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Interactions between demersal fish body condition and density during the regime shift of the Gulf of Lions

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Abstract :

Environmentally driven changes in small pelagic fish condition and size have been observed in the Gulf of Lions (GOL) since 2008, leading to a significant fishery crisis. However, the effect of changes in environment and/or in the small pelagic community on the demersal community remain unknown. For the first time, this study examines the body condition (bc) and population density of 22 demersal species since 1994, using dynamic factor analysis (DFA). Most (but not all) of demersal species have shown a common shift between 2006 and 2009, which is synchronous with that observed in small pelagic species and the environmental conditions in the GOL. It had been concluded that the environmentally driven changes detected in the pelagic fish community also affected the demersal fish community, but with less drastic and lasting consequences. As the DFA revealed that the bc displayed important variations for several species, notably hake (Merlucius merluccius), the interaction between the bc and population density was investigated using the Multivariate Autoregressive (MAR) model on hake population at three life stages (recruits, juveniles, and adults). Results showed that adult bc, while negatively affected by density, had a positive effect on recruitment. So hake bc could have affected population dynamics by promoting higher recruitment at low densities. Further work is needed to ascertain whether such effects exist in other demersal species.

Keywords : body condition, demersal fish, dynamic factor analysis, Gulf of Lions, Merluccius merluccius, multivariate autoregressive models

Introduction

The Gulf of Lions (GOL) is one of the most productive regions of the Mediterranean Sea, due to its wide continental shelf and a combination of large inflows from the Rhone River and small-scale coastal upwelling (Millot, 1982, 1990). This area has been intensively exploited for decades, with

total landings reaching 30,000 to 50,000 tonnes from the 1970s to the 1990s, but only amounting to 13,604 tonnes (tuna excluded) in 2018 (STECF, 2019a, 2019b). Today, fish stocks of commercial interest are heavily overfished, according to the report of the State of Mediterranean and Black Sea Fisheries (SoMFi) (FAO, 2018a). It is therefore a high-stakes sector from an ecological, social and economic perspective, where the consequences of unexpected changes could be considerable (Barange *et al.*, 2018).

Around 2008, the pelagic ecosystem of the GOL had shown signs of disruption, characterized by the drastic changes in size, age and condition of its two main small commercial pelagic fish stocks (European sardine, *Sardina pilchardus*; European anchovy, *Engraulis encrasicolus*). This "small pelagic crisis" in the GOL was attributed to slower growth and higher natural mortality in the older age groups (Van Beveren *et al.*, 2014). Different hypotheses about the causes of such changes have been tested and finally seemed to result from a bottom-up control induced by a change in plankton composition and/or density (Brosset *et al.*, 2015; Saraux *et al.*, 2019). Subsequent studies indicated that environmental conditions in the GOL broadly changed in the mid-2000s (Feuilloley *et al.*, 2020). These types of large-scale disturbances are known for their effects on fish species biology, directly – physiological threshold – or indirectly – by modifying the food resource (plankton), thereby affecting bottom-up mechanisms (Jørgensen, 1992). This has consequences on the energy storage dynamics of individuals (Jakob *et al.*, 1996), reflected in their body condition (BC), and ultimately in their natural mortality and growth, affecting population dynamics. Fluctuations in population density and BC therefore provide information on population health. The small pelagic crisis first induced a crash in landings, followed by a historic collapse of the fishing activity in the area (Van Beveren *et al.*, 2016) and the shift of fishing efforts towards demersal stocks, which increased an already unsustainable fishing pressure on the demersal species. As such, the demersal stocks became crucial for the survival of the trawl and small-scale fisheries in the region. The captures during the decade preceding the crisis (outside of tuna catches) were composed of around 3/4 of small pelagic species, mainly sardine and anchovy, and around 1/4 of demersal species, while post-crisis (after 2008) the pattern reversed to 1/3 of small pelagic species and almost 2/3 of demersal species (FAO, 2018b).

While the small-pelagic shift of the GOL has been the center of an intense research activity (summarized in Saraux *et al*. 2019), not much has been done to discover whether demersal stocks have also been affected, since studies on demersal species' BC in the GOL are over a decade old (Lloret *et al.*, 2002, 2008; Ferraton *et al.*, 2007). Similar changes in BC are likely to be observed in the demersal community, especially since many demersal species depend on environmental conditions when they are in a larval or juvenile stage, and, once adult, certain demersal species feed mainly on small pelagic fishes (Banaru *et al.*, 2013; Mellon-Duval *et al.*, 2017). BC can have a strong

impact on growth (Ratz and Lloret, 2003) and natural mortality, as fish in poor condition are more susceptible to disease, predation, and fishery (Martinez *et al.*, 2003). BC can also affect reproduction or reproductive potential, which is crucial for the recovery of a declining stock. Some fish populations in poor condition invest their energy in growth rather than reproduction, reducing fecundity and the quality of the eggs, or leading to delayed maturation (Lambert and Dutil, 2000; Lloret *et al.*, 2008), while others, such as small pelagic fish in the GOL, continue their energy investment in reproduction, whatever their BC, leading to an increased mortality after spawning (Brosset *et al.*, 2016). The search for possible links between BC and population dynamics is therefore interesting.

This paper has two goals. First, we explore the demersal species' response to an ecosystem shift detected in the GOL around 2008. Then, we investigate the population dynamics of a highly documented species, the European hake (*Merluccius merluccius)*, to better understand how BC and density interact at a population level. Hence, the first part of the paper is dedicated to determining whether the BC and/or density of demersal species has changed over time. More precisely, we have looked for common trends between 22 demersal species (in terms of BC and density) and investigated if these common trends match those already detected by Feuilloley *et al.* (2020) in the environmental conditions and small pelagic fish species of the GOL. In the second section, we use the European hake as a study model to examine to what extent changes in BC and/or density could affect one another, using Multivariate Autoregressive (MAR) models. The choice of hake was mostly motivated by its central role in the demersal fishery (Mellon-Duval *et al.*, 2017) and by data availability. Hake was the only species which had enough information available to set up a three-stage population dynamics model suitable for searching for interactions between BC and the density of hake at various stages (recruits, juveniles, and adults).

With this study, we hope to uncover crucial information that helps provide a better understanding of the dynamics of the demersal stocks in the GOL, and ultimately contribute to the establishment of a more ecosystem-oriented approach to fisheries management in this area.

Materials and methods

Data description: The MEDITS survey

Data used in the analyses were collected from annual international bottom trawl surveys performed in May-July since 1994 over the continental shelf (10 m to 200 m depth) and the continental slope (200 m to 800 m) of the Mediterranean Sea through the MEDITS scientific program (Bertrand *et al.*, 2002). The sampling procedures were standardized according to a common protocol over countries and years. The MEDITS survey (Jadaud, 1994) aims to annually estimate and monitor the demersal fish stocks in the GOL and east of Corsica. The current study focuses on the GOL (Figure 1). The fishing gear used is a bottom trawl GOC-73 with 20 mm of stretched cod-end mesh size. The average

vertical and wing opening of the gear are around 2 m and 18 m, respectively. All the tows were performed during daylight hours, 30 min for shelf stations, and 60 min for the continental slope. The MEDITS database documents the distribution and density of roughly 400 Mediterranean species collected over 25 years of sampling. However, for many reasons such as a lack of data or appropriate biological measurements throughout the whole time series (see e.g. Morfin *et al.*, 2012), we restricted our analysis to 22 species that were regularly caught (i.e. there were no missing values in the time series) during the survey and for which length measurements were consistently taken during the whole time period (see Table 1). The survey provides the population density for each species, obtained by dividing the number of individuals of each species obtained in any given trawl by the trawled surface (the annual densities being the average of all densities obtained in any given year for each species, see Supplementary Figure S1). Density is here used as a proxy of abundance in the GOL relative to the trawl catchability, which is assumed to be constant through time, since the fishing protocol has carefully been kept constant since 1994 (Morfin *et al.*, 2012).

Body condition index

To measure the BC, the residual index (Gould, 1975) was used, which is the residual of the length-weight log-linear relationship. Positive residuals indicate the BC is above average, while negative residuals indicate the BC is below average. This index is convenient as it allows to separate the BC from the body size effect (Jakob *et al.*, 1996).

The MEDITS protocol includes systematic measurements of individual size for the 22 selected species, but few of them are individually weighed. In the absence of individual weights for each species and in each haul sample, the data available consists of a total biomass and an associated size spectrum. However, it is still possible to estimate a length-weight relationship from these data. The classical length-weight relationship is written as follows:

$$w_{s,i} = a_s l_{s,i}^{b_s} \quad (1)$$

The $w_{s,i}$ and $l_{s,i}$ are the weight and length of individual i of species s, respectively. The total biomass in one haul h of a given species s, thereafter denoted $B_{h,s}$, is equal to the sum of the n individuals' weight (w_i) contained in the haul h, as described in equation (2).

$$B_{h,s} = \sum_{i=1}^{n} w_{h,s,i} = a_s \sum_{i=1}^{n} l_{h,s,i}^{b_s} \quad (2)$$

Where $B_{h,s}$ is the observed biomass of species s in the h^{th} haul and a_s and b_s are the typical constants of the length-weight relationship of the given species s, and $l_{h,s,i}$ is the length of the i^{th} fish in the h^{th} haul of the species s.

The number of hauls varies slightly from year to year (the average number being 65). To calculate the residual index based on the same number of hauls each year and produce confidence intervals, the residual index time series were extracted using 100 non-parametric bootstraps. For each species

and bootstrap, 40 hauls were randomly selected each year, resulting in a 1000-point data set (40 haul * 25 years). Then the estimates of parameters a_s and b_s were obtained by fitting the equation (2) to the 1000 pairs of $B_{h,s}$ and their corresponding sum of sizes, then finally, residuals were calculated from the fit of the equation (2). Averaging these residuals per year for each bootstrap sample resulted in 100 time series of 25 years, from which the median – and 2.5% and 97.5% quantiles for confidence intervals – were extracted to build the BC index series for each species. These steps are described graphically in Figure 2 and the BC time series can be consulted in Supplementary Figure S2. Furthermore, to check for consistency, bootstrapped estimates of a_s and b_s parameters were compared to parameters from the bibliography, and the obtained results were satisfactory (Supplementary Table S1).

Dynamic Factor Analysis (DFA)

DFA is a dimension reduction technique specifically designed for time series since it takes into account the time factor, unlike other dimension reduction techniques like principal component analysis (PCA) or canonical correspondence analysis (CCA). DFA aims to identify common trends between different time series and relationships between these series (Zuur *et al.*, 2003). It fits linear multivariate autoregressive state-space models with Gaussian errors (Holmes *et al.*, 2018). The model is written as follows:

$$y_t = Zx_t + v_t \text{ where } v_t \sim MVN\,(0, R) \quad \text{(3a)}$$

$$x_t = x_{t-1} + w_t \text{ where } w_t \sim MVN\,(0, Q) \quad \text{(3b)}$$

The y equation (3a) represents the observation process, and the x equation (3b) is termed the state process. The vector y_t of n time series (corresponding to the number of analyzed species, n=22) is modeled as a linear combination of m hidden common trends (x_t vector) and the factor loadings matrix Z, and observation errors vector v_t, which were distributed as a multivariate normal distribution with mean vector 0 and variance-covariance matrix R. The m hidden common trends at time t (x_t) follow random walks with process error vector w_t, which was distributed as a multivariate normal distribution with mean vector 0 and variance-covariance matrix Q (Holmes *et al.*, 2018). For any given time t and species s, the linear form of the model can be written as follows:

$$y_{st} = z_{s1}x_{1t} + z_{s2}x_{2t} + \ldots + z_{sm}x_{mt} + v_{st} \quad \text{(4)}$$

Two DFA were carried out, one for the BC time series and another for the density time series. In both cases, several models were fitted, which had from m=1 to m=3 latent variables, and a covariance matrix R starting from its simplest form "diagonal and equal" (i.e. the same variance and no covariance) to a more complex form "equalvarcov" (i.e. one value for the variance and one for the covariance). Model selection was based on Akaike's information criterion for small samples (AICc;

Burnham and Anderson, 2002) to identify the most parsimonious model containing the least number of common trends without experiencing much information loss. The Multivariate Autoregressive State-Space (MARSS) package developed in *R* (Holmes *et al.*, 2018; R Core Team, 2020) was used to perform these analyses. As input data for the DFA, we used log-transformed and centered density, and standardized BC time series.

Trends identified by this DFA analysis were then compared to the time series retrieved from the study by Feuilloley *et al.* (2020). These authors investigated whether an environmental change could have triggered the small pelagic crisis based on two DFA analyses, one including the time series of 10 biological variables (biomass, condition and size for sardine, anchovy and sprat plus abundance for sardine) and one including the time series of 10 environmental variables (chlorophyll-a (Chla) concentration, Rhone flow, thermal fronts, Sea Surface Temperature (SST), Western Mediterranean Oscillation Index, convection, upwelling, stratification index, N and P nutrient concentration). These two DFA analyses revealed common trends with a shift in the mid-2000's, which led the authors to suggest that changes in environmental conditions could have affected plankton production and hence the small pelagic fish community (Feuilloley *et al.*, 2020). Those two common trends have been thus retrieved and compared with the results of the DFA analyses carried out in this study on the demersal community to investigate a potential match between trends in environment, small pelagic and demersal fish communities in the GOL.

Multivariate Autoregressive (MAR) Model

This part of the study looks for interaction between BC and density, using the Granger causality (GC) concept (Granger, 1969). The basic idea of GC is that a variable x impacts a variable y if it improves the prediction of the latter. This concept can be based on the fitted interaction matrix obtained from a MAR model (Ives *et al.*, 2003; Certain *et al.*, 2018). MAR(p) models, in their linear formula, have demonstrated a particular efficiency in detecting interactions in nonlinear systems (Barraquand *et al.*, 2021). This analysis was based on a conditional GC (Geweke, 1984; Barnett and Seth, 2014), in which, when focusing on the causal relationship between two variables, the confounding relationships are accounted for due to the remaining variables.

We focused on European hake because: (i) it is a well-sampled species and the most documented of the MEDITS survey; (ii) its life cycle is well known and the timing of the MEDITS survey (late spring) has been designed to capture hake recruitment; (iii) it is one of the most important and abundant species of the demersal community in the GOL; (iv) it is a major commercial species; and (v) its BC increased significantly through the study period. European hake is widely distributed in the GOL, with juvenile and young adults concentrated mainly on the continental shelf, and the largest individuals deeper on the slope and canyons (Maynou *et al.*, 2003). Hake is a key predator in this

area, feeding mainly on crustaceans and small benthic fish when juvenile, then switching to a more piscivorous diet at 15 cm (small pelagics and blue whiting representing 40% to 80% of its diet, Mellon-Duval *et al.*, 2017). It is a highly mobile species, with long lifespan and slow growth (Mellon-Duval *et al.*, 2010). The European hake is a batch spawner that spawns throughout the year with a peak in winter (Ferrer-Maza *et al.*, 2014), and recruitment also happens throughout the year with a peak in late spring. Juveniles are fished as soon as they reach a catchable size (i.e. in their first year of life).

A MAR(1) analysis was done using density and BC as variables. Both the BC and density were split into three stages using an age-length key (Bensebaini *et al*., 2019): juveniles (or recruits) age 0-1; juveniles age 1-2; and adults age 2+ (Supplementary Figure S3). Separating adults from juveniles permits the verification of whether maturation and modifications in physiological processes, leading to changes in the body's energy resources management (Kooijman, 2009), affects the BC-density relationship. In addition, natural mortality is higher in juveniles – which are more vulnerable to predation compared to adults (Vetter, 1988) – and possibly act as a confounding factor. Recruits (juveniles age 0-1) were separated from other juveniles (juveniles age 1-2) in an attempt to acquire recruitment dynamics. The MAR analysis was restricted to a one-year lag due to the shortness of the time series (i.e. 25 points), as increasing the lag also greatly increases model dimensionality.

In matrix form, MAR models with one time lag (MAR (1) models) are written as follows:

$$x_t = Bx_{t-1} + w_t \text{where } w_t \sim MVN(0, Q) \quad (5)$$

with x_t a vector whose elements corresponds to the response variables of the model; either total log-density or BC, each being divided by three stages. B is the 6*6 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. w_t is a multivariate normally distributed error vector with mean 0 and variance-covariance matrix Q. Matrix B parameters were estimated by a maximum likelihood estimation using a Kalman filter (Harvey, 1989). Each parameter was considered significant with a p-value lower than a significance level of 5% and was associated with a 95% confidence interval.

Considering the high number of parameters to be estimated in the full model and the relatively short length of the available time series, we designed a specific approach to avoid a potential overfitting issue. To do so, we first set all parameters that had no biological meaning (see Supplementary Table S2) to 0, such as b_{14}, because the BC of the recruits at time t cannot affect the density of recruits at time t+1 (since the latter are not yet born, see Supplementary Table S3). Then, backward elimination was based on the AICc to keep the most relevant coefficients and to penalize overly complex models. However, some coefficients related to the population dynamics have not been included in the

backward elimination because of their key biological meaning: b_{21} and b_{32} (i.e. the growth in density of recruits age 0-1 and of juveniles age 1-2, respectively) as juveniles age from one year to the next; b_{13} (i.e. the adults reproductive output) because adults reproduce and give birth to recruits; and b_{33} (i.e. density-dependent effects within the adult density) because adult density cannot grow indefinitely.

Because the aim of this study is to determine whether recruit density is better predicted with an adult BC effect, The sum of squares of residuals (SSR) of recruit density were computed and compared for the models with and without the effect of adult BC on recruit density.

Results

DFA

For the BC, the AICc (Supplementary Table S4) selected two models as the most parsimonious (ΔAICc=1.9). One contained one common trend and an "equalvarcov" covariance matrix R (i.e. a common variance for all series and common covariance between them), and the other contained two common trends, and an "equalvarcov" covariance matrix R. Both models were tested and showed similar results. However, the model with a common trend (Supplementary Figure S4) had lower factor loadings, probably because a single common trend was insufficient to properly describe the common dynamics of demersal fish BC, which forms the rationale for the selection of the model with two common trends (Figure 3). The first common trend showed a sharp drop in 1994, then a gradual increase from 2006 to 2016. The second common trend displayed a typical regime shift pattern: it dropped sharply between 2006 and 2009, after which it remained below zero until the end of the series. Species with factor loadings (Figure 3) smaller than a threshold of 0.2, in absolute values, have not been included in the interpretation of results (Zuur *et al.*, 2003), as they did not have a particular trend over time. Factor loadings resulting from the DFA on BC (Figure 3) seemed clustered by taxonomic categories, suggesting that the BC of species within a taxonomic group followed a similar temporal dynamics. Cephalopods (three species) mainly displayed negative loadings on trend 2, while perciforms (five species) and John dory displayed positive loadings on trend 2. Pleuronectiforms (two species) were mostly positively associated with trend 1, while gadiforms (four species) and scorpaeniforms (two species) were positively associated with both trends 1 and 2, except hake, which only displayed positive loadings on trend 1. Lophiiforms (two species) were poorly associated with both trends.

When looking at the overall model fits for each BC time series (Supplementary Figure S5), most species showed a good fit with the observations, except for a few species (Norway lobster, blackbellied angler, red mullet, and blackspot seabream series). As several species were associated with both common trends, the contribution of each BC time series to the two common trends was plotted in different colors (Figure 4) to determine at which point in the series the model was more driven by trend 1 or 2. In the shift period (2006-2009), almost all species were driven by trend 2 (i.e. blue points) except for European hake, spotted flounder, and angler, whose BCs were only associated with trend 1 (Figure 3).

For density, the AICc (Supplementary Table S5) selected the model containing one common trend, and an "equalvarcov" covariance matrix R. This common trend (Figure 5) showed low values until 2006, then values quickly increased until 2010, and finally the increase slowed until it reached what appears to be a plateau in 2014. Again, species with factor loadings smaller than 0.2 were not included

in the interpretation of results (bottom part of Figure 5 for factor loading; and Supplementary Figure S6 for density model fits versus observed time series), leaving only shortfin squid and three perciforms (blackspot seabream, common pandora, and Mediterranean horse mackerel), which were positively associated with this trend, while blue whiting was negatively associated with it.

The common trend from DFA on demersal fish densities, the trend 2 from the DFA on demersal fish BC and the common trends of the DFA analyses on environmental conditions and small pelagic fishes in the GOL performed by Feuilloley *et al.* (2020) are displayed in Figure 6. This figure highlights a strikingly concomitant period of shift (2006-2009), when the strongest changes in these four trends occurred.

Multivariate Autoregressive (MAR) Model

The model selected by backward elimination is illustrated in Figure 7. Results show that coefficients that have not been included in the backward elimination (b_{21}=0.01±0.32, b_{32}=0.12±0.40, b_{33}=0.1±0.48) were low and not statistically significant, except b_{13}, which revealed the strong positive effect of the density of adults age 2+ at time *t* on recruits age 0-1 at time *t+1* (b_{13}=0.90±0.46). The density of adults age 2+ at time *t* also had a negative effect on the BC of juveniles age 1-2 (b_{53}=-0.22±0.14), and adults age 2+ (b_{63}=-0.33±0.2) at time *t+1*. Finally, the BC of adults age 2+ had a positive effect (b_{16}=0.83±0.69) on the density of recruits age 0-1 at time *t+1* and was negatively autocorrelated (b_{66}=-0.36±0.29). The calculation of the SSR shows that there was a reduction of the SSR in the model with the effect of the BC, as compared with the model without this effect (a reduction of 17.20%). This means that juvenile density was better predicted when accounting for the BC.

Discussion

One of the first goals of this study was to explore whether the environmentally driven changes in small pelagic fish BC could also be detected in the demersal fish community of the GOL. DFA performed on the BC and density time series of 22 demersal species tended to confirm this impact. This was documented by a common shift between 2006 and 2009 for most (but not all) demersal fishes and a striking synchrony between the common trends extracted from the DFA of this study (on demersal fish) and those performed on the small pelagic fishes and environmental conditions in the GOL (Feuilloley *et al.*, 2020). The authors have clearly depicted an overall change in the environmental conditions of the GOL over the last 30 years, characterized by a rapid decline in Chla concentration in the mid-2000s, a continuous increase in SST, an intensification of coastal upwellings and frontal activities, a decrease in the nutrient inputs from the Rhone river as well as in the deep winter convection and modifications in the regional atmospheric conditions (as described by the Western Mediterranean Oscillation Index). Those environmental changes have probably affected the lower trophic levels (plankton) of the GOL ecosystem, and consequently the small pelagic fish compartment, as already stressed by previous studies (see Saraux *et al*., 2019; Brosset *et al*., 2015). The present study shows that these environmental changes may also have affected the demersal fish community. However, the exact cause and pathways of these changes are yet to be discovered. Hence, the processes through which environmental changes might have affected energy storage and fish BC will probably remain a challenging research topic for the next decade, requiring more theoretical approaches before it is solved.

The BC of many demersal species were both positively correlated with trend 1 (a continuous BC improvement) and with trend 2 (the shift in the mid-2000s). For these species, the contribution of trend 2 is substantial during the shift period (blue points in fig 4), while the contribution of trend 1 is more significant at the end of the time series. Hence the BC of these species (blue whiting, greater forkbeard, capelan, Mediterranean and Atlantic horse mackerel, grey gunnard, blackbelly rosefish and John dory), while momentarily altered during the shift, saw an improvement in recent years, contrary to the small pelagic fishes whose BC has still not recovered up to this day (Saraux *et al*. 2019). This study therefore confirms that, as revealed by BC-DFA in trend 2, the impacts of the shift experienced by the small pelagics in the GOL also affected the demersal system, but without triggering the same drastic and long-lasting consequences at the biological (for most species), ecological and economic level.

The pelagic community (3 major species of small pelagics) appears to have a strong and lasting response to the shift, while the demersal community appears to have more diverse responses in both direction and intensity. Depending on their turnover rates, species respond differently to changes in

the abiotic environment, for example, small pelagic fish that have fast turnover rates react quickly to an abrupt change (Stenseth *et al.*, 2002). Small pelagic fish communities have lower species diversity (Angel, 1993) and are known to have short trophic chains, a short lifespan, and an explosive demography, making them very sensitive to environmental fluctuations (Alheit and Hagen, 2001). Regime shifts were often observed in these communities, like sardines in the California Current (Hill *et al.*, 2015), or anchovies in the Humboldt Current (Guiñez *et al.*, 2014). Conversely, demersal communities often have a greater species diversity (Angel, 1993), live longer and tend to grow slower (Pauly, 1998). They usually display longer trophic chains and are capable of feeding on both benthic and pelagic resources (Garrison and Link, 2000; Bulman *et al.*, 2001). The demersal community food web is therefore generally characterized by higher complexity and modularity, numerous interactions, and these elements are thought to provide a greater stability and inertia to their dynamics (MacArthur, 1955; Paine, 1966; Möllmann and Diekmann, 2012). The difference in responsiveness between small pelagic and demersal systems may explain why the demersal one is usually less affected by environmental changes than the pelagic (Tian *et al.*, 2008; Moyano *et al.*, 2021). It is therefore not surprising that the strong shift signature observed in the small pelagic species of the GOL is only partly mirrored within the demersal community.

The shift period seems to be rather advantageous to cephalopods in terms of their BC. This is particularly interesting as cephalopods are species with a short lifespan that respond very quickly to changing environmental conditions compared to other demersal species (Rodhouse *et al.*, 2014). It has been demonstrated that the increase of water temperature (Mangold, 1983), and the intensification of coastal upwelling (Otero *et al.*, 2016) may have a positive impact on the density and growth of cephalopods and especially the common octopus, as this has been shown in the GOL by Feuilloley *et al.*, (2020). During the shift, a significant and sudden increase in density was noticed for shortfin squid. Again, the increase of shortfin squid density can be explained by the availability of a favorable environment for the development of cephalopods, such as the rise in the SST (Mangold, 1983) and the intensification of upwellings (Otero *et al.*, 2016) during the mid-2000's.

Identifying the precise drivers of BC changes for each species is beyond the scope of the present study, as it requires further species-centered analyses, that would account for both the effects of fishing and the environment. Depending on the species, these drivers are most likely multiple, and our analysis revealed some degree of inter-specific variability in the temporal patterns, but species of the same taxonomic group tended to exhibit similar patterns. In the absence of knowing what triggered the shift in the GOL, it is difficult to provide a clear explanation for this clustering beyond the fact that taxonomically related species may have more similar physiology, diet and behaviour, and so are more likely to be affected in a similar way by any given change.

365 On a more general note, the results of the two DFA show that BC time series have more patterns in
366 common across species than density time series. Such an outcome can emerge from a greater
367 sensitivity of BC to common environmental drivers. If the trend 2 on BC time series displays the
368 same patterns of variations as the small pelagic fish and environmental conditions in the GOL, the
369 gradual increase observed in BC (trend 1), to which most species – except cephalopods and anglers
370 – are positively associated, may result from reduced competition among fishes due to increased
371 fishing pressure. Indeed, it is worth pointing out that the drastic response of the small pelagics to the
372 shift led to a collapse of the fishery, the effort of which has been redirected to the demersal stocks.
373 So increased fishing pressure, due to relaxing (perhaps mostly intra-specific) competition, could be
374 one explanation for improved BC in species positively correlated to trend 1.

375 The objective of the MAR analysis on the hake case study was to determine whether changes in BC
376 may impact population density or vice versa. This analysis displayed the negative effect of the adult
377 density on adult BC, possibly due to intra-specific competition (Hixon and Jones, 2005; Hixon *et al.*,
378 2012), while adult BC positively affected recruitment, most likely through higher reproductive
379 investment, a better quality of eggs and thus higher recruitment success (Booth and Beretta, 2004;
380 Grote *et al.*, 2011). The search for prey by fish larvae and early fish juveniles, as well as predatory
381 escape, is more efficient in developed individuals (with better BC), assuring that they can overcome
382 the critical larval stage with a better survival rate (Brown and Taylor, 1992; Morgan, 2004). Lloret *et*
383 *al.* (2008) also confirmed that maternal condition may affect the reproductive potential of hake in the
384 north-western Mediterranean. Interestingly, hake responded positively to trend 1 of the DFA
385 performed on the BC time series and displayed a continuous positive increase in BC while showing
386 a decrease in density. So, the positive link between BC and recruitment suggests that recruitment of
387 the depleted hake population in the GOL can be enhanced through a higher BC in adults, which may
388 be a mechanism that would partly compensate for population decline due to overfishing (GFCM,
389 2018). The case study of hake clearly demonstrated the importance of investigating the relationship
390 between BC and density for the other species when information is available.

391 In the MAR analysis on hake, the model was unable to detect the growth of recruits age 0-1 to
392 juveniles age 1-2, and then to adult. This lack of apparent connection between ages 0-1 and 1-2, and
393 ages 1-2 and 2+ has multiple explanations. First, natural mortality in the first year is known to be high
394 and variable (because of changes in environmental conditions) for Teleosts, masking cohort tracking
395 from ages 0-1 (Cushing, 1990). Secondly, the area of distribution of the hake population is wider than
396 the GOL (WGSAD, 2019), so immigration/emigration processes with neighboring areas might be
397 another confounding factor. Thirdly, adult hake are known to take refuge in marine canyons (at the
398 shelf break) and are hence more difficult to track by the MEDITS survey. Still, the model was able

to recover a strong positive link between adults' (2+) density and recruits, illustrating that spawning stock density affects to some extent the recruitment in the following year. Such relationships are often difficult to observe in fish populations, mostly because recruitment density is more strongly influenced by environmental variations than spawning biomass (Cury *et al.*, 2014) and because the low survival rate of recruits is unrelated to the fishing activity. But in cases when the fishing effort on adults increased beyond a certain threshold (termed recruitment-overfishing by Pauly, 1984; Sparre and Venema, 1992), stock-recruitment relationships can become more visible in the data, which is precisely the case for hake in GSA 7 (GFCM, 2018).

To summarize, we detected some changes in the BC and density of the demersal species in the GOL that appeared synchronous with those observed in small pelagic fish populations and in the environmental conditions of the GOL, but to a lesser extent. We also highlighted strong interactions between the BC and density in the European hake population, which could partly explain the rather high resilience of this population to high fishing pressure. This is a good reason to scrutinize relationships between BC and density for commercial fish stocks.

Supplementary material

Supplementary material is available at the ICESJMS online version of the manuscript.

Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author or to the second author G. Certain (gregoire.certain@ifremer.fr).

Author's contributions

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

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428 **Table 1.** List of 22 species selected for the DFA analyses with their contribution to the commercial
429 landings, as well as their estimated density (in number and percentage) in the MEDITS survey catches
430 of 2018 (study area: Gulf of Lions).

Species	Scientific name	Density (%)	Density (individuals)	Commercial landings (%)
Horned octopus	*Eledone cirrhosa*	1,38	15263	16.81
Shortfin squid	*Illex coindetii*	1,54	17010	4.23
Common octopus	*Octopus vulgaris*	0,19	2109	8.96
Norway lobster	*Nephrops norvegicus*	0,65	7145	0.13
European hake	*Merluccius merluccius*	5,62	61943	18.13
Blue whiting	*Micromesistius poutassou*	2,69	29698	0.11
Greater forkbeard	*Phycis blennoides*	0,83	9123	0.43
Capelan	*Trisopterus capelanus*	22,88	252325	10.7
Blackbellied angler	*Lophius budegassa*	0,72	7970	11.1
Angler	*Lophius piscatorius*	0,07	746	1.94
Red mullet	*Mullus barbatus barbatus*	4,78	52751	7.11
Surmullet	*Mullus surmuletus*	0,09	1038	1.93
Axillary seabream	*Pagellus acarne*	0,05	502	3.95
Blackspot seabream	*Pagellus bogaraveo*	0,43	4722	0.7
Common pandora	*Pagellus erythrinus*	0,37	4103	3.6
Mediterranean horse mackerel	*Trachurus mediterraneus*	0,35	3905	9.03
Atlantic horse mackerel	*Trachurus trachurus*	50,63	558400	
Spotted flounder	*Citharus linguatula*	0,20	2233	0.09
Four-spot megrim	*Lepidorhombus boscii*	0,32	3522	0.04
Grey gurnard	*Eutrigla gurnardus*	5,84	64402	0.73
Blackbelly rosefish	*Helicolenus dactylopterus*	0,35	3861	0.04
John dory	*Zeus faber*	0,01	103	0.24

Figure 1. Map of the sampling stations of the MEDITS survey in the Gulf of Lions.

Figure 2. Process diagram of BC time series extraction.

Figure 3. Common trends (top part of the figure) for the residual index series obtained by the model with two common trends and an "equalvarcov" covariance matrix R, and the factor loadings on these trends (bottom part of the figure). The dashed grey lines show the threshold -/+ 0.2 (Zuur *et al*., 2003), above which factor loadings will be interpreted.

Figure 4. Contribution of the two common trends represented in Figure 2 to the fitted series of BC of each species. The dotted line represents the effect of the first common trend on each BC time series ($z_{s1}x_{1t}$). The dashed line represents the effect of the second common trend ($z_{s2}x_{2t}$). And the solid line is the model fit ($z_{s1}x_{1t} + z_{s2}x_{2t}$). Colored points represent the proportion of contributions from each trend (example for species *s* and trend 1: $\mathbf{p_{1t}}=z_{s1}x_{1t}/(z_{s1}x_{1t} + z_{s2}x_{2t})$) to the fit of the models (red for trend 1, and blue for trend 2). **(a)** is the "shift" phase (2006-2009).

Figure 5. Common trend (top part of the figure) for the density time series obtained by the model with one common trend and an "equalvarcov" covariance matrix R, and the factor loadings on this trend (bottom part of the figure). The dashed grey lines show the threshold -/+ 0.2 (Zuur *et al*., 2003), above which factor loadings will be interpreted.

Figure 6. Comparison of all common trends obtained by DFA from the current study and the study of Feuilloley *et al*. (2020). The dashed line in blue represents BC trend 2 and dotted line in green represents density common trend. The brown line with points represents the common trend of small pelagics, while the yellow line with diamonds represents the common trend of environmental factors from the study of Feuilloley *et al*. (2020). The shaded area of the graph delimits the period for the shift between 2006 and 2009.

Figure 7. Schematic view of the model selected for European hake *M. merluccius*. Red arrows represent negative effects, green arrows represent positive effects, arrows with non-significant p-value were grayed out. x_1: recruits age 0-1 log density, x_2: juveniles age 1-2 log density, x_3: adults age 2+ log density, x_4: recruits age 0-1 BC, x_5: juveniles age 1-2 BC, x_6: adults age 2+ BC.

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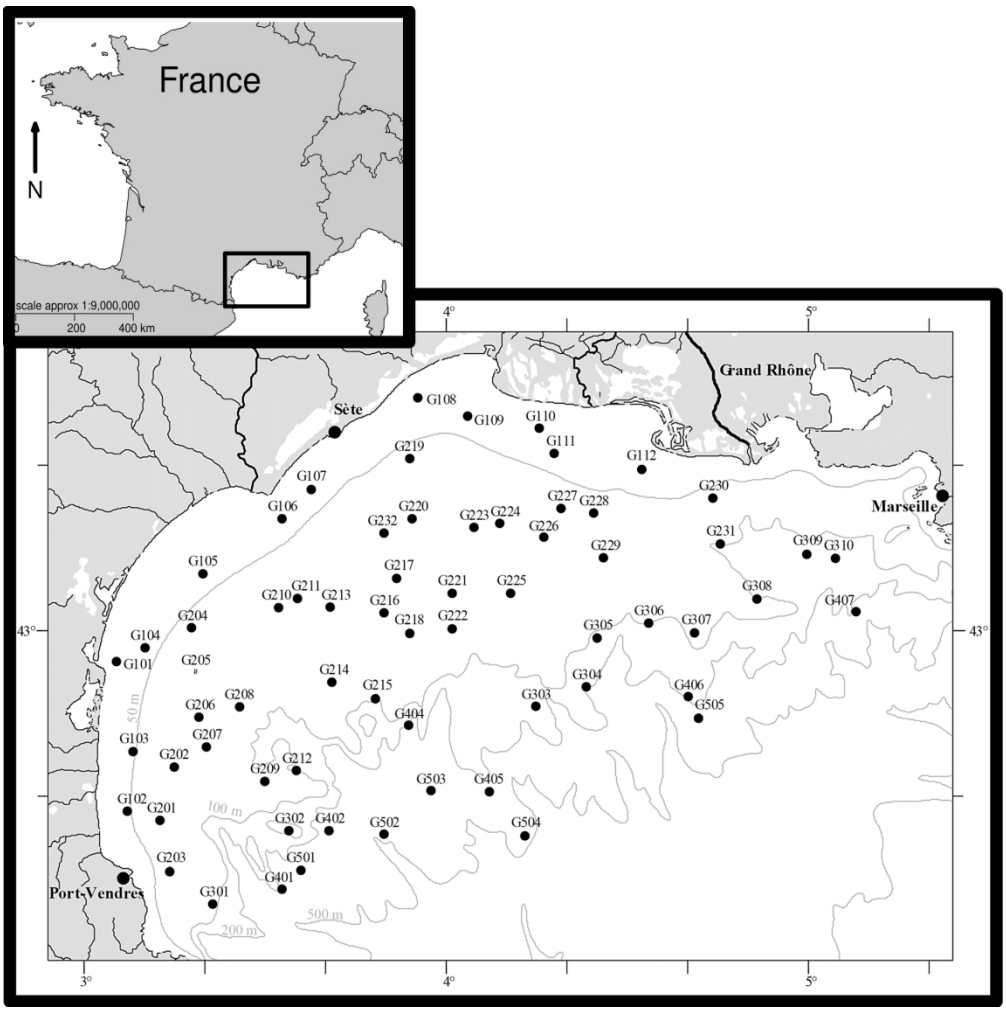

Map of the sampling stations of the MEDITS survey in the Gulf of Lions.

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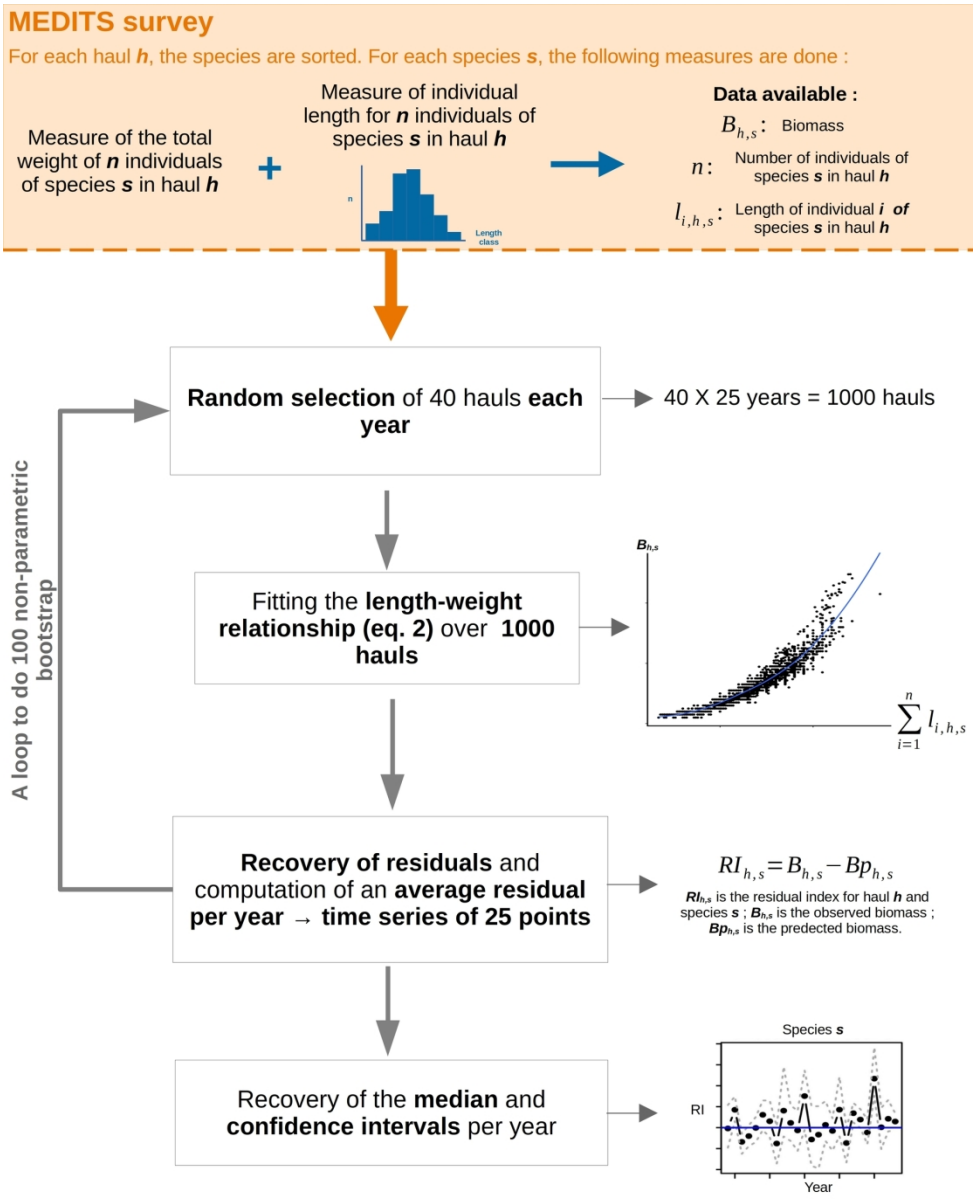

Process diagram of BC time series extraction.

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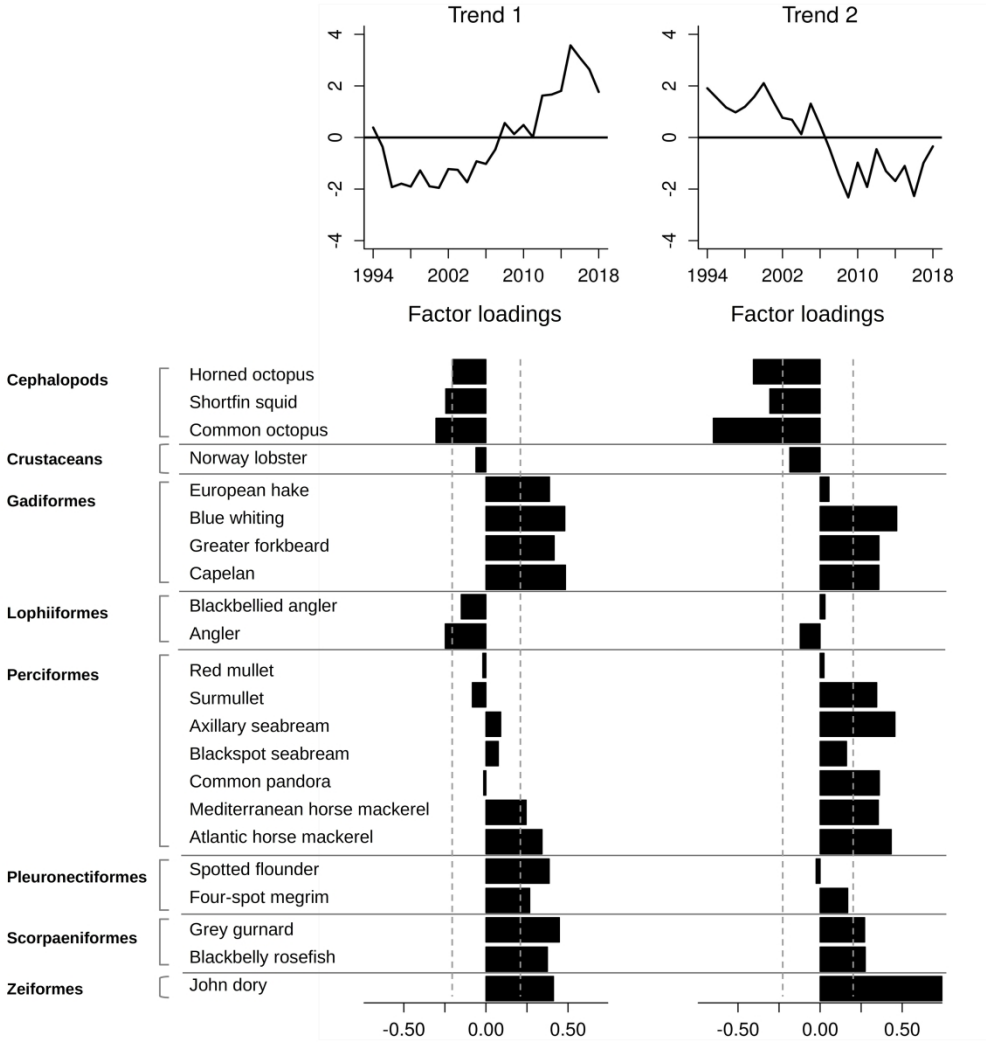

Common trends (top part of the figure) for the residual index series obtained by the model with two common trends and an "equalvarcov" covariance matrix R, and the factor loadings on these trends (bottom part of the figure). The dashed grey lines show the threshold -/+ 0.2 (Zuur *et al*., 2003), above which factor loadings will be interpreted.

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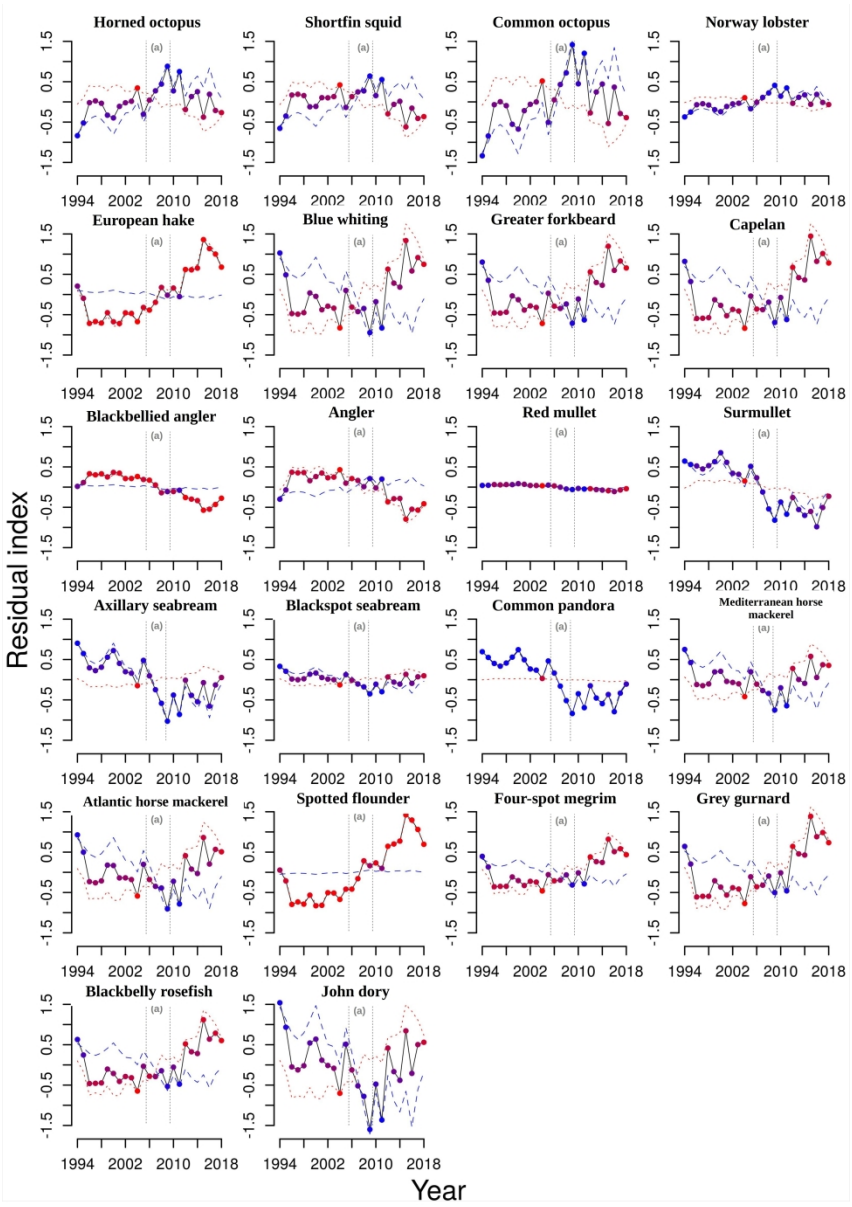

Contribution of the two common trends represented in Figure 2 to the fitted series of BC of each species. The dotted line represents the effect of the first common trend on each BC time series ($z_{s1}x_{1t}$). The dashed line represents the effect of the second common trend ($z_{s2}x_{2t}$). And the solid line is the model fit ($z_{s1}x_{1t} + z_{s2}x_{2t}$). Colored points represent the proportion of contributions from each trend (example for species s and trend 1: $p_{1t}=z_{s1}x_{1t}/(z_{s1}x_{1t}+z_{s2}x_{2t})$) to the fit of the models (red for trend 1, and blue for trend 2). (a) is the "shift" phase (2006-2009).

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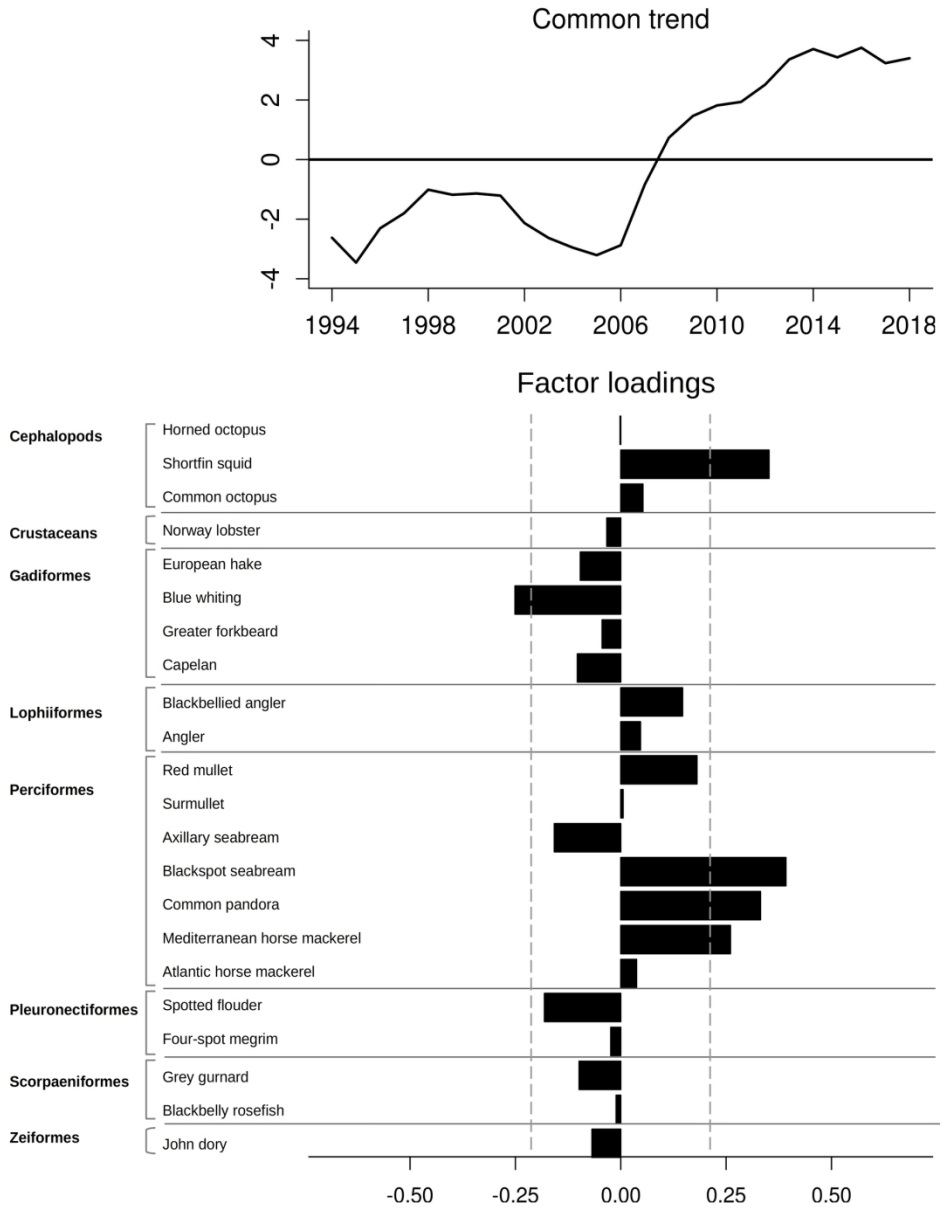

Common trend (top part of the figure) for the density time series obtained by the model with one common trend and an "equalvarcov" covariance matrix R, and the factor loadings on this trend (bottom part of the figure). The dashed grey lines show the threshold -/+ 0.2 (Zuur *et al*., 2003), above which factor loadings will be interpreted.

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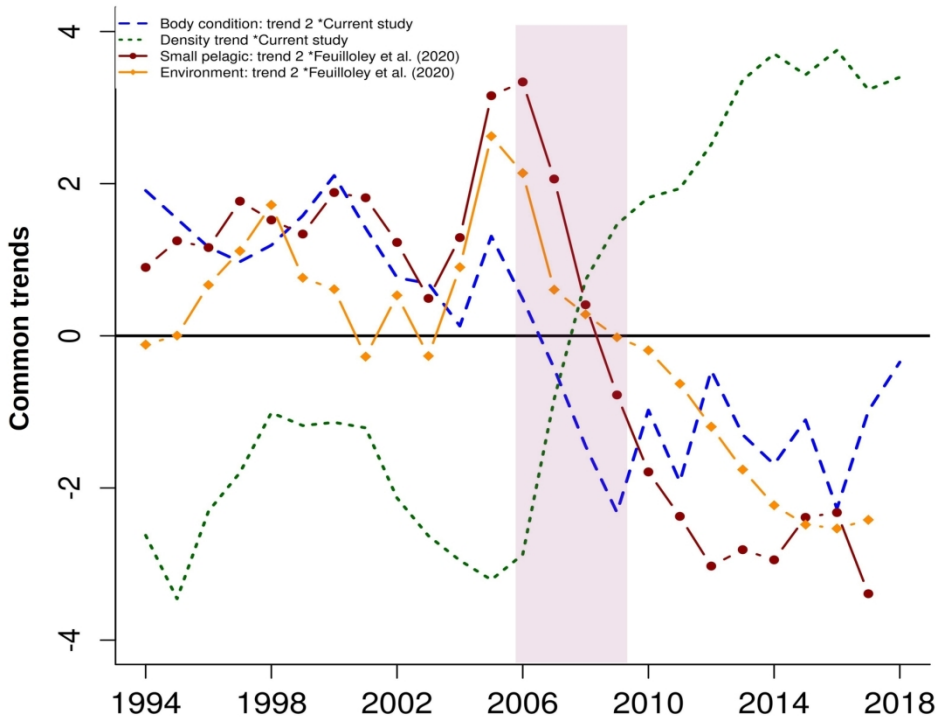
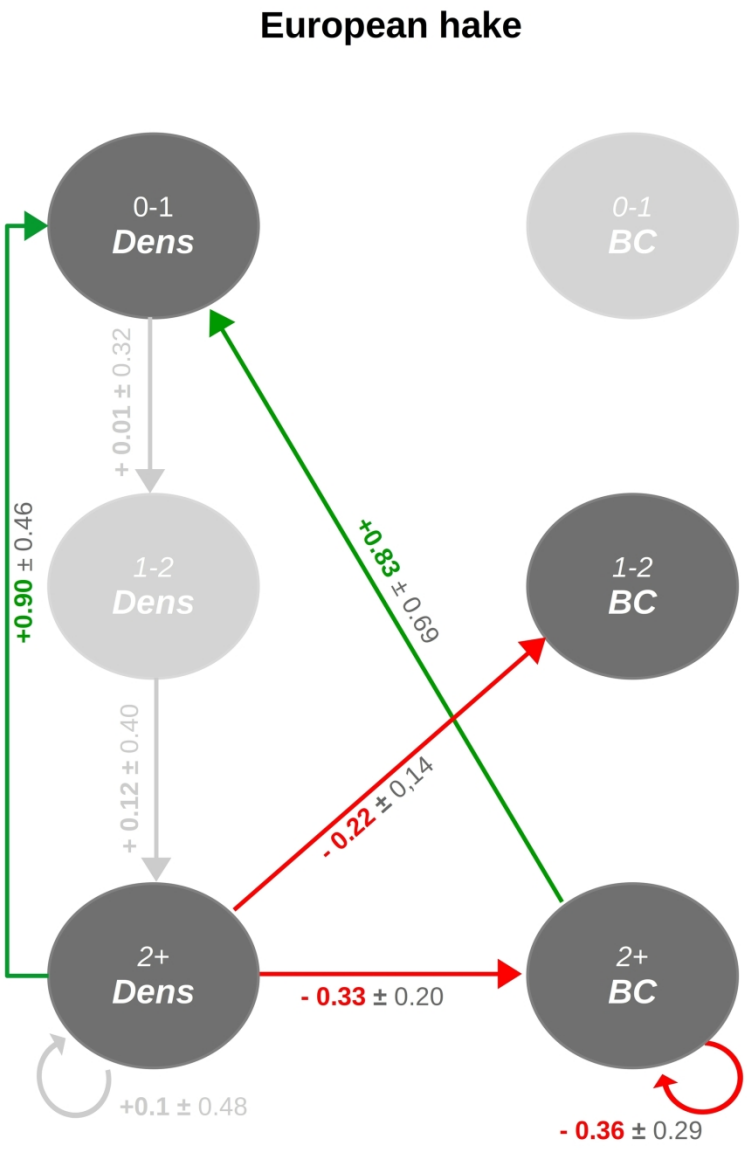


Comparison of all common trends obtained by DFA from the current study and the study of Feuilloley *et al*. (2020). The dashed line in blue represents BC trend 2 and dotted line in green represents density common trend. The brown line with points represents the common trend of small pelagics, while the yellow line with diamonds represents the common trend of environmental factors from the study of Feuilloley *et al*. (2020). The shaded area of the graph delimits the period for the shift between 2006 and 2009.

85x68mm (600 x 600 DPI)



Schematic view of the model selected for European hake M. merluccius. Red arrows represent negative effects, green arrows represent positive effects, arrows with non-significant p-value were grayed out. x_1: recruits age 0-1 log density, x_2: juveniles age 1-2 log density, x_3: adults age 2+ log density, x_4: recruits age 0-1 BC, x_5: juveniles age 1-2 BC, x_6: adults age 2+ BC.

85x127mm (600 x 600 DPI)