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Progressive changes in the Western English Channel foster a reorganization in the plankton food web

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ABSTRACT

Growing evidence has shown a profound modification of plankton communities of the North East Atlantic and adjacent seas over the past decades. This drastic change has been attributed to a modification of the environmental conditions that regulate the dynamics and the spatial distribution of ectothermic species in the ocean. Recently, several studies have highlighted modifications of the regional climate station L4 (50° 15.00′N, 4° 13.02′W) in the Western English Channel. We here focus on the modification of the plankton community by studying the long-term, annual and seasonal changes of five zooplankton groups and eight copepod genera. We detail the main composition and the phenology of the plankton communities during four climatic periods identified at the L4 station: 1988–1994, 1995–2000, 2001–2007 and 2008–2012. Our results show that long-term environmental changes underlined by Molinero et al. (2013) drive a profound restructuration of the plankton community modifying the phenology and the dominance of key planktonic groups including fish larvae. Consequently, the slow but deep modifications detected in the plankton community highlight a climate driven ecosystem shift in the Western English Channel.

1. Introduction

Time-series data have been shown to be fundamental in understanding marine ecosystem function in an era of global environmental change (Harris, 2010). In the last half-century, modifications of the natural environmental equilibrium in the global ocean have complicated our understanding of natural ecosystem dynamics. Resolving how marine communities deal with these changes challenges the sustainable management of resources, and therefore represents a major endeavour in marine science. In this regard, the thorough assessment of plankton dynamics appears essential to forecast pelagic food web changes. Indeed, by virtue of the role of plankton at the base of the food web and their non-linear responses to external forces, these organisms are valuable indicators of ecosystem health (Hays et al., 2005). Hence, understanding the temporal variability of plankton communities can help anticipate changes in the marine ecosystem (Behrenfeld, 2014).

The Western English Channel has a long history of marine ecosystem investigations. First reports appeared in the late 1880s and were followed by a number of investigations that focused on the effect of environmental and climatic variations on marine resources. Southward et al. (2004) provided a compelling overview of the long-term research in the Western English Channel and showed that field data are fundamental to identify climate-induced environmental changes and their effects on marine populations. Recent studies using the Plymouth Marine Laboratory dataset showed conspicuous changes in plankton over the period 1988–2007 (Eloire et al., 2010). These results portrayed an asymptotic trend in zooplankton abundance together with an increased species richness in pelagic copepods. These changes echoed modifications in the magnitude and length of the seasonal temperature influence and, consequently, in the timing and depth of the thermocline (Molinero et al., 2013). The latter authors further warned of the increasing climate variance that might change plankton species' structure and function, thereby promoting bottom-up controls in food webs. Plankton resilience is of central importance for the entire marine ecosystem, for which a thorough understanding of structural changes, i.e. taxa/species replacement.

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On the basis of the result found in Molinero et al. (2013), we here examine plankton community response to climate forcing over the period 1988–2012. As the strength of the climate influence on populations varies over time, we may expect different type of response between the different planktonic groups and species. To quantify the effects of climate cascades on the plankton ecosystem we first assessed the time-varying strength of the climate influence and identified regimes of environmental variability that governed the period investigated. Subsequently, we examined temporal changes of plankton taxa and identified structural changes related to dominant taxa, composition and phenology for the whole planktonic system, as well as for pelagic copepods.

2. Materials and methods

2.1. Biological data

All biological data used in the study are from the Plymouth Marine Laboratory L4 dataset (www.westernchannelobservatory.org.uk). This is based on quasi-weekly sampling at station L4 (50° 15.00′N, 4° 13.02′W). The temporal resolution has been averaged for monthly resolution for all biological parameters to compensate for non-homogenous sampling effort (i.e. occasional missed sampling and variations in day of the week sampled).

Phytoplankton samples were collected from a depth of 10 m using a 10 L Niskin bottle over the period 1992–2012. Samples were immediately fixed with 2% (final concentration) Lugol's iodine solution (Throndsen, 1978). A 200 mL sub-sample was taken and preserved with neutral formaldehyde for the enumeration of coccolithophores. Samples were stored in cool, dark conditions until analysis using light microscopy and the Utermöhl counting technique (Utermöhl, 1958). Samples were gently homogenized before settling a 50 mL subsample from the Lugol's-preserved sample, and a 100 mL subsample from the formaldehyde-preserved sample. Further details of sampling processing are given in Widdicombe et al. (2010). To quantify the chlorophyll-a concentration, fluorimetric techniques were used from 1992 to 1999 and HPLC from 1999 to 2012.

Zooplankton records cover the period from March 1988 to December 2012. Zooplankton was sampled during daylight by two consecutive vertical net hauls from near bottom (average depth 55 m) to the surface at station L4 using a WP2 net (57 cm inlet diameter, mesh size 200 μm). Sub-sampling of the catch was carried out using a Folsom splitter and organisms counted under a dissecting microscope. The abundance (ind. m^{-3}) of the two vertical hauls was averaged to reduce the variability related to sampling. In this study, only time series (i.e. total abundance of biological stage) of abundant species (Southward et al., 2004) with no major breaks in the dataset have been analyzed to evaluate temporal change of representative zooplankton species of the Western English Channel. Consequently, the study has focused particularly on the main copepod groups: *Oithona* spp., *Pseudocalanus* spp., *Oncaea* spp., *Paracalanus* spp., *Temora* spp., *Acartia* spp., *Corycaeus* spp. and *Calanus* spp. Also, to represent the different zooplanktonic communities of the L4 station five taxonomic groups have been computed: total copepods, cladocerans, tunicates (Appendicularia, Doliolida Ascidian tadpole), meroplankton (gastropod, malacostraca, echinoderm, cirripedia and echinoderm larvae), gelatinous carnivores and total fish larvae. The gelatinous carnivore group is composed of Narcomedusae, Trachymedusae, Hydromedusae, Siphonophora and Ctenophora. All groups have been computed with the monthly mean total abundance of all biological stages.

Abundance of fish larvae was obtained from the same WP2 vertical net hauls. This methodology gives adequate sampling of larvae and early post-larvae (referred to here all as ''larvae'') but will not include the more motile later post-larval stages. Other sampling in the Western English Channel (Coombs and Halliday, 2012) indicates that over 50% of the larvae will be clupeids including sprat (*Sprattus sprattus*) and sardine (*Sardina pilchardus*).

2.2. Physical data

The regional climate variability in the Western English Channel was assessed using monthly anomalies of surface air temperature, sea surface temperature, atmospheric sea level pressure, 300 hPa geopotential height and precipitation records over the period 1988–2012 from the Climate Diagnostics Center (NCEP/NCAR) reanalysis fields (Kalney et al., 1996).

2.3. Statistical analysis

To depict long-term trends of each trophic level sampled in the Western English Channel, a Principal Component Analysis (PCA) was performed on regional climate variables. The first principal component (PC1) accounted for 56.6% of regional climate variability. The general trends of climate, phytoplankton, zooplankton and fish data were obtained by means of Eigen Vector Filtering (EVF) (Ibañez and Etienne, 1992). The EVF method corresponds to a PCA calculated on an autocovariance matrix based on the original series z plus several copies of it, lagged by one time unit (equal to 1 month in our case). An objective number of P lagged series corresponds to the number of lags at which autocorrelation of the original series first approaches zero (Ibañez and Etienne, 1992). This technique acts as a weighted moving average with the advantage that no observation is lost at the boundaries of the time series.

The timing of structural changes in monthly fluctuations of each trophic group and climate parameters was detected using a fluctuation test, based on the cumulative sum of standardized ordinary least square residuals (OLS-based CUSUM test) (Zeileis et al., 2003), which computes the probability p of significant changes in a time series. Results of the OLS-based CUSUM test are represented in Fig. 1. To link the impact of environmental conditions on the plankton pool over the whole studied period, monthly climatologies of chlorophyll-a concentration (Chla) and sea surface temperature (SST) were calculated for each period identified and plotted in Fig. 2. In addition, monthly fluctuations of total zooplankton and copepods sampled at L4 were represented as scatter plots in Fig. 3a and 3b.

To quantify and discriminate the changes in the zooplankton groups observed in Fig. 1c, two analyses were performed on the main zooplankton groups and copepod genera. First, dominant zooplankton groups and copepods were identified as the highest abundance for each month from March 1988 to December 2012, and represented on Fig. 3c and d. Second, a PCA was performed on the time series of zooplankton groups and copepod abundance. Results from each PCA are shown on Fig. 4. Subsequently, a CUSUM transformation (Ibañez et al., 1993) was applied on the first two principal components (PCs) of zooplankton and copepod groups to depict changes in zooplankton composition.

To quantify changes in seasonality we used a wavelet-based procedure (hereafter SWaP) to extract several phenological indices from zooplankton time series, as in Demarcq et al. (2012). The SWaP is based on a Continuous Wavelet Transform (CWT) and uses the Morlet wavelet function. The seasonal signal's amplitude at 1 year of periodicity is calculated as the annual average of each zooplankton group between 1989 and 2012 by averaging the Wavelet power spectrum (Demarcq et al., 2012). The seasonal duration was obtained at yearly resolution using a surrogated methodology. The timings of onset blooms are identified for each parameter following Racault et al. (2012). The trend of each