Recent changes in ichthyoplanktonic assemblages of the eastern English Channel

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Abstract :

ish assemblages vary through time in both abundance and diversity, often due to changes in climate. The potential consequences of these changes on the larval phase need to be considered. In the Eastern English Channel, fish larvae of 30 taxa, from surveys conducted during spring in the nineties and in 2017 with bongo nets, were used to investigate seasonal and interannual changes in larval assemblages with different statistical tests and multivariate analyses (Outlying Mean Index, Principal Coordinate Analysis and variance partitioning). The major change observed was significant lower abundances in 2017 (in April and May) compared to the nineties. Most of the dominant taxa were two to three-fold less abundant in 2017 than the 1990s. We suggest that the reduced larval abundances in 2017 could be a consequence of lower adult abundances in the area from a switch from a colder to a warmer phase of the Atlantic Multidecadal Oscillation.

Highlights

► Larval assemblages were dominated by ten species. ► Overall abundances and diversity increased across the spring season. ► Larval abundances were significantly lower in 2017 compared to the nineties. ► Several larval and adult fish species responded similarly to a shift in the AMO.

1. Introduction

In the context of global change, fish communities have undergone shifts in both abundance and species composition (Reid et al., 2001; Hawkins et al., 2013). In the Eastern English Channel (ECC), Auber et al. (2015, 2017) noted an increase in sea surface temperature at the end of the nineties to explain the significant decrease in fish abundance at the community level. However, the underlying mechanism remains unclear and the potential role of the larval phase in these changes has not been investigated. In spring, the spatial distribution of larval assemblages on the southern side of the EEC is influenced by a coastal front (Grioche and Koubbi, 1997) which varies according to the winds and the megatidal regime of the EEC. The coastal waters along the French coast differ in terms of hydrobiological characteristics (e.g. salinity, turbidity, phytoplankton, zooplankton) from the central waters (Brylinski and Lagadeuc, 1990). Most of the fish larvae in this area are distributed according to this coastal/offshore separation (Grioche et al., 1999, 2000, 2001; Koubbi et al., 2006) with younger larvae in the central waters and older larvae closer to the southern coast. On the northern side, while observations are more limited, the absence of this frontal structure leads to a different configuration in larval assemblages (Koubbi et al., 2006).

The crucial role of the larval phase in fish population dynamics has been widely recognised (see Miller and Kendall, 2009; Somarakis et al., 2018). Fish larvae are influenced by fluctuations of abiotic and biotic conditions including species interactions such as

predation, competition and food availability (Miller and Kendall, 2009; Houde, 1987). Ichthyoplanktonic studies, thanks to oceanographic surveys, aim to acquire essential data on fish early life stages in terms of abundances, diversity, spatio-temporal distributions and physiological condition. These data can be used to compute recruitment indices as well as indicators of spawning dynamics and changes in the ecosystem that can be integrated within ecosystem models. While spring surveys were regularly programmed during the nineties on the southern EEC, no survey was conducted from 1999 to 2017. The completion of three new surveys conducted in 2017 in the same area of the EEC throughout the springtime allowed comparisons of larval assemblages between the nineties and 2017.

The main objective of this paper is to compare fish larvae assemblages in terms of species composition between these two contrasting periods of sea surface temperature. In particular, the role of different sources of variation, including spatial, seasonal, inter-annual and environmental effects, on the fluctuations of larval assemblages has been investigated.

2. Materials and Methods

2.1 Sampling strategy

Data came from thirteen ichthyoplanktonic surveys that were conducted in the EEC, especially in its southern part, between March and June in 1993, 1994, 1995, 1999 and 2017 (Table 1). Coastal-offshore sampling was primarily performed between the Bay of Seine and Belgium and between the Isle of Wight and the Thames estuary (Figure 1). At each of the 308 stations where ichthyoplankton was sampled, environmental variables were recorded.
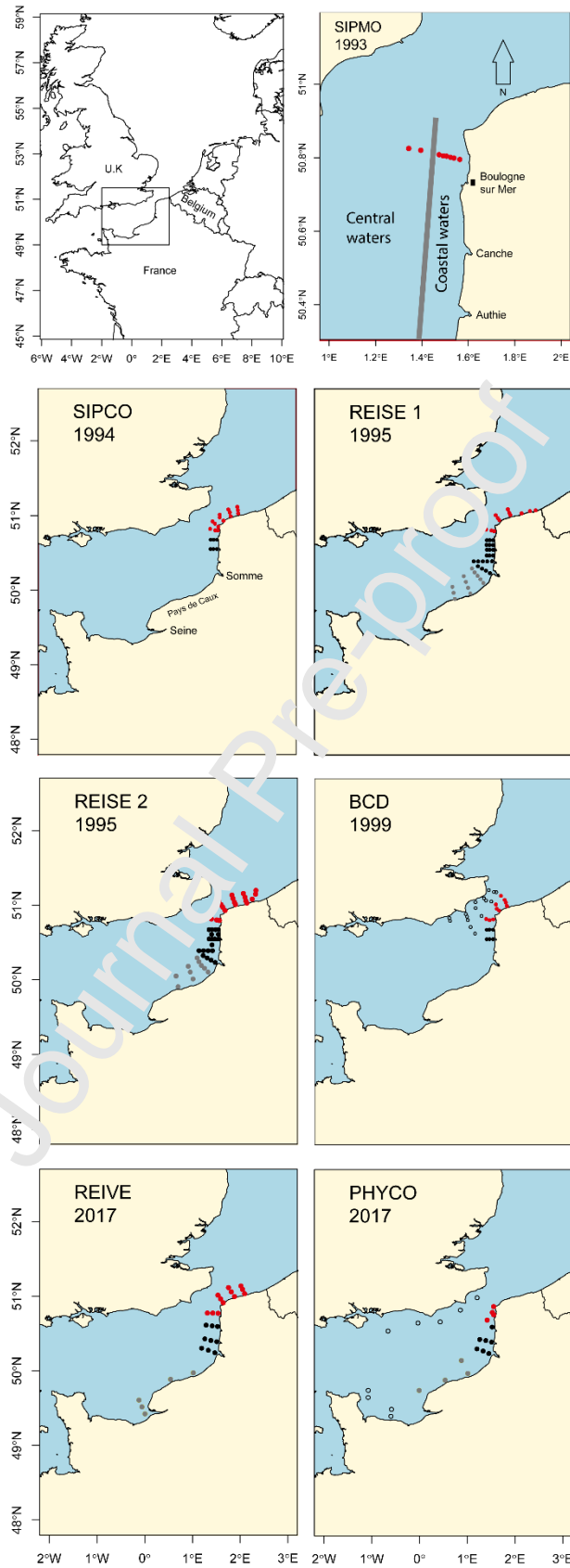
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Table 1: List of the sampling surveys. Dates of sampling and number of stations are indicated.

Survey	Start	End	Number of stations
SIPMO 4	01/04/1993	01/04/1993	8
SIPMO 5	14/05/1993	14/05/1993	8
SIPMO 6	25/06/1993	25/06/1993	8
SIPCOI	28/04/1994	29/04/1994	21
SIPCOII	27/05/1994	31/05/1994	20
SIPCOIII	23/06/1994	27/06/1994	21
REISEI	11/04/1995	13/04/1995	45
REISEII	02/05/1995	04/05/1995	48
SIPCOIV	24/05/1995	26/05/1995	21
BCD	27/04/1999	01/05/1999	32
REIVE1	23/03/2017	30/03/2017	26
PHYCO	21/04/2017	29/04/2017	24
REIVE2	05/05/2017	12/05/2017	26

2.2 Fish larvae sampling and identification

Fish larvae were sampled using a bongo net (60 cm diameter, Smith, 1977) fitted with either two 500 μm nets or with one 500 and one 330 μm net. The net was deployed at two knots through a double oblique-tow between the surface and five meters above the seabed during at least 10 minutes. The filtered volume of seawater was estimated using a digital flowmeter fixed at the entry of each net. For this study, only the first net of 500 μm mesh size was considered. The content of the net was fixed in a buffered-formalin seawater solution for later identification at the laboratory. Fish larvae were sorted under a stereomicroscope and identified at the species, genus or family levels according to Russell (1976). Abundances of each taxon (ind.100 m^{-3}) were calculated using the filtered volume of seawater.

Figure 1: Location of sampling stations. Colors correspond to the three areas used for the Kruskal-Wallis test (grey = area A; black = area B and red = area C). Open circles are stations which were not allocated to an area. Coastal and central waters, separated by the front are represented.

2.3 Environmental variables

Vertical profiles of temperature (°C) and salinity were recorded using a Seabird SBE 19 CTD (Conductivity Temperature Depth) profiler. Geographical factors such as the distance to the coast and to the nearest estuary were post-calculated with a geographic information system (ArcMap 9.2 from ESRI). Bedstress (N.m^{-2}) and depth (m) were also mapped.

2.4 Statistical analyses

Of the 80 taxa encountered, statistical analyses were performed on the 30 taxa that were present in at least five percent of all the stations sampled. Abundances were log-transformed (log[x+1]). Statistical and multivariate analyses were applied under the R software (R Core Team, 2018) and the threshold of significance for all analyses was set at an alpha of 0.05.

Annual differences in total larval abundance were tested using non-parametric Kruskal-Wallis tests (Hollander and Wolfe, 1973) performed on April and May surveys. Only taxa accounting for 80% of the total abundance were analysed. The southern side of EEC between the Bay of Seine and Belgium, i.e. the common area for all surveys, was also divided into three areas based on sampling regularity between years and larval composition from previous studies (Grioche et al., 2001; Koubbi et al., 2006): the Seine estuary to the south of the Somme estuary along the Pays de Caux (A), the three estuaries (Somme, Authie and Canche) of the Opale coast (B) (the most regularly sampled between years) and from Boulogne-sur-Mer to Belgium (C, Figure 1). Monthly and annual quantiles of abundances were also calculated for taxa that accounted for 80% of the total abundance from all surveys.

A Principal Coordinates Analysis (PCoA) was used to compare the similarity of larval assemblages between all samples and surveys. PCoA is the generalization of the PCA to any

distance matrix (Legendre and Legendre, 2012). Here, the Bray Curtis distance was used to calculate the dissimilarity matrix from the fauna matrix.

The collinearity between the environmental and geographical variables was assessed using a Pearson correlation test. When two variables had a significant correlation coefficient higher than or equal to 0.6, one of the two variables was removed.

Taxa-environment relationships were studied using an Outlying Mean Index analysis (OMI, Dolédec et al., 2000) performed using all surveys. Temperature, salinity, distance to the coast and to the nearest estuary, bedstress, depth and latitude were used as explanatory variables. This method is a co-inertia analysis between an environmental data matrix, in the form of a PCA, and a fauna data matrix. OMI investigates the relevance of the environmental factors by separating taxa according to the characteristics of their habitat. Average conditions are represented by the origin of the axes. OMI analysis provides for each taxon a marginality index (called OMI) that represents the distance between the average conditions of the habitat used by the taxon and the average conditions over all of the stations (*i.e.* axes origin). It also provides a tolerance index (Tol), which is the spatial variance of the niche across environmental conditions. Taxa having low OMI and high Tol values are represented close to the axes origin and are considered ubiquitous (*i.e.* they occupy a wide range of environmental conditions). Conversely, high OMI and low Tol values represent marginal or specialist taxa. Significance of the OMI values was tested by a Monte Carlo permutation test (999 permutations).

Influence of the environment, space and time on larval composition variation was investigated using a variance partitioning approach (Mood, 1971; Peres-Neto et al., 2006) as proposed by Legendre and Legendre (2012). Using all the surveys and their data available, the aim of this approach was to calculate the amount of variance explained in the fauna matrix by

each of the set of explanatory variables once the effect of the other variables (called co-variables) had been removed. It also permitted calculations of the amount of explained variation that was shared by the different variables. For the environment, temperature and salinity were used as the explanatory variables. For time and space, variables were built using Moran's eigenvector maps (MEM) approach which was proposed by Dray et al. (2006) based on Borcard and Legendre (2002). The principle of MEM is the construction of a series of variables representing either spatial (Loots et al., 2010) or temporal (Baho et al., 2015) structures. Three sets of variables: spatial, annual and seasonal, were created. For the seasonal and annual variables, the mean day of the month and the year of each survey were used to calculate the Euclidean distance matrix. For the spatial variables, the distance matrix was calculated on the latitude and corrected longitude (longitude*cos[(latitude*Pi)/180]) of the sampling stations (Loots et al., 2010). Distance matrices were then truncated by changing all values above a threshold (*i.e.* the highest distance between two neighbors) to four times that threshold, so that all the points remained connected. Eigenvectors (MEMs) with positive eigenvalues were extracted from a PCoA performed on each truncated matrix. A redundancy analysis (RDA) was then performed between the detrended table and all positive MEMs variables from each set of variables before checking significance by a Monte-Carlo permutation test (999 permutations). Significant MEMs variables were selected using a forward selection based on their adjusted R-square (R^2adj) with regard to the fauna data matrix, which was linearly detrended beforehand according to latitude and corrected longitude (Blanchet et al., 2008; Miller and Farr, 1971). The forward selection performs a Monte Carlo permutation test (999 permutations) on each variable and stops when either the R^2adj threshold is reached when adding a new variable or when the added variable is not significant. The variable inflation factor (VIF; Gross, 2003) was computed for each set of variables in order to examine the collinearity between environment, space and time (James et al., 2013).

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This method provides the ratio of variance between a model containing all variables and a model with a single variable. Only variables with a VIF below 15 were kept. Finally, variation partitioning was performed to quantify the part of variation in the larval assemblages explained by each set of variables (Anderson and Cribble, 1998), as well as the amount of explained variation shared by the different variables. The significance of the variation explained by each set of variables was assessed by a Monte Carlo permutation test (999 permutations).

3. Results

Table 2: List of the most frequently found fish larval taxa between 1993 and 2017 in the sampling area. Codes used in figures are also indicated.

Scientific name	Common name	Code
Ammodytidae	Sandeels	Amm spp
Buglossidium luteum	Solenette	Bug lut
Callionymidae	Dragonets	Cal spp
Clupea harengus	Atlantic herring	Clu har
Cottidae	Cottids	Cot spp
Dicentrarchus labrax	European bass	Dic lab
Diplecogaster bimaculata	Two-spotted clingfish	Dip bim
Echiichthys vipera	Lesser weever	Ech vip
Gadidae	Gadids	Gad spp
Gobiidae	Gobies	Gob spp
Labrus bergylta	Ballan wrasse	Lab ber
Limanda limanda	Common dab	Lim lim
Liparis liparis	Common seasnail	Lip lip
Liparis montagui	Montagu's seasnail	Lip mon
Lotidae	Lings	Lot spp
Merlangius merlangus	Whiting	Mer mer
Micrenophrys lilljeborgii	Norway bullhead	Mic lil
Microchirus variegatus	Thickback sole	Mic var
Platichthys flesus	European flounder	Pla fle
Pleuronectes platessa	European plaice	Ple pla
Sardina pilchardus	European pilchard	Sar pil
Scophthalmus maximus	Turbot	Sco max
Scomber scombrus	Atlantic mackerel	Sco sco
Solea solea	Dover sole	Sol sol
Sprattus sprattus	European sprat	Spr spr
Taurulus bubalis	Longspined bullhead	Tau bub

Trachurus trachurus	Atlantic horse mackerel	Tra tra
Trisopterus luscus	Pouting	Tri lus
Trisopterus minutus	Poor cod	Tri min
Trisopterus	Trisopterus	Tri spp

Kruskal-Wallis tests performed on total abundances between April and May for the three areas indicated that abundances in 2017 were significantly different from those in the nineties except for April in area C and with 1999 in area B (Table 3). There were also differences within the nineties, in particular between 1999 and the other years for April in area A and B. The only difference among 1993, 1994 and 1995 was found in April in area C between 1993 and 1994.

Table 3: results of the Kruskal-Wallis tests comparison between years and areas (see figure 1) for April and May surveys.

Area	Years comparison	p-value	
		April	May
A	1995-2017	<0.01	<0.01
B	1994-1995	0.27	0.99
	1994-1999	<0.01	-
	1994-2017	<0.01	<0.01
	1995-1999	<0.01	-
	1995-2017	<0.01	<0.01
	1999-2017	0.95	-
C	1993-1994	<0.05	0.96
	1993-1995	0.09	0.96
	1993-1999	0.38	-
	1993-2017	0.99	<0.01
	1994-1995	0.98	0.99
	1994-1999	0.98	-
	1994-2017	0.37	<0.01
	1995-1999	0.97	-
	1995-2017	0.59	<0.01
	1999-2017	0.97	-

Larval abundances per taxa were summarized by year and month (Figure 2). Of the 30 taxa initially used in the analysis, ten of them accounted for 80% of the cumulative abundance

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by month or year. These included two clupeids (sprat and herring), dragonets, gobies, sandeels, horse mackerel, whiting and three flatfishes (solenette, dab and sole). Sprat was the most abundant taxa in all years and months, accounting for 40% to 64.5% of the total abundance, followed by dragonets, gobies and sandeels. From 1993 to 1999, four or five taxa accounted for 80% of the total abundance and six in 2017 due to lower taxa abundances.
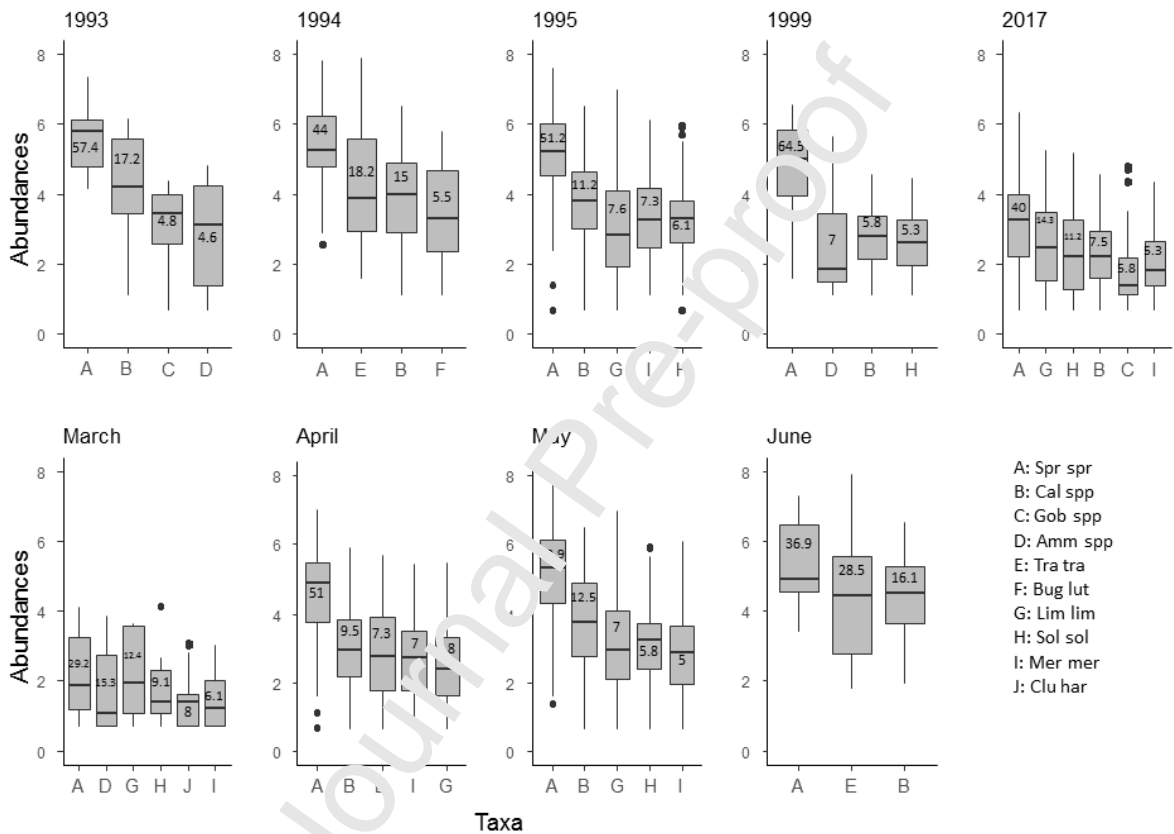

Figure 2: Larval abundances (ind.100m⁻³, log-transformed) by year (top) and month (bottom). Numbers inside the box plots are the proportions (%). For each plot, only the taxa accounting for 80% of the cumulative abundance are represented. Taxa abbreviations are given in Table 2. Note that March was only sampled in 2017 and June only in 1993 and 1994 (Table 1).

Differences in larval fish composition between months were also found. In March six taxa accounted for 80% of the total abundance (sprat, sandeels, dab, sole, herring and

whiting). In April, five dominant taxa emerged: sprat, dragonets, sandeels, whiting and dab whereas in May sandeels were replaced by sole. In June, the number of dominant taxa decreased to three with sprat, horse mackerel and dragonets. Sprat was always the most abundant taxa regardless of the month with a proportion ranging from 29.2% in March to 53.9% in May.

A PCoA was performed on larval assemblages per station and survey (Figure 3). The first two axes explained 50% and 23 % of the variability respectively. The different surveys were distributed along the first axis with March 2017 on the right, the ones of April and May in the middle and the June surveys of 1993 and 1994 on the left. Annual succession was also distributed along this axis with 1993 and 1994 mainly on the left, 1995 and 1999 in the middle and 2017 on the right. On the second axis, April and May of the nineties were separated from the other surveys.
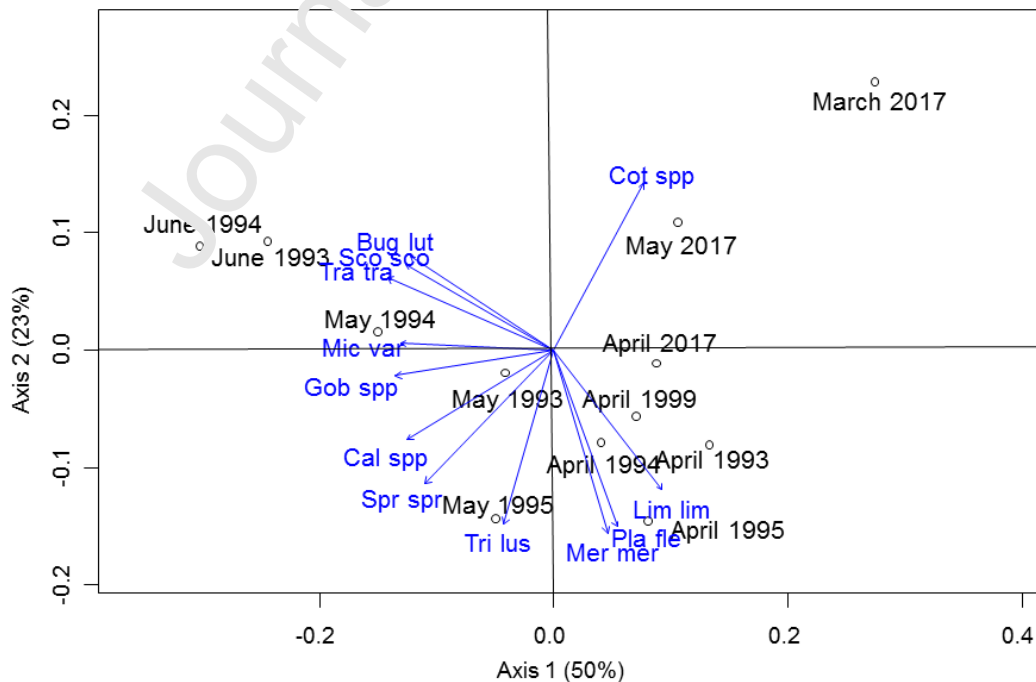
Figure 3: Principal coordinate analysis, factorial plane of the first two axes. Only taxa contributing significantly to the period separation along the axes are represented (permutation test, 999 permutations). Taxa abbreviations are given in Table 2. The barycentric position of each survey (indicated as month and year) is also represented.

All significant taxa, except cottids, were associated with, i.e. more abundant in, the nineties surveys. Dab, flounder and whiting were correlated with April surveys, thickback sole, gobies, dragonets, sprat and pouting with May surveys and solenette, mackerel and horse mackerel with June surveys.

A Pearson correlation test performed on the set of environmental and geographical variables revealed a strong correlation between latitude and bedstress ($R^2= 0.61$; F-statistic: 159.7; $p < 2.2e^{-16}$), and latitude was therefore removed from further analyses.

Results of the OMI analysis built upon the PCA on environmental factors, selected by the correlation test, and the fauna matrix were used to explore fish larval environmental preferences and dependencies (Figure 4). The total inertia represented 60% of the fauna matrix variation. Both axes had a cumulative projected inertia of 86% (53% and 33% respectively). The total number of taxa was related to depth and distance to the coast and not correlated with temperature. Most of the taxa were related with these geographical variables and low temperatures whereas solenette, mackerel, horse mackerel and lesser weever were related with high temperatures. Plaice and flounder appeared corelated with stations far from estuaries with low temperatures.
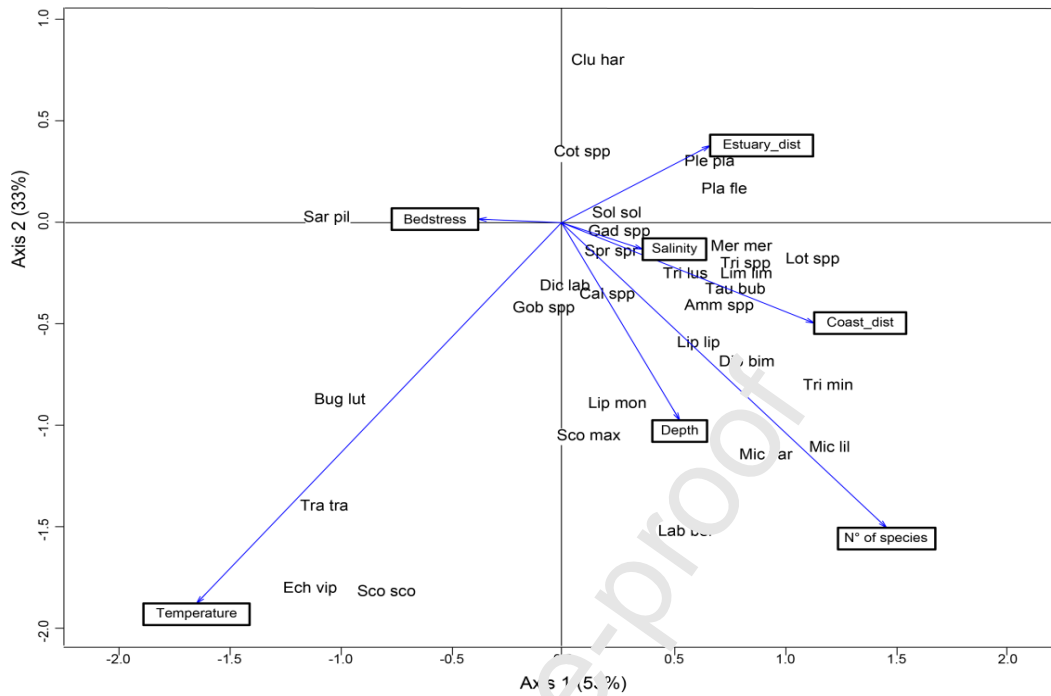
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Figure 4: OMI analysis: scatter plot of the first two axes. Arrow lengths represent the quality of representation of variables in boxes. Taxa abbreviations are given in Table 2. Note that all surveys were included in the analysis.

OMI and tolerance values were obtained (Figure 5). OMI values ranged from 0.06 (sprat) to 4.85 (lesser weever). The Monte Carlo permutation test showed that sea bass, two-spotted clingfish and gobies (other than whiting, pouting and poor cod) were not influenced by the set of variables used for the analysis. Sprat, sole, dragonets, gobies, pouting, whiting and sandeels had the lowest OMI values and high tolerance values, indicating ubiquitous taxa. Conversely, several taxa including lesser weever, mackerel, horse mackerel, sardine, wrasses, snailfishes and poor cod had the highest OMI values and lower tolerance values indicating specialist taxa. Other taxa such as cottids and solenette had intermediate OMI and tolerance values, characteristic of neither specialist nor generalist taxa.
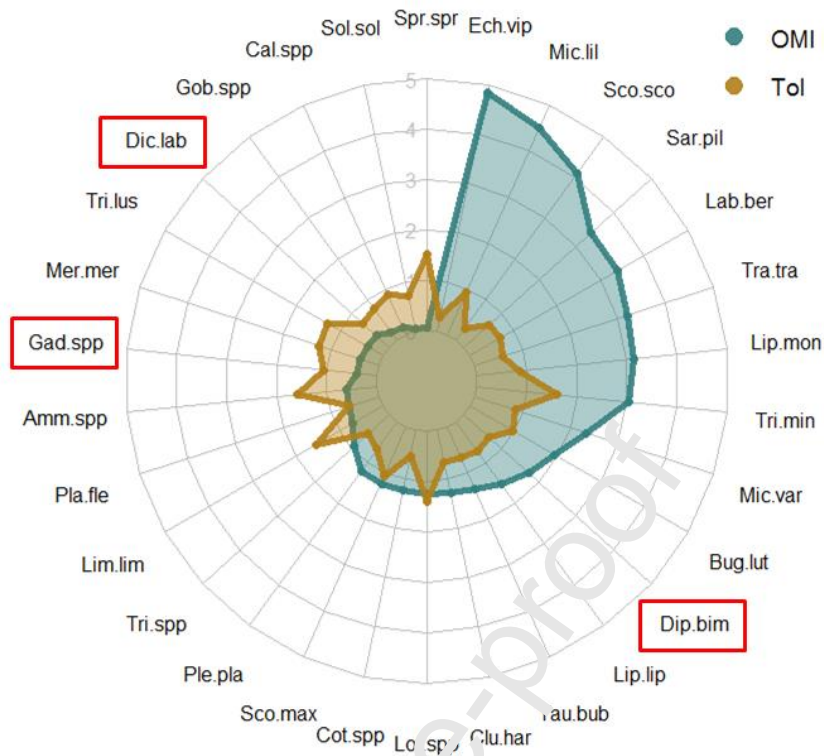
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Figure 5: radarchart of OMI (marginality) and tolerance (Tol) values for the 30 taxa. Red boxes show non-significant taxa. Taxa abbreviations are given in Table 2.

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Nine spatial (R²adj= 0.104), six seasonal (R²adj= 0.309) and four annual (R²adj= 0.158) variables were kept at the end of the MEM analysis. The variation partitioning results (Figure 6) indicated that 44% of the total variation was explained, 33% by the seasonal effect, 16% by the year effect, 10% by the spatial effect and 13% by the environmental effect. In terms of pure effect, season explained the most (12%) followed by space (5%), environment (3%) and year (2%). A large amount of variation was shared between the different variables, in particular between year and season (8%) and season and environment (7%), while environment and year shared no variation, and environment and space only 1%.
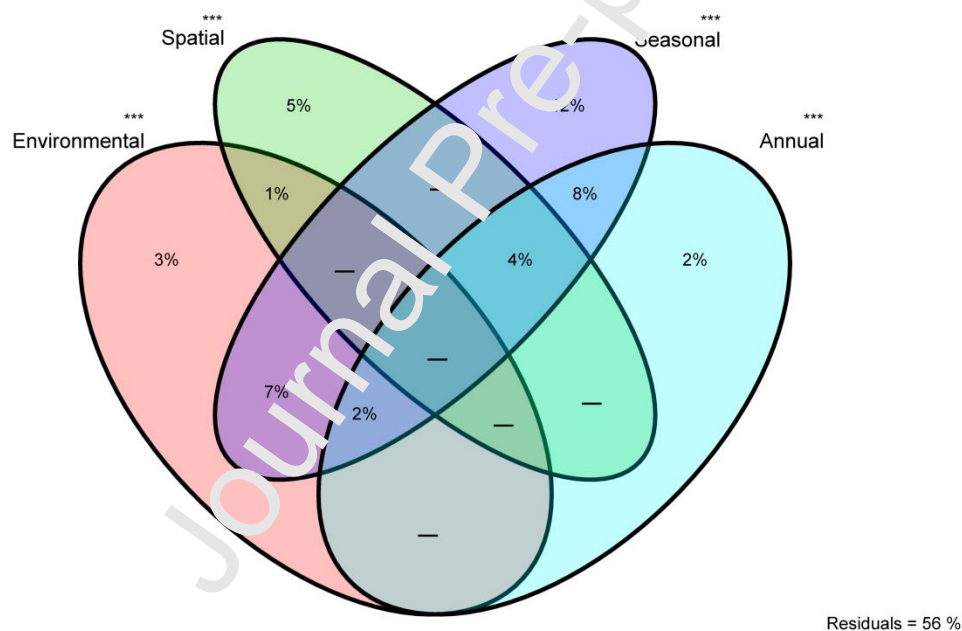

Figure 6: Variance partitioning analysis. Venn diagram showing the percentage of variation explained in the larval assemblages by each of the spatial, environmental, seasonal and annual effects. ***: p-value< 0.001. Note that all surveys were included in the analysis.

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4. Discussion

The contribution of different sources of variation including environment, year, season and geography on spring larval assemblages in the EEC was investigated. Whereas the present study area pertains to a limited part of the English Channel, the eastern part provides important spawning and nursery areas for many species (Carpentier et al., 2009; Eastwood et al., 2003). This paper gives an update on the seasonal succession of the main larval fish species encountered in spring. It appeared that the year and seasonal effects linked to environmental conditions were the main drivers explaining the observed variation whereas the spatial effect did not substantially change between the nineties and 2017. OMI analysis revealed that the number of species was positively correlated with the distance to the coast and depth. This could stem from the frontal zone impact on larval assemblages well described by Grioche and Koubbi (1997) and Grioche et al. (1999) who showed a spatial segregation of fish larvae assemblages between coastal and central waters in the south of the EEC due to a frontal zone acting more or less as a permeable barrier (depending on the tidal regime). This spatial pattern is accentuated by the ontogenetic migration of several larval species from the offshore spawning grounds towards coastal nurseries (Grioche et al., 2001; Koubbi et al., 2006). However, the variance partitioning analysis also revealed that this spatial effect only accounted for 10% of the explained variation, which is fairly low compared to inter-annual and seasonal effects.

A temporal succession of larval taxa was observed during spring. Of the ten dominant taxa that were identified, some were characteristic of a particular month (*e.g.* herring in March, horse mackerel in June) whereas others were dominant throughout the season (*i.e.* sprat). This temporal pattern can be explained by fish strategies in terms of spawning period, time duration of the larval development and foraging. Sprat was clearly the most abundant

larval fish species in the EEC throughout the spring season, which is in accordance with its protracted reproductive season (Alheit, 1988). Sprat is a batch spawner and females can lay nine batches of eggs during the reproductive season. It is also the most abundant adult fish species (Vaz et al., 2007) in the EEC and recently reached a record abundance in the North Sea (ICES, 2018). Moreover, the OMI analysis revealed a low marginality and a high tolerance meaning that sprat larvae were ubiquitous and tolerate a high range of temperatures allowing an extended spawning period. These findings are in agreement with previous studies showing that viable eggs of sprat can be found at a wide range of temperatures from 2°C to 20°C, although survival for North Sea sprat decreases at temperatures below 6°C (Thomson et al., 1981).

In March 2017, larval assemblages were dominated by six taxa including, apart from sprat, a combination of larvae from winter spawners (*e.g.* herring, plaice) and early-spring spawners (*e.g.* sole, dab, whiting). The presence of herring larvae is in accordance with the spawning time of the Downs spawning component of North Sea herring, which hatches in the EEC mainly in December-January (Corten, 2013; Heath et al., 1997). Plaice is also a winter spawning fish and generally spawns in early January in the EEC (Fox et al., 2005).

In April and May, larval assemblages that were observed in the different years were dominated by five other taxa including sole, dab, whiting, sandeels and dragonets. Sandeels and whiting were more abundant in April contrary to sole and dab. Dragonets were abundant in both months. While they represented only 0.9% of the March assemblage, they became the second most abundant taxa in April (9.5%) and May (12.5%) and finally reached 16.1% in June. Hence dragonets, like sprat, were not specially affiliated to late spring conditions but were ubiquitous and supported a high range of temperatures.

In June, larval assemblages were different compared to the earlier months. Apart from sprat and dragonets, horse mackerel was the second most abundant species and was associated with other less abundant species like lesser weever, solenette and mackerel in the OMI analysis. Their high marginality and low tolerance regarding temperature indicated a "warm water" affinity of these larvae hatching during late spring and early summer. Although, Russel (1976) and Clark (1920) reported that horse mackerel spawns in the EEC from July onwards, our results show that horse mackerel larvae can already be found in June suggesting that the spawning season may start earlier than July.

In terms of inter-annual variations, our results from the Kruskal-Wallis tests combined with those from PCoA clearly showed a significative difference in larval abundances for April and May in the southern part of the EEC (except between Boulogne sur Mer and Belgium) between 2017 and the nineties. Indeed, the overall abundance of the dominant taxa was more than two times lower during 2017 (even when only considering April and May that were sampled every year) compared to the nineties. In the PCoA all significant taxa (including both generalists and specialists), except cottids, were clearly more abundant during the nineties' surveys, suggesting changes in the abundance of the main larval fish species of the EEC ecosystem. From the Kruskal-Wallis test, we also found more significant differences between 1999 and the early nineties (at least in April) than with 2017. This suggests that changes in the level of larval abundances in the EEC might have already started at the end of the nineties.

With no shared variation between year and environment, temperature and salinity do not appear to be the only factors that could explain changes in larval assemblages. Auber et al. (2017) studied adult fish abundances in the EEC between 1980-1997 and 1998-2012. They showed a significant decrease of abundances in the recent period as we found with larval abundances. This was particularly the case for five taxa, namely sprat, dab, plaice, dragonets

and gobies, which correspond to the larval taxa more associated with the nineties surveys in the PCoA. In agreement with our results, they found cottids to be one of the rare adult fish taxa more abundant in the 1998-2012 period. Adults of all the other taxa (except horse mackerel) were also less abundant during the 1998-2012 period (but this was not significant). Concerning horse mackerel, the discrepancy between larvae, more abundant during the nineties, and adults, more abundant in the recent period, is potentially due to the fact that in 2017 no survey was conducted in June whereas June has been shown to be relevant for larval occurrence of this species.

Auber et al. (2017) hypothesized that these changes between the two periods were linked to the AMO, which reflects the variation of sea surface temperature in the North Atlantic Ocean at a multidecadal scale. In the middle of the nineties, the EEC experienced an increase of temperature due to a shift from a cold to a warm phase of the AMO (Drinkwater et al., 2014). In the English Channel, the AMO and the Russell Cycle vary together (Edwards et al., 2013; Russell et al., 1971). The Russell cycle is a well-known phenomenon illustrating the influence of climate variations (warm and cool conditions) on marine plankton at the decadal scale which leads to changes in fish distribution and abundances. Even if the truly cyclical nature of planktonic changes is not proven, phase changes in major climatic cycles, such as the AMO, lead to variations in assemblages (McManus et al., 2016). A shift in 1998 in dinoflagellate and dominant zooplankton groups has been shown by Beaugrand (2003) and Alvarez-Fernandez et al. (2012) who established a link with a rapid change in environmental conditions. Several studies also found that plankton and fish larvae were more abundant during a cold period than during a warm period of the AMO (Alheit et al., 2014; Cushing and Dickson, 1976, Southward et al., 1988). Since fish larvae survival highly relies on food availability, it could have been impacted by recent changes in plankton communities, due to increasing surface temperature. Higher temperatures also enhance larval growth rates (Pepin,

1991) which can in turn increase mortality due to starvation (Montero-Serra et al., 2015). Consequently, a lower survival rate during the larval phase could have led to fewer adults as observed by Auber et al. (2017). An alternative hypothesis is that lower larval abundance could come from a more northward distribution and spawning location in response to warming (Jansen and Gislason, 2011; Montero-Serra et al., 2014). While adults abundances of mainly small bodied species decreased drastically in the EEC (Aubert et al., 2017, McLean et al., 2018a) found a northward increase of these species in the connected ecosystem of the south bay of the North Sea that appeared simultaneously due to a rapid sea surface warming (McLean et al., 2018b). This hypothesis would mean that the EEC's spawning potential rapidly declined during the climate oscillation of the end of nineties.

Conclusion

Studying assemblage variation of early life stages of fish is essential to understanding changes in fish population dynamics in the context of global change. The monthly succession of larval species remains the main source of variability in larval assemblages during spring in the EEC. However, the present study also showed lower abundances in 2017 compared to the nineties. This decrease appeared to be in line with observations on the adults in the same area. This clear decline in the EEC does not necessarily mean that spawning populations are going down, but it would be worthwhile to investigate if the signal in a small part of the distribution area signifies a change in geographical distribution or indeed a decrease of the whole spawning population. The climatic regime shift could have led to a decrease in the larval survival rate and/or to a northward shift in the geographical distribution of adults, both leading to the observed decrease of the spawning population in the area and consequently in the number of fish larvae. Whereas these observations during one year will need to be

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confirmed through a multiannual sampling, they may reflect true changes, as they were also observed for phyto- and zooplankton communities as well as fish adults.

Acknowledgments

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Declaration of interests

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☒   The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships whi ch may be considered as potential competing interests:

Highlights

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Larval assemblages were dominated by ten species

Overall abundances and diversity increased across the spring season

Larval abundances were significantly lower in 2017 compared to the nineties

Several larval and adult fish species responded similarly to a shift in the AMO