strong discrepancy between expected trophic interactions and the recovered GC interactions (Fig. 6) is a good example showing that trophic relationships should not be the sole driver to build models of marine ecosystem dynamics. For example, in the case of hake, despite their known preference for small pelagics (Mellon-Duval *et al.*, 2017), no links have been evidenced between hake and sardine or anchovy, suggesting that their dynamics are either independent, or not interacting strongly enough to be detected by our analysis. Other studies in the same region have shown that the population dynamics of small pelagic fish (mainly sardines and anchovies) is not affected by the increased abundance of their major predators, such as bluefin tuna (*Thunnus thynnus*) (Van beveren *et al.*, 2017) and dolphins (Queiros *et al.*, 2018). In fact, most of the trophic links issued from our literature survey did not translate into a retained statistical interaction, which suggests that trophic interactions have a rather weak impact on population dynamics in the GOL. In addition, the recovered dynamic interactions are not necessarily attributable to direct trophic interactions, which suggests that non-trophic and indirect interactions have a non-negligible role as co-drivers of community dynamics. There is a growing appreciation of this idea in the field of terrestrial ecology as shown by a study on multi-trophic communities in insects (Kawatsu *et al.*, 2021), or another study on terrestrial plants (Ohgushi, 2008), but still not widely spread in the field of marine ecology. This is probably due to the difficulty of observing indirect interactions in marine environment.

4.4. The unknown interactions

GC provides one approach that, in its most basic form, is relatively easy to implement and rests on a firm statistical foundation. However, GC does not provide any ecological or biological insight on the relationship between the variables. For example, in the case of the positive effect of John dory on juvenile hake, the negative effect of juvenile capelan on sardine, or the negative effect of anchovy on adult red mullet, no clear ecological processes can be advocated to support the observed interactions. These apparently spurious causalities may arise when the interaction actually occur though some other hidden variables not accounted for in the analysis (Hsiao, 1982).

Causal inference requires careful consideration of confounders and mediators. The case of the interaction between adult blackbellied angler and juvenile hake is a good example of confounding effect. The interaction coefficient between the two species was reduced when the effect of the "shift" covariate was added to the model. we can therefore easily deduce that there is indeed a confounding effect of the environmental "shift" on this interaction, but it is not the main cause here, since the interaction has not completely disappeared.

In the case of the negative effect of anchovy on adult red mullet, it could be a third species which is impacted positively by anchovy and has a negative impact on adult red mullet. This third species could be a predator in common for both species whose population is poorly sampled. Putting forward hypotheses likely to explain the underlying process(es) of a causal relationship is not obvious in some cases, and would require more information on the biology and ecology of the studied species. Nevertheless, the absence of logical explanations for some interactions was not an obstacle in itself if the interaction, even if unknown, enabled better prediction of the variable of interest.

4.5. Contribution to the management of the Gulf of Lions Ecosystem.

One important challenge of stock assessment is to include further processes, notably biotic interactions and environmental forcing, to better explain and predict the dynamics of the target stocks. Identifying which process to include, with which covariate, and how to include it can be difficult questions and addressing them requires a certain amount of direct data on biological and ecological processes such as feeding habits, growth, recruitment, or natural mortality (Maunder and Piner, 2015). Our analysis demonstrates how to highlight and combine the different elements of an interaction network while overcoming the lack of data issues using multivariate analysis of time series produced directly from survey data. The SINs identified in the GOL unravel (1) the importance of abiotic drivers (nitrate and phosphate inputs, temperature and demersal trawling effort) on the dynamics of our target stocks; and (2) the coupling between various stock dynamics that could benefit from a joint modeling approach. In addition to the 6 target species initially considered, our analysis revealed the importance of three other interacting species: John dory, grey gurnard and capelan. Two of them (capelan and grey gurnard) are important species in terms of abundance (Certain *et al.*, 2022), and John dory has a great commercial interest (FranceAgriMer, 2022). As such, they are good candidates to be included in the list of potential species to be assessed (Certain *et al.*, 2022).

The MAR(1) models described in our study, in their current implementation, are not designed to provide the classical reference points expected for fisheries assessment or management (see Caddy and Mahon, 1995 for a review of reference points in fisheries management). However, they can serve as a basis for computing Ecologically Sustainable Exploitation Rates ("ESER", see Säterberg *et al.*, 2019) in a multi-specific context, and they can provide long-term projections of log-density under different management scenarios in a context of global warming and taking into account biotic interactions, and this can help to support stock conservation and management (Ward *et al.*, 2014). Indeed, a fitted MAR(1) model can predict the trend of a population over longer period under a “PRES” perturbation (i.e. a change in the mean of a covariate Bender *et al.*, 1984). This kind of projection can provide an idea of the fate of some species that are not modeled in conventional stock assessments (like grey gurnard or blackbellied angler) and are generally considered to be static (i.e. species whose dynamics are not described, see example of the IAM model in STECF, 2022).

5. Conclusion

In conclusion, in this study a relatively simple method has been carried out to statistically detect and select key interactions in an ecosystem from relatively short time series obtained from different data sets. This approach has shown some effectiveness in detecting strong statistical relationships and thus in reducing a complex multivariate system to the most essential interactions. Results showed 3 SINs of intermediate complexity that provide a synthetic overview of the most important biotic interactions and abiotic drivers in the GOL fisheries. This case study showed that there could be some limitations in the use of GC to identify an interaction network within a complex and unknown ecosystem. However, this method remains one of the most appropriate to overcome the problem of lack of data to build ecosystem models in data-limited regions, as well as to restrict the complexity of the ecosystem to a few key interactions and drivers.

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Author's contributions

Bensebaini and Certain: conceptualization, methodology, formal analysis, writing and reviewing. Fromentin, Thebaud, and Gourguet: conceptualization and reviewing. Billet, Jadaud and Hattab: data providing and reviewing.

Data Availability Statement

All aggregated data of densities, fishing efforts, and environmental factors in this study are publicly available on: https://github.com/cyriabens/Git_Statistical_Interaction_Network.git All R codes used in this study are also available on: https://github.com/cyriabens/Git_Statistical_Interaction_Network.git

Conflict of Interest Statement

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.

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Tables

Table 1. Landings in euros and tons of the most fished species in the Gulf of Lions area, cumulated over 2018 and 2020 (compiled from Certain *et al.*, 2022). Species are sorted according to the quantity landed, the economic importance, by category of stock assessment (going from “yes” indicating that a stock assessment exists to “hard” to have a stock assessment), and the availability of routine sampling by MEDITS and PELMED surveys. Species in blue are the targeted species in this study.

Common name	**Scientific name**	**Total value k€ (2018-20)**	**Total landings Tons (2018-20)**	**Survey (MEDITS - PELMED)**	**Stock assessment**
European hake	*Merluccius merluccius*	14307,5	2344,45	Yes	Yes
Red mullet	*Mullus barbatus*	5459,57	1002,91	Yes	Yes
Anchovy	*Engraulis encrasicolus*	3234,2	3165,84	Yes	Yes
Sardine	*Sardina pilchardus*	1820,84	1414,41	Yes	Yes
Blackbellied angler	*Lophius budegassa*	8081,71	1497,23	Yes	Possible
Horned octopus	*Eledone cirrhosa*	5403,65	1602,77	Yes	Possible
Squid	*Illex spp*	2859,69	584,92	Yes	Possible
Capelan	*Trisopterus minutus*	2385,57	1439,93	Yes	Possible
Red gurnard	*Chelidonycthys cuculus*	1541,75	802,31	Yes	Possible
Gurnard	*Triglidae*	1190,97	586,31	Yes	Possible
Mediterranean horse mackerel	*Trachurus mediterraneus*	981,23	1021,77	Yes	Possible
Gilthead seabream	*Sparus aurata*	39473,15	3141,85	No	Hard
European eel	*Anguilla anguilla*	15165,82	2153,20	No	Hard
European seabass	*Dicentrarchus labrax*	15001,64	833,65	No	Hard
Mullet	*Mugil spp*	7629,33	1978,43	No	Hard
Mediterranean mussel	*Mytilus galloprovincialis*	1084,65	779,19	No	Hard
Thicklip grey mullet	*Chelon labrosus*	1061,07	771,42	No	Hard
Common octopus	*Octopus vulgaris*	14605,3	2010,73	Yes	Hard
Octopus	*Octopodidae*	10682,93	1147,71	Yes	Hard
Atlantic mackerel	*Scomber scombrus*	5267,3	2280,26	Yes	Hard

Table 2. The 36 biotic and the 9 abiotic time series used for the pairwise Granger causality (GC) tests, with the time period covered by the series, the data source, and precision on life stage for the biotic series. The 6 targeted species of our study are indicated in blue.

		Scientific name	Life stage	Time series	Source
Biotic time series	**Sardine**	***Sardina pilchardus***	**No stage**	**1995-2021**	**PELMED**
	Anchovy	***Engraulis encrasicolus***	**No stage**	**1995-2021**	**PELMED**
	Spotted flounder	*Citharus linguatula*	No stage	1994-2021	MEDITS
	Four-spot megrim	*Lepidorhombus boscii*	No stage	1994-2021	MEDITS
	Shortfin squid	*Illex coindetii*	No stage	1994-2021	MEDITS
	European squid	*Loligo vulgaris*	No stage	1994-2021	MEDITS
	Surmulet	*Mullus surmuletus*	No stage	1994-2021	MEDITS
	Blue whiting	*Micromesistius poutassou*	No stage	1994-2021	MEDITS
	Angler	*Lophius piscatorius*	No stage	1994-2021	MEDITS
	Common octopus	*Octopus vulgaris*	No stage	1994-2021	MEDITS
	Axilary seabream	*Pagellus acarne*	No stage	1994-2021	MEDITS
	Blackspot seabream	*Pagellus bogaraveo*	No stage	1994-2021	MEDITS
	Common pandora	*Pagellus erythrinus*	No stage	1994-2021	MEDITS
	Common sole	*Solea vulgaris*	No stage	1994-2021	MEDITS
	John dory	*Zeus faber*	No stage	1994-2021	MEDITS
	Red mullet	***Mullus barbatus***	**Adult**	**1994-2021**	**MEDITS**
	Horned octopus	***Eledone cirrhosa***	**Adult**	**1994-2021**	**MEDITS**
	Horned octopus	***Eledone cirrhosa***	**Juvenile**	**1994-2021**	**MEDITS**
	European hake	***Merluccius merluccius***	**Adult**	**1994-2021**	**MEDITS**
	European hake	***Merluccius merluccius***	**Juvenile**	**1994-2021**	**MEDITS**
	Blackbellied angler	***Lophius budegassa***	**Adult**	**1994-2021**	**MEDITS**
	Blackbellied angler	***Lophius budegassa***	**Juvenile**	**1994-2021**	**MEDITS**
	Grey gurnard	*Eutrigla gurnardus*	Adult	1994-2021	MEDITS
	Grey gurnard	*Eutrigla gurnardus*	Juvenile	1994-2021	MEDITS
	Blackbelly rosefish	*Helicolenus dactylopterus*	Adult	1994-2021	MEDITS
	Blackbelly rosefish	*Helicolenus dactylopterus*	Juvenile	1994-2021	MEDITS
	Norway lobster	*Nephrops norvegicus*	Adult	1994-2021	MEDITS
	Norway lobster	*Nephrops norvegicus*	Juvenile	1994-2021	MEDITS
	Greater forkbeard	*Phycis blennoides*	Adult	1994-2021	MEDITS
	Greater forkbeard	*Phycis blennoides*	Juvenile	1994-2021	MEDITS
	Atlantic horse mackerel	*Trachurus trachurus*	Adult	1994-2021	MEDITS
	Atlantic horse mackerel	*Trachurus trachurus*	Juvenile	1994-2021	MEDITS
	Mediterranean horse mackerel	*Trachurus mediterraneus*	Adult	1994-2021	MEDITS
	Mediterranean horse mackerel	*Trachurus mediterraneus*	Juvenile	1994-2021	MEDITS
	Capelan	*Trisopterus capelanus*	Adult	1994-2021	MEDITS
	Capelan	*Trisopterus capelanus*	Juvenile	1994-2021	MEDITS
Abiotic time series	SST	-	-	1982-2021	Copernicus Marine Service
	MLD	-	-	1993-2020	Copernicus Marine Service
	WeMOI	-	-	1821-2020	Cru data
	Rhône flow	-	-	1993-2020	hydro.eaufrance
	P Concentration	-	-	1990-2021	naiades.eaufrance
	N Concentration	-	-	1990-2021	naiades.eaufrance
	F.E. of demersal trawlers	-	-	2000-2020	SACROIS data base and expertise
	F.E. of pelagic trawlers	-	-	2000-2020	SACROIS data base and expertise
	F.E. of seiners	-	-	2000-2020	SACROIS data base and expertise

F.E.: Fishing effort **; P :** phosphate ; **N :** nitrate ; **WeMOI** : Western Mediterranean Oscillation Index ; **MLD** : Mixed Layer Depth ; **SST :** Sea Surface Temperature

Table 3. Results of the selection of the pairwise Granger causality test applied to test biotic interactions (interactions with strong effect, i.e. $G_{obs} \geq 0.28$, and significant, i.e. p-value≤ 0.1). The right column indicates the main hypotheses assigned to the selected interactions.

ID	***x***	***y***	**G_{obs}**	***p*-value**	**b_{11}**	**Main hypothesis**
1	Hake juv	Hake adu	0.38	0.003	0.35	Growth
2	Caplan juv	Sardine	0.37	0.004	-0.43	None
3	G. gurnard adu	Hake adu	0.35	0.004	0.38	Predation
4	Bb. angler adu	Hake juv	0.32	0.006	0.77	None
5	Hake adu	Hake juv	0.3	0.008	0.8	Reproduction
6	J. dory	Hake juv	0.3	0.007	0.48	None
7	Anchovy	R. mullet adu	0.3	0.004	-0.51	None
8	H. octopus juv	H. octopus adu	0.29	0.008	-0.42	Reproduction
9	Sardine	H. Octopus juv	0.28	0.01	0.52	Predation
10	R. mullet adu	Bb. angler juv	0.28	0.007	0.64	Predation

ID: link identifier; b_{11}: the interaction coefficient between the two variables; $G_{obs:}$ the observed value of the effect size; **juv**: juvenile; **adu**: adult.

Table 4. Results of the selection of the pairwise Granger causality applied to test the effects of abiotic drivers (abiotic driver with strong effect, i.e. $G_{obs} \geq 0.28$, and significant, i.e. p-value≤ 0.1).

ID	**Abiotic driver**	**Variable**	$\mathbf{G_{obs}}$	p**-value**	b_{11}
a	SST	Red mullet adu	0.79	0.0	0.34
b	Nitrate concentration	Sardine	0.62	0.0	-0.34
c	Demersal trawlers	Red mullet adu	0.39	0.007	-0.46
d	Nitrate concenration	Blackbellied angler juv	0.37	0.003	-0.46
e	Demersal trawlers	Blackbellied angler juv	0.30	0.024	-0.44
f	Phosphate concentration	Grey gurnard adu	0.28	0.011	0.30

ID: link identifier; b_{11}: is the effect of the covariable at time t on the variable at time t; G_{obs}: is the observed value of the effect size; **juv**: juvenile; **adu**: adult.

Figure legends

Fig. 1. Map of the sampling stations of the MEDITS survey and the radials of the PELMED survey in the Gulf of Lions.

Fig. 2. Process diagram for building the statistical interaction network(s).

Fig. 3. Variation of *p*-values according to G_{obs} values obtained by the pairwise GC tests. On the left, the results of the biotic interaction tests. On the right, the results of abiotic effect tests. In green, the area corresponding to strong and significant interactions ($G_{obs} \geq 0.28$ and *p*-value≤ 0.1). In orange, the area corresponding to weak but significant interactions ($0 < G_{obs} \leq 0.28$ and *p*-value≤ 0.1). In red, the area corresponding to interactions that are weak and not significant.

Fig. 4. Example of graphical representation of time series (left) and scatter-plot (right) for a biotic interaction (top) and an abiotic effect (bottom), both selected with strong and significant interactions: $G_{obs} \geq 0.28$ and *p*-value≤ 0.1) among the results of the pairwise Granger Causality test.

Fig. 5. Diagram of selected biotic interactions and abiotic effects (strong and significant interactions: $G_{obs} \geq 0.28$ and *p*-value≤ 0.1) showing the comparison between coefficients from the pairwise Granger Causality test (in black), and coefficients from MAR(1) models (in orange). 1, 2, and 3 are the three Statistical interaction networks that could be identified and each of them is surrounded by a gray area. The size of the species in the diagram is relative to their average size and according to their life stage (adult or juvenile).

Fig. 6. Diagram of comparison between the causal interactions (in black) highlighted in this study and the trophic interactions (in orange) summarized from diet studies (Appendix D: Table D.1). Bold arrows outline causal interactions that are probably due to trophic links. Dashed

arrows always point from prey to predator. The size of the species in the diagram is relative to their average size and according to their life stage (adult or juvenile).