

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 restructuring 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.

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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).

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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.

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 ([Thronsdon, 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

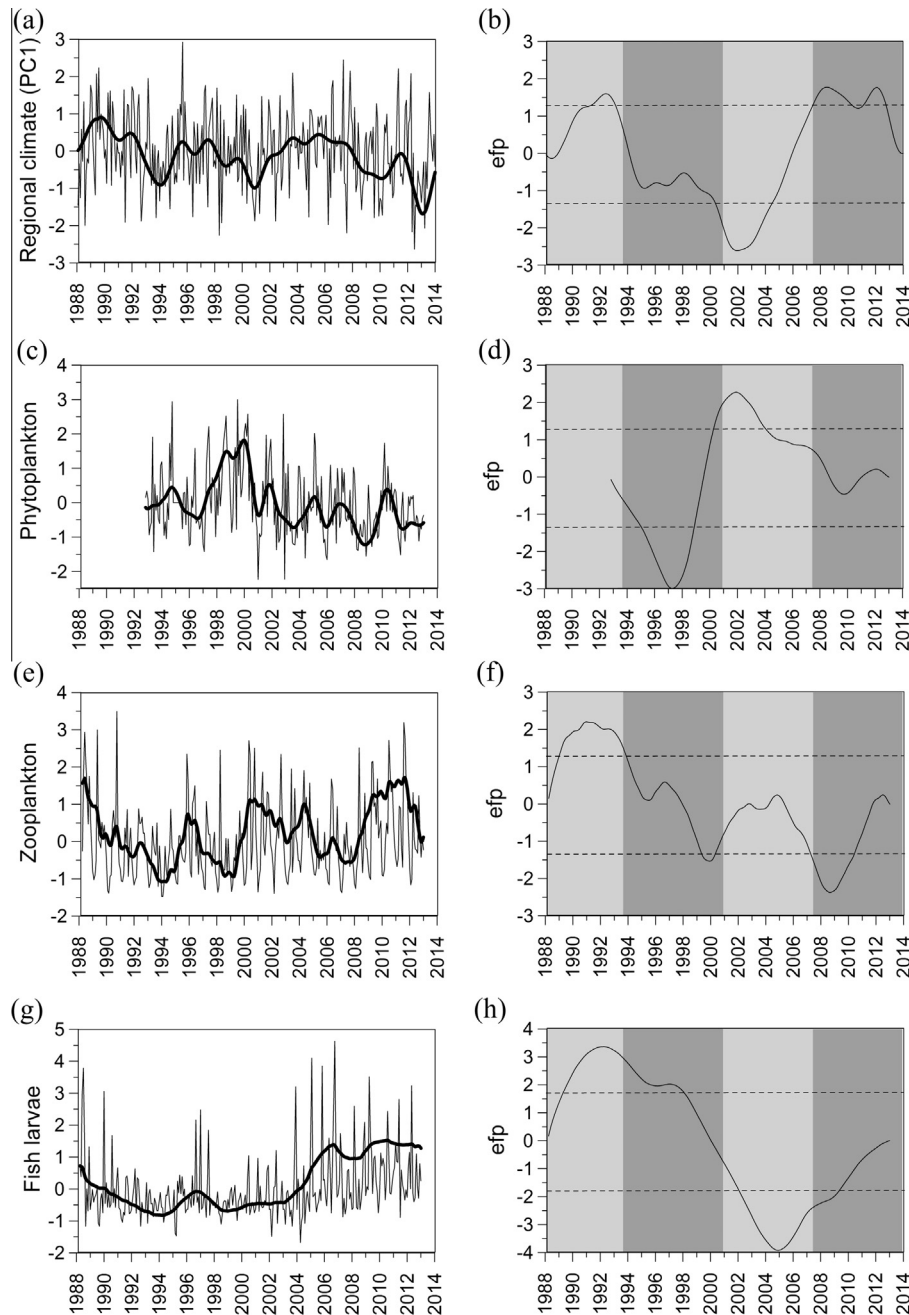


Fig. 1. Long term variations of environmental conditions and phytoplankton and zooplankton communities in the Western English Channel, Station L4. Panels (a), (c), (e) and (g) portray the monthly variability and trend (thick line) of regional hydroclimate, phytoplankton and zooplankton. Panels (b), (d), (f) and (h) show structural changes in the time series depicted by the cumulative sum of ordinary least square residuals (OLS-based CUSUM process). Confidence intervals ($p < 0.05$) are indicated by horizontal dashed lines. efp: empirical fluctuation process.

phenological parameter (amplitude, duration, onset timing) was calculated over the whole period from 1989 to 2012 using a robust linear regression (DuMouchel and O'Brien, 1989) and are presented in Figs. 5 and 6.

3. Results

Climate conditions for the Western English Channel, as represented by PC1 of regional atmospheric variables, showed the expected inter-annual variability, with a trend indicating multi-annual cycles of 6–7 years (Fig. 1a). The OLS-based CUSUM test identified four major periods of forcing during the years

examined (Fig. 1b): January 1988 to circa 1994, 1994 to circa 2001, 2001–2007 and 2008 onwards. These changes, primarily driven by the expanding climate variance envelope, i.e. interval of variation of climate parameters, together with the increasing temperatures in the middle-late 1990s, cascaded down influencing phytoplankton and zooplankton communities including fish larvae. Records of phytoplankton did not cover all the period examined, however the temporal variations did show significant changes during the periods 1994 to circa 2001 and 2001–2007 (Fig. 1c and d). In turn, the temporal variations of zooplankton parallel the main trend of climate (Fig. 1e) while significant changes were also depicted by the OLS-based CUSUM test (Fig. 1f). Similarly, the ensemble of fish larvae showed comparable changes;

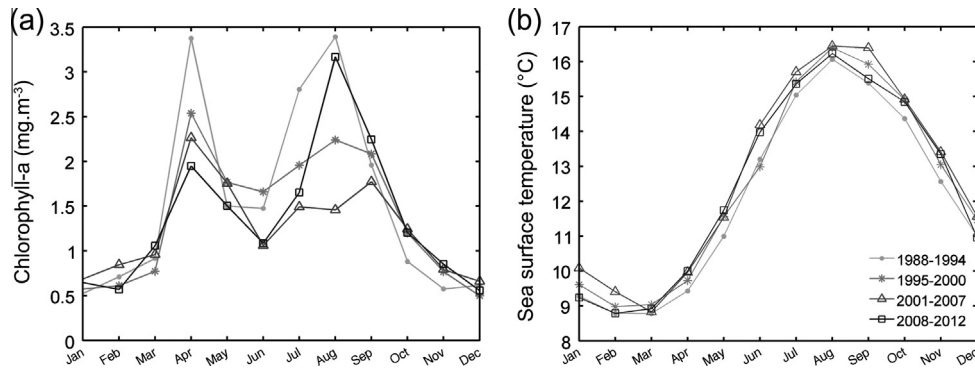


Fig. 2. Plot of the monthly average of (a) chlorophyll-a concentration (mg m^{-3}) and (b) sea surface temperature ($^{\circ}\text{C}$) for the four climatic periods identified on Fig. 1b.

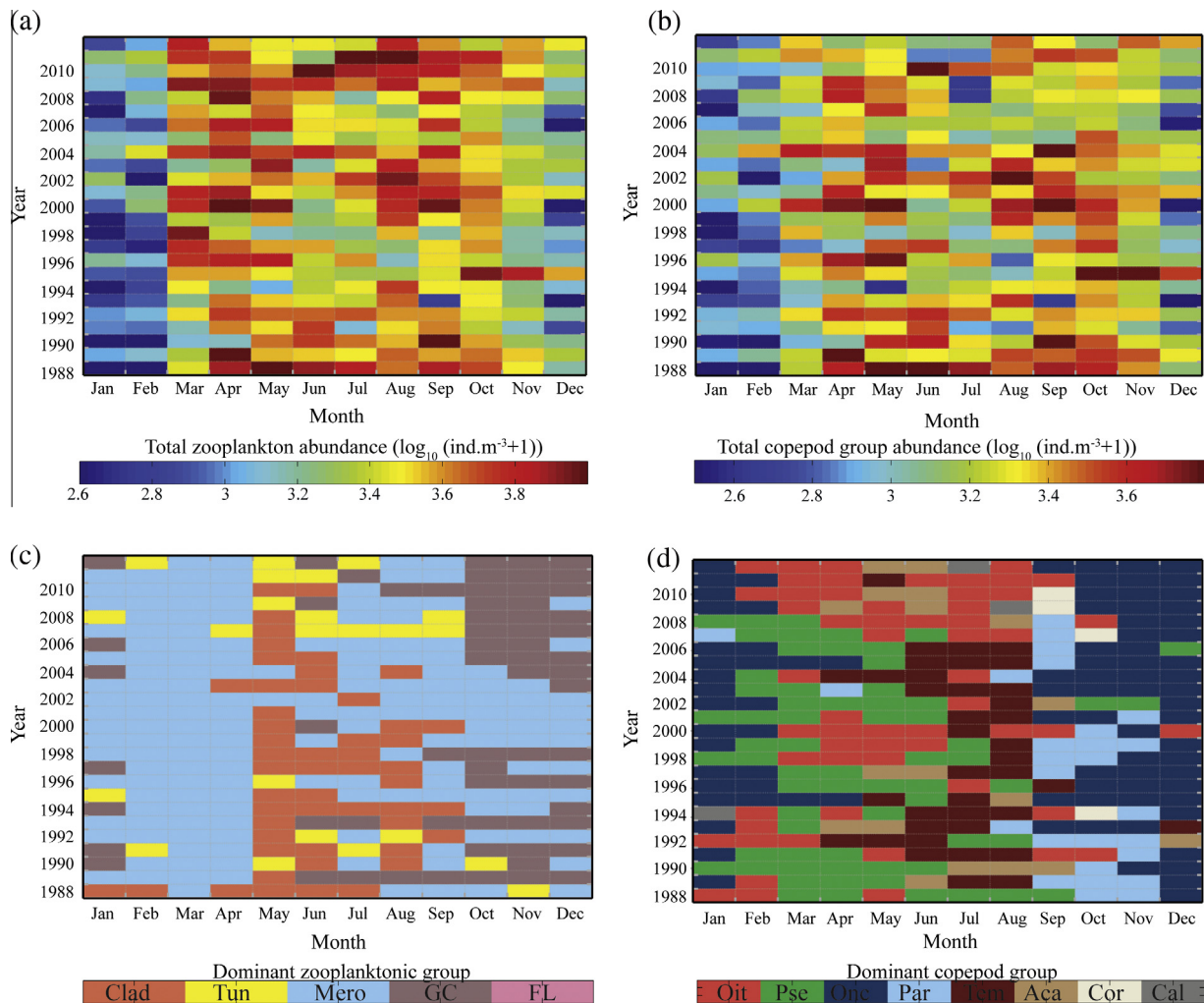


Fig. 3. Plots by month and year for the mean abundance of (a) total zooplankton and (b) total copepods. Plots for dominant groups (i.e. maximal abundance) is represented in (c) by functional group and in (d) for copepod species only. Annotations in the color bar of Fig. 3c represent: Clad = Cladoceran; Tun = Tunicata; Mero = Meroplankton; GC = Carnivorous Gelatinous; FL = Fish Larvae. Annotations in the color bar of Fig. 3d represent: Oit = *Oithona* spp.; Pse = *Pseudocalanus* spp.; Onc = *Oncaea* spp.; Par = *Paracalanus* spp.; Tem = *Temora* spp.; Aca = *Acartia clausi*; Cor = *Corycaeus* spp.; Cal = *Calanus helgolandicus*.

their abundance was low prior to 2000 and increased markedly from the early 2000s (Fig. 1g). Significant changes in fish larval abundance were also apparent around 1994, 2001 and 2008 (Fig. 1h), the same as seen in the phytoplankton and zooplankton results.

As revealed in Molinero et al. (2013), environmental conditions have significantly changed over the sampling period. These

modifications are particularly marked in the seasonality of each environmental parameter studied (Fig. 2). Indeed, amplitude and duration of the seasonality of SST have increased progressively from 1988 to 2007 with a slight decrease in the amplitude the last climate period (2008–2012). In addition, seasonality of the primary producers approximated by the Chla reveals strong changes during the spring and autumn blooms. A drastic decrease in amplitude of

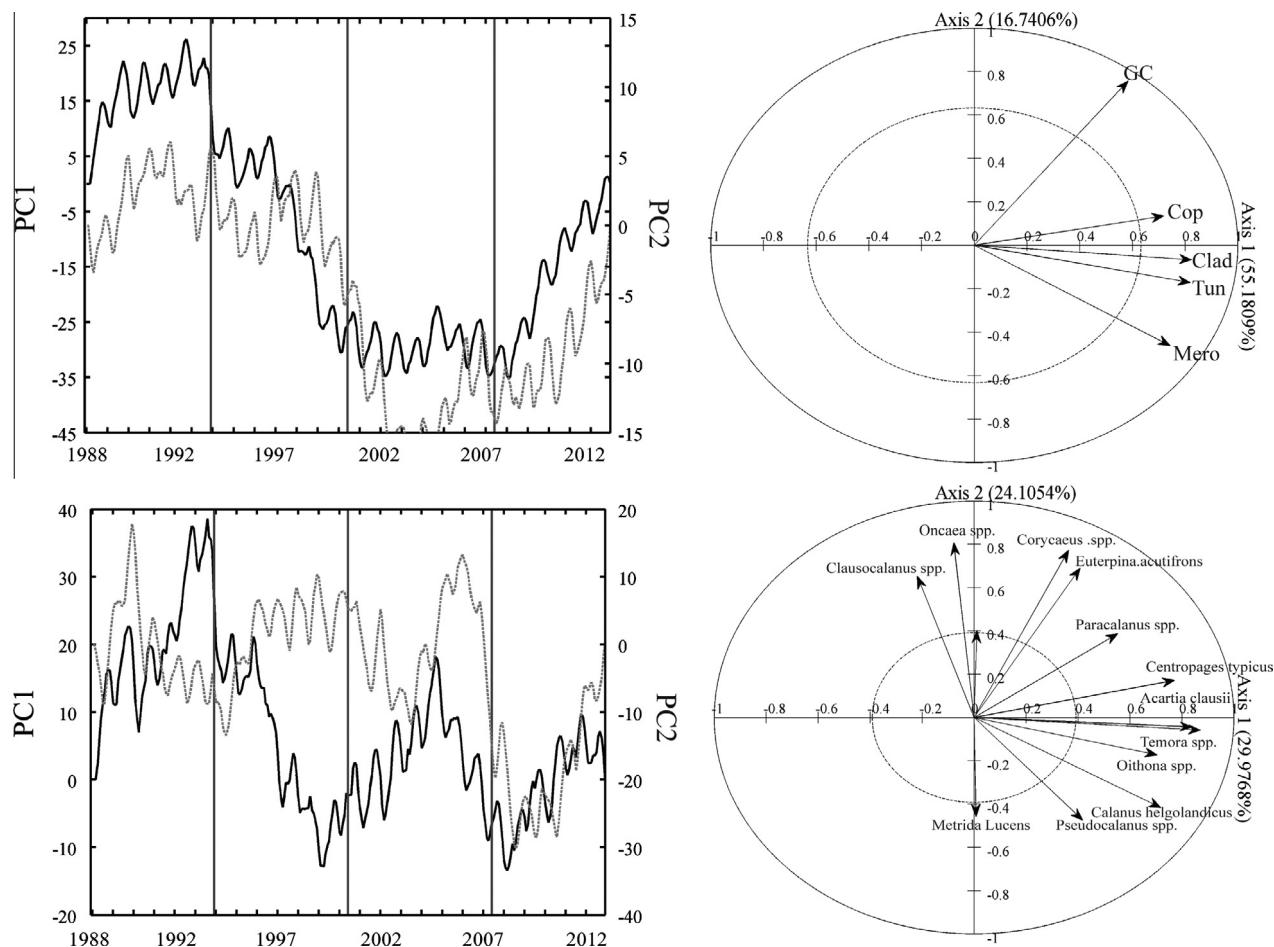


Fig. 4. (a) Principal Component Analysis performed on the time series of functional group abundance and plot of the CUSUM of the corresponding first and second components. Annotations on the PCA represent: Clad = Cladoceran; Tun = Tunicata; Mero = Merozooplankton; GC = Carnivorous Gelatinous. (b) Principal Component Analysis performed on the abundance time series of copepods species abundance and plot of the CUSUM of the corresponding first and second component. Periods identified on Fig. 1 are represented by gray vertical lines.

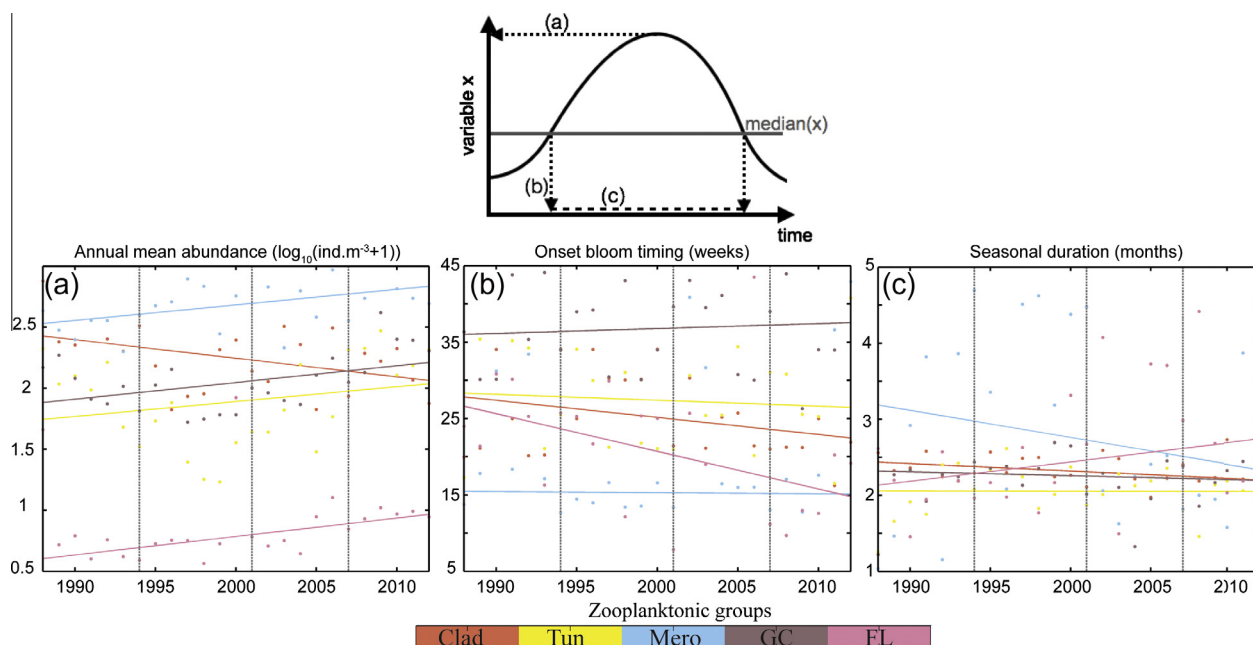


Fig. 5. Plot of phenological indices for the zooplankton groups from 1988 to 2012: (a) annual mean abundance ($\log_{10}(\text{ind. m}^{-3} + 1)$), (b) timing of the onset of the spring bloom (weeks) and (c) duration of the bloom (months). Each point represents the year value of the index. Each line represents the robust linear regression performed over the complete time series.

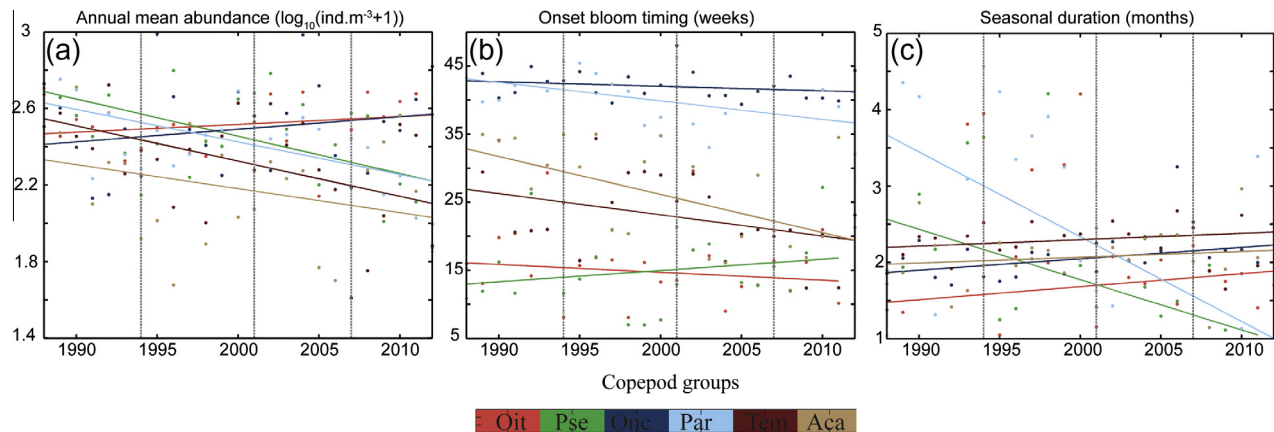


Fig. 6. Plot of phenological indices for the copepod groups from 1988 to 2012: (a) annual mean abundance ($\log_{10}(\text{ind. m}^{-3} + 1)$), (b) timing of the onset of the spring bloom (weeks) and (c) duration of the bloom (months). Each point represents the year value of the index. Each line represents the robust linear regression performed over the complete time series.

the spring bloom is detected over the entire sampling period. This change is contrasted by a very noticeable modification of the autumn bloom that decreases in amplitude between 1988 and 2007 and then from 2008 onwards becomes the dominant bloom. In addition, the duration of the autumn bloom increases over the whole time series.

The above inter-annual fluctuations of zooplankton were further investigated by quantifying the raw monthly variation of total zooplankton and copepod abundance over the entire sampling period (Fig. 3a and b). Fluctuations in total zooplankton abundance were mainly driven by copepod numbers that represent more than 80% of all zooplankton. Conspicuous seasonal variations were observed in total zooplankton as well as the copepod groups, which showed low abundance during the winter and high values in spring and autumn. Yearly changes of total zooplankton abundance show a small increase during the summer from 2000 to 2011. This trend was not correlated with total copepod abundance suggesting an increasing contribution of other zooplankton groups in the community.

These modifications of the plankton community were driven by a restructuring of species and group associations at each trophic level. Indeed, changes in dominance (Fig. 3c and d) and species association (Fig. 4) reveal a drastic modification of the planktonic pool consistent with the climatic periods identified in Fig. 1b. A clear increase of gelatinous species dominance (Narcomedusae, Trachymedusae, Ctenophora and Tunicata) is observed as for *Oithona* spp. and *Oncaea* spp. since 2002. Simultaneously a marked decrease of meroplankton, Cladocera, *Pseudocalanus* spp. and *Temora* spp. was detected. This modification in the community composition was underlined by the PCA analysis in Fig. 4. Indeed, the observed change in dominance (Fig. 3c and d) resulted from a progressive modification of total plankton represented by the first two components of each PCA, which revealed a profound restructuring of the plankton species' association since the year 2000 (Fig. 4).

Environmental changes can induce modifications in plankton community structure and also phenological responses which are species dependent. To track potential changes in phenology we here focused on the annual mean abundance, the timing of bloom onset and the seasonal duration (Figs. 5 and 6). All functional groups, except cladocerans, showed an increase in mean annual abundance over the time series (Fig. 5a). While the meroplankton and the gelatinous carnivores did not exhibit significant changes in the onset of their bloom (no change for the first 1 and 2 week delay period), tunicates, cladocerans and fish larvae have all

undergone advances in their period of occurrence of respectively 2, 6 and 12 weeks (Fig. 5b). The seasonal duration was not modified for the cladocerans, gelatinous carnivores and tunicates (between 2 and 2.5 months) while meroplankton had a shorter seasonal abundance by 0.8 month and the seasonal duration of fish larvae increased by half a month (Fig. 5c).

When looking at the copepod species assemblage, both *Oncaea* and *Oithona* showed an increase in annual mean abundance while for the other copepod genera, *Pseudocalanus*, *Paracalanus*, *Temora*, *Acartia* mean annual abundance declined (Fig. 6a). All copepods, apart from *Pseudocalanus*, occurred earlier in the year (Fig. 6b). *Oncaea* and *Oithona* showed moderate changes (1.5 and 2.5 weeks in advance, respectively) while the onset blooming time for *Paracalanus*, *Temora* and *Acartia* occurred 5, 7 and 13 weeks in advance, respectively (Fig. 6b). It is worth noticing that *Pseudocalanus* and *Paracalanus* totally disappeared from the copepod community, while the other copepod taxa slightly increased their seasonal duration from 0.2 to 0.4 months (Fig. 6c).

4. Discussion

4.1. Progressive changes in environmental conditions

Environmental conditions in the Western English Channel biotope are mainly controlled by global atmospheric (Beaugrand, 2009) and hydrographic (Hátún et al., 2005) processes that regulate the entire North Atlantic. The effect of these macro-processes varies between different North Atlantic marine ecosystems due to variations in basin shape and local meso-scale features such as river run-off, coastal orientation or interface with adjacent open seas areas. For example, the North Atlantic Oscillation (NAO) partially drives the multi-decadal oscillations of several environmental parameters of the eastern margin of the North Atlantic including at station L4 (Ottersen et al., 2001). Indeed, basin scale atmospheric conditions, such as the NAO cascade down to the oceans through restructuring the macro-hydrological conditions in the North Atlantic such as a modification of the area and location of sub-tropical and sub-polar gyres (Reygondeau et al., 2013). Consequently, inter-annual change of the NAO is closely related to seasonal variability, timing and amplitude of both atmospheric (wind speed and direction) and hydrographic (SST and stratification) parameters at station L4 (Molinero et al., 2013). The inter-annual and seasonal

variations of environmental parameters thus define the conditions for the Western English Channel biotope.

In recent years, analysis of hydroclimatic conditions at station L4 has suggested a progressive long-term modification of this environmental biotope. Indeed, a progressive intensification of the warm period (increase in amplitude and duration of summer SST, Fig. 2) has been identified since the early 1990s. For instance, Molinero et al. (2013) found a conspicuous decrease in the intensity and depth of the thermocline suggesting a decline in the temperature gradient between upper and lower water layers. Such a pattern is in line with the ongoing warming trend in the North East Atlantic deep waters, which has favoured the shallower depth of the thermocline (Dulvy et al., 2008; Hinder et al., 2012). Consequently, the significant long term warming of water column temperature attributed to global climate change (IPCC, 2013) has progressively altered much of the biogeochemical and hydrological dynamics.

This progressive change in the mean environmental conditions driven by the increase of temperature also altered the annual variance of each parameter. Our results showed four distinct periods marked by significant environmental change: 1988–1994, 1995–2000, 2001–2007 and 2008–2012. While the two first periods are mainly driven by natural macro-processes (shift in the NAO index), the two latter periods are driven more by the effect of the increasing warming periods. Consequently, while natural environmental parameters define the width of the envelope, the consistent warming trend has modified the environmental stability reference point of the biotope to a warmer range.

4.2. Impact on plankton community structure

In the English Channel, the non-stationary climate forcing promoted significant variations in the seasonal pattern in both the atmospheric and marine systems. These changes impacted the plankton through modifications of the water column, as shown by the phenological changes in autotroph communities where the spring bloom amplitude declined markedly at the same time as a slight increase of the autumn bloom (Fig. 2). Hydroclimatic variation also influenced the timing and duration of the seasonal cycle represented by maximum chlorophyll concentration, thereby enhancing bottom up control of the planktonic food web (Molinero et al., 2013). The observed biotope modifications are consistent with previous reports showing covariance in environmental conditions and structure and trophodynamics of marine ecosystems (Kirby and Beaugrand, 2009; Cury et al., 2008).

Along with the changes in primary producers, our results further underline a gradual modification of zooplankton composition consisting of a decrease of crustacean zooplankton, e.g. cladocerans, while the copepod assemblage experienced a shift toward a dominance of small-sized cosmopolitan species and a reduction in abundance of specialized cold/temperate water species, e.g. *Pseudocalanus*. These changes suggest a decline in the biomass of crustacean zooplankton, a major food component for fish larvae, and therefore a potential detrimental effect on fish larval nutrition. Similar biotope modifications were recently reported in northern locations, such as the Irish Sea (a decline in copepod biomass, Lynam et al. 2011), or the Baltic Sea (an increase of small sized copepods, Garzke et al., 2014). Likewise, our results portrayed a noticeable increase of gelatinous zooplankton, e.g. tunicata and jellyfish, which also agrees with recent findings in the Northeast Atlantic (Lynam et al. 2011). The observed reorganisation has occurred concurrently with significant changes in the pattern of climate variability, as we have shown here, supporting the hypothesis of the predominant role of climate variation in the long-term changes in jellyfish abundance (Lynam et al. 2011). Under this hypothesis climate effects may act both directly (effect on

metabolism, growth and/or reproduction) and indirectly (via ecosystem interactions); it is acknowledged, however, that competing factors, such as eutrophication, particularly in coastal areas, have also promoted ecosystem-wide structural changes in the Northeast Atlantic and adjacent seas.

It is worth noting that zooplankton assemblages shifted from dominance by temperate species to a dominance of cosmopolitan ones; the former with a narrow temperate water affinity, whereas the latter showing a wide range of temperature tolerance. These results are in line with biogeographic shifts, i.e. expansion (retraction) of the spatial distribution of warm (cold)-water calanoid copepod assemblages in the Northeast Atlantic over the past decades (Beaugrand et al., 2002), and further emphasize that the climate impact on zooplankton is noticeable within and across taxa.

Changes in the physical environment can modify the dominance of species and structure, diversity and functioning of marine ecosystems. In the present study the four identified periods showed wide changes at the base of the food web; that is, an increase in total zooplankton abundance and specifically for *Oncaea* spp., *Oithona* spp. and *Acartia clausi* or a decline for *Pseudocalanus elongatus*, *Paracalanus parvus* and *Temora* spp. and changes in the phenology in several species, with predominant forward shifts in the timing of the maximum peak. It is worth noting that most of the taxa exhibited a shift in the timing of the initiation time greater than 8 weeks, as well a shift in the timing of maximum abundance. Our results also indicate the large, possibly critical, reduction in the abundance of *Pseudocalanus elongatus*, a preferential prey for the larvae of cod (*Gadus morhua*) and herring (*Clupea harengus*). A similar finding was reported in the Gulf of Trieste in the northern Adriatic (Conversi et al., 2009), and in the wider North Atlantic (Beaugrand et al., 2002), showing that this cold water species is experiencing changes both locally and in other regions.

4.3. Bottom up control of ichthyoplankton

Small pelagic fish constitute the bulk of the fish biomass in many areas of the oceans and are in a mid-trophic position in the food web. Therefore their ecological role in the ecosystem is crucial, as being plankton-feeders they may have an important effect on lower trophic levels and, at the same time, potentially affect the dynamics of their main predators (Costalago et al., 2014). Survival of young fish stages depends greatly on their ability to capture and digest sufficient quantities of appropriate prey. For example, sardine juveniles (*S. pilchardus*) widely distributed in the eastern North Atlantic from west Africa to the North Sea (Coombs et al., 2010) should benefit compared to other clupeids such as herrings under an increase of small copepod species abundance because of their feeding adaptations (viz short distance between gill rakers) and their greater filtering capacity (Costalago et al., 2014). This planktivorous species is short-lived with population dynamics strongly associated with changing environmental conditions (e.g. Alheit and Hagen, 1997), and the number of fish eggs spawned is typically a reflection of stock size. Coombs et al. (2010) have shown that the higher overall numbers of sardine eggs in the English Channel at the beginning of the 21st century is mostly due to increased autumn spawning, which implied higher stock levels at that time. Our results showed that the autumn phytoplankton bloom has progressively decreased during the three first periods identified in the time series to finally recover in period 4 (post 2008) and reach approximatively the same intensity as in period 1 (1994–2001). This has probably favoured zooplankton abundances in the autumn and consequently egg production in sardines.

Long term changes in zooplankton communities have been widely demonstrated in the North Sea with strong consequences

for exploited fish recruitment (e.g. on cod *Gadus morhua*, Beaugrand et al., 2003). A more recent paper (Montero-Serra et al., 2014) indicates strong long-term changes in several pelagic fish species assemblages in the North Sea and Baltic Sea; while occurrence of those pelagic fish species were correlated with temperature, other species including sardine (*S. pilchardus*) anchovy (*Engraulis encrasicolus*), mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*) also showed positive associations with the abundance of the copepod *Calanus helgolandicus* (Montero-Serra et al., 2014) supporting our results in the English Channel.

Our study has highlighted important modifications of trophodynamics of the zooplankton community. However, compensatory dynamics may have buffered the effects as suggested by the roughly consistent total zooplankton abundance throughout the time series, while zooplankton structure has changed drastically, implying effects on pelagic fish predators and possibly top predators. For example, off eastern Tasmania zooplankton changes have increased the relative abundance of redbait (*Emmelichthys nitidus*) and consequently reduced the effort of surface fisheries (McLeod et al., 2012). Consequently, the present findings have relevance in modern ecosystem approaches to fish stock management.

4.4. Concluding remarks

In recent years, with the growing availability of long-term data, substantial efforts have been devoted to investigate regime shifts in marine ecosystems (see de Young et al., 2004). Regime shifts are profound reorganizations in system structure, function and feedback, which can lead to changes in the provision of ecosystem services with significant impacts on human well-being (Crépin et al., 2012). These major changes have been reported world-wide over recent decades generally relating to the compound effects of climate and anthropogenic forces such as fishing or habitat destruction (IPCC, 2013). Although plankton dynamics may have the ability to buffer external perturbations to a certain extent, the close connection between climate, hydrography and plankton shown in the present results suggest that continued global warming may shift plankton toward novel dynamics (Casini et al., 2009). Hence, the expected climate variance in warming scenarios can lead to profound modifications in plankton structure and function (IPCC, 2013), tending to enhanced bottom-up controls in pelagic food webs (Molinero et al., 2013). Such uncertain scenarios are likely to be further accelerated by continued climate and anthropogenic perturbations.

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