




Review Article

Disentangling the influence of fishing, demography, and environment on population dynamics of Iberian Peninsula waters fish stocks

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Quinzán, M., Castro, J., Massutí, E., Rueda, L., and Hidalgo, M. Disentangling the influence of fishing, demography, and environment on population dynamics of Iberian Peninsula waters fish stocks. – ICES Journal of Marine Science, 77: 1–11.

Received 4 December 2018; revised 7 September 2019; accepted 12 September 2019; advance access publication 13 December 2019.

Overexploitation and climate change are increasingly causing unanticipated changes in marine ecosystems such as higher variability in fish recruitment or shifts in species dominance and distribution that alter the productivity of fish stocks. This study analyses how external and internal drivers influence population dynamics of hake (*Merluccius merluccius*), white anglerfish (*Lophius piscatorius*), four-spot megrim (*Lepidorhombus boschii*), and horse mackerel (*Trachurus trachurus*) of Iberian Peninsula waters of the Northeast Atlantic across different spatiotemporal scales. Available spawning stock biomass and recruitment have been used as biological data, whereas fishing mortality, demographic data as well as climatic and oceanographic data have been used as drivers. The obtained results indicate that population dynamics of these species are mainly driven by oceanographic variability at regional scale along with fishing pressure and demographic factors, while the impact of large-scale climate indices was minimal. The identified variables represent relevant oceanographic regional processes candidate to be potentially integrated into the stock assessment models and management procedures of these important fishery resources.

Keywords: ecosystem approach, NE Atlantic, nonlinearity, spatiotemporal scales

Introduction

It is of fundamental importance for fisheries management to understand the environmental and ecological mechanisms by which the abundance of the populations is regulated. Unravelling the driving forces of population fluctuations has been the aim of an intensive ongoing research effort that has attracted particular interest in the field of fisheries ecology for its implications in conservation and management in the context of global change (O'Brien *et al.*, 2000; Cury *et al.*, 2008; Horswill *et al.*, 2016). Lack of understanding of the sources of temporal variability in fish abundance affects biological reference points, decision making and risk assessment in precautionary fisheries management whereas it is largely responsible for the uncertainty that has led to past failures in managing fisheries (Hilborn *et al.*, 2001). Future sustainable management of fisheries will require well-founded

knowledge on the resilience capabilities of populations to the effects of environmental variability and climate change affecting the stock productivity. In this sense, new generation of stock assessment methods envisions a progressive implementation of environmental and ecological drivers. As the most outstanding example, it is widely acknowledged that environmental factors do drive substantially recruitment variability, which appears to be in general largely independent of the spawning stock biomass (SSB; Szuwalski *et al.*, 2015). However, it does not mean that the role of the other important drivers such as fishing exploitation or regulatory density-dependent mechanisms might be undermined. A wide number of studies have focused on the influence of fishing exploitation (e.g. Pauly *et al.*, 2002; Planque *et al.*, 2010), density-dependence (e.g. Andersen *et al.*, 2017; Zimmermann *et al.*, 2018) and environment (e.g. Rouyer *et al.*, 2014; Pécuchet *et al.*, 2015)

in fish marine population dynamics. Yet, effects of self-regulating forces as well as external factors on fish populations are complex, and their combined effect is often non-linear and still to be fully understood (e.g. Bjørnstad and Grenfell, 2001; Hidalgo *et al.*, 2012). As it is evidenced by recent and strategic calls of scientific projects within Europe {e.g. H2020 [“Advancing basic biological knowledge and improving management tools for commercially important fish and other seafood species” (<http://ec.europa.eu/research/participants/portal/desktop/en/opportunities/h2020/topics/sfs-21-2016-2017.html>)]}, there is a pressing need to provide a more efficient fisheries management of European fish stocks and novel stock assessment models. A pre-requisite for this critical step forward is to disentangle the influence of fishing, demography, and environment on population dynamics of fish stocks, as well as the spatial and temporal scale at which these drivers impact fish populations.

Fisheries exploitation, understood as human-made predation, can alter the structure of marine populations (Planque *et al.*, 2010), either by direct effects such as the removal of individuals by increasing fishing mortality or indirect ones that can affect at the population and community level, such as intra- and inter-specific relationships, survival, and demography (Audzijonyte *et al.*, 2013). Furthermore, the mean age of the spawning stock, which may be important in determining the reproductive potential of fish stocks (Trippel *et al.*, 1997; Marteinsdottir and Begg, 2002), is impacted by the overexploitation of marine fish populations. That typically results in the loss of the largest individuals making marine populations more sensitive to climate forcing (e.g. Anderson *et al.*, 2008; Planque *et al.*, 2010).

Fish population dynamics are intimately associated with climatic and oceanographic features, which influence early life stage survival and determine species distributions, migrations, abundance, and interactions (Lees *et al.*, 2006). Climate-driven large-scale decadal fluctuations affect marine ecosystems worldwide (Stenseth *et al.*, 2002). More specifically, a wide range of studies have investigated the North Atlantic climate variability and its long-term influence on marine community structures and commercial fish abundance in the Atlantic ecosystems (Lees *et al.*, 2006; Ottersen *et al.*, 2013). Furthermore, changes in key oceanographic variables, such as sea surface temperature (SST), upwelling, and poleward flow, can also affect marine ecosystems (Sánchez and Gil, 2000; Hoegh-Guldberg and Bruno, 2010). Nonetheless, sensitivity to the environment is not uniform across populations. The response to the stimuli is time lagged, and the delay can vary with species, life stage, geographical location within the range of the species' repartition and type or frequency of forcing (Tommasi *et al.*, 2017). Interest is increasing in the complex ways in which age-structured populations respond selectively to different time scales of variability in the environment (Rouyer *et al.*, 2012). Previous studies have documented time-lags up to 5 years in the biological response of the Iberian Atlantic pelagic ecosystem to changes in climate (Bode *et al.*, 2006). In other cases, highly dynamics oceanographic process (e.g. meso-scale structures, upwelling strength) occurring in a relevant timing within the life cycle of a species can affect the inter-annual variability of species distributions (e.g. mesoscales structures shaping spatial pattern of recruitment in the north Spain, Sánchez and Gil, 2000). These highly dynamic processes are often difficult to identify because they operate at short temporal and spatial scales (ICES, 2016a). Indeed, ecologically similar species may be affected by different drivers when their habitats

requirements differ. Thus, a more complete mechanistic understanding is likely to arise only by incorporating observations at a variety of scales.

Here we investigate how fishing exploitation, environmental drivers, and internal population properties, such as age structure, modulate the population dynamics of four commercially exploited stocks in the Iberian Peninsula waters of the Northeast Atlantic across different spatiotemporal scales. In this regard, estimates of recruitment (R) were investigated in terms of short-term drivers whereas SSB were related to drivers at larger temporal scales applying different time-lags. The study area comprises the regions of the southern Bay of Biscay in the north of Spain and the Atlantic Iberian waters, corresponding to the International Council for the Exploration of the Sea (ICES) fishing areas 27.8c and 27.9a. The stocks analysed in this study were hake (*Merluccius merluccius*), white anglerfish (*Lophius piscatorius*), four-spot megrim (*Lepidorhombus boschii*), and horse mackerel (*Trachurus trachurus*), as they are among the most important species in the study area in terms of their commercial interest, and their life history and ecology have been extensively studied (Muus and Dahlström, 1989; Sánchez *et al.*, 1998; Muus and Nielsen, 1999; FAO-FIGIS, 2005). Ecologically, they occupy separate segments of the Atlantic ecosystem. The Atlantic Iberian stocks of hake, white anglerfish, and four-spot megrim share the same geographical distribution, covering the ICES Divisions 8c and 9a whereas the Iberian stock of horse mackerel is reduced to Division 9a. In 2004, it was separated from the previously named Southern stock, while the horse mackerel population of ICES Division 8c was added to the current Western stock (ICES, 2004). Spanish, French, and Portuguese fleets operate in those waters and consist of gillnetters, longliners, trawlers, and artisanal boats targeting those species among a wide variety. Landings of these species have fluctuated in the region over the years along with their main population parameters. Despite varying fishing mortality levels, which for hake and four-spot megrim have been considered above the F_{MSY} , the stock sizes of the four stocks are nowadays considered to be in “full reproductive capacity” (ICES, 2019a, b, c, d).

Although several studies have investigated density-dependent and independent mechanisms that affect ecological dynamics of fish populations of the study species (Santos *et al.*, 2007; Hidalgo *et al.*, 2014; Punzón *et al.*, 2016), little has been done concerning the study of the variability of these stocks together within the same analytical framework. In terms of fishing impact, the state of north-east Atlantic populations has shown signs of recovery (Modica *et al.*, 2014), though it is still unclear how this improvement has affected the dynamics and the structure of the Atlantic communities and ecosystems. We perform a comparative analysis in which the results of identical analyses of individual stocks are compared, as such studies can help to determine what is fundamental and what is specific to particular ecosystems.

Material and methods

Population data

Estimates of recruitment (R) and SSB of the four commercial stocks considered from the Iberian Peninsula waters of Northeast Atlantic (hake, white anglerfish, four-spot megrim, and horse mackerel) were obtained from the data compiled by two ICES Working Groups: the Bay of Biscay and the Iberian waters Ecoregion (WGBIE: ICES, 2017a) and the Southern Horse

Mackerel, Anchovy, and Sardine (WGHANSA: ICES, 2017b). These ICES Working Groups used different models to evaluate their corresponding stocks, being GADGET (Begley and Howell, 2004) for hake (period 1982–2016, ICES Division 8c–9a), SS3 (Methot, 2000) for white anglerfish (period 1980–2016, ICES Division 8c–9a), XSA (Shepherd, 1999) for four-spot megrim (period 1986–2016, ICES Division 8c–9a), and AMISH (Lowe et al., 2009) for horse mackerel (period 1992–2016, ICES Division 9a). All the assessments groups use quarterly-based information to calculate yearly abundances. In addition, a relative measure of recruitment success was used as response, i.e. survival, the ratio between the annual numbers of recruits (all these stocks consider R at age 0) and the SSB of the previous year (R/SSB_{t-1}). The study area corresponds to the distribution of the stocks analysed as shown in Figure 1: ICES Divisions 8c (southern Bay of Biscay: 43–44.5 N, 2–11 W) and 9a (Atlantic Iberian waters: 36–43 N, 5–11 W).

Anthropogenic data

A time series of fishing mortality (F) was obtained for each stock by averaging over the most harvested age or length classes (based on stock-specific reports, ICES 2017a, b): $F_{\text{bar}(1-3)}$ for hake, $F(30-130\text{cm})$ for white anglerfish, $F_{\text{bar}(2-4)}$ for four-spot megrim, and $F_{\text{bar}(2-10)}$ for horse mackerel.

Demographic data

To describe the demographic characteristics, the mean age of the spawning population (A), determined for each year and stock separately, was estimated by calculating a spawning biomass weighted mean value, added over all age groups potentially contributing to the spawning stock.

Trophic data

Blue whiting is known to be the main prey of hake (Velasco and Olaso, 1998). Hence, to assess the potential trophic influence of blue whiting on hake dynamics, estimates of recruitment of blue whiting (R_{WHB}) were obtained from the data compiled by ICES Working Group on Widely Distributed Stocks (WGWIDE: ICES, 2016b) and used as predictor when considered SSB of hake.

Climatic data

Global indices were used to determine whether regional changes in the populations were triggered by large-scale climatic processes. The application of climate indices by definition reduces complex space and time variability into simple measures, “packages of weather” (Stenseth et al., 2003).

Two climate indices were used to capture complex spatio-temporal variability into a simple metric and to investigate the influence of large-scale climatic processes. These were the North Atlantic Oscillation index (NAO) and the Eastern Atlantic annual pattern (EA) because they are the most representative patterns of atmospheric variation in the Atlantic Northern hemisphere and are known to affect marine populations of the European seas. The NAO index consists of a north–south dipole of anomalies; one centre is located over Greenland and the other centre with the opposite sign spans the central latitudes of the North Atlantic between 35° and 40°N. We used the winter average (December–March) of the NAO index because its influence in the Atlantic is higher during winter when the coupled ocean–atmosphere system

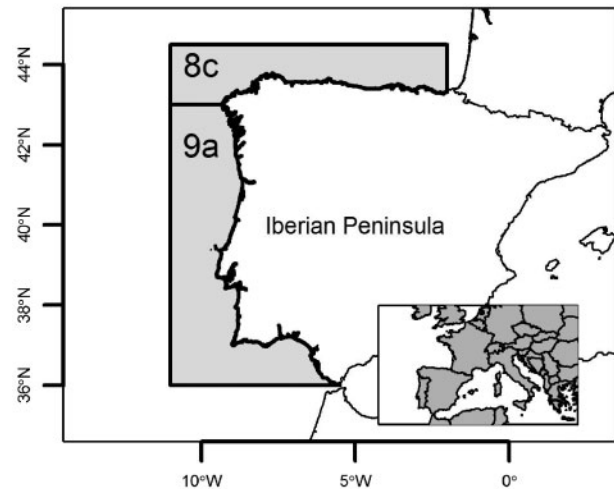


Figure 1. Map of the study area corresponding to NE Atlantic waters. Rectangles represent the ICES Divisions 8c and 9a.

is more active (Hurrell, 1995). The anomaly centres of EA pattern are displaced south-eastward to the approximate nodal lines of the NAO index (Barnston and Livezey, 1987; more information on the calculation process can be found at www.cpc.ncep.noaa.gov). It is precisely in the northern part of the Iberian Peninsula where the EA pattern best explains temperature variations and plays a key role in long-term variability of winds across the North Atlantic, thereby affecting coastal upwelling intensity (deCastro et al., 2008). The effect of EA is particularly strong in autumn and winter.

Oceanographic data

Regional and local hydroclimatic variables off Spanish coast were selected to represent oceanographic conditions in the distribution area of the analysed stocks.

Many studies have described the impact of sea temperature on fish population dynamics, distributions and life-history traits. Moreover, temperature may influence the physiological processes indirectly through alterations of ecosystem composition, resource availability or hydrographic conditions. For our analysis, annually averaged temperatures over the study area were obtained at two considered bathymetric levels, i.e. at surface (SST) and at 200 m depth (T200). Satellite estimates of SST were obtained from the Climate Diagnostics Center (NCEP/NCAR) reanalysis field (Kalnay et al., 1996), which provides monthly mean SST on selected region. Temperatures at 200 m depth (T200) were obtained from the EN4 quality controlled ocean data (version EN4.1.1, Good et al., 2013). This dataset spans from 1950 to 2016 and includes data from bathythermographs (MBTs and XBTs), hydrographic profiles (CTDs and predecessors), moored buoys, and profiling floats (Argos data).

Finally, local variables were selected at a measurement point chosen to be representative of the oceanographic characteristics along the Iberian Peninsula waters: the Upwelling Index (UI) and the Iberian Poleward Current (IPC) index. During summer, the intensity peaks of cold and nutrient-rich upwelling waters increase primary production (Manson et al., 2005) while in autumn, the warm IPC waters flow northwards along the shelf break (about 200 m depth) (Frouin et al., 1990). Monthly values

of Ekman transport were computed by the Instituto Español de Oceanografía from geostrophic winds centred at 43°N 11°W (<http://www.indicedeafloramiento.ieo.es/>), and averaged between April and September (UI) and between October to December of the previous year (IPC). Values represent strength and direction of the Ekman transport. The Atlantic north-western coast of the Iberian Peninsula shows a north–south orientation, hence, winds from the North produce offshore transport. The magnitude of offshore transport in the upper layer is considered an indicator of the amount of water upwelled along the coast into the surface layers (Mann and Lazier, 1991). Positive values of these indices indicate offshore water transport whereas negative values indicate onshore water transport.

Statistical analysis

Prior to analysis, all data sets were first explored for outliers, correlation, collinearity, and normality following protocols proposed by Zuur et al., 2010. Collinearity of variables was tested by analysing linear pairwise correlation coefficients and calculating the variance inflation factor (VIF). Variables that gave a VIF > 4 were sequentially dropped out, and then recalculated until all VIFs were smaller than the preselected threshold (Zuur et al., 2010). The response variables were log-transformed to ensure normality in the residual error.

Anthropogenic index (F), demographic index (A), two climate indices (NAO and EA), two regional temperatures as two averaged temperatures over the study area (SST and T200), and two local oceanographic indices (UI and IPC) were used as predictors. When analysing R and survival, SSB_{t-1} was also used as predictor. As abovementioned, SSB for hake was analysed including recruitment of blue whiting (R_{WHB}) as predictor.

The analysis consisted of examining the fishing, demographic, and environmental influence on population parameters of each stock when predictors were lagged 1 year. In addition, the influence on SSB was also explored when predictors were lagged 2 and 3 years, respectively. For hake, trophic influence on SSB was additionally explored.

Given that non-linear relationships were expected between the response variables and the predictors, Generalized Additive Models (GAMs: Hastie and Tibshirani, 1990) were used to analyse density-dependent and density-independent effects in population dynamics.

The fully additive GAM fit was given by

$$y_t = b + \sum_j f_j(E_{t-1,t-2,t-3}^j) + \varepsilon_t \quad (1)$$

where y_t is the logarithm of the population parameter at year t ; b is the intercept; $E_{t-1,t-2,t-3}^j$ is a vector of predictors at year $t-1$, $t-2$ or $t-3$, respectively, whose single components are identified by the superscript j ; f_j is non-parametric smoothing function (cubic splines with a maximum 2 degrees of freedom (3 knots, points where the cubic polynomials of the cubic spline meet) and ε_t denotes a Gaussian error term.

A backwards strategy was adopted to select the best model based on the lowest Akaike Information Criterion (AIC; Akaike, 1974). This means that all the predictors were initially included in the GAM model, and then they were sequentially eliminated, one by one, as a result of the low significance in their partial effect, until AIC is minimized with a set of significant covariates.

According to the length of the time series the number of predictors in final models was limited to 3.

All model residuals were checked for the absence of temporal correlation. If autocorrelation in residuals was still observed after model fitting, the log-transformed SSB of previous year, $\log SSB_{t-1}$, was also included as predictor to take into account the potential temporal autocorrelation related to density-dependence in the SSB time series (Hjermann et al., 2004; Minto et al., 2008; Quinzán et al., 2016).

GAM was developed with R package [R Development Core Team (2005), R: A language and environment for statistical computing, reference index version 3.5.1] by using variations of GAM, as implemented in the *mgcv* library (Wood, 2011).

Results

Time series of the variables used in the analysis are plotted in Figure 2a–i. The SSB showed two different levels, a lower level in which it gathered the demersal and benthic stocks, i.e. hake, white anglerfish, and four-spot megrim, and an upper one for horse mackerel. SSB of hake and white anglerfish were high at the beginning of their time series, and dramatically decreased to minimum in mid-90s. Since then, SSB of those stocks has continuously increased. Although less dramatic, similar trend is observed for four-spot megrim. For horse mackerel, SSB showed a marked increase from 2011 onwards (Figure 2a). R of the analysed stocks was highly variable showing three different levels: the lowest for white anglerfish, a medium level for hake and four-spot megrim, and the highest for horse mackerel (Figure 2b). Survival of both hake and white anglerfish (R/SSB_{t-1}) showed two differentiated periods. While starting from similar levels, survival of those stocks diverged from the 90 s (Figure 2c).

Hake and white anglerfish stocks experienced high levels of F in the beginning of their time series. For white anglerfish, F reached the highest value in 1988 ($F=1.52$). It has, however, steadily decreasing afterwards. F on hake has also decreased from 1997 onwards. Estimates of F of four-spot megrim showed a subtle decrease with years. For horse mackerel, the F was the lowest of the four stocks analysed (Figure 2d).

The change in A is illustrated in Figure 2e, which describes the evolution of the demographic structure for each of the analysed stocks. Hake and white anglerfish mean ages started from similar levels but from the 90 s they separated: A of hake declined to the four-spot megrim level, which showed a steady mean age value around 2 throughout the time series, while A of white anglerfish rose to the horse mackerel level.

R of blue whiting is shown in Figure 2f. It was significantly higher in 1997, 2001, 2003 and 2015 than in the years with the historically lowest recruitments (2007–2009). The mean values were much higher than those obtained for the four stocks targeted for analysis; however, the size of the blue whiting stock is not comparable and extends beyond Iberian waters, covering all western European waters.

The time series of climatic and oceanographic indices are shown in Figure 2g–i. For the studied period, NAO showed positive values however a negative phase appeared in 1985, 1987, 1996–1998, 2003 and 2009–2011. It is remarkable the substantial negative value in 2010. In contrast to negative values in late 80 s and 90 s, the EA pattern showed a positive phase from 2000, excluding 2004, 2008 and 2011. Figure 2h reveals that there has been a gradual increase in temperatures (SST and T200). Finally,

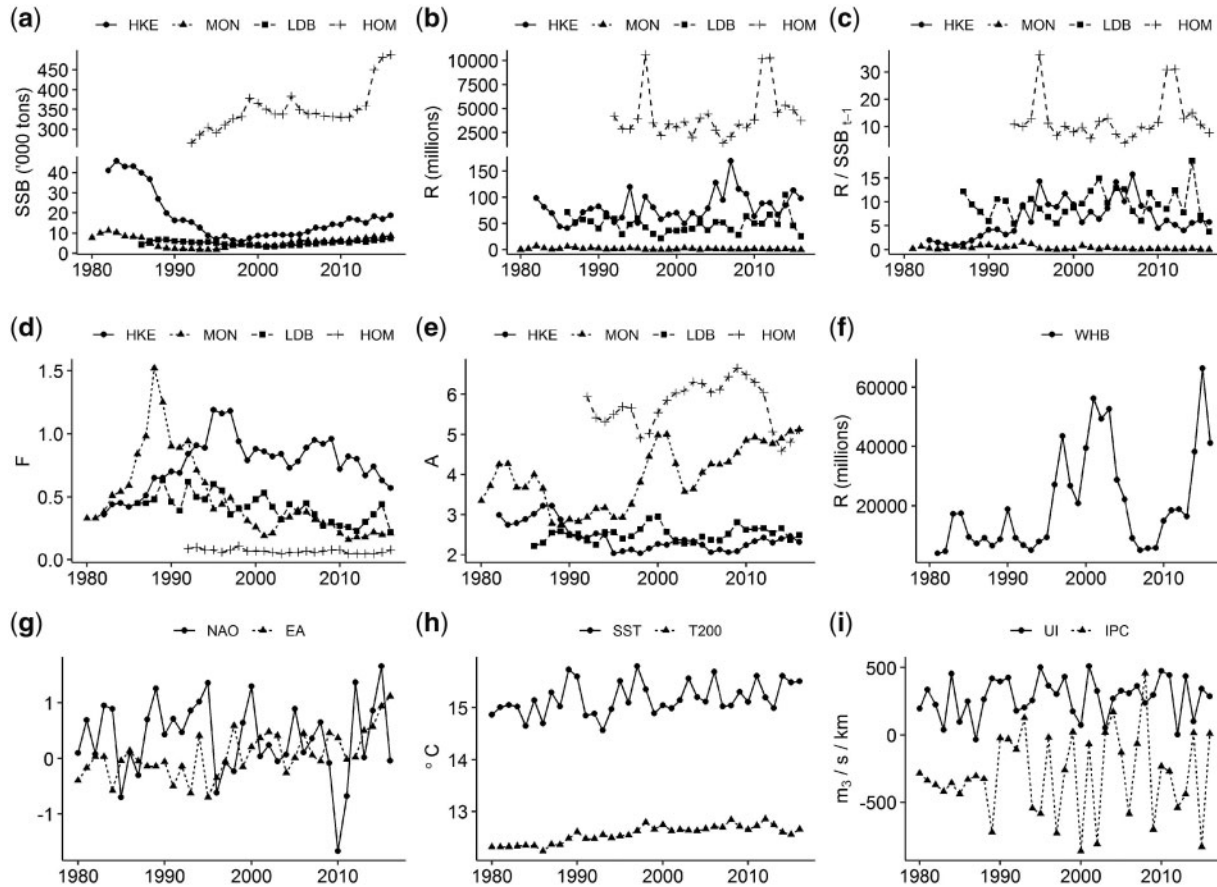


Figure 2. Time series of the variables used in the analysis: (a) SSB; (b) recruitment (R); (c) survival (R/SSB_{t-1}); (d) fishing mortality (F); (e) weighted average of age in spawners abundance (A). Coding line for the four stocks investigated: HKE (hake, continuous, and solid circle), MON (white anglerfish, dotted, and triangle), LDB (four-spot megrim, dotted, and square), and HOM (horse mackerel, dotted, and cross); (f) recruitment of blue whiting (Rwhb); (g) global indices: winter North Atlantic Oscillation (NAO) and East Atlantic pattern (EA); (h) regional parameters: SST and Temperature at 200 m depth (T200) over the study area; (i) local parameters: UI and IPC at 43N 11W.

the maximum values of UI coincide with minimum values of IPC throughout their time series.

Table 1 summarizes the results from the best fitted models selected based on the lowest AIC. Partial effects resulted either linear or almost linear thus indicated by arrows with the aim to help interpretation. The complete combined partial effects for each time-lag scenario are given in the [Supplementary Material](#).

F displayed a negative effect for all SSB analysed (for hake, it was not included due to collinearity with SSB_{t-1}) and a significant positive effect on the survival of white anglerfish.

When included as a predictor, \logSSB_{t-1} affected \logSSB of all stocks analysed, having a positive effect, whereas survival of hake and horse mackerel were negatively affected by that predictor. A weak negative effect of \logSSB_{t-1} on \logR of horse mackerel was also observed. The contribution of this term to the variance explained varies from 6% in model SSB.hom1 to 74.8% in model SSB.mon3. Furthermore, A displayed a negative effect on \logSSB of four-spot megrim and horse mackerel, respectively, though at different time-lags.

The $\log R_{WHB}$ did not show any significant effect on the SSB of hake.

Regarding climatic predictors, the NAO index did not show a significant effect in any of the stocks analysed. However, the EA

pattern showed a negative effect on SSB of white anglerfish with a time-lag of 1 year. In addition, EA displayed opposite effects on both R and survival of four-spot megrim and horse mackerel, respectively, being negative for four-spot megrim but positive for horse mackerel.

Oceanographic predictors showed significant effects on population responses. The effects of SST and IPC on recruitment and survival of hake were both positive. In contrast, when analysing the effect of SST on the same response variables of white anglerfish, a negative effect was observed. There was a significant positive effect of T200 on SSB of hake that seems to last throughout time as well on white anglerfish when lagged 3 years. In contrast, the effect of T200 was negative on SSB of four-spot megrim with a time lag of both 1 and 3 though positive when lagged 2 years. T200 was also observed to negatively affect \logR of white anglerfish. The analysis also suggested a positive effect of UI when lagged 3 years on SSB of horse mackerel, although the intensity of the effect was small.

Discussion

We have analysed the influence of exploitation, demography, and environment on the population parameters of four commercial stocks in Iberian Atlantic waters and the results show species-specific

Table 1. Selected GAMs considering predictors with lag 1 year when modelled against all response variables, and lag 2 and lag 3 years when modelled against parental stock (SSB) of analysed species.

Species	Response variable	lag in predictor (years)	Predictor																Formulation	Model deviance			
			Anthropogenic		Demographic				Trophic		Climatic				Oceanographic								
			F	logSSB _{t-1}	A		logR _{WHB}		NAO		EA		SST		T200		UI				IPC		
p-value	effect	p-value	effect	p-value	effect	p-value	effect	p-value	effect	p-value	effect	p-value	effect	p-value	effect	p-value	effect						
HKE	logSSB	1	***	↘	***	↗	ns		ns		ns		ns		ns		ns		ns		SSB.hke1	94.7	
		2	***	↘	***	↗	ns		ns		ns		ns		ns		ns		ns		SSB.hke2	95.2	
		3	***	↘	***	↗	ns		ns		ns		ns		ns		ns		ns		SSB.hke3	93.6	
	logR	1	ns		ns		ns		ns		ns		**	↗	ns		ns		**	↗	R.hke	29.6	
		log(R/SSB _{t-1})	1	***	↘	***	↗	ns		ns		ns		*	↗	ns		ns		*	↗	R.SSB1.hke	88.6
			2	***	↘	***	↗	ns		ns		ns		ns		ns		ns		ns			
MON	logSSB	1	***	↘	***	↗	ns		ns		*	↘	ns		ns		ns		ns		SSB.mon1	96.6	
		2	***	↘	***	↗	ns		ns		ns		ns		ns		ns		ns		SSB.mon2	96.3	
		3	***	↘	***	↗	ns		ns		ns		ns		ns		ns		ns		SSB.mon3	94.1	
	logR	1	ns		ns		ns		ns		ns		*	↘	*	↘	ns		ns		R.mon	40.3	
		log(R/SSB _{t-1})	1	***	↘	ns		ns		ns		ns		**	↘	ns		ns		ns		R.SSB1.mon	47.6
			2	***	↘	ns		ns		ns		ns		ns		ns		ns		ns			
LDB	logSSB	1	***	↘	***	↗	ns		ns		ns		ns		***	↘	ns		ns		SSB.ldb1	86.1	
		2	ns		***	↗	***	↘	ns		ns		ns		*	↘	ns		ns		SSB.ldb2	88.6	
		3	**	↘	ns		*	↘	ns		ns		ns		**	↘	ns		ns		SSB.ldb3	69.5	
	logR	1	ns		ns		ns		ns		ns		ns		ns		ns		ns		R.ldb	31.4	
		log(R/SSB _{t-1})	1	ns		ns		ns		ns		**	↘	ns		ns		ns		ns		R.SSB1.ldb	32.9
			2	ns		ns		ns		ns		ns		ns		ns		ns		ns			
HOM	logSSB	1	*	↘	**	↗	*	↘	ns		ns		ns		ns		ns		ns		SSB.hom1	89.3	
		2	**	↘	ns		*	↘	ns		ns		ns		ns		ns		ns		SSB.hom2	64.3	
		3	***	↘	ns		ns		ns		ns		ns		ns		.	↗	ns		SSB.hom3	68.5	
	logR	1	ns		.	↘	ns		ns		ns		*	↗	ns		ns		ns		R.hom	26.7	
		log(R/SSB _{t-1})	1	ns		**	↘	ns		ns		*	↗	ns		ns		ns		ns		R.SSB1.hom	33.1
			2	ns		ns		ns		ns		ns		ns		ns		ns		ns			

HKE, hake; MON, white anglerfish; LDB, four-spot megrim; HOM, horse mackerel. The significance (p -value: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $\cdot < 0.1$; ns, not significant) and partial effect (↗: positive; ↘: negative) of each predictor is also indicated. Shaded cell indicates predictor was not included, either due to collinearity or absence of autocorrelation in residuals. F, Fishing mortality; SSB_{t-1}, Spawning Stock Biomass of previous year; A, Weighted average of age in spawners abundance; R_{WHB}, Recruitment of blue whiting; NAO, winter North Atlantic Oscillation; EA, East Atlantic pattern; UI, Upwelling Index (m³/s/km); IPC, Iberian Poleward Current (m³/s/km); SST, Sea Surface Temperature (°C) in the study area; T200, Temperature at 200 m depth (°C) in the study area. [Supplementary material](#) is shown in Appendix 1.

effects while certain consistency was observed between species more attached to the bottom and those more connected to the pelagic realm. Our observations lead us to conclude that the population dynamics of these species are mainly driven by oceanographic variability at regional scale along with fishing pressure and demographic factors.

Fishing mortality resulted, as expected, one of the main drivers of SSB. A negative relation between fishing mortality and SSB has been found in the analysed stocks within the three time-lagged scenarios. It is known that harvesting has direct effects on the biotic components of ecosystems through mortality inflicted as catch or injury (Pope *et al.*, 2006) and in the adaptive life-history traits (Jørgensen *et al.*, 2007). A direct consequence is a reduction in population size and the reduced contribution of larger and older individuals to total abundance (Planque *et al.*, 2010). As increased fishing pressure truncates the age structure, reproductive potential declines rapidly, and this decline outpaces concurrent declines in SSB, while increases the sensitivity to climate variability as it has already been observed for hake (Hidalgo *et al.*, 2009, 2011, 2012, 2014). Exploitation acts therefore as a removal function reducing the mean biomass and the mean age of exploited populations (Planque *et al.*, 2010).

Furthermore, the positive effect of fishing mortality on survival of white anglerfish found in this study may be explained as an indirect consequence of diminished intra-specific competition. Previous studies on the feeding ecology of *Lophius* species found cannibalism was relatively important (Maravelias and Papaconstantinou, 2003). Cannibalism has been suggested as a

regulatory mechanism for recruitment success, including in the case of hake (Hidalgo *et al.*, 2014). That is to say that the major competitor and predator is the adult stock itself. Therefore, reducing SSB by exploitation also reduces competition and predation exerted by large fish on smaller ones (Pope *et al.*, 2006), which may be the plausible mechanism that explains our findings.

Except sparingly in horse mackerel, SSB of the previous year has not shown a significant effect on the recruitment of any of the stocks analysed. This corroborates the weak adjustment of stock–recruitment relationships obtained in the assessment of these and most of stocks, where instead of Ricker or Beverton–Holt models a segmented regression was considered to be more appropriate to calculate biological reference points (ICES, 2017c). In contrast, the results showed SSB of the previous year to be a significant factor of the survival of hake and horse mackerel, which is consistent with Hidalgo *et al.* (2012, 2014) in the case of hake. Minto *et al.* (2008) determined that the interannual variability in survival of a number of marine, anadromous and freshwater fish species increases at low adult abundance in an inversely density-dependent fashion. Recent studies highlight that density-dependence in marine fish population is more complex than it can be captured by models of spatially homogeneous population dynamics or by models based on stock–recruitment relationships, as it is related to the size of the habitat (Andersen *et al.*, 2017). In habitats of small and medium size as those off Iberian Peninsula (in contrast to northern larger habitats such as North Sea), density-dependent regulation of populations does not occur only in early life stages as currently assumed in fish advice, but also

late in life, such as density-dependent adult growth (van Gemert and Andersen, 2018). Thus, competition in the juvenile stages may lead to stunted growth and to overcompensated regulation of the populations at small scales, which was already proposed as a main regulatory process in the southern European hake (Hidalgo *et al.*, 2014).

As shown in this study, the negative effect of mean age of the spawners at different time-lags on analysed SSB evidence that removal of the oldest and largest individuals can have substantial consequences on dynamics as populations are mainly supported by young age classes (Anderson *et al.*, 2008). Older populations contributing less to the SSB in a stock might be a consequence of higher natural mortality in older age-classes. On the other hand, strong evidence were found that age-truncated or juvenescent populations have increasingly unstable population dynamics because of changing demographic parameters (Anderson *et al.*, 2008; Hidalgo *et al.*, 2009). For instance, demographic erosion may trigger changes in the regulatory mechanisms to ensure the long-term persistence of populations (i.e., a long-term constant intrinsic growth rate; Hidalgo *et al.*, 2014). The mechanisms involved are, however, many and complex.

The present work also provided evidence for the importance of oceanographic drivers on the population dynamics of marine stocks. In particular, our results indicated that temperature of intermediate waters along with sea surface temperature plays a key role in regulating population dynamics of demersal species. In our analysis, the influence of temperature of the intermediate waters was found to enhance SSB of hake and the positive effect is observed to persist throughout time. It is known that spawning of hake is located close to the 200 m depth isobath in the southern area of the North-East Atlantic waters (Alvarez *et al.*, 2001). Although previous studies focused on sea surface temperature as a determinant factor driving the timing of the spawning season (Alvarez *et al.*, 2004), no study had investigated to date the influence of intermediate waters characteristics. Our results reveal the importance of at depth temperature in SSB of hake which characterizes the habitat of adults of this species.

Regarding SSB of megrim, it showed opposite responses to the temperature of intermediate waters depending on the time lag scenario evaluated. However, it is not yet clear whether the different signals shown by this predictor influence this species, and longer time series might be required to further investigate this effect. *L. boschii* has a preferential depth range of between 100 and 450 m (mode in 250 m) in ICES Divisions 8c and 9a and has been observed to be significantly correlated with the temperature of intermediate waters (Punzón *et al.*, 2016). The expected response under a scenario of increased temperature of intermediate waters is changed in species distribution (geographic and bathymetric) and abundance. An increase in temperature of intermediate waters has already been detected (González-Pola *et al.*, 2005), which could enhance increases in occurrence and abundance of Lusitanian species at depths where they are normally less frequent, affecting their distributions and abundances.

Our results also evidence that the surface temperature of the previous year has a significant although the opposite effect on recruitment and survival of two species out of four analysed, being positive on hake whereas negative on white anglerfish. Several studies found that higher seawater temperatures contribute to increase development rates and consequently enhance growth during early life stages (e.g. Fernandes *et al.*, 2010; Tsoukali *et al.*, 2016). This implies a reduction in the time spent in such early

vulnerable life stages and thus a greater survival of larvae and juvenile individuals, with the subsequent increase in survival. The positive effect of surface temperature on recruitment of hake resulted from our analysis is in accordance with these observations. By contrast, the increasing temperature can also have negative effects depending on the life history of the species as we here observed on white anglerfish. The northerly spatial range of white anglerfish seems to be limited by low seawater temperatures (Solmundsson *et al.*, 2010). A northward shift of the distribution limits of this species has been already documented due to climate change (Perry *et al.*, 2005; Solmundsson *et al.*, 2010). The observed positive trend in both temperatures at the surface and 200 m depth makes plausible to infer a negative effect on the distribution of this species in southern Atlantic stocks, i.e. a similar effect to the one observed in the North where increasing temperatures cause the northward shift of the species. The observed increase in seawater temperatures could be the reason behind the negative effect of temperature on the recruitment and survival of white anglerfish in this southern Atlantic stock. This response has already been reported by Stige *et al.* (2006), who found a negative effect of increasing temperatures on the recruitment of cod in the southernmost stocks. Temperature affects the timing of ontogenetic transitions, as it may decouple changes in the larval environment from the thermal cues used by the adult population (Stige *et al.*, 2006). Eggs and larvae of white anglerfish are pelagic, and therefore, phenology of important ecosystem processes and stratification of the water column may have significant impacts on the survival of this species. However, further research is needed to confirm the temperature–recruitment links and to understand the underlying mechanisms through the early life stage.

For fish species that spawn offshore and recruit inshore, like hake, the retention processes over the nursery areas of eggs and larvae from spawning areas constitute a critical process in its life cycle that largely depends on oceanographic processes (e.g. shelf-break currents) (Sánchez and Gil, 2000). The preferential habitats identified for hake recruits in the northern continental shelf waters off the Iberian Peninsula are areas affected by Poleward Current within a bathymetry range of 150–175 m (Sánchez and Gil, 2000), and we observed in our results that its strength influences hake recruitment. Currents, such as the Poleward Current, determine the major nursery grounds of hake by producing meso-scale eddies which retain larvae and favour the feeding behaviour of recruits (Sánchez and Gil, 2000).

NAO and EA indices are structurally similar, although some differences are expected in their effects on the analysed stock dynamics due to the more regional character of EA index. The NAO (December–March) was not found to influence the population parameters of the stocks analysed from the Iberian Peninsula waters although many authors have reported links between long-term trends in NAO and different components of the Atlantic ecosystem (e.g. Brander, 2005; Engelhard *et al.*, 2014). Previous studies have shown EA to be more influential than NAO in some areas of the Northeast Atlantic, such as the Bay of Biscay, as it accounts for a much higher fraction of variance (Sáenz *et al.*, 2001a, b). Indeed, EA pattern is a proxy for some of the processes affecting recruitment over the study area (Valencia *et al.*, 2009). Our results showed a negative effect of this index on recruitment and survival of four-spot megrim. In the western coast of the Iberian Peninsula, the main upwelling variability can be explained in terms of the EA pattern, with a significant negative correlation

along the entire coast (deCastro *et al.*, 2008). Recruitment of megrim and post-summer upwelling were positively correlated in the Northern Spanish continental shelf (Sánchez *et al.*, 2003), is consistent with the negative effect of extremely positive EA values on recruitment of four-spot megrim observed in our analysis. Furthermore, Santos *et al.* (2001) evaluated the effect of upwelling intensity on the west coast of Portugal on horse mackerel, revealing that increasing upwelling intensity during winter (January–March) negatively affected recruitment. Upwelling events during small pelagic fish spawning season have been reported to promote egg and larvae offshore transport, thus having a negative effect on recruitment (Bakun, 1996). Our results underlining a positive influence of EA pattern on recruitment of horse mackerel are consistent with these findings.

In contrast with previous studies, no significant effects of climate predictors were found on hake population dynamics. It should also be noticeable that no relation was found among SSB of hake and recruitment of blue whiting. These results may be associated with the potential mismatch of the management structure and the biological structure of European hake in the Atlantic. Currently, the Atlantic population of European hake is managed on the basis of two recognized stocks, the so-called Northern and Southern stocks (ICES, 2006). ICES consider both as management units based on two main criteria: the first is the presence of a geographical barrier, Cape Breton Canyon, which separates the Iberian shelf from the French shelf in the extreme corner of the Bay of Biscay; the second reason is the observation of two spawning areas, one located from the French coast to the Celtic Sea and the other located on the northwest coast of the Iberian Peninsula. However, some controversy exists about the stock structure and the spatial complexity of European hake in the Atlantic (Hidalgo *et al.*, 2014; Pita *et al.*, 2016). In our study, only Southern stock of hake is considered, thus potential drivers on population dynamics may be masked due to connectivity between subpopulations or misrepresentation of the stock boundary. Similar explanations can be argued to justify no effect of upwelling on hake, as not only misrepresentation of the stock can affect but also that the stock distribution is so large that it is not affected by local processes. MacKenzie and Schiedek (2007) stated that interpreting and predicting how individual populations and species in a local ecosystem respond to oceanographic variations is more likely to be reliable when data are scaled closely to their perceived environments and life histories. In this sense, upwelling index of three years earlier was found to have a weak positive influence on horse mackerel SSB, and this is mostly related to the fact that this index is constrained to the stock distribution area.

The present study sheds new light on the short- and long-term sensitivity of population dynamics of different species harvested off the Iberian Peninsula to exploitation, demography and environment. The ecological factors or environmental conditions impacting on population dynamics of the stock analysed here are neither taken into account at present in the assessment nor in the management. It is worth emphasizing that the proposed additive effects may be useful for integrating the identified drivers into stock assessment models and management procedures of these important fishery resources. Models of fish populations that do systematically use these indicators may provide valuable information for developing adaptive management strategies. Our findings may help to understand and forecast climate change effects on population dynamics as it affects biological processes from the genetic to ecosystem level of organization and they may be affected

by regional oceanographic changes, with implications for commercial fisheries and food security. Modifications in the spatial variability mechanisms associated with the climate change has already been observed along with water warming (Thompson *et al.*, 2012), which increases the importance of taking into account these factors in management. Particularly, a key assumption in the projections of the mixed-fisheries analysis covering some of the stocks in Iberian waters analysed here (hake, white anglerfish, and four-spot megrim: ICES, 2018e) is that catchability by stock and métier remain constant. However, fishing patterns may change over time, in response to significant changes in policy, such as the introduction of landing obligation, or to oceanographic changes such as the increase in temperature. In practice, such changes in catchability would have paramount implications on the outcomes of mixed-fisheries projections. In addition, future research making use of longer time series could be orientated to analyse the combined effect of those drivers as interactive rather than additive.

Supplementary data

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

Funding

This study was carried out within the framework of two projects: “Synergistic effects of climate and fishing on the demersal ecosystems of the North Atlantic and the Western Mediterranean” (ECLIPSAME; CTM2012-37701) and “Climate variability and fisheries in the 21st century: Effects of global change on populations and nectobenthic communities” (CLIFISH; CTM2015-66400), both funded by the Spanish National R&D&I Plan.

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Handling editor: Valerio Bartolino