Synchronous combined effects of fishing and climate within a demersal community

Antoni Quetglas[1]*, Francesc Ordines[1], Manuel Hidalgo[1], Sebastià Monserrat[2,3], Susana Ruiz[4], Ángel Amores[3], Joan Moranta[1], and Enric Massutí[1]

[1]Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Moll de Ponent s/n, Apdo. 291, 07015 Palma, Spain
[2]CSIC/UIB – Institut Mediterrani d'Estudis Avançats, Miquel Marquès 21, 07190 Esporles, Spain
[3]Universitat de les Illes Balears, Departament de Física, 07122 Palma, Spain
[4]Instituto Español de Oceanografía, Centro Oceanográfico de Santander, Promontorio de San Martín s/n, Apdo. 240, 39080 Santander, Spain

*Corresponding Author: tel: +34-971-401-561; fax: +34-971-404-945; e-mail: toni.quetglas@ba.ieo.es

Accumulating evidence shows that fishing exploitation and environmental variables can synergistically affect the population dynamics of exploited populations. Here, we document an interaction between fishing impact and climate variability that triggered a synchronic response in the population fluctuations of six exploited species in the Mediterranean from 1965–2008. Throughout this period, the fishing activity experienced a sharp increase in fishing effort, which caused all stocks to shift from an early period of underexploitation to a later period of overexploitation. This change altered the population resilience of the stocks and brought about an increase in the sensitivity of its dynamics to climate variability. Landings increased exponentially when underexploited but displayed an oscillatory behaviour once overexploited. 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 lifespan, while the global-scale El Niño Southern Oscillation index (ENSO) positively influenced the population abundances of species with a narrow age structure and short lifespan. 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 environmental variability (Perry *et al.*, 2010; Planque *et al.*, 2010). Interactions 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, which increase the instability of population dynamics (e.g. Hsieh *et al.*, 2006; Anderson *et al.*, 2008). In addition, demographic structure erosion makes populations more dependent on recruitment strength, and tightens the link between population and environmental variability (Botsford *et al.*, 2011; Hidalgo *et al.*, 2011; Rouyer *et al.*, 2011). This evidence calls for

a more comprehensive management approach that accounts for the combined effects of fishing and environment on ecological processes and population regulatory mechanisms.

Growing evidence from historical time-series analysis shows that climate can trigger large fluctuations in marine populations in the absence of fishing pressure, mainly described with respect to large and small pelagic species (Baumgartner *et al.*, 1992; Ravier and Fromentin, 2001). However, the relationship between climate oscillations and fish populations has been demonstrated to be transitory, largely because of the non-stationary link between climate oscillations and regional-scale hydrography (Hsieh *et al.*, 2009). In addition, natural populations 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 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 populations fluctuations (Bjornstad and Grenfell, 2001); ultimately, this results in a complex interplay between deterministic and stochastic processes. Most studies investigating how fishing affects this interplay focus on stock-specific case studies (but see CalCOFI database related studies, e.g. Hsieh *et al.*, 2006; Anderson *et al.*, 2008). However, fishing quite often harvests several species with a broad spectrum of life histories within a community, particularly the case for multi-specific fisheries, so a deep understanding of the way in which the same environmental variability can affect species with different life histories and demographic structure is required.

The Mediterranean is one of the most impacted upon seas in the world (Coll *et al.*, 2008; Halpern *et al.*, 2008; Lejeusne *et al.*, 2010). Among ecological factors, such as direct habitat modification, species tropicalization, and seawater acidification (Calvo *et al.*, 2011), fishing represents the activity having the greatest impact because it has driven most stocks to overexploitation (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 the abundance of some species seem to be linked not only to exploitation, but also to the influence of climate on these populations (Oliver, 1993; Quetglas *et al.*, 1998; Maynou, 2008b). Climate oscillations, such as the NAO (North Atlantic Oscillation), the 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 1965–2008 for six exploited species differing in 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 the time-series of population biomass between periods of different exploitation levels. Finally, we tested the potential influence of climatic variability on the population fluctuations.

Material 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 analysed 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 being the category "elasmobranchs", which includes the catshark, *Scyliorhinus canicula*, and the thornback ray, *Raja clavata,* the rest of the categories are composed chiefly of 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 in the use of commercial categories, we do not consider that they significantly affect 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 of the catshark, *S. canicula*, and the skate, *R. clavata*. In our study area, both inhabit the same depth range (80–400m) (Massutí and Moranta, 2003) and share similar population characteristics (http://www.fishbase.org/): (i) maximum age: 9 years; (ii) trophic level: 3.69 vs 3.76; (iii) low resilience, with minimum population doubling time 4.5–14 years.

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 ($HP \cdot y^{-1}$) was subsequently calculated by 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 (Figure 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 northwestern Mediterranean (Monserrat *et al.* 2008). The IDEA index is based on the air/sea heat fluxes in the Gulf of Lion during the winter months, and 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 (100–300 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 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 by 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). The 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 Jacobeit, 2011).

Fishing exploitation
To analyse the temporal variation of the fishing exploitation level throughout the study period, a surplus production model was
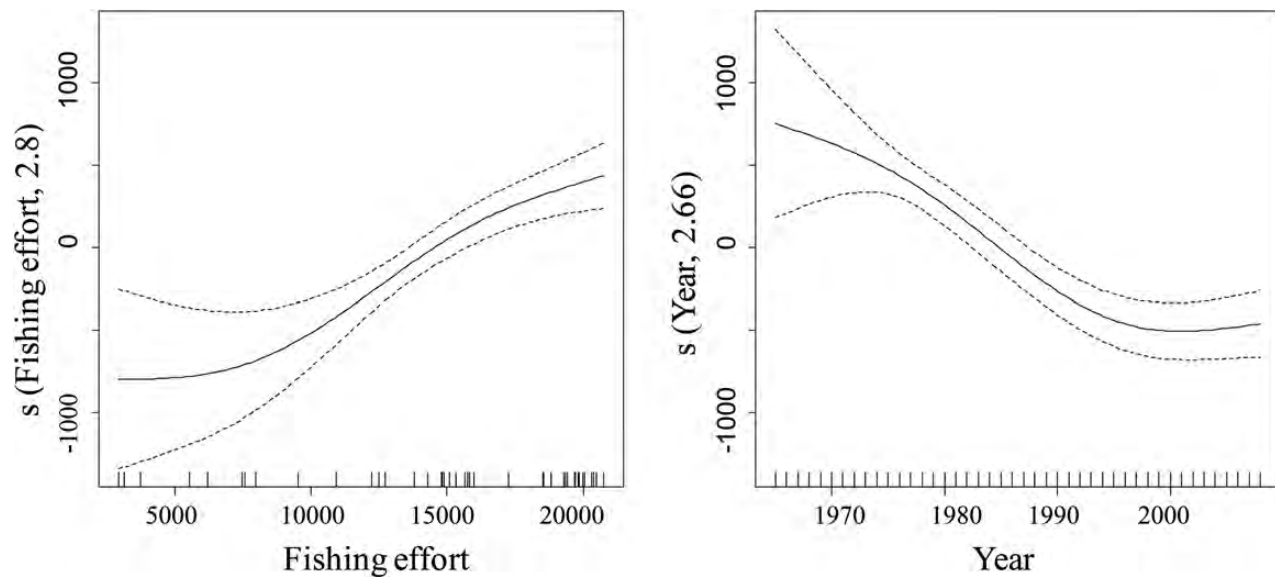
Figure 1. Results of a generalized additive model (GAM) describing landings as a function of fishing effort (in HP) and year. Landings and effort data correspond to the trawl fleet fishery off Mallorca (Balearic Islands, western Mediterranean) from 1965–2008. In the GAM, both effects (effort and year) were significant at $p < 0.001$, and the total deviance explained by the model was 71%.

fitted to data (using the ASPIC software) for each selected species (Prager, 2004). In addition to the maximum sustainable yield (MSY), ASPIC estimates several benchmarks and stock status indicators such as population biomass (B), relative biomass (B/B_{MSY}) and relative fishing mortality (F/F_{MSY}); B_{MSY} and F_{MSY} stand for the B and F when stocks are exploited at their MSY. As a general consensus, the species with $B/B_{MSY} < 1$ and $F/F_{MSY} > 1$ are indicative of an overexploitation state, while $B/B_{MSY} > 1$ and $F/F_{MSY} < 1$ are indicative of an underexploitation state (Prager, 2004). ASPIC requires starting guesses of the following estimated parameters: (i) K, the stock's maximum biomass or carrying capacity; (ii) MSY, the maximum sustainable yield; (iii) B_1/K, the ratio of the biomass at the beginning of the first year to K; and (iv) q, the catchability coefficient. In the first trials, we followed the recommendations of Prager (2004) in setting 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_1/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_1/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 ($B_1/K = 0.7$).

Population fluctuations

Monthly time-series of landings and catches per unit effort (CPUEs) were analysed 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 (Massutí *et al.*, 2008; Hidalgo *et al.*,

2009): 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 did 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 analysed 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

$$y = \bar{x} + A\cos(\omega t) + B\cos(\omega t) \tag{1}$$

was used (Bloomfield, 1976), where ω is the frequency of the series searched for, first independent term is the mean of the catch data and A and B are as follows

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

$$B = \frac{2}{n}\sum_{n=1}^{t}(x_t - \bar{x})\sin(\omega t), \tag{3}$$

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 of 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; Massutí *et al.*, 2008; Maynou, 2008b), the GAMs were performed using lags from 0–7 years to include the highest periodicity reported for these indices (ENSO, 3–7 years). Consequently, eight (0–7 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/) 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 1965–2008, the bottom trawl fishery off Mallorca showed large variations in the number of vessels, mean engine power and the fishing time at sea (Figure 2). Three main phases can be distinguished in the evolution of the total fleet fishing effort over time: (i) from 1965 to the mid 1970s it increased by a factor of 2.5; (ii) from the mid 1970s to 1994 it continued to grow but at a slower rate; and (iii) 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 (Figure 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_{MSY}) and biomass (B/B_{MSY}) throughout the time-series showed a similar trend for all species (Figure 4). From the beginning of the series to the mid 1970s the stocks were underexploited, since the fishing effort was lower than the fishing effort that should be exerted to attain the maximum sustainable yield ($F/F_{MSY} < 1$); consequently, the stocks' biomass was higher than the expected biomass at MSY ($B/B_{MSY} > 1$). All the species turned to an overexploited state (i.e. $B/B_{MSY} < 1$ and $F/F_{MSY} > 1$) around the early 1980s, which 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_{2009}/B_{MSY}, F_{2008}/F_{MSY}, and Ye_{2009}/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 fluctuations

The time-series analyses showed that analysing monthly landings or CPUEs rendered similar results. Both series showed an increase during the first period (1965–1980) with absence of interannual periodicities, best fitted in all species using a positive exponential function for landings and a negative exponential function for CPUEs. This period ended simultaneously for all species at the beginning of the 1980s, when an interannual oscillatory behaviour became 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 was the seasonal oscillation. This annual cycle, present throughout the entire series of all species, was clearly revealed by the Fourier analysis, and showed 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 overexploited and oscillatory period (1980–2008). For each of the six species investigated, eight GAM models were performed, corresponding to the eight lag times (0–7 years) considered. Model selection and outputs of all these 48 models (8 lags × 6 species) are displayed in 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 26–33%. 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 has been synchronously affected by the combined effect of fishing exploitation and environment variability during the last forty-four years. Such a synchronic effect has been twofold. First, the fact
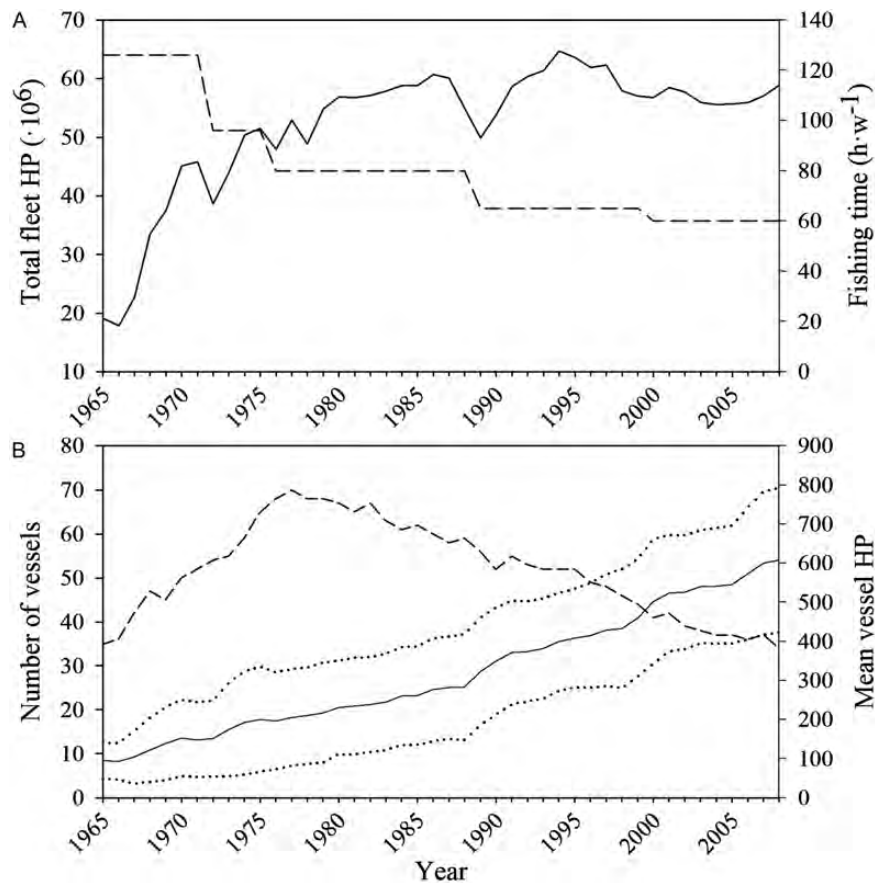
Figure 2. (**A**) Annual horse power (HP) (continuous line) of the entire bottom trawl fleet of Mallorca (Balearic Islands, western Mediterranean) and fishing time at sea (in hours per week, h·w^{-1}) (stippled line) permitted by different regulations throughout the time-series 1965–2008. (**B**) Total number of vessels (stippled line) along with mean and standard deviation (continuous and dotted lines, respectively) of mean vessel HP during the same time-series.

that all the species here studied became overexploited (i.e. $B/B_{MSY} < 1$) around the early 1980s seems unlikely to be an exclusive effect of fishing. We hereafter discuss how changes in the Mediterranean hydroclimate in the early 1980s could have contributed to synchronizing the changes observed. And second, by turning to an overexploited state, populations seem to have been more susceptible to environmental variability (Perry *et al.*, 2010; Planque *et al.*, 2010), displaying synchronic fluctuations in the population biomass.

The six species analysed followed a general trend characterized by an early period of underexploitation that shifted to overexploitation in the early 1980s. This community shift affected the population dynamics of all the species, since their landings and CPUEs showed an increasing trend during the underexploitation phase (1965–1980) but an oscillatory behaviour during the overexploitation phase (1980–2008). These natural fluctuations, however, would have been 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 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) seems to have had the major effect of

sudden depletion. However, growing evidence shows that the hydroclimate of the northwest Mediterranean also changed suddenly, around the early 1980s, to an overall dominance of higher temperatures and atmospheric pressure, and weaker wind stress and precipitation (Fernandez de Puelles and Molinero, 2007, 2008; Molinero *et al.*, 2009; Conversi *et al.*, 2010). These changes in the hydrography influenced the seasonal and interannual plankton dynamics around the Balearic Islands (Fernandez de Puelles and Molinero, 2007, 2008) that could have affected the survival of early life stages of exploited species, and, in turn, synergistically magnified 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
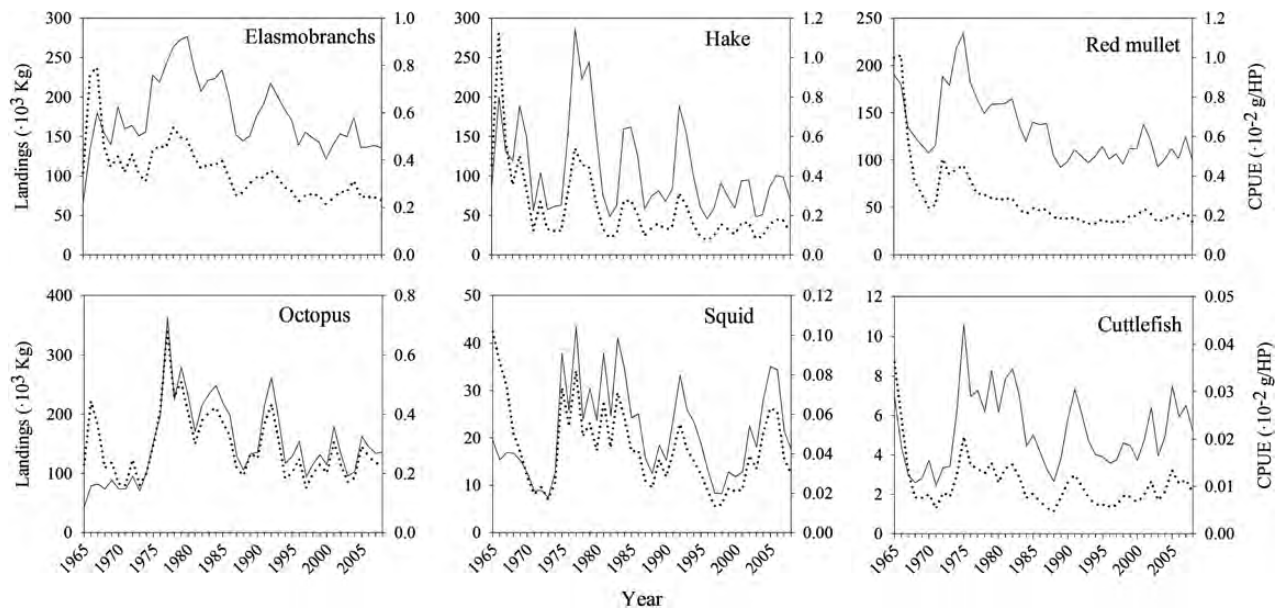
Figure 3. Landings (continuous line) and catch per unit effort (CPUE) (dotted line) of six demersal species caught by the bottom trawl fleet off Mallorca (Balearic Islands, western Mediterranean) during the period from 1965 to 2008.
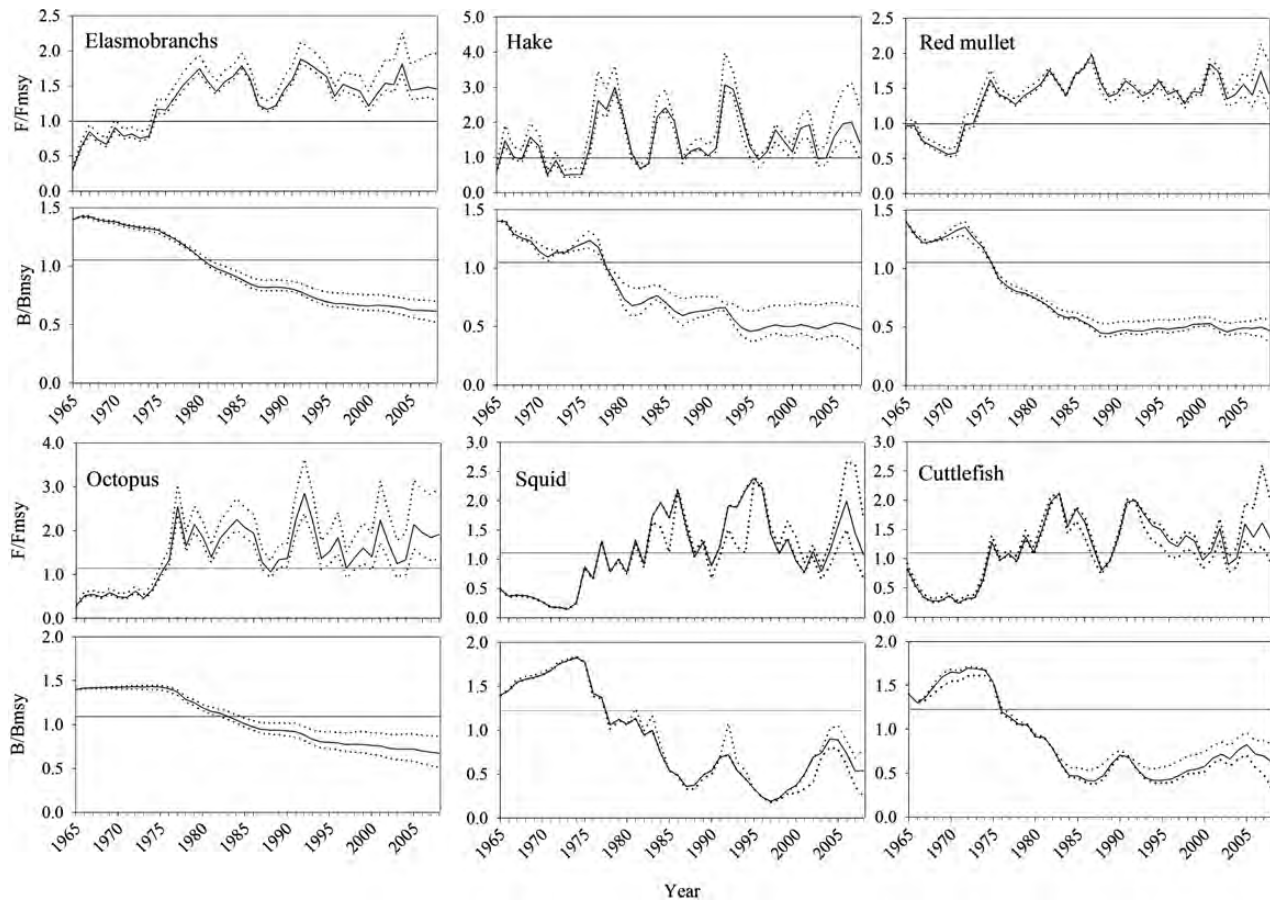

Figure 4. Time trajectories of the relative fishing mortality rate (F/F_{MSY}) and relative population biomass (B/B_{MSY}) estimated using non-equilibrium surplus production models for six different demersal species from Mallorca (Balearic Islands, western Mediterranean) under the assumption $B_1/K = 0.7$. Dotted lines are 80% bias-corrected confidence intervals from bootstrapping.
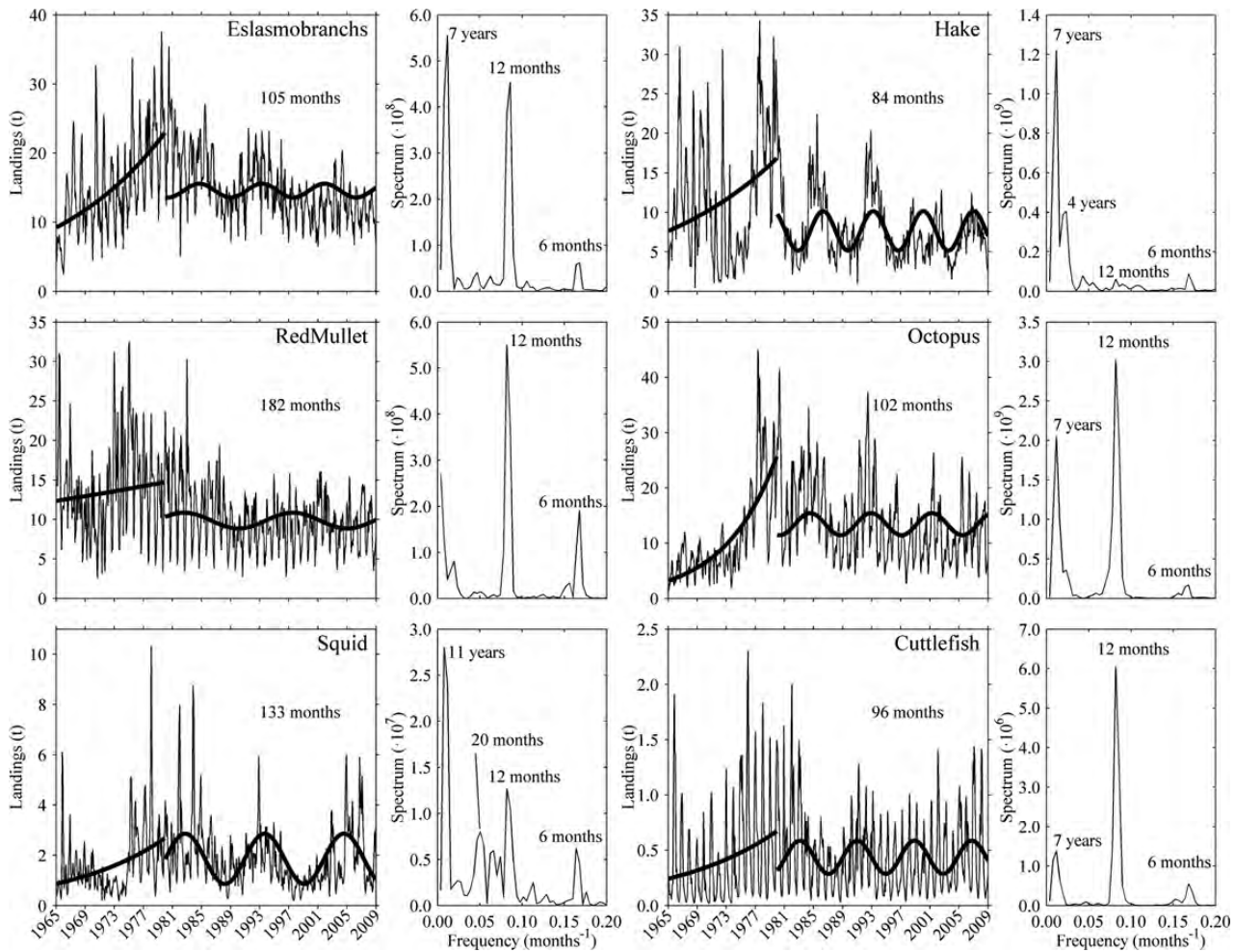
Figure 5. Spectrum analysis and least squares fitting to the monthly data (landings) of six demersal species caught by the bottom trawl fleet off Mallorca (Balearic Islands, western Mediterranean) during the period from 1965 to 2008. The best fit to the data is shown superimposed on the landings: an 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.

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 an independent variable.

	Elasmobranch	Hake	Red mullet	Octopus	Cuttlefish
Hake	0.62***				
Red mullet	0.17	−0.13			
Octopus	0.61***	0.60***	0.14		
Cuttlefish	0.39*	−0.02	0.30	0.61***	
Squid	0.50***	0.25	0.15	0.62***	0.57***

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.
*$p < 0.05$; **$p < 0.005$; $p < 0.001$.

due to the elevated variability of recruitment and the increased sensitivity to environmental variability resulting from the demographic truncation caused by fishery exploitation (Hsieh *et al.*, 2006; Anderson *et al.*, 2008).

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 analysed (red mullet, octopus, squid, and cuttlefish). Identical responses in these four species (Figure 5) point to an ENSO signal in some Mediterranean marine populations. This signal might, in fact, interact with, or have masking effects on, other influences such as the NAO, which has displayed a multidecadal component of ca. 8 years during recent decades (e.g. Massei *et al.*, 2007 and references therein), close to the periodicity found in most of our time-series (7 years). 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 rainfall (e.g. Mariotti *et al.*, 2002). Recent evidence also demonstrated the influence of ENSO variability on Mediterranean hydrographical

Table 2. Results of generalized linear models (GAMs) fitting the abundance indices 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.

Species	Lag time (years)	IDEA	NAO	ENSO	DE (%)
Red mullet	6	n.s.	n.s.	0.024	26.0
Octopus	6	n.s.	n.s.	0.008	33.3
Squid	5	n.s.	n.s.	0.011	30.3
	6	n.s.	n.s.	0.013	30.2
Cuttlefish	0	n.s.	n.s.	0.052	16.8
	6	n.s.	n.s.	0.010	31.9
Hake	2	n.s.	0.022	n.s.	25.5
	5	n.s.	0.065	n.s.	18.7
	7	0.030	n.s.	n.s.	38.5
Elasmobranch	2	0.043	n.s.	n.s.	19.2

$*p < 0.05$, $**p < 0.005$, $***p < 0.001$, n.s. = non-significant.
The following indices of increasing spatial scale were used: the IDEA index, the North Atlantic Oscillation (NAO) and the 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).

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 are those inhabiting the shallow continental shelf, they should be more influenced by the interannual dynamics of zooplankton affecting prey–predator relationships and survival of early life stages. Links between ENSO and coastal species outside the Mediterranean are not new and have been reported for other organisms worldwide (Urban *et al.*, 2000; Rimbu *et al.*, 2003).

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-year lag of the ENSO effect on the population biomass of the four continental shelf species is a striking result of our study (but see, Gonzalez-Herraiz *et al.*, 2009; Zimmerman and Palo, 2012). 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 have not taken 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 consecutive years due to the relative good level of 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 have shown that variability in recruitment increases with fishing and becomes 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.*, 1999,

2004) and has been recently suggested for hake in the Balearic Islands (Hidalgo *et al.*, 2011). 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 the hypothesis 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 elasmobranch species have a broader age structure and longer life span compared with squid, cuttlefish, and 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 population fluctuations are likely to be more affected by climate variability. It is worth noting 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 CPUE data with age-structure (stage-structure) information for assessment groups that will allow investigation as to whether and how climate can affect the same species through several demographic processes.

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

Supplementary Data
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.

Acknowledgements

Funding

References

Abraham, B., and Ledolter, J. 1983. Statistical Methods for Forecasting. John Wiley and Sons, New York. 445 pp.

Anderson, C. N. K., Hsieh, C. H., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M., et al. 2008. Why fishing magnifies fluctuations in fish abundance. Nature, 452: 835–839.

Astudillo, A., and Caddy, J. F. 1986. Periodicidad de los desembarcos de merluza (*Merluccius merluccius*) y salmonete (*Mullus* sp.) en la isla de Mallorca. International Symposium on Long Term Changes in Marine Fish Populations, 221–234.

Baumgartner, T. R., Soutar, A., and Ferreirabartrina, V. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past 2 millennia from sediments of the Santa-Barbara Basin, California. California Cooperative Oceanic Fisheries Investigations Reports, 33: 24–40.

Bjornstad, O. N., Fromentin, J. M., Stenseth, N. C., and Gjosaeter, J. 1999. Cycles and trends in cod populations. Proceedings of the National Academy of Sciences of the United States of America, 96: 5066–5071.

Bjornstad, O. N., and Grenfell, B. T. 2001. Noisy clockwork: time series analysis of population fluctuations in animals. Science, 293: 638–643.

Bjornstad, O. N., Nisbet, R. M., and Fromentin, J. M. 2004. Trends and cohort resonant effects in age-structured populations. Journal of Animal Ecology, 73: 1157–1167.

Bloomfield, P., 1976. Fourier Analysis of Time Series: An Introduction. John Wiley and Sons, Inc., New York. 258 pp.

Botsford, L. W., Holland, M. D., Samhouri, J. F., White, J., and Hastings, A. 2011. Importance of age structure in models of the response of upper trophic levels to fishing and climate change. ICES Journal of Marine Science, 68: 1270–1283.

Calvo, E., Simo, R., Coma, R., Ribes, M., Pascual, J., Sabates, A., Gili, J.M., et al. 2011. Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. Climate Research, 50: 1–29.

Carbonell, A., Carbonell, M., Demestre, M., Grau, A., and Monserrat, S. 1999. The red shrimp *Aristeus antennatus* (Risso, 1816) fishery and biology in the Balearic Islands, Western Mediterranean. Fisheries Research, 44: 1–14.

Coll, M., Lotze, H. K., and Romanuk, T. N. 2008. Structural degradation in Mediterranean Sea food webs: testing ecological hypotheses using stochastic and mass-balance modelling. Ecosystems, 11: 939–960.

Colloca, F., Cardinale, M., Maynou, F., Giannoulaki, M., Scarcella, G., Jenko, K., Bellido, J.M., et al. 2011. Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. Fish and Fisheries, doi: 10.1111/j.1467-2979.2011.00453.x.

Conversi, A., Fonda Umani, S., Peluso, T., Molinero, J. C., Santojanni, A., and Edwards, M. 2010. The Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallelisms with other European basins. Plos One, 5: e10633.

Fernandez de Puelles, M. L., and Molinero, J. C. 2007. North Atlantic climate control on plankton variability in the Balearic Sea, western Mediterranean. Geophysical Research Letters, 34: L04608, doi:10.1029/2006GL028354.

Fernandez de Puelles, M. L., and Molinero, J. C. 2008. Decadal changes in hydrographic and ecological time-series in the Balearic Sea (western Mediterranean), identifying links between climate and zooplankton. ICES Journal of Marine Science, 65: 311–317.

Gonzalez Herraiz, I., Torres, M., Farina, A., Freire, J., and Cancelo, J. 2009. The NAO index and the long-term variability of *Nephrops*

norvegicus population and fishery off West of Ireland. Fisheries Research, 98: 1–7.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., et al. 2008. A global map of human impact on marine ecosystems. Science, 319: 948–952.

Hertig, E., and Jacobeit, J. 2011. Predictability of Mediterranean climate variables from oceanic variability. Part II: Statistical models for monthly precipitation and temperature in the Mediterranean area. Climate Dynamics, 36: 825–843.

Hidalgo, M., Massutí, E., Guijarro, B., Moranta, J., Ciannelli, L., Lloret, J., Oliver, P., et al. 2009. Population effects and changes in life history traits in relation to phase 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.

Hidalgo, M., Rouyer, T., Molinero, J., Massutí, E., Moranta, J., Guijarro, B., and Stenseth, N. 2011. Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. Marine Ecology-Progress Series, 426: 1–U18.

Hsieh, C. H., Chen, C. S., Chiu, T. S., Lee, K. T., Shieh, F. J., Pan, J. Y., and Lee, M. A. 2009. Time series analyses reveal transient relationships between abundance of larval anchovy and environmental variables in the coastal waters southwest of Taiwan. Fisheries Oceanography, 18: 102–117.

Hsieh, C. H., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., and Sugihara, G. 2006. Fishing elevates variability in the abundance of exploited species. Nature, 443: 859–862.

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

Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C. F., and Pérez, T. 2010. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends in Ecology & Evolution, 25: 250–260.

Lloret, J., Lleonart, J., Sole, I., and Fromentin, J. M. 2001. Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. Fisheries Oceanography, 10: 33–50.

Mariotti, A., Zeng, N., and Lau, K. M. 2002. Euro-Mediterranean rainfall and ENSO, a seasonally varying relationship. Geophysical Research Letters, 29: 591–594.

Massei, N., Durand, A., Deloffre, J., Dupont, J., Valdes, D., and Laignel, B. 2007. Investigating possible links between the North Atlantic Oscillation and rainfall variability in northwestern France over the past 35 years. Journal of Geophysical Research-Atmospheres, 112: D09121.

Massutí, E., Monserrat, S., Oliver, P., Moranta, J., Lopez-Jurado, J. L., Marcos, M., Hidalgo, M., et al. 2008. The influence of oceanographic scenarios on the population dynamics of demersal resources in the western Mediterranean: Hypothesis for hake and red shrimp off Balearic Islands. Journal of Marine Systems, 71: 421–438.

Massutí, E., and Moranta, J. 2003. Demersal assemblages and depth distribution of elasmobranchs from the continental shelf and slope off the Balearic Islands (western Mediterranean). ICES Journal of Marine Science 60, 753–766.

Maynou, F. 2008a. Environmental causes of the fluctuations of red shrimp (*Aristeus antennatus*) landings in the Catalan Sea. Journal of Marine Systems, 71: 294–302.

Maynou, F. 2008b. Influence of the North Atlantic Oscillation on Mediterranean deep-sea shrimp landings. Climate Research, 36: 253–257.

Molinero, J., Vukanic, V., Lucic, D., Ibanez, F., Nival, P., Licandro, P., Calbet, A., et al. 2009. Mediterranean marine copepods: basin-scale trends of the calanoid *Centropages typicus*. Hydrobiologia, 617: 41–53.

Monserrat, S., Lopez-Jurado, J. L., and Marcos, M. 2008. A mesoscale index to describe the regional circulation around the Balearic Islands. Journal of Marine Systems, 71: 413–420.

Moranta, J., Quetglas, A., Massutí, E., Guijarro, B., Ordines, F., and Valls, M. 2008. Research trends on demersal fisheries oceanography in the Mediterranean. *In* Biological Oceanography Research Trends, pp. 9–65. Ed. by L. P. Mertens. Nova Science Publishers, Inc., New York.

Oliver, P. 1993. Analysis of fluctuations observed in the trawl fleet landings of the Balearic Islands. Scientia Marina, 57: 219–227.

Ottersen, G., Stenseth, N. C., and Hurrell, J. W. 2004. Climatic fluctuations and marine systems: a general introduction to the ecological effects. *In* Marine ecosystems and climate variation, pp. 3–14. Ed. by G. Ottersen, N. C. Stenseth, and J. W. Hurrell. Oxford University Press, Oxford, UK. 252 pp.

Overland, J. E., Alheit, J., Bakun, A., Hurrell, J. W., Mackas, D. L., and Miller, A. J. 2010. Climate controls on marine ecosystems and fish populations. Journal of Marine Systems, 79: 305–315.

Perry, R. I., Cury, P., Brander, K., Jennings, S., Moellmann, C., and Planque, B. 2010. Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. Journal of Marine Systems, 79: 427–435.

Planque, B., Fromentin, J. M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I, and Kifani, S. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? Journal of Marine Systems, 79: 403–417.

Prager, M. H. 2004. Uséŕs manual for ASPIC: a stock-production model incorporating covariates (ver. 5) and auxiliary programs. National Marine Fisheries Service, Beaufort Laboratory Document BL-2004-01: 1–27.

Pyper, B. J., and Peterman, R. M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data.

Canadian Journal of Fisheries and Aquatic Sciences, 55: 2127–2140.

Quetglas, A., Alemany, F., Carbonell, A., Merella, P., and Sanchez, P. 1998. Biology and fishery of *Octopus vulgaris* Cuvier, 1797, caught by trawlers in Mallorca (Balearic Sea, western Mediterranean). Fisheries Research, 36: 237–249.

Ravier, C., and Fromentin, J. M. 2001. Long-term fluctuations in the eastern Atlantic and Mediterranean bluefin tuna population. ICES Journal of Marine Science, 58: 1299–1317.

Rimbu, N., Lohmann, G., Felis, T., and Patzold, J. 2003. Shift in ENSO teleconnections recorded by a northern Red Sea coral. Journal of Climate, 16: 1414–1422.

Rouyer, T., Ottersen, G., Durant, J. M., Hidalgo, M., Hjermann, D. O., Persson, J., Stige, L. C., *et al.* 2011. Shifting dynamic forces in fish stock fluctuations triggered by age truncation? Global Change Biology, 17: 3046–3057.

Tzeng, W. N., Tseng, Y. H., Han, Y. S., Hsu, C. C., Chang, C. W., Di Lorenzo, E., and Hsieh, C. H. 2012. Evaluation of multi-scale climate effects on annual recruitment levels of the Japanese Eel, *Anguilla japonica*, to Taiwan. Plos One, 7: e30805.

Urban, F. E., Cole, J. E., and Overpeck, J. T. 2000. Influence of mean climate change on climate variability from a 155-year tropical Pacific coral record. Nature, 407: 989–993.

Wood, S. N. 2001. mgcv: GAMs and Generalized Ridge Regression for R. R News, 1: 20–25.

Zimmerman, J. K. M., and Palo, R. T. 2012. Time series analysis of climate-related factors and their impact on a red-listed noble crayfish population in northern Sweden. Freshwater Biology, 57: 1031–1041.

Handling editor: Howard Browman