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# Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species

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## Abstract :

Fisheries ecologists traditionally aimed at disentangling climate and fishing effects from the population dynamics of exploited marine fish stocks. However, recent studies have shown that internal characteristics and external forcing (climate and exploitation) have interactive rather than additive effects. Thought most of these studies explored how demographic truncation induced by exploitation affected the response of recruitment to climate, identifying a general pattern revealed to be difficult as interactions are often case-specific. Here we compared five exploited stocks of European hake *Merluccius merluccius* from the Atlantic Ocean and Mediterranean Sea to investigate how the interaction between internal characteristics and external forces affect the variability of the population growth rate and their consequences on recruitment. Our results show that demographic truncation induces a novel population scenario in which the growth rate is maximized when the reproductive stock is younger and less diverse. This scenario is shaped by the climate variability and the fishing pattern. The population growth rate becomes more dependent on the maturation schedule and less on the survival rates. The consequences for the recruitment dynamics are twofold; the effect of density-dependent regulatory processes decreases while the effect of the density-independent drivers increases. Our study shows that the interaction between internal characteristics and external forces changes across geographic locations according to 1) the importance of demographic truncation, 2) the influence of the climate on the regional hydrography and 3) the spatiotemporal heterogeneity of the physical environment to which fish life history is adapted.

## Introduction

Human activities in the worldwide seas affect the maintenance of marine diversity and undermine the long-term sustainability of marine ecosystems. This loss of diversity also modifies the communities' structure and the demography within single populations. Heterogeneous communities, characterized by high population and life history diversity, produce more temporal stability because of the independent but complementary dynamics among species (Hilborn et al. 2003). From a single population perspective, a diverse age structure provides biological and ecological advantages to cope with a variable environment, stabilizing population dynamics and fluctuations (Hsieh et al. 2010). Fishing typically harvests larger individuals, eroding the size/age structure and displaying a demographic structure dominated by fewer and younger age classes. This demographic truncation (DT) is often referred to as the age truncation effect and has already been documented for numerous stocks (Anderson et al. 2008, Ottersen 2008 and review in Hsieh et al. 2010).

Growing research is investigating the biological, ecological and evolutionary consequences of DT. Larger and older individuals have higher fecundity (number of eggs released), better quality eggs that increase the offspring survival (i.e., 'maternal effect', Berkeley et al. 2004a), and more variable strategies to colonize different spatial locations and time for reproduction (Berkeley et al. 2004b). However, for a truncated population, fewer older individuals allocate their reproductive effort to a large spatial and temporal range of conditions, which reduces the probability of ensuring reproductive success in unfavorable and/or heterogeneous environmental conditions. Additionally, a fish population can be seen as a filter of the environmental stochasticity and can generate long-term fluctuations in population size through the echoing of stochastic variations of the new incoming cohorts over age classes by inter-cohort interactions (i.e., 'cohort resonance effect', Bjørnstad et al. 2004). The modification of the demographic structure may therefore result in the alteration of the cohort resonant effect, which has recently been put forward to explain changes in the response of fish stocks to the environment (Hidalgo et al. 2011, Rouyer et al. 2011). Finally, if the age-specific selectivity of exploitation remains stable over time, life history strategies may shift through plastic and/or adaptive phenotypic responses such as maturation schedules (Law 2000, Jørgensen et al. 2007).

Several recent studies have suggested that DT might have consequences for recruitment (e.g., number of recruits, sensitivity to environment or recruitment variability), with direct implications on the population variability (Hsieh et al. 2006, Ottersen et al. 2006, Anderson et al. 2008). However, in a recent meta-analysis Brunel (2010) did not find any evidence for such a process to be general. This result suggests that the interaction between demographic structure, fishing and climate may be highly context- and species-dependent (Perry et al. 2010, Planque et al. 2010). In order to investigate how potential geographical differences in this interaction affect the population dynamics, we studied the temporal variation of population growth rate of five different stocks of the same species from different locations.

Leslie matrices (Leslie 1945) were used to represent the population dynamics of these stocks because they provide a common basis for comparison. The different vital rates (survival, fecundity and recruitment success) that compose the matrix can be independently affected by both climate and exploitation (Durant et al. 2008). However, vital rates interact among each other displaying trade-offs between fecundity and survival (Roff and Fairbairn 2007) or between fecundity and recruitment success (Aubry et al. 2009). This makes it difficult to disentangle whether climate and fishing affect a single vital rate or the interaction among rates. In order to simplify this issue, we first investigated the combined effects of fishing and climate on partial demographic matrices (Oli et al. 2003) composed of survival and maturity rates (i.e, independent of the recruitment success). Secondly, we studied the consequences of these interplays on the recruitment dynamics. We hypothesize that geographical variation in the potential of a population to grow as a function of maturity and survival is shaped by the interaction of climate and fishing, which can affect the density-dependent and -independent regulation of the recruitment dynamics. To test this hypothesis we focus on five stocks of European hake (*Merluccius merluccius* L.).

European hake is an overexploited groundfish species inhabiting the North Atlantic European coast and the whole Mediterranean Sea (inset in Fig. 1) with a long history of exploitation elsewhere (Murua 2010). The studied stock units cover different geographic areas that represent a broad range of environmental conditions to which the species displays adapted traits (see Study systems). Obvious large scale differences in environmental conditions separate the Atlantic and the Mediterranean systems. At regional scales, environmental heterogeneity is particularly relevant in the Mediterranean as the general oligotrophic conditions in this basin make fish life history adapted to the most favorable hydro-climatic characteristics at smaller geographical (Recasens et al. 2008, Hidalgo et al. 2009) and temporal scales (Hidalgo et al 2011). The Mediterranean and the Atlantic stocks also display different exploitation patterns. While Mediterranean fisheries are characterized by a high exploitation rate of young individuals (i.e., juveniles' fishery, Lleonart and Maynou 2003), Atlantic fisheries display a comparatively more even exploitation of immature and mature individuals (Fernández et al. 2010). The five studied stocks thus represent contrasting systems well suited for a comparative study.

The objective of this study is twofold. Firstly, we aim at investigating the geographic differences in the interaction between internal population processes and external forcing (climate and exploitation), by studying its effect on the variability of the population growth. Secondly, we explore how the complexity of these interacting processes affects recruitment dynamics in each geographical area.

## Methods

### Study systems

We considered five geographical (management) areas for which age-structured information on hake was available. We used two Atlantic stocks, the Northern Atlantic (NA) and the Southern Atlantic (SA) stocks and three Mediterranean stocks, Balearic Islands (BI), Gulf of Lions (GL) and Tyrrhenian Sea (TS) (Fig. 1). The main hydrographical features differ in each area. NA is considered a homogeneous environment whose hydrography depends on the water masses and circulation of the Bay of Biscay, which are affected by the regional climatic conditions such as rainfall and storms (Pingree et al. 1993). In contrast, environmental conditions are more heterogeneous in SA which integrates two contrasted hydrographic regions: the Atlantic dominated by wind driven oceanographic processes and summer coastal upwelling (Álvarez et al. 2010) and the Cantabric, which depends on the variability of the central (i.e., intermediate in the water column) water masses and on mesoscale structures (Llope et al. 2006). In the Mediterranean, winter processes such as the vertical mixing and the amount of intermediate waters formed by deep convection dominate the hydrography in the NW Mediterranean (Lloret et al. 2001), while spring processes such as cyclonic and anticyclonic gyres generated by the wind also favor productivity in the TS (Artale et al. 1994).

### The data

We gathered time- and age-specific estimates of stock abundance and spawning stock biomass from five hake assessment groups from the Atlantic Ocean (International Council for the Exploration of the Sea, ICES 2009) and the Mediterranean Sea (General Fisheries Commission for the Mediterranean, FAO-GFCM 2009). All the assessment groups used a similar approach based on a virtual population analysis (Hilborn and Walters 1992). A time series of fishing mortality (F) was obtained for each stock by averaging over the most harvested age classes (based on stock-specific reports, FAO-GFCM 2009, ICES 2009): $F_{2\text{-}6}$ for NA, $F_{2\text{-}5}$ for SA and GL, and $F_{2\text{-}4}$ for BI and TS. All the assessments groups use monthly-based information to calculate yearly abundances except TS, which is based on seasonal scientific trawl surveys performed in summer (FAO-GFCM 2009). Time series of recruitment, spawning stock biomass and fishing mortality are displayed in the Supplementary material Appendix 1 (Fig. A1).

In order to describe the demographic characteristics of each stock, three variables were defined. The mean length ($L_{SSB}$) and mean age ($A_{SSB}$) of the spawners were calculated as the weighted average of length and age, respectively, in the spawners' abundance. Age diversity was calculated using the Shannon diversity index ($H_{SSB}$, Shannon 1948) to summarize the homogeneity of age classes in the spawning stock. $H_{SSB}$ is independent of stock size and describes both the number of age classes in the spawning stock and the diversity of the distribution of fish among cohorts (Marteinsdottir and Thorarinsson 1998). $H_{SSB}$ is calculated as follows: $H_{SSB} = -\sum_{i=1}^{n} p_i \cdot log(p_i)$, where $n$ is the number of age classes, and $p_i$ is the proportion of age class $i$ in the total spawning abundance.

We used both global climate indices and regional hydro-climatic variables as environmental information (Supplementary material Appendix 1, Fig. A2). The North Atlantic Oscillation (NAO) index, which is described as an out-of-phase behaviour between the climatological low pressure centre near Iceland and the high-pressure centre near the Azores, was used as a proxy of the North Atlantic climate (Hurrell 1995). NAO is often found to account for ecological processes better than local weather variables because it reduces complex space and time variability into simple measures (Stenseth et al. 2003). 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 is more active (Hurrell 1995). A mesoscale (regional) hydro-climatic index based on the air-sea heat fluxes in the Gulf of Lions during winter months (IDEA index hereafter) was used as a proxy of the strength of the southward current and vertical mixing activity in the NW Mediterranean (Monserrat et al. 2008). Lower values of the IDEA index indicate a larger formation of Western Mediterranean Intermediate Waters in winter at intermediate layers (100-300 m) in the Gulf of Lions; this implies a larger presence of these water masses in the NW Mediterranean platform during spring, which increases the productivity (Massutí et al. 2008).

Sea surface temperature (SST) obtained from the Climate Diagnostics Center (NCEP/NCAR) reanalysis fields (Kalney et al. 1996) on a 1x1-degree grid was also used as a proxy of regional hydro-climatic conditions. Winter (December to February) and spring (March to May) averages were calculated for each stock over each study area (e.g., Lloret et al. 2001, Bartolino et al. 2008, Fernandes et al. 2010).

## Modeling approach

We investigated the potential effects of climate, fishing and demographic characteristics of the spawning stock on time series of the population growth rate using generalized additive models (GAM, Hastie and Tibshirani 1990). Population growth rates were calculated using the Leslie matrix approach, which is an age-structured model that relies on estimates of demographic rates to project population dynamics (Caswell 2001). The fundamental relationship is given by $N_{t+1}=A_tN_t$, where $N_t$ is a vector representing the number of individuals for each age class at time t, and $A_t$ is a transition (Leslie) matrix that summarizes the dynamics of the populations between time t and time t+1 (Leslie 1945, Caswell 2001). $A_t$

summarizes the vital rates and the logarithm of its dominant eigenvalue ($\lambda$) provides the population growth rate, *r*. For a given year, the transition matrix ($A_t$) is defined as follows:

$$A_t = \begin{pmatrix} RS_{0,t} & RS_{1,t} & RS_{2,t} & \ldots & RS_{i\max,t} \\ S_{1-0,t} & 0 & 0 & \ldots & 0 \\ 0 & S_{2-1,t} & 0 & \ldots & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & S_{i\max-(i\max-1),t} & S_{i\max-(i\max-1),t} \end{pmatrix} \qquad (1)$$

with $S_{i-(i-1),t}$ the survival between age-class *i* at year *t* and age-class *i-1* at year *t-1*, assuming that individuals of the oldest age classes within the tail of the length distributions displayed the same survival $S_{imax-(imax-1)}$ at year *t*. $RS_{i,t}$ is the recruitment success of the year-class *i* at year *t* defined as follows:

$$RS_{i,t} = \frac{R_t Mat_{i,t-1}}{\sum_{i=1}^{i=i\max} Mat_{i,t-1} N_{i,t-1}} \qquad (2)$$

where $Mat_{i,t-1}$ is the maturity rate at age *a* and at time *t-1*, $N_{i,t-1}$ the abundance at age-class *i* and at time *t-1* and $R_t$ the recruitment at time *t*. Therefore, $RS_{i,t}$ represents the interaction between the ratio $R_t/N_{spawners,\, t-1}$ (recruitment / total abundance of spawners), which is age-specific independent, and the maturity rates. Since in the present study we specifically aimed at investigating the effects of climate, fishing and the spawning properties on a partial demography dependent on age-specific rates (survival and the maturity), we assume the ratio $R_t/N_{spawners,\, t-1}$ was constant over time. That is, we explored the impact of the aforementioned effects on the capability of a population to grow independently of the recruitment (i.e., new incomers) variability. Similar approaches, so called ‘partial life cycle analyses’ are often used when part of the age-specific estimates are lacking (e.g., Oli and Zinner 2001, Oli et al. 2003, Dillingham 2010). For fisheries sciences, Jensen (1974) proposed alternative modifications of matrix models such as the fecundity-based or the recruitment-based matrix models.

Here, $A_t$ was built depending only on survival and maturity rates, and our growth estimates were called the recruitment-independent growth rate ($r^{RI}$). We constructed one transition matrix per year and estimated a time series of $r^{RI}$ for each population. To investigate the relative contribution of each demographic rate (survival and maturity) to the variability of $r^{RI}$, we computed the elasticity ($e_{ij}$) of $r^{RI}$ to each survival and maturity rate as $e_{ij} = [\partial\lambda/\partial a_{ij}][a_{ij}/\lambda]$ (Caswell 2001), where $a_{ij}$ was an element of the matrix $A_t$, $\lambda$ the dominant eigenvalue of the matrix, and $[\partial\lambda/\partial a_{ij}]$ the sensitivity of $\lambda$ to changes in a matrix element $a_{ij}$ estimated as:

$$\frac{\partial\lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle v, w\rangle} \qquad (3)$$

where $\boldsymbol{v}$ and $\boldsymbol{w}$ are the left and right eigenvectors, respectively, corresponding to the dominant eigenvalue of the matrix $A_t$.

To asses how internal characteristics and external forces and their interactions contributed to the recruitment-independent growth rate ($r^{RI}$) variability, we used generalized additive models (GAMs). We used three types of covariates describing: the environmental conditions (E: climate indices or sea surface temperature), the demographic properties of the spawners (SP: mean age, mean length or age-structure diversity index of the spawning stock) and the fishing mortality (F). Two types of GAM formulations were used: (*i*) additive, assuming that the effect of the covariates was stationary over the years and independent of the other covariate effects, and (*ii*) threshold (non-additive), to test the hypothesis of interaction among the covariate effects. The two formulations were then compared using a measure of prediction error. The additive formulation used was:

$$r_t^{RI} = \beta_t + f(E_t) + g(F_t) + h(SP_t) + \varepsilon_t \qquad (4)$$

where $r^{RI}_t$ is the recruitment-independent population growth rate in year t, $\beta_t$ is the intercept, *f*, *g* and *h* are one dimensional non parametric smoothing functions (cubic splines with maximally 3 degrees of freedom [4 knots, points where the cubic polynomials of the cubic spline meet], Wood 2004) for the effect of the environment (E), exploitation (F) and the population properties (SP), respectively. ε denotes a Gaussian error term.

To test the hypothesis of combined effects of E, F and SP on the response of $r^{RI}$, we fitted a threshold GAM (TGAMs, Ciannelli et al. 2004) to the data. TGAM is a semi-parametric regression where the shape of a smoothing function can change according to whether an external covariate is below or above an estimated threshold value. The change in the form of the smoothing function may occur in one or several terms of the TGAM (in our model from $f_1$ to $f_2$, from $g_1$ to $g_2$ and from $h_1$ to $h_2$):

$$r^{RI}{}_t = \begin{cases} \beta_1 + f_1(E_t) + g_1(F_t) + h_1(SP_t) + \varepsilon_t & \text{if} \quad \alpha C_t \le z \\ \beta_2 + f_2(E_t) + g_2(F_t) + h_2(SP_t) + \varepsilon_t & \text{if} \quad \alpha C_t > z \end{cases} \tag{5}$$

with *z* the threshold of one of the smoothing functions of the covariates (E, F or SP) or a combination of them, which can switch in the model, while the additive effects of the other two covariates remain unaltered. Potential changes in the intercept (from $\beta_1$ to $\beta_2$) were also accounted for. Though TGAM allows for threshold effects in more than one covariate to be tested simultaneously, the thresholds were introduced for one covariate at a time because of the limitation of the length of observations. *C* is a vector containing all the covariates analysed (E, F or SP) and α being a row vector of coefficients. The threshold value *z* can be uni- or bi-dimensional, that is, *z* can be estimated from a unique covariate or from a combination of two of them. For uni-dimensional thresholds, α equals one. Threshold estimation (z and α values) is based on the minimization of the Generalized Cross Validation (GCV) − a proxy for the model's out-of-sample predictive performance analogous to the Akaike's Information Criterion (AIC). Further details of the threshold estimation procedure can be obtained in Ciannelli et al. (2004). Note that two out of the three Mediterranean stocks, Gulf of Lions and Tyrrhenian Sea, were not analysed for threshold (i.e., non-additive) effects due to the shortness of the available time series. Results for these stocks were used to discuss the geographic changes in the relative importance of covariates.

Similar formulations were applied on the longest recruitment (log-transformed, R) time series available (NA, SA and BI) to investigate the potential effect of the variability of $r^{RI}$ on the recruitment dynamics in addition to the other external and internal drivers (E, F, and SP). In this case, the covariates of the additive formulation were the spawning stock biomass (log transformed, *SSB*) and a regional-scale environmental variable (*E*). *E* variables were winter and spring averages of sea surface temperature. The IDEA index was also used for the BI stock. Using the TGAM formulation, we then investigated the consequences of changes in the $r^{RI}$ on both the effect of density (*SSB*) and the environmental covariate. In this case, the TGAM fitted was:

$$R_t = \begin{cases} \beta_1 + f_1(SSB_t) + g_1(E_t) + \varepsilon_t & \text{if} \quad \alpha C_t \leq r \\ \beta_2 + f_2(SSB_t) + g_2(E_t) + \varepsilon_t & \text{if} \quad \alpha C_t > r \end{cases} \qquad (6)$$

where the vector *C* also contains in this case $r^{RI}$ as a potential threshold variable in addition to E, F and SP (*C*{E, F, SP, $r^{RI}$}).

Because the GCV does not account for the additional parameter used in the threshold search and can not be used to compare GAM to TGAM, the best models were selected by computing the genuine cross validation (gCV, see Ciannelli et al. 2004 for details). gCV was calculated as the average squared leave-one-out prediction error, that is removing one data point at a time from the original model and predicting its value from the resulting model. All the potential threshold effects were applied for each covariate and scored against all the potential additive formulations based in the minimization of gCV. For every model, residuals were checked for homogeneity of variance, absence of temporal autocorrelation and violation of normality assumptions.

# Results

## Demographic structure of the spawning stocks

Figure 2 shows the time series of the diversity index $H_{SSB}$, the mean age $A_{SSB}$ and the mean length $L_{SSB}$, which all describe the evolution of the demographic structure. NA and SA displayed a decrease in the three variables, which suggested that a demographic truncation (DT) with a change of average values occurred between the middle eighties and early nineties. In contrast, these three indices displayed a high inter-annual variability with no sign of decrease for the Mediterranean stocks. However, values of these indices of the Mediterranean stocks are lower or comparable to those of the truncated stated in of the Atlantic stocks, which suggests certain degree of DT in the Mediterranean stocks since the beginning of the time period investigated. The high consistency between the three proxies for the TS was likely to be a consequence of the high dependency on the young age classes due to the seasonal and the trawl-oriented sampling. Since $H_{SSB}$ and $A_{SSB}$ were highly correlated in all the stocks and since $H_{SSB}$ could have broader and different ecological implications, which encompass those of $L_{SSB}$ and $A_{SSB}$, we used $H_{SSB}$ and $L_{SSB}$ as the indices of the spawner properties (SP) to simplify the statistical analyzes.

## Recruitment-independent growth rate time series

The estimated $r^{RI}$ displayed very different variability patterns for each area (Fig. 3A). Clear temporal trends were only found for the Atlantic stocks with low and high inter-annual variability for NA and SA respectively. The contribution (i.e., elasticity) of the maturity rates to the $r^{RI}$ increased over the whole period for NA and SA (Fig. 3B) and high values of $r^{RI}$

were observed as the contribution of maturity to the $r^{RI}$ increased (Fig. 3C). In the Mediterranean, the BI stock showed two extreme periods of high contribution of maturity with high survival in the nineties (Fig. 3B). For both BI and TS, the inter-annual pattern of the contribution of survival was closely related to the variability of $r^{RI}$ (Fig. 3C), which suggested a high dependency of the $r^{RI}$ estimates upon the young age classes. For GL, high values of $r^{RI}$ were associated with a high contribution of the maturity rates in accordance with the Atlantic stocks pattern (Figs. 3B−C).

## Combined effects of spawners' characteristics, climate and fishing mortality on $r^{RI}$

The most parsimonious models of $r^{RI}$ were always obtained with threshold formulations (TGAM) except for the two areas with short time series (TS and GL), for which only additive (GAM) formulations were fitted (Table 1 and Fig. 4). The best models for each area are given in the Supplementary material Appendix 1 (Table A1). The percentage of variance explained ranges from 89% for NA to 53% for TS (Table 1). The climate variable was always additively retained in the best models, but never as an interaction. The NAO displayed a non-linear effect on the Atlantic stocks; low values of NAO had a positive effect for the NA stock (Fig. 4A) while the opposite pattern was observed for SA (Fig. 4B). Such a pattern for the NA stock was mainly due to positive NAO values (> 2, Fig. 4B) occurring in the period 1989-1995, when the lowest values of $r^{RI}$ were estimated (Fig. 3A) and a drastic demographic truncation was observed for this stock (Fig. 2A). In the Mediterranean, the IDEA index displayed a negative effect for BI (Fig. 4C) and the SST in winter displayed a negative effect for the GL (Fig. 4D) and TS (Fig. 4E), though the effect for GL was observed as inverted dome-shaped likely due to the low number of observations in upper range of temperature. It is worth to note that SST in spring may be also relevant for the TS stock (Supplementary material Appendix 1, Table A1).

Although fishing mortality (F) was expected to additively affect $r^{RI}$, this was only observed for the SA stock in the Atlantic (Fig. 4B) and the TS stock (Fig. 4E) in the Mediterranean Sea. However, fishing mortality was retained as an interaction with the spawners' characteristics ($H_{SSB}$ and $L_{SSB}$) in all the areas where interactive effects were explored. Figure A3 (Supplementary material Appendix 1) shows the fishing mortality regimes obtained for each stock according to the Generalized Cross Validation (GCV) profile. In low fishing regimes (low F), high values of $r^{RI}$ were related to low values of $H_{SSB}$ (a less diverse age structure) in NA (Fig. 4A) and to low values of $L_{SSB}$ (comparatively smaller spawners) in SA (Fig. 4B) through a negative linear effect. In contrast, under high fishing regimes a weaker and non-linear effect of $H_{SSB}$ and $L_{SSB}$ on $r^{RI}$ was observed. In contrast to the Atlantic, in a low fishing regime $H_{SSB}$ had a positive effect on the BI stock (Fig. 4C), while it showed a similar pattern for GL but with a positive effect of $L_{SSB}$ (Fig. 4D).

## Combined effects on the recruitment dynamics

The most parsimonious models for the two Atlantic stocks displayed an interactive effect between *SST* and the spawner characteristics, while a non-additive effect of the spawning stock biomass (*SSB*) with a threshold on the IDEA index was observed for the BI stock (Fig. 5). The best models for each area are given in the Supplementary material Appendix 1 (Table A2). The percentage of variance explained was 60.3%, 59.4% and 59.9% for NA, SA and BI, respectively (Table 1). Two of the models fitted to recruitment retained a bivariate threshold effect involving $r^{RI}$. Under low values of $r^{RI}$ and $H_{SSB}$ for the NA, the effect of the $SST_{winter}$ on the recruitment was positive, whereas the relationship became negative in the other regime (Fig. 5A). Thought the dome-shaped effect of *SSB* found for the NA stock could be slightly overestimated do to the variance explained by the interacting environmental effect, this functional form suggested an overcompensatory behaviour at high population densities (i.e., negative density-dependent survival) supported by the opposed trends displayed by *SSB* and recruitment during the first decade of the period investigated (Supplementary material Appendix 1, Fig. A1A). This was not the case for the SA stock where the effect of spawners abundance was linearly positive over the whole range of abundance (Fig. 5B). The effect of the $SST_{spring}$ for SA was only observed for low values of $H_{SSB}$, while no significant effect was observed for high $H_{SSB}$ values (diverse age structure of the spawners). In the case of BI (Fig. 5C), *SSB* was linear and negatively related to the recruitment abundance under high values of $r^{RI}$ and *IDEA* index, while a negative non-linear response was observed under the opposite conditions. The effect of the environment for this area was positive and linear over the whole period.

## Discussion

The long term exploitation of the North Atlantic fish stocks has reduced their biomass to levels hardly comparable to those of the early XX$^{th}$ century (c.a., 'pristine state'). Recently, a 95% biomass reduction was documented over the last 118 years for the demersal populations off the UK (Thurstan et al. 2010). The exploitation pattern, typically size-selective, targeted older age classes and resulted in a long-term demographic truncation for several stocks (e.g., Ottersen et al. 2006, Ottersen 2008 and reviews in Jørgensen et al. 2007 and Hsieh et al. 2010). Therefore, the picture given by the contemporary age-structured data (i.e., last three or four decades) often depicts already truncated populations, which may affect the baseline for the evaluation of the recent decades.

Though the hake populations we studied are likely the result of long-term demographic erosion, the Atlantic stocks displayed a drastic change in the demographic structure, which is not as evident for the Mediterranean stocks. This results in an increasing contribution of the maturation schedule on the population growth rate of the Atlantic stocks over time. The potential consequences can be seen under three aspects. Firstly, the relative importance of the young spawners in the reproductive potential of the population increased. Secondly, the realized growth rate can become more sensitive to the recruitment variability (Rouyer et al. 2011). Thirdly, the contribution of the survival rates decreased along with the increase of the contribution of the maturity rates, which may affect the density-dependent regulation mechanisms of populations. For instance, such regulation may occur by altering the mortality rates of adults or relaxing overcompensation that operates on the survival of the young age classes (Warner and Chesson 1985). The Mediterranean populations displayed, however, high inter-annual variability of the recruitment-independent population growth rates and high contribution of the maturity rates, though it decreased as the growth rate increased. Recent study showed that the BI stock was highly dependent on recruitment in the last three decades due to the long-term erosion of its demographic structure (Hidalgo et al. 2011). This study is in resonance with our results, which show similar actual levels $H_{SSB}$, $A_{SSB}$ and $L_{SSB}$ of the Mediterranean population to those of the Atlantic stocks after the truncation. These findings therefore suggests that a high DT is long-lasting in the Mediterranean Sea, while no clear trend can be observed in the more recent years.

### Synergistic effects on the recruitment-independent growth rate

Since the effect of climate on vital rates (i.e., maturity or survival) can vary with age and sex (Coulson et al. 2001) and since the demographic structure of hake stocks changed over time (Fig. 2), an interacting effect between the climate and the other covariates on the growth rate was expected. No such effect was observed, which we attribute to the different temporal scales at which climate affects fish stocks compared to exploitation and demography (Ottersen et al. 2010). On a comparative time scale to the present study, the North Atlantic Oscillation (NAO) has been found to affect population growth rate of Northeast Arctic cod

(Durant et al. 2008). In the case of the SA hake stock, our results are in accordance with previous studies. An increase of marine productivity during positive phases of NAO may favor its reproduction (Dominguez-Petit et al. 2008), while a negative phase may strengthen the Iberian poleward current (de Castro et al. 2011) decreasing the survival (Sanchez and Gil 2000). By contrast, the opposite climate effect observed in the NA stock seems counterintuitive. The causal basis for this difference is not clear, but we note that only high NAO values negatively influenced the growth rate and that those values were restricted to a short period in the early nineties. Beaugrand (2009) evidenced that early nineties were an inflexion point for ecosystem changes in different areas of the North Atlantic, included North Sea and adjacent areas as the Bay of Biscay (Dufour et al. 2010, see discussion below). We speculate that this climate-induced ecosystem change could contribute, in addition to the DT, to the low population performance observed in the early nineties for NA. In the Mediterranean, regional hydro-climatology shapes the population dynamics at a smaller spatial scale. Our results are supported by previous studies that showed that winter conditions affect the population dynamics in the NW Mediterranean stocks (GL and BI) (Lloret et al. 2001, Massutí et al. 2008), while both spring and winter conditions can be relevant for the TS stock (Bartolino et al. 2008).

The interaction that maximized the parsimony of our models was always found between the fishing mortality and the spawners' characteristics, which is evidence for the sensitivity of the growth rate to changes in the spawners’ demography. Under low fishing regimes in the Atlantic, a truncated age structure favors the increase of the population growth rate, while under a heavy exploitation pattern spawners may not be able to contribute to the growth rate. Because the contribution of maturity rates increases with the demographic truncation, our results suggest that for highly exploited stocks, the population growth rate would be maximized when the spawners are younger. This implies that the population may increase reproductive investment in younger spawners, for instance by increasing fecundity-at-age (e.g., Yoneda and Wright 2004, Rijnsdorp et al 2005, Wright 2005). Mehault et al. (2010) documented similar changes in hake as the contribution to total egg production in the SA spawning stock shifted from older age classes to young spawners in the recent years.

In the Mediterranean, the BI stock showed a different interaction between fishing and spawner characteristics compared to the Atlantic stocks, with a positive effect of the age diversity of the spawning stock on the growth rate when fishing mortality was low. This relationship is analogous to the positive effect of the mean length of the spawners on the growth rate of the GL stock. These results suggest that Mediterranean stocks may exhibit higher growth rates with comparatively less truncated demographic structure within the study period, which could increase the contribution of survival to growth rate. In consequence, highly truncated populations (which is the case for BI, Hidalgo et al. 2011) characterized by low reproductive potential may improve the stability of the spawning stocks by maximizing the survival rates of young age classes. This strategy is common in long-lived unexploited vertebrates which exhibit stable adult survival (e.g., Warner and Chesson 1985, Tavecchia et al 2001).

## Consequences on recruitment

Our results show that recruitment-independent growth rates, through an increase of the contribution of the maturity rates of young spawners, can modify the sensitivity of recruitment to climate. However, this interaction changes geographically. For the NA stock, the combination of low growth rates and spawners' characteristics (i.e., truncated demography) resulted in a positive effect of SST on recruitment, which is in accordance with recent studies (Fernandes et al. 2010). However, changes in hydro-climatic conditions can *per se* modify the recruitment dynamics through different pathways (see review in Ottersen et al.

2010). The hydroclimatilogy of the Bay of Biscay changed in the early nineties in a fashion comparable to the well-known regime shift in the North Sea (Dufour et al. 2010). Beaugrand (2004) showed how climate modified the composition, size structure and abundance of zooplankton in the North Sea, which had consequences for the predator-prey interactions at the early life stages of fish. In the Bay of Biscay, such trophic implications have been demonstrated to affect other fish species such as anchovy (Irigoien et al. 2009). This suggests that observed changes in population dynamics of hake in the NA can result from a combination of demographic truncation and climate-induced changes in the trophic interactions during the early life stages of hake. Further research is required to understand how these mechanisms operate.

Under elevated environmental heterogeneity such as the contrasting hydrographies experienced by the SA stock, a more diverse demographic structure of the spawning stock might facilitate colonizing and meeting favorable environmental/trophic conditions for planktonic larvae, both in space and time (Marteinsdottir and Thorarinsson 1998). Such environmental heterogeneity would then make it difficult to identify a link between the favorable environmental conditions and recruitment success. The emerging effect of the sea surface temperature under a low age diversity of the spawners has already been documented for other species and has been suggested to be a consequence of an increase of the sensitivity of recruitment to climate (e.g., Marteinsdottir and Thorarinsson 1998, Ottersen et al. 2006).

The contrasting functional relationships observed between spawner abundance and recruitment suggests different regulatory mechanisms. Hake in SA does not exhibit overcompensation under high spawner density, as it is the case for the NA stock. Since the strength of population regulation increases as a function of the population size (Minto et al. 2008), the decrease of spawner density and diversity due to fishing increases the importance of the density-independent processes (i.e., environment), which then controls the recruitment survival when the density-dependent regulation is undermined. By contrast, the high density-dependence observed in NA could be partially explained by the high cannibalistic pattern of this species. High levels of cannibalism have been reported in areas with a broad continental shelf such as Bay of Biscay, where hake of different lengths coexist (Mahe et al. 2007). Since cannibalism of older age classes on recruits has been demonstrated to be very high for recent and truncated periods (Mahe et al. 2007), cannibalism rate could be higher in the pre-truncated state explaining partially the overcompensation observed.

Finally, in populations with strong recruitment dependency the population dynamics are mainly driven by environmental fluctuations (Hidalgo et al. 2011, Rouyer et al. 2011). This could promote instability of the density-dependent regulatory mechanisms, which could explain the observed change in the spawner biomass effect in the BI stock under different levels of growth rate and environmental conditions. However, the negative density dependence observed for this Mediterranean stock is ecologically difficult to explain and may therefore suggest alternative sources of population maintenance. Connectivity via passive drift of early life stages has already been proposed as a mechanism to complement the auto-recruitment of archipelagos (Cowen and Sponaugle 2009) such as the BI (Hidalgo et al. 2009).

## Conclusions

The increased dependency of population growth rate upon age classes of young spawners may occur concomitant to a loss of temporal stability of adult survival. Thus, demographic truncation may increase the importance of maternal effects on the persistence of the population and alter the population regulatory processes shaping the population dynamics. As a consequence, the ability of populations to cope with variable and/or heterogeneous environments decreases and the dependence of the recruitment dynamics on the hydro-climatic variability increases.

Several studies have demonstrated that stocks located in the limits of geographical distribution of the species are more sensitive to the hydroclimatic variability (e.g., Planque and Fredou 1999, Brunel and Boucher 2006, Stige et al 2006, Mantzuoni et al. 2010), which can be magnify due to the demographic truncation (Ottersen et al. 2006, Rouyer et al. 2011). Our study add to this picture the importance of embracing general ecological patterns with the context-dependence processes that emerge at intermediate latitudes within the range of the species distribution (see Fig. 1), in which the environmental effects often shows high heterogeneity. These regional scale synergies depend on: 1) the degree of demographic truncation, 2) the influence of the climate on the regional hydrography and 3) the spatiotemporal heterogeneity of the physical environment to which fish life histories are regionally adapted. Since truncated populations will be difficult to manage because of their high dependence on unpredictable environmental variability, our conclusions highlight the need to consider the interaction between fishing and climate in future scientific-based management programs.

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## References

Álvarez, M. et al. 2010. Summer upwelling frequency along the western Cantabrian coast from 1967 to 2007. − J. Mar. Syst. 79: 218-226.

Anderson, C. N. K. et al. 2008. Why fishing magnifies fluctuations in fish abundance. − Nature 452: 835−839.

Artale, V. et al. 1994. Seasonal variability of gyre-scale circulation in the northern Tyrrhenian Sea. − J. Geophys. Res. 99 (C7): 14127–14137.

Aubry, L. M. et al. 2009. Consequences of recruitment decisions and heterogeneity on age-specific breeding success in a long-lived seabird. − Ecology 90: 2491− 2502.

Bartolino, V. et al. 2008. Modelling recruitment dynamics of hake, *Merluccius merluccius*, in the central Mediterranean in relation to key environmental variables. − Fish. Res. 92: 277–288.

Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. − Prog. Oceanogr. 60: 245–262.

Beaugrand, G. 2009. Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. − Deep Sea Res. II 56: 656–673.

Berkeley, S. A. et al. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. − Ecology 85: 1258–1264

Berkeley, S. A. et al. 2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. − Fisheries 29: 23–32.

Bjørnstad, O. N. at al. 2004. Trends and cohort resonant effects in age-structured populations. − J. Anim. Ecol. 73: 1157–1167.

Brunel, T. and Boucher, J. 2006. Pattern of recruitment variability in the geographical range of the exploited northeast Atlantic fish species. – J. Sea Res. 55: 156–168.

Brunel, T. 2010. Age-structure-dependent recruitment: a meta-analysis applied to Northeast Atlantic fish stocks. − ICES J. Mar. Sci. 67: 1875−1866.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. − Sinauer Associates, Sunderland, MA.

Ciannelli, L. et al. 2004. Nonadditive effects of the environment on the survival of a large marine fish population. − Ecology 85: 3418–3427.

Coulson, T. et al. 2001. Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep. − Science 292: 1528−1531.

Cowen, R.K. and Sponaugle, S. 2009. Larval dispersal and marine population connectivity. − Annu. Rev. Mar. Sci. 1: 443-466.

De Castro, M. et al. 2011. Atmospheric modes influence on Iberian Poleward Current variability. − Cont. Shelf Res. 31: 425-432.

Dillingham, P. J. 2010 Generation time and the maximum growth rate for populations with age-specific fecundities and unknown juvenile survival. − Ecol. Mod. 221: 895–899.

Domínguez-Petit, R. et al. 2008. Changes in size at maturity of European hake Atlantic populations in relation with stock structure and environment regimes. − J Mar Syst. 71: 2060−278.

Dufour, F. et al. 2010. Climate impacts on albacore and bluefin tunas migrations phenology and spatial distribution. − Prog. Oceanog. 86: 283–290.

Durant, J. M. et al. 2008. Northeast Arctic cod population persistence in the Lofoten - Barents Sea system under fishing. − Ecol. Appl. 18: 662−669.

FAO-GFCM, 2009 Report of the eleventh session of the Scientific Advisory Committee. Marrakech, Morocco, 1-5 December 2008. − FAO Fisheries Report, Nº 890. Rome, FAO, 95 p.

Fernandes, J. A. et al. 2010. Fish recruitment prediction, using robust supervised classification methods. − Ecol. Mod. 221: 338−352.

Fernández, C. et al. 2010. Stock assessment and projections incorporating discard estimates in some years: an application to the hake stock in ICES Divisions VIIIc and IXa. − ICES J. Mar. Sci. 67: 1185–1197.

Hidalgo, M. et al. 2009. Intra-annual recruitment events of a shelf species around an island system in the NW Mediterranean. − Estuar. Coast. Shelf. Sci. 83: 227–238.

Hidalgo, M. et al. 2011. Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. − Mar. Ecol. Prog. Ser. 426: 1-12.

Hilborn, R. and Walters, C. J. 1992. Quantitative Fisheries Stock Assesment: Choice, Dynamics & Uncertainy. − Chapman & Hall, New York.

Hilborn R. et al. 2003. Biocomplexity and fisheries sustainability. − Proc. Natl Acad. Sci. USA 100: 6564–6568.

Hsieh, C. H. et al. 2006. Fishing elevates variability in the abundance of exploited species. − Nature 443: 859–862.

Hsieh, C. H. et al. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. − Aquat. Sci. 72: 165–178.

Hurrell, J. W. (1995). Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitations. − Science 269: 676–679.

Hastie, T. J. and Tibshirani, R. J. 1990. Generalized additive models. − Chapman and Hall, London, UK.

ICES, 2009. Report of the Working Group on the Assessment of Southern Shelf Stocks of Hake, Monk, and Megrim [WGHMM]. 5-11 May 2009. − ICES CM 2009/ACOM:08.

Irigoien, X. et al. 2009. Spring zooplankton distribution in the Bay of Biscay from 1998 to 2006 in relation with anchovy recruitment. − J. Plankton Res. 31: 1−17.

Jensen, A. L. 1974. Leslie matrix models for fisheries studies. − Biometrics 30: 547-551.

Jørgensen, C. et al. 2007. Managing Evolving Fish Stocks. − Science 318: 1247−1248.

Kalney, E. et al. (1996). The NCEP/NCAR 40-year reanalysis project. − B. Am. Meteorol. Soc 77: 437–471.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33, 183–222.

Law, R. 2000. Fishing, selection, and phenotypic evolution. − ICES J. Mar. Sci. 57: 659–668.

Lleonart, J. and Maynou, F. 2003. Fish stock assessments in the Mediterranean: state of the art. − Sci. Mar. 67: 37–49.

Lloret, J. et al. 2001. Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. − Fish. Oceanogr. 10: 33−50.

Llope, M. et al. 2006. Hydrography of the southern Bay of Biscay shelf-break region: Integrating the multiscale physical variability over the period 1993-2003. − J. Geophys. Res-Oceans 111: Art. No. 9021.

Mantzouni, I. et al. 2010. Hierarchical modelling of temperature and habitat size effects on population dynamics of North Atlantic cod. – ICES J. Mar. Sci. 67: 833–855.

Marteinsdottir, G. and Thorarinsson, K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. − Can. J. Fish. Aquat. Sci. 55: 1372−1377.

Massutí, E. et al. 2008. The influence of oceanographic scenarios on the population dynamics of demersal resources in the western Mediterranean: hypotheses for hake and red shrimp off the Balearic Islands. − J. Mar. Syst. 71: 421−438.

Mahe, K. et al. 2007. Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. – ICES J. Mar. Sci. 64: 1210–1219.

Mehault, S. et al. 2010. Variability in total egg production and implications for management of the southern stock of European hake. − Fish. Res. 104: 111−122.

Minto, C. et al. 2008. Survival variability and population density in fish populations. − Narture 452: 344−347.

Monserrat, S. et al. 2008. Interannual variability of Winter Intermediate Water at the Balearic Islands. − J. Mar. Syst. 71: 413−420.

Murua, H. 2010. The biology and fisheries of European hake, *Merluccius merluccius*, in the North-East Atlantic. − Adv. Mar. Biol. 58:97−154.

Oli, M. K. 2003. Partial life-cycle models: how good are they? − Ecol. Mod. 169: 313-325.

Oli, M.K. and Zinner, B. 2001. Partial life cycle analysis: a model for birth-pulse populations. − Ecology 82: 1180–1190.

Ottersen, G. 2008. Pronounced long-term juvevation in the spawning stock of Arcto-Norwegian cod and possible consequences for recruitment. − Can. J. Fish. Aquat. Sci. 65: 523−534.

Ottersen, G. et al. 2006 Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. − Fish. Oceanog. 15: 230−243.

Ottersen, G. et al. 2010. Major pathways by which climate may force marine fish populations. − J. Mar. Syst. 79: 343−360.

Perry, R. I. et al. 2010. Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. − J. Mar. Syst. 79: 403−417.

Pingree, R. D. 1993. Flow of surface waters to the west of the British Isles and in the Bay of Biscay. − Deep Sea Res. Part II. 40: 369–388.

Planque, B. and Frédou, T. 1999. Temperature and the recruitment of Atlantic cod (Gadus morhua). Can. J. Fish. Aquat. Sci. 56: 2069–2077.

Planque, B. et al. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? − J. Mar. Syst. 79: 430−417.

Recasens, L. et al. 2008. Spawning pattern and batch fecundity of the European hake (*Merluccius merluccius* (Linnaeus, 1758)) in the western Mediterranean. − Sci. Mar. 71: 721−732.

Rijnsdorp, A. D. et al. 2005. Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? − Can. J. Fish. Aquat. Sci. 62, 833−843.

Roff, D. A. and Fairbairn, D. J. 2007. The evolution of trade-offs: where are we? − J. Evol. Biol. 20: 433−447.

Rouyer, T. et al. 2011. Shifting dynamical forces in fish stock fluctuations triggered by age truncation. Glob. Chang. Biol. (in press, doi:10.1111/j.1365-2486.2011.02443.x).

Sánchez, F. and Gil, J. 2000. Hydrographic mesoscale structures and Poleward Current as a determinant of hake (*Merluccius merluccius*) recruitment in southern Bay of Biscay. − ICES J. Mar. Sci. 57:152−170.

Stige, L. C. et al. 2006. Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. − Mar. Ecol. Prog. Ser. 325: 227−241.

Shannon, C. E. 1948. A mathematical theory of communication. − AT&T. Tech. J. 27: 379−423.

Stenseth, N.C. et al. 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 270: 2087–2096.

Tavecchia, G. R. et al. 2001. Sex- and age-related variation in survival and cost of first reproduction in Greater Flamingos. − Ecology 82: 165–174.

Thurstan, R. H. et al. 2010. The effects of 118 years of industrial fishing on UK bottom trawl fisheries. − Nature Communications 1: 15.

Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. − J. Am. Stat. Assoc. 99: 637–686.

Warner, R. R. and Chesson, P. L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. − Am. Nat. 125: 769–787.

Wright P. J. Temporal and spatial variation in reproductive investment of haddock in the North Sea. − ICES CM 2005 Q:07.

Yoneda, M. and Wright P. J. 2004. Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. − Mar. Ecol. Prog. Ser. 276: 237–248.

Supplementary material (Appendix E7314 at <www.oikosoffice.lu.se/appendix>). Appendix 1.

Table caption

Table 1. Final best formulations selected, threshold variable used, adjusted $R^2$ ($R_{adj}^2$, i.e., proportion of variance explained), and genuine cross validation (gCV) of the best models for recruitment-independent growth rate estimates ($r^{RI}_{t}$) and recruitment abundance ($R_t$). All the terms included in these models were statistically significant ($p < 0.05$).

Table 1

| Response | Area | Formula | Threshold variable/s | $R_{adj}^2$ | gCV |
|---|---|---|---|---|---|
| $r^{RI}$ | NA | $r^{RI}{}_t = f(NAO_t) + \varepsilon_t + \begin{cases} 0.13 + h_1(H_t^{SSB}) & if \quad F_{2-6} \le 0.28 \\ 0.06 + +h_2(H_t^{SSB}) & if \quad F_{2-6} > 0.28 \end{cases}$ | $F_{2-6}$ | 89.8 | 0.00056 |
| | SA | $r^{RI}{}_t = -0.1 + g(F_{2-5}) + f(NAO_t) + \varepsilon_t + \begin{cases} h_1(L_t^{SSB}) & if \quad F_{2-5} \le 0.47 \\ h_2(L_t^{SSB}) & if \quad F_{2-5} > 0.47 \end{cases}$ | $F_{2-5}$ | 80.3 | 0.0027 |
| | BI | $r^{RI}{}_t = -0.59 + f(IDEA_t) + \varepsilon_t + \begin{cases} h_1(H_t^{SSB}) & if \quad F_{2-4} \le 1.06 \\ h_2(H_t^{SSB}) & if \quad F_{2-4} > 1.06 \end{cases}$ | $F_{2-4}$ | 60.6 | 0.035 |
| | GL | $r^{RI}{}_t = -0.47 + f(SST_t^{Winter}) + h(L_t^{SSB}) + \varepsilon_t$ | - | 83.4 | 0.25 |
| | TS | $r^{RI}{}_t = -0.46 + f(SST_t^{Winter}) + h(H_t^{Tot}) + \varepsilon_t$ | - | 53.6 | 0.033 |
| Recruitment | NA | $R_t = 12.23 + f(SSB_t) + \varepsilon_t + \begin{cases} h_1(SST_t^{Winter}) & if \quad \{H_{SSB}, r^{RI}{}_t\} \le r \\ h_2(SST_t^{Winter}) & if \quad \{H_{SSB}, r^{RI}{}_t\} > r \end{cases}$ | $H_{ssb}$, $r^{RI}$ | 60.3 | 0.045 |
| | SA | $R_t = f(SSB_t) + \varepsilon_t + \begin{cases} 4.79 + h_1(SST_t^{Spring}) & if \quad H_{SSB} \le 0.54 \\ 4.68 \quad if \quad H_{SSB} > 0.54 \end{cases}$ | $H_{ssb}$ | 59.4 | 0.0086 |
| | BI | $R_t = 7.58 + f(IDEA_t) + \varepsilon_t + \begin{cases} h_1(SSB_t) & if \quad \{IDEA, r^{RI}{}_t\} \le r \\ h_2(SSB_t) & if \quad \{IDEA, r^{RI}{}_t\} > r \end{cases}$ | IDEA, $r^{RI}$ | 59.9 | 0.091 |

Notes*:* Abbreviations and variables are: *NAO*, North Atlantic Oscillation index; *IDEA*, mesoscale hydro-climatic index of the NW Mediterranean; $SST^{Winter}$ and $SST^{Spring}$, sea surface temperature averaged for winter and spring; *SSB*, spawning stock biomass; $H^{SSB}$, age diversity index of *SSB*; $L^{SSB}$, mean length of SSB; $F^{2-6}$, $F^{2-5}$ and $F^{2-4}$ fishing mortality averaged from age classes 2 to 6, 2 to 5 and 2 to 4.

Figure captions

Figure 1. Geographic location of the five stocks of European hake analysed: North Atlantic stock (NA), South Atlantic stock (SA), Balearic Islands (BI), Gulf of Lions (GL) and Tyrrhenian Sea (TS). The inset map displays the geographic distribution of the species.

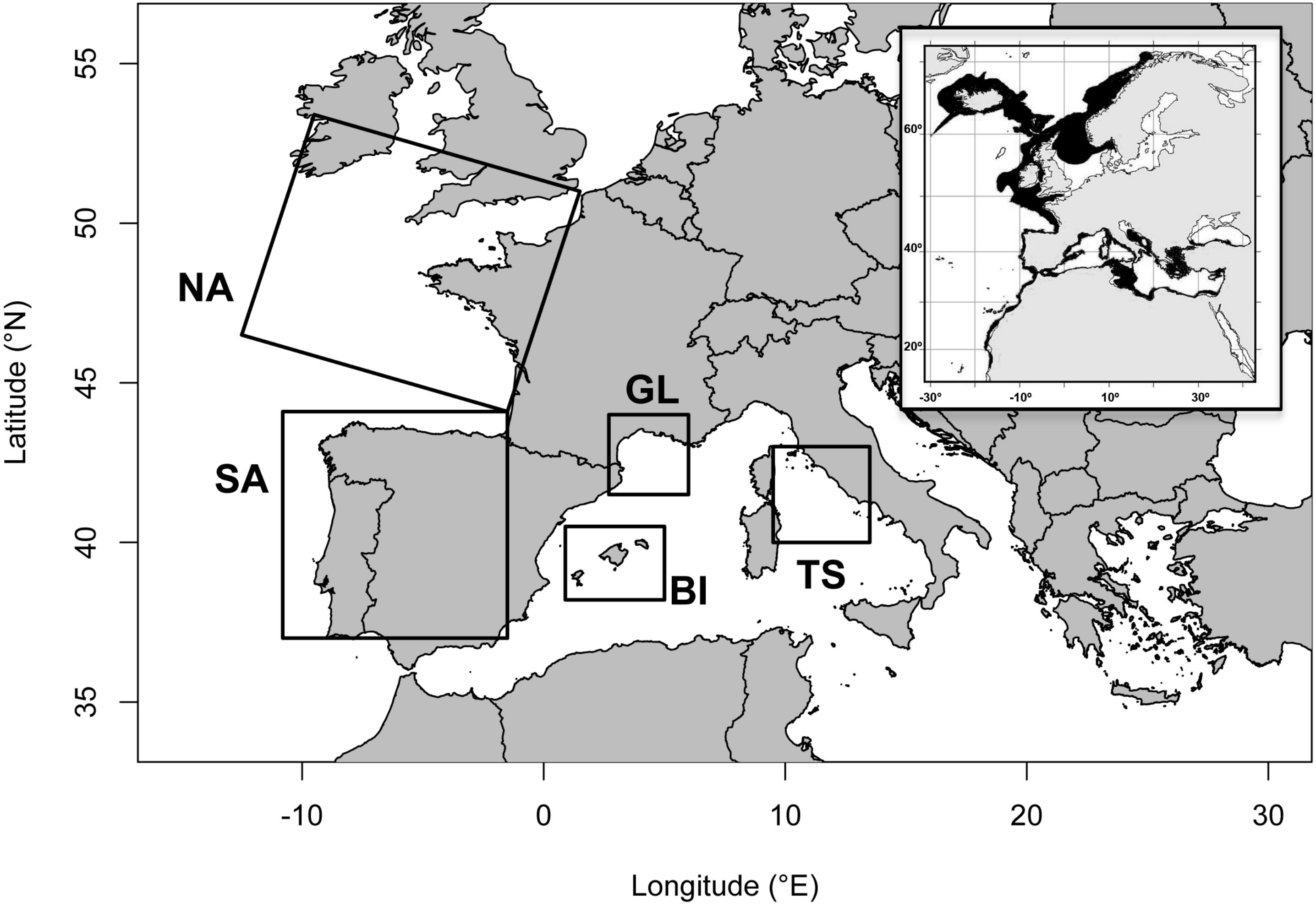
Figure 2. Age diversity ($H_{SSB}$), mean length ($L_{SSB}$) and mean age ($A_{SSB}$) of the spawning stock biomass for the five stocks investigated: North Atlantic stock (A), South Atlantic stock (B), Balearic Islands (C), Gulf of Lions (D) and Tyrrhenian Sea (E).

Figure 3. Recruitment-independent growth rate time series ($r^{RI}$) for each stock (A), relative contribution (i.e., elasticity) of maturity (white) and survival (grey) to $r^{RI}$ variability (B) and relationship between maturity contribution and $r^{RI}$ (C).

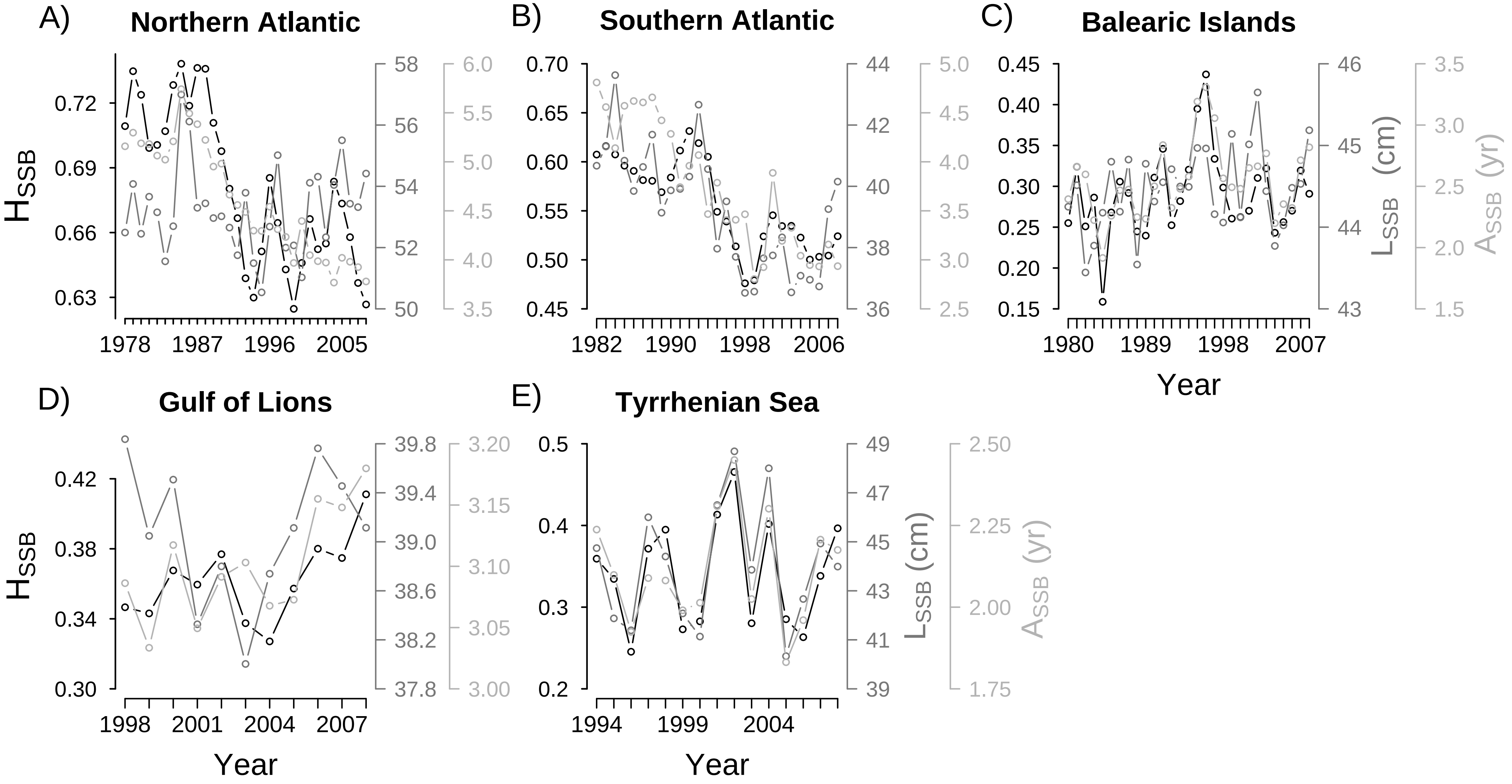
Figure 4. Effect of climate (left column), spawning properties (middle column) and fishing (right column) on the recruitment-independent growth rate for each stock: North Atlantic stock (A), South Atlantic stock (B), Balearic Islands (C), Gulf of Lions (D) and Tyrrhenian Sea (E). Note that the effect of spawning properties in A, B and C is partitioned by two fishing regimes as indicated in Table 1 and shown in Figure S3 (Supplementary material): the effects under low and high fishing regimes are shown in dark and light grey respectively.

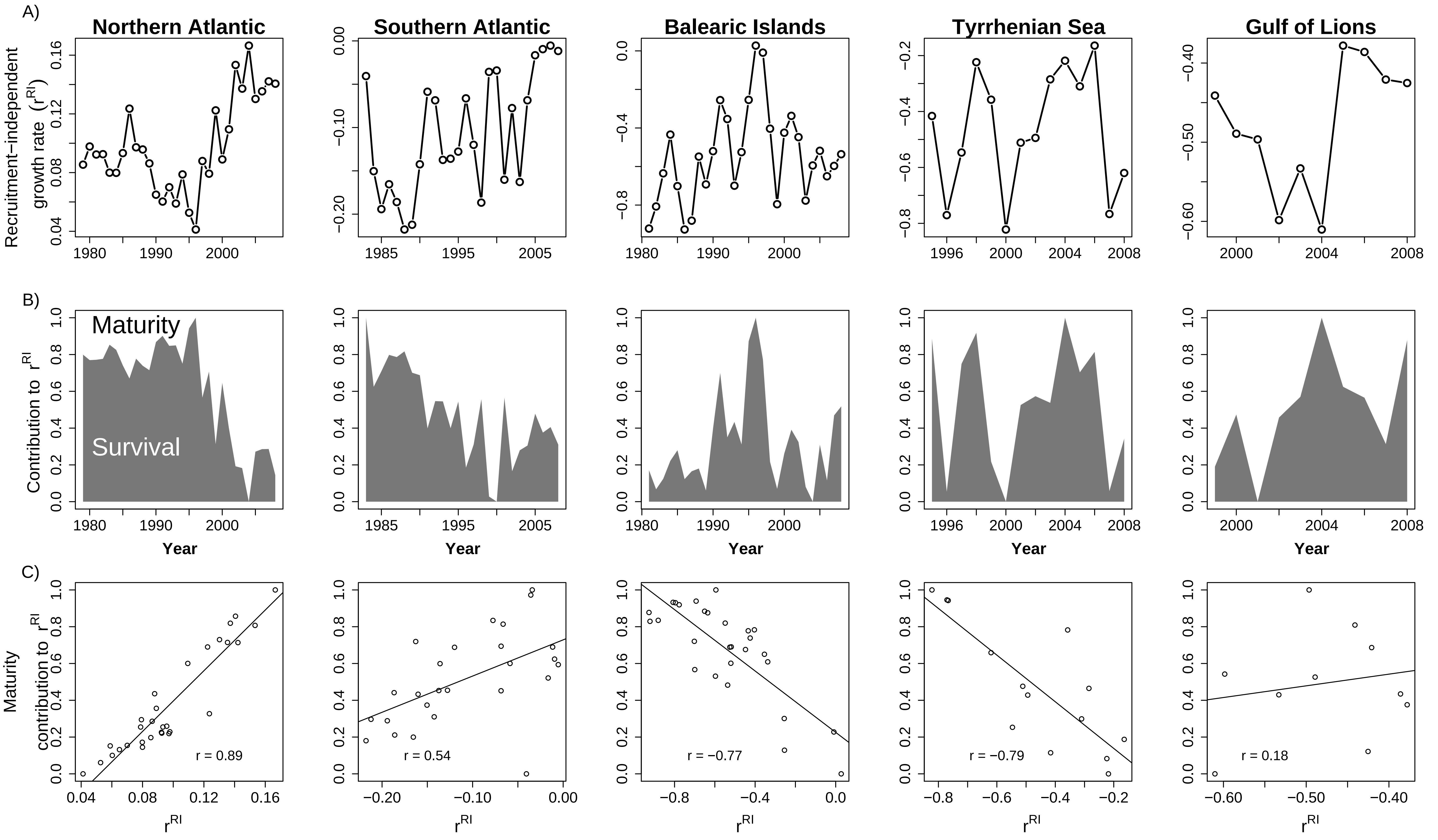
Figure 5. Effect of spawning stock biomass (SSB, left column) and environment (middle column) on the recruitment abundance for each stock analysed: North Atlantic stock (A), south Atlantic stock (B) and Balearic Islands (C). The environment effect for A and B, and SSB effect for C are partitioned into two regimens (dark and light grey), which are shown in the right column and indicated in Table 1. Note that threshold interaction of A and C is

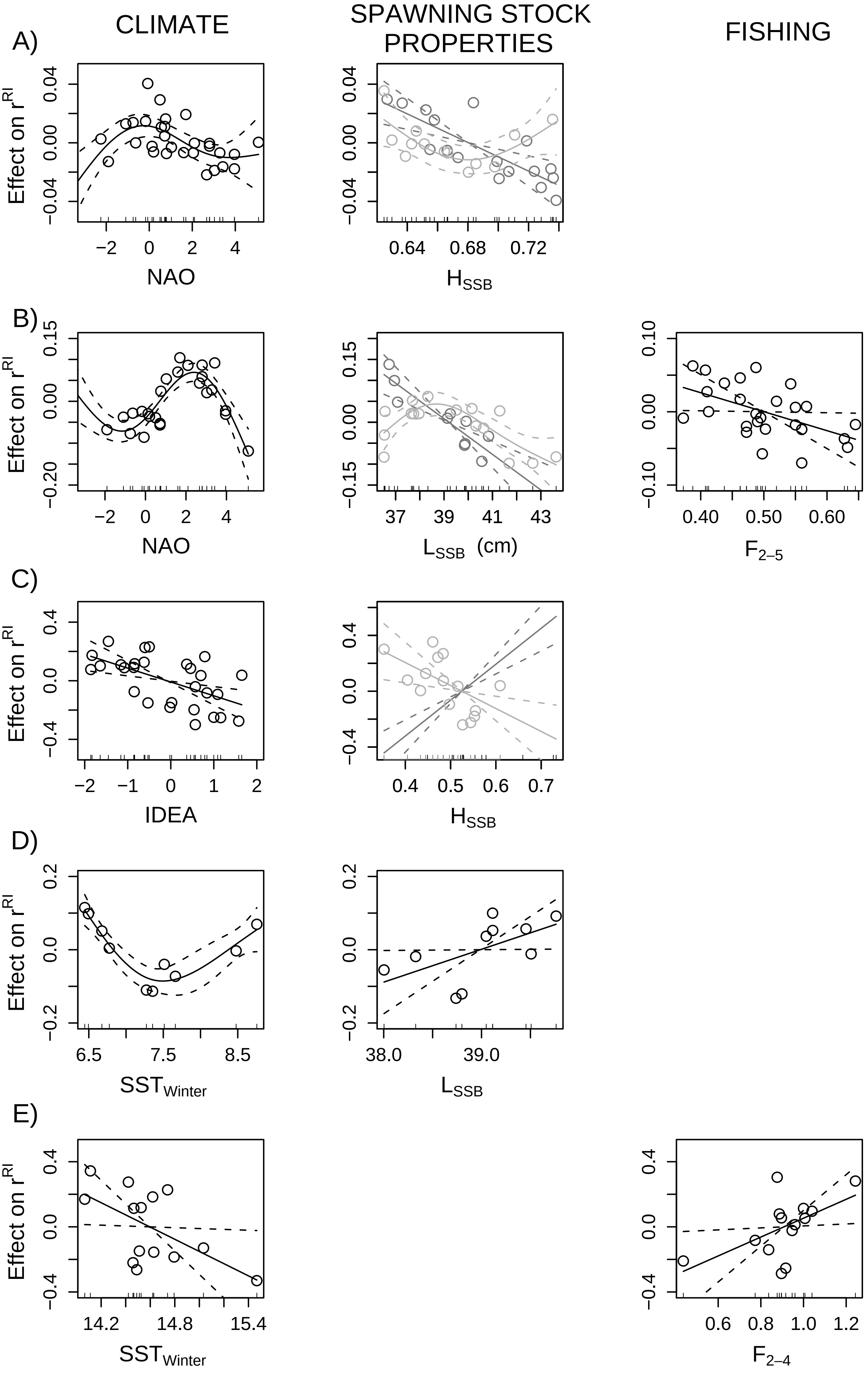
bivariate, while the threshold is univariate for B For the North Atlantic stock, the scatter plot shows two biological regimes as the interaction between $r^{RI}$ and $H^{SSB}$ that modified the form of the environment effect. For the South Atlantic, low values of $H_{SSB}$ let the $SST_{Winter}$ affect negatively the recruitment while no significant effect (shown as the mean value for this regime) was observed for high values. For the Balearic Islands, a scatter plot shows a biological/environmental interacting regime of $r^{RI}$ and IDEA index that modified the form of effect of the SSB covariate. The threshold lines (detected by the GCV criteria, Ciannelli et al. 2004) that divide the plot of interacting variables in two regions are also shown in the right column.

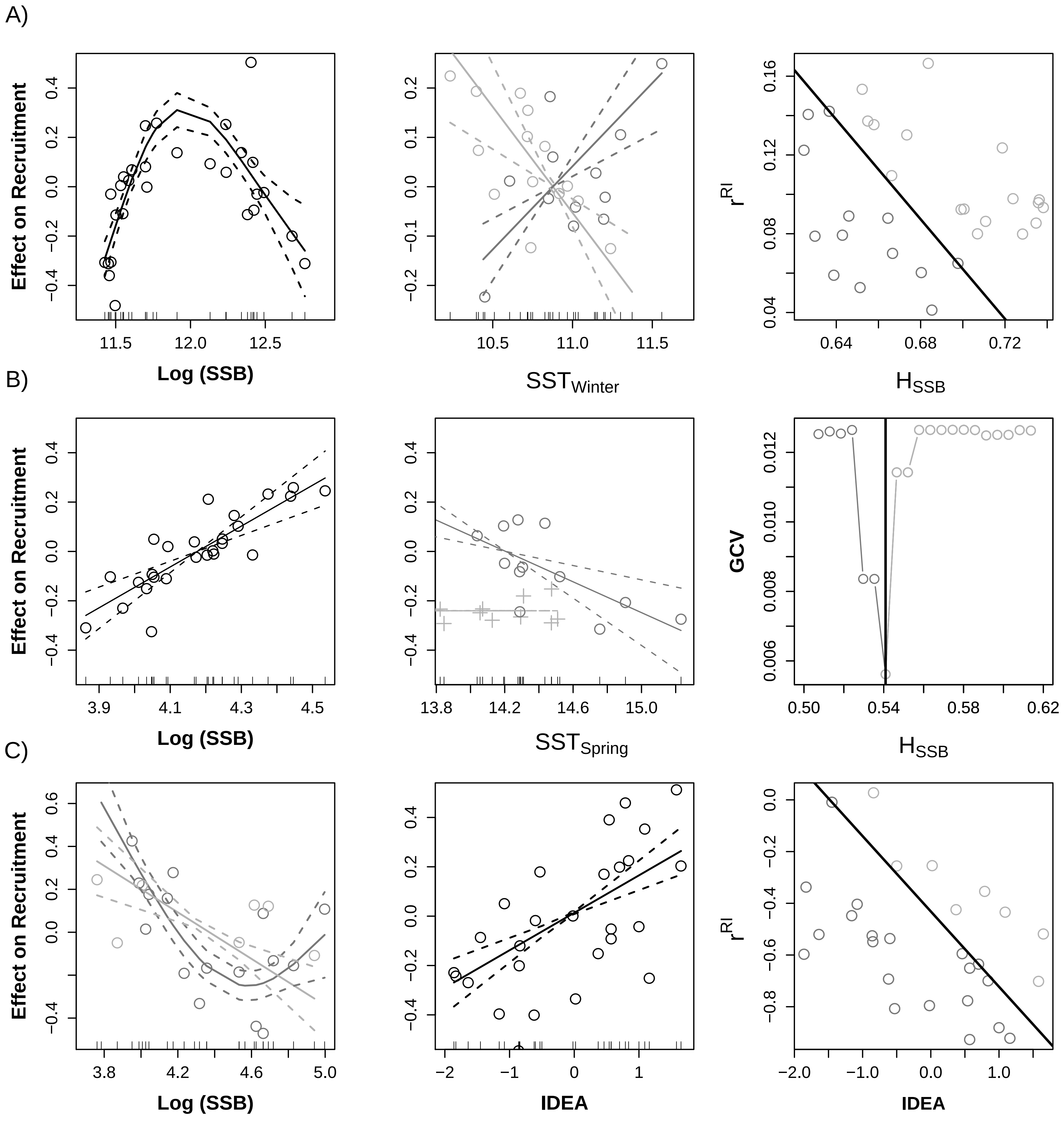


NA
SA
GL
BI
TS
55
50
45
40
35
Latitude (°N)
-10
0
10
20
30
Longitude (°E)
60º
40º
20º
-30º
-10º
10º
30º


A)
Northern Atlantic
B)
Southern Atlantic
C)
Balearic Islands
D)
Gulf of Lions
E)
Tyrrhenian Sea
$H_{SSB}$
$L_{SSB}$ (cm)
$A_{SSB}$ (yr)
Year
0.72
0.69
0.66
0.63
58
56
54
52
50
6.0
5.5
5.0
4.5
4.0
3.5
1978
1987
1996
2005
0.70
0.65
0.60
0.55
0.50
0.45
44
42
40
38
36
5.0
4.5
4.0
3.5
3.0
2.5
1982
1990
1998
2006
0.45
0.40
0.35
0.30
0.25
0.20
0.15
46
45
44
43
3.5
3.0
2.5
2.0
1.5
1980
1989
1998
2007
0.42
0.38
0.34
0.30
39.8
39.4
39.0
38.6
38.2
37.8
3.20
3.15
3.10
3.05
3.00
1998
2001
2004
2007
0.5
0.4
0.3
0.2
49
47
45
43
41
39
2.50
2.25
2.00
1.75
1994
1999
2004


A)
Northern Atlantic
Southern Atlantic
Balearic Islands
Tyrrhenian Sea
Gulf of Lions
Recruitment−independent growth rate ($r^{RI}$)
0.04
0.08
0.12
0.16
1980
1990
2000
0.00
−0.10
−0.20
1985
1995
2005
0.0
−0.4
−0.8
1980
1990
2000
−0.2
−0.4
−0.6
−0.8
1996
2000
2004
2008
−0.40
−0.50
−0.60
2000
2004
2008
B)
Maturity
Survival
Contribution to $r^{RI}$
0.0
0.2
0.4
0.6
0.8
1.0
Year
Year
Year
Year
Year
C)
Maturity contribution to $r^{RI}$
r = 0.89
r = 0.54
r = −0.77
r = −0.79
r = 0.18
0.04
0.08
0.12
0.16
−0.20
−0.10
0.00
−0.8
−0.4
0.0
−0.8
−0.6
−0.4
−0.2
−0.60
−0.50
−0.40
$r^{RI}$
$r^{RI}$
$r^{RI}$
$r^{RI}$
$r^{RI}$


CLIMATE
SPAWNING STOCK PROPERTIES
FISHING
A)
Effect on $r^{RI}$
−0.04
0.00
0.04
−2
0
2
4
NAO
0.64
0.68
0.72
$H_{SSB}$
B)
−0.20
0.00
0.15
NAO
−0.15
0.00
0.15
37
39
41
43
$L_{SSB}$ (cm)
−0.10
0.00
0.10
0.40
0.50
0.60
$F_{2-5}$
C)
−0.4
0.0
0.4
−2
−1
0
1
2
IDEA
0.4
0.5
0.6
0.7
$H_{SSB}$
D)
−0.2
0.0
0.2
6.5
7.5
8.5
$SST_{Winter}$
38.0
39.0
$L_{SSB}$
E)
14.2
14.8
15.4
$SST_{Winter}$
0.6
0.8
1.0
1.2
$F_{2-4}$


A)
Effect on Recruitment
−0.4 −0.2 0.0 0.2 0.4
11.5 12.0 12.5
Log (SSB)
−0.2 −0.1 0.0 0.1 0.2
10.5 11.0 11.5
SST_Winter
r^RI
0.04 0.08 0.12 0.16
0.64 0.68 0.72
H_SSB
B)
Effect on Recruitment
−0.4 −0.2 0.0 0.2 0.4
3.9 4.1 4.3 4.5
Log (SSB)
−0.4 −0.2 0.0 0.2 0.4
13.8 14.2 14.6 15.0
SST_Spring
GCV
0.006 0.008 0.010 0.012
0.50 0.54 0.58 0.62
H_SSB
C)
Effect on Recruitment
−0.4 0.0 0.2 0.4 0.6
3.8 4.2 4.6 5.0
Log (SSB)
−0.4 −0.2 0.0 0.2 0.4
−2 −1 0 1
IDEA
r^RI
−0.8 −0.6 −0.4 −0.2 0.0
−2.0 −1.0 0.0 1.0
IDEA