
Temporal synchrony among juvenile marine fishes and potential climate and environmental drivers in the Bay of Biscay

Saulnier Erwan ^{1,*}, Brind'Amour Anik ¹, Lecomte Jean Baptiste ¹, Piette Semeril Eloise ¹,
Trenkel Verena ¹

¹ DECOD (Ecosystem Dynamics and Sustainability), IFREMER, INRAE, Institut Agro, Nantes, France

* Corresponding author : Erwan Saulnier, email address : esaulnier.ecology@gmail.com

Abstract :

The existence of synchronous fluctuations among sympatric species is an important property of a community, potentially reducing temporal stability of ecosystem services. Yet, community synchrony and its potential drivers has rarely been studied in marine ecosystems. Here, we analyzed a 14-year time-series (2007-2020) of fish abundance data collected by a scientific beam trawl survey in the Bay of Biscay, a temperate marine ecosystem located in the North-east Atlantic. We used dynamic factor analysis to reveal common trends in abundance among juvenile demersal marine fishes, and to identify potential environmental drivers. Our results revealed synchronous changes in juvenile fish abundance among the 12 marine species examined in the study. This strong temporal coherence was likely related to the influence of climate and environmental factors, notably sea bottom temperature and the East Atlantic Pattern. We also found some support for alternative drivers of early-life fish dynamics, namely the North Atlantic Oscillation and sea surface chlorophyll-a concentration, the later suggesting bottom-up trophic control. In the context of ongoing environmental changes, our findings raise questions about the future stability of the demersal marine fish community in the Bay of Biscay.

Highlights

► We analysed the temporal dynamics of 12 juvenile marine fishes in the Bay of Biscay. ► Time-series of annual fish abundance were derived from beam trawl survey data. ► Dynamic factor analysis detected synchronous changes in abundance among species. ► Interspecific synchrony was explained by climate and environmental factors. ► Potential drivers were sea bottom temperature and the East Atlantic Pattern.

Keywords : Interspecific synchrony, Time-series analysis, Demersal fish, Early-life history, Climate forcing, Bay of Biscay

1. Introduction

Synchrony - the tendency of wild populations to display similar temporal fluctuations in abundance or in life-history traits (e.g., growth rate, body condition) – is a longstanding issue in ecology (Elton and Nicholson 1942; Moran 1953), with important implications for species conservation and management (Earn et al. 2000; Stier et al. 2020). Synchrony among spatially distinct populations (i.e., spatial synchrony) has been extensively studied and detected in wide range of taxa, both aquatic and terrestrial (reviewed in Koenig 1999; Liebhold et al. 2004). The main causes of spatial synchrony (environmental forcing, trophic interactions, dispersal between populations; Liebhold et al. 2004) and its consequences for species conservation are well-known. For example, a metapopulation has a higher risk of collapse or extinction if local populations are synchronized (Heino et al. 1997; Palmqvist and Lundberg 1998). Conversely, synchrony among sympatric populations of different species (i.e., community synchrony) has received less attention (but see, e.g., Raimondo et al. 2004; Cheal et al. 2007; Zimmermann et al. 2019), despite its potential influence on community and ecosystem dynamics. In particular, the stability of a community and the ecosystem services it delivers to society can be reduced if various species fluctuate synchronously, because the decline of one species is not

buffered by an increase of others (Yachi and Loreau 1999; Morin et al. 2014; Zhang et al. 2016). For example, a climatic shift has increased the coherence in survival rates of two salmon species in the northeast Pacific Ocean since the 1980s, reducing the aggregate stability of economically important salmon populations which support commercial fisheries along the west coast of North America (Kilduff et al. 2015). Detecting community synchrony and identifying its potential drivers can provide valuable information on ecosystems dynamics, and contribute to ecosystem-based management of exploited living resources (Latour et al. 2017; Zimmermann et al. 2019).

This study focused on demersal marine fishes inhabiting the Bay of Biscay, a temperate marine ecosystem located in the North-east Atlantic. This large bay is widely open to the Atlantic Ocean, bounded on the north and the east by France, and on the south by Spain. The bay is characterized by a weak oceanic circulation, seasonal eddies and a consistent poleward current over a large continental shelf that narrows southwards (Koutsikopoulos and Le Cann 1996). The area is very productive, notably due to high freshwater discharges from large French rivers and to upwelling events occurring in the south-western part of the bay (Corrales et al. 2022). High primary production has supported intense fisheries since at least the 1950s (Guénette and Gascuel 2012), which in turn have strongly affected the structure and functioning of the marine food web (Quero and Cendrero 1996; Blanchard et al. 2004; Gascuel et al. 2016; Bentorcha et al. 2017). However, total fish and shellfish biomass has been slowly increasing in recent years (Hosack and Trenkel 2019). The Bay of Biscay ecosystem has been affected by various other human pressures including pollution, habitat alteration, and species invasion (Lorance et al. 2009). Effects of anthropogenic climate change have also been reported. A decline in the abundance of northern species and an increase in the abundance of southern species (Poulard and Blanchard 2005; Hermant et al. 2010) have been related to a warming of sea surface temperature in the area (Costoya et al. 2015).

Several scientific surveys are conducted annually in the Bay of Biscay, notably to inform the stock assessment of commercial fish species. For example, the objective of the ORHAGO beam trawl survey is to provide an abundance index of common sole *Solea solea* for stock assessment. Although this

survey samples many other demersal fish species, these data have not been analyzed so far. Yet, they provide a unique opportunity to examine temporal synchrony among demersal marine fishes in the area. In marine fish, interannual fluctuations in abundance are notoriously high. This is mainly because of density-independent environmental factors which can induce a high mortality of pelagic eggs and larvae and thus yield variable levels of recruitment (Myers and Cadigan 1993; Houde 2008). Consequently, the year class strength of marine fishes is generally determined early in life, a period which is therefore critical for the replenishment of adult populations (Hjort 1914; Leggett and Deblois 1994). Here, we investigated whether 12 demersal marine fishes inhabiting the Bay of Biscay exhibited synchronous changes in abundance during their early life. We analyzed fourteen years of data collected by the ORHAGO survey using dynamic factor analysis, a dimension reduction technique designed specifically for multivariate time-series analysis. The objectives of the study were two-fold: (1) test the hypothesis that juvenile demersal marine fishes shared common trends in abundance in the Bay of Biscay and evaluate the degree of interspecific synchrony (if any), and (2) quantify the relative importance of environmental variables and large-scale climate indices in explaining abundance variations of juvenile fishes and interspecific synchrony.

2. Materials and methods

2.1. Fish sampling

Fish data were collected annually from 2007 to 2020 in the Bay of Biscay by the ORHAGO survey (<https://doi.org/10.18142/23>). The study area extends from 44° to 48° N and from the west coast of France to the 100-m isobath (Fig. 1). The survey follows a stratified sampling design, based on latitude (three regions: northern, central, southern) and depth (two strata in the central region: < 50m and 50-100m). Depending on weather conditions, approximately 48 fixed stations (range: 38-49) were sampled each year in November, as this period is appropriate for sampling both juvenile and adult sole and other fishes. Indeed, at the juvenile stage, many demersal fish species are found in estuarine and coastal shallow areas from late spring to late summer, and then move in fall to deeper

waters where they are sampled by the ORHAGO survey. At each station, a 4-m beam trawl with ten tickler chains and a 40-mm stretched mesh in the cod-end was towed during daylight hours at an average speed of 5 knots for 30 minutes. The swept area was calculated for each tow using vessel GPS position data (beam width multiplied by towed distance). All fishes retained in the net were identified, counted, measured to the nearest 1-cm in total length, and weighed by species on board. Otoliths of common sole were collected for laboratory-based age-determination.

We selected 12 demersal fish species that were sampled each year in at least 10% of hauls: lesser silver smelt (*Argentina sphyraena*), Mediterranean scaldfish (*Arnoglossus laterna*), solenette (*Buglossidium luteum*), common dragonet (*Callionymus lyra*), wedge sole (*Dicologlossa cuneata*), grey gurnard (*Eutrigla gurnardus*), thickback sole (*Microchirus variegatus*), common sole, greater weever (*Trachinus draco*), Atlantic horse mackerel (*Trachurus trachurus*), pouting (*Trisopterus luscus*), and poor cod (*Trisopterus minutus*). These demersal species have various functional characteristics in common (e.g., diet; Table 1). Although Atlantic horse mackerel is often considered pelagic, it was selected because it generally forms large shoals near the bottom during daylight hours (Macer 1977), which explains its occurrence and high abundance in bottom trawl catches. We estimated the age-composition of common sole using age-length keys generated from data collected during the ORHAGO survey. For all remaining species, we established length boundaries between age groups by examining length-frequency distributions. We used the von Bertalanffy growth function when a distinct mode was not obvious or the length distribution was unimodal. We focused on a single age group to identify more easily the potential driving environmental factors. We selected one-year olds because they were more consistently sampled than young-of-the-year individuals due to the mesh size used in the cod-end of the beam trawl and the location of the trawl hauls. We calculated for each species annual abundance indices for age one (A_t in ind.km⁻²) as follows:

$$A_t = \frac{\sum_k \alpha_k \cdot \bar{A}_{t,k}}{\sum_k \alpha_k}$$

where $\bar{A}_{t,k}$ is the mean density (ind.km⁻²) at age one, year t , in stratum k , and α_k is the area (km²) of stratum k .

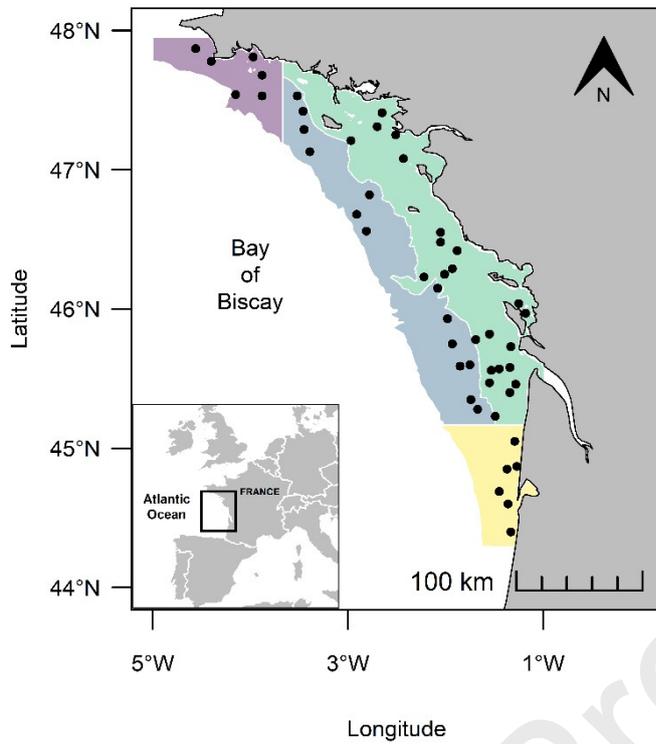


Fig. 1. Study area in the Bay of Biscay and sampling design of the ORHAGO survey. Colored surfaces are sampling strata and black dots fixed stations. The study area extends from the coast to the 100-m isobath.

Table 1. Functional traits of 12 marine fish species studied in the Bay of Biscay. Commercial species are underlined.

Common name	Latin name	Morphology	Biogeography	Vertical habitat	Spawning	Diet
Lesser silver smelt	<i>Argentina sphyraena</i>	Roundfish	Lusitanian	Benthopelagic	Winter - spring	Benthivore
Mediterranean scaldfish	<i>Arnoglossus laterna</i>	Flatfish	Lusitanian	Benthic	Spring - summer	Benthivore
Solenette	<i>Buglossidium luteum</i>	Flatfish	Lusitanian	Benthic	Winter - spring	Benthivore
Common dragonet	<i>Callionymus lyra</i>	Roundfish	Lusitanian	Benthic	Winter - spring	Benthivore
<u>Wedge sole</u>	<i>Dicologlossa cuneata</i>	Flatfish	Lusitanian	Benthic	Summer	Benthivore
<u>Grey gurnard</u>	<i>Eutrigla gurnardus</i>	Roundfish	Lusitanian	Benthic	Winter - summer	Benthivore
<u>Thickback sole</u>	<i>Microchirus variegatus</i>	Flatfish	Lusitanian	Benthic	Winter - spring	Benthivore
<u>Common sole</u>	<i>Solea solea</i>	Flatfish	Lusitanian	Benthic	Winter - spring	Benthivore
<u>Greater weever</u>	<i>Trachinus draco</i>	Roundfish	Lusitanian	Benthic	Summer	Benthivore
<u>Atlantic horse mackerel</u>	<i>Trachurus trachurus</i>	Roundfish	Lusitanian	Benthopelagic	Spring	Planktivore
<u>Pouting</u>	<i>Trisopterus luscus</i>	Roundfish	Lusitanian	Benthopelagic	Winter - spring	Benthivore
Poor cod	<i>Trisopterus minutus</i>	Roundfish	Lusitanian	Benthopelagic	Winter - spring	Benthivore

2.2. Explanatory variables

Based on the literature, we identified several processes that may induce abundance variations (cohort strength) and interspecific synchrony of the studied species at age one and selected suitable explanatory variables (Table 2). When appropriate, we also tested whether the selected drivers acted at specific ages (young-of-the-year or age one), in specific habitats (e.g., coastal areas) and/or during specific seasons (e.g., winter-spring versus summer-early fall). We selected three environmental variables to describe the biotic and abiotic conditions experienced by marine fishes in the Bay of Biscay: sea temperature, surface chlorophyll-a (Chl-a) concentration, and river discharge. Time-series of sea temperature (°C) and surface chl-a concentration ($\text{mg}\cdot\text{m}^{-3}$) were derived from ocean physics and biogeochemistry model outputs (reanalysis datasets) for the North-West European shelf (<http://marine.copernicus.eu/services-portfolio/access-to-products/>). These datasets were produced using ocean models (NEMO and ERSEM) that assimilate observations of sea surface temperature

(SST), vertical temperature profiles, and sea surface chlorophyll concentration from ocean color satellite data. They provide monthly mean estimates of each variable at a $0.111^\circ \times 0.067^\circ$ spatial resolution and for 24 depth levels (0 to -5000m). We calculated mean annual sea temperature and Chl-a indices by averaging values over a spatial domain that ranged from latitude 44° to 48° N and extended from the coastline to either the 50-m or the 100-m isobaths (Table 2). We used the mean temperature of the water column (average from January to June) and the sea bottom temperature (average from July to October) to describe the pelagic and demersal phases, respectively. Time-series of daily river discharge ($\text{m}^3 \cdot \text{s}^{-1}$) were obtained from the HYDRO database (<http://www.hydro.eaufrance.fr/>) for nine major rivers flowing into the Bay of Biscay. We calculated a comprehensive index of river discharge as the first component of a principal component analysis (PCA) performed on the nine standardized time-series of mean annual river discharge (average from January to June), because preliminary analyses revealed that these time-series were strongly correlated (Fig. S1). The PCA was implemented in the *FactoMineR* R package (Lê et al. 2008). We also selected two large-scale climate indices that represent major environmental forcing factors of climatic and ecological processes in the Northeast Atlantic (Stenseth et al. 2003): the North Atlantic Oscillation (NAO), and the East Atlantic Pattern (EAP). The NAO is defined as the normalized sea level pressure difference between Iceland and the Azores. It is the main pattern of atmospheric variability in the North Atlantic region (Barnston and Livezey 1987). The NAO exhibits interannual to multidecadal variations that strongly influence temperatures and precipitations in Europe (Hurrell 1995). The EAP corresponds to a north-south dipole in the North Atlantic sea-level pressure field. Its configuration is similar to that of the NAO, albeit displaced southeastwards. It is the second mode of interannual atmospheric variability in the North Atlantic region (Barnston and Livezey 1987). We calculated mean annual time-series of each climate index by averaging monthly mean values provided by the Physical Sciences Laboratory (PSL) (unsmoothed NAO index: <https://www.psl.noaa.gov/data/climateindices/list/>) and by the NOAA Climate Prediction Center (CPC) (EAP index: https://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/ea_index.tim). We also

calculated a winter (December-February) index of the NAO and the EAP, because these two climate patterns are prominent in winter (Barnston and Livezey 1987). We examined each climate and environmental driver with and/or without a one-year lag to test the influence of the environment on juvenile marine fishes during their first and second year of life, respectively (Fig. S2). Although it is well known that fishing is an important driver of fish abundance variations and may induce or increase synchrony among marine species (e.g., Frank et al. 2016; Morrongiello et al. 2021), it was not included as an explanatory variable in the analysis because fishing mortality (F) of both young-of-the-year and one-year-old individuals was assumed to be low for the selected species (e.g., $F = 0$ at age zero and one in the stock assessment of common sole in the Bay of Biscay; ICES 2021).

Table 2. Environmental variables and large-scale climate indices included in the analysis. Potential processes relating these variables to early-life fish dynamics are detailed. Coastal areas: from the coast to the 50-m isobath; Bay of Biscay: from the coast to the 100-m isobath.

Variable	Acronym	Temporal scale	Spatial scale	Age	Processes
River discharge	RIVER_JJ	January-June	Bay of Biscay	0 or 1	High river discharge can increase fish survival and abundance through different potential processes, including (i) bottom-up trophic control: higher amount of nutrients and particulate organic matter leads to higher planktonic (Grimes and Finucane 1991; Wetz et al. 2011) and/or macrobenthic production (Salen-Picard et al. 2002; Darnaude et al. 2004; Kostecki et al. 2010), (ii) enhanced larval drift to or retention in nursery grounds (Grimes and Kingsford 1996; James et al. 2008), and (iii) spatial extension of suitable nursery habitats (Le Pape et al. 2003).
Mean temperature of the water column	TEMP_JJ	January-June	Bay of Biscay	0	Water temperature is known to affect development, growth and survival of pelagic fish eggs and larvae (Houde 1989; Garrido et al. 2016), as well as those of juvenile demersal fish after their settlement in coastal and estuarine areas (Akimova et al. 2016).
Sea bottom temperature	SBT_JJ	January-June	Bay of Biscay	1	
	SBT_JO	July-October	Coastal areas	0 or 1	
Surface chlorophyll a	S_Chla	Annual	Bay of Biscay	0 or 1	Proxy for primary production (Ryther and Yentsch 1957; Boyce et al. 2010). At the base of the marine food web, primary production determines the amount of food available for higher trophic levels (Lindeman 1942), notably fish larvae and juveniles, which in turn can affect fish growth, survival and production (bottom-up trophic control; Ware and Thomson 2005; Chassot et al. 2010; Capuzzo et al. 2018).
	S_Chla_JJ	January-June	Bay of Biscay	0 or 1	
North Atlantic Oscillation	NAO	Annual	North Atlantic	0 or 1	Major forcing factors driving ecosystem dynamics in the North Atlantic. The NAO and the EAP are known to influence marine plankton and/or higher trophic levels through various processes (Drinkwater et al. 2003; Tanner et al. 2019), including demersal marine fishes at the juvenile stage (Attrill and Power 2002).
	NAO_w	December-February	North Atlantic	0 or 1	
East Atlantic Pattern	EAP	Annual	North Atlantic	0 or 1	
	EAP_w	December-February	North Atlantic	0 or 1	

2.3. Statistical analysis

We used dynamic factor analysis (DFA) to investigate whether demersal marine fishes shared common temporal trends in abundance at the juvenile stage in the Bay of Biscay, and to identify potential environmental drivers of these dynamics. DFA is a dimension reduction technique designed specifically to analyze multivariate time-series, including those that are relatively short, non-stationary or contain missing values (Zuur et al. 2003b). Time-series are modeled as a linear combination of shared hidden trends, potential environmental covariates, and observation errors.

The DFA model can be written in matrix form as follows:

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

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

where y_t is the $n \times 1$ vector of observations (here, the standardized abundance indices of the n fish species) in year t , x_t is a $m \times 1$ vector of m hidden trends ($m \ll n$), Z is a $n \times m$ matrix of factor loadings on the trends, d_t is a $q \times 1$ vector of environmental covariates, D is a $n \times q$ matrix of the effects of the covariates on the observations, and v_t is a $n \times 1$ vector of the observations errors, which are assumed to follow a multivariate normal (MVN) distribution with mean vector 0 and $n \times n$ variance–covariance matrix R .

The m hidden trends in year t (x_t) are modeled as random walks with process errors w_t , a $m \times 1$ vector of errors which are assumed to follow a multivariate normal distribution with mean vector 0 and a $m \times m$ variance–covariance matrix I . The hidden trends represent temporal patterns shared by the abundance time-series that are not explained by the covariates. In order to make the model identifiable, the matrix I was set to the identity matrix (Zuur et al. 2003a; Holmes et al. 2012). The matrix Z contained species-specific factor loadings. We examined a matrix D with either species-specific or shared covariate effects (i.e., which contained a single common parameter for each covariate applied to all species). The magnitude and sign of the factor loadings (and the covariate effects) indicated the extent to which the common trends (and the environmental covariates, respectively) were related to the abundance time-series of each fish species. Factor loadings and

covariate effects were statistically significant when their 95% confidence interval (CI) did not overlap zero. We examined three structures for the variance-covariance matrix R: (i) shared variance but no covariance (*diagonal and equal*), (ii) shared variance and covariance (*equalvarcov*), and (iii) different variances and no covariance (*diagonal and unequal*) between fish species. Preliminary analyses showed that models with an *unconstrained* variance-covariance matrix R did not converge, likely due to the relatively short length of the time-series (14 years). Before its inclusion in the DFA model, each time-series of fish abundance and environmental covariate was standardized by subtracting its mean and dividing by its standard deviation (Zuur et al. 2003a). Incorporating covariates in DFA models is optional. In the present study, we fitted and examined two kinds of DFA models: (i) models without covariates to detect common trends in the abundance time-series and estimate the degree of temporal synchrony among species, and (ii) models with covariates to identify potential environmental drivers of fish abundance variations.

Given the small number of abundance time-series ($n = 12$), we allowed a maximum of three hidden trends and two environmental covariates in any single model. We conducted model selection using the Akaike's information criterion corrected for small sample size (AICc). Models with AICc values two units apart or less were considered competitive models with similar support from the data (Burnham and Anderson 2008). We calculated an additional measure of model fit, called 'fit ratio', by dividing the sum-of squared residuals by the sum-of-squared observations for each species' time-series. Lower fit ratios indicate better model fit (Zuur et al. 2003b). We also averaged fit ratios across species and used this metric, denoted 'mean fit', to compare models (Peterson et al. 2017). We tested DFA models in two steps. First, we examined models with all combinations of one, two or three hidden trends, zero or one covariate and the three structures of the variance-covariance matrix R. The rank order of the models with one covariate (based on their AICc) determined the order in which the second covariate was added (Jorgensen et al. 2016). We restricted the list of second covariates to those, which were not collinear with the first covariate (Fig. S3), and which were previously included in models with an AICc value at least two units lower than that of the 'best'

model without covariates ('baseline' model). We verified that parameter estimation converged for each model, and conducted visual inspection of residuals plots and model fits to data for the top 20 models. We further calculated Pearson's correlation coefficients between the hidden trends of the best DFA model and environmental variables that were not included in that model to search for potential environmental explanations for the trends (Zuur et al. 2003b). The DFA models were fitted using the *MARSS* R package (Holmes et al. 2012). All analyses were conducted using R version 4.0.5 (R Core Team 2021).

3. Results

3.1. Detecting common trends in the abundance time-series

The best DFA model *without covariates* (baseline model) had one common hidden trend to describe the abundance time-series of the 12 demersal marine fishes studied in the Bay of Biscay (Fig. 2a, Table S1). This trend was characterized by a steep increase in abundance at the beginning of the time-series followed by a short and abrupt decline from 2010-2012. A similar but smoother pattern was observed during the rest of the time-series, with a peak in 2017. Remarkably, all fish species except *T. draco* had positive factor loadings on the common trend (Fig. 2b). Loadings were high (≥ 0.5) and statistically significant for six species (*B. luteum*, *A. sphyraena*, *C. lyra*, *A. laterna*, *M. variegatus*, and *D. cuneata*) and fairly high (≥ 0.25) and but not statistically significant for four other species (*T. minutus*, *T. trachurus*, *E. gurnardus* and *S. solea*). The baseline model included an observation error structure of shared variance but no covariance between species (*diagonal and equal* R matrix). Time-series of fish abundance were moderately well fitted by the baseline model (Fig. S4), with poor model fit for six species (*E. gurnardus*, *S. solea*, *T. draco*, *T. trachurus*, *T. luscus* and *T. minutus*, fit ratio > 0.7 , Table S2); all but *T. minutus* are commercial species. Internannual fluctuations in fish abundance were better explained by including covariates in DFA models.

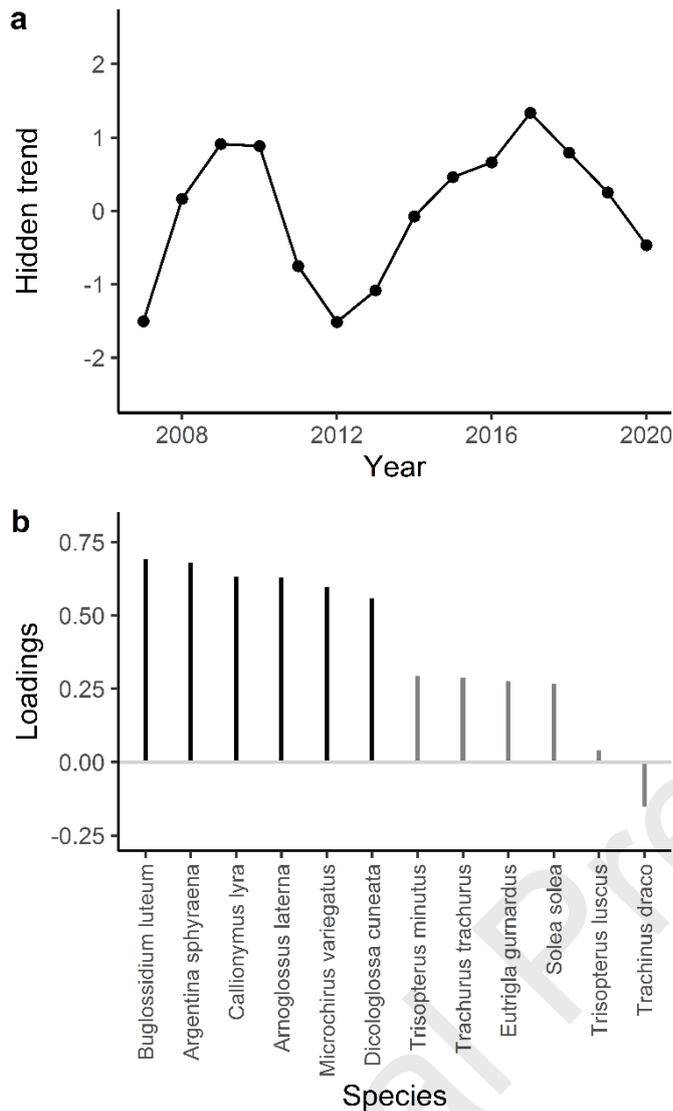


Fig. 2. Common hidden trend in 12 fish abundance time-series from the Bay of Biscay (a) and factor loadings (b) estimated by the 'baseline' model (best DFA model *without covariates*). Factor loadings were arranged in descending order (b); those which were statistically significant (at $\alpha=0.05$ level) were displayed in black (otherwise, in grey).

3.2. Including environmental covariates in DFA models

Nine DFA models including environmental covariates had more data support than the baseline model (Table 3). The best model included one hidden trend and two environmental covariates: sea bottom temperature (mean from January to June, SBT_JJ) and the EAP lagged one year (annual mean, Lag.EAP). The hidden trend of the best model showed some similarities with that of the baseline

model, notably a short steep decline in abundance which occurred however one year earlier (2009-2011), followed by a long increase until 2017 (Fig. 3a). Conversely, the trend was flat at the beginning of the time-series and ended with a slight decrease. Again, factor loadings were mostly positive (Fig. 3b), being statistically significant for *M. variegatus*, *A. sphyraena*, *T. draco*, *T. luscus* and *D. cuneata*, of which only *A. sphyraena* is non-commercial. Loadings were low (either positive: < 0.1 , or negative: > -0.1) and not significant for five species (*E. gurnardus*, *B. luteum*, *C. lyra*, *T. minutus* and *S. solea*). Only *T. trachurus* showed a high negative and significant loading on the hidden trend. The observation error structure in the best model was diagonal and equal (shared variance and no covariance) but a model with the same covariates and an error structure of shared variance and covariance performed similarly well ($\Delta AICc < 2$, equal mean fit values, Table 3). Sea bottom temperature (SBT_JJ) had a single shared negative (-0.43) and statistically significant effect (95% CI: [-0.56; -0.30]) on fish abundance (Fig. 3d). Interannual variations in SBT_JJ were opposite to those of the hidden trend estimated by the baseline model, except during the period 2014-2017 characterized by moderate variations around the mean (Fig. 3c). The Lag.EAP was also included as a covariate in the best model. After a short decrease during 2007-2009, the Lag.EAP showed a progressive increase until 2017, followed by a steep decline. The species-specific effect of the Lag.EAP was either negative or positive, and statistically significant for some of the species (e.g. *T. luscus*, Fig. 3d). Based on the estimates of the factor loadings and the Lag.EAP effect, fish species could be clustered into two groups: species that showed a high positive significant loading on the hidden trend and mostly a negative Lag.EAP effect, versus species that showed a low and/or negative loading on the hidden trend and mostly a positive Lag.EAP effect. Interestingly, the hidden trend of the best DFA model was strongly and positively correlated with Lag.NAO_w (Pearson's $r = 0.75$, Fig. S5), and to a lesser extent with NAO_w ($r = 0.66$). Correlations with other environmental variables were either negative or positive, and generally much lower (Table S3). Overall, the time-series of fish abundance were well fitted by the best DFA model (Fig.4), except for *E. gurnardus*, *S. solea*, and *T. draco* (fit ratio > 0.7 , Table S2).

Table 3. The top nine DFA models, which all have more data support than the best model without covariates (i.e., the baseline model, $|\Delta\text{AICc}| > 2$). The variance-covariance structure (R), the number of hidden trends (m), the log-likelihood (logLik), the number of parameters estimated (K), the mean fit and the AICc of each model are listed. The ΔAICc values are relative to the AICc score of the baseline model, which is denoted in italics. The prefix 'Lag' indicates covariates with a one-year lag, and an asterisk (*) indicates a shared covariate effect across all species (otherwise, the covariate effect was species-specific). The acronym of each covariate is defined in Table 2. Note that several other DFA models had an AICc value lower than that of the baseline model (see Table S4).

Model	Covariates	R	m	logLik	K	Mean fit	AICc	ΔAICc
1	SBT_JJ*, Lag.EAP	diagonal and equal	1	-194	26	0.54	450	-22
2	SBT_JJ*, Lag.EAP	equalvarcov	1	-193	27	0.54	451	-21
3	SBT_JJ*	diagonal and equal	1	-212	14	0.68	455	-17
4	SBT_JJ*	equalvarcov	1	-211	15	0.67	456	-16
5	Lag.NAO_w*	diagonal and equal	1	-218	14	0.67	467	-5
6	Lag.S_Chla*	diagonal and equal	1	-218	14	0.72	467	-5
7	NAO_w*	diagonal and equal	1	-219	14	0.70	469	-3
8	Lag.EAP	diagonal and equal	1	-205	25	0.57	469	-3
9	Lag.NAO_w*	equalvarcov	1	-218	15	0.67	469	-3
<i>Baseline</i>	<i>no covariate</i>	<i>diagonal and equal</i>	<i>1</i>	<i>-222</i>	<i>13</i>	<i>0.71</i>	<i>472</i>	<i>0</i>

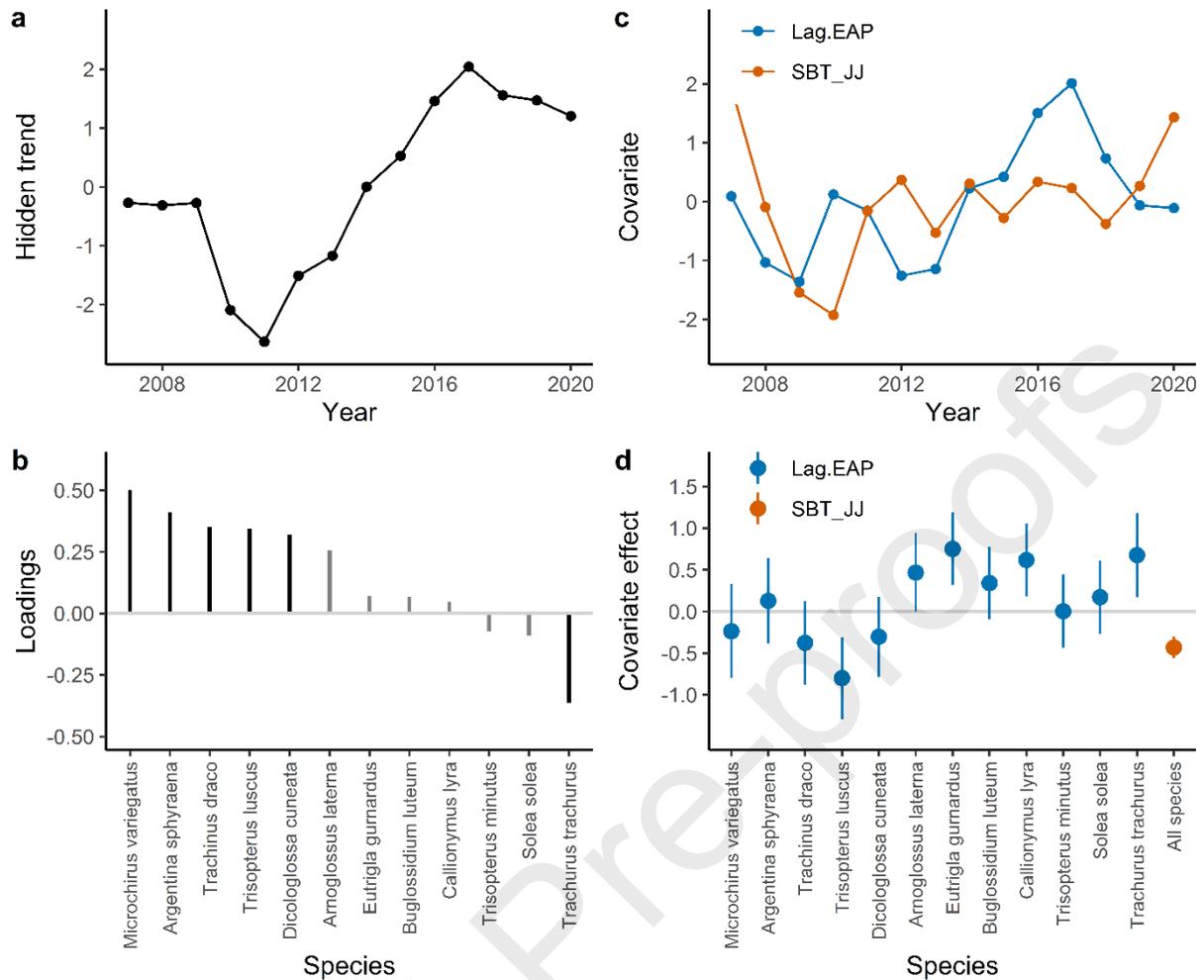


Fig. 3. Common hidden trend in 12 fish abundance time-series from the Bay of Biscay (a) and factor loadings (b) estimated by the best DFA model. It included sea bottom temperature (mean from January to June, SBT_JJ) and the East Atlantic Pattern lagged one year (annual mean, Lag.EAP) as standardized covariates (c) with a single shared negative effect and a species-specific effect, respectively (d). Factor loadings were arranged in descending order (b); those which were statistically significant were displayed in black (otherwise, in grey). Estimates of the species-specific effect of the EAP (blue dots) and their 95% confidence interval (blue lines) (d) were displayed in the same order as for factor loadings.

Seven other DFA models with one hidden trend and a single environmental covariate outperformed the baseline model ($|\Delta\text{AICc}| \geq 3$), but they had all much less data support than the best DFA model

(Table 3). These models included the two covariates included in the best DFA model individually (SBT_JJ and Lag.EAP), but also alternative environmental drivers such as the winter NAO (with or without a one-year lag) and the surface Chl-a index lagged one year. The environmental covariates included in these models had a single shared and significant effect on juvenile fish abundance, except Lag.EAP whose effect was species-specific and significant for some of the species. The effect of Lag.NAO_w, Lag.EAP and Lag.S_Chla was positive while that of SBT_JJ and NAO_w was negative in the nine top models. The R matrix with the most data support was consistently diagonal and equal, for all environmental covariates and number of hidden trends included in DFA models (Tables 3 and S3).

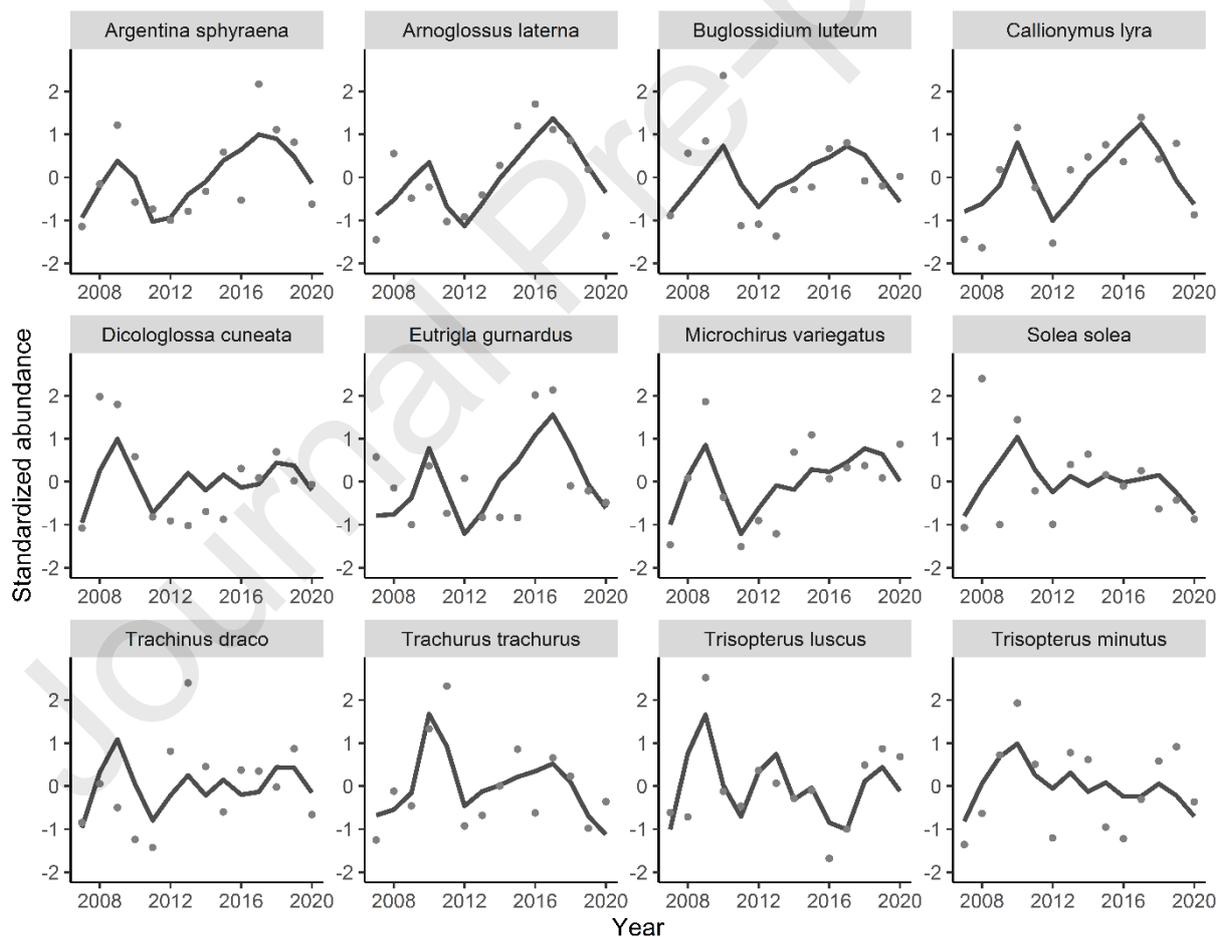


Fig. 4. Model fits (lines) to the time-series of standardized fish abundance (dots) by species. Fitted values from the best DFA model (Table 3).

4. Discussion

Our analysis revealed strong evidence for synchronous changes in abundance among most of the 12 studied juvenile demersal marine fishes in the Bay of Biscay over the past two decades. We showed that this strong temporal coherence was likely explained by environmental and climate factors, notably sea bottom temperature and the EAP. We discuss below these findings and their implications for management and interpret the potential processes behind the drivers identified in our study.

4.1. Temporal synchrony and consequence for management

Fitting DFA models without covariates enabled us to identify the main temporal pattern in the abundance time-series of the studied juvenile fishes, and to quantify the degree of synchrony among species using factor loadings. The fact that the loadings on the trend estimated by the baseline model had the same sign for all species except *T. draco* and had high or fairly high values for most of the species examined (9 out of 12, significant for 6) revealed a high interspecific synchrony in the dynamics of juvenile demersal marine fishes in the Bay of Biscay. These synchronous fluctuations in abundance might be explained by shared life history traits and other functional characteristics, which may lead to similar responses to environmental forcing (Lepš et al. 2018; Viviani et al. 2019; Rocha et al. 2021). However, such a degree of synchrony among species was not expected and raises critical questions about the structure and the dynamics of the demersal fish community in the Bay of Biscay. For example, does this interspecific synchrony detected during early-life stages persist until recruitment to the fisheries, or even older ages? Is it generalizable to other fish species, notably commercial ones? Was the stability of the Bay of Biscay demersal fish community reduced by this interspecific synchrony, as suggested by both theoretical and empirical studies (Yachi and Loreau 1999; Blüthgen et al. 2016; van Klink et al. 2019)? The existence of synchrony can have implications for fisheries if it reduces the stabilizing portfolio effect stemming from the exploitation of several species by a fishery (e.g., Minnegal and Dwyer 2008; Kilduff et al. 2015; Cline et al. 2017). In the Bay

of Biscay, fishing fleets typically exploit 4–19 species (Trenkel et al. 2013). Among the studied species, only *S. solea*, *T. trachurus* and *T. luscus* are among the 20 major commercial species for French fisheries in this area (Daurès et al. 2009). Synchrony was relatively low among these species, as indicated by opposite signs or low estimates for the Lag.EAP effect and the loadings on the common trend of the best DFA model. Further, the three species are exploited by different fleets (Daurès et al. 2009). Hence, overall the results of this study provided little indications for synchrony in young-of-the-year or one-year-old individuals challenging fisheries for the three major species. However, further studies are needed for investigating the fisheries and management consequences for *M. variegatus*, *D. cuneata* and *T. draco*, as these three minor commercial species showed a higher level of synchrony. Whether synchronous fluctuations in abundance occur among other species in the Bay of Biscay also requires further investigations.

4.2. A synchronizing influence of sea bottom temperature?

Including covariates in DFA models provided a means to determine the potential environmental drivers of juvenile fish dynamics in the Bay of Biscay, and helped to identify the life stage (via time lags) and the season (via season for explanatory variables) at which they were likely at play. It also revealed a temporal trend shared by the abundance time-series which was not explained by the covariates included in the best DFA model.

The shared effect of the SBT_JJ suggests that sea bottom temperature during the first half of the year had a synchronizing influence on the abundance of juvenile (age 1) demersal fishes in November, and partly explained the common temporal pattern detected by the baseline model in the abundance time-series. Interestingly, the first years of the studied period were characterized by extreme winter temperatures in Europe. The winter 2006/2007 was exceptionally warm (Yiou et al. 2007; Rempfer et al. 2010), while the winters 2008/2009 and 2009/2010 were among the coldest of the past decades (Cattiaux et al. 2010; Wetthey et al. 2011). Extreme weather events are expected to synchronize population dynamics across species (Hansen et al. 2013; Black et al. 2014), though there is little

empirical evidence for fishes. The winter temperature anomalies recorded in 2007, 2009 and 2010 in the Bay of Biscay might have been high enough to simultaneously affect several demersal fish species at the juvenile stage. However, we would expect effects of extreme sea temperatures on pelagic eggs and larvae, which are characterized by high mortality rates, rather than on demersal one-year-old fishes which have higher survival (Houde 2008; Nash and Geffen 2012). In addition, the negative effect of the SBT on the species examined was surprising, because the Bay of Biscay does not correspond to the southern limit of their latitudinal range. A negative effect of winter sea temperature on the year-class strength of European plaice (*Pleuronectes platessa*) (van der Veer and Witte 1999; Fox et al. 2000) and Atlantic cod (*Gadus morhua*) (Planque and Fox 1998) has been reported in the North Sea and in the Irish Sea, respectively. However, in these studies the influence of winter sea temperature was on early-life stages (eggs and/or larvae), and these two boreal species have colder thermal affinities than those of the Lusitanian species examined in the present study.

Beyond direct physiological effects, environmental drivers may affect marine fishes indirectly through trophic interactions (e.g., Beaugrand et al. 2003). For example, high recruitments of some bivalve species have been documented after severe winters in the Wadden Sea (Strasser et al. 2003), as well as recruitment failures after mild winters (Beukema 1992). However, this negative effect of extreme sea temperatures seems to be restricted to the recruitment success of a few prey species. In the Bay of Biscay, the extreme cold weather in winter 1963 led to an unusual decrease in nearshore water temperature, which strongly impacted oysters (*Ostrea edulis*) and nearly wiped out the common octopus (*Octopus vulgaris*) from the shores of Britany for several decades (P. Lorange, pers. comm.). A reduction in predation pressure exerted by crustaceans on juvenile plaice was also reported after severe winters on the Swedish west coast (Pihl 1990) and in the Wadden Sea (van der Veer and Bergman 1987; van der Veer et al. 2000), but only for young-of-the-year fish. More generally, severe winters tend to induce a decline in macrobenthic biomass and abundance (Beukema 1979; Armonies et al. 2001; Kröncke et al. 2013; Beukema and Dekker 2020), which likely results in a lower food supply for benthivore species, at least in early spring (Beukema et al. 1993). In

summary, we found no plausible explanation in the literature for the observed negative effect of the SBT on one-year-old fishes in the Bay of Biscay.

Interannual fluctuations in abundance indices from bottom trawl surveys could reflect changes in the spatial distribution of demersal fish, rather than variations in year-class strength or population size. Indeed, extreme water conditions such as marine heat waves have been found to lead to simultaneous spatial shifts of several fish species (Auth et al. 2018; Li et al. 2019). Such shifts would decrease abundance if individuals moved outside the survey area. However, we did not find any underlying mechanism explaining why the SBT recorded during the first half of the year could affect the spatial distribution of one-year-old fishes five months later in November. Consequently, we cannot exclude that the relationship between the abundance of one-year-old fishes and the SBT_JJ was spurious, indicating simply temporal concurrence rather than causation. An alternative explanation might be that the SBT_JJ was correlated to another variable which actually affected the dynamics of juvenile demersal fishes in the Bay of Biscay, but which was not included in the present study.

4.3. Species-specific effect of the EAP

Temporal variations in climate indices represent broad-scale environmental changes that can affect multiple trophic levels (Drinkwater et al. 2003), with potential consequences for the growth and survival of early-life stages of fishes. The effects of the EAP on marine organisms in the North Atlantic have been less studied and are thus less well-known than those of other climate patterns like the NAO (Stenseth et al. 2003). However, previous studies revealed changes in zooplankton phenology along the European shelf associated with seasonal and annual indices of the EAP (Uriarte et al. 2021), as well as a positive effect of the autumn EAP index on growth variations of Atlantic horse mackerel off the Iberian Atlantic coast (Tanner et al. 2019). In the Bay of Biscay, anchovy (*Engraulis encrasicolus*) recruitment has been negatively related to the EAP in spring-early summer (March to

July), which has been explained by its influence on wind speed and direction and, in turn, on upwelling events (Borja et al. 2008). Our findings further suggest that the EAP can affect the abundance of demersal young-of-the-year fishes in the Bay of Biscay. Understanding the processes underlying this EAP effect is not straightforward, notably because climate patterns reflect the temporal variations of various weather variables (Stenseth et al. 2003). A positive significant correlation between the winter EAP index and precipitation has been previously reported in the northern part of France (Casanueva et al. 2014) and in southern England (Hall and Hanna 2018). Consequently, the winter EAP index also correlated positively with river discharge in western Brittany (Tréguer et al. 2014) and more globally, in the Bay of Biscay (Fig. S6). Hence, the effect of the EAP on juvenile demersal fishes might be partially mediated by river discharge, involving a bottom-up trophic control and/or modulating larval drift to estuarine and coastal nursery grounds. However, the influence of the EAP on climate variability extends beyond the winter period (Báez et al. 2021). For example, in the United Kingdom, the summer EAP correlated positively with precipitation and negatively with temperature (Hall and Hanna 2018). This lasting influence of the EAP throughout the year may explain why the annual index (rather than its winter component) was included in the best DFA model. It also highlights that the effect of the EAP in Western Europe is more complex than a simple influence on precipitation and river discharge during the first half of the year. Furthermore, our results indicated that the effect of the EAP was species-specific, which was not necessarily expected because the species examined in the present study have many functional and life-history traits in common (Table 1). The reason why the fish species were clustered into two groups based on the EAP effect can be explained by the additive structure of DFA models: the hidden trend in the best model represented the temporal pattern shared by the species that were not affected by the EAP. However, we did not find any explanation for why abundance changes of some species were significantly explained by the EAP while others were not. Despite a growing number of studies focusing on the EAP, a better understanding of the effects of this large-scale climate pattern on oceanographic processes and marine organisms requires further investigations.

4.4. Alternative drivers of juvenile fish abundance

Besides the effects of the SBT and the EAP, the presence of alternative covariates in DFA models that outperformed the baseline model suggests that fluctuations in fish abundance may also be related to other environmental variables, notably the winter NAO and Chl_a indices. The strong positive correlation found between the winter NAO index lagged one year and the hidden trend of the best DFA model supports this hypothesis. The one-year lag associated with these two covariates in the top DFA models indicates an influence of environmental forcing factors on demersal fishes during their first year of life. In the North Atlantic, influence of the NAO has been observed on various marine organisms, from phytoplankton to large fish and seabirds (Drinkwater et al. 2003). For example, a positive relationship was established between a winter NAO index and larval survival rates of common sole in the Bay of Biscay (Savina et al. 2016). The authors hypothesized that strengthened westerly winds over northern Europe during positive phases of the NAO index (Hurrell 1995; Hurrell and Deser 2010) enhance the drift of sole larvae from offshore spawning areas to estuarine and coastal nurseries in the Bay of Biscay. Because most of the species examined in our study share early-life history characteristics, the same mechanism might explain the observed positive significant effect of the winter NAO index on the abundance of juvenile demersal fishes in this study. The relationship might also involve sea temperature, although the effect of the winter NAO index on this weather variable seems weak (Planque et al. 2003) or restricted to northern coastal areas in the Bay of Biscay (Costoya et al. 2015). The cold winter of 2010 was an exception, as this extreme weather event was caused by long-lasting negative winter NAO anomalies (Cattiaux et al. 2010).

It seems plausible that the surface Chl_a index used in the present study did not reflect interannual fluctuations in prey biomass or production well, which may explain the moderate data support for the corresponding DFA model. Unfortunately, other indices of food availability for fish larvae (zooplankton) and juveniles (macrobenthic invertebrates) were not available at a relevant spatial or temporal scale for the Bay of Biscay. Nonetheless, the identified positive significant effect of the

Chl_a index on the abundance of young-of-the-year fishes suggests a bottom-up trophic control in the study area. During their pelagic larval stage, demersal fish feed on planktonic prey, notably copepods (Nunn et al. 2012). Hence, primary production may have affected zooplankton dynamics during 2007-2020, as observed previously in the southern Bay of Biscay (Stenseth et al. 2006; Dessier et al. 2018), and in turn, early-life stages of demersal fishes. Lastly, we assumed that fishing pressure during the first and second year of life was low for the studied species in the Bay of Biscay, but we could not verify this assumption due to the lack of fishing mortality estimates for these ages and the absence of stock assessments for certain species. Consequently, we cannot exclude that fishing pressure amplified synchronous interspecific fluctuations of species caught together in the Bay of Biscay mixed fisheries. Indeed, four out of the five species found to be significantly positively associated with the hidden trend of the best DFA model are commercial species, which could mean fishing could have driven the hidden trend. Thus, due to these data limitations, the potential importance of bottom-up trophic processes and fishing in driving early-life fish dynamics in the Bay of Biscay may have been underestimated. Similarly, it is noteworthy that DFA tests for linear relationships (Zuur et al. 2003b). Therefore, certain non-linear relationships between demersal fish abundance and explanatory variables may not have been detected in this study.

4.5. Conclusion and future directions

We found strong support for temporal synchrony among several juvenile demersal fishes, which raises questions about the stability of the demersal fish community in the area. We also found evidence for climate and environmental forcing on the sensitive early-life stages of these demersal fishes, as revealed by the one-year lag associated with most of the covariates included in the best fitting DFA models. Further, the significant effect of SBT in the best model suggests that abiotic conditions may also influence the abundance of one-year-old fish, although the underlying mechanisms remain unclear. Finally, our study searched for common trends in fish abundance at the scale of the Bay of Biscay. Yet, the range of movements of demersal fish is limited during the juvenile

stage (e.g., for flatfish, Le Pape and Cognez 2016), so that individuals that settled in the North are for instance unlikely to mix at this stage with those that settled in the South of the bay. Thus, future research may focus on spatial synchrony within and among species at smaller spatial scales to disentangle the effects of large-scale or regional drivers investigated in the present study and those of local drivers acting at specific locations on population dynamics. Because the degree of synchrony among species can vary through time (Kilduff et al. 2015; Marshall et al. 2019), another key issue would be to investigate whether temporal coherence in abundance or in life-history traits strengthens or decreases in the coming years.

Acknowledgments

We thank Gérard Biais, Yann Coupeau and the crews of the ORHAGO surveys for their efforts to collect field data. We are grateful to David Eme for sharing a R script for handling netCDF files. We also thank two anonymous reviewers for providing valuable comments on an earlier version of the manuscript. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

References

- Armonies, W., E. Herre, and M. Sturm. 2001. Effects of the severe winter 1995/96 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the island of Sylt. *Helgol. Mar. Res.* **55**: 170–175.
- Auth, T. D., E. A. Daly, R. D. Brodeur, and J. L. Fisher. 2018. Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean. *Glob. Change Biol.* **24**: 259–272. doi:10.1111/gcb.13872
- Báez, J. C., L. Gimeno, and R. Real. 2021. North Atlantic Oscillation and fisheries management during global climate change. *Rev. Fish Biol. Fish.* **31**: 319–336. doi:10.1007/s11160-021-09645-z

- Barnston, A. G., and R. E. Livezey. 1987. Classification, seasonality and persistence of low-frequency atmospheric circulation patterns. *Mon. Weather Rev.* **115**: 1083–1126.
- Beaugrand, G., K. M. Brander, J. A. Lindley, S. Souissi, and P. C. Reid. 2003. Plankton effect on cod recruitment in the North Sea. *Nature* **426**: 661–664.
- Bentorcha, A., D. Gascuel, and S. Guénette. 2017. Using trophic models to assess the impact of fishing in the Bay of Biscay and the Celtic Sea. *Aquat. Living Resour.* **30**: 7.
- Beukema, J. J. 1979. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter. *Neth. J. Sea Res.* **13**: 203–223.
- Beukema, J. J. 1992. Expected changes in the Wadden Sea benthos in a warmer world: lessons from periods with mild winters. *Neth. J. Sea Res.* **30**: 73–79.
- Beukema, J. J., and R. Dekker. 2020. Half a century of monitoring macrobenthic animals on tidal flats in the Dutch Wadden Sea. *Mar. Ecol. Prog. Ser.* **656**: 1–18.
- Beukema, J. J., K. Essink, H. Michaelis, and L. Zwarts. 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? *Neth. J. Sea Res.* **31**: 319–330.
- Black, B. A., W. J. Sydeman, D. C. Frank, and others. 2014. Six centuries of variability and extremes in a coupled marine-terrestrial ecosystem. *Science* **345**: 1498–1502.
- Blanchard, F., F. LeLoc'h, C. Hily, and J. Boucher. 2004. Fishing effects on diversity, size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. *Mar. Ecol. Prog. Ser.* **280**: 249–260.
- Blüthgen, N., N. K. Simons, K. Jung, and others. 2016. Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. *Nat. Commun.* **7**: 10697.
doi:10.1038/ncomms10697
- Borja, Á., A. Fontán, J. O. N. Sáenz, and V. Valencia. 2008. Climate, oceanography, and recruitment: the case of the Bay of Biscay anchovy (*Engraulis encrasicolus*). *Fish. Oceanogr.* **17**: 477–493.

- Burnham, K. P., and D. R. Anderson. 2008. Model selection and multimodel inference, 2nd ed. Springer New York, NY.
- Casanueva, A., C. Rodríguez-Puebla, M. D. Frías, and N. González-Reviriego. 2014. Variability of extreme precipitation over Europe and its relationships with teleconnection patterns. *Hydrol. Earth Syst. Sci.* **18**: 709–725.
- Cattiaux, J., R. Vautard, C. Cassou, P. Yiou, V. Masson-Delmotte, and F. Codron. 2010. Winter 2010 in Europe: A cold extreme in a warming climate. *Geophys. Res. Lett.* **37**.
- Cheal, A. J., S. Delean, H. Sweatman, and A. A. Thompson. 2007. Spatial synchrony in coral reef fish populations and the influence of climate. *Ecology* **88**: 158–169.
- Cline, T. J., D. E. Schindler, and R. Hilborn. 2017. Fisheries portfolio diversification and turnover buffer Alaskan fishing communities from abrupt resource and market changes. *Nat. Commun.* **8**: 1–7.
- Corrales, X., I. Preciado, D. Gascuel, and others. 2022. Structure and functioning of the Bay of Biscay ecosystem: A trophic modelling approach. *Estuar. Coast. Shelf Sci.* **264**: 107658.
- Costoya, X., M. Decastro, M. Gómez-Gesteira, and F. Santos. 2015. Changes in sea surface temperature seasonality in the Bay of Biscay over the last decades (1982–2014). *J. Mar. Syst.* **150**: 91–101.
- Daurès, F., M.-J. Rochet, S. Van Iseghem, and V. M. Trenkel. 2009. Fishing fleet typology, economic dependence, and species landing profiles of the French fleets in the Bay of Biscay, 2000–2006. *Aquat. Living Resour.* **22**: 535–547. doi:10.1051/alr/2009031
- Dessier, A., P. Bustamante, T. Chauvelon, and others. 2018. The spring mesozooplankton variability and its relationship with hydrobiological structure over year-to-year changes (2003–2013) in the southern Bay of Biscay (Northeast Atlantic). *Prog. Oceanogr.* **166**: 76–87.
- Drinkwater, K. F., A. Belgrano, A. Borja, and others. 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation, p. 211–234. *In* The North

- Atlantic Oscillation: Climatic Significance and Environmental Impact. American Geophysical Union.
- Earn, D. J., S. A. Levin, and P. Rohani. 2000. Coherence and conservation. *Science* **290**: 1360–1364.
- Elton, C., and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. *J. Anim. Ecol.* 215–244.
- Fox, C. J., B. P. Planque, and C. D. Darby. 2000. Synchrony in the recruitment time-series of plaice (*Pleuronectes platessa* L) around the United Kingdom and the influence of sea temperature. *J. Sea Res.* **44**: 159–168.
- Frank, K. T., B. Petrie, W. C. Leggett, and D. G. Boyce. 2016. Large scale, synchronous variability of marine fish populations driven by commercial exploitation. *Proc. Natl. Acad. Sci.* **113**: 8248–8253. doi:10.1073/pnas.1602325113
- Gascuel, D., M. Coll, C. Fox, and others. 2016. Fishing impact and environmental status in European seas: a diagnosis from stock assessments and ecosystem indicators. *Fish Fish.* **17**: 31–55.
- Guénette, S., and D. Gascuel. 2012. Shifting baselines in European fisheries: the case of the Celtic Sea and Bay of Biscay. *Ocean Coast. Manag.* **70**: 10–21.
- Hall, R. J., and E. Hanna. 2018. North Atlantic circulation indices: links with summer and winter UK temperature and precipitation and implications for seasonal forecasting. *Int. J. Climatol.* **38**: e660–e677.
- Hansen, B. B., V. Grøtan, R. Aanes, and others. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. *Science* **339**: 313–315. doi:10.1126/science.1226766
- Heino, M., V. Kaitala, E. Ranta, and J. Lindström. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. *Proc. R. Soc. Lond. B Biol. Sci.* **264**: 481–486.
- Hermant, M., J. Lobry, S. Bonhommeau, J.-C. Poulard, and O. Le Pape. 2010. Impact of warming on abundance and occurrence of flatfish populations in the Bay of Biscay (France). *J. Sea Res.* **64**: 45–53.

- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp P-V Reun Cons Int Explor Mer* **20**: 1–228.
- Holmes, E. E., E. J. Ward, and K. Wills. 2012. MARSS: Multivariate Autoregressive State-space Models for Analyzing Time-series Data. *R J.* **4**: 11–19.
- Hosack, G. R., and V. M. Trenkel. 2019. Functional group based marine ecosystem assessment for the Bay of Biscay via elasticity analysis. *PeerJ* **7**: e7422. doi:10.7717/peerj.7422
- Houde, E. D. 2008. Emerging from Hjort's shadow. *J. Northwest Atl. Fish. Sci.* **41**: 53–70.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science* **269**: 676–679.
- Hurrell, J. W., and C. Deser. 2010. North Atlantic climate variability: the role of the North Atlantic Oscillation. *J. Mar. Syst.* **79**: 231–244.
- ICES. 2021. Working Group for the Bay of Biscay and the Iberian Waters Ecoregion (WGBIE). *ICES Sci. Rep.* **3:48**: 1101 pp. doi:https://doi.org/10.17895/ices.pub.8212
- Jorgensen, J. C., E. J. Ward, M. D. Scheuerell, and R. W. Zabel. 2016. Assessing spatial covariance among time series of abundance. *Ecol. Evol.* **6**: 2472–2485.
- Kilduff, D. P., E. Di Lorenzo, L. W. Botsford, and S. L. Teo. 2015. Changing central Pacific El Niños reduce stability of North American salmon survival rates. *Proc. Natl. Acad. Sci.* **112**: 10962–10966.
- van Klink, R., J. Lepš, R. Vermeulen, and F. de Bello. 2019. Functional differences stabilize beetle communities by weakening interspecific temporal synchrony. *Ecology* **100**: e02748.
- Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. *Trends Ecol. Evol.* **14**: 22–26.
- Koutsikopoulos, C., and B. Le Cann. 1996. Physical processes and hydrological structures related to the Bay of Biscay anchovy. *Sci. Mar.* **60**: 9–19.
- Kröncke, I., H. Reiss, and J. W. Dippner. 2013. Effects of cold winters and regime shifts on macrofauna communities in shallow coastal regions. *Estuar. Coast. Shelf Sci.* **119**: 79–90.

- Latour, R. J., J. Gartland, and C. F. Bonzek. 2017. Spatiotemporal trends and drivers of fish condition in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **579**: 1–17.
- Le Pape, O., and N. Cognez. 2016. The range of juvenile movements of estuarine and coastal nursery dependent flatfishes: estimation from a meta-analytical approach. *J. Sea Res.* **107**: 43–55. doi:10.1016/j.seares.2015.06.001
- Lê, S., J. Josse, and F. Husson. 2008. FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* **25**: 1–18. doi:10.18637/jss.v025.i01
- Leggett, W. C., and E. Deblois. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Neth. J. Sea Res.* **32**: 119–134.
- Lepš, J., M. Májerková, A. Vítová, J. Doležal, and F. de Bello. 2018. Stabilizing effects in temporal fluctuations: management, traits, and species richness in high-diversity communities. *Ecology* **99**: 360–371.
- Li, L., A. B. Hollowed, E. D. Cokelet, and others. 2019. Subregional differences in groundfish distributional responses to anomalous ocean bottom temperatures in the northeast Pacific. *Glob. Change Biol.* **25**: 2560–2575. doi:10.1111/gcb.14676
- Liebhold, A., W. D. Koenig, and O. N. Bjørnstad. 2004. Spatial synchrony in population dynamics. *Annu Rev Ecol Evol Syst* **35**: 467–490.
- Lorance, P., J. A. Bertrand, A. Brind'Amour, M.-J. Rochet, and V. M. Trenkel. 2009. Assessment of impacts from human activities on ecosystem components in the Bay of Biscay in the early 1990s. *Aquat. Living Resour.* **22**: 409–431.
- Macer, C. T. 1977. Some aspects of the biology of the horse mackerel [*Trachurus trachurus* (L.)] in waters around Britain. *J. Fish Biol.* **10**: 51–62.
- Marshall, K. N., J. T. Duffy-Anderson, E. J. Ward, S. C. Anderson, M. E. Hunsicker, and B. C. Williams. 2019. Long-term trends in ichthyoplankton assemblage structure, biodiversity, and synchrony in the Gulf of Alaska and their relationships to climate. *Prog. Oceanogr.* **170**: 134–145.

- Minnegal, M., and P. Dwyer. 2008. Managing risk, resisting management: Stability and diversity in a southern Australian fishing fleet. *Hum. Organ.* **67**: 97–108.
- Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. *Aust. J. Zool.* **1**: 291–298.
- Morin, X., L. Fahse, C. de Mazancourt, M. Scherer-Lorenzen, and H. Bugmann. 2014. Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. *Ecol. Lett.* **17**: 1526–1535.
- Morrongiello, J. R., P. L. Horn, C. Ó Maolagáin, and P. J. Sutton. 2021. Synergistic effects of harvest and climate drive synchronous somatic growth within key New Zealand fisheries. *Glob. Change Biol.* **27**: 1470–1484. doi:10.1111/gcb.15490
- Myers, R. A., and N. G. Cadigan. 1993. Is juvenile natural mortality in marine demersal fish variable? *Can. J. Fish. Aquat. Sci.* **50**: 1591–1598.
- Nash, R. D., and A. J. Geffen. 2012. Mortality through the early life-history of fish: What can we learn from European plaice (*Pleuronectes platessa* L.)? *J. Mar. Syst.* **93**: 58–68.
- Nunn, A. D., L. H. Tewson, and I. G. Cowx. 2012. The foraging ecology of larval and juvenile fishes. *Rev. Fish Biol. Fish.* **22**: 377–408.
- Palmqvist, E., and P. Lundberg. 1998. Population extinctions in correlated environments. *Oikos* **83**: 359–367. doi:10.2307/3546850
- Peterson, C. D., C. N. Belcher, D. M. Bethea, W. B. Driggers III, B. S. Frazier, and R. J. Latour. 2017. Preliminary recovery of coastal sharks in the south-east United States. *Fish Fish.* **18**: 845–859.
- Pihl, L. 1990. Year-class strength regulation in plaice (*Pleuronectes platessa* L.) on the Swedish west coast. *Hydrobiologia* **195**: 79–88.
- Planque, B., P. Beillois, A.-M. Jégou, P. Lazure, P. Petitgas, and I. Puillat. 2003. Large-scale hydroclimatic variability in the Bay of Biscay: the 1990s in the context of interdecadal changes. *ICES Marine Science Symposia.* 61–70.
- Planque, B., and C. J. Fox. 1998. Interannual variability in temperature and the recruitment of Irish Sea cod. *Mar. Ecol. Prog. Ser.* **172**: 101–105.

- Poulard, J.-C., and F. Blanchard. 2005. The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay. *ICES J. Mar. Sci.* **62**: 1436–1443.
- Quero, J.-C., and O. Cendrero. 1996. Incidence de la pêche sur la biodiversité ichthyologique marine : le bassin d'Arcachon et le plateau continental sud Gascogne. *Cybiurn* **20**: 323–356.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Raimondo, S., M. Turcáni, J. Patoëka, and A. M. Liebhold. 2004. Interspecific synchrony among foliage-feeding forest Lepidoptera species and the potential role of generalist predators as synchronizing agents. *Oikos* **107**: 462–470.
- Rempfer, J., D. M. Livingstone, C. Blodau, R. Forster, P. Niederhauser, and R. Kipfer. 2010. The effect of the exceptionally mild European winter of 2006–2007 on temperature and oxygen profiles in lakes in Switzerland: A foretaste of the future? *Limnol. Oceanogr.* **55**: 2170–2180.
- Rocha, B. S., E. García-Berthou, J. L. C. Novaes, L. M. Bini, and M. V. Cianciaruso. 2021. Interspecific synchrony is related to body-length similarity in a fish community under prolonged drought conditions. *Sci. Total Environ.* **781**: 146721. doi:10.1016/j.scitotenv.2021.146721
- Savina, M., M. Lunghi, B. Archambault, L. Baulier, M. Huret, and O. Le Pape. 2016. Sole larval supply to coastal nurseries: Interannual variability and connectivity at interregional and interpopulation scales. *J. Sea Res.* **111**: 1–10. doi:10.1016/j.seares.2015.11.010
- Stenseth, N. C., M. Llope, R. Anadón, L. Ciannelli, K.-S. Chan, D. Ø. Hjermann, E. Bagøien, and G. Ottersen. 2006. Seasonal plankton dynamics along a cross-shelf gradient. *Proc. R. Soc. B Biol. Sci.* **273**: 2831–2838.
- Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, K.-S. Chan, N. G. Yoccoz, and B. Ådlandsvik. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc. R. Soc. Lond. B Biol. Sci.* **270**: 2087–2096.

- Stier, A. C., A. Olaf Shelton, J. F. Samhuri, B. E. Feist, and P. S. Levin. 2020. Fishing, environment, and the erosion of a population portfolio. *Ecosphere* **11**: e03283.
- Strasser, M., R. Dekker, K. Essink, and others. 2003. How predictable is high bivalve recruitment in the Wadden Sea after a severe winter? *J. Sea Res.* **49**: 47–57.
- Tanner, S. E., A. R. Vieira, R. P. Vasconcelos, S. Dores, M. Azevedo, H. N. Cabral, and J. R. Morrongiello. 2019. Regional climate, primary productivity and fish biomass drive growth variation and population resilience in a small pelagic fish. *Ecol. Indic.* **103**: 530–541.
- Tréguer, P., E. Goberville, N. Barrier, and others. 2014. Large and local-scale influences on physical and chemical characteristics of coastal waters of Western Europe during winter. *J. Mar. Syst.* **139**: 79–90.
- Trenkel, V. M., F. Daurès, M.-J. Rochet, and P. Lorance. 2013. Interannual variability of fisheries economic returns and energy ratios is mostly explained by gear type. *PLoS One* **8**: e70165.
- Uriarte, I., F. Villate, A. Iriarte, Á. Fanjul, A. Atkinson, and K. Cook. 2021. Opposite phenological responses of zooplankton to climate along a latitudinal gradient through the European Shelf. *ICES J. Mar. Sci.* **78**.
- van der Veer, H. W., and M. J. Bergman. 1987. Predation by crustaceans on a newly settled 0-group plaice *Pleuronectes platessa* population in the western Wadden Sea. *Mar. Ecol. Prog. Ser.* **35**: 203–215.
- van der Veer, H. W., A. J. Geffen, and J. I. Witte. 2000. Exceptionally strong year classes in plaice *Pleuronectes platessa*: are they generated during the pelagic stage only, or also in the juvenile stage? *Mar. Ecol. Prog. Ser.* **199**: 255–262.
- van der Veer, H. W., and J. I. Witte. 1999. Year-class strength of plaice *Pleuronectes platessa* in the Southern Bight of the North Sea: a validation and analysis of the inverse relationship with winter seawater temperature. *Mar. Ecol. Prog. Ser.* **184**: 245–257.

- Viviani, J., C. Moritz, V. Parravicini, D. Lecchini, G. Siu, R. Galzin, and L. Viriot. 2019. Synchrony patterns reveal different degrees of trophic guild vulnerability after disturbances in a coral reef fish community. *Divers. Distrib.* **25**: 1210–1221.
- Wetthey, D. S., S. A. Woodin, T. J. Hilbish, S. J. Jones, F. P. Lima, and P. M. Brannock. 2011. Response of intertidal populations to climate: effects of extreme events versus long term change. *J. Exp. Mar. Biol. Ecol.* **400**: 132–144.
- Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci.* **96**: 1463–1468.
- Yiou, P., R. Vautard, P. Naveau, and C. Cassou. 2007. Inconsistency between atmospheric dynamics and temperatures during the exceptional 2006/2007 fall/winter and recent warming in Europe. *Geophys. Res. Lett.* **34**.
- Zhang, Y., M. Loreau, X. Lü, N. He, G. Zhang, and X. Han. 2016. Nitrogen enrichment weakens ecosystem stability through decreased species asynchrony and population stability in a temperate grassland. *Glob. Change Biol.* **22**: 1445–1455.
- Zimmermann, F., M. Claireaux, and K. Enberg. 2019. Common trends in recruitment dynamics of north-east Atlantic fish stocks and their links to environment, ecology and management. *Fish. Fish.* **20**: 518–536.
- Zuur, A. F., R. J. Fryer, I. T. Jolliffe, R. Dekker, and J. J. Beukema. 2003a. Estimating common trends in multivariate time series using dynamic factor analysis. *Environmetrics* **14**: 665–685.
- Zuur, A. F., I. D. Tuck, and N. Bailey. 2003b. Dynamic factor analysis to estimate common trends in fisheries time series. *Can. J. Fish. Aquat. Sci.* **60**: 542–552.

Declaration of interests

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

considered as potential competing interests:

Journal Pre-proofs