A shift in a hake (*Merluccius merluccius*) population of the NW Mediterranean induced by a combined effect of climate and fishery harvesting

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ABSTRACT

Climate and fisheries are often interacting with each other and producing complex synergic effects on the population dynamics of marine species. The drastic change in the climatic conditions in the North Atlantic (NA) in the early eighties triggered changes in local weather and hydrographical conditions in the Mediterranean Sea. In the other hand, the long term fishery harvesting on the stock of European hake (*Merluccius merluccius*) off the Balearic Islands (BA, NW Mediterranean) changed the properties of the population and its structure in the early eighties, which could have triggered a different response to the environmental variability. Using time series analysis (on the environmental and hake CPUE time series) and a population simulation model, we examine the hypothesis that these processes are linked and, in turn, a combined effect of fishery harvesting and environmental changes in the NA induced an ecological shift in the hake population off BA. The results points out that the changes in the variance and modes of hake CPUE were consistent with changes in the hydroclimatic variability in the NW Mediterranean induced by the North Atlantic climate. Population simulations show that age-structured populations act like a filter of the environmental fluctuations and can intrinsically generate cycles ('cohort-resonance effect') consistent with the 12 yr mode observed in the CPUE before the eighties. Size selective fishing mortality could erode the age structure and change the population filter properties. The population would have changed from internally-generated fluctuations to an externally-forced fluctuations mode after the eighties, increasing its dependency on the recruitment variability. This fits with the observations which show the high dependency of the CPUE on the recruitment variability and the winter condition modes predominating after eighties. Our results emphasize the importance of the interaction between fisheries, environment and internal dynamics that can cause transitory shifts in the behaviour of a population.

Keywords: European hake, juvenescent populations, juveniles' fishery, North Atlantic climate, NW Mediterranean climate, phase transitions, regimen shifts.

Introduction

Climatic variability has major effects on the population dynamics of exploited fish populations at different spatial and temporal scales (e.g., Alheit and Bakun 2009, Anderson et al. 2008, Duffy-Anderson et al. 2005, Ottersen et al. 2009). However, the population responses of harvested stocks to climatic variability can not be separated from the fishing impacts because climate and fisheries effects are often interacting with each other rather than being additive (Planque et al. 2009, Kirby et al. 2009). Drastic population responses as sudden depletions of abundance (i.e., 'phase transitions' events, Duffy-Anderson et al. 2005) are often observed and studied in the contest of regiment shifts in the marine ecosystems. Fisheries independent climatically-induced regime shifts have been documented worldwide (e.g., Alheit and Bakun 2009 Beaugrand et al. 2003 Ciannelli et al 2005, Hjermann et al. 2004). In addition, exploitation can also be a key factor that triggers regime shifts, for example by changing trophodynamic interactions caused by the overexploitation of predators (e.g., top-down effects and trophic cascades, Daskalov et al. 2007).

Harvesting also produces complex responses on a single population perspective. These responses range from obvious alterations in abundance and biomass in different age-classes, changes in demographic parameters such as the life-span, to more hidden and often overlooked evolutionary changes in life history traits (e.g. Jørgensen et al. 2007). These effects can be often translate into changes in the resistance and resilience of fish populations to anthropogenic and natural environmental perturbations (Hutchings et al. 2007), or in other words in changes in the sensitivity of fish populations to environmental forcing (see Planque et al. 2009). Since animals of different ages can respond in different ways to density and environmental changes, identical environmental conditions can results in different dynamics in populations of equal sizes but different demographic structure (Coulson et al. 2001, Fromentin and Fontaneau 2001). Alternatively, theoretical and empirical studies have also shown that the age-structure of fish-populations can act as a filter of environmental conditions and can intrinsically generate large changes in abundance (e.g., 'cohort-resonance effects', Bjørnstad et al. 1999, 2004). Consequently changes in demographic parameters, such as the life-span of the population or its rate of increase, can also change how the population filters environmental fluctuations. For instance, the juvenescence of marine fish populations due to the overexploitation of the older age-classes makes the populations more dependent upon the abundance of the youngest age classes and to the recruitment dynamics. Because younger fishes are less able to buffer environmental changes and because they are also less efficient for reproduction, the age-truncation of the population increases the potential non-linear coupling between the environmental fluctuations and recruitment, and ultimately lead to changes in the variability of the population (Anderson et al. 2008, Ottersen et al. 2006, Ottersen 2008, Stenseth and Rouyer 2008).

The stock of European hake (*Merluccius merluccius*) off the Balearic Islands (NW Mediterranean, Figure 1) is an overexploited small population. Previous studies showed evidence of a strong linkage between this population and the environment through the recruitment during the last three decades (Hidalgo et al. 2008, Massutí et al. 2008). Two population transitions were identified in 1980 and 1995 and preliminary attributed to the long term fishery exploitation of this species (Hidalgo et al. 2009a). Changes in the population properties as population growth rate, demographic structure or density-dependent relationships were related to these transitions affecting the sensitivity of the population to the environmental variability (Hidalgo et al. 2009a). Simultaneously, several studies have also

identified in the very same years (early eighties and mid nineties) changes in climatic variability in the North Atlantic linked to the regional climatic shifts in the NW Mediterranean that ultimately affected the pelagic food webs (Fernadez de Puelles and Molinero 2007, 2008; Molinero et al. 2005). However, to date, any study has demonstrated whether climatic shift in the Atlantic and NW Mediterranean were related to the transitions in this hake population. In this study we hypothesise that these two processes were linked and , in turn, a combined effect of fishery harvesting and environmental changes in the North Atlantic could have produced an ecological shift for hake population off the Balearic Islands.

In addition to the observed time series, a positive identification of a system transition also requires a mechanistic understanding of how internal (e.g. density dependence) and external (e.g. environmental forcing and fishery) variables affect key properties of the system. We then combined time series analyses of the population and environmental conditions with population dynamics simulations given exploitation and climatic scenarios. This will let to reproduce the main population properties under a no- and fishery scenario, and to compare with available information with the aim to improve the understanding of the underlying mechanisms triggering shifts in the marine fish populations.

Methods

Data
Available catch per unit effort (CPUE, kg hp^{-1}) data series were used as an index of population biomass (1940-2004) (Massutí et al. 2008). North Atlantic Oscillation (NAO) index is the north-south alternation in the atmospheric mass between the subtropical Atlantic and the Artic (i.e., out-of-phase behaviour between the climatological low pressure centre near Iceland and the high-pressure centre near Azores, Hurrell 1995) and was used a proxy of Atlantic climate. Winter average (December-March) was used as the best index of Atlantic-induced climatic variability (Hurrell 1995). A mesoscale hydro-climatic index based in the air-sea heat fluxes at the Gulf of Lions during winter months (IDEA index hereafter; defined as the standardized air temperature anomalies at 1000 hPa in the Gulf of Lions during winter, December-March, Monserrat et al. 2008) was used as a proxy of strength current circulation in the NW Mediterranean for the period 1960-2004 (Monserrat et al. 2008). Lower values of this IDEA index indicate a larger presence of Western Mediterranean Intermediate Waters (WIW) of the Balearic Islands in spring. These waters are associated with an increment in productivity in late winter and spring and consequently have a positive effect on hake recruitment (Hidalgo et al. 2008, Massutí et al. 2008). Sea Surface Temperature (SST) around the Balearic Islands for the period 1960-2004 was obtained from ICOADS (International Comprehensive Ocean-Atmosphere Data Set Project) data set with resolution 1x1-degree boxes. The selected area extends from 1° to 5°E and from 38.5° to 40.5°N. Mean values for autumn (SST-autumn, September-November) and winter (SST-winter, December-February) were used respectively as a proxy of temperature conditions experienced by early life stages after the spawning season (Recasens et al 1998), and the high productive scenarios occurring after winters with low temperature. These variables can be related with early life stages survival, and thus recruitment variability of hake.

Analyses
Because the mean and the variance of both the environmental and hake time series are changing through time (i.e. non-stationary) we used wavelet analysis to investigate their

fluctuations (Cazelles et al. 2008, Lau and Weng 1995). The wavelet transform is a technique that allows decomposing the variance of time-series on a time-frequency diagram. A mathematical function (the mother wavelet) is first chosen, then dilated and translated (daughter wavelets) and compared with the time series. For a given set of parameters *a* (scale parameter related to frequencies) and *tau* (translation parameter related to time position) the wavelet function *ψ* is defined at time *t* as follows:

$$\Psi_{a,\tau}(t) = \frac{1}{\sqrt{a}} \Psi\left(\frac{t-\tau}{a}\right)$$

Since these functions are local they allow detecting changes of behaviour in the time-series. The wavelet transform *W* of the time series *x* is obtained by the convolution product between the wavelets and the time-series:

$$W_x(a,\tau) = \frac{1}{\sqrt{(a)}} \int x(t)\Psi\left(\frac{t-\tau}{a}\right)dt = \int x(t)\Psi_{a,\tau}dt$$

We used the Morlet wavelet, a continuous and complex wavelet with a simple relationship between scales and frequencies (Menard et al. 2007, Cazelles et al. 2008). The wavelet power spectrum S for the time series *x* is then defined as:

$$S_x(a,\tau) = \left|W_x(a,\tau)\right|^2$$

S is represented on a 2D time frequency plot with the intensity of the variance at each time/frequency being represented on a colour-scale from blue (low variance) to red (high variance). In order to study potential links between two time series one can also extend the wavelet analysis to bidimensional cases and compute the cross spectrum and the cross-coherencies, to study respectively the transient covariance and the transient correlation between the two signals (see Cazelles et al. 2008 for details).

In order to describe the variability of the time series through time, and particularly during the periods where major shifts occurred, univariate wavelet spectra were investigated for the global climatic index (NAO), the biomass index of hake of the Balearic Islands (CPUE) and the three Mediterranean mesoscale variables (SST-autumn, SST-winter and IDEA index). Using the bivariate wavelet approach, we compared NAO and hake CPUE time series between them and with the three Mediterranean mesoscale variables (SST-autumn, SST-winter and IDEA index). SST-winter and IDEA index were also cross analysed to find out whether these two winter indicators had consistent modes.

In order to investigate how the dynamics of a population change when subjected to environmental forcing and to an age-selective removal, we performed population simulations. We used the following stochastic age-structured model based on the fundamental equation of fish stocks dynamics:

$$N_{a,t} = N_{a-1,t-1}\, e^{(M_{a-1}+F_{a-1})t}$$

where, $N_{a,t}$ is the number of fish of age (a) at time (t), and M and F respectively the natural and the fishing mortality from age (a-1) to age (a). The biological parameters were obtained from published estimations used in the assessment working groups for this species (FAO 2006). Natural mortality vector (M_0=1.3, M_1=0.8, M_2=0.4, M_3=0.3 and M_{4+}=0.2) was obtained from previous estimations of a close Mediterranean population (Ligurian Sea, Bartolino 2008, Caddy and Abella 1999). Fishing mortality vector (Figure 2a) was obtained from population models for the assessment of the species (FAO 2006) showing the intensive exploitation of hake juveniles which is characteristic of Mediterranean demersal populations (Caddy 1993, Lleonart and Maynou 2003). The fishing mortality was initially set at 0 during the 250 first years in order to observe dynamics of the model. After the 250 years a linear increase of the fishing mortality has been simulated (Figure 2b), to mimic the increase observed in the data.

The age-structured model was forced by a stochastic Ricker curve previously fitted on the dataset (Massutí et al 2008):

$$R_t = \alpha SSB_{t-1} e^{\beta SSB_{t-1}} \gamma \varepsilon_t$$

where, R_t is the recruitment (number of fish which grow into the age class 0 the first year of life) at time (t), SSB the spawning stock biomass, and ε is a stochastic environment. α, β and γ parameters were taken from Massutí et al. 2008.

In order to investigate how the population model filters environmental fluctuations, we defined two environmental scenarios: (i) white noise (balanced mixed of frequencies) that is used as a control experiment and (ii) a sinusoidal environment at pre-defined long and short-term frequencies. The wavelength of the oscillations was arbitrarily set at 5 and 100 yrs. For both scenarios the total variance of the environmental signal was calibrated on the variance of the environmental signal used for the fit of the recruitment curve in Massutí et al. 2008. Outputs of the model, namely biomass and catches, were investigated using wavelet analyses in order to detect potential changes of behaviour occurring through time, as well as to compare with the original data. We also investigated trends in the demographic structure of the population through the mean length of the population and the diversity of the age structure through the Shannon diversity index H (Shannon 1948):

$$H = -\sum_{i=1}^{n} p_i \cdot \log(p_i)$$

where n is the number of age groups, p_i the proportion in age group i of the total population abundance. Large values of H denote similar within-year group composition in abundance, while low values indicate large differences within-year groups.

Simulations were run over 500 years and fishery was introduced after 250 years and steady increasing (Figure 2b). The procedure was repeated 100 times and the biomass and catches were obtained by averaging over the simulations.

Results

Wavelet analyses

Univariate wavelet spectra (UWS) investigated show the variability of all the time series changed early 1980s (Figure 3). The analysis of the CPUE time series displayed a 12 years mode of fluctuation which disappeared after the eighties (Figure 3a). Due to the important drop in variance after the eighties the main frequency pattern for the last 3 decades did not appear on the colour plot. A UWS focussed on the last three decades shows a 7 yr mode in the CPUE (Figure 3b). The wavelet spectrum of the NAO showed a change in frequency from 7-8 years before the eighties to c.a. 5 years afterwards (Figure 3c). In contrast, the IDEA index showed that a 7 years pattern emerged after eighties while no clear periodicity was observed in the previous period (Figure 3f). As for the CPUE time series, the UWS of SST-autumn showed a nine years mode which started to disappear after the eighties (Figure 3d). The wavelet spectrum of SST-winter showed however the presence of a 6-8 yr mode after eighties (Figure 3e).

Potential direct associations between time series were then investigated using cross-wavelet spectra (CWS). A change in the signal during the early eighties was detected for almost all the combinations (Figure 4). CWS of CPUE showed consistent modes of 8-11 yr before the eighties with the NAO (Figure 4a) and the SST-autumn time series (Figure 4c). In contrast CWS showed an association around 7 yr after the early eighties with the regional winter-related variables (Figures 4e and 4g, IDEA index and SST-winter respectively). In the case of the CWS between the IDEA index and CPUE a secondary 10-11 yr was observed, but the cross coherence of this signal was very low and this mode was not observed in the UWS of these variables. CWS of the NAO and the IDEA showed consistent associations at 5-7 yr after the early eighties (Figure 4d) and the same pattern was found for the CWS between NAO and the SST-winter (Figure 4f). By contrast, NAO and SST-autumn were the only cross-wavelet spectra which did not show a change in the eighties, showing a 9 yr association over the whole period studied (Figure 4b). CWS between IDEA index and SST-winter show a clear mode around 6-7 years evidencing the strong signal of winter weather in the NW Mediterranean after early eighties (Figure 4h). The wavelet results show that the change in the dominant modes in the CPUE time series before and after the eighties were consistent with the environmental changes induced in the Mediterranean by the Atlantic climate.

Population dynamics simulations

The simulated total biomass for both the white noise (Figure 5a) and the controlled environment (Figure 5b) displayed the 12 yr mode observed in the CPUE time series prior to the intensive exploitation (Figure 3a). The drop of variance that appears after exploitation made us unable to detect particular changes of frequencies on the wavelet colour plots. In order to study how the capacity of the population to filter the environmental time series changes as the intensity of the exploitation increases, we produced time series of the importance (percentage) of the variance explained by determined environmental frequencies. That is, high frequencies (2-15 years) and the low frequencies (>15 years) where extracted from the wavelet outputs of the model simulations.

For both the white noise and the controlled environments, as soon as the variance of the biomass of the simulated population decreased sharply due to exploitation a change in the frequencies occur in the signal (Figures 5a, 5b). In the white noise environment, the percentage of variance explained by the low frequencies decrease in the signal, while that explained by high frequencies increased (Figures 5a, 5b). In the controlled environment, the amount of variance of the population explained by the high frequencies increased with the

intensity of exploitation (Figure 5c). The high frequency in the simulated biomass also corresponded to the high frequency fluctuations that were arbitrarily set for the environment. This result suggests that with the increase of exploitation, the fluctuations of the population seem to switch from internally generated (12 years cycle) to more environmentally forced fluctuations.

The both traits analyses (mean length and H diversity index) followed consistent oscillations with the population biomass before the occurrence of the fishery. It was expected as both the population biomass and the traits are dependent of the age structure. After the exploitation started, the mean length of the population decreased as well as the diversity index, displaying the increase of dependency of younger individuals (juvenescent population, Figure 5d).

Discussion

We show that the phase transitions observed in the hake stock off the Balearic Islands in the early eighties occurred as a combination of sudden climatic conditions in the Mediterranean and the long term effect of fishery exploitation. In this study we focused on how exploitation stresses the intrinsic properties of fish stocks that ultimately lead to a change of behaviour of the population fluctuations. This has been shown to be a key factor to understand how the environmental effect on the population dynamics changed over time. It is worldwide observed that current climate change and overfishing are affecting the productivity and structure of marine ecosystems. However, the synergic effects of fishing and climate can not be neglected in marine populations and ecosystems (e.g., Kirby et al. 2009). Here we show with simple assumptions how fisheries can interact with the internal properties of the population and cause transitory relationships with environmental fluctuations. Particularly, using time series analysis and a more mechanistic approach we managed to mimic the major features of the transitory shifts occurring in the hake stock off the Balearic Islands. Our results suggest that changes in the Mediterranean climate (North Atlantic-induced) triggered a drastic population decline which was facilitated by the juveniles' fishery ('growth overexploitation'). This long term fishing pattern would have eroded the age structure of the population becoming highly recruitment–dependent (i.e., juvenescent), and thus increasing the sensitivity to climatic variability.

North Atlantic forcing, Mediterranean climate and the European hake modes

Several studies have already given evidence on the sensitivity of Mediterranean regional fields of atmospheric parameters and temperature to the North Atlantic climate, which is summarized on an inter-annual basis by the North Atlantic Oscillation (NAO) index (e.g., Lloret et al. 2001, Gomis et al 2006, Trigo et al. 2000, Tsimplis et al 2005). On the whole, NAO negative phases are associated with wetter and cooler conditions in the western Mediterranean increasing the marine productivity (e.g. Bolle 2003, Lloret et al 2001). The climatic shift in the North Atlantic climate during the early eighties has been characterized in different studies with higher, in average, occurrence of positive NAO periods (e.g., Hurrell 1995). For the western Mediterranean, this translates into lower rainfall regimes (lower runoff) and weaker winter western winds (less advective process) which are both linked to a decrease of the primary production (Lloret et al. 2001). Our results confirm that this climatic shift in the North Atlantic climate triggered changes in the Western Mediterranean systems.

The wavelet analyses performed on the Mediterranean environmental variables displayed changes consistent with the change in the North Atlantic climatic conditions. However, our results show that the winter-related variables (SST-winter and the IDEA index) displayed both an increase of variance and a change in the main mode of fluctuations after the early eighties. Consequently, the shift was also characterized by a change in the environmental winter conditions despite the higher presence of weaker winters (positive NAO periods). The hard winters (associated with negative NAO events), which occur with a mode of c.a. 6-7 years, increased the western Mediterranean productivity as we discuss hereafter; lower values of IDEA index and SST-winter are a regional responses to those hard winters.

Though there is evidence of ecological effects induced by negative-NAO periods on the Mediterranean marine populations for the last decades (Cartes et. al. 2009, Fernández de Puelles and Molinero 2007, 2008, Grbec et al. 2002, Lloret et al. 2001, 2004, Massutí et al. 2008, Santojani et al. 2006) only a few studies investigated changes in these effects before and after eighties (Molinero et al. 2005, 2008) due to the lack of long-term data sets (Lleonart and Maynou 2003). Despite Massutí et al (2008) identified changes in the effect of the climatic conditions on the CPUE of hake off the Balearic Islands after the early eighties, such changes have not been linked to variation in the proper climatology. The present study points out that the changes in the variance and periodicity of hake CPUE were consistent with changes in the hydroclimatic variability in the NW Mediterranean induced by the North Atlantic climate as depicted by the NAO. Before the eighties the hake stock showed consistent periodicities with SST-autumn and NAO index on 8-11 yrs mode while afterwards hake modes were linked to winter variables on the 5-7 yr mode. Consequently, c.a. 8 yrs modes of favourable environmental conditions (higher productivity events in the NW Mediterranean) are positively related to the 12 yr cycles shown by hake CPUE before the eighties (Massutí et al. 2008), but they are also consistent to the intrinsically-generated cycles as we showed using the simulation model. However, patterns of variations in fisheries time series only poorly reflect the underlying dynamics of fish populations; they appear to be shaped by several successive embedded processes, each interacting with each other (Rouyer et al. 2008). We tried to understand how 8 yr (climate) and 12 yr (biology) oscillations are related by studying the population dynamics.

Long term population dynamics and the response to the size selective mortality of Mediterranean fishery

Population dynamics simulated using a simple age-structured model was able to reproduce the 12 yr mode observed in the CPUE data before the eighties. Furthermore, this cyclicity was internally generated and occurred irrespectively of the environmental scenario chosen (i.e. random or controlled frequencies). Age-structured populations act like a filter of the environmental fluctuations and can intrinsically generate cycles whose properties depend upon the life histories of the species and particularly upon its demography (Bjørnstad et al. 1999, 2004, Bjørnstad and Grenfell 2001). This effect, known as 'cohort-resonance effect', occurs for age-structured populations which echo the recruitment through the age-classes.

As soon as the size selective fishing mortality starts to erode and truncate the age/size structure, the properties of the population filter are changed. In other words, heavy fishing modifies how the population integrate environmental fluctuations and so do the importance and the characteristics of the internally-generated fluctuation. Our results suggest that fishing exploitation can switch the population from internally-generated fluctuations mode to an

externally-forced fluctuations mode by altering the demographic structure of the population. By changing the demographic structure, fishing links more closely the population to the recruitment, accelerate its life cycle, and consequently reflects more closely the environmental fluctuations. However, our simulations assume stationary dynamic of the life history traits and several studies have already shown that fishing can affect the life history traits, in the short- or in the long-term, and affect the response of fish stocks to exploitation (Jennings et al. 1998, 1999; Jørgensen et al. 2007, Stenseth and Rouyer 2008). Empirical studies have also shown that in some cases these "maladaptative" (i.e., if they have genetic basis, 'fishery-induced evolution') changes in multiple traits caused by fishing reduce the capacity of the population to recover after depletions (i.e. reduce its resilience, Walsh et al. 2006). This could slow down the demographic alterations produced by the fishing activity, but it would unlikely affect the fact that it would end occurring, either the two main conclusions we obtain from the simulations and observe in the data. On the one hand, 12 yr cycles simulated and observed the CPUE data before the eighties were likely to be internally created by the population though they would have been forced by environmental fluctuations occurring on the same or lower frequencies. On the other hand, over the last three decades exploitation increased and hake population off the Balearic Islands has been demonstrated to highly depend upon the recruitment variability (Hidalgo et al. 2009a, Massutí et al. 2008). Simulations also reproduce this pattern showing the increase in the dependency of the population upon recruitment while the exploitation persists. Conversely, the size selective pattern of the Mediterranean fishery has been shown to be long-term focused in the younger age classes ('juveniles' fishery', e.g., Caddy 1993, Lleonart and Maynou 2003). However, the long term effect on the population dynamics and the size structure is the same because the fishery exploitation is removing the adult individuals some years before as juveniles.

Synthesis on the combined effect climate-fishery on the European hake off the Balearic Islands

The results obtained in this study allow proposing that the long-term fishery exploitation on this species make this population more sensitive to both inter-annual environmental variability and regimen climatic shifts due to its high recruitment dependency in the last decades (i.e., juvenescent population). Several studies have already shown that size structure truncation induced by the size selective fishing pressure on the old age classes make the population more dependent of the younger age classes (juvenescent populations; e.g., Anderson et al. 2008, Ottersen et al 2006, 2008, Stenseth and Rouyer 2008). Thought our study evidenced the climatic influence on the population transition early eighties, we do not explain which is the mechanism triggering such as sudden transition. Recent studies (Fernadez de Puelles and Molinero 2008) and analyses in progress suggest that a change in seasonal pattern of the environmental variables, mainly in the autumn-winter season, is linked to sudden changes in the inter-annual pattern. The oligotrophy of Mediterranean makes the phenology (e.g. timing of seasonal activities) of marine species to be adapted to match the favourable environmental circumstances that occur in a narrow window in the Mediterranean (Hidalgo et al. 2009b). In our case, sudden alteration of this seasonal pattern in winter likely would lead to a mismatch between hake eggs hatched and early life stages of hake and the favourable environmental conditions, with a consequent depletion of the population abundance.

Finally, we should take into account the island identity of the Balearic populations that make them likely dependent upon the connectivity processes (i.e., incoming of early life stages from the mainland through the currents, Cowen and Sponauglue 2009). In our case, connectivity processes are proposed to be related with the strong winters (negative NAO events) in the NW Mediterranean (Hidalgo et al. 2009b, Massutí et al. 2008), and the recruitment variability would depend on the combination of inter-annual variability of the connectivity process and the mainland spawning stock abundance. The spawning stock abundance in the W Mediterranean have been proposed to depend on a cryptic stock ('*spawning refugia*', Caddy 1993) hidden in less exploited areas (e.g., canyons in the Gulf of Lions). As a consequence of technological improvements in fishing, this hidden spawning stock was made vulnerable (Lleonart and Maynou 2003), with the consequent undermining of the so-called '*spawning refugia*' (FAO 2005). This could have a negative synergic effect with the higher occurrence of positive NAO phases as the both of them would have a negative effect on the population. Thought this could affect to the stochastic forcing of the recruitment, it does not alter the main conclusions of the present study.

Conclusions

The 12 yrs mode displayed by the European hake population studied responds to internal cyclicity generated by echoing the recruitment through the age-classes. This made the population able to filter high environmental frequencies. The change in periodicity and the drop of mean abundance after the early 1980s can be explained by a combination of the following factors: *i*) long term fishing exploitation made the population more dependent upon younger age classes (recruitment) and to the environment variability; *ii*) the Atlantic climatic shift in the early 1980s produced, on average, weaker winter conditions in the NW Mediterranean. In contrast, the occurrence of strong winters (favourable for marine productivity) became highly noticeable and regularly periodic with a clear ca. 6-7 yr modes; and *iii*) the undermining of the '*spawning refugia*' in the last decades in the W Mediterranean could also have negatively affected the Balearic populations decreasing the connectivity process. As a consequence it would produce a negative synergic effect on the population with less mainland spawners contributing to the population and a decrease of the currents strength pattern due to weaker winter conditions. Our results emphasize the importance of the interaction between fisheries, environment and internal dynamics that can cause transitory shifts in the behaviour of a population.

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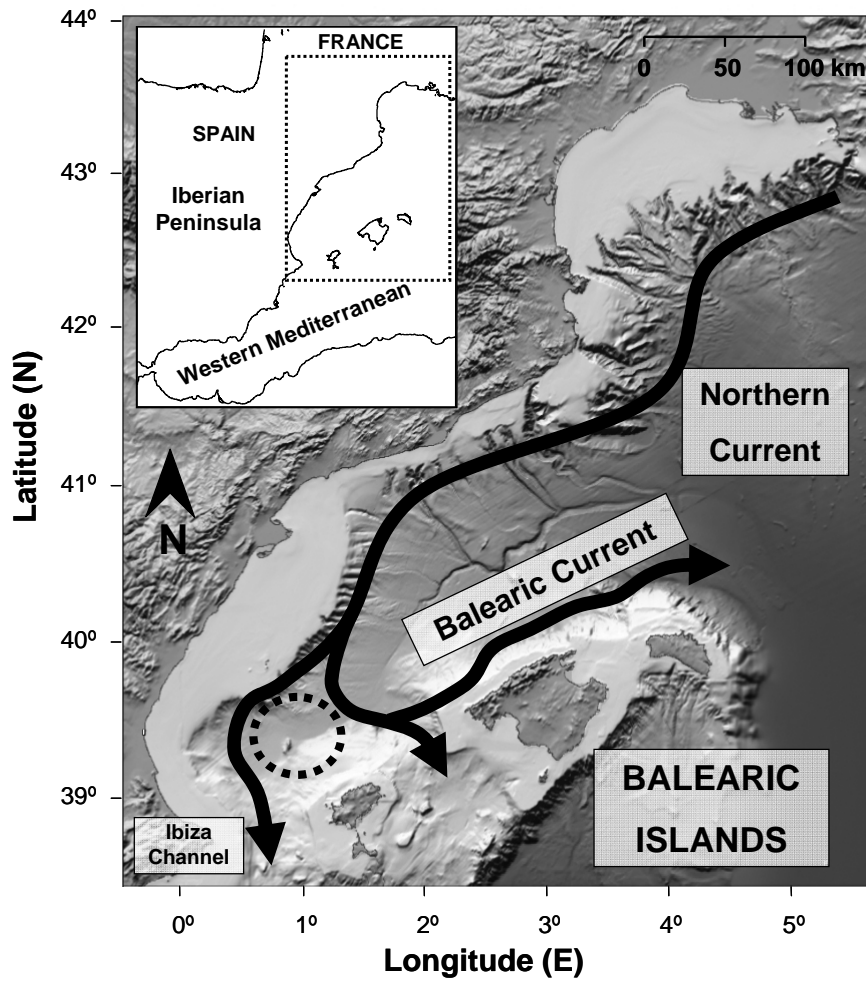
Figure 1. Map of the NW Mediterranean showing the Balearic Islands System. Northern (NC) and Balearic (BC) slope currents are also shown on the map. NC flows southward reaching the Ibiza channel where it bifurcates into two branches. One branch continues southward and one forms the BC, which flows towards the northeast along the northwestern slope of the Balearic Islands. Mesoscale structures in the Ibiza channel determine the degree of bifurcation each year, and affect the annual oceanographic regime (more details in Monserrat et al. 2008). Map adapted from http://www.icm.csic.es/geo/gma/MCB/CBSmaps.htm, morpho-bathymetry of the Mediterranean Seam MediMap Group, 2005, CIESM/Ifremer.
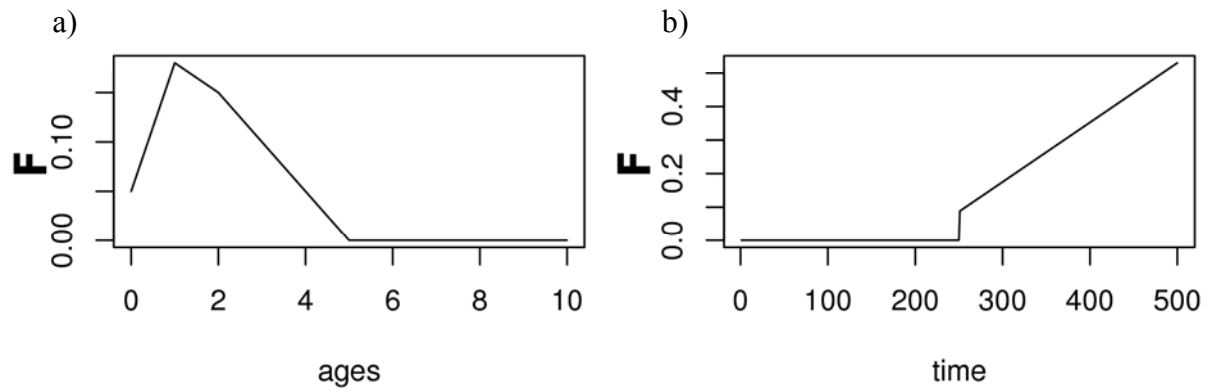
a)

b)

Figure 2. a) Mean fishing mortality vector applied in the simulations and (b) the evolution of fishing mortality with the time.
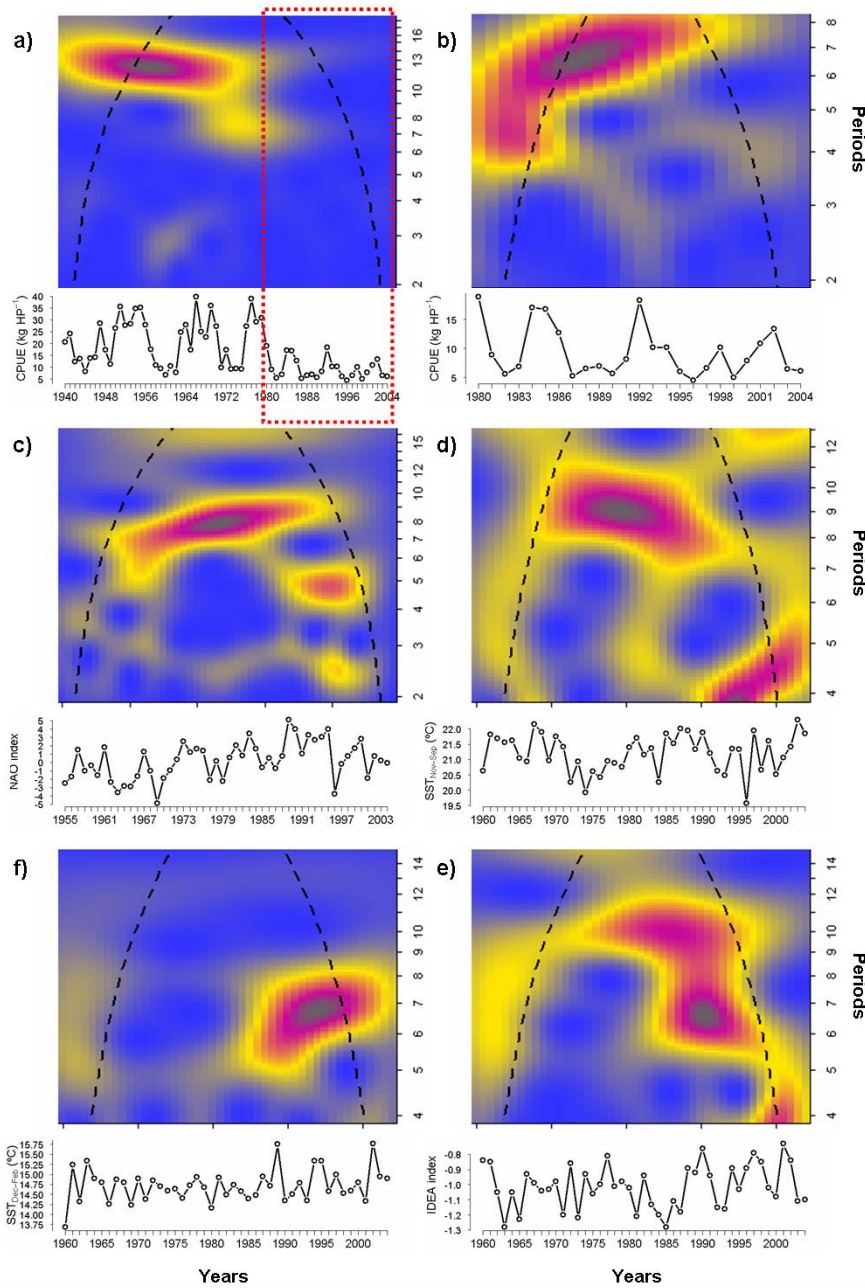
Figure 3. Univariate wavelets spectra and time series analysed: a) hake CPUE (kg HP^{-1}), the red-dotted outlined area square from 1980 to 2004 refers to a period separately analysed and shown in the figure b), c) NAO winter index, d) SST-autumn (ºC), e) SST-winter (ºC) and f) IDEA index. The wavelet spectra decompose the variance of time series over time (x axis) and periods (y axis), enabling to follow the time evolution of the relative importance of modes (periodicities) in the signal. The colours gradient, from dark blue to dark red, codes for low- to high-power values. Broken lines indicate significant areas at 5% level.
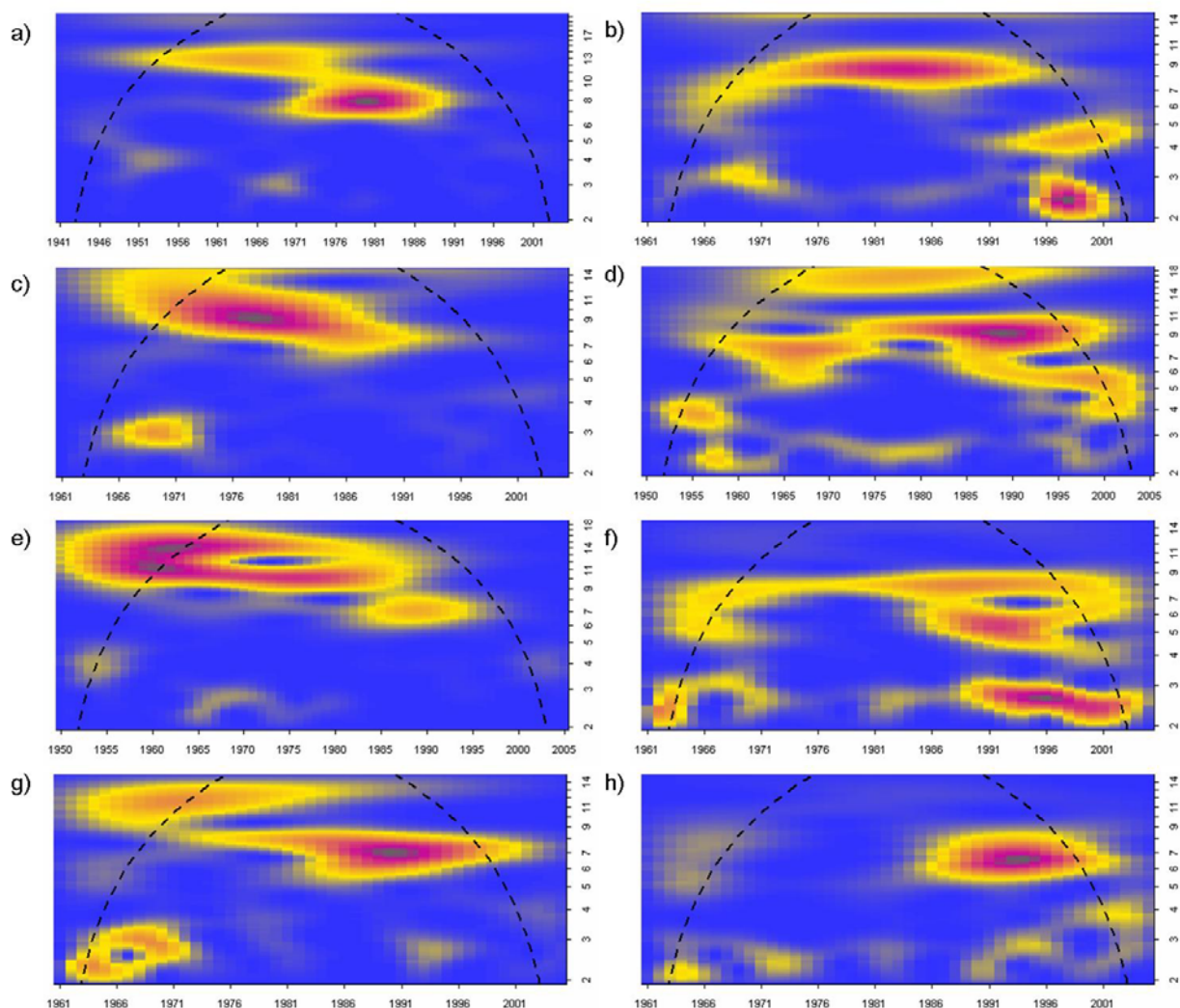
Figure 4. Cross (bivariate) wavelets spectra for all the combination of time series analysed: a) hake CPUE vs NAO, b) NAO vs SST-autumn, c) hake CPUE vs SST-autumn, d) NAO vs IDEA, e) hake CPUE vs IDEA, f) NAO vs SST-winter, g) hake CPUE vs SST-winter and h) IDEA vs SST-winter. Colours code range from dark blue (low values) to dark red (high values) for low to high cross-power values. X-axis represents time and y-axis represents periods. The colours gradient, from dark blue to dark red, codes for low- to high-power values. Broken lines indicate significant areas at 5% level.
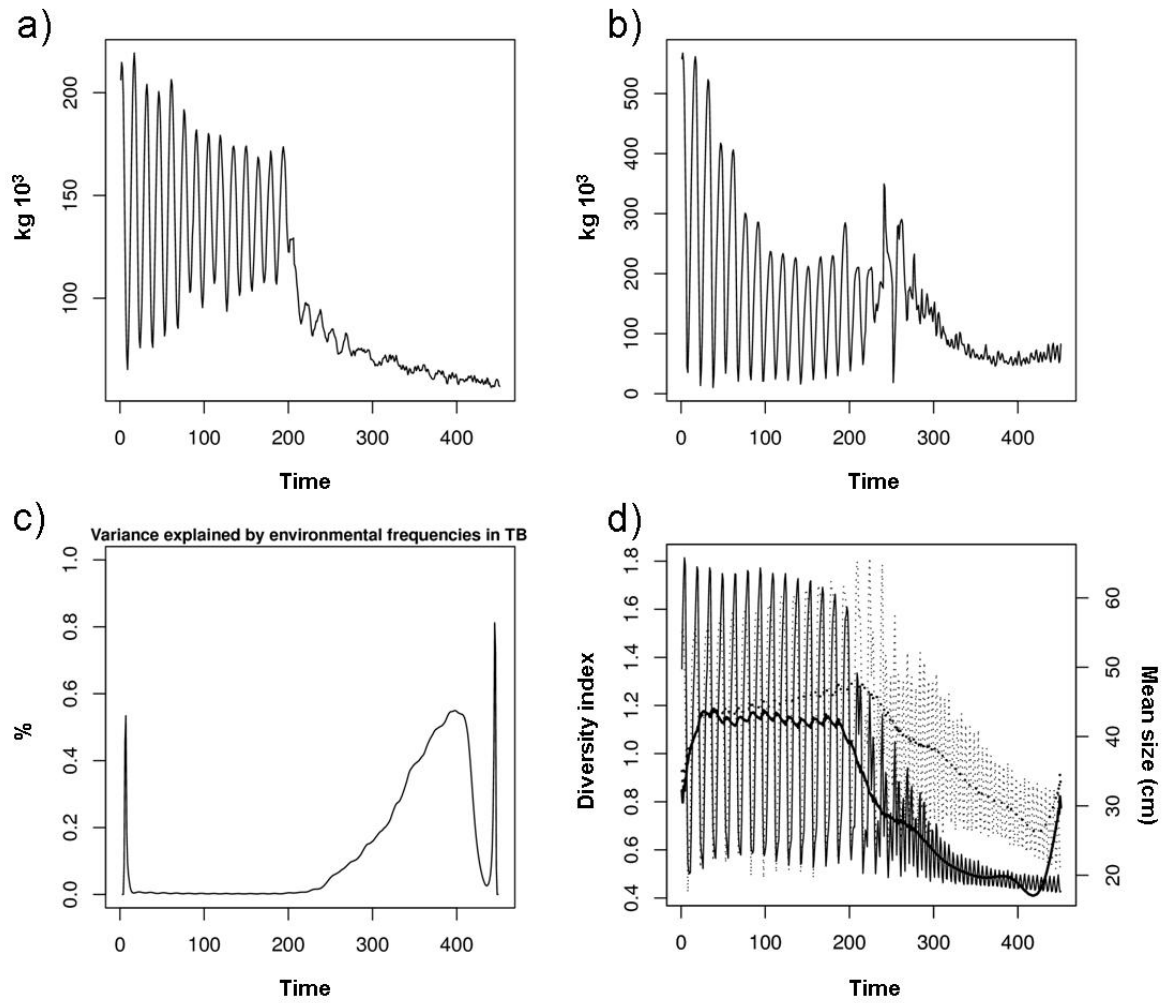
Figure 5. Outputs (Total biomass, kg 10^3) from the hake population simulation modelling for the random (a) and controlled (b) frequencies scenario. (c) Percentage of frequencies introduced in the controlled frequencies environment scenario that were observed in the simulated population output. (d) Straight and dotted lines refer to the mean length (cm) and H diversity index of the population respectively; long-term trends are represented with thicker lines.