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Spatial and temporal variation of seasonal synchrony in the deep-sea shrimp *Aristeus antennatus* in the Western Mediterranean

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ABSTRACT

Resolving drivers of spatial synchrony in marine species is fundamental for the management and conservation of deep-sea ecosystems. Here we examine an 11-year data set of monthly catches per unit of effort (CPUE) of the red-shrimp *Aristeus antennatus*. These data comprise 16 locations of two population subunits in the Western Mediterranean, the Catalan coast and the Balearic archipelago. The analysis of their seasonal covariation and its space–time structure showed small-scale geographical segregation of locations linked with the seasonal fluctuations of CPUE. Results further revealed that seasonal synchrony dominates at short spatial scales (ca. 50 km), while asynchrony prevails are broader spatial scales (ca. 200–300 km). This spatial pattern, however, varied over the period examined, although it was specific for each population subunit suggesting contrasting drivers of seasonal synchrony. The Balearic Islands, a patchier population subunit, displayed a seasonal synchrony pattern mainly dependent on biological and oceanographic processes at local scales. By contrast, in the Catalan coast, the pattern appeared related with regional-scale climate, which triggers spatial differences in the phenology of primary producers and the timing of food advection to the seabed. These cascading processes depicted by our investigation shed light on underlying mechanisms shaping the temporal synchrony of broadly distributed deep-sea populations.

1. Introduction

Spatial synchrony refers to covariation in abundance or time-varying ecological processes of geographically separated populations or demes (see reviews in Bjørnstad et al., 1999; Liebhold et al., 2004). At the intra-specific level, synchrony is mainly ascribed to three non-exclusive primary mechanisms: environmental variability (i.e., Moran effect, Moran, 1950), dispersal and connectivity processes among populations or demes, and ecological interactions with other species. The relative contribution of each mechanism, however, varies along with the spatial scale and the spatial structure of the population. For instance, climate variability is the main driver of synchrony over large areas, as described by Myers et al. (1997), who found concurrent variations in the recruitment of several marine species in the North Atlantic due to the common influence of large-scale environmental variables. By contrast, at smaller spatial scales or in complex populations (e.g., metapopulations) demographic and dispersal processes comparatively appear more relevant (Abbot, 2011). This is commonly observed in coastal populations, where synchronic fluctuations are primarily driven by the strength and efficiency of connectivity processes of early life stages (e.g., Gouhier et al., 2010; Lagos et al., 2007).

To date, much attention has been devoted to identify the aforementioned factors shaping spatial synchrony at inter-annual scales, while little is known about seasonal synchrony patterns and causes. For instance, inter-annual variations of phenology have been broadly investigated in marine systems (e.g., 'match–mismatch' hypothesis), but few studies addressed their spatial synchrony (but see Otero et al., 2014). Life cycles of marine organisms in high latitudes or oligotrophic systems (e.g., Mediterranean Sea) are seasonally adapted to short periods of high productivity, often clustered spatially (D'Ortenzio and d'Alcala, 2009), which subsequently shape the extent of covariation in population responses (e.g., Friedland et al., 2008). In addition, the phenology of primary producers appears as a key element in synchronizing life history events of marine species over large areas in the North Atlantic (e.g., shrimps, Koeller et al., 2009; zooplankton, Batchelder et al., 2012). Hence, seasonality and spatial synchrony should be assessed in a combined manner to resolve interconnections between the physical environment, species life history, and the population dynamics.

Synchrony is often investigated as a time invariant (i.e., stationary) process and attribute of populations. However, it can change with time. To date, only few studies have addressed the causes of the time-varying strength of synchrony (see Kelly et al., 2009; Kilduff et al., 2014; Post and Forchhammer, 2004). For instance, inter-annual changes

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in the phenology of phytoplankton over a large area can alter the way local populations are seasonally synchronized (e.g., Durant et al., 2007; Friedland et al., 2008). Likewise, at inter-annual scales, climate processes (Kilduff et al., 2014) and their influence on local weather (Post and Forchhammer, 2004) can also alter the degree of covariation. Also, fishing impact has been shown to buffer synchronous signals. For instance, the removal or erosion of demes by fishing in metapopulations impairs dispersal pathways, thereby reducing synchrony dependent on dispersal (Ciannelli et al., 2013; Kelly et al., 2009).

Investigating seasonal synchrony may improve the understanding of species with poor knowledge of its spatiotemporal dynamics. This is particularly true for deep-sea species that lack reliable or continuous temporal and spatial population sampling (Gordon, 2001; Herring, 2002). This work is crucial for deep-sea species that have experience a dramatic increase in exploitation in recent decades (Villasante et al., 2012). Hence, there is a pressing need to understand and quantify ecological processes driving deep-sea exploited populations given current limitations. In the Mediterranean Sea, the red shrimp (*Aristeus antennatus*) is a deep-sea species of high ecological and economic importance, particularly in the Western basin (Sardà et al., 2003; WWF/IUCN., 2004). At the inter-annual scale, abundance covariation has been observed in geographically distant spawning locations of this species in the Catalan coast (northwest Mediterranean Sea, Maynou, 2008a, 2008b). This was mainly attributed to two non-exclusive processes: the variation in the food advection from upper layers to seabed spawning aggregations (Cartes et al., 2009), and the formation of dense shelf waters and their subsequent downslope cascade through submarine canyons that negatively affect the occurrence and distribution of the species (i.e., cascading events, Company et al., 2008). However, the red shrimp also displays regular seasonal variations, although the seasonal synchrony of the species across geographical gradients remains unknown. Resolving these processes may reveal spatial associations relevant for management purposes, as well as additional drivers shaping the seasonal spatiotemporal dynamics of the species.

The main goal of the present study is to investigate the seasonal synchrony of the deep-sea red shrimp *A. antennatus* in the northwest Mediterranean Sea. We also hypothesize that the strength of seasonal synchrony between locations where the species is harvested varies along with the spatial structure of the population at inter-annual scales. To tackle this question, we use spatial information of monthly catches per unit of effort (CPUE) from 2000 to 2010 to compare two differentiated red shrimp population subunits inhabiting different areas in the NW Mediterranean (Catalan coast and Mallorca Island, see Methods and Fig. 1a). The two subunits are part of a complex metapopulation (Fernández et al., 2011; Sardà et al., 2010) but they display contrasting characteristics in spatial structure, as well as in the demographic and biological characteristics (Guijarro et al., 2008; Quetglas et al., 2012). Our study has three objectives: i) to identify small-scale patterns of seasonal synchrony at each population subunit, ii) to detect non-stationary patterns investigating temporal variation in the strength of seasonal synchrony and iii) to assess the role of local demography and climate in the covariation pattern across each population subunit.

2. Methods

2.1. Two contrasting systems

The red shrimp from Catalan coast (CA) (Sardà et al., 2004) and Mallorca Island (MA) (Guijarro et al., 2008) shares a common spawning season (i.e., summer, mainly from June to August), but these regions differ in ecosystem structure and function providing a 'natural experiment' to investigate contrasting mechanisms influencing the spatial synchrony in this species in the Western Mediterranean. CA is a high productive region due to the influence of climate on winter mesoscale processes, such as runoff and vertical mixing particularly in the Gulf of Lions, that increase productivity (D'Ortenzio and d'Alcala, 2009; Lloret et al., 2001). Submarine canyons at Palamós and Blanes are prominent bathymetric features marking discontinuities in the spatial continuity of the CA region (Fig. 1a). These canyons are important pathways channelling advective inputs of productivity from the shelf (Fig. 1a) (Canals et al., 2009), and have specific currents systems that favour the occurrence of red shrimp (Sardà et al., 2009). By contrast, MA is comparatively more oligotrophic lacking nutrient input from continental runoff or vertical mixing (Estrada, 1996). Recent studies showed that inter-annual variations of intermediate- and deep-water circulation in terms of termohaline characteristics and water masses occupancy affect red shrimp population at MA (Massutí et al., 2008). Also, earlier impact of currents in the north of the archipelago and a higher influence of productivity of the north basin trigger spatial differences in the population dynamics between the north and the south of the archipelago (Guijarro et al., 2008). Lastly, further differences between MA and CA are related to the efficiency and complexity of trophic pathways. Oligotrophic waters, such as those of MA, have more efficient and simpler trophic pathways compared to more productive ecosystems like CA, which have more diverse and less efficient trophic pathways (Fanelli et al., 2013).

2.2. Biological data

Daily landings of red shrimp (*A. antennatus*) from all fishing ports in Catalan coast (CA) and Mallorca (MA) in the Balearic Islands were available from the sale slips for the period 2000–2010 (Fig. 1b). Monthly catch per unit effort (CPUE) was calculated using fishing trips of the bottom trawl fleet, which accounts for effort information of number of fishing days and number of boats that target exclusively this species between 600 and 800 m depth (Guijarro et al., 2008; Sardà et al., 2004). Thus, CPUE is a proxy of the presence and density of the species in the fishing grounds of the middle slope due to the daily presence of trawlers targeting the red shrimp and the absence of discards (Company et al., 2008; Guijarro et al., 2008). No changes in fishing effort exist from 2000–2010 that could bias CPUE (e.g., increasing number of hours fished per day, increased engine power, etc.). Hence, red shrimp CPUE in the Western Mediterranean can be used as indicators of both presence and relative density in the fishing grounds (Keller et al., 2014; Quetglas et al., 2013). These CPUE estimates, however, do not reflect absolute population density over the entire region, because the fishing fleet does not target non-reproductive, young recruits found in depths greater than 1000 m (Sardà and Company, 2012; Sardà et al., 2004). Thus, the fleet completely harvests the adult component of the population (Guijarro et al., 2008; Sardà et al., 2004), potentially triggering a size-selective effect of fishing on the demography (e.g., demographic erosion, Hidalgo et al., 2012).

Because monthly age–structure is not available for red shrimp during the study period, we used indirect stage–structure demographic information using the fraction of commercial landings in the small (juvenile) and large (adult) categories to investigate the general spatial variation in demography. Previous studies show that large individuals are bigger than ca. 32 mm (carapace length) and correspond with reproductive adults older than 2 years old, while individuals of the small category are below ca. 32 mm and corresponds with non-reproductive large juveniles younger than two years old (Carbonell et al., 1999; Guijarro et al., 2008).

2.3. Time series analyses

We apply two complementary time series techniques, clusterized wavelet analyses and time-varying correlograms, to investigate the non-stationary behaviour of seasonal fluctuations of CPUE and how the strength of seasonal synchrony of this species changes with time at inter-annual scales.