Spatial structuring of Mediterranean fisheries landings in relation to their seasonal and long-term fluctuations

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ABSTRACT

The Western Mediterranean fisheries significantly contribute to the regional blue economy, despite evidence of ongoing, widespread overexploitation of stocks. Understanding the spatial distribution and population dynamics of species is crucial for comprehending fisheries dynamics combining local and regional scales, although the underlying processes are often neglected. In this study, we aimed to (i) evaluate the seasonal and long-term spatio-temporal fluctuations of crustacean, cephalopod, and fish populations in the Western Mediterranean, (ii) determine whether these fluctuations are driven by the spatial structure of the fisheries or synchronic species fluctuations, and (iii) compare groupings according to the individual species and life history-based groups. We used dynamic factor analysis to detect underlying patterns in a Landing Per Unit Effort (LPUE) time series (2009–2020) for 23 commercially important species and 33 ports in the Western Mediterranean. To verify the spatial structure of ports and species groupings we investigated the seasonal and long-term spatio-temporal fluctuations and common LPUE trends that exhibit non-homogeneous and species-specific trends, highlighting the importance of life history, environmental and demographic preferences. Long-term trends revealed spatial segregation with a north-south gradient, demonstrating complex population structures of Western Mediterranean resources. Seasonal patterns exhibited a varying spatial aggregation based on species-port combinations. These findings can inform the Common Fishery Policy on gaps challenging their regionalisation objectives in the Mediterranean Sea. We highlight the need for a nuanced and flexible approach and a better understanding of sub-regional processes for effective management and conservation – a current challenge for global fisheries. Our LPUE approach provides insight into population dynamics and changes in regional fisheries, relevant beyond the Mediterranean Sea.

1. Introduction

The majority of marine biota are not distributed uniformly or randomly but rather display grouping structures such as gradients or patches that are dictated by biotic, abiotic and historical factors (Ciannelli et al., 2013; Letourneur et al., 2003). Most of the information on species behaviour, spatial aggregations and their distribution over continental shelves and slopes come from scientific bottom trawl surveys, which are primarily suited to give seasonal snapshots of communities and populations (Maureaud et al., 2021). However, whilst investigating seasonal fluctuations can shed new light on recruitment dynamics and population structure of individual species, fisheries-dependent information can provide an understanding of both seasonal and inter-annual fish and fisheries dynamics. Landings data can be used to reveal the long-term trajectories of populations and can inform of the effectiveness of management efforts and responses to climatic forcing. A combination of spatial and temporal analyses of fisheries landings at small and large scales could therefore provide a more

holistic overview of the primary triggers and the scale of response for both individual species and entire communities, but also how these aggregations and the scale of response relate to the broader objectives set by fisheries management (Alglave et al., 2022; Poulard, 2002). Such knowledge can be particularly relevant for ecosystems with strong ecological and environmental structuring such as the Mediterranean Sea (D'Ortenzio and Ribera d'Alcalà, 2009; Nieblas et al., 2014; Rossi et al., 2014; Veloy et al., 2022), which may constrain the spatial dynamics of local fisheries. The majority of landings on the Spanish Mediterranean coast originate from the vicinity of a port, as fishing expeditions tend to be short and boats tend to stay loyal to their regular fishing grounds, resulting in them usually docking at the same harbour where they are registered (Aragão et al., 2022).

Within European waters, Mediterranean fisheries are worth over $2.7 billion USD and support around 166,000 vessel-based jobs in the area, driving the regional blue economy (FAO, 2022). However, numerous assessments of Mediterranean stocks showed a rapid decline in commercial fish populations, with about 75% of the EU Mediterranean fish stocks currently experiencing overexploitation and anthropogenic pressures (Colloca et al., 2017; FAO, 2018, 2020a; Fortibuoni et al., 2010, 2017; Hassoun et al., 2015). These constraints result in a high and diverse accumulation of threats in a sea of relatively small size, with some of the changes linked to biodiversity shifts and losses (Costello et al., 2010). For example, The increased dominance of thermotolerant, thermophilic species can occur at the expense of stenothermal, cold-adapted organisms due to water warming (Lejeusne et al., 2010). Moreover, a 2009 climate change-associated regime shift in the ecosystem of the Western Mediterranean (WM) has already been reported, with the environmental shift favouring short-lived invertebrates at the expense of opportunistic fish (Hidalgo et al., 2022c; Paradinas et al., 2022). Determining which organisms prevail and for how long complicates short and medium-term management plans, as it can be species-specific and responsive to regional hydrodynamics of the Mediterranean.

The western part of the Mediterranean basin is characterised by high biodiversity combined with spatial and temporal heterogeneity in hydrographic and climatic conditions as well as fisheries structures (Agostini and Bakun, 2002; Gaertner et al., 2005; Nieblas et al., 2014; Rossi et al., 2014). Differences along the north-south gradient help to define five distinct environmental provinces of the WM (Fig. 1a), with higher surface temperature as well as a smaller depth profile in the north and high and changeable primary productivity toward the south near the Strait of Gibraltar (Coll et al., 2010; Nieblas et al., 2014; Veloy et al., 2022). This spatial structure contributes to complex population dynamics and species-specific spatial and temporal patterns, associated with responses to changes in local conditions and fishing pressure based on life traits and population demography (Keller et al., 2017; Pecuchet et al., 2017; Quetglas et al., 2013; Rouyer et al., 2011). Due to the environmental heterogeneity along the coastline, the structures of seasonal and long-term responses of the same species might not be uniform across regions, posing a challenge to assessment and for management (Hidalgo et al., 2008; Puerta et al., 2015, 2016).

Considering the historical trends of stock decline in the Mediterranean and its exploitation (FAO, 2022), knowledge of past and present structures of WM marine communities can help not only to understand how WM multispecies fisheries will change in the future, but also how to improve their assessment in the present by distinguishing between local and regional scale processes. Under the overarching hypothesis that continued yet heterogeneous alterations to WM marine population dynamics can be expected on seasonal and temporal scale, this study aimed to *(i)* evaluate the seasonal and long-term spatio-temporal fluctuations of commercial species populations along the WM coastline (2009–2020), *(ii)* ascertain whether these fluctuations respond to the spatial structure of the fisheries or the synchronic fluctuations of species, *(iii)* assess how the overall models represent the trends in comparison with individual species models. By utilising LPUE data from ports along the south-eastern Iberian Peninsula coast and the Balearic Archipelago, this analysis provides insight not only into the population dynamics but also into the changes in regional fisheries, which could see broad application beyond the Mediterranean Sea.

2. Materials and methods

2.1. Data sources

Spanish fisheries landings data between 2009 and 2020 were obtained from the Ministry of Agriculture, Fisheries and Food (MAPA) of Spain. Daily weights of landings at species level were standardised for monthly Landing Per Unit Effort considering the weight of landings per fishing trip (LPUE; kg fishing trip^{-1}), which was used as a proxy of local abundance. The mean monthly LPUE was calculated for each landing port and each species per month and year based only on the landings from bottom trawling vessels (outrigger, twin otter and beam trawls; single and pair boat trawls) that operate on a daily basis.

The initial dataset with 74 species (Supplementary Materials (SM) Table 1) and 113 landing ports (i.e. ports where the landings were registered on return; Fig. 1a) was filtered through a four-step selection process to include only the most relevant port-species combinations (see SM for details, Supplement 1; SM Figs. S1–2). The northernmost port considered was Rosas while the southernmost port in the Western Mediterranean retained was Estepona. All the other ports located closer to the Strait of Gibraltar were discounted due to possible fishing outside

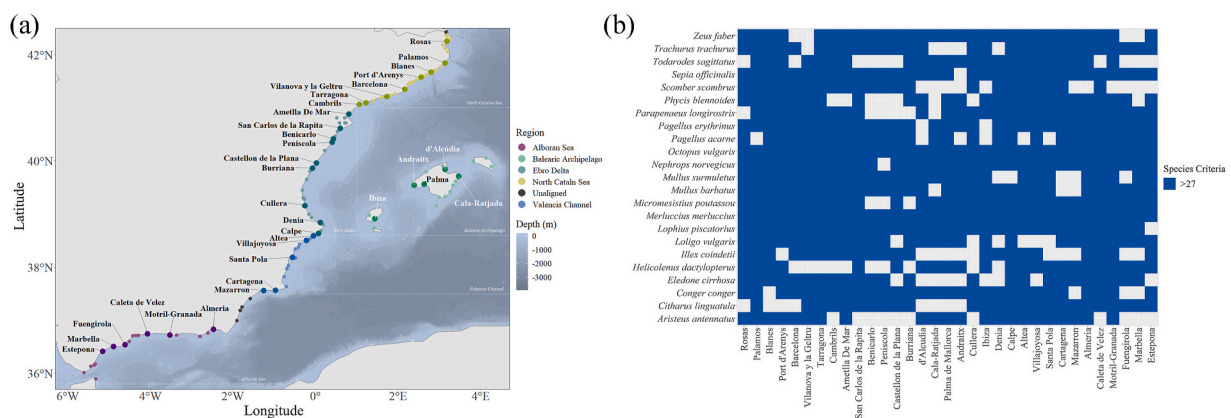**Fig. 1.** (a) Locations of landing ports, with colours separating five identified regions of Spanish Western Mediterranean and the unaligned ports (grey). The labelled ports were used in the final analysis while the other ports were eliminated during the selection process. (b) The final combination of landing ports and species present in the investigated region that were used for the analysis.

of the Western Mediterranean (Fig. 1a). The selection process resulted in the final 23 species and 33 ports that were subsequently used in the regional Dynamic Factor Analysis (Fig. 1, SM Tables S1 and 2).

As an additional step for the species-specific analyses, a second subset of six species was chosen from among the 23 species. These species were selected based on their different life histories (SM Table 1), widespread coverage along the WM coast, consistent occurrence throughout the years and ports (Fig. 1b), as well as high importance within the demersal fishery (FAO, 2022). The six species selection included long and short-lived fish, cephalopods and crustaceans with demersal, pelagic and benthic lifestyles. This subset comprised: common monkfish (*Lophius piscatorius*), Norway lobster (*Nephrops norvegicus*), European hake (*Merluccius merluccius*), common octopus (*Octopus vulgaris*), deep-water rose shrimp (*Parapenaeus longirostris*), blue whiting (*Micromesistius poutassou*). Those six species were used for separate, individual models to assess the consistency of the regional models' outputs and evaluate how well they represent the trends for distinct species with unique characteristics.

2.2. Time series analysis

A preliminary time series (TS) analysis to obtain the individual decomposition components was performed separately for each species in each of the ports between January 2009 and December 2020. The aim was to obtain both, long-term (interannual) and seasonal (monthly) trends together with the random component obtained from the decomposition, later referred to as TR and SR, respectively (SM Fig. 3). The decomposition of the obtained TS was conducted by extracting the opposite decomposition component from the observed values (SM Fig. 2) for *Merluccius merluccius*. In case of incomplete records, missing data was first interpolated for existing port-species combinations using linear interpolation. Due to the mismatch between records from 2015 and other years and to avoid biased time series analysis outputs, the entire year was eliminated before fitting the statistical models. Finally, the TS outputs obtained from the decomposition analyses were log-transformed before being graphically represented.

2.3. Dynamic factor analysis (DFA)

Dynamic Factor Analysis (DFA) with latent processes modelled as random walks (Zuur et al., 2003a,b) was used to determine the underlying common trends within the SR and TR calculated from the LPUE TS analysis, both spanning 11 years (discounting the eliminated 2015), for the 23 species in the 33 associated ports located in the five subregions of the WM (North Catalan Sea, Ebro Delta, Valencia Channel, Alboran Sea, Balearic Archipelago; Fig. 1), identified from previous literature (Veloy et al., 2022). In the DFA, new variables (factor loadings) are created in order to explain the majority of the variation in the data and in this case, how different ports are associated with the common trends (i.e. dimensions) identified. The common trends are smooth functions with the smoothing estimated in the two-step expectation–maximization (EM) algorithm. Those dynamic factor models (DFMs) belong to the family of Multivariate Autoregressive State-Space (MARSS) models, available through the R MARSS package (Holmes et al., 2012, 2021a,b), and constitute a state process (Equation (1)) and observation equations (Eq. (2)):

$$m_t = m_{t-1} + w_t \text{ where } w_t \sim MVN(0,I) \quad (1)$$

$$y_t = Zm_t + a + Dd_t + v_t \text{ where } v_t \sim MVN(0,R) \quad (2)$$

DFA models sets of observed times series (*n*) as a linear combination of unobserved trends (*m*; where $m \ll n$), factor loadings (*Z*), error terms (*w*, *v*), additional model parameters specifying the DFA model (*a*) and optionally the covariates (*Dd*) to explain temporal variability (Eq. (1) and (2)), although the latter was not implemented in this work. The model components are assumed to be stochastic. The correlation of the observation errors can be specified with one of four potential error matrices (unconstrained, equalvarcov, diagonal and equal, diagonal and unequal). The calculated factor loadings demonstrate the resemblance of each time series to the common trend.

Here, two separate pathways of DFA were implemented. For the selection of the six species (SM Table 1) with different life history traits, the individual DFA (iDFA) was conducted (SM Table 3), while the regional DFA (rDFA) included the entire community present in each WM region (SM Table 4). The DFAs were run considering two possible trends to balance the complexity and accuracy of the model, and four matrix structures for iDFA or three for rDFA as the unconstrained matrix resulted in an unstable solution, possibly due to the volume of the data and its homogeneity. Models were fit separately for SR and TR until convergence, with the exception of the iDFAs with unconstrained error structure, Ebro Delta rDFA with the equalvarcov matrix structure and all Alboran Sea long-term time series rDFAs, which did not reach convergence (at maximum iteration >100,000). However, repeated fits of the models at constant iteration resulted in the same values for the computed factor loadings, indicating uniform and clear direction of the model solution calculations, despite non-convergence between trials. As such, the models were retained for further selection. The best model structures for the DFA for each time series were selected based on the lowest Corrected Akaike's Information Criterion (AICc) (Holmes et al., 2021a,b; Zuur et al., 2003a,b).

In all DFA analyses performed, the ports were segregated by latitude, from south to north. For visual analysis, factor loadings were differentiated based on species' habitat (benthic, benthopelagic, demersal, pelagic), lifespan and growth (denoted by the K constant) sourced from the FishBase and SeaLifeBase websites (Froese and Pauly, 2022; Palomares and Pauly, 2022) available in the Supplementary Materials.

All exploratory and statistical analyses were performed using R (version 4.2.1) through R studio software (R Core Team, 2023). Handling was supported by the use of packages included in 'tidyverse' (Wickham et al., 2019). For the DFA analysis, the MARSS package was used (Holmes et al., 2012, 2021a,b).

3. Results

The best model structures from DFA were obtained by comparing the goodness of fit of different variance and covariance matrices of the error terms for the observations and the number of trends (SM Tables S1–4). The best fits for all the iDFA and rDFA included two common trends (hereafter trend 1, T1, and trend 2, T2) with the exception of iDFA blue whiting which had one common trend for the SR time series.

3.1. Individual species DFA

3.1.1. Underlying trends for the seasonal component

Patterns present in the seasonal analysis revealed the importance of port location, with marked groupings observable along the latitude gradient (Fig. 2a–f). Three general seasonal patterns could be distinguished: a summer peak (T2 common monkfish, European hake, deep-water rose shrimp; T1, T2 Norway lobster; T1 common octopus), an autumn peak (T1 common monkfish, European hake, blue whiting) and a winter peak (T2 common octopus; T1 deep-water rose shrimp). On balance, the Balearic Archipelago resonated more strongly with the summer trends for most species, while the mainland presented a more varied and species-specific response.

The summer and autumn trends for the common monkfish were structured over the mainland area in a nearly alternating fashion (Figs. 2a and 3a). Conversely, for the Norway lobster, T1 and T2 followed a similar pattern in the same timeframe, with an increase over the summer months and a decrease in winter accompanied by mostly positive factor loadings (Figs. 2b and 3b). The ports in the south were associated more with the spring/summer trend T1, while the north was influenced most by T2 with the peak in June (Figs. 2b and 3b). Centrally
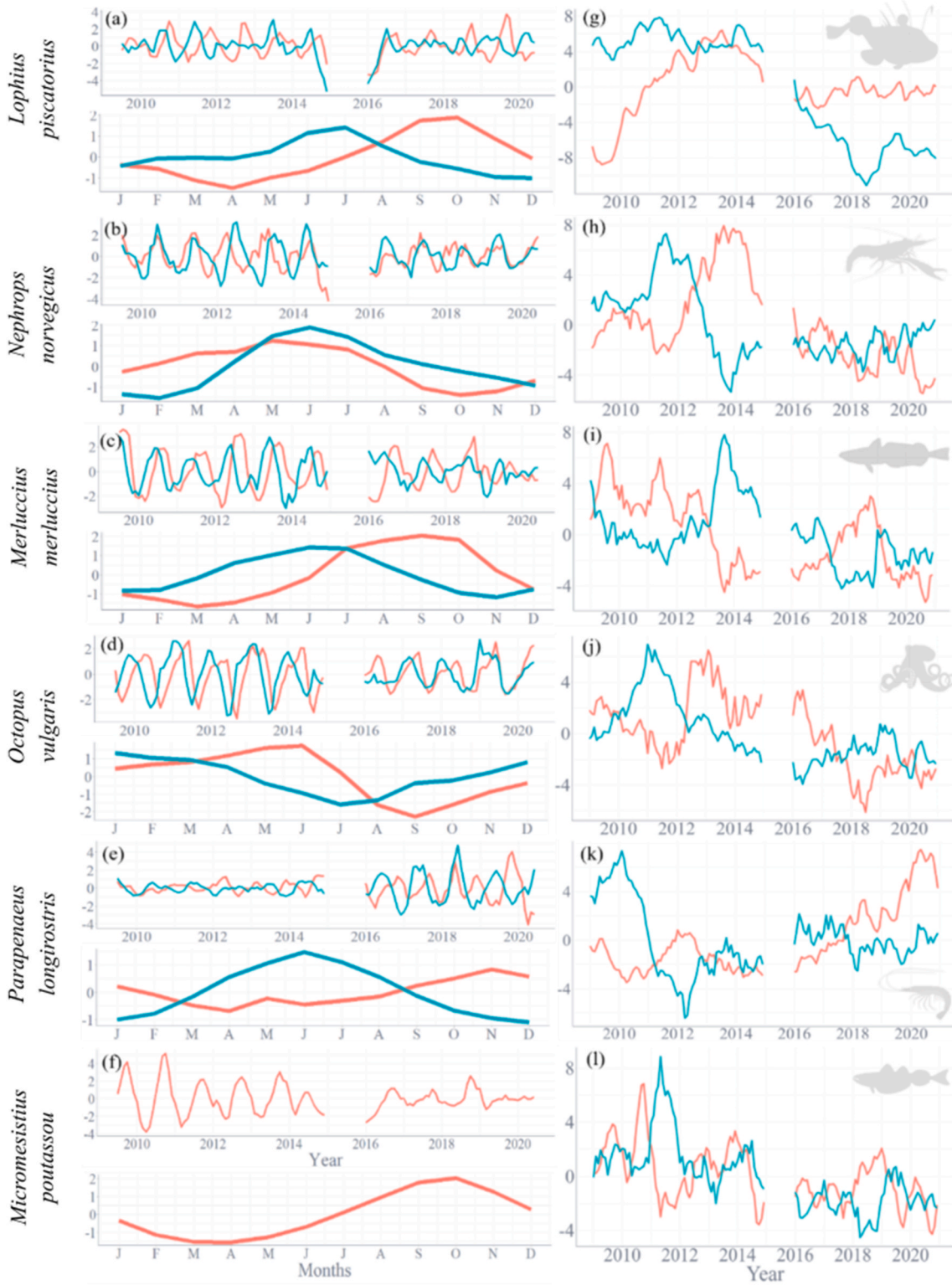
Fig. 2. Seasonal (left; a-f) and long-term (right; g-l) individual species DFA outputs. Underlying seasonal common trends (top) are presented with averaged seasonal patterns (bottom). Common trends in orange – trend 1 (T1); blue – trend 2 (T2). All axes are unitless. Y-axis represents the magnitude of the common trends.

located ports, including the archipelago, were nearly equally driven by both trends. The Balearic ports located in the northeast were associated with T2 more than ports in the south responding to T1.

A trend with a peak in June (T2) was also observed for the European hake, although factor loadings were predominantly low or negative, especially in the north, indicating an opposite behaviour (Figs. 2c and

3c). The autumn trend dominated, particularly in the southern part of the North Catalan Sea, Ebro Delta and Palma de Mallorca (Figs. 2c and 3c). For the octopus, the LPUE in the southern ports, including the Alboran Sea and Valencia Channel, and the Balearic Archipelago was associated with the spring/summer trend with an increasing strength toward the south (Figs. 2d and 3d). Central and northern mainland ports
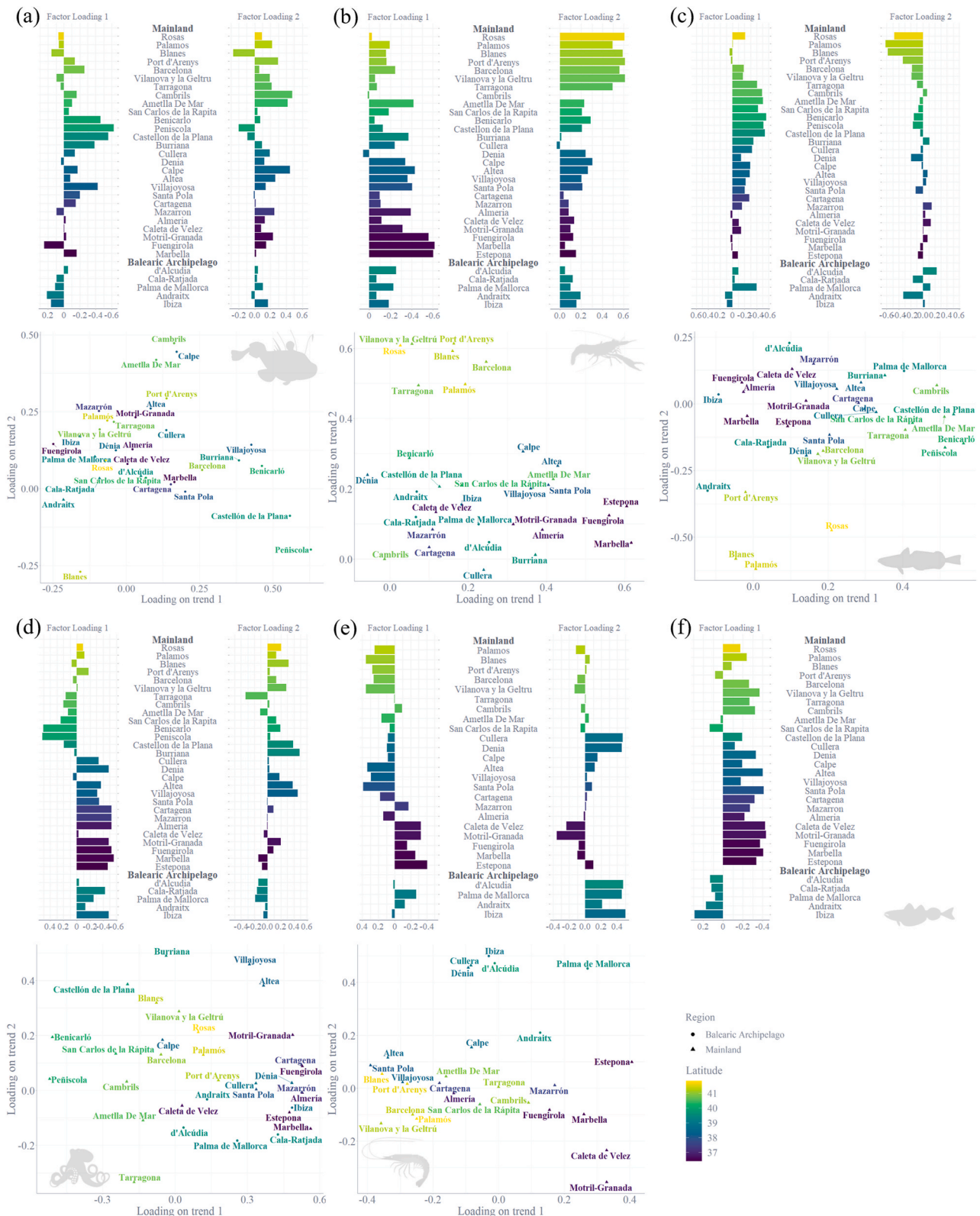
Fig. 3. Seasonal individual species DFA factor loading outputs. All axes are unitless. The ports are sorted by latitude, from south to north and separated by mainland and archipelago. (a) *Lophius piscatorius*, (b) *Nephrops norvegicus*, (c) *Merluccius merluccius*, (d) *Octopus vulgaris*, (e) *Parapenaeus longirostris*, (f) *Micromesistius poutassou*. Factor loadings on trend one (left), trend two (right) and scatter plot of both (below).

were better defined by the winter trend. The factor loadings for the T2 of Islands and T1 of Ebro delta were negative, indicating opposite patterns. In the case of the deep-water rose shrimp, the winter trend T1 was prominent in the southern parts whilst an opposite pattern was indicated for the rest of the mainland. Few ports from the Valencia Channel and Cullera port, together with the archipelago resonated strongly with T2, suggesting that the highest LPUE occurred there in the summer (Figs. 2e and 3e). The remaining locations were characterised by negative factor loadings, pointing towards an opposite pattern in the shrimp LPUE. Finally, the seasonal analysis of the whiting revealed only a single underlying trend with a peal from September to October and a clear geographic gradient decreasing from south to north (Figs. 2f and 3f). Negative factor loadings for the Balearic Archipelago indicated an opposite seasonal trend in the region.

3.1.2. Underlying trends for the long-term component

Despite a period of an increase in landings evident for most species between 2010 and 2014, an overall decrease in landings can be observed for all species, with the exception of T2 of the deep-water rose shrimp (Figs. 2g–l). Landings of the common monkfish resonated strongly with the T2, where, after a relatively stable pre-2015 period, the LPUE trend dropped abruptly with a slight recovery in 2019 (Figs. 2g and 4a). On the other hand, T1 showed a milder decline that stabilised after 2016. The North Catalan Sea and Balearic Archipelago followed the decreasing trend while the Ebro Delta showed a more stable trend.

For both, Norway lobster and European hake, T1 and T2 presented time-lagged peaks and alternating fluctuations post-2015 (Figs. 2h, i and 4b, c). T1 of the lobster showed low values in the early 2000s, with a sharp increase leading to a peak in 2013–14 while T2 reached a maximum peak earlier, in 2011–12. A geographic, opposite gradient of dominance for T1 and T2 from south to north was visible (Figs. 2h and 4b). In the case of hake overall increasing dominance gradients from south to north and, although less visibly, north to south can be seen for the T2 and T1 respectively.

The patterns of the common octopus trends were most comparable to Norway lobster, although the 2014 drop in T2 was not as sharp and the range of fluctuations was greater for the cephalopod (Figs. 2j and 4d). Mainland factor loadings of the common octopus were also consistently higher for the delayed T1, while the archipelago was better described by the early T2, with the exception of Ibiza (Figs. 2j and 4d). For the deep-water rose shrimp, long-term trends of the deep-water rose shrimp were in complete opposition to each other (Fig. 2k). However, the increasing trend T1 was less influential, dominating the most northern part of the North Catalan Sea and having little influence on the remaining mainland and island locations (Figs. 2k and 4e). For blue whiting, both trends decreased after 2015, with a partial recovery throughout 2018 (T1) and 2019 (T2) (Fig. 2l). All factor loading estimates were, except for Ibiza, positive and indicated that all trends have some influence over the investigated region and a mild geographic gradient can be discerned for both trends (Figs. 2l and 4f). Northern ports and the Balearic Archipelago were described more by the slightly delayed T2, while the southern ports formed a grouping associated primarily with the early T1.

3.2. Regional DFA

The regional analysis has revealed unique trends across the Iberian Peninsula and the Balearic Archipelago. Here, two contrasting cases are included: the North Catalan Sea and the Balearic Archipelago (Fig. 5). The remaining visual representations of the trends and corresponding factor loadings (per port and classified based on species' lifespan and habitat) for the other regions are available in the Supplementary Materials (SM Figs. 4–11).

3.2.1. Underlying trends for the seasonal component

Based on the season when the peaks of the trends were observed, three general patterns could be discerned (Fig. 5a–b; SM Fig. 4a–c):

winter/early spring peak (T2 Alboran Sea, Balearic Archipelago; T1 Valencia Channel), summer peak (T1 Alboran Sea, North Catalan Sea, Ebro Delta, Balearic Archipelago; T2 Valencia Channel) and autumn peak (T2 North Catalan Sea, Ebro Delta). The factor loadings presented a diverse combination of positive and negative scores, although negative loadings dominated in some ports.

For the North Catalan Sea, T2 lagged behind T1, reaching its peak in autumn (Fig. 5a). Benthic species were more affected by the summer trend (T1), while demersal and pelagic species, associated with autumn/winter trend (T2) (Figs. 5a and 6a). The T1 for the Ebro Delta had a wider span than the North Catalan Sea, starting in April and slowly declining over August and September (SM Fig. 4a). Similarly to their northern neighbours, demersal species of the Ebro Delta were connected to the autumn trend, although pelagic species were more consistently associated with the summer trend (SM Figs. 4a and 5). No clear latitudinal gradient was present and the responses of other habitat classes were more port-specific. In contrast to the Ebro Delta and the North Catalan Sea, species from the Valencia Channel and the Alboran Sea displayed greater association with the late summer trend. Notably, *O. vulgaris* correlated strongly with the early spring trend, most resemblant of the T1 dominant in the southern regions in iDFA. In the Balearic Archipelago, the benthic, benthopelagic and pelagic species showed a greater dependence on the summer trend whilst the winter/early-spring trend resonated stronger with the demersal class, as seen in the North Catalan Sea (Figs. 5b and 6c).

3.2.2. Underlying trends for the long-term component

With the exception of the Alboran Sea and the North Catalan Sea, regions did not show a universal decrease or increase, with trends heading in both directions (Fig. 5; SM Fig. 4). However, the period between 2012 and 2016 remained a reoccurring, important moment where the biggest shift transpired for both trends in nearly all investigated regions. In terms of the timing in the long-term trend changes, three main groups can be distinguished: decrease in the trend prior to 2012 (T2, T1 Balearic Archipelago, Ebro Delta; T2 North Catalan Sea, Alboran Sea); increase in the trend until around 2015 followed by a decrease (T2 Valencia Channel; T1 Alboran Sea, North Catalan Sea) and increase in the trend past 2015 (T1 Balearic Archipelago; T2 Ebro Delta). High factor loadings on the first and second group trends in combination with negative factor loadings for the third group indicate a progressing decline in the LPUE of mainland regions (Figs. 5–6; SM Figs. 4–6). The similarities in trend patterns of non-neighbouring regions are noteworthy, particularly the North Catalan Sea and the Alboran Sea, located on opposing sides of the peninsula. The factor loadings for the North Catalan Sea were primarily positive, indicating that most species were affected by one or both of the trends, with a slight dominance of the initially increasing T2 (Fig. 6c). The Balearic Archipelago, with a decrease in T2 over time with a simultaneous increase in T1, presented a more even distribution between the influence of the two underlying trends, with no clusters forming based on port or habitat classification (Fig. 6d–SM Fig. 11).

The groupings based on habitat, lifespan and K were investigated although neither of those traits showed consistent and distinct groupings or patterns across all five regions (SM Figs. 8–11). Some of the smaller clusters identified resulted from the aggregation of the same species across different ports, rather than a common habitat class within the same port.

3.3. DFA results overview

Seasonal and long-term spatio-temporal fluctuations of Western Mediterranean fisheries landings showed that two common trends were best at representing the underlying changes in the LPUE, highlighting a clear difference in responses on species and regional levels. Both analyses also revealed a long-term LPUE decline, affecting five out of six species and the region as a whole. Seasonal synchronies were visible
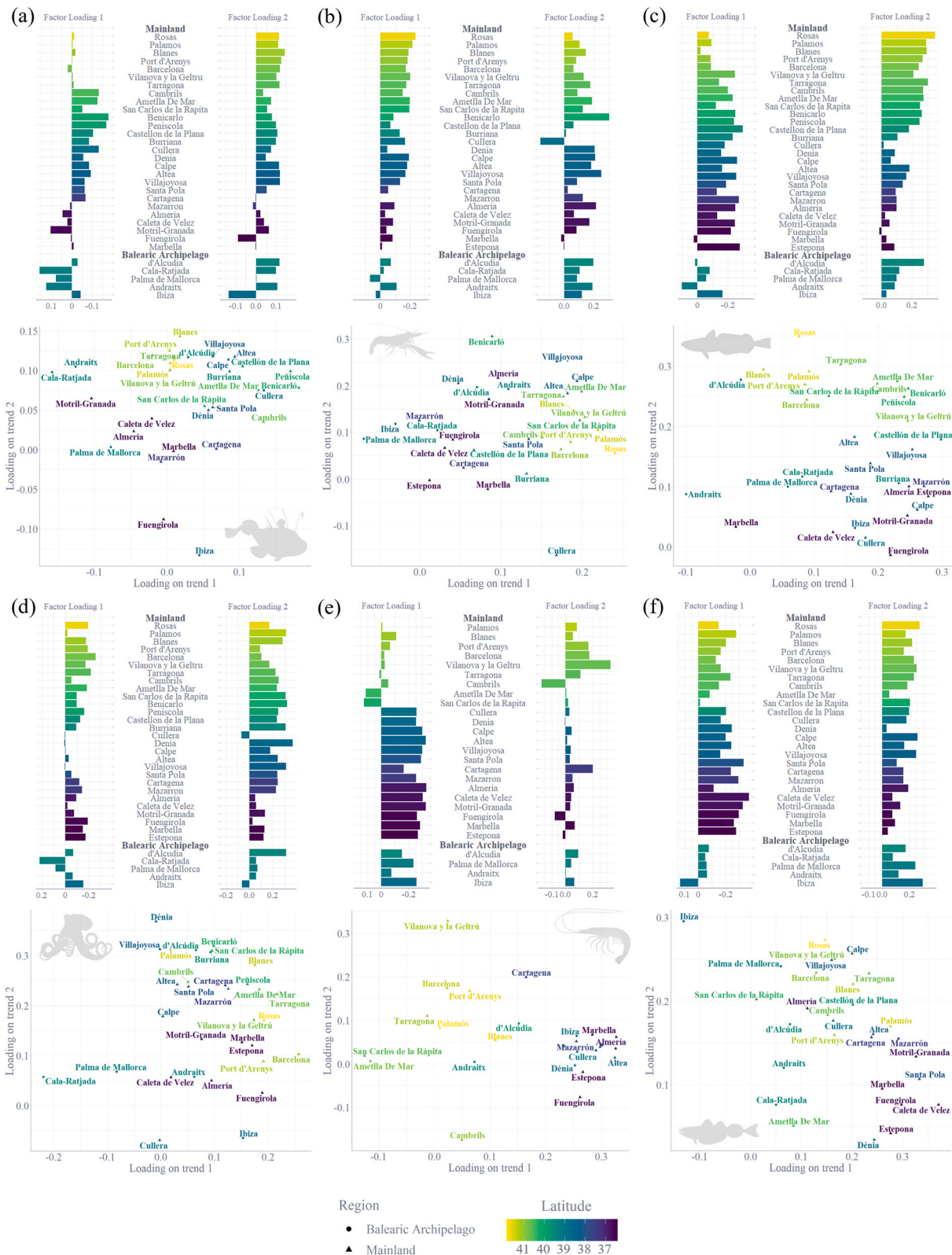
Fig. 4. Long-term individual species DFA factor loading outputs. All axes are unitless. The ports are sorted by latitude, from south to north and separated by mainland and archipelago. (a) *Lophius piscatorius*, (b) *Nephrops norvegicus*, (c) *Merluccius merluccius*, (d) *Octopus vulgaris*, (e) *Parapenaeus longirostris*, (f) *Micromesistius poutassou*. Factor loadings on trend one (left), trend two (right) and scatter plot of both (below).

Seasonal analysis   **Long-term analysis**

North Catalan Sea

Balearic Archipelago
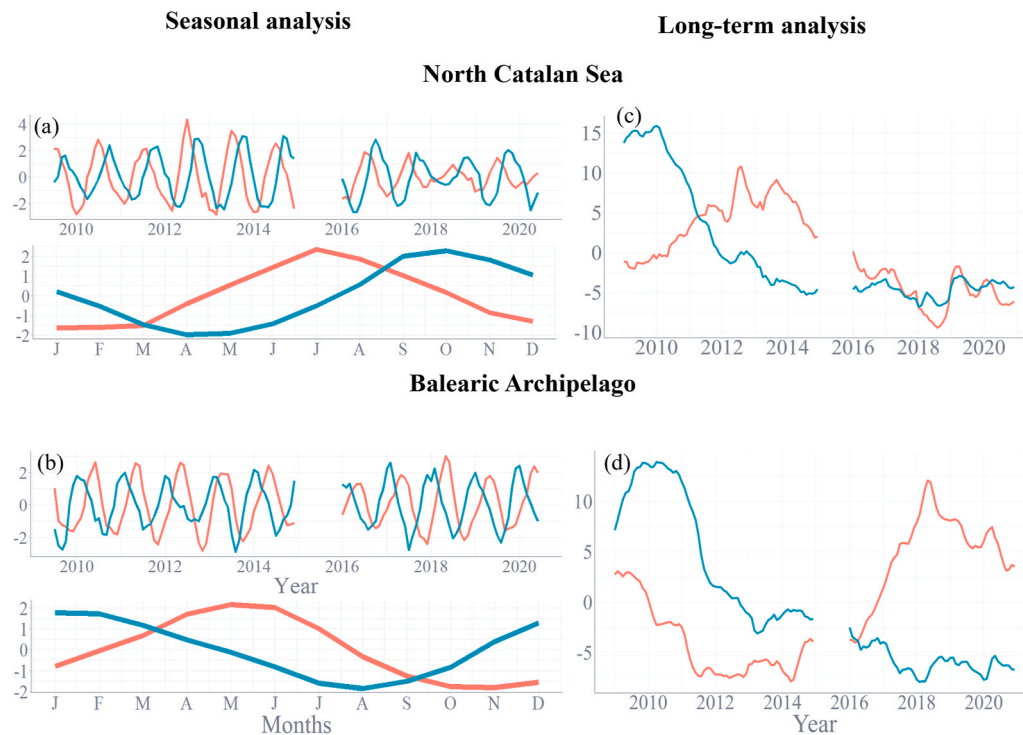
Fig. 5. Common trends resulting from regional dynamic factor analyses for landings per unit effort (LPUE) time series seasonal (left; a–b) and long-term (right; c–d) components between 2009 and 2020. Common trends in orange – trend 1 (T1); blue – trend 2 (T2). All y-axis are unitless. Y-axis represents the magnitude of the common trends.

through species and regional analysis, with marked groupings observable along the north-south gradient underlining the importance of port location. Progression of summer, autumn and winter peaks, with later seasons dominating in the north was also noted. Regional analysis revealed unique trends across the Iberian Peninsula and the Balearic Archipelago, although nearly all have been affected by the change between 2012 and 2016 and show a continued decline in the LPUE of mainland regions.

4. Discussion

Our study reports strong spatial segregation of fisheries resources along the Western Mediterranean geographic gradient attending to the seasonal and long-term variation of landings in most ports. As expected, and based on preceding analyses in other components of the Mediterranean ecosystems, a geographical aggregation was reported, yet species grouping based on life history traits was not explicit. On the scale of the Spanish region of the Western Mediterranean, the DFA revealed seasonal synchronies at the species level as well as the whole regional community level with complex individual patterns and some degree of a north-south gradient for the peak LPUE timeline. In the long-term, the dominance of a downward trajectory of LPUE was evident on species-specific and regional scales with observable synchrony along the north-south gradient of the Iberian Peninsula. The Western Mediterranean, a biodiversity hotspot and economic support system for local communities, is experiencing varied environmental changes, including regime shifts, and intense anthropogenic pressure that are projected to alter fish communities by 2040 (Clark et al., 2020; Coll et al., 2010; Hidalgo et al., 2022b; Nykjaer, 2009; Vargas-Yáñez et al., 2008), along with long-lasting overexploitation of harvested stocks. This study provides the structural spatial basis of fisheries and their resources to further investigate and understand potential changes in the future and design sound adaptation measures to the emerging climate change impacts (Hidalgo et al., 2022b).

At the individual species level, models showed distinct seasonal responses, which were expected based on the differing life histories of the investigated species. The spatial segregation of seasonal trends was overall more patchy rather than following directional gradients, indicating a complex dynamic possibly related to fisheries dynamics and local environmental processes (e.g. the influence of Ebro Delta or primary production bloom originated in the winter in the Gulf on Lion, Puerta et al. (2016). For instance, the common monkfish exhibited the highest catches in the Ebro Delta during autumn, while other regions had increased landings during the early summer months. Small-scale segregation observed for blue and red shrimp (*Aristeus antennatus*) can be attributed to the phenology of primary producers and the timing of food advection to the seabed (Fanelli et al., 2013; Hidalgo et al., 2015). The only species where a somewhat directional pattern can be discerned were Norway lobster and the European hake. Norway lobster showed dominant seasonal peaks between May and August, a known high-catch season (Ligas et al., 2011), as well as the most synchronised seasonal trends of all species considered, likely due to its benthic lifestyle and lower mobility (Farmer, 1974). Southern ports were characterised by an earlier peak (May) while the northern regions experienced later highs in June, supporting spatial segregation as the main driver in Norway lobster population dynamics. The late high season (from June until October) of the European hake was observed in nearly all the ports with an increasing dominance from south to north (except for the northernmost ports of the North Catalan Sea). This could correspond to high catches following spring and summer recruitment peaks recorded in the numerous ports of the Western Mediterranean (Maynou, 2003; Recasens et al., 1998). The North Catalan Sea expressed the opposite of the expected pattern of the early summer peak (T2), as the spawning in that area peaks in colder months (Maynou, 2003), with the Alboran Sea also showing independent dynamics as the spawning in this region occurs in spring.

For the common octopus, the seasonal analysis revealed two consecutive peaks in January (T2) and June (T1) and a compatible

Fig. 6. Factor loadings resulting from North Catalan Sea (a, c) and Balearic Archipelago (b, d) regional dynamic factor analyses for landings per unit effort (LPUE) time series seasonal (left; a–b) and long-term (right; c–d) components between 2009 and 2020. All y-axis are unitless.

pattern was discovered in Mallorca, which coincides with the highest catch rates and recruitment peaks observed in the Balearic Sea (Puerta et al., 2016; Quetglas et al., 1998). However, no such behaviour was previously seen for the mainland ports in the south, where the highest LPUE values occurred over autumn and winter (Puerta et al., 2016). Compared to preceding analyses (Puerta et al., 2016; Sonderblohm et al., 2014), the trends presented here were shifted and expanded into late spring and early autumn, however, the difference could be explained by a greater spatial coverage that incorporated more ports along an uninterrupted latitudinal gradient. This would support that spatial segregation occurs along the gradient as a result of hydrological and environmental factors acting together with fishing pressure. The shift in abundance from north to south between winter and summer could also be associated with spawning aggregations and migratory behaviours exhibited by some cephalopods (Garcia Martinez, 2017; Pierce et al., 2008; Puerta et al., 2014, 2016). On the regional scale, the synchronies in cephalopods can be determined by environmental factors like temperature (Chen, 2010; Zuur and Pierce, 2004) that can act as a direct driver of growth or survival of paralarvae, but also indirect, exerting pressure from the bottom of the food chain (Keller et al., 2017). Primary productivity of the area also plays a role in shaping their dynamics in the generally oligotrophic waters of the Mediterranean through increased competition with small pelagic fish species (Coll et al., 2006; Keller et al., 2017). Climate change, as well as human activities such as fishing, can also alter the stability of marine ecosystems, leading to a competitive advantage for opportunistic groups such as cephalopods (André et al., 2010; Keller et al., 2017).

Although the spatial structure was less obvious at the regional level due to the complementarity among species' patterns, the sub-regional communities also displayed some synchronies in seasonal patterns, with autumn, summer and winter/spring peaks progressing from north to south and the Balearic Archipelago falling somewhat closer to the Alboran Sea seasonal pattern. This supports the regional adaptation of species to their local environmental conditions, which was reported here and in preceding studies (García-Ruiz et al., 2021; Keller et al., 2017; Puerta et al., 2016). Synchrony or sometimes asynchrony throughout the populations can have a buffering role that provides resilience and aids the recovery of connected populations, making them important aspects of management mitigation measures (Aragão et al., 2022; Hidalgo et al., 2015, 2022a; Keller et al., 2017). The overall spatial segregation of seasonal trends was patchy, indicating a more complex dynamic possibly related to sub-regional and local fisheries dynamics and pressures.

Five out of the six species analysed showed a decrease in abundance over time, with unique oscillations accompanying these changes. The decrease of some of those, like the blue whiting (Mir-Arguimbau et al., 2022b, p.), Norway lobster and European hake (FAO, 2022) was already reported previously. For the Norway lobster and blue whiting, the downward trend could be associated with the negative relationship between their biomass and SST as well as the reduced freshwater influx bringing less organic matter for the Norway lobster (Cartes et al., 2009; Sbrana et al., 2020) or reducing the spawning period of blue whiting (Cushing, 1990; Mir-Arguimbau et al., 2022a). This is particularly visible in the 2018–2020 peaks from both long-term trends and the seasonal trends, which could be the aftermath of a mild 2017 winter, followed by the more severe winter of 2018 that benefited the Norway lobster and blue whiting populations (Mir-Arguimbau et al., 2022a, p.). Interestingly, the decline in the common octopus LPUE was in opposition to the expected increase in cephalopod production (Hidalgo et al., 2022c; Keller et al., 2017; Sonderblohm et al., 2014; Veloy et al., 2022), which should be positively affected by water warming as well as the negative effect of fishing pressure on their competitors and predators (Coll et al., 2021; Keller et al., 2017). The dichotomy between this and preceding research could be reflective of an alternative theory, where increasing temperatures are not so broadly beneficial for cephalopod populations due to the likely influence of other environmental drivers

and extreme weather events brought about by climate change (André et al., 2010).

Only the deep-water rose shrimp, has shown a positive trend (T1), which was correlated with the southern, central and Balearic ports and was already observed in other regions of the Mediterranean Sea (Colloca et al., 2014; FAO, 2022; Ligas et al., 2011, 2010; Vasilakopoulos and Maravelias, 2016). This could be attributed to the warming of the water layers inhabited by the deep-water rose shrimp (García-Lafuente et al., 2022; Vargas-Yáñez et al., 2008, 2009), which has a preference for warm water conditions (Abelló et al., 2002a; Colloca et al., 2014; Sobrino et al., 2005) and is likely one of the 'winners' of the generalized warming associated to the climate change (Hidalgo et al., 2022a).

The overall decline in Mediterranean stocks is supported by other accounts regarding the entire basin dating back to 1990 (Vasilakopoulos et al., 2014). The preceding increase in landings observed between 2010 and 2015 was also already noted for individual species as well as regional populations (Keller et al., 2017; Ligas et al., 2011; Sonderblohm et al., 2014; Vasilakopoulos and Maravelias, 2016). Certainly, the alternating increases and decreases could be a part of periodic oscillations, already reported in the Western Mediterranean for some species (Karametsidis et al., 2023; Martin et al., 2016; Quetglas et al., 1998). The upward trends visible for Ebro Delta, Valencia Channel and Balearic Archipelago were not the dominant trends, possibly resulting from local fishery dynamics. Indeed, frequent negative factor loadings indicated opposite trends (i.e. decreasing) for some of the port-species combinations. Some of the landings increase could also be attributed to the masked effect of fishing depth range expansion, which can target more abundant, unexploited populations (Damalas et al., 2015), or species of higher economic value (Farriols et al., 2020; Hidalgo et al., 2009). The continued decline in 2020 could also be attributed to the decrease in fishing activities resulting from COVID-19 restrictions and closures as well as shortages of resources and labour (Clavelle, 2020; FAO, 2020b). However, given the long-term trends and extensive time series of our study (2009–2020), the patterns and conclusions obtained in our study are not affected by the COVID-19 period.

On both, species and regional community levels, the majority of the modelled long-term trends displayed at least a partial downward trajectory and species-specific trends were clearly driven by spatial segregation with some degree of a north-south gradation. This was likely led by the spatially varying dependence of the seasonal dynamics of key environmental processes – mainly primary producers' blooms, cyclic convection and temperature which drive the high seasonality of the Mediterranean (Coll et al., 2010; Hidalgo et al., 2019; Martin et al., 2016) as well as fishing patterns (Lloret-Lloret et al., 2021). The spatial gradient was clear for the long-term trends of the European hake or blue whiting, which have shown an opposing dominance in the north and south of the peninsula or the Norway lobster with the increasing dominance of T1 from south to north. This highlights the complex and fluctuating nature of fish populations in the Mediterranean Sea and the importance of considering seasonal factors in understanding their trends and spatial dynamics.

The heterogeneous responses at species and region levels suggest that regional hydrodynamics, ecological pressures, potential complex population structures (e.g. metapopulations) and fisheries dynamics at shorter scales all play an important role in defining the seasonal and interannual fluctuations of landings (Cuttitta et al., 2018; Hanski, 1998; Hidalgo et al., 2019; Quattrocchi and Maynou, 2017). Furthermore, the lack of anticipated distinct grouping based on the three life history traits for long-term and seasonal analysis indicated a species-specific response, not shared across the groups. Some differences in the response of the same species across ports within the same regions point to a high relevance of fisheries pressure in the local dynamics, as purely environmental drivers would result in a more uniform behaviour on such a small scale. A solely climate change-driven response would also be more homogeneous and not express the timeline differences. These could be attributed to environmental variations and buffering

capabilities between the regions. The Alboran Sea is characterised by strong productivity (Abelló et al., 2002b) and the influence of Atlantic currents (Millot, 1999), representing a transitional area of Atlantic macrofauna with high turnover (Gaertner et al., 2005), which could benefit local demersal and benthic communities. This could have contributed to a later decrease in fish abundance that occurred at a gentler rate than the North Catalan Sea observed here. Similarly, the presence of the Ebro River constitutes an important local nutrient inflow source (Gaertner et al., 2005) and could have buffered the climate change-related decline through bottom-up control (AllEnviAlliance nationale de recherche pour l'environnement, 2016; Caddy, 2000; Deleivamoreno et al., 2000; Gaertner et al., 2005). Lastly, the Balearic archipelago is characterised by high hydrodynamic variability, which can have a significant impact on the demersal and benthic communities of its two main fishing zones (Amores and Monserrat, 2014; Ordines et al., 2011). This could account for the dichotomous behaviour of local populations, experiencing an evenly-matched increase and decrease, already observed in other deep-sea species (Hidalgo et al., 2015).

5. Implications, future and broad applications

By highlighting the decline in fisheries landings and the existence of seasonal and long-term spatial synchronies, our study shows the importance of implementing management practices based on substantiated knowledge of seasonal and spatial resource dynamics, which are specific to a particular area. As the Mediterranean boasts a diverse, efficient fishing fleet with high catchability (Sánchez Lizaso et al., 2020), fishing pressure is one of the more important drivers that can be addressed directly. Considering the reported progressing decline of fish stocks, attempts at the management of Mediterranean fishery in line with the Common Fisheries Policy (CFP) continue in their unsuccessful record (Vasilakopoulos et al., 2014; Vasilakopoulos and Maravelias, 2016), while more time is needed to assess the impact of the most recently applied measures (e.g. Multiannual Management Plan). Understanding of the regional segregation of species and future expansion of species analysis, particularly on the seasonal scale, could support tailored management measures that fall in line with current CFP policies and help identify key periods of protection (Puerta et al., 2016), or seasons with a higher fisheries portfolio (Anderson et al., 2017). The dichotomous DFA approach used has shown considerable overlap between individual and regional models that cover diverse ecosystems and management areas with high spatial variability in the catches. As regional analysis revealed a small to moderate shift in the peak timeline of each region, supporting the management with regional analysis is advisable.

6. Conclusions

This study evaluated the seasonal and long-term spatio-temporal fluctuations of Western Mediterranean fisheries landings and revealed the dominance of a downward trend affecting the majority of species and the Western Mediterranean region as a whole. Seasonal synchronies were also observed for individual species and within each region. Divergence from the decreasing trend was species-specific and shown by organisms with warm water affinity or ones that benefit from the indirect effects of climate change (Ligas et al., 2010; Sobrino et al., 2005). Spatial segregation along the north-south gradient was revealed to have a clear influence on the underlying long-term trends and, to a lesser degree, on the progression of summer, autumn and winter peaks, with later seasons dominating in the north. Spatial segregation of seasonal trends was more irregular, indicating a complex dynamic possibly resulting from multiple pressures (Lloret-Lloret et al., 2021; Vasilakopoulos et al., 2014). Incorporation of the regional adaptation of species to the local environmental conditions and the presence of synchronies, as well as asynchronies, is crucial in understanding the resilience of ecosystems and the adaptive capacities of local fisheries communities to

environmental changes (Hidalgo et al., 2022a; Keller et al., 2017). Considering the progressing and generalized decline of Mediterranean fish stocks, the CFP applied to the Mediterranean appears to be still in need of information on dynamics at the sub-regional scale. This data is essential for enhancing the implementation of CFP regionalisation approaches and spatial fishing restrictions in a more effective direction.

CRediT authorship contribution statement

Konstancja Woźniacka: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Georgios Kerametsidis:** Methodology, Writing – original draft, Writing – review & editing. **Lucía López-López:** Funding acquisition, Project administration, Writing – original draft, Writing – review & editing. **Christian Möllmann:** Supervision, Writing – original draft, Writing – review & editing. **Manuel Hidalgo:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

Manuel Hidalgo reports administrative support, statistical analysis, and travel were provided by Biodiversity Foundation of the Spanish Ministry for the Ecological Transition and the Demographic Challenge. Manuel Hidalgo reports article publishing charges was provided by Spanish Ministry of Science and Innovation. Konstancja Wozniacka reports financial support was provided by Erasmus Plus. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106453.

References

Abelló, P., Abella, Á., Adamidou, A., Jukic-Peladic, S., Maiorano, P., Spedicato, M.T., 2002a. Geographical patterns in abundance and population structure of *Nephrops norvegicus* and *Parapenaeus longirostris* (Crustacea: Decapoda) along the European Mediterranean coasts. Sci. Mar. 66, 125. https://doi.org/10.3989/scimar.2002.66s2125.

Abelló, P., Carbonell, A., Torres, P., 2002b. Biogeography of epibenthic crustaceans on the shelf and upper slope off the Iberian Peninsula Mediterranean coasts: implications for the establishment of natural management areas. Sci. Mar. 66, 183. https://doi.org/10.3989/scimar.2002.66s2183.

Agostini, V.N., Bakun, A., 2002. 'Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*): "Ocean triads" in the Mediterranean Sea. Fish. Oceanogr. 11, 129–142. https://doi.org/10.1046/j.1365-2419.2002.00201.x.

Alglave, B., Rivot, E., Etienne, M.-P., Woillez, M., Thorson, J.T., Vermard, Y., 2022. Combining scientific survey and commercial catch data to map fish distribution. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 79, 1133–1149. https://doi.org/10.1093/icesjms/fsac032.

AllEnvi, Alliance nationale de recherche pour l'environnement, 2016. The Mediterranean Region under Climate Change: a Scientific Update. IRD éditions, Marseille.

Amores, A., Monserrat, S., 2014. Hydrodynamic comparison between the north and south of Mallorca Island. J. Mar. Syst. 138, 40–50. https://doi.org/10.1016/j.jmarsys.2014.01.005.

Anderson, S.C., Ward, E.J., Shelton, A.O., Adkison, M.D., Beaudreau, A.H., Brenner, R.E., Haynie, A.C., Shriver, J.C., Watson, J.T., Williams, B.C., 2017. Benefits and risks of diversification for individual Fishers. Proc. Natl. Acad. Sci. U.S.A. 114, 10797–10802. https://doi.org/10.1073/pnas.1702506114.

André, J., Haddon, M., Pecl, G.T., 2010. Modelling climate-change-induced nonlinear thresholds in cephalopod population dynamics: climate change and octopus population dynamic. Global Change Biol. 16, 2866–2875. https://doi.org/10.1111/j.1365-2486.2010.02223.x.

Aragão, G.M., López-López, L., Punzón, A., Guijarro, E., Esteban, A., García, E., González-Irusta, J.M., Polo, J., Vivas, M., Hidalgo, M., 2022. The importance of regional differences in vulnerability to climate change for demersal fisheries. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 79, 506–518. https://doi.org/10.1093/icesjms/fsab134.

Caddy, J., 2000. Marine catchment basin effects versus impacts of fisheries on semi-enclosed seas. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 57, 628–640. https://doi.org/10.1006/jmsc.2000.0739.

Cartes, J.E., Maynou, F., Fanelli, E., Papiol, V., Lloris, D., 2009. Long-term changes in the composition and diversity of deep-slope megabenthos and trophic webs off Catalonia (western Mediterranean): are trends related to climatic oscillations? Prog. Oceanogr. 82, 32–46. https://doi.org/10.1016/j.pocean.2009.03.003.

Chen, C.-S., 2010. Abundance trends of two neon flying squid (*Ommastrephes bartramii*) stocks in the North Pacific. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 67, 1336–1345. https://doi.org/10.1093/icesjms/fsq063.

Ciannelli, L., Fisher, J., Skern-Mauritzen, M., Hunsicker, M., Hidalgo, M., Frank, K., Bailey, K., 2013. Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. Mar. Ecol. Prog. Ser. 480, 227–243. https://doi.org/10.3354/meps10067.

Clark, N.J., Kerry, J.T., Fraser, C.I., 2020. Rapid winter warming could disrupt coastal marine fish community structure. Nat. Clim. Change 10, 862–867. https://doi.org/10.1038/s41558-020-0838-5.

Clavelle, T., 2020. Global fisheries during COVID-19. Global Fishing Watch. URL. https://globalfishingwatch.org/data/global-fisheries-during-covid-19/ (accessed 3.10.24).

Coll, M., Ortega-Cerdà, M., Mascarell-Rocher, Y., 2021. Ecological and economic effects of COVID-19 in marine fisheries from the Northwestern Mediterranean Sea. Biol. Conserv. 255, 108997 https://doi.org/10.1016/j.biocon.2021.108997.

Coll, M., Palomera, I., Tudela, S., Sardà, F., 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. J. Mar. Syst. 59, 63–96. https://doi.org/10.1016/j.jmarsys.2005.09.001.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglia, C., Galil, B.S., Gasol, J.M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M.-S., Koukouras, A., Lampadariou, N., Laxamana, E., López-Fé de la Cuadra, C.M., Lotze, H.K., Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., San Vicente, C., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., Voultsiadou, E., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PLoS One 5, e11842. https://doi.org/10.1371/journal.pone.0011842.

Colloca, F., Mastrantonio, G., Lasinio, G.J., Ligas, A., Sartor, P., 2014. *Parapenaeus longirostris* (Lucas, 1846) an early warning indicator species of global warming in the central Mediterranean Sea. The wrapping up of the IDEADOS project: International Workshop on Environment, Ecosystems and Demersal Resources, and Fisheries J. Mar. Syst. 138, 29–39. https://doi.org/10.1016/j.jmarsys.2013.10.007.

Colloca, F., Scarcella, G., Libralato, S., 2017. Recent trends and impacts of fisheries exploitation on Mediterranean stocks and ecosystems. Front. Mar. Sci. 4 https://doi.org/10.3389/fmars.2017.00244.

Costello, M.J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H., Miloslavich, P., 2010. A census of marine biodiversity knowledge, resources, and future challenges. PLoS One 5, e12110. https://doi.org/10.1371/journal.pone.0012110.

Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In: Blaxter, J.H.S., Southward, A.J. (Eds.), Advances in Marine Biology. Academic Press, pp. 249–293. https://doi.org/10.1016/S0065-2881(08)60202-3.

Cuttitta, A., Torri, M., Zarrad, R., Zgozi, S., Jarboui, O., Quinci, E.M., Hamza, M., Abdulfatah, E., Haddoud, D., El Turki, A., Ramadan, A., Missaoui, H., Mifsud, R., Bonomo, S., Mazzola, S., Patti, B., 2018. Linking surface hydrodynamics to planktonic ecosystem: the case study of the ichthyoplanktonic assemblages in the Central Mediterranean Sea. Hydrobiologia 821, 191–214. https://doi.org/10.1007/s10750-017-3483-x.

Damalas, D., Maravelias, C.D., Osio, G.C., Maynou, F., Sbrana, M., Sartor, P., 2015. "Once upon a time in the mediterranean" long term trends of mediterranean fisheries resources based on Fishers' traditional ecological knowledge. PLoS One 10, e0119330. https://doi.org/10.1371/journal.pone.0119330.

Deleivamoreno, J., Agostini, V., Caddy, J., Carocci, F., 2000. Is the pelagic-demersal ratio from fishery landings a useful proxy for nutrient availability? A preliminary data exploration for the semi-enclosed seas around Europe. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 57, 1091–1102. https://doi.org/10.1006/jmsc.2000.0705.

D'Ortenzio, F., Ribera d'Alcalà, M., 2009. On the trophic regimes of the Mediterranean Sea: a satellite analysis. Biogeosciences 6, 139–148. https://doi.org/10.5194/bg-6-139-2009.

Fanelli, E., Cartes, J.E., Papiol, V., López-Pérez, C., 2013. Environmental drivers of megafaunal assemblage composition and biomass distribution over mainland and insular slopes of the Balearic Basin (Western Mediterranean). Deep Sea Res. Oceanogr. Res. Pap. 78, 79–94. https://doi.org/10.1016/j.dsr.2013.04.009.

FAO, 2022. The State of Mediterranean and Black Sea Fisheries 2022. FAO. https://doi.org/10.4060/cc3370en.

FAO, 2020a. The State of Mediterranean and Black Sea Fisheries 2020, General Fisheries Commission for the Mediterranean. https://doi.org/10.4060/cb2429en. Rome.

FAO, 2020b. Summary of the Impacts of the COVID-19 Pandemic on the Fisheries and Aquaculture Sector. FAO. https://doi.org/10.4060/ca9349en.

FAO, 2018. The State of Mediterranean and Black Sea Fisheries 2018.

Farmer, A.S.D., 1974. Burrowing behaviour of the Norway lobster, *Nephrops norvegicus* (*L.*) (Decapoda: Nephropidae). Estuar. Coast Mar. Sci. 2, 49–58. https://doi.org/10.1016/0302-3524(74)90027-9.

Farriols, M.T., Ordines, F., Carbonara, P., Casciaro, L., Di Lorenzo, M., Esteban, A., Follesa, C., García-Ruiz, C., Isajlovic, I., Jadaud, A., Ligas, A., Manfredi, C., Marceta, B., Peristeraki, P., Vrgoc, N., Massutí, E., 2020. Spatio-temporal trends in diversity of demersal fish assemblages in the Mediterranean. Sci. Mar. 83, 189. https://doi.org/10.3989/scimar.04977.13A.

Fortibuoni, T., Giovanardi, O., Pranovi, F., Raicevich, S., Solidoro, C., Libralato, S., 2017. Analysis of long-term changes in a mediterranean marine ecosystem based on fishery landings. Front. Mar. Sci. 4 https://doi.org/10.3389/FMARS.2017.00033.

Fortibuoni, T., Libralato, S., Raicevich, S., Giovanardi, O., Solidoro, C., 2010. Coding early naturalists' accounts into long-term fish community changes in the Adriatic sea (1800-2000). PLoS One 5, 1–8. https://doi.org/10.1371/journal.pone.0015502.

Froese, R., Pauly, D., 2022. FishBase [WWW document]. World Wide Web electronic publication. URL. www.fishbase.org (accessed 9.8.22).

Gaertner, J., Bertrand, J., de Sola, L., Durbec, J., Ferrandis, E., Souplet, A., 2005. Large spatial scale variation of demersal fish assemblage structure on the continental shelf of the NW Mediterranean Sea. Mar. Ecol. Prog. Ser. 297, 245–257. https://doi.org/10.3354/meps297245.

Garcia Martinez, M. del C., 2017. Short comment about the octopus life cycle in the northern Alboran Sea (western Mediterranean Sea), 01 Fisher.-Res.. https://doi.org/10.35841/fisheries-research.1.1.34-37.

García-Lafuente, J., Sammartino, S., Sanchez Leal, R., Nadal Ariza, I., Naranjo, C., 2022. Increased Warming Trend of the Mediterranean Outflow into the North Atlantic Ocean.

García-Ruiz, C., Delgado, M., Hidalgo, M., 2021. Patterns of spatial changes on demersal species in the Gulf of Cadiz and northern Alboran Sea. Mediterr. Mar. Sci. https://doi.org/10.12681/mms.27386.

Hanski, I., 1998. Metapopulation dynamics. Nature 396, 41–49. https://doi.org/10.1038/23876.

Hassoun, A.E.R., Gemayel, E., Krasakopoulou, E., Goyet, C., Abboud-Abi Saab, M., Guglielmi, V., Touratier, F., Falco, C., 2015. Acidification of the Mediterranean Sea from anthropogenic carbon penetration. Deep Sea Res. Oceanogr. Res. Pap. 102, 1–15. https://doi.org/10.1016/j.dsr.2015.04.005.

Hidalgo, M., Bartolino, V., Coll, M., Hunsicker, M.E., Travers-Trolet, M., Browman, H.I., 2022a. 'Adaptation science' is needed to inform the sustainable management of the world's oceans in the face of climate change. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 79, 457–462. https://doi.org/10.1093/icesjms/fsac014.

Hidalgo, M., Hernández, P., El-Haweet, A.E., Tirasin, E.M., Fortibuoni, T., Ronchi, F., Lauria, V., Abdallah, O.B., Arnieri, E., Milone, N., Lelli, S., Bernal, M., Vasconcellos, M., Tsikliras, A.C., 2022b. Risks and adaptation options for the Mediterranean fisheries in the face of multiple climate change drivers and impacts. https://doi.org/10.1093/icesjms/fsac185.

Hidalgo, M., Massutí, E., Guijarro, B., Moranta, J., Ciannelli, L., Lloret, J., Oliver, P., Stenseth, N.C., 2009. Population effects and changes in life history traits in relation to phase transitions induced by long-term fishery harvesting: European hake (*Merluccius merluccius*) off the Balearic Islands. Can. J. Fish. Aquat. Sci. 66, 1355–1370. https://doi.org/10.1139/F09-081.

Hidalgo, M., Massutí, E., Moranta, J., Cartes, J., Lloret, J., Oliver, P., Morales-Nin, B., 2008. Seasonal and short spatial patterns in European hake (*Merluccius merluccius L.*) recruitment process at the Balearic Islands (western Mediterranean): the role of environment on distribution and condition. J. Mar. Syst. 71, 367–384. https://doi.org/10.1016/j.jmarsys.2007.03.005.

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Hidalgo, M., Rossi, V., Monroy, P., Ser-Giacomi, E., Hernández-García, E., Guijarro, B., Massutí, E., Alemany, F., Jadaud, A., Perez, J.L., Reglero, P., 2019. Accounting for ocean connectivity and hydroclimate in fish recruitment fluctuations within transboundary metapopulations. Ecol. Appl. 29 https://doi.org/10.1002/eap.1913.

Hidalgo, M., Rueda, L., Molinero, J.C., Guijarro, B., Massutí, E., 2015. Spatial and temporal variation of seasonal synchrony in the deep-sea shrimp *Aristeus antennatus* in the Western Mediterranean. J. Mar. Syst. 148, 131–141. https://doi.org/10.1016/j.jmarsys.2015.02.007.

Hidalgo, M., Vasilakopoulos, P., García-Ruiz, C., Esteban, A., López-López, L., García-Gorriz, E., 2022c. Resilience dynamics and productivity-driven shifts in the marine communities of the Western Mediterranean Sea. J. Anim. Ecol. 91, 470–483. https://doi.org/10.1111/1365-2656.13648.

Holmes, E.E., Ward, E.J., Wills, K., 2012. MARSS: multivariate autoregressive state-space models for analyzing time-series data. R J. 4, 11. https://doi.org/10.32614/RJ-2012-002.

Holmes, E.E., Ward, E.J., Scheuerell, M.D., 2021a. Analysis of multivariate time series using the MARSS package. Version 3.11.4. https://doi.org/10.5281/ZENODO.5781847.

Holmes, Elizabeth Eli, Ward, Eric J., Scheuerell, Mark D., Wills, K., 2021b. MARSS: multivariate autoregressive state-space modeling. R package version 3.11.4 [WWW Document]. CRAN. URL. https://CRAN.R-project.org/package=MARSS.

Karametsidis, G., Rueda, L., Bellido, J.M., Esteban, A., García, E., Gil De Sola, L., Pennino, M.G., Pérez-Gil, J.L., Hidalgo, M., 2023. The trade-off between condition and growth shapes juveniles' survival of harvested demersal fish of the Mediterranean sea. Mar. Environ. Res. 184, 105844 https://doi.org/10.1016/j.marenvres.2022.105844.

Keller, S., Quetglas, A., Puerta, P., Bitetto, I., Casciaro, L., Cuccu, D., Esteban, A., Garcia, C., Garofalo, G., Guijarro, B., Josephides, M., Jadaud, A., Lefkaditou, E., Maiorano, P., Manfredi, C., Marceta, B., Micallef, R., Peristeraki, P., Relini, G., Sartor, P., Spedicato, M.T., Tserpes, G., Hidalgo, M., 2017. Environmentally driven synchronies of Mediterranean cephalopod populations. Prog. Oceanogr. 152, 1–14. https://doi.org/10.1016/j.pocean.2016.12.010.

Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C.F., Pérez, T., 2010. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends Ecol. Evol. 25, 250–260. https://doi.org/10.1016/j.tree.2009.10.009.

Letourneur, Y., Ruitton, S., Sartoretto, S., 2003. Environmental and benthic habitat factors structuring the spatial distribution of a summer infralittoral fish assemblage in the north-western Mediterranean Sea. J. Mar. Biol. Ass. 83, 193–204. https://doi.org/10.1017/S0025315403006970h.

Ligas, A., De Ranieri, S., Micheli, D., Reale, B., Sartor, P., Sbrana, M., Belcari, P., 2010. Analysis of the landings and trawl survey time series from the Tyrrhenian Sea (NW Mediterranean). Fish. Res. 105, 46–56. https://doi.org/10.1016/j.fishres.2010.03.003.

Ligas, A., Sartor, P., Colloca, F., 2011. Trends in population dynamics and fishery of *Parapenaeus longirostris* and *Nephrops norvegicus* in the Tyrrhenian Sea (NW Mediterranean): the relative importance of fishery and environmental variables: trends in P. congirostris and N. norvegicus. Mar. Ecol. 32, 25–35. https://doi.org/10.1111/j.1439-0485.2011.00440.x.

Lloret-Lloret, E., Pennino, M.G., Vilas, D., Bellido, J.M., Navarro, J., Coll, M., 2021. Main drivers of spatial change in the biomass of commercial species between summer and winter in the NW Mediterranean Sea. Mar. Environ. Res. 164, 105227 https://doi.org/10.1016/j.marenvres.2020.105227.

Martin, P., Maynou, F., Recasens, L., Sabatés, A., 2016. Cyclic fluctuations of blue whiting (*Micromesistius poutassou*) linked to open-sea convection processes in the northwestern Mediterranean. Fish. Oceanogr. 25, 229–240. https://doi.org/10.1111/fog.12147.

Maureaud, A., Frelat, R., Pécuchet, L., Shackell, N., Mérigot, B., Pinsky, M.L., Amador, K., Anderson, S.C., Arkhipkin, A., Auber, A., Barri, I., Bell, R.J., Belmaker, J., Beukhof, E., Camara, M.L., Guevara-Carrasco, R., Choi, J., Christensen, H.T., Conner, J., Cubillos, L.A., Diadhiou, H.D., Edelist, D., Emblemsvåg, M., Ernst, B., Fairweather, T.P., Fock, H.O., Friedland, K.D., Garcia, C.B., Gascuel, D., Gislason, H., Goren, M., Guitton, J., Jouffre, D., Hattab, T., Hidalgo, M., Kathena, J.N., Knuckey, I., Kidé, S.O., Koen-Alonso, M., Koopman, M., Kulik, V., León, J.P., Levitt-Barmats, Y., Lindegren, M., Llope, M., Massiot-Granier, F., Masski, H., McLean, M., Meissa, B., Mérillet, L., Mihneva, V., Nunoo, F.K.E., O'Driscoll, R., O'Leary, C.A., Petrova, E., Ramos, J.E., Refes, W., Román-Marcote, E., Siegstad, H., Sobrino, I., Sólmundsson, J., Sonin, O., Spies, I., Steingrund, P., Stephenson, F., Stern, N., Tserkova, F., Tserpes, G., Tzanatos, E., Rijn, I., Zwieten, P.A.M., Vasilakopoulos, P., Yepsen, D.V., Ziegler, P., Thorson, J., 2021. Are we ready to track climate-driven shifts in marine species across international boundaries? - A global survey of scientific bottom trawl data. Global Change Biol. 27, 220–236. https://doi.org/10.1111/gcb.15404.

Maynou, F., 2003. Seasonal and spatial variability of hake (*Merluccius merluccius L.*) recruitment in the NW Mediterranean. Fish. Res. 60, 65–78. https://doi.org/10.1016/S0165-7836(02)00062-0.

Millot, C., 1999. Circulation in the western Mediterranean Sea. J. Mar. Syst. 20, 423–442. https://doi.org/10.1016/S0924-7963(98)00078-5.

Mir-Arguimbau, J., Flexas, M.M., Salat, J., Martín, P., Balcells, M., Raventós, N., Sabatés, A., 2022a. Severe winter conditions improve recruitment success of blue whiting (*Micromesistius poutassou*), a temperate water fish species, in the NW Mediterranean sea. Prog. Oceanogr. 205, 102818 https://doi.org/10.1016/j.pocean.2022.102818.

Mir-Arguimbau, J., Martín, P., Balcells, M., Sala-Coromina, J., Sabatés, A., 2022b. Fishery dynamics of blue whiting, *Micromesistius poutassou*, a highly discarded

bycatch species in the NW Mediterranean Sea. Sci. Mar. 86, e025. https://doi.org/10.3989/scimar.05240.025.

Nieblas, A.-E., Drushka, K., Reygondeau, G., Rossi, V., Demarcq, H., Dubroca, L., Bonhommeau, S., 2014. Defining mediterranean and black sea biogeochemical subprovinces and synthetic ocean indicators using mesoscale oceanographic features. PLoS One 9, e111251. https://doi.org/10.1371/journal.pone.0111251.

Nykjaer, L., 2009. Mediterranean Sea surface warming 1985-2006. Clim. Res. 39, 11–17. https://doi.org/10.3354/cr00794.

Ordines, F., Jordà, G., Quetglas, A., Flexas, M., Moranta, J., Massutí, E., 2011. Connections between hydrodynamics, benthic landscape and associated fauna in the Balearic Islands, western Mediterranean. Continent. Shelf Res. 31, 1835–1844. https://doi.org/10.1016/j.csr.2011.08.007.

Palomares, M.L.D., Pauly, D., 2022. SeaLifeBase [WWW document]. World Wide Web electronic publication. URL. www.sealifebase.org (accessed 7.6.22).

Paradinas, I., Giménez, J., Conesa, D., López-Quílez, A., Pennino, M.G., 2022. Evidence for spatiotemporal shift in demersal fishery management priority areas in the western Mediterranean. Can. J. Fish. Aquat. Sci. https://doi.org/10.1139/cjfas-2021-0327 cjfas-2021-0327.

Pecuchet, L., Lindegren, M., Hidalgo, M., Delgado, M., Esteban, A., Fock, H.O., Gil de Sola, L., Punzón, A., Sólmundsson, J., Payne, M.R., 2017. From traits to life-history strategies: deconstructing fish community composition across European seas: Pecuchet et al. Global Ecol. Biogeogr. 26, 812–822. https://doi.org/10.1111/geb.12587.

Pierce, G.J., Valavanis, V.D., Guerra, A., Jereb, P., Orsi-Relini, L., Bellido, J.M., Katara, I., Piatkowski, U., Pereira, J., Balguerias, E., Sobrino, I., Lefkaditou, E., Wang, J., Santurtun, M., Boyle, P.R., Hastie, L.C., MacLeod, C.D., Smith, J.M., Viana, M., González, A.F., Zuur, A.F., 2008. A review of cephalopod–environment interactions in European Seas. Hydrobiologia 612, 49–70. https://doi.org/10.1007/s10750-008-9489-7.

Poulard, J., 2002. Interaction between marine populations and fishing activities: temporal patterns of landings of La Rochelle trawlers in the Bay of Biscay. Aquat. Living Resour. 15, 197–210. https://doi.org/10.1016/S0990-7440(02)01182-8.

Puerta, P., Hidalgo, M., González, M., Esteban, A., Quetglas, A., 2014. Role of hydro-climatic and demographic processes on the spatio-temporal distribution of cephalopods in the western Mediterranean. Mar. Ecol. Prog. Ser. 514, 105–118. https://doi.org/10.3354/meps10972.

Puerta, P., Hunsicker, M.E., Quetglas, A., Álvarez-Berastegui, D., Esteban, A., González, M., Hidalgo, M., 2015. Spatially explicit modeling reveals cephalopod distributions match contrasting trophic pathways in the western Mediterranean Sea. PLoS One 10, e0133439. https://doi.org/10.1371/journal.pone.0133439.

Puerta, P., Quetglas, A., Hidalgo, M., 2016. Seasonal variability of cephalopod populations: a spatio-temporal approach in the Western Mediterranean Sea. Fish. Oceanogr. 25, 373–389. https://doi.org/10.1111/fog.12159.

Quattrocchi, F., Maynou, F., 2017. Environmental drivers of sardine (*Sardina pilchardus*) in the Catalan sea (NW Mediterranean Sea). Mar. Biol. Res. 13, 1003–1014. https://doi.org/10.1080/17451000.2017.1331039.

Quetglas, A., Alemany, F., Carbonell, A., Merella, P., Sánchez, P., 1998. Biology and fishery of *Octopus vulgaris* Cuvier, 1797, caught by trawlers in Mallorca (Balearic Sea, western mediterranean). Fish. Res. 36, 237–249. https://doi.org/10.1016/S0165-7836(98)00093-9.

Quetglas, A., Ordines, F., Hidalgo, M., Monserrat, S., Ruiz, S., Amores, Á., Moranta, J., Massutí, E., 2013. Synchronous combined effects of fishing and climate within a demersal community. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 70, 319–328. https://doi.org/10.1093/icesjms/fss181.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Recasens, L., Lombarte, A., Morales-Nin, B., Tores, G.J., 1998. Spatiotemporal variation in the population structure of the European hake in the NW Mediterranean. J. Fish. Biol. 53, 387–401. https://doi.org/10.1111/j.1095-8649.1998.tb00988.x.

Rossi, V., Ser-Giacomi, E., López, C., Hernández-García, E., 2014. Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves. Geophys. Res. Lett. 41, 2883–2891. https://doi.org/10.1002/2014GL059540.

Rouyer, T., Ottersen, G., Durant, J.M., Hidalgo, M., Hjermann, D.Ø., Persson, J., Stige, L. Chr, Stenseth, N.Chr, 2011. Shifting dynamic forces in fish stock fluctuations triggered by age truncation?: dynamic forces in fish stock fluctuations. Global Change Biol. 17, 3046–3057. https://doi.org/10.1111/j.1365-2486.2011.02443.x.

Sánchez Lizaso, J.L., Sola, I., Guijarro-García, E., Bellido, J.M., Franquesa, R., 2020. A new management framework for western Mediterranean demersal fisheries. Mar. Pol. 112, 103772 https://doi.org/10.1016/j.marpol.2019.103772.

Sbrana, M., Zupa, W., Ligas, A., Capezzuto, F., Chatzispyrou, A., Follesa, M.C., Gancitano, V., Guijarro, B., Isajlovic, I., Jadaud, A., Markovic, O., Micallef, R., Peristeraki, P., Piccinetti, C., Thasitis, I., Carbonara, P., 2020. Spatiotemporal abundance pattern of deep-water rose shrimp, *Parapenaeus longirostris*, and Norway lobster, *Nephrops norvegicus*, in European Mediterranean waters. Sci. Mar. 83, 71. https://doi.org/10.3989/scimar.04858.27A.

Sobrino, I., Kapiris, K., Silva, C., Sbrana, M., 2005. A review of the biology and fisheries of the deep water rose shrimp, *Parapenaeus longirostris*, in European Atlantic and Mediterranean waters (Decapoda, Dendrobranchiata, Penaeidae). Crustaceana 78, 1153–1184. https://doi.org/10.1163/156854005775903564.

Sonderblohm, C.P., Pereira, J., Erzini, K., 2014. Environmental and fishery-driven dynamics of the common octopus (*Octopus vulgaris*) based on time-series analyses from leeward Algarve, southern Portugal. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 71, 2231–2241. https://doi.org/10.1093/icesjms/fst189.

Vargas-Yáñez, M., Jesús García, M., Salat, J., García-Martínez, M.C., Pascual, J., Moya, F., 2008. Warming trends and decadal variability in the Western

Mediterranean shelf. Global Planet. Change 63, 177–184. https://doi.org/10.1016/j.gloplacha.2007.09.001.

Vargas-Yáñez, M., Moya, F., Tel, E., García-Martínez, M.C., Guerber, E., Bourgeon, M., 2009. Warming and salting in the western Mediterranean during the second half of the 20th century: inconsistencies, unknowns and the effect of data processing. Sci. Mar. 73, 7–28. https://doi.org/10.3989/scimar.2009.73n1007.

Vasilakopoulos, P., Maravelias, C.D., 2016. A tale of two seas: a meta-analysis of crustacean stocks in the NE Atlantic and the Mediterranean Sea. Fish Fish. 17, 617–636. https://doi.org/10.1111/faf.12133.

Vasilakopoulos, P., Maravelias, C.D., Tserpes, G., 2014. The alarming decline of mediterranean fish stocks. Curr. Biol. 24, 1643–1648. https://doi.org/10.1016/j.cub.2014.05.070.

Veloy, C., Hidalgo, M., Pennino, M.G., Garcia, E., Esteban, A., García-Ruiz, C., Certain, G., Vaz, S., Jadaud, A., Coll, M., 2022. Spatial-temporal variation of the Western Mediterranean Sea biodiversity along a latitudinal gradient. Ecol. Indicat. 136, 108674 https://doi.org/10.1016/j.ecolind.2022.108674.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. JOSS 4, 1686. https://doi.org/10.21105/joss.01686.

Zuur, A.F., Fryer, R.J., Jolliffe, I.T., Dekker, R., Beukema, J.J., 2003a. Estimating common trends in multivariate time series using dynamic factor analysis. Environmetrics 14, 665–685. https://doi.org/10.1002/env.611.

Zuur, A.F., Pierce, G.J., 2004. Common trends in northeast Atlantic squid time series. J. Sea Res. 52, 57–72. https://doi.org/10.1016/j.seares.2003.08.008.

Zuur, A.F., Tuck, I.D., Bailey, N., 2003b. Dynamic factor analysis to estimate common trends in fisheries time series. Can. J. Fish. Aquat. Sci. 60, 542–552. https://doi.org/10.1139/F03-030.