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.

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**

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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/): 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 Jacobeit, 2011).

Fishing exploitation

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_{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 over-exploitation state while $B/B_{MSY}>1$ and $F/F_{MSY}<1$ 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_1/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_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's fluctuations

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

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165   two distinct periods for all species with different variance in the fluctuations, already reported in

166   previous studies (Hidalgo *et al.*, 2009; Massutí *et al.*, 2008): a period with increasing landings from

167   1965 to 1980, followed by a period with interannual oscillatory behaviour from 1980 to 2008.

168   Therefore, the two time periods were treated differently. Preliminary analyses of the first period do

169   not reveal any clear periodicity and non-linear regressions were fitted by means of the least squares

170   method. The period from 1980 to 2008 was first analyzed using a classical Fourier analysis to

171   obtain the relative importance of the different frequencies present in the time series. Given that the

172   time series is rather short and the frequency resolution achieved with a Fourier transform too low to

173   quantify interannual oscillations, least squares fittings were used to better quantify the interannual

174   variability observed in the time series. A function of the form

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

176   was used (Bloomfield, 1976), where ω is the frequency of the series searched for, $\bar{x}$ is the mean of

177   the catch data and A and B are as follows

178
$$A = \frac{2}{n}\sum_{n=1}^{t}(x_t - \bar{x})\cos(\omega t), \tag{2}$$

179
$$B = \frac{2}{n}\sum_{n=1}^{t}(x_t - \bar{x})\sin(\omega t), \tag{3}$$

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

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182   **Climate effects**

183   Climate effects on the population dynamics of the six stockswere investigated by means of

184   Generalized Additive Models (GAMs). As a previous step to the GAM analyses, which bear the

185   implicit assumption of additivity (covariates are mutually independent), we checked the lack of

186   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; Massutí *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/) 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.

213   **Results**

214   During the period from 1965 to 2008, the bottom trawl fishery off Mallorca showed large

215   variations in the number of vessels, mean engine power and the fishing time at sea (Fig. 2). Three

216   main phases can be distinguished in the evolution of the total fleet fishing effort over time: 1) from

217   1965 to the mid 1970s it increased by a factor of 2.5; 2) from the mid 1970s to 1994 it continued to

218   grow but at a slower rate; and 3) from 1994 to the present it has gradually decreased. Consistently

219   for all species, time series of landings showed a marked increase during the late 1970s that was

220   followed by a progressive decrease comparatively less pronounced for squid and cuttlefish (Fig. 3).

221   Although with some exceptions, occurring mainly during the first years of the time series, annual

222   CPUEs followed the same general pattern as the landings.

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224   **Fishing exploitation**

225   The evolution of the relative fishing mortality (F/F_{MSY}) and biomass (B/B_{MSY}) throughout the time

226   series showed a similar trend for all species (Fig. 4). From the beginning of the series to the mid

227   1970s the stocks were under-exploited, since the fishing effort was lower than the fishing effort that

228   should be exerted to attain the maximum sustainable yield ($F/F_{MSY}<1$); consequently, the stocks'

229   biomass was higher than the expected biomass at MSY ($B/B_{MSY}>1$). All the species turned to an

230   over-exploited state (i.e., $B/B_{MSY}<1$ and $F/F_{MSY}>1$) around the early 1980s that continues to the

231   present day. Although estimates of exploitation status of stocks expressed in relative terms were

232   very similar for all the species studied (Supplementary Table S1), two main groups could be

233   distinguished. The first group contained the two target species of the trawl fishery, red mullet and

234   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

235   respectively. The second group included the by-catch species (elasmobranchs, octopus, squid and

236   cuttlefish), whose central estimates for the same three parameters were 0.61-0.66, 1.08-1.58, and

237   0.85-0.89 respectively.

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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

265 model showed a significant positive effect of the ENSO index at a lag time of 6 years. The variance

266 explained for these four models ranged from 26 to 33%. The two remaining species only showed

267 significant effects of the NAO (hake at lag times of 2 and 5 years) and IDEA (hake and

268 elasmobranchs at lag times of 7 and 2 years, respectively) indexes.

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Discussion

271 This study showed that the population dynamics of the main commercial species of the demersal

272 community off the Balearic Islands was synchronously affected by the combined effect of fishing

273 exploitation and the environment variability during the last forty-four years. Such a synchronic

274 effect was twofold. First, the fact that all the species here studied turned to over-exploited (i.e.,

275 $B/B_{MSY}<1$) around the early 1980s seems to be unlikely an exclusive effect of fishing. We hereafter

276 discuss how changes in the Mediterranean hydroclimate in the early 1980s could contribute to

277 synchronize the changes observed. And second, by turning to an over-exploited state, populations

278 seemed to be more dependent on the environmental variability (Planque *et al.*, 2010; Perry *et al.*,

279 2010) displaying synchronic fluctuations on the population biomass.

280 The six species analysed followed a general trend characterized by an early period of

281 under-exploitation that shifted to over-exploitation in early 1980s. This community shift affected

282 the population dynamics of all the species, since their landings and CPUEs showed an increasing

283 trend during the under-exploitation phase (1965-1980) but an oscillatory behaviour during the over-

284 exploitation phase (1980-2008). These natural fluctuations, however, would be masked during the

285 first part of the series, when landings displayed an exponential growth due to the rapid increase in

286 fishing effort. Therefore, our results would indicate a phase-transition event in the population

287 dynamics of demersal stocks from the Balearic Islands in 1980, a scenario already reported for

288 hake in this area (Hidalgo *et al.*, 2009). The rapid increase in the exploitation rate observed during

289 the previous years (namely, it increased 2.5 times during 1965-1977) seemed to have a major effect

290 on the sudden depletion. However, growing evidence showed that the hydroclimate of the NW

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291 Mediterranean also suddenly changed around the early 1980s to an overall dominance of higher

292 temperatures and atmospheric pressure, and weaker wind stress and precipitation (Conversi *et al.*,

293 2010; Fernandez de Puelles and Molinero, 2007, 2008; Molinero *et al.*, 2009). These changes in the

294 hydrography influenced the seasonal and inter-annual plankton dynamics around the Balearic

295 Islands (Fernandez de Puelles and Molinero, 2007, 2008) that could affect the survival of early life

296 stages of exploited species, and, in turn, synergistically magnify the effect of fishing (Hidalgo *et*

297 *al.*, 2011).

298 Fluctuations in landings of demersal species in the western Mediterranean are well documented.

299 Astudillo and Caddy (1986) found a marked periodicity of 12 years in the landings of hake and red

300 mullet from the Balearic Islands, which they hypothesized to be independent of fleet activity. In the

301 same area, a periodicity of about 8 years was reported for octopus (Quetglas *et al.*, 1998) and red

302 shrimp (Carbonell *et al.*, 1999). In a nearby area, however, fluctuations in red shrimp landings

303 ranged between 7 and 13 years among different ports (Maynou, 2008a). Our results showed

304 interannual oscillations with a periodicity of 7-9 years in the last three decades for four out of the

305 six species investigated. There is increasing evidence that harvested species fluctuate more than

306 unharvested ones, which is probably due to the elevated variability of recruitment and the increased

307 sensitivity to the environmental variability resulting from the demographic truncation caused by

308 fishery exploitation (Anderson *et al.*, 2008; Hsieh *et al.*, 2006).

309 To determine whether the causes of the interannual fluctuations in CPUEs were linked to

310 climatic variability, climate indices at increasing spatial scales (local, meso-, and global-scale)

311 were examined. NAO and IDEA showed significant effects on the elasmobranches and hake

312 consistent with previous studies (Massutí et al 2008). Unexpectedly, however, our models found

313 much support for an effect of ENSO with a lag time of 6 years for four out of the six species

314 analyzed (red mullet, octopus, squid and cuttlefish). Identical responses in these four species (Fig.

315 5) points to an ENSO signal on some Mediterranean marine populations. **This signal might, in**

316 **fact, interact with, or have masking effects on, other influences such as the NAO, which**

317 **displayed a multidecadal component of ca. 8 years during the last decades (e.g. Massei et al.**

318   **2007 and references therein) close to the periodicity found in most of our time series (7 years).**

319   Indeed, the interaction between North Atlantic climate (i.e. NAO) and Pacific modes (i.e. ENSO)

320   has been shown to affect the Mediterranean climate through the rainfall (e.g. Mariotti *et al.*, 2002).

321   Recent evidences also demonstrated the influence of ENSO variability on the Mediterranean

322   hydrographical characteristics, particularly on the sea surface temperature (Hertig and Jacobeit,

323   2011). In the Balearic Islands, rainfall and sea surface temperature variability strongly affect the

324   nutrients, phytoplankton and zooplankton variability (Fernandez de Puelles and Molinero, 2007,

325   2008). Since the species displaying a close link with ENSO were those inhabiting on the shallow

326   continental shelf, they should be more influenced by the inter-annual dynamics of zooplankton

327   affecting the prey-predator relationships and survival of the early life stages. Links between ENSO

328   and coastal species outside the Mediterranean are not new and have been reported for other

329   organisms worldwide (Rimbu *et al.*, 2003; Urban *et al.*, 2000).

330   Though a time lag between the climatic and the biological signal was expected (e.g. Ottersen *et*

331   *al.*, 2004; Overland *et al.*, 2010), the 6 years lag of the ENSO effect on the population biomass of

332   the four continental shelf species is likely the more striking result of our study (but see,

333   Zimmerman and Palo, 2012; Gonzalez-Herraiz *et al.*, 2009). Since the ENSO signal on the

334   Mediterranean hydroclimate is transmitted within some months (Hertig and Jacobeit, 2011), there

335   must be additional factors modulating the population fluctuations that we did not take into account

336   in our study. We suggest that internal properties of the life cycle of these species can interact with

337   the climate signal, which makes plausible potential inter-cohort and density-dependent effects

338   (Bjornstad and Grenfell, 2001). Favourable climatic events can produce strong annual cohorts,

339   favouring the recruitment in the consecutive years due to the relative good level of the reproductive

340   stock. This could magnify the climatic signal in the next generations and thus bring forth

341   population cycles (Tzeng *et al.*, 2012) that could explain the lagged oscillatory response observed.

342   Recent studies on species with a broad demographic structure show that variability in recruitment

343   increased with fishing and became particularly sensitive to forcing at time-scales near the mean age

344   of reproduction (Botsford *et al.*, 2011). This is consistent with the cohort resonance effect

345   (Bjornstad *et al.*, 2004; Bjornstad *et al.*, 1999) and has been recently suggested for hake in the

346 Balearic Islands (Hidalgo *et al.*, 2011). Our study adds to this picture of how species of the same

347 harvested community with different life history and demographic structure cope with

348 environmental variability. Our results support that population fluctuations result from the

349 interaction of deterministic and stochastic processes (Bjornstad and Grenfell, 2001), while the

350 relative contribution of each component depends on the life history and demographic structure of

351 the species. Hake, red mullet and elasmobranches species have a broader age structure and longer

352 life span compared to squid, cuttlefish or octopus, and thus deterministic mechanisms (e.g., internal

353 demographic processes) may have higher impact on population fluctuations. By contrast,

354 cephalopods display a narrow age structure, fast life cycle and short life span, and thus the

355 population fluctuations are likely more affected by climate variability. **It is worth noticing that**

356 **our results suggest potential effects of the same climatic phenomena at different temporal**

357 **lags that may be further evaluated in a unique model structure for each species, as well as**

358 **potential interactions among the different climatic indices. Future studies should tackle this**

359 **challenge combining long term information of CPUEs with age(stage)-structure information**

360 **from assessment groups that will allow to investigate whether and how climate can affect the**

361 **same species through several demographic processes.**

362 To conclude, our results demonstrate that the interaction between fishing and climate can

363 have synchronic effects on the population fluctuations of different species within an overexploited

364 community. An intense fishing exploitation might increase the susceptibility, and therefore reduce

365 the resilience, of harvested populations to climate variability (Botsford *et al.*, 2011). We also

366 showed that, as a consequence of this increased susceptibility, populations might also increase their

367 sensitivity to subtle climate signals that could previously be masked by more influential factors.

368 Our study expands this conclusion to the community scale and highlights that species sensitivity to

369 climate and thus population fluctuations depend on the demographic characteristics, life history and

370 bathymetric distribution of each species.

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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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528

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

533

	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^{***}

534 *p<0.05; **p<0.005; p<0.001

535

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

544

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

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

546

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, $h \cdot w^{-1}$) 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 $B_1/K=0.7$. Dotted lines are 80% bias-corrected confidence intervals from bootstrapping.

Figure 5. Spectrum analysis and least squares fitting to the monthly data (landings 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).