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Non-stationary synchrony and asynchrony in the deep sea driven by climate variability and populations spatial structure

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Summary
Spatial synchrony in population size changes is often referred as a time-invariant process, although it shows non-stationary dynamics driven by compound effects of ecological and environmental mechanisms. Understanding these interactions is particularly relevant for species whose population dynamics is little known such as those inhabiting the deep sea. We here address this question by using monthly abundance data over the period 2000-2010 of a deep-sea harvested species in the Mediterranean Sea, the red shrimp *Aristeus antennatus*. We investigated two subpopulations in the Mediterranean that contrast in the complexity of the spatial structure. We show evidence on the non-stationary seasonal synchrony and asynchrony, which are shaped by a varying contribution of external (climate) and internal drivers (demography and life history) at each subpopulation. We also show that the subpopulation with larger spatial complexity displayed seasonal synchronic fluctuations dependent on the local dynamics. By contrast, in the subpopulation with a low level of complexity, climatic variability triggered a trade-off between synchronic and asynchronic behaviour. We argue that climate influences the regional environment and spatially drives the phenology of primary producers, thereby modifying the timing of food advection from upper layers to benthic communities. These cascading links ultimately shape the temporal synchrony of broad distributed deep-sea populations.

Introduction
Synchronous ecological processes among spaced populations occur in a variety of taxa and are often used to understand space-time abundance changes (Liehold et al. 2004). Intra-specific synchrony is mainly ascribed to environmental variability, dispersal and connectivity processes among populations or population subunits, and ecological interactions with other species. Much attention has been devoted to identify the aforementioned factors, though few studies have addressed non-stationary processes underlying the time-varying strength of synchrony (but see Kelly et al. 2009). This remains a challenging endeavour in fisheries ecology because fishing can either magnify or buffer the synchronous signal in harvested populations depending on the contribution of mechanisms leading to synchrony. In the Mediterranean Sea, the relative young deep-sea fisheries is already threatening several species with the red shrimp (*Aristeus antennatus*) as one of the more relevant examples of the deep Mediterranean ecosystem. Here, we investigate the non-stationary pattern of a/synchrony of two red shrimp subpopulations inhabiting different areas in the NW Mediterranean and displaying contrasting complexity in spatial structure. Our objective is to evaluate the relative contribution of drivers determining temporal variation of a/synchrony: 1) the role of the Atlantic climate as potential large scale driver of seasonal a/synchrony of the species, and 2) the extent to which variations in the degree of synchrony are controlled by changes in the demographic structure, including a potential eroding effect of fishing.

Material and Methods
We used daily landings of red shrimp from all boats and fishing ports in Catalonian coast (CA) and Mallorca (MA, in the Balearic Islands) for the period from 2000 to 2010 to calculate monthly CPUEs. CA and MA are two contrasting systems within the general oligotrophy of the NW Mediterranean. CA is a highly productive system at seasonal scale and is characterized by the presence of submarine canyons, which are pathways channelling advective inputs of productivity from the shelf (Sardà et al. 2009). By contrast, MA displays a lack of canyons and a pronounced oligotrophy due to the lack of nutrient supply from continental runoff or vertical mixing, while with reported influence intermediate- and deep-water circulation on red shrimp population (Massutí et al. 2008). To investigated the non-

stationary link between North Atlantic climate and the regional hydroclimatic variability as a potential factor affecting synchrony, we correlate the influence of the North Atlantic Oscillation index as a proxy of large-scale climate variability on the monthly variations of hydroclimate conditions at regional scale, updating the approach of Molinero et al. (2005). Our study combines analytical techniques that allow depicting spatiotemporal signals in time series: 1) clustering analyses of wavelet spectra and 2) a time-varying approach of spatial correlograms (i.e. Moran's index *I* profiles).

Results and Discussion

Attending to the non-stationary pattern on the seasonal signal, the cluster of the wavelet spectra obtained for CA shows groups related to the geographical gradient (the northern and southern CA) with the two ports operating in two submarine canyons as non-clustered signals evidencing the independence on the dynamics at each canyon. For MA, the cluster obtained from the wavelet spectra also indentified a geographic pattern with two groups corresponding with the north and the south of the island.

Correlograms applied for the whole period displayed a similar pattern for the two areas with significant positive values observed at short spatial scales (Fig. 1A for CA) due to clustering seasonal dynamics. Significant negative values were observed at larger spatial scales for CA (Fig. 1A) and MA, suggesting a significant phase-shifted pattern of seasonal dynamics. By contrast, the temporal variation of the 24-months moving window correlograms displayed a contrasting pattern for each area. For CA (Fig. 1A), positive *I* values (synchrony) at short spatial scale were found during the early 2000s and progressively disappeared in concomitance with a strengthening pattern of negative *I* values (asynchrony) at large distances. Though, is does not seem to be related with a change in density (Fig. 1B), the correlation between NAO index and the hydroclimatic index at CA was significant, but only for the second period (Fig. 1C) characterized by negative *I* values (Fig. 1A). We argue that during periods of high influence of Atlantic climate on the regional environment, largely separated locations might increase the phase-shifted phenology of primary production. This phenological variation may trigger the marked seasonal asynchrony in spawning habitats of red-shrimp that attempts to maximize favourable trophic conditions during the reproductive season due to the seasonal shift in the phytodetritus sinking. This pattern was not observed at MA.

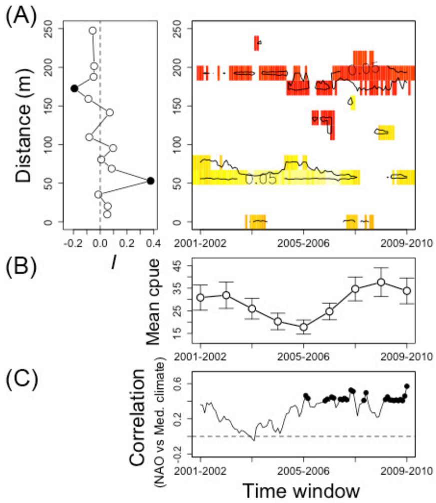

Fig. 1. Non-stationary behaviour of synchrony at CA. (A) Left panel shows the correlogram for the whole period; filled dots represent significant Moran's *I* index. Right colour panel shows a 24-months moving window correlograms with yellow and red colours positive and negative *I* values respectively (only significant values are plotted). (B) 24-months moving averages and standard deviations of the monthly cpue (kg boat^{-1} d^{-1}). (C) 24-months Pearson correlations between monthly NAO index and monthly Mediterranean hydroclimatic index (filled dots are significant values).

We observed influence of spatiotemporal variation in the demography, while it was not related to the effect of fishing. Our study stresses that ecological responses of deep-sea populations to climatic variability encompasses both local and regional scales, which is of paramount importance for the conservation and management of deep-sea ecosystems.

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