Synchronous combined effects of fishing and climate within a demersal community

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Abstract: Accumulating evidence shows that fishing exploitation and environmental variables can synergistically affect the population dynamics of exploited populations. Here, we document that the interaction between fishing impact and climate variability triggered a synchronic response in the population fluctuations of six exploited species in the Mediterranean during 1965-2008. Through this period, the fishing activity experienced a sharp increase of fishing effort, which caused that all stocks shifted from an early period of under-exploitation to a later period of over-exploitation. This change altered the population resilience of the stocks and brought about an increase in the sensitivity of its dynamics to the climate variability. Landings increased exponentially when under-exploited but displayed an oscillatory behaviour once over-exploited. Climatic indices related to the Mediterranean mesoscale hydrography and large-scale north Atlantic climatic variability seemed to affect the species with broader age structure and longer life span, while the global-scale El Niño Southern Oscillation index (ENSO) positively influenced the population abundances of species with a narrow age structure and short life span. The species affected by ENSO preferentially inhabit the continental shelf, suggesting that Mediterranean shelf ecosystems are sensitive to the hydroclimatic variability linked to global climate.

Keywords: climate, ENSO, fishing, Mediterranean, synchrony, trawling
Introduction

A current view among fisheries ecologists is that the effect of fishing exploitation on the population dynamics of harvested species cannot be separated from that of the environmental variability (Perry et al., 2010; Planque et al., 2010). These interacting effects between fishing and climate trigger a variety of complex and often unpredictable biological responses. For instance, fishing exploitation may magnify the response of populations to environmental fluctuations by means of changes in demographic parameters, such as growth rate, that increase the instability of the population dynamics (e.g. Anderson et al., 2008; Hsieh et al., 2006). In addition, the demographic structure erosion makes populations more dependent to the recruitment strength and tightens the link between population and environmental variability (Rouyer et al., 2011; Botsford et al., 2011; Hidalgo et al., 2011). These evidences call for a more comprehensive management approach accounting for the combined effects of fishing and environment on the ecological processes and the population regulatory mechanisms.

Growing evidence from historical time series analysis shows that climate can trigger large fluctuations in marine populations in absence of fishing pressure, which has been mainly described for large and small pelagic species (Ravier and Fromentin, 2001; Baumgartner et al., 1992). However, the relationship between climate oscillations and fish populations has been demonstrated to be transitory, mainly because of the non-stationary link between climate oscillations and the regional-scale hydrography (Hsieh et al., 2009). In addition, natural populations can also fluctuate irrespective of the environmental scenario (i.e., relative contributions of low and high frequencies in the spectrum) because age-structure can act as a filter of the environmental forcing (Bjornstad et al., 2004). Thus, depending on the species life cycle and life history traits, recruitment signal spreads among age classes shaping the population fluctuations, which finally results from a complex interplay between deterministic and stochastic processes (Bjornstad and Grenfell, 2001). Most studies investigating how fishing affects this interplay focused on stock-specific case studies (but see CalCOFI database related studies, e.g, Anderson et al., 2008; Hsieh et al., 2006). However, fishing quite often harvests several species with a
broad spectrum of life histories within a community. This is particularly the case for the multi-
specific fisheries, which thus requires a deep understanding of how the same environmental
variability affects species of different life histories and demographic structure.

The Mediterranean is one of the most impacted seas in the world (Coll et al., 2008; Halpern et
al., 2008; Lejeusne et al., 2010). Among other ecological impacts, such as direct habitat
modification, species tropicalisation or seawater acidification (Calvo et al., 2011), fishing
represents the most impacting activity because it has driven most stocks to over-exploitation
(Colloca et al., 2011). Specifically, demersal fisheries, which are both multifleet and multispecific,
demand an integrated multispecies approach to management (Moranta et al., 2008). In addition,
marked cyclical fluctuations in abundance of some species do not seem to be linked only to
exploitation, suggesting the influence of climate on these populations (Maynou, 2008b; Oliver,
1993; Quetglas et al., 1998). Climate oscillations such as NAO (North Atlantic Oscillation), MO
(Mediterranean Oscillation) and IDEA (a recently described mesoscale index from the western
Mediterranean; Monserrat et al., 2008), have been reported to affect the cyclic abundance of
demersal resources in the Mediterranean Sea (Lloret et al., 2001; Massutí et al., 2008; Maynou,
2008b).

In this study we aimed at investigating the combined effects of fishing and climate on the
demersal community off the Balearic Islands (Western Mediterranean) using monthly information
from 1965 to 2008 of six exploited species, which differ in the life history characteristics and
demographic structure. To do that, we first evaluated the temporal variation of the fishing
exploitation level. Second, we investigated the oscillatory pattern of time series of population
biomass between periods of different exploitation levels. Finally, we tested the potential influence
of climatic variability on the population fluctuations.
Materials and methods

Data sources

This study focuses on the bottom trawl fishery off Mallorca, the largest island of the Balearic Archipelago (western Mediterranean), that works on the continental shelf and upper slope, where it mainly targets striped red mullet *Mullus surmuletus* and European hake *Merluccius merluccius* respectively. We analyzed these two main target species and a set of four representative commercial by-catch species for which long term series of landings data were also available. Since the work is based on official statistics, the term species is used to refer both to the taxonomic species and to commercial categories. With the only exception of the category elasmobranchs, which includes mainly the catshark *Scyliorhinus canicula* and the thornback ray *Raja clavata*, the rest of categories are composed mainly by the following taxonomic species: red mullet, *Mullus surmuletus*; hake, *Merluccius merluccius*; octopus, *Octopus vulgaris*; squid, *Loligo vulgaris*; and cuttlefish, *Sepia officinalis*. Although we are aware of the limitations inherent to the use of commercial categories, we also consider that they do not affect significantly the main conclusions of this work because when there are mixtures of species in our study area, such mixtures contain sympatric or co-generic species having similar life-history traits. Consider, for instance, the worst case, the elasmobranch category composed by the catshark *S. canicula* and the skate *R. clavata*. In our study area both inhabit the same depth range (80-400 m; (Massuti & Moranta 2003) and share similar population characteristics ([http://www.fishbase.org/](http://www.fishbase.org/)): 1) maximum age: 9 yr; 2) trophic level: 3.69 vs 3.76; 3) low resilience, with minimum population doubling time 4.5-14 yr.

Monthly time series of landings of these commercial species, along with the monthly fishing activity of each individual vessel from the trawling fleet of Mallorca during 1965 to 2008 were taken from official statistics. Communications with fishermen allowed us to use the actual, not nominal (declared), engine power (in HP) for each vessel, including changes in engine power over time and the corresponding increase in HP. The monthly fishing effort was obtained as the sum
of the HP of all the vessels working during that month weighted by the permitted time at sea (number of days per week and hours per day); the annual fishing effort (HP·y⁻¹) was subsequently calculated adding the monthly values. Previous to these calculations, however, we demonstrated that landings and effort acted proportionally during the time series analysed, which is a required property if effort has to be summed for the entire fleet (Fig. 1).

In order to determine the influence of the climate on the population dynamics of the six stocks, we investigated three climatic indices of increasing spatial scale. The mesoscale (regional) IDEA index is a proxy of the hydroclimate in the north-western (Monserrat et al. 2008). IDEA index is based on the air/sea heat fluxes in the Gulf of Lion during winter months was used as a proxy for the strength of the current in the northwest Mediterranean Sea (Monserrat et al. 2008). Lower values of the IDEA index indicate a larger formation of Western Mediterranean Intermediate Waters (WIW) in winter at intermediate layers (100 to 300 m depth) in the Gulf of Lion; this implies a larger presence of these water masses in the Balearic Sea during spring. 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). We used the winter average (December–March) of the NAO index (www.cru.uea.ac.uk/cru/data/nao.htm) because its influence in the Atlantic is higher during winter when the coupled ocean–atmosphere system is more active (Hurrell 1995). The global-scale El Niño Southern Oscillation (ENSO) was also investigated analysing the Southern Oscillation Index (www.cdc.noaa.gov/enso/enso.current.html), which measures the difference of sea level pressure between two localities situated in the eastern and central Pacific (Darwin and Tahiti, respectively). NAO and ENSO indices have been demonstrated to influence the regional climate and the surface hydrographical conditions in the Mediterranean Sea (e.g., Mariotti et al., 2002, Hertig and Jacobite, 2011).
To analyze the temporal variation of the fishing exploitation level throughout the study period, a surplus production model was fitted to data using the ASPIC software for each selected species (Prager, 2004). In addition to the maximum sustainably yield (MSY), ASPIC estimates several benchmarks and stock status indicators such as population biomass (B), relative biomass (B/B<sub>MSY</sub>) and relative fishing mortality (F/F<sub>MSY</sub>); B<sub>MSY</sub> and F<sub>MSY</sub> stand for the B and F when stocks are exploited at their MSY. As a general consensus, the species with B/B<sub>MSY</sub>&lt;1 and F/F<sub>MSY</sub>&gt;1 are indicative of an over-exploitation state while B/B<sub>MSY</sub>&gt;1 and F/F<sub>MSY</sub>&lt;1 are indicative of a under-exploitation state (Prager, 2004). ASPIC requires starting guesses of the following estimated parameters: 1) K, the stock’s maximum biomass or carrying capacity; 2) MSY, the maximum sustainable yield; 3) B<sub>1</sub>/K, the ratio of the biomass at the beginning of the first year to K; and 4) q, the catchability coefficient. In the first trials, we followed the recommendations of Prager (2004) to set the starting guesses for these parameters, which were then interactively adjusted depending on the program outputs. The initial conditions for the MSY and K were half and ten times respectively the largest catch observed for each species during the period from 1965 to 2008. The starting value of the relative biomass (B<sub>1</sub>/K) was fixed at a range of values, as this can considerably reduce variance in the estimates and is a common practice when fitting surplus production models (Prager, 2004). The range of B<sub>1</sub>/K values used (0.5, 0.7, 0.9) reflects the lightly fished status of the stocks before 1965. For each estimated parameter, 80% bias-corrected confidence intervals were calculated using bootstrapping with 1000 iterations on the central set of estimates (B<sub>1</sub>/K=0.7).

Monthly time series of landings and catches per unit effort (CPUEs) were analyzed to determine any periodicity during the period from 1965 to 2008. In addition to a marked seasonal oscillation throughout the entire time series, preliminary analyses of the landings data showed the existence of...
two distinct periods for all species with different variance in the fluctuations, already reported in previous studies (Hidalgo et al., 2009; Massutí et al., 2008): a period with increasing landings from 1965 to 1980, followed by a period with interannual oscillatory behaviour from 1980 to 2008. Therefore, the two time periods were treated differently. Preliminary analyses of the first period do not reveal any clear periodicity and non-linear regressions were fitted by means of the least squares method. The period from 1980 to 2008 was first analyzed using a classical Fourier analysis to obtain the relative importance of the different frequencies present in the time series. Given that the time series is rather short and the frequency resolution achieved with a Fourier transform too low to quantify interannual oscillations, least squares fittings were used to better quantify the interannual variability observed in the time series. A function of the form

\[ y = \bar{x} + A \cos(\omega t) + B \cos(\omega t) \]  

was used (Bloomfield, 1976), where \( \omega \) is the frequency of the series searched for, \( \bar{x} \) is the mean of the catch data and \( A \) and \( B \) are as follows

\[ A = \frac{2}{n} \sum_{n=1}^{n} (x_t - \bar{x}) \cos(\omega t), \]  

and

\[ B = \frac{2}{n} \sum_{n=1}^{n} (x_t - \bar{x}) \sin(\omega t), \]  

where \( n \) and \( x_t \) are the number of points and the value of \( x \) in time \( t \) (in months) respectively.

**Climate effects**

Climate effects on the population dynamics of the six stocks were investigated by means of Generalized Additive Models (GAMs). As a previous step to the GAM analyses, which bear the implicit assumption of additivity (covariates are mutually independent), we checked the lack of correlation among these three climatic indices (NAO vs IDEA: \( R=0.099, p=0.608 \); NAO vs
ENSO: $R=0.229$, $p=0.232$; IDEA vs ENSO: $R=0.136$, $p=0.482$). To remove any possible effect of fishing effort in the oscillatory behaviour, the analyses were performed using CPUEs rather than landings. Furthermore, given that a decrease in the CPUEs series was observed for most species, which can be explained in part by increased fishing effort, the series were detrended (Maynou, 2008b). Detrending the original series renders this series stationary and consisted in fitting an exponential regression to the data, with time as an independent variable (Abraham and Ledolter, 1983). The residuals obtained in these regressions were then used in the GAM analyses to model CPUEs as a function of the IDEA, NAO and ENSO indices. Previous to GAM analyses, Spearman correlations (accounting for temporal autocorrelations, Pyper and Peterman, 1998) were performed among species to inspect potential synchronic patterns.

Since in many cases climatic indices and CPUEs or landings are found to be correlated at different lag times (Lloret et al., 2001; Massuti et al., 2008; Maynou, 2008b), the GAMs were performed using lags from 0 to 7 years to include the highest periodicity reported for these indices (ENSO, 3 to 7 years). Consequently, eight (0 to 7 years) different GAMs were developed in which the abundance of each species was modelled against the IDEA, NAO and ENSO indices as explanatory variables. GAM analyses were carried out with the R package (version 2.5.1; [http://www.r-project.org/](http://www.r-project.org/)) using the mgcv library (Wood, 2001). The model selection criterion was based on minimizing the generalized cross validation (GCV), which measures the predictive squared error of the model; low values show the best compromise between model complexity and fit to the observed data (Wood, 2001). The goodness of fit in the GAMs was assessed using the percentage of deviance explained (DE) and the final GCV. For every model, residuals were checked for homogeneity of variance, absence of temporal autocorrelation and violation of normality assumptions.
Results

During the period from 1965 to 2008, the bottom trawl fishery off Mallorca showed large variations in the number of vessels, mean engine power and the fishing time at sea (Fig. 2). Three main phases can be distinguished in the evolution of the total fleet fishing effort over time: 1) from 1965 to the mid 1970s it increased by a factor of 2.5; 2) from the mid 1970s to 1994 it continued to grow but at a slower rate; and 3) from 1994 to the present it has gradually decreased. Consistently for all species, time series of landings showed a marked increase during the late 1970s that was followed by a progressive decrease comparatively less pronounced for squid and cuttlefish (Fig. 3). Although with some exceptions, occurring mainly during the first years of the time series, annual CPUEs followed the same general pattern as the landings.

Fishing exploitation

The evolution of the relative fishing mortality (F/F<sub>MSY</sub>) and biomass (B/B<sub>MSY</sub>) throughout the time series showed a similar trend for all species (Fig. 4). From the beginning of the series to the mid 1970s the stocks were under-exploited, since the fishing effort was lower than the fishing effort that should be exerted to attain the maximum sustainable yield (F/F<sub>MSY</sub>&lt;1); consequently, the stocks’ biomass was higher than the expected biomass at MSY (B/B<sub>MSY</sub>&gt;1). All the species turned to an over-exploited state (i.e., B/B<sub>MSY</sub>&lt;1 and F/F<sub>MSY</sub>&gt;1) around the early 1980s that continues to the present day. Although estimates of exploitation status of stocks expressed in relative terms were very similar for all the species studied (Supplementary Table S1), two main groups could be distinguished. The first group contained the two target species of the trawl fishery, red mullet and hake, whose central estimates of B<sub>2009</sub>/B<sub>MSY</sub>, F<sub>2008</sub>/F<sub>MSY</sub> and Y<sub>e2009</sub>/MSY were 0.48, 1.4 and 0.73 respectively. The second group included the by-catch species (elasmobranchs, octopus, squid and cuttlefish), whose central estimates for the same three parameters were 0.61-0.66, 1.08-1.58, and 0.85-0.89 respectively.
Population’s fluctuations

The time series analyses showed that analysing monthly landings or CPUEs rendered similar results. Both series show an increasing behaviour during the first period (1965-1980) with absence of interannual periodicities, best fitted in all species using a positive (negative) exponential function for landings (CPUEs). This period ends simultaneously for all the species at the beginning of the 1980s and then an interannual oscillatory behaviour becomes apparent from 1980 to 2008.

The best fitting sinusoidal function for each species is superimposed on the 1980-2008 data series in Figure 5, which, for clarity purposes, only shows the landings fits. As previously mentioned, the most evident signal observed in the monthly series is the seasonal oscillation. This annual cycle, present throughout the entire series of all species, is clearly revealed by the Fourier analysis, and shows two main peaks at 12 and 6 months corresponding to the seasonal cycle and the first harmonic respectively. The discrete Fourier transform and the harmonic analysis showed interannual oscillations of 7 years for four out of the six species analysed (elasmobranchs, hake, octopus and cuttlefish). In the case of squid and red mullet these oscillations were longer (11 and 15 years, respectively).

Climate effects

Residuals retained after removing the non-linear trend were significantly correlated in most species pairs (Table 1). Such residuals were then used in the GAM analyses to model CPUEs as a function of the IDEA, NAO and ENSO indices. To determine whether the fluctuations in the population dynamics were due to climate variability, we focused our analysis on the over-exploited and oscillatory period (1980-2008). For each of the six species investigated, eight GAM models were performed, corresponding to the eight lag times (0 to 7 years) considered. Model selection and outputs of all these 48 models (8 lags × 6 species) are displayed in the Supplementary Table S2, whereas Table 2 shows exclusively the best model for each species. Consistent results were obtained for four out of the six species (red mullet, octopus, squid and cuttlefish), whose best
model showed a significant positive effect of the ENSO index at a lag time of 6 years. The variance explained for these four models ranged from 26 to 33%. The two remaining species only showed significant effects of the NAO (hake at lag times of 2 and 5 years) and IDEA (hake and elasmobranchs at lag times of 7 and 2 years, respectively) indexes.

Discussion

This study showed that the population dynamics of the main commercial species of the demersal community off the Balearic Islands was synchronously affected by the combined effect of fishing exploitation and the environment variability during the last forty-four years. Such a synchronic effect was twofold. First, the fact that all the species here studied turned to over-exploited (i.e., $B/B_{MSY}\text{<}1$) around the early 1980s seems to be unlikely an exclusive effect of fishing. We hereafter discuss how changes in the Mediterranean hydroclimate in the early 1980s could contribute to synchronize the changes observed. And second, by turning to an over-exploited state, populations seemed to be more dependent on the environmental variability (Planque et al., 2010; Perry et al., 2010) displaying synchronic fluctuations on the population biomass.

The six species analysed followed a general trend characterized by an early period of under-exploitation that shifted to over-exploitation in early 1980s. This community shift affected the population dynamics of all the species, since their landings and CPUEs showed an increasing trend during the under-exploitation phase (1965-1980) but an oscillatory behaviour during the over-exploitation phase (1980-2008). These natural fluctuations, however, would be masked during the first part of the series, when landings displayed an exponential growth due to the rapid increase in fishing effort. Therefore, our results would indicate a phase-transition event in the population dynamics of demersal stocks from the Balearic Islands in 1980, a scenario already reported for hake in this area (Hidalgo et al., 2009). The rapid increase in the exploitation rate observed during the previous years (namely, it increased 2.5 times during 1965-1977) seemed to have a major effect on the sudden depletion. However, growing evidence showed that the hydroclimate of the NW
Mediterranean also suddenly changed around the early 1980s to an overall dominance of higher temperatures and atmospheric pressure, and weaker wind stress and precipitation (Conversi et al., 2010; Fernandez de Puelles and Molinero, 2007, 2008; Molinero et al., 2009). These changes in the hydrography influenced the seasonal and inter-annual plankton dynamics around the Balearic Islands (Fernandez de Puelles and Molinero, 2007, 2008) that could affect the survival of early life stages of exploited species, and, in turn, synergistically magnify the effect of fishing (Hidalgo et al., 2011).

Fluctuations in landings of demersal species in the western Mediterranean are well documented. Astudillo and Caddy (1986) found a marked periodicity of 12 years in the landings of hake and red mullet from the Balearic Islands, which they hypothesized to be independent of fleet activity. In the same area, a periodicity of about 8 years was reported for octopus (Quetglas et al., 1998) and red shrimp (Carbonell et al., 1999). In a nearby area, however, fluctuations in red shrimp landings ranged between 7 and 13 years among different ports (Maynou, 2008a). Our results showed interannual oscillations with a periodicity of 7-9 years in the last three decades for four out of the six species investigated. There is increasing evidence that harvested species fluctuate more than unharvested ones, which is probably due to the elevated variability of recruitment and the increased sensitivity to the environmental variability resulting from the demographic truncation caused by fishery exploitation (Anderson et al., 2008; Hsieh et al., 2006).

To determine whether the causes of the interannual fluctuations in CPUEs were linked to climatic variability, climate indices at increasing spatial scales (local, meso-, and global-scale) were examined. NAO and IDEA showed significant effects on the elasmobranches and hake consistent with previous studies (Massutí et al 2008). Unexpectedly, however, our models found much support for an effect of ENSO with a lag time of 6 years for four out of the six species analyzed (red mullet, octopus, squid and cuttlefish). Identical responses in these four species (Fig. 5) points to an ENSO signal on some Mediterranean marine populations. This signal might, in fact, interact with, or have masking effects on, other influences such as the NAO, which displayed a multidecadal component of ca. 8 years during the last decades (e.g. Massei et al.
Indeed, the interaction between North Atlantic climate (i.e. NAO) and Pacific modes (i.e. ENSO) has been shown to affect the Mediterranean climate through the rainfall (e.g. Mariotti et al., 2002).

Recent evidences also demonstrated the influence of ENSO variability on the Mediterranean hydrographical characteristics, particularly on the sea surface temperature (Hertig and Jacobeit, 2011). In the Balearic Islands, rainfall and sea surface temperature variability strongly affect the nutrients, phytoplankton and zooplankton variability (Fernandez de Puelles and Molinero, 2007, 2008). Since the species displaying a close link with ENSO were those inhabiting on the shallow continental shelf, they should be more influenced by the inter-annual dynamics of zooplankton affecting the prey-predator relationships and survival of the early life stages. Links between ENSO and coastal species outside the Mediterranean are not new and have been reported for other organisms worldwide (Rimbu et al., 2003; Urban et al., 2000).

Though a time lag between the climatic and the biological signal was expected (e.g. Ottersen et al., 2004; Overland et al., 2010), the 6 years lag of the ENSO effect on the population biomass of the four continental shelf species is likely the more striking result of our study (but see, Zimmerman and Palo, 2012; Gonzalez-Herraiz et al., 2009). Since the ENSO signal on the Mediterranean hydroclimate is transmitted within some months (Hertig and Jacobeit, 2011), there must be additional factors modulating the population fluctuations that we did not take into account in our study. We suggest that internal properties of the life cycle of these species can interact with the climate signal, which makes plausible potential inter-cohort and density-dependent effects (Bjornstad and Grenfell, 2001). Favourable climatic events can produce strong annual cohorts, favouring the recruitment in the consecutive years due to the relative good level of the reproductive stock. This could magnify the climatic signal in the next generations and thus bring forth population cycles (Tzeng et al., 2012) that could explain the lagged oscillatory response observed.

Recent studies on species with a broad demographic structure show that variability in recruitment increased with fishing and became particularly sensitive to forcing at time-scales near the mean age of reproduction (Botsford et al., 2011). This is consistent with the cohort resonance effect (Bjornstad et al., 2004; Bjornstad et al., 1999) and has been recently suggested for hake in the
Our study adds to this picture of how species of the same harvested community with different life history and demographic structure cope with environmental variability. Our results support that population fluctuations result from the interaction of deterministic and stochastic processes (Bjornstad and Grenfell, 2001), while the relative contribution of each component depends on the life history and demographic structure of the species. Hake, red mullet and elasmobranches species have a broader age structure and longer life span compared to squid, cuttlefish or octopus, and thus deterministic mechanisms (e.g., internal demographic processes) may have higher impact on population fluctuations. By contrast, cephalopods display a narrow age structure, fast life cycle and short life span, and thus the population fluctuations are likely more affected by climate variability. It is worth noticing that our results suggest potential effects of the same climatic phenomena at different temporal lags that may be further evaluated in a unique model structure for each species, as well as potential interactions among the different climatic indices. Future studies should tackle this challenge combining long term information of CPUEs with age(stage)-structure information from assessment groups that will allow to investigate whether and how climate can affect the same species through several demographic processes.

To conclude, our results demonstrate that the interaction between fishing and climate can have synchronic effects on the population fluctuations of different species within an overexploited community. An intense fishing exploitation might increase the susceptibility, and therefore reduce the resilience, of harvested populations to climate variability (Botsford et al., 2011). We also showed that, as a consequence of this increased susceptibility, populations might also increase their sensitivity to subtle climate signals that could previously be masked by more influential factors. Our study expands this conclusion to the community scale and highlights that species sensitivity to climate and thus population fluctuations depend on the demographic characteristics, life history and bathymetric distribution of each species.
**Supplementary Material**

Supplementary material is available at the *ICESJMS* online version of the paper:

**Supplementary Table S1.** Surplus-production model results.

**Supplementary Table S2.** Outputs of 48 GAMs (8 lags × 6 species) modelling CPUEs as a function of the climatic indexes IDEA, NAO and ENSO.

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**References**


W ell, you're quite the scholar, aren't you? It seems you're quite the expert on the topic of sustainable management of Mediterranean ecosystems.

Your work on the Mediterranean Sea regime shift at the end of the 1980s has been particularly influential. Your research on the long-term variability of the NAO index and the long-term variability of Nephrops norvegicus population and fishery off West of Ireland has provided valuable insights into the impacts of climate change on marine ecosystems.

Your studies on the effects of climate change on Mediterranean marine ecosystems have been groundbreaking. You've shown how human impact on marine ecosystems has led to significant changes in the Mediterranean Sea.

Your research on the importance of age structure in models of the response of upper trophic levels to fishing and climate change has been particularly relevant in the context of sustainable fisheries management.

Your work on the effects of climate change on Mediterranean marine ecosystems has been crucial in developing new paradigms for ecological sustainability. Your research on the Mediterranean Sea regime shift at the end of the 1980s has provided valuable lessons for understanding the impacts of climate change on marine ecosystems.

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transitions induced by long-term fishery harvesting: European hake (*Merluccius merluccius*) off the Balearic Islands. Canadian Journal of Fisheries and Aquatic Sciences, 66: 1355–1370.


Table 1. Correlation of residuals among the six species investigated (elasmobranchs, hake, red mullet, octopus, squid and cuttlefish) obtained from fitting an exponential regression to CPUE data with time as independent variable. The residuals obtained in these regressions were then used in the GAM analyses to model CPUEs as a function of the IDEA, NAO and ENSO indices.

<table>
<thead>
<tr>
<th></th>
<th>Elasmobranch</th>
<th>Hake</th>
<th>Red mullet</th>
<th>Octopus</th>
<th>Cuttlefish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hake</td>
<td>0.62***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red mullet</td>
<td>0.17</td>
<td>-0.13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Octopus</td>
<td>0.61***</td>
<td>0.60***</td>
<td>0.14</td>
<td></td>
<td></td>
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<tr>
<td>Cuttlefish</td>
<td>0.39*</td>
<td>-0.02</td>
<td>0.30</td>
<td>0.61***</td>
<td></td>
</tr>
<tr>
<td>Squid</td>
<td>0.50**</td>
<td>0.25</td>
<td>0.15</td>
<td>0.62***</td>
<td>0.57***</td>
</tr>
</tbody>
</table>

*p<0.05; **p<0.005; ***p<0.001
Table 2. Results of generalized linear models (GAMs) fitting the abundance index of six commercial species from the Mallorca trawling fleet (Balearic Islands, western Mediterranean) as a function of three different climatic indices with several lag times. The following indices of increasing spatial scale were used: the IDEA index, the North Atlantic Oscillation (NAO) and El Niño/Southern Oscillation (ENSO). The significance of each index and the best model fit based on the percentage of deviance explained (DE) are shown. The GAMs displayed were performed on the statistically significant fittings resulting from the entire set of 48 models considering eight lag times (0 to 7 years) (see Supplementary Table S2).

<table>
<thead>
<tr>
<th>Species</th>
<th>Lag time (years)</th>
<th>IDEA</th>
<th>NAO</th>
<th>ENSO</th>
<th>DE (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red mullet</td>
<td>6</td>
<td>n.s.</td>
<td>n.s.</td>
<td>0.024</td>
<td>26.0</td>
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<tr>
<td>Octopus</td>
<td>6</td>
<td>n.s.</td>
<td>n.s.</td>
<td>0.008</td>
<td>33.3</td>
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<tr>
<td>Squid</td>
<td>5</td>
<td>n.s.</td>
<td>n.s.</td>
<td>0.011</td>
<td>30.3</td>
</tr>
<tr>
<td>Cuttlefish</td>
<td>0</td>
<td>n.s.</td>
<td>n.s.</td>
<td>0.052</td>
<td>16.8</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>n.s.</td>
<td>n.s.</td>
<td>0.010</td>
<td>31.9</td>
</tr>
<tr>
<td>Hake</td>
<td>2</td>
<td>n.s.</td>
<td>0.022</td>
<td>n.s.</td>
<td>25.5</td>
</tr>
<tr>
<td></td>
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<td>0.065</td>
<td>n.s.</td>
<td>18.7</td>
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<tr>
<td></td>
<td>7</td>
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<td>n.s.</td>
<td>n.s.</td>
<td>38.5</td>
</tr>
<tr>
<td>Elasmobranch</td>
<td>2</td>
<td>0.043</td>
<td>n.s.</td>
<td>n.s.</td>
<td>19.2</td>
</tr>
</tbody>
</table>

* p<0.05; ** p<0.005; *** p<0.001; n.s. non significant
Figure legends

Figure 1. Results of a generalized additive model (GAM) describing landings as a function of fishing effort (in HP) and year. Landings and effort data correspond to the trawl fleet fishery off Mallorca (Balearic Islands, western Mediterranean) from 1965-2008. In the GAM, both effects (effort and year) were significant at p<0.001 and the total deviance explained by the model was 71%.

Figure 2. Annual horse power (HP) of the entire bottom trawl fleet of Mallorca (Balearic Islands, western Mediterranean) and fishing time at sea (in hours per week, h·w⁻¹) permitted by different regulations throughout the time series 1965 to 2008 (A). Total number of vessels (stippled line) along with mean and standard deviation (continuous and dotted line respectively) vessel HP during the same time series (B).

Figure 3. Landings (continuous line) and catch per unit effort (CPUE) (dotted line) of six demersal species caught by the bottom trawl fleet off Mallorca (Balearic Islands, western Mediterranean) during the period from 1965 to 2008.

Figure 4. Time trajectories of the relative fishing mortality rate (F/F_{MSY}) and relative population biomass (B/B_{MSY}) estimated using non-equilibrium surplus production models for six different demersal species from Mallorca (Balearic Islands, western Mediterranean) under assumption B₁/K=0.7. Dotted lines are 80% bias-corrected confidence intervals from bootstrapping.

Figure 5. Spectrum analysis and least squares fitting to the monthly data (landings and/or CPUEs) of six demersal species caught by the bottom trawl fleet off Mallorca (Balearic Islands, western Mediterranean) during the period from 1965 to 2008. The best fit to the data is shown superimposed on the landings: an exponential function for the series 1965-1980 and a sinusoidal function for 1980-2008. The periodicity of the oscillations (in months) found in this last period is also shown for each species considering both landings (black line) and CPUEs (grey line).