Research papers

The impact of environmental variability on Atlantic mackerel *Scomber scombrus* larval abundance to the west of the British Isles

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ABSTRACT

The value of the Continuous Plankton Recorder (CPR) fish larvae dataset, with its extensive spatio-temporal coverage, has been recently demonstrated with studies on long-term changes over decadal scales in the abundance and distribution of fish larvae in relation to physical and biological factors in the North Sea. We used a similar approach in the west and southwest area of the UK shelf and applied a principal component analysis (PCA) using 7 biotic and abiotic parameters, combined with Hierarchical Cluster Analysis (HCA), to investigate the impact of environmental changes in the west and southwest area of the UK shelf on mackerel larvae during the period 1960–2004. The analysis revealed 3 main periods of time (1960–1968; 1969–1994; 1995–2004) reflecting 3 different ecosystem states. The results suggest a transition from an ecosystem characterized by low temperature, high salinity, high abundances of zooplankton and the larger phytoplankton groups, to a system characterized by higher temperature, lower salinities, lower abundances of zooplankton and larger phytoplankton and higher abundances of the small phytoplankton species. Analysis revealed a very weak positive correlation between the Second principal component and mackerel larvae yearly abundance, attributed to the North Atlantic Oscillation (NAO). The results presented here are in broad accord with recent investigations that link climatic variability and dynamics of mackerel reproduction. However, the growing body of literature that documents statistical correlations between environment and mackerel needs to be supplemented by local process studies, to gain more insight and to be able to predict mackerel response to climate change scenarios. Utilising the strength of the CPR dataset, namely its unique temporal coverage, in an analysis where other data (such as egg surveys) are drawn in to compensate for the spatial issues could prove to be the way forward.

1. Introduction

Atlantic mackerel *Scomber scombrus* is one of the most abundant migratory fish species in the North East Atlantic. It is pelagic in all life stages and its distribution encompasses the entire ICES area (ICES, 2012). The most important spawning areas in recent decades are located to the south and west of Ireland. Outside the spawning season, the centre of distribution shifts northwards as the mackerel migrate to the feeding grounds between Greenland, Norway and in the North European shelf Seas. Over the years, great variability in abundance and distribution of mackerel population has been observed (ICES, 2012; Jansen, 2014). Substantial quantities of mackerel are now being landed from Icelandic and Greenland EEZs where mackerel was not caught in great quantities

before (ICES, 2014). The changing spatial dynamics of the mackerel population is a challenge for the international management. This is clear from the fact that, despite protracted negotiations over Total Allowable Catches (TACs), no international agreement that includes all fishing nations has been achieved since 2007. A deeper understanding of the abundance and distribution dynamics of this commercially important species may facilitate international agreements and in turn, a more optimal utilisation of the resource.

The Continuous Plankton Recorder (CPR) Survey's marine monitoring programme was established in 1931, and has been collecting data from the North Atlantic and the North Sea on the ecology and biogeography of plankton, consistently since 1946. The spatio-temporal coverage of the CPR is therefore one of the longest and largest offered by any biological monitoring programmes worldwide. The utility of this dataset has been established with the many, and increasingly complex, studies published, aiming to relate spatio-temporal changes in plankton distribution to underlying ecosystem changes. It has also provided valuable

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information concerning the scale and nature of processes affecting fish stocks (Brander et al., 2003). As well as zooplankton and phytoplankton (the main focus of the CPR), fish larvae have been analysed up until-through 2005 (Edwards et al., 2011). The value of the CPR fish larvae dataset, with its extensive spatio-temporal coverage, has been recently demonstrated with studies on long-term changes over decadal scales in the abundance and distribution of fish larvae in relation to physical and biological factors (Pitois et al., 2012), on blue-whiting populations in the North Atlantic (Pointin and Payne, 2014), and on the use of a larval index to inform stock assessments for sandeels (Lynam et al., 2013) and mackerel (Jansen et al., 2012b) in the North Sea. Analyses in the North Sea (Pitois et al., 2012) suggest that the larvae of clupeids, sandeels, dab and gadoids seem to be affected mainly by changes in the plankton ecosystem via bottom-up effects, while the larvae of migratory species such as mackerel respond more to hydrographic influences. Here we use a similar approach to this previous work and focus on the larvae of mackerel collected by the CPR in the west and southwest of the British Isles. Firstly we attempt to identify regimes with defined environmental conditions and second, to identify potential linkages between the environment and fish larvae. We then compare our results with those obtained from the North Sea by Pitois et al. (2012).

2. Materials and methods

2.1. The CPR survey

The CPR device is towed by ships of opportunity at speeds of 15 to 20 knots, at an approximate depth of 10 m. Water enters the recorder through an aperture of 1.27 cm^2, and is filtered through a continuously moving band of silk with an average mesh size of 270 µm. Each sample represents $\sim$3 m^3 of filtered seawater. Methods of counting and data processing have been described by Colebrook (1975) and Batten et al. (2003). All plankton data were extracted from the CPR dataset.

2.2. Area of study

Results from the CPR survey show two separate spawning areas for mackerel in the central North Sea and to the west and southwest of the British Isles (Fig. 1a). Mackerel larvae caught by the CPR have declined substantially over the period 1948–2005 reflecting a decline of first the North Sea stock and subsequently the western population (Edwards et al., 2011). This was however followed by a period of stock extension, not included here (ICES,

2014). The area of study for this analysis was selected according to the distribution of mackerel larvae from CPR samples within the west and southwest area of the UK Shelf (Fig. 1b). We extracted a total of 43,882 data points within the area delimited by latitude 47°N to 60°N and longitudes 14°W and 2°W, over the period 1960–2004, this ensured consistency across all datasets used. It is important to bear in mind that the study area does not cover the total spawning grounds of NE Atlantic mackerel; an important spawning grounds also exists in the Bay of Biscay (ICES, 2013). The CPR also collects samples from the Bay of Biscay but this only includes one route from Bilbao (Spain) to Land's End (England). Based on limited coverage and resolution of the data and the low number of larvae caught from the Bay of Biscay (Fig. 1b), we decided to limit our work to the area which the highest number of larvae caught in CPR samples.

2.3. Plankton data

Zoo- and phytoplankton data were extracted from the CPR dataset along with the mackerel larvae data. As a proxy for zooplankton, we extracted the total abundance of copepods and of cladocerans. These 2 groups were selected because they are important prey of many fish larvae, including mackerel, in their early stages of life (Last, 1980). The CPR underestimates zooplankton abundance compared with other datasets (Clark et al., 2001; John et al., 2001). As we thought it important to take into account the relative contribution of each potential prey species to the total zooplankton abundance, undersampling was corrected using species-specific WP-2/CPR ratios (Pitois and Fox, 2006). We gathered together all these species-specific corrected abundances to create an index of total zooplankton abundance.

A lot of recent work has shown notable prey selectivity in mackerel larvae that does not support the view that all copepods are the same (Paradis et al., 2012; Peterson and Ausubel, 1984; Robert et al., 2014). Because, prey selectivity seems to vary from area to area depending on the particular prey available; we could not extract some selectivity index that could be applied on the CPR data as a whole.

Fish larvae caught by the CPR are very small. Johnson (1977) reported that the larvae of Atlantic mackerel caught by the CPR were $<$7 mm long, on average 5 mm; and Jansen et al. (2012b) estimated that these had a length of 4.8 mm using a backwards-advection model based upon an estimate of time-since-spawning. Such larvae are very young and likely to be 5–12 days old (Robert et al., 2014; Jansen et al., 2012b) depending on temperature and food conditions mainly. These small larvae tend to feed on the smallest prey available, such as phytoplankton and copepod eggs
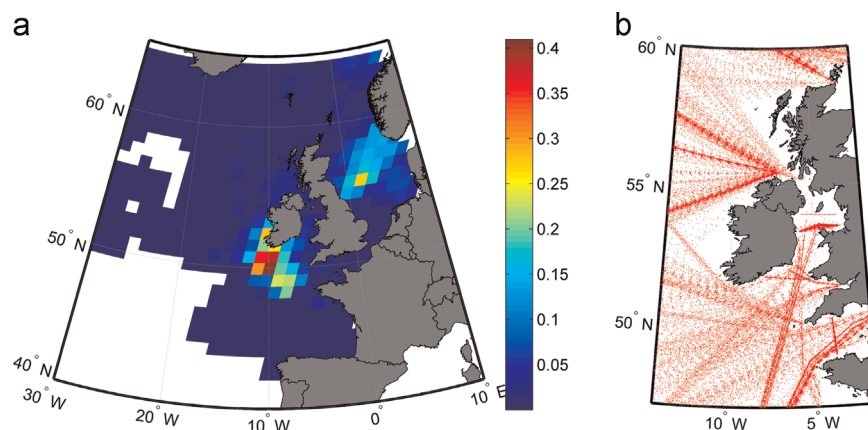
Fig. 1. (a) Mackerel larvae distribution from Continuous Plankton Recorder (CPR) samples collected between 1948 and 2005. (b) Area of study (47°N to 60°N, 14°W to 2°W) and ichthyoplankton sampling locations over the period 1960–2004 (43,882 data-points).

and nauplii (Last, 1980; Paradis et al. 2012; Peterson and Ausubel, 1984; Robert et al., 2014). The zooplankton index used here has been corrected for undersampling by the CPR, but it still only comprises the larger copepodites and adults and does not include nauplier stages. For lack of better information, it seems reasonable to assume that abundances of copepod nauplii are linked to similarly high abundances of copepods during summer.

The plankton chlorophyll index (CHLO) was also extracted. This index of greenness provides a semi-quantitative indication of primary production and hence phytoplankton, and has also been referred to as the Plankton Colour Index. We further extracted information on the abundance of the larger groups of phytoplankton, namely diatoms and dinoflagellates; abundances of individual species were collated within each of these 2 groups to create separate indices of abundance.

2.4. Potential biases and limitations

As might be expected, the CPR instrument, with its very small aperture and fixed sampling depth, is known to substantially under-sample fish larvae more than it does zooplankton, but this has not yet been quantified. Therefore, generalisations based on this study concerning long-term changes in mackerel larvae abundance and distribution must be treated with some caution.

Due to the mesh size of CPR silks, many phytoplankton species are only semi-quantitatively sampled due to the small size of the organisms. There is thus a bias toward recording larger armoured flagellates and chain-forming diatoms, and smaller species abundance estimates from cell counts will probably be underestimated in relation to other sampling methods. However, Robinson (1970) found that the proportion of the population that is retained by the CPR silk reflects the major changes in abundance, distribution and composition, i.e. the percentage retention is roughly constant within each species even for very small-celled species.

Due to the subsurface sampling of the CPR, the survey cannot take into account long-term changes in the depth of the pycnocline. If there were significant changes to the depth of the pycnocline over a decadal time scale, this could potentially bias CPR results. Due to the lack of sufficient physical data at the same scales of this study, this potential bias could not be tested. It is worth noting, however, that the water immediately behind a large, fast-moving vessel is likely to be mixed and homogenised well below the CPR towing depth (Batten et al., 2003).

2.5. Mid-column temperature and salinity data

Monthly water mid-column temperature and salinity data for $0.111° \times 0.167°$ (latitude × longitude) grid cells, covering the selected area and time frame, were obtained from the POLCOM model, at the National Oceanography Centre (NOC, Liverpool, UK).

2.6. The NAO index

The NAO index, as calculated by Hurrell (1995), is defined as the normalised winter (December–March) sea-level pressure difference between a station on the Azores and one in Iceland, and it is used to represent North Atlantic climate variability. The winter NAO index was provided by the Climate Analysis Section, NCAR, Boulder, Colorado, and downloaded from www.cgd.ucar.edu/cas/jhurrell/indices.html. We also used a monthly index of the NAO.

2.7. Data analysis

Data analysis was performed using the Matlab computing language. Due to the highly skewed statistical distance of abundance values within the CPR data, these were log-transformed using a $\log(x+1)$ function (Colebrook, 1960). The CPR survey collects samples at different times of day and at locations that do not follow a regular grid. All CPR data therefore need to be regularised in time and space before being subjected to numerical analyses (Beare et al., 2003). This was undertaken on a 50×50 nautical mile (92.6×92.6 km) grid using Inverse Distance Weighing Interpolation (Lam, 1983; Legendre and Legendre, 1998). We used a search radius of 100 miles (i.e. 185.2 km), and a minimum and maximum number of neighbours of 3 and 20, respectively. These values were chosen as a compromise between numerical efficiency and the need to keep the number of missing values in the interpolated grid to a minimum. CPR data also show major seasonal and diel patterns (Beare et al., 2003; Beaugrand et al., 2003), and these were taken into account when calculating annual values. The procedure used was adapted from (Beaugrand et al., 2001). The samples covering our area and period of study were grouped into day and night periods for each month and year; day/night periods were defined from calculation of the sun zenith angle at each sampling location. Spatial interpolation was performed for each month for both day and night, resulting in 24 matrices per year that were then combined to produce 45 annual matrices covering the period 1960–2004. The monthly gridded temperature and salinity data were also combined per year to produce 45 annual matrices.

The values of each annual matrix for each parameter were averaged to produce yearly mean values of abundances of mackerel larvae, zooplankton, dinoflagellates, diatoms, as well as yearly mean values of CHLO, temperature and salinity. Standardised anomalies in the long-term trends of every variable were calculated by removing the mean from every yearly value before reducing it by the standard deviation of that variable across 45 years of data.

2.8. Multivariate analysis

As fluctuations in the abundance of fish larvae are likely to be influenced by several biotic and abiotic factors, correlated or independent, we used a multivariate technique to investigate the combined effect of the 7 environmental and biological variables described above (i.e. mid-column temperature and salinity, NAO, CHLO, abundances of diatoms, dinoflagellates and zooplankton).

First, a standardized principal component analysis (PCA) was performed on the matrix of annual values (1960–2004) of the selected parameters (PCA, 45 yr × 7 variables). We considered external conditions to influence larvae, adults prior to spawning and the quality and quantity of eggs produced; so in order to match the seasonality of mackerel (Fig. 2) with environmental conditions, we performed the PCA by using annual means for all 7 variables covering 12 months up to the last month of larval presence (i.e. September the previous year to August).

A Hierarchical Cluster Analysis (HCA, with Euclidian distance and agglomerative ward criteria) was then applied on the table of scores obtained from PCA analysis. Only those components explaining 70–80% of total variance were used. The aim of the PCA with HCA was to identify major patterns of year-to-year changes in the environmental composition of the study area.

Second, a PCA was performed on the matrix of monthly values of the same parameters (PCA, 540 months × 7 variables). The aim of this PCA was to also consider seasonal variability of the selected variables and identify monthly changes in environmental composition of the studied ecosystem, and their impacts on mackerel larvae in the study area.

2.9. Correlations

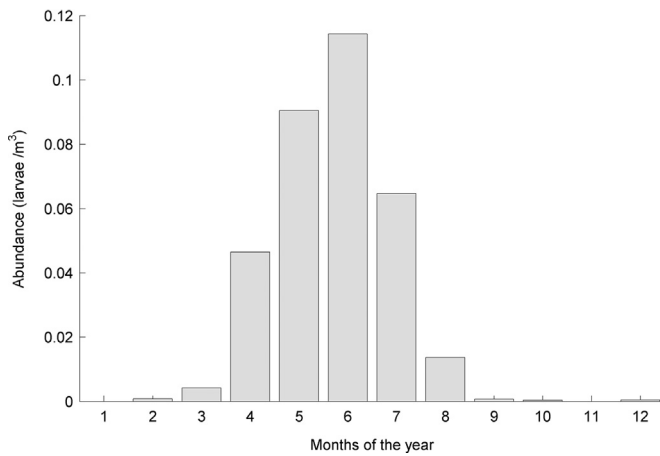In order to explore relationships and synchrony between fish

Fig. 2. Monthly abundance and seasonality of Atlantic mackerel larvae caught in Continuous Plankton Recorder samples, within area of study and 1960–2004.

larvae and environmental conditions, year-to-year fluctuations in abundance of fish larvae were correlated with the results from the PCA on the matrix of annual values. Pearson linear correlation coefficients were calculated, but to account for autocorrelation, the degrees of freedom were adjusted for autocorrelation via the modified Chelton method, with the Chatfield estimator, and the number of lags to be considered in computing autocorrelation taken as one-fifth of the length of the time-series (Pyper and Perterman, 1998).

3. Results

3.1. PCA on the matrix of annual (September–August) environmental values

The results are shown in Table 1 (first set of loadings (a)). The first principal component (PC1) contributes 42.57% of the variance, the greatest loadings on PC1 being zooplankton (0.48) followed by dinoflagellate (0.45) and diatom abundance (0.44), and salinity (0.41). PC2 (16.58% of variance) mostly reflects the winter NAO (0.78), and PC3 (15.34% of variance) is largely driven by

Table 1
Principal component analysis (PCA) of seven environmental and biological parameters for the period 1960 to 2004, showing annual values September–August (a) and monthly values (b). Bold values indicate the greatest loading for each principal component.

PCA loadings and variability by component	PC1	PC2	PC3
(a) PCA, table years (September–August) × variables			
Zooplankton abundance	**0.48**	0.35	−0.20
Diatoms abundance	**0.44**	0.10	0.27
Dinoflagellates abundance	**0.45**	0.31	−0.01
CHLO	−0.38	0.27	0.01
Temperature	−0.24	0.10	**0.81**
Salinity	**0.41**	−0.30	**0.47**
Winter NAO	−0.12	**0.78**	0.13
Percentage total variance explained	*42.57*	*16.58*	*15.34*
(b) PCA, table months–years × variables			
Zooplankton abundance	**0.49**	−0.07	−0.02
Diatoms abundance	**0.46**	−0.23	−0.12
Dinoflagellates abundance	**0.49**	0.03	0.03
CHLO	0.40	**−0.42**	−0.17
Temperature	0.32	**0.42**	0.31
Salinity	0.22	**0.67**	0.17
NAO	−0.02	−0.37	**0.91**
Percentage total variance explained	*53.67*	*17.50*	*13.92*

temperature (0.81) and salinity (0.47). In summary, PC1 is driven mainly by plankton and potential prey for fish larvae, while PC2 and PC3 are driven by climate and physical variables respectively.

Application of the HCA on the matrix of scores (3 first components, 74.79% of total variance) reveals 3 ecosystem states, each with a specific combination of the environmental variables selected for in the PCA (Figs. 3 and 4). State A is characterized by the highest values of PC1, the most important drivers being high abundances of zooplankton, diatoms and dinoflagellates and high salinity combined with low abundances of the smaller phytoplankton species (CHLO), in combination with generally positive values of PC2 driven by the NAO. State B is characterized by mostly negative values of all 3 principal components. State C is characterized by the lowest values of PC1, therefore in opposition to State A.

There is a chronological progression from State A to State C via State B (Table 2). 1960–1968 (Period 1) is characterised by State A. 1969–1985 (Period 2a) fluctuates between States A and B with ecosystem State C appearing for the first time in 1982. 1986–1994 (Period 2b) is mostly defined by State B with State C occurring again in 1990. Finally, 1995–2004 (Period 3) is characterised by ecosystem State C. These results suggest that there have been a change in the ecosystem state of the west and south-west area of the British Isles from an ecosystem characterized by high values of salinity, abundances of zooplankton and the larger phytoplankton groups, and low abundances of the smaller phytoplankton groups (1961–1968, Period 1), passing through a transition period (1969–1994, Period 2), to an ecosystem characterized with high temperature and abundances of the small phytoplankton groups, and low values of salinity and abundances of zooplankton and the larger groups of phytoplankton (1994–2004, Period 3) (Fig. 5).

3.2. PCA on the matrix of monthly environmental values

Results are listed in Table 1 (second set (b)). PC1 contributes 53.67% of the variance, the greatest loadings being zooplankton and dinoflagellate abundances (both 0.49) followed by diatoms (0.46). Potential prey for the fish larvae are again the major drivers of PC1. PC2 (17.50% of variance) is mainly driven by salinity (0.67) followed by temperature and CHLO (0.42 and −0.42 respectively). PC3 (13.92% of variance) is largely dominated by the NAO (0.91).

Visual examination of long-term monthly changes in the first three principal components (Fig. 6) revealed some distinctions between the 3 periods: Period 1 is characterized by the highest PC1 anomalies and generally positive PC2 anomalies; Transition Period 2 (2a+2b) is chacterised by generally negative PC1 and PC2 anomalies; And Period 3 is characterized by generally negative PC1 anomalies. However, the distinction between the periods of time is not as strong as for the results obtained from PCA analysis performed on annual matrices, indicating that the annual variability is not always strong enough to mask the seasonal variability.

3.3. Atlantic mackerel larvae and PCA

We correlated larval fish abundance with PC1, PC2 and PC3 from the yearly analysis (Table 3). The only significant correlation was between PC2 and the annual abundances of mackerel larvae (Fig. 7, $R=0.41$, $p=0.01$). The link between PC2 and Atlantic mackerel larvae was attributable mainly to the winter NAO (loading of 0.78 on PC2, Table 1). Indeed, the highest values of mackerel larvae abundances recorded during the early 1990s coincided with a period of high NAO (Fig. 5). However, PC2 as a predictor only explains 16.58% of the environmental variability and the NAO index is only a part of that (78%); consequently the correlation between larval abundance and NAO is very weak.
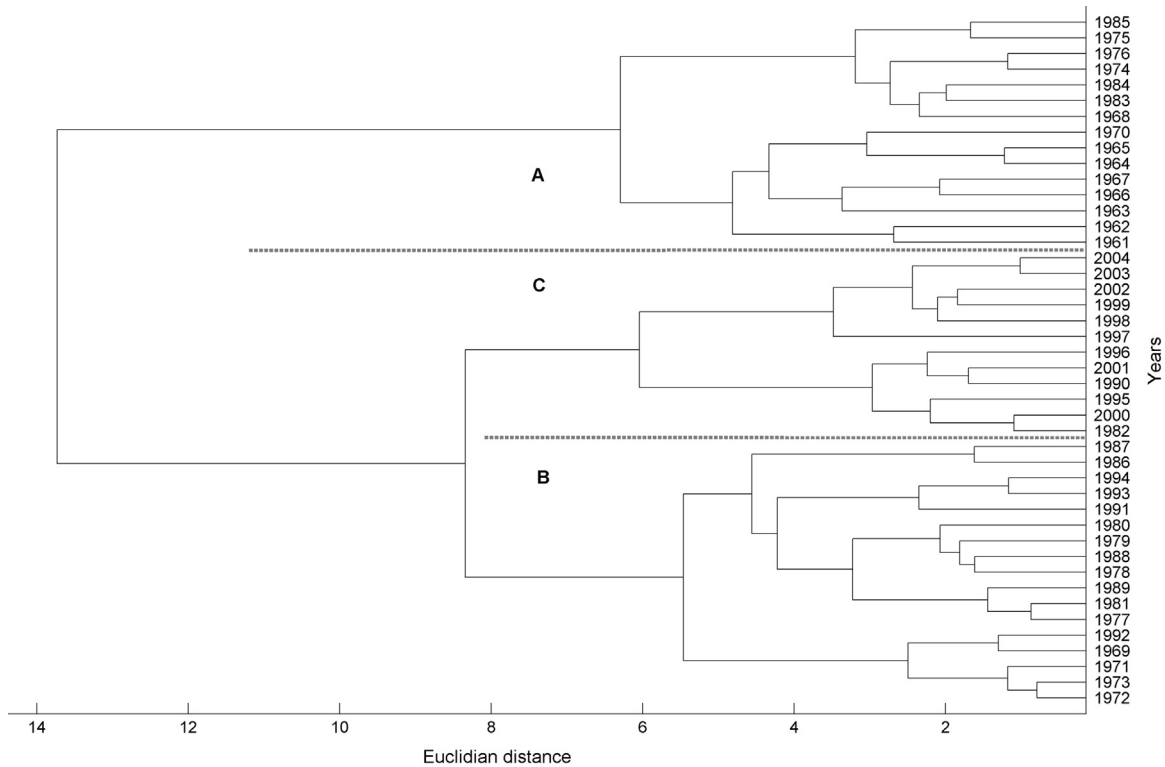
Fig. 3. Dendrogram produced from Hierarchical Cluster analysis (HCA) applied on the table of scores obtained from PCA performed on the matrix of annual values (September 1960–August 2004) of seven selected environmental parameters. The dashed black lines indicate the separation between the 3 main groups of years: A, B and C, each characterized by a specific "ecosystem state" as defined by values of first 3 principal components.
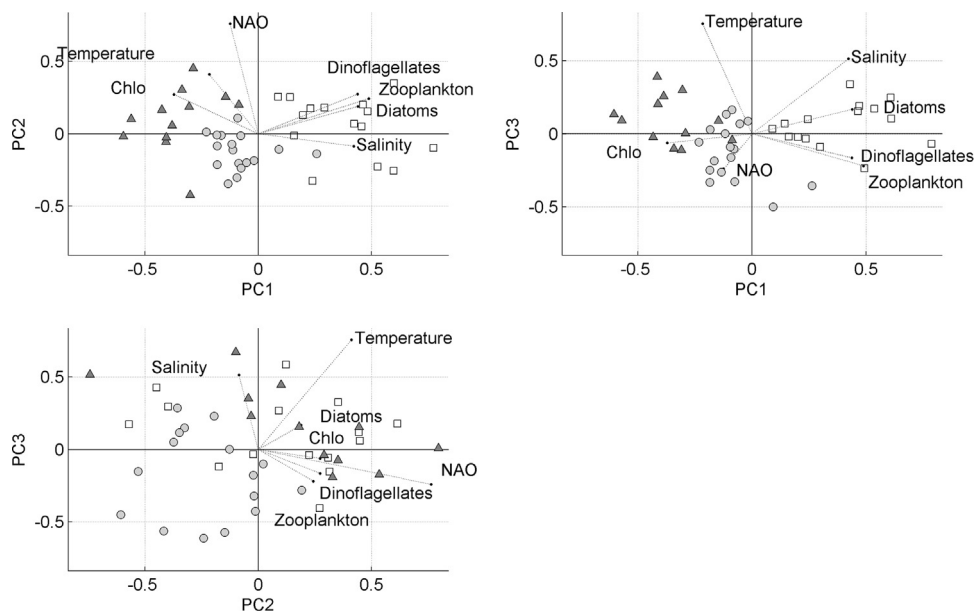
Fig. 4. Scores plots of the first 3 principal components (PC2 vs. PC1, PC3 vs. PC1 and PC3 vs. PC2) for the analysis performed on the matrix of annual values (September–August) of 7 selected environmental variables and biological parameters (PCA, 45 yr × variables, Table 1(a)). Markers and colours indicate the ecosystem state from HCA (Fig. 3, Table 2): State A: black clear square, State B: light grey circle, State C: dark grey triangle.

4. Discussion and conclusions

When comparing the results obtained here with results obtained in previous work using similar datasets and techniques in the North Sea (Pitois et al., 2012), we find both differences and similarities:

In the North Sea results showed that long-term environmental changes were critical in defining the status of the ecosystem, as the results from the PCA analysis were still visible when seasonal variability was taken into consideration. The present results suggest that the effects of long-term variability in the variables are obscured by the seasonal variability of the selected variables. This could be because the two areas are very different in their hydrological features: the west and south-west area of the British Isles is entirely open to the influence of the Atlantic ocean, while the North Sea is semi-enclosed thus rendering it more sensitive to

Table 2
Results obtained from Hierarchical Cluster analysis (HCA) applied on the table of scores obtained from PCA performed on the matrix of annual values (Fig. 3). Years represented by ecosystem state A have a clear background, years represented by ecosystem state B a light grey one and years represented by ecosystem state C a darker grey one.

Years (September–August)				
1961	1970	1979	1988	1997
1962	1971	1980	1989	1998
1963	1972	1981	1990	1999
1964	1973	1982	1991	2000
1965	1974	1983	1992	2001
1966	1975	1984	1993	2002
1967	1976	1985	1994	2003
1968	1977	1986	1995	2004
1969	1978	1987	1996	

environmental changes. This could also explain why the periods of time defined by the multivariate analysis were different in the two areas. Indeed, several studies point towards two regime shifts in the North Sea, first in the mid-late 1980s and then in the mid-late 1990s (Beaugrand, 2004; Beaugrand and Ibañez, 2004); these apparent events were seen in the previous North Sea study (Pitois et al., 2012). Spencer et al. (2012) also found regime shifts in the Celtic Sea in the early 1990s and in the west of Scotland in the mid 1990s. Our results show a transition from Period 2 to Period 3 consistent with a regime shift at that time. Furthermore, the transition from ecosystem state A to B and C seems to follow the fluctuations of the Atlantic Multi-decadal Oscillation (AMO, Schlesinger and Ramankutty, 1994) signal, with Period A and C corresponding with positive anomalies and Period B with negative anomalies (Fig. 5). The AMO signal is defined from the patterns of SST variability in the North Atlantic once any linear trend has been removed; It has been found to accounts for the second most important macro-trend in North Atlantic plankton, and to be responsible for habitat switching (abrupt ecosystem/regime shifts) over multi-decadal scales impacting on the fortunes of various fisheries such as sardine and anchovies over many centuries (Edwards et al., 2013). It is therefore possible that fluctuations in the AMO may also affect the health of the mackerel population.

North Sea PCA results suggested a cascading effect from climate variability to plankton via hydrographical changes within the North Sea: The NAO appeared to be an underlying driving force on the physical status of the North Sea ecosystem, in turn impacting on the ecological status of the North Sea ecosystem as characterised by PC1 (zooplankton and phytoplankton). In the present study, plankton and salinity were the main contributors to PC1, the NAO the greatest contributor to PC2 while temperature and salinity contribute to PC3 (Table 1); However the relative contribution to the total variability is only 16.58% and 15.34% for PC2 and PC3 respectively, thus making the relative importance of the second and third principal component very close to each other. In agreement with our results and in the context of climate change, other recent studies have found the long term effects of bottom-up effects to be weaker in the Celtic Sea compared to the North Sea (Lauria et al., 2013). In any case, In both the North Sea and the west–southwest areas our results show a similar transition from an ecosystem characterized with high salinity, low temperature, high abundances of zooplankton and the larger phytoplankton species to a system characterized by higher temperature, lower salinities, lower abundances of zooplankton and larger phytoplankton and more abundant small phytoplankton species.

Similar to results obtained in the North Sea study, no relationship was found between plankton and mackerel larvae (i.e. via the first principal component), zooplankton is nonetheless important as food for both the adults and larvae in both regions. Mackerel is a relatively fast and constantly swimming species, thus able to react to the environment by migrating over long distances. This dynamic spatial behaviour enables the mackerel to avoid poor temperature conditions during its migration in search of optimal areas for reproduction and feeding. Our study over the entire area covering 47°N to 60°N and longitudes 14°W and 2°W, did not take into account year to year spatio-temporal variability in spawning within this large area, as mackerel adapt to environmental variability, and this could be a reason for the lack of an apparent relationship between yearly mackerel abundance and plankton and temperature in this study.

We found a statistically significant positive correlation between mackerel larvae yearly abundance and PC2. This was also found in the North Sea study; however, while PC2 primarily reflected salinity in the North Sea, it was dominated by the NAO in the present
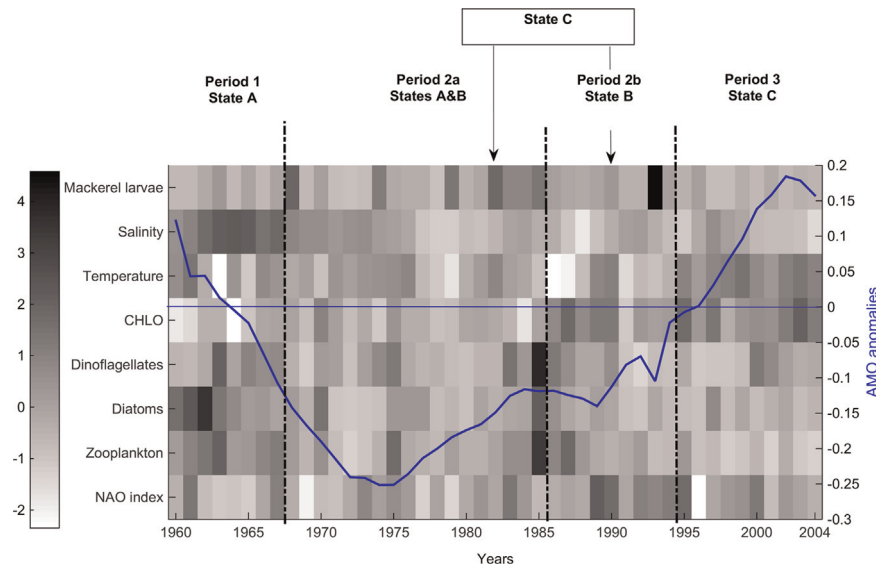
Fig. 5. Standardised anomalies in annual fluctuations in the abundance of mackerel larvae, and the environmental and biological variables selected for multivariate analysis. Dashed vertical lines show the boundaries between the periods of time (1, 2a, 2b and 3) identified by the PCA/HCA. The signal for the Atlantic Multi-decadal Oscillation (AMO) is superimposed onto the figure. The data for the AMO was provided by the National Centre for Atmospheric Research Staff (2013).
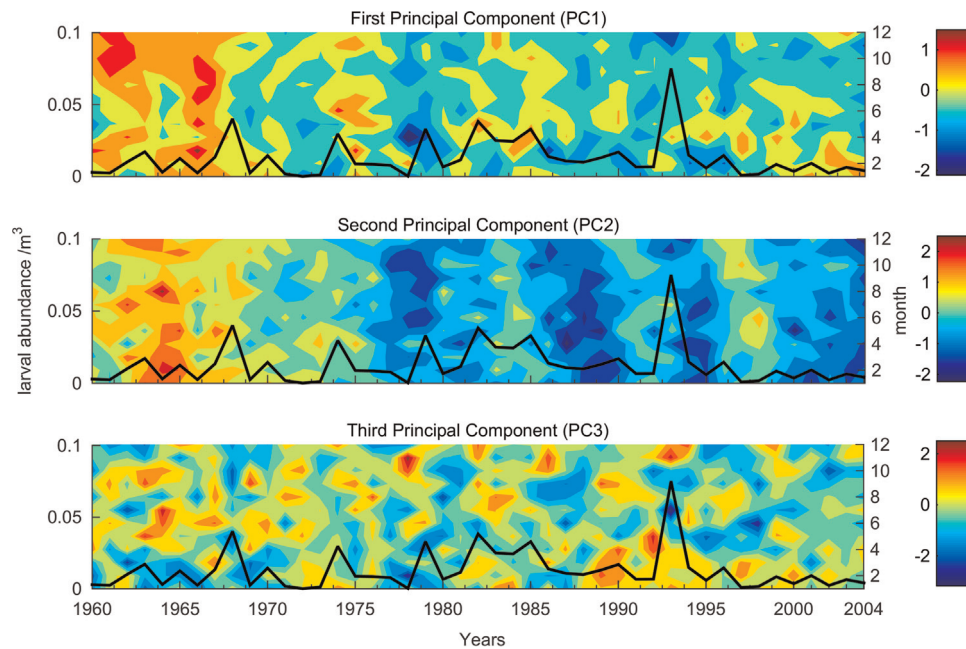
Fig. 6. Long-term monthly variability (1960–2004) in the 7 environmental variables used simultaneously as first (PC1), second (PC2) and third (PC3) principal components (respectively explaining 53.67%, 17.50% and 13.92% of total variability). The black line represents the annual abundance of Atlantic mackerel larvae, superimposed on monthly principal component anomalies.

Table 3

Pearson's correlation coefficients (with associated *p*-values) between annual abundance of fish larvae and the first (PC1) second (PC2) and third principal components (PC3) resulting from analysis of the annual average to match the seasonality of fish larvae (April–August). The *p*-value was adjusted taking into account autocorrelation. A value in bold type indicates that the relationship is significant within a 95% level confidence interval.

	Mackerel larvae yearly abundance	
	R	p
PC1	0.19	0.32
PC2	**0.41**	**0.01**
PC3	− 0.11	0.55

study. The NAO index expresses the atmospheric pressure gradient over the North Atlantic, which affects the speed and direction of westerly winds, heat and moisture transport (Hurrell, 1995). The wind pushes the water masses and the currents and circulation patterns influence some ecological processes (Hurrell et al., 2003). Many authors have speculated about the link between prevailing weather or climatic conditions and the 'recruitment' (year class strength) of commercial fish species. Borja et al. (2002) suggested that the southern pre-spawning migration pattern of Atlantic mackerel is directed towards areas with low turbulent mixing at spawning time, providing a 'stable environment' for egg and larval survival. In contrast, in the northern areas, the role of turbulence over the entire year becomes increasingly more relevant; this is related, to the high levels of turbulence during autumn and winter, which may become limiting to the survival of juveniles. Patterns in the NAO have been found to correlate with recruitment variability in a number of important North Atlantic fish species, including sandeel and cod (e.g. Arnott et al., 2002; Brander and Mohn, 2004). However, in the present study, PC2 only explains 16.58% of the environmental variability and the NAO index is only a part of that (78%). Consequently, in the broader perspective, the correlation between larval abundance and NAO is extremely weak indeed, and caution must be applied when interpreting such results.

There is however a growing body of literature that relates

mackerel ecology and the physical environment, suggesting that mackerel is sensitive and highly responsive to variations in these physical variables. Timing and location of migration during autumn and winter as well as timing and location of spawning appear to be related to temperature (Jansen et al., 2012a; Jansen and Gislason, 2011; Jansen and Gislason, 2013; Reid et al., 1997). Furthermore, the abundance of juvenile recruits has been shown to be related to wind induced turbulence (Borja et al., 2002; Villamor et al., 2011). The weak but significant relation between PC2 and the number of larvae caught by the CPR may thus be a consequence of a number of environment-mediated processes. The strongest effect may, however, come from processes involving wind-induced turbulence related to mackerel recruitment, because of the tight link between NAO and wind, and a likely link between abundance of larvae and of juvenile recruits. The actual mechanisms behind this correlation are not known. Potential mechanisms include effects on vertical distribution (availability to the CPR sampler), productivity of food and the match/mismatch between food and appearance of early life stages.

According to the most recent assessment (AR5) of the UN Intergovernmental Panel on Climate Change (IPCC), the NAO is one of the climate modes for which it is most difficult to provide accurate future projections (Stocker et al., 2013). Wintertime NAO is very likely to exhibit large natural variations in the future of similar magnitude to those observed in the past, but different climate models suggest different long-term outcomes in terms of whether or not the NAO will tend towards more positive or negative values in the future. Recent multi-model studies (e.g. Gillett and Fyfe, 2013; Karpechko, 2010) suggest overall that the NAO is likely to become slightly more positive (on average) in the future due to increases in greenhouse gas emissions (Stocker et al., 2013). From the present results, we might therefore expect a slight tendency towards increasing mackerel larvae abundance and potentially recruitment in the future if the relationships observed in the past continue to hold. This prediction is however based on "unsure" climate projections and weak links between mackerel larvae abundance and NAO from data stretching from 1960 to 2005. For the most recent years (after 2005) when the stock expanded (ICES, 2014), the NAO fluctuated without clear trend (Hurrell, 2014).
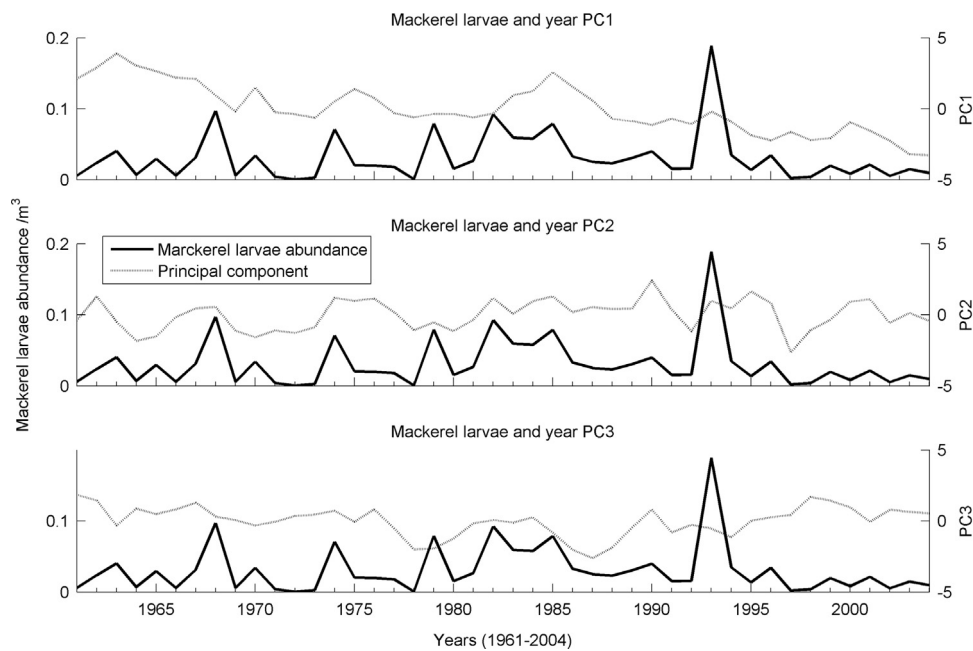
Fig. 7. Long-term variability in larval mackerel annual abundance in the area of study superimposed on changes in the first three principal components (PC1, PC2 and PC3). The standardized PCA was carried out on annual means of the 7 selected environmental variables calculated according to larval seasonality.

Nonetheless, such a hypothesis would be worth investigating further. In addition, more recently, the ecological importance of the variability in the AMO has been recognised (Drinkwater et al. 2014; Edwards et al., 2013; Nye et al. 2014), in particular in the subpolar gyre region (Harris et al., 2014); and it is possible that these two climate variability patterns interact with each other, thus making it difficult to discern the effect of either the AMO or the NAO on their own.

Traditionally, the North Sea and Western mackerel stocks have been viewed as two different components of the wider North East Atlantic mackerel stock, according to their distinct spawning locations (Fig. 1). Although, the mackerel caught in the North Sea was found to be generally larger at age than the typical Western mackerel, even in the years and seasons when Western mackerel dominated in the catches in the North Sea (Skagen, 1989), no study has managed so far to conclusively identify any physiological or genetic difference between the individuals of these two components, and recent work by (Jansen and Gislason, 2013) have suggested that the two spawning populations are connected by straying mackerel and these stock components are therefore not isolated. This latest result is an added challenge to our understanding of the behavioural, environmental and anthropogenic drivers of mackerel population dynamics.

The present analysis did not reveal substantial new aspects of mackerel ecology, but the results presented are in broad accord with recent investigations that link climatic variability and dynamics of mackerel reproduction. Furthermore, extra caution is required when attempting to draw conclusions concerning the development of the total stock of the NEA mackerel on the basis of a part of their spawning area: an important spawning ground also exists in the Bay of Biscay (ICES, 2013) but is not represented here. In a climate change scenario, our results combined with those extracted from the latest studies on NEA mackerel life cycle and population dynamics suggest that mackerel is likely to be affected in the future with subsequent consequences for the fishery and for mackerel predators and prey. Juvenile mackerel are thought to be an important prey item for demersal predators such as hake and whiting in the Celtic Sea (Trenkel et al., 2005) and predation by adult mackerel is known to have a very important influence on

juvenile survivorship of commercial fish species in the North Sea (Sparholt, 1990). However, the growing body of literature that documents statistical correlations between environment and mackerel need to be supplemented by local process studies, to gain more insight and to be able to predict mackerel responses to future climate change scenarios. In future studies, the abundance signals in this unique long dataset may be more clearly extracted by lcg-modelling as it has recently been shown (Jansen et al., 2014). Furthermore, utilising the primary strength of the dataset, namely the unique temporal coverage, in an analysis where other data (such as egg surveys) are drawn in to compensate for the spatial issues could prove to be the way forward.

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