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Decline of cold-water fish species in the Bay of Somme (English Channel, France) in response to ocean warming

Auber Arnaud [1, *], Gohin Francis [2], Goascoz Nicolas [3], Schlaich Ivan [3]

[1] IFREMER, Laboratoire Ressources Halieutiques, 150 quai Gambetta, BP699, 62321 Boulogne-sur-Mer, France
[2] IFREMER, Département Dynamiques de l'Environnement côtier, Centre Ifremer Brest, BP 70, 29280 Plouzané, France
[3] IFREMER, Laboratoire Ressources Halieutiques, Avenue du Général de Gaulle, BP32, 14520 Port-en-bessin, France

* Corresponding author : Arnaud Auber, email address : Arnaud.Auber@ifremer.fr

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Abstract :

A growing number of studies have documented increasing dominance of warm-water fish species ("tropicalisation") in response to ocean warming. Such reorganization of communities is starting to occur in a multitude of local ecosystems, implying that tropicalisation of marine communities could become a global phenomenon. Using 32 years of trawl surveys in the Bay of Somme (English Channel, France), we aimed to investigate the existence of a tropicalisation in the fish community at the local scale of the estuary during the mid-1990s, a period where an exceptional temperature rise occurred in Northeast Atlantic. A long-term response occurred (with a major transition over 6 years) that was characterized by a marked diminution in the abundance of cold-water species in parallel to a temperature rise generated by the ocean-scale phenomenon, the Atlantic Multidecadal Oscillation, which switched from a cool to a warm phase during the late 1990s. Despite finding no significant increase in the dominance of warm-water species, the long-term diminution of cold-water species suggests that the restructuring of the fish community was mainly influenced by global-scale environmental conditions rather than local ones and that indirect effects may also occurred through biological interactions.

1. Introduction

One of the main challenges in ecology is to understand how biodiversity responds to environmental changes, and the consequences this can generate for ecosystem functioning, especially when aiming to anticipate long-term biological responses to future environmental changes (Bengtsson, 1998) and predict impacts on ecosystem services (Duffy et al., 2007). In marine environments, community structure is highly variable and depends on both natural and human-induced environmental variation (Collie et al., 2004), which may act concomitantly (Chavez et al., 2003), rendering the quantification of their relative contributions difficult (Beaugrand, 2004).

Among human-induced environmental variation, climate change alters environmental conditions including global temperature, sea-ice extent, nitrogen levels in the biosphere, atmospheric and oceanic carbon dioxide concentrations which tend to affect water acidity (Doney et al., 2009), oxygen availability (Koenigstein et al., 2016), rainfall patterns, wind, biogeochemical cycles (Zepp et al., 2003) including salinity (Durack et al., 2012), frequency of extreme weather events, sea level, ocean circulation (IPCC, 2007), thermal stratification of water-columns (Hordoir and Meier, 2012), and the size of the oxygen minimum zone (Stramma et al., 2010). Climate change has a wide variety of effects on the physiology, distribution and phenology of marine organisms (IPCC, 2014) (Perry et al., 2005; Cheung et al., 2009; Cheung et al., 2013) including phytoplankton (e.g., Wetz et al., 2011; Rossoll et al., 2012), zooplankton (e.g., Hays et al., 2005, Richardson, 2008), fishes (e.g., Cheung et al., 2012b; Pinsky and Fogarty, 2012; Perry et al., 2005; Hawkins et al., 2013), birds (e.g., Şekercioğlu et al., 2012; Niven et al., 2009), and marine mammals (e.g., McMahon and Burton, 2005; Learmonth et al., 2006), which ultimately affects humans (Patz et al., 2005; McMichael et al., 2006). These impacts are fundamentally linked to the close relationship between ocean conditions and the ecophysiology of marine organisms, notably water-breathing ectotherms (Somero 2010; Sunday et al., 2011).

Climate change has mainly been characterized by an ongoing rise in the global temperature of the world's oceans since the mid-20th century (IPCC, 2007), which can be more or less pronounced in different regions (Belkin, 2009; Alexander et al., 2014). Water temperature is recognized as an abiotic "master factor" controlling physiological processes of aquatic organisms (Beitinger and Fitzpatrick, 1979; Singh et al., 2013), and therefore controls the behaviour, growth, metabolism, abundance and species composition of fishes (e.g., Thiel et al., 1995; Stenseth et al., 2002), notably in estuarine ecosystems (Thiel et al., 1995; Harrison and Whitfield, 2006). Marine fishes mainly respond to temperature increases through changes in distribution (e.g., Perry et al., 2005), generally to higher latitudes (Parmesan, 2006; Mueter and Litzow, 2008; Jung et al., 2014; Punzón et al., 2016) and deeper waters (Dulvy et al., 2008; Punzón et al., 2016). Latitudinal shifts can also result in changes in community composition through increasing dominance by tropical or subtropical fish species preferring warm-waters. Such a reorganization of fish communities, or so-called "tropicalisation", appears to be occurring in a multitude of local ecosystems, suggesting that this reorganization of marine communities could become a global phenomenon (Verges et al., 2014). Previous works have indicated that tropicalisation of fish communities has occurred in response to global warming in several areas/scales, including Western Australia (Cheung et al., 2012a), the Aegean Sea (Keskin and Pauly, 2014), Italian seas (Fortibuoni et al., 2015) and in fisheries of Large Marine Ecosystems (Cheung et al., 2013). In addition to potential cascading effects within biological communities, modifications in species assemblages may lead to substantial impacts on socio-economic components (Chapin et al., 2000, Cheung et al., 2012a).

In the North Atlantic, several natural climate oscillations also occur and act concomitantly with human-induced climate change. Over the last three decades in northeast Atlantic marine systems, abundant evidence of natural, climate-driven changes in biotic assemblages has been mounting. Among natural climate cycles, the Atlantic Multidecadal Oscillation (AMO) reflects natural oscillations of sea surface temperature (SST) from cool to warm phases with a periodicity varying between 60 and 80 years (Edwards et al., 2013; Auber et al., 2015). The AMO is progressively considered as a “proxy for complex processes in the coupled atmosphere-ocean system of the North Atlantic” (Alheit et al. 2014a); this system involves the North Atlantic Oscillation (NAO), the Atlantic Meridional Overturning Circulation (AMOC), the Mediterranean Overflow Water (MOW) and the subpolar gyre (Hátún et al., 2009; Alheit et al., 2014b). Alheit *et al.,* (2014b) indicated that these complex climatic processes began building in the North Atlantic in the 1960s and culminated in the 1990s, which had pervasive ecosystem and ecological repercussions. In the Western English Channel, the AMO is synchronous with the Russell Cycle (Russell *et al.,* 1971; Edwards *et al.,* 2013), which has characterized profound changes in species’ abundances and distributions since the mid-19th century, including fishes (Alheit et al., 2014b; Mieszkowska et al., 2014). Another well-known climate cycle, the NAO, corresponds to decadal variations in atmospheric and oceanic circulation in the North Atlantic (Dickson and Turrell, 2000).

This climate phenomenon has been widely announced as a major forcing factor acting on marine communities (Fromentin and Planque, 1996; Beaugrand et al., 2002) because it affects precipitation patterns, which can influence river run-off and therefore nutrient inputs, salinity, and turbidity (e.g. Enfield et al., 2001; Trigo et al., 2004; Harley et al., 2006). The NAO and AMO are partly linked through atmospheric-oceanic circulation coupling, since SST depends and acts upon atmospheric circulation (Drinkwater *et al.*, 2014; Harris *et al.*, 2014).

Several studies have shown SST warming from 0.2 to 0.6°C in the North Atlantic since the late 1980s (Dulvy et al., 2008; Wang and Dong, 2010), with exceptional warming after the mid-1990s (Wang and Dong, 2010), notably in the English Channel (Saulquin and Gohin, 2010). The combined effects of anthropogenic climate change and the positive phase of the AMO after the 1990s may have caused higher warming in the North Atlantic than would be expected from climate change alone (Andronova and Schlesinger, 2000; Knudsen et al., 2011). Such a strong temperature rise during the late-1990s raises the question of whether a tropicalisation also occurred at local scales. A recent work (Auber et al., 2015) documented a persistent structural change in the exploited fish community of the Eastern English Channel in the mid-1990s, characterized by a strong decrease of cold-water fish species and a moderate increase of warm-water species, which was synchronous with a change from a cold to a warm phase of the AMO. According to these authors, a question remains of whether this community change was or was not visible at even more local scales than the Eastern English Channel, notably in fish nursery ecosystems.

Estuaries are essential ecosystems for the life cycles of many fish species (Lipcius et al., 2008; Nicolas et al., 2010) since they act temporarily as nursery and feeding areas for marine juveniles, offering a highly nutrient-rich environment and shallow turbid refuges suitable for development (Potter et al., 1990; Nicolas et al., 2010). Additionally, fish species encompass a wide diversity of biological cycles and ecological compartments, making them relevant indicators of estuarine conditions at multiple spatial and temporal scales (Whitfield and Elliott, 2002). In Northern France, the estuarine ecosystem of the Bay of Somme provides a nursery area for many species of the English Channel (Rybarczyk et al., 2003) that shifted spatially during the late-1990s, likely in response to the AMO switch. Because several tropicalisation events have occurred in multiple local ecosystems, because an exceptional temperature rise occurred in the mid-1990s in Northeast Atlantic, and because the Bay of Somme constitutes a nursery for fish species living in the Eastern English Channel (where many species shifted during the late-1990s), we suspect that a tropicalisation also occurred in the Bay of Somme during this period.

Based on the ecosystem of the Bay of Somme (English Channel, France), the aims of this study are (i) to investigate the temporal dynamics of the taxonomic structure of the fish community, (ii) to better understand the underlying mechanisms of community dynamics in this estuary by assessing the respective effects of global climate-related conditions and local conditions in the Bay, and (ii) to investigate, through a functional approach, the potential tropicalisation of this community during the last 32 years in response to temperature rise.

2. Materials and Methods

2.1 Study site and Fish community sampling

The Bay of Somme (50°14’N, 1°33’E; Figure 1) is the second largest coastal ecosystem in Northwestern France, after the Seine Estuary (Rybarczyk et al., 2003). With an intertidal surface of more than 50km², the Bay is a macrotidal system of the Eastern Channel (Rybarczyk et al., 2003) and is fed by the Maye River in north and the Somme River in south (Figure 1). Marine influences dominate, making this complex ecosystem mostly a marine bay with an estuary system reduced to the channel of the Somme (Rybarczyk et al., 2003).

The fish community (including cephalopods) of the Bay of Somme was sampled through the ecological and fisheries monitoring of the CNPE of Penly (Centrale Nucléaire de Production d’Electricité) in late summer of each year since 1987. Gastropods and crustaceans were not considered since the gear used was adapted to harvest fishes, not benthic invertebrates. The study period was chosen in order to maximize the availability of juveniles. Thus, since 1987, monitoring has been conducted annually according to an experimental protocol that has remained unchanged through time. The sampling scheme was defined according to three depth strata (see Figure 1). The stratified sampling scheme aimed to achieve 44 hauls, 28 hauls using a beam trawl with a 3-m horizontal opening (CP3) and a 20-mm stretched mesh size in strata B and C, and 16 hauls using a beam trawl with a 2-m horizontal opening (CP2) and a 20-mm stretched mesh size in stratum A. The vertical opening was 0.5 m for both beam trawls.

All CP2 hauls lasted 7 min while CP3 hauls lasted 15 min. These trawling lines were carried out during daylight hours at an average speed of 2.5 knots.

Fig. 1 here

Within each haul, fish species were identified, counted and weighed. A total of 62 taxonomic groups were recorded over the study period. All abundance values were standardized to numbers of individuals per km².

2.2 Global conditions

The North Atlantic Oscillation (NAO) is an intradecadal, basin-scale alternation of atmospheric mass over the North Atlantic between the high atmospheric pressure centered on the Azores and low atmospheric pressure around Iceland (Dickson and Turrell, 2000). The index used here is based on the difference in normalized sea level atmospheric pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland since 1864 (Dickson and Turrell, 2000). During the positive phase of the NAO, Northern Europe is exposed to warm, wet conditions with both more frequent and stronger winter storms crossing the Atlantic Ocean in a northerly track (Reid et al., 2001; Ottersen et al., 2001; Walker and Graf, 2005). The opposite trends occur during the negative phase: fewer and weaker winter storms, a west-east pathway, and cold, dry conditions in Northern Europe. Concerning biotic compartments, the NAO has already led to shifts in phytoplankton abundance and species composition, followed by changes in the dominant zooplanktonic species, *Calanus spp.*, in the North Sea (Fromentin and Planque, 1996). For fishes, the NAO is now considered as a driver acting on assemblage composition, abundance, and juvenile growth (Attrill and Power, 2002). Additionally, from one fish species to another, the influence of NAO on recruitment may vary, notably in European Shelf seas (Dippner, 1997; Attrill and Power, 2002). The annual NAO index for the period 1988-2011 was obtained from the National Oceanographic and Atmospheric Administration (NOAA, US).

The Atlantic Multidecadal Oscillation (AMO) refers to a 60-80 year cycle of the North Atlantic SST (Edwards *et al.*, 2013). Its determinants are not fully understood nor are they predictable. The AMO index is computed as a monthly area-weighted average of SST anomalies over the North Atlantic (from 0 to 70°N). The obtained time series is then detrended in order to remove the effect of global warming. This index has recently been reported to influence plankton and fish abundance in some North Atlantic ecosystems (Edwards et al., 2013; Alheit et al., 2014b). AMO values were provided by NOAA, US.

Northern Hemisphere air temperature anomalies ($NHT_{anomalies}$) were also used in this work. This index is indicative of temperature conditions at a global scale; it reflects both human and natural variations, and previous work (Beaugrand et al., 2002) indicated that NHT anomalies could play a synergistic role with NAO on SST in the Northeast Atlantic and thus on marine biota. NHT anomalies have already been correlated with the abundance/biomass of several biological compartments: phytoplankton, zooplankton, fishes (Beaugrand et al., 2002; Beaugrand and Reid, 2003) and also with community indices like species richness of calanoid copepods in the northwestern North Atlantic (Beaugrand et al., 2002). The values of $NHT_{anomalies}$ were calculated from the average temperature over the period 1950-2014 and produced by the Hadley Centre Research and Climate Prediction (MetOffice, 2014).

2.3 Local conditions

Sea surface temperatures were extracted from a database provided by the Hadley center, Met Office (http://www.metoffice.gov.uk/hadobs/hadisst/). The data were interpolated to provide a 1-month resolution SST dataset composed of *in situ* and satellite data (advanced very high resolution radiometer). SST values were interpolated from this database from 1980 to 2012 from nodes of a 1° latitude-longitude spatial grid (Rayner *et al*., 2003) located between 50°17'N and 50°6'N, and 1°24W and 1°40E (2 nodes located in the Bay of Somme). Annual mean SST values were computed over this area ($\text{SST}_{HadISST}$).

Additional SST values were obtained from the Ifremer SST data derived from AVHRR/Pathfinder products interpolated by kriging (Saulquin and Gohin, 2010) for the period 1986-2009, the OSTIA data provided by the Met Office using the Operational SST and Sea Ice Analysis (OSTIA) system described in Donlon *et al.*, (2011) for 2010, and the ODYSSEA data, also derived from multi-sensor data incorporating microwave instruments, provided by MyOcean (Autret and Piollé, 2011) for 2011-2012. A comparison with a homogeneous time series covering the entire period, stemming from global low-resolution GHRSST, showed that the inhomogeneity of the high-resolution time series used here did not generate bias (L'Hévéder et al., 2016). The three sets of satellite-derived SST data were projected onto the same regular grid --- 0.075° in longitude and 0.05° in latitude --- allowing a relatively high spatial resolution of about 5 km x 5 km. SST was assessed from this satellite dataset at each sampling site and date from the year when this trawl was performed. The mean of all temperature values within each year was then calculated and used in this work (SST_{sat}).

Other SST values were collected through *in situ* measurements carried out during the ecological monitoring of the CNPE of Penly. The mean between April, July and September sessions from 1989 to 2012 were used in this work (SST_{hydro}). Finally, SST and bottom temperatures measured were also included in this work (mean between May and June sessions: SST_{ichtyo} and BottomTEMP).

Salinity can also influence fish community structure through physiological responses at the individual scale (e.g., Peterson and Meador, 1994; Rowe and Dunson, 1995). Bottom and surface salinity were obtained through the ecological monitoring of the CNPE of Penly (the mean between May and June sessions was used in this work). For this work, the mean between bottom and surface values was used as an index of salinity in the overall water column.

Ecosystem productivity, which is usually assessed through the concentration of chlorophyll *a* (Cravo *et al*., 2010; Horta e Costa *et al*., 2014) can also influence the structure of fish communities through trophic cascades. Concentration of chlorophyll *a* was recorded during the ecological monitoring of the CNPE of Penly (the mean between April, July and September sessions was used for this study). Additional Chlorophyll *a* data were extracted from satellite data (Gohin, 2011). Chlorophyll *a* concentrations were assessed from the satellite dataset at each sampling site and date when each trawling line was performed. For each year, the mean between all Chl. a values (i.e., between all trawling lines during the survey period) was used.

The concentration of suspended matter has previously been documented as a non-negligible factor that can affect aquatic organisms through “disruptions in migrations and spawning, movement patterns, sublethal effects like disease susceptibility, growth, and development, reduced hatching success, and direct mortality” (Kjelland *et al.*, 2015). The concentration of suspended matter was recorded during the ecological monitoring of the CNPE of Penly from 1980 to 2012. The mean between April, July and September sessions was used for this study. Non-algal suspended matter was also obtained from satellite data from 1998 to 2015 (Gohin *et al.*, 2005; Gohin, 2011). These data were assessed from the satellite dataset at each sampling site and date when each trawling line was performed. For each year, the mean between all satellite-derived suspended matter concentrations was used (i.e., between all trawling lines during the survey period).

Among meteorological parameters, rainfall has often been identified as one of the main forces acting on the structure of fish communities (e.g., Castillo-Rivera et al., 2002; Meynecke *et al.*, 2006). River flow, which is directly linked to rainfall, was also included in this study because nutrient content, and thus ecosystem productivity, may vary with river flow. Summer river flow (mean from July to September) from 1980 to 2015 was available from the Data Centre for French Coastal Operational Oceanography (Fichaut *et al.*, 2011). Rainfall data (mean between July, August and September at Noyelles-sur-Mer; Figure 1) from 1980 to 2015 were extracted from the Météo France website (https://donneespubliques.meteofrance.fr/). Wind speed can also act as a forcing factor, as several studies have already shown that wind may influence recruitment dynamics, predator-prey relationships, and assemblage structure (e.g., Menge and Menge, 2013; Horta e Costa *et al.*, 2014). Therefore, wind speed (mean between July, August and

September at Dieppe; see Figure 1) and air temperature (annual mean: AirTemp at Dieppe), from 1980 to 2015, were also extracted from the Météo France website (https://donneespubliques.meteofrance.fr/).

2.4 Analysis of community structure changes

Only taxa with abundances above 0.1% of total abundance across the study period were included in this study (Kortsch *et al.*, 2012), which resulted in a collection of 49 taxa. Spatially aggregated abundance indices at the scale of the whole Bay of Somme were used in the analyses described below. Aggregated indices were computed for each species and each year as the mean of the numbers of individuals per km² between all trawling lines. The resulting data was a matrix of spatially aggregated abundance indices per species (columns) and per year (lines) that represents the times series of community's taxonomic structure.

A correlation-based Principal Component Analysis was performed on the species abundance matrix in order to characterize temporal changes in the fish community (see PCA biplot in supplementary material S1.A.). The two first components of the PCA ($PC1_{taxo}$ and $PC2_{taxo}$) were used as indices of community structure.

The existence and timing of potential shifts in community structure was assessed by chronological clustering using a multivariate regression tree (MRT) with the species abundance matrix as the explained matrix and time as the explanatory variable (Borcard *et al.*, 2011). The shift in community structure was first characterized by testing for changes in the abundance of each species, between the period before and that after the shift. A Monte-Carlo permutation test was then performed on the spatially aggregated abundance indices using the “max statistic” method described below in order to account for the increase in the family-wise type 1 error rate due to multiple testing (Groppe *et al.*, 2011). Lines of the species abundance matrix corresponding to years were randomly permuted between the period before and that after the shift. This randomized any potential association between the abundance index of each species and the period, while preserving any correlative structure between species abundance indices themselves. A one-way ANOVA with period as the explanatory factor was then performed on the abundance index of each species in the permuted matrix, and the maximum F value across species was recorded. This procedure was repeated 5000 times and the resulting distribution of permuted maximum F values was used as the empirical null distribution against which observed F values, computed through one-way ANOVAs on the actual time series of species average abundance indices, were tested. A change in species abundance was declared significant when less than 5% of the permuted maximum F values were larger than the observed F value.

In order to assess potential changes in the community in terms of balance between warmer-water and colder-water species, the MTC index (Cheung et al., 2013) was computed from the average inferred temperature preference of species weighted by their density:

$$MTC = \frac{\sum_i^n Ti.Ci}{\sum_i^n Ci}$$

Here *Ci* corresponds to the density of species *i* (nb.ind./km²), *Ti* corresponds to the thermal preference of species *I*, and *n* is the total number of species. Thermal preference of each species was obtained from Cheung et al. (2013). First, a one-way ANOVA with period as the explanatory factor was performed on the MTC index. Second, in order to identify which members of the community (cold-water or warm-water species) mostly contributed to temporal changes of MTC, several groups of species were built based upon their thermal preferences (e.g., [11-12°C]). As for the abundance of each species, the max statistic method was used to test for differences in the abundance of each thermal preference group between compared time periods.

2.5 Effects of global and local conditions on community structure

The dynamics of global conditions were assessed using the first principal component ($PC1_{global}$) coordinates of a correlation-based PCA applied to the matrix of variables relative to global conditions (see supplementary material S1.B; variables: NAO, AMO, $NHT_{anomalies}$). The same procedure was used for local conditions ($PC1_{local}$; variables: sea surface temperature, air temperature, suspended matters, river flow, rainfall, wind speed, Chl.*a* and salinity; see supplementary material S1.C). The Pearson correlations between $PC1_{global}$ and $PC1_{taxo}$ and between $PC1_{local}$ and $PC1_{taxo}$ were then investigated through a cross-correlation analysis at several time-lags (0 to 6 years).

Temporal changes in the fish community were also assessed by analyzing a "thermal matrix" containing the abundance of 14 groups defined by thermal preferences ([7-8°C],]8-9°C], …,]20-21°C]). Like with the taxonomic approach, the shift(s) in community structure was/were characterized by testing for changes in the abundance of each thermal group, between the period before and that after each shift by using the max statistic method (Groppe et al., 2011). A correlation-based Principal Component Analysis was performed on the thermal matrix and the coordinates of the first principal component

($PC1_{therm}$) were used in order to describe the dynamics of the "thermal structure" of the community. Additionally, cross-correlation analyzes were performed between the MTC index and all indices relative to temperature (SST_{sat}, $SST_{HadISST}$, SST_{hydro}, SST_{ichtyo}, BottomTEMP, AirTemp, AMO, $NHT_{anomalies}$ and NAO) with time-lags ranging from 0 to 3 years. In order to investigate which index (i.e., $PC1_{taxo}$ or $PC1_{therm}$) mostly responded to AMO, p-values and determination coefficients of a cross-correlation analysis between the AMO index and $PC1_{therm}$ were compared to those provided by the cross-correlation between the AMO index and $PC1_{taxo}$ (with several time-lags ranging from 0 to 3 years). Finally, the same procedure was performed with the "local SST" variable (i.e., the mean between all SST variables: SST_{sat}, $SST_{HadISST}$, SST_{hydro}, SST_{ichtyo}, BottomTEMP).

Statistical analyzes were performed using the R software version 3.1.3 (R Core Team, 2015). Potential temporal autocorrelations of explained variables (i.e., $PC1_{taxo}$ and $PC1_{therm}$, and the MTC index) were checked before all statistical analyses, and effects were declared statistically significant with an alpha value of 0.05.

3. Results

3.1. Temporal changes of the fish community

The multivariate regression tree of community data against time detected the existence of a significant change in community structure in 1998 (permutation test: $p < 0.001$). This change represents 34% of community structure variation over the overall study period. In view of the first and second principal components extracted from the PCA (see Supplementary material S1.A.) and applied on the fish community matrix (PC1 and PC2 explained 20 and 10% of total variation, respectively), the change in the taxonomic structure of the fish community especially occurred from 1998 to 2003 (Figure 2). As indicated by the first principal component, the taxonomic structure was relatively stable before 1998 and quickly changed until 2003, before stabilizing again (Figure 2). Similarly, the second principal component also indicated 1998 as the breaking year (Figure 2).

Fig. 2 here

The change in community structure was characterized by a diminution in the abundance of the majority of species during the mid-1990s (Figure 3). In the overall fish community, five taxa significantly decreased in abundance from the period “before 1998” to the period “after 1998”: Gobiidae family (permutation test: $p < 0.001$), *Callionymus lyra* (Dragonet; $p = 0.004$), *Limanda limanda* (Dab; $p = 0.008$), *Pleuronectes platessa* (Plaice; $p = 0.004$), and *Sprattus sprattus* (sprat; $p = 0.008$), whereas only one genus, Arnoglossus (Scaldfish), significantly increased in abundance ($p = 0.023$) (Figure 3).

Fig. 3 here

3.2. Effects of environmental conditions on the taxonomic structure of the fish community

Significant relationships were found between the global conditions index ($PC1_{global}$: 82% of total variation; Supplementary material S1.B.) and the structure of the fish community ($PC1_{taxo}$: 20% of total variation) with 0, 1, 2, 4, 5 and 6-year lags (Figure 4A), and a significant correlation was observed with the local conditions index ($PC1_{local}$: 33% of total variation; Supplementary material S1.C.) with a 2-year lag (Figure 4B).

Fig. 4 here

3.3. Effects on the thermal structure of the fish community

In parallel with a significant temperature rise in the Bay of Somme ($p < 0.05$) and the switch from a cold to a warm phase of the AMO, the MTC index increased at an average rate of 0.2 °C per decade from 1987 to 2012, especially from the mid-1990s to early 2000s (Figure 5), and significantly increased from 11.49 ± 0.36 to 11.91 ± 0.45 °C between the periods “before 1998” and “after 1998” (ANOVA: F(1,28) = 7.075, $p < 0.05$). Significant positive correlations were detected between MTC and the majority of temperature-related variables: SST_{sat} (time lag = 0 year), $SST_{HadISST}$ (time lag = 0 year), SST_{ichtyo} (time lag = 0 year), AirTemp (time lag = 0 and 1 year), $NHT_{anomalies}$ (time lag = 0 and 1 year) and AMO (time lag = 0 and 3 years) (see Table 2 for detailed results).

Fig. 5 here

According to Figures 6A and 6B, the increase of the MTC index was especially due to a decrease in the abundance of species preferring cold-waters. Significant diminutions in abundance were observed for three thermal groups: [9-10°C], [10-11°C], and [11-12°C] (Figure 6A). We also observed that several species with significant diminutions (Gobiidae family, *Callionymus lyra*, *Limanda limanda;* Figure 3) belonged to the [11-12°C] thermal group, which largely explains the significant decrease of this group. The two last species showing a significant decrease (*Pleuronectes platessa* and *Sprattus sprattus*), belonged to the [9-10°C] thermal group, and thus contributed to the significant decrease of this group. Figure 6B indicates that flounders (*Platichthys flesus*), which did not significantly change in abundance, also contributed to the decrease of the [9-10°C] thermal group. The [10-11°C] thermal group, represented by mackerel (*Scomber scombrus),* sculpins (Cottidae family), whiting (*Merlangius merlangus*), European eel (*Anguilla anguilla*), European pollock (*Pollachius pollachius*) and lemon sole (*Microstomus kitt*), showed a significant decrease, although no individual species significantly decreased over time. Despite observing some abundance increases for “warm-water species” these increases were not significant (e.g., *Sardina pilchardus*, *Mullus surmuletus*), except for Arnoglossus, which was characterized by intermediate thermal preference (Figure 6B). A significant change occurred in the thermal structure of the community (characterized by a decrease in the dominance of cold-water species) between the two periods (permutation test: $p < 0.001$). A significant positive correlation was also observed between the amplitude of abundance variation and thermal preference (Pearson’s r = 0.342, $p = 0.022$; Figure 6B), and a significant difference was noted between the thermal preferences of species that decreased in abundance and the thermal preferences of species that increased in abundance (ANOVA: F(1,43) = 6.376, $p = 0.015$; Figure 6C).

Fig. 6 here

The AMO index was significantly correlated to the taxonomic structure of the community with 1 and 2 year time-lags and significantly correlated to the thermal structure of the community for all tested time-lags (Figure 7A, 7B and Table 1). In parallel, local SST was not significantly correlated with $PC1_{taxo}$ or $PC1_{therm}$ (for any time-lag) (Figure 7C, 7D and Table 1). We can note here that all local temperature-related variables in the Bay of Somme were positively and significantly correlated to the global AMO index (SST_{sat}: $p < 0.05$ with time-lag = 4 years; $SST_{HadISST}$: $p < 0.001$ for time-lag = 0 and 1 year, and $p < 0.01$ for time-lag = 2 years; AirTemp: $p < 0.001$ for time-lag = 1 and $p < 0.01$ for time-lag = 0 and 2 years).

The results (p-values and R² coefficients) extracted from cross-correlation analyzes between $PC1_{therm}$ and AMO compared to those relative to the correlation between $PC1_{taxo}$ and AMO revealed that, whatever the considered time-lag, the thermal structure of the community was better correlated to the AMO than to taxonomic structure (Table 1). This result was not observed with local SST, except with time lag = 3 years.

Table 1 here

4. Discussion

Our analyses revealed a noteworthy change in the structure of the Bay of Somme fish community at the end of 1990s (from 1998 to 2003) that was related to an increase of SST at the global scale. This change in the fish community was mainly characterized by a decrease in the abundance of species preferring cold-waters. Several other fish species (bream, squids from the loliginidae family**,** sardine, red mullet), characterized by higher thermal preference, increased (non-significantly) in abundance over time. These dynamics, which led to the observed increase of the MTC index, are in line with numerous works (e.g., Perry et al., 2005; Cheung et al., 2012a; Fortibuoni *et al*., 2015, Tsikliras *et al*., 2014, 2015) documenting a tropicalisation of fish communities in response to temperature rise. Such a tropicalisation is characterized by an increase in the dominance of warm-water species in temperate areas in response to ocean warming (Cheung *et al.,* 2013). Our results differ from what we expected and from the majority of documented tropicalisations in the sense that the response of the community to warming was mainly characterized by a diminution in the abundance of cold-water species rather than an increase of warm-water species. We also noticed that, at the local scale of the Bay of Somme, the MTC index increased at a similar rate (0.2°C/decade) to the rate of increase of non-tropical MTC observed at the global scale (0.23°C/decade, according to Cheung et al., 2013) during the last four decades.

Whatever the considered approach (taxonomic or functional), the fish community has changed in relation to temperature conditions measured at the local scale of the bay, which appear themselves highly dependent on global conditions. A reason that could explain why global conditions (especially conducted by the AMO and NHT) mainly determined the community structure at the local scale is that certain fish species do not spend their entire life cycle in the Bay of Somme, which indicates that they might also be exposed to other conditions (e.g., at the basin-wide scale of the English Channel, North Sea). Species rely on different coastal habitats to fulfill their life cycles (Seitz et al., 2014), therefore, habitat quality and connectivity are considered essential characteristics of coastal ecosystems (Lipcius et al., 2008). For example, adult common sole (*Solea solea*) spawn in the continental shelf whereas juveniles grow in coastal nurseries where environmental conditions differ, notably in water temperature (MacPherson and Duarte, 1991).

In this study, most of the local temperature variables were significantly correlated with the AMO index, which therefore suggests that the Bay of Somme is substantially dependent on global phenomena like climate oscillations, although several local processes occur. We therefore inferred that the long-term increase in local SST, which is reflected by the AMO index, was the main forcing factor affecting the structure of the fish community. The idea that temperature was a major contributing forcing factor was reinforced by the fact that the MTC index was correlated with the majority of temperature measures and several time lags. Much more significant correlations were indeed observed between community indices and global conditions (i.e., many more time lags above zero) than between community indices and local conditions (see for example Table 1 and Figure 4). This potentially means that the fish community may have presented a long-term response to global conditions during the last three decade.

The long-term characteristic of the response (over 6 years here) of the fish community notably suggests the existence of indirect effects through biological interactions (that may necessitate delays in response time) like trophic cascades following direct effects on other biological compartments (e.g., phyto-zooplankton and benthic macroinvertebrates), or direct impacts on the growth of larvae and/or juveniles, or on the physiology of adults like fecundity that potentially generate inter-cohort effects. Long-term responses at community scale are increasingly detected in marine ecosystems like for example in the North Sea, where Daan et al. (2005) observed a minimum of 6 year-lagged response of fish communities to indirect effects of fishing pressure. Our understanding of long-term changes in exploited fish communities necessitates to consider numerous aspects like species interactions (Ferretti et al., 2013) that are now recognized as one of the main driving mechanism leading to community changes over time and space (Ferretti et al., 2010). In a next step, investigating how the trophic structure of the entire biocoenose (or at least the fish community) have changed over time in the Bay of Somme will be therefore extremely helpful to better understand the reason leading to the observed long-term response. The long-term characteristic of the response can be also explained by several other mechanisms like physiological effects of sea warming on fish larvae and/or juvenile and/or adults, or also progressive shifts in latitudinal distributions. We present in Figure 8 potential processes that may explain the community changes.

First, potential changes in fish community structure may have occurred following the physical movement of fishes, possibly in response to climate-induced latitudinal shifts in food resources (e.g., zoo-planktonic communities, Beaugrand *et al.,* 2002; Perry *et al.,* 2005) or the direct influence of temperature increase (Figure 8). Fish movements may have been encouraged by northeastward water masses flowing into the Channel in the mid-1990s from the Bay of Biscay, which characterized the beginning of a new warm phase (positive AMO index values) (Mieszkowska *et al.*, 2014). Several cold-water fish species (e.g., *Scomber scombrus, Trisopterus luscus*, *Trisopterus minutus*) decreased in abundance in the Bay of Somme, showing opposite trends to what has been observed since the mid-1990s in the North Sea (Beare *et al.,* 2004; Astthorsson *et al.,* 2012). As proposed by these authors, our results also support the hypothesis of a northward migration of fishes from the Channel to the North Sea in response to ocean warming. In parallel, we documented a decrease in the abundance of sprats and herring, two cold-water species, similar to previous observations in the Eastern, North, and Central Atlantic Seas, which also varied in synchrony with warm and cool AMO phases (Alheit et al., 2012, 2014b). We also observed an increase in the abundance of some warm-water species (e.g., red mullet: *Mullus surmuletus*; although non-significant), similar to previous studies (Cheung et al., 2012b), which observed an increase in catches of red mullet (*Mullus barbatus*) around the UK in response to ocean warming. In the same manner, we observed similar trends to those presented by several authors concerning sardine, another warm-water species, which increased in abundance in response to AMO variations in the Western English Channel, North Sea, and Baltic Sea (Petitgas *et al.*, 2012; Alheit *et al.*, 2012) through northward migrations, particularly in the mid-1990s (Alheit et al., 2014b). Several works have documented northward movements of Lusitanian fish species into the English Channel, Celtic and North Seas over the last few decades (Perry *et al.*, 2005; ter Hofstede *et al.*, 2010; Simpson *et al.*, 2011; Petitgas *et al.*, 2012).

Fig.8 here

Second, the observed changes in the fish community may be the result of modifications in hydrodynamic connectivity between habitats that are vital for successive life-stages, especially for eggs and larvae that depend highly on ocean circulation (Figure 7; Kendall et al., 2016). We can suppose that larval dispersion patterns were modified following the exceptional inflow of oceanic water in the mid-1990s (Toresen and Østvedt 2000; Mieszkowska et al., 2014). According to Kendall et al. (2016), climate change is "predicted to alter ocean currents that transport eggs and young larvae through changes in atmospheric circulation and ocean stratification," which may therefore impact the structure of the fish community.

Third, fish recruitment may have been affected by temperature rise through:

(i) physiological effects on larval and/or juvenile growth and mortality rates (Pepin, 1991; Green and Fisher, 2004; Genner et al., 2010) (Figure 8). For example, Arula et al., (2015) showed that exceeding the physiological thermal preferences of fish larvae can cause decreased growth rates and increased mortality. In the specific case of this study in the Bay of Somme, despite no significant increase in the abundance of warm water species was observed, the temperature increase may have improved juvenile growth rates, resulting in higher recruitment and abundance of certain of these species (Nye *et al.*, 2014). In contrast, the temperature increase may have reduced the growth rates of cold-water species, leading to substantial diminutions in abundance.

(ii) physiological effects on adults themselves (Figure 8; Rijnsdorp *et al.*, 2009), which could cause changes in community dynamics. A study on tropical fish species (Pankhurst and Porter, 2003) showed that relatively small changes in temperature lead to changes in fishes' endocrine systems, which by consequence influenced reproductive activity. However, for some species, areas that were previously unsuitable may have become more favourable (Cheung et al., 2013). Complementary investigations on the temperature tolerance range of species rather than their thermal preferences would be useful, notably because rates of temperature variation may be decisive for fish communities.

(iii) physiological effects on the prey of fish larvae and/or juveniles therefore causing a trophic cascade on fish larvae and/or juveniles themselves (e.g., Arula et al., 2015; Hátún et al., 2009) (Figure 8). Several observations have confirmed this climate-induced change. For example, in the Western English Channel, the zooplanktonic community quickly changed from large to small-sized copepods with warm-water affinities in parallel to the AMO (Hátún *et al.*, 2009; Eloire *et al.*, 2010). This trophic cascade hypothesis could therefore be tested by investigating spatio-temporal changes in prey species within the Bay of Somme but also at a more global scale (at least the Eastern English Channel scale). In opposite, the observed changes in fish community structure may have led to a series of cascading effects through trophic relationships, potentially impacting planktonic communities, seabirds or marine mammals. The study of Hernandez-Farinas et al., (2014) indicated that several dinoflagellate genera and some diatoms (e.g., *Pseudo-nitzschia*) increased from 2001 to 2007/2010 in the Bay of Somme in relation to the AMO. Such an increase during the 2000s is probably linked to the decrease of total fish abundances we describe in this study. In their work, Hernandez-Farinas et al., (2014) also inferred that, in this estuary, global conditions (AMO and NAO, especially AMO) may be stronger than local conditions in impacting the structure of phytoplanktonic communities. Lefebvre et al., (2011) also showed that, in the Bay of Somme, several exceptional changes occurred between the late 1990s and early 2000s, such as an increase in chlorophyll *a* concentration (from 1996 to 2005), an increase of the standard molar ratio for dissolved inorganic nitrogen (from 1999 to 2003), and an increase in the density of phytoplanktonic cells (from 1999 to 2003), with exceptional dominance of Prymnesiophyceae algae (especially *Phaeocystis globosa*). These results therefore indicate that the changes we observed in the fish community also concerned phytoplanktonic communities. According to Lefebvre et al., (2011), changes in the phytoplanktonic compartment were mainly due to global climate processes through the direct effects of AMO and NAO, but we can also suppose that indirect effects (e.g., trophic cascades) occurred. We can indeed assume that the Bay of Somme fish community changes were due to the observed modification of the phytoplanktonic community, and vice versa. Nonetheless, because the change in the fish community was mainly characterized by a decrease of fish densities, and because thermal preference appears to be a structuring trait, we believe that the fish community was directly impacted by temperature increase and that phytoplanktonic communities (e.g., increase of algae density) were both directly impacted by temperature increase and indirectly through a top-down effect. We are therefore convinced that investigating the dynamics of the phyto-zooplanktonic and macroinvertebrates communities of the Bay constitutes the best next step for understanding the ecological mechanisms that occurred in this estuary.

Unfortunately, the effects of fishing were not assessed in this work because no data were available. Despite its known catastrophic effects on fish assemblages, fishing mortality has declined in the Northeast Atlantic since the beginning of 1990s (ter Hofstede *et al.*, 2010). However, the long history of exploitation in the EEC may have facilitated the observed community change by rendering the entire fish community more sensitive to climatic variations (Hsieh et al., 2006; Auber et al., 2015). Furthermore, caution must be taken concerning the non-implication of fishing in the observed reorganization of the fish community, since several species spend part of their life cycle in the open English Channel, an ecosystem that has been subjected to intense fishing pressure for multiple decades, which can be also accompanied of time-lagged effects on fish communities (e.g., Daan *et al*., 2005). Consequently, future investigations are needed to assess the potential effects of fishing at the local scale of the bay, notably by focusing initially on species that are known to move between the Bay of Somme and the English Channel.

In conclusion, the observed change of the Bay of Somme fish community constitutes an additional observation of 'tropicalisation' since it is now added to the numerous previous works showing such type of community reorganization. It therefore reinforces the hypothesis that a global scale phenomenon is occurring in fish communities. This study also tends to show that the restructuring of the fish community was mainly influenced by global-scale sea warming rather than local environmental conditions. The response was characterized by a long-term change in the structure of the community and thus reinforces the idea that the effect of warming is, the most often, not detectable in the short term (Godbold and Solan, 2013). This highlights the necessity to mostly consider the appropriate timescales for assessing ecological repercussions of climate forcings (e.g., Hettinger et al., 2012; Godbold and Solan, 2013), especially in the aim to better identify responsible drivers, to better understand mechanisms of action and finally, to support decision making in the context of the policy adaptation to global warming.

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Figure captions:

Fig. 1. The Bay of Somme with locations of sampling sites and meteorological stations of Dieppe and Noyelles-sur-Mer.

Fig. 2. Temporal dynamics of the fish community structure in the Bay of Somme from 1980 to 2012. Shaded grey represents the "breaking year" (1998). PC1 and PC2 explained 20 and 10% of total variation, respectively.

Fig. 3. Radar plot comparing fish abundances before and after 1998 in the Bay of Somme (nb.ind.km²; $\log_{10}$ transformed). Results of permutation tests for changes in taxa abundance before and after 1998 accounting for multiple testing: ***: $p < 0.001$; **: $0.001 < p < 0.01$; *: $0.01 < p < 0.05$.

Fig. 4. A. Cross-correlation plot between the index of global conditions ($PC1_{global}$) and the index of fish community structure ($PC1_{taxo}$). **B.** Cross-correlation plot between the index of local conditions ($PC1_{local}$) and the index of fish community structure ($PC1_{taxo}$).

Fig. 5. Temporal dynamics of the Mean Temperature of the Catch index (MTC).

Fig. 6. A. Structure of the fish community before and after 1998 according to thermal preferences. Results of permutation tests for change in each "thermal group" before and after 1998 accounting for multiple testing: ***: $p < 0.001$; **: $0.001 < p < 0.01$; *: $0.01 < p < 0.05$. **B**. Thermal preferences and trends of abundance variation (increase/decrease) of each species between the two tested periods. Underlined species changed significantly in abundance between the two periods. **C**. Thermal preferences of species that decreased in abundance over time.

Fig. 7. A. Temporal dynamics of the taxonomic structure of the fish community ($PC1_{taxo}$) and AMO. **B.** Thermal structure ($PC1_{therm}$) and AMO. **C.** Taxonomic structure ($PC1_{taxo}$)

and local SST. **D.** Thermal structure (PC1$_{therm}$) and local SST. PC1$_{taxo}$ explains 19% of total variation of the taxonomic structure of the community and PC1$_{therm}$ explains 27% of total variation of the thermal structure of the community.

Fig. 8. Potential mechanisms of effects related to temperature change on the structure of the fish community. Each arrow indicates a potential effect.

Table 1. Pearson correlation results (p-values and R²) between PC1$_{taxo}$ and AMO, PC1$_{taxo}$ and local SST, PC1$_{therm}$ and AMO, PC1$_{therm}$ and local SST with four time-lags (0, 1, 2 and 3 years). Shaded cells correspond to significant correlations.

		AMO		local SST	
		PC1$_{taxo}$	PC1$_{therm}$	PC1$_{taxo}$	PC1$_{therm}$
time lag (years)	0	p = 0.113 ; R²= 0.13	p = 0.001 ; R²= 0.43	p = 0.219 ; R²= 0.078	p = 0.439 ; R²= 0.03
	1	p = 0.048 ; R²= 0.2	p = 0.022 ; R²= 0.26	p = 0.05 ; R²= 0.19	p = 0.169; R²= 0.11
	2	p = 0.008 ; R²= 0.35	p = 0.004 ; R²= 0.38	p = 0.193 ; R²= 0.09	p = 0.428 ; R²= 0.04
	3	p = 0.396 ; R²= 0.04	p = 6.7e-04 ; R²= 0.52	p = 0.065 ; R²= 0.19	p = 0.055 ; R²= 0.21

Table 2. Pearson correlation results (p-values and r) between MTC and temperature-related indices with four time-lags (0, 1, 2 and 3 years). Shaded cells correspond to significant correlations.

			time-lags (years)	Spearman correlation coefficient r	*p* value
MTC vs.	SSTsat	local temperature indices	0	0.558	0.003
			1	0.085	0.686
			2	0.131	0.543
			3	-0.064	0.771
	SSTHadISST		0	0.565	0.001
			1	0.349	0.064
			2	0.317	0.1
			3	0.091	0.651
	SSTichtyo		0	0.407	0.043
			1	-0.125	0.56
			2	0.188	0.39
			3	-0.157	0.407
	BottomTEMP		0	0.398	0.059
			1	6.10^{-4}	0.998
			2	0.127	0.574
			3	-0.159	0.477
	AirTemp		0	0.494	0.005
			1	0.473	0.009
			2	0.339	0.078
			3	0.059	0.771
	SSThydro		0	0.347	0.114
			1	0.322	0.154
			2	0.09	0.706
			3	-0.031	0.9
	NHTanomalies	global temperature indices	0	0.465	0.009
			1	0.53	0.003
			2	0.344	0.073
			3	0.344	0.078
	NAO		0	0.153	0.417
			1	-0.159	0.408
			2	-0.132	0.505
			3	-0.289	0.144
	AMO		0	0.358	0.052
			1	0.404	0.029
			2	0.334	0.083
			3	0.392	0.042

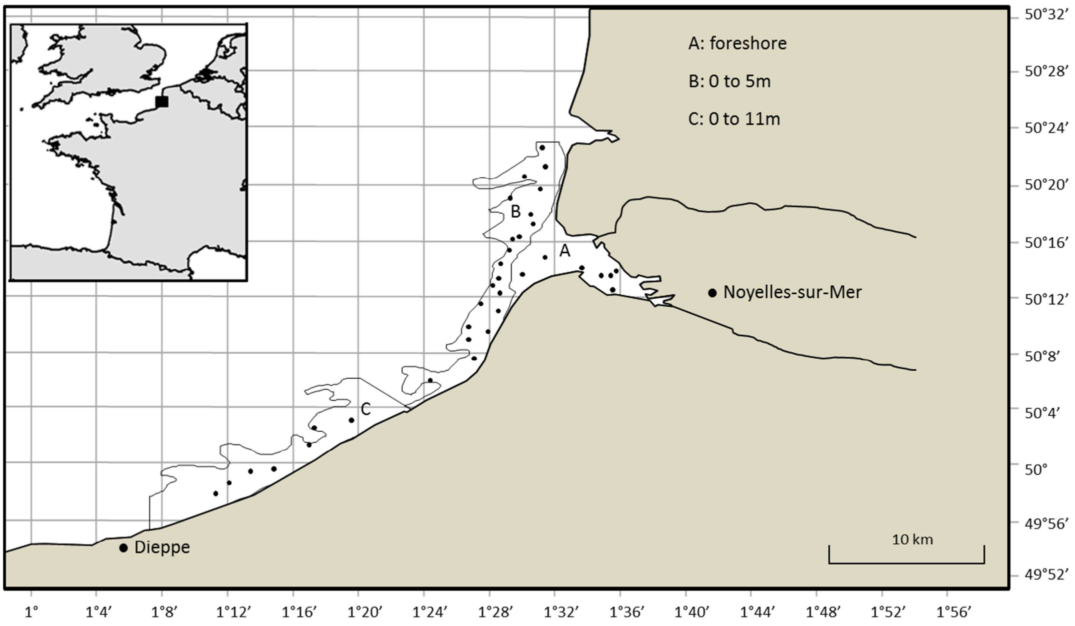
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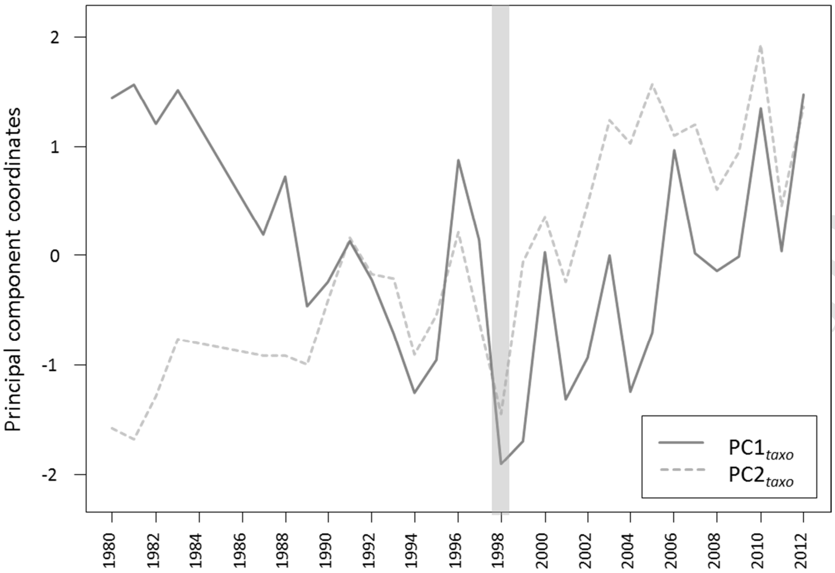
Figure 1.



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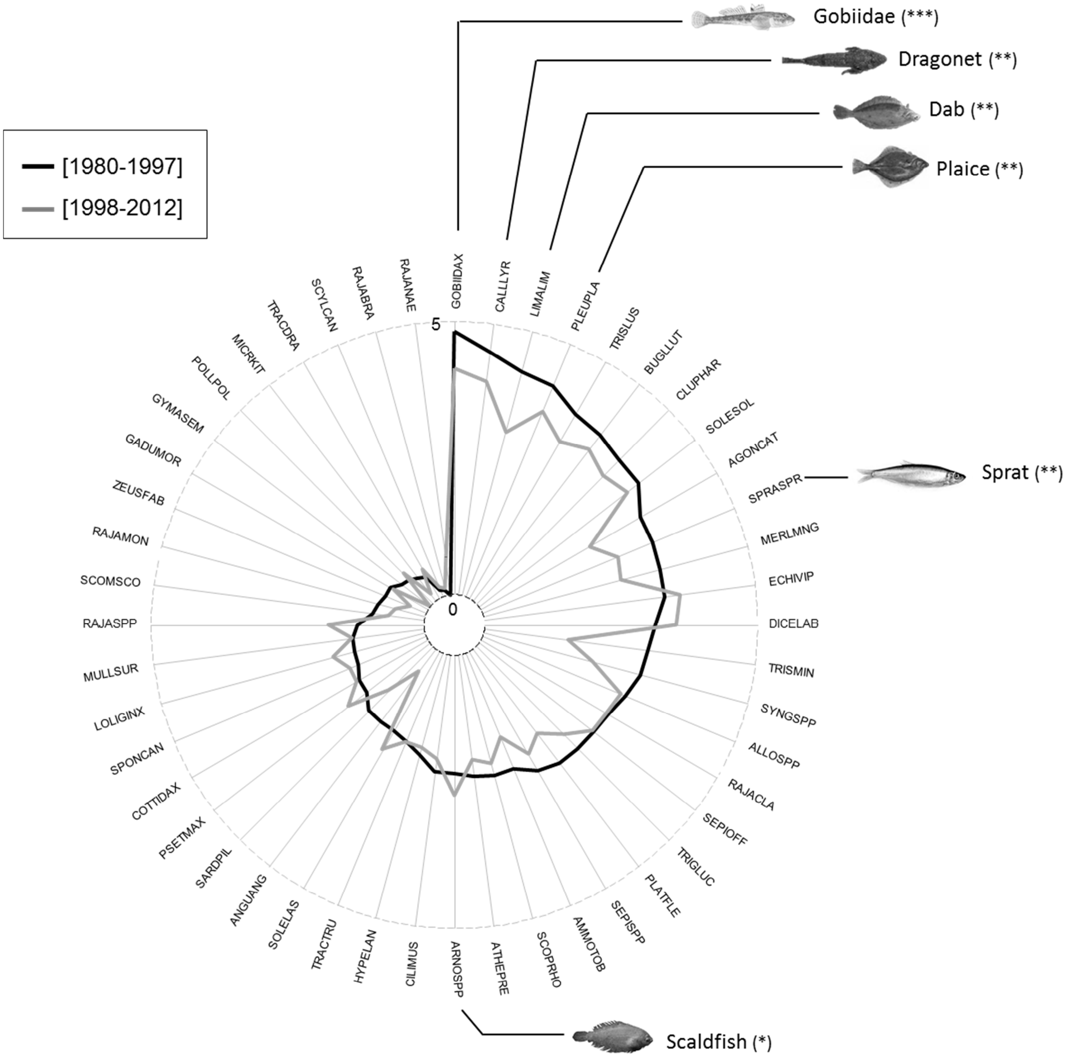
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BUGLLUT
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SOLESOL
AGONCAT
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MERLMNG
ECHIVIP
DICELAB
TRISMIN
SYNGSPP
ALLOSPP
RAJACLA
SEPIOFF
TRIGLUC
PLATFLE
SEPISPP
AMMOTOB
SCOPRHO
ATHEPRE
ARNOSPP
CILIMUS
HYPELAN
TRACTRU
SOLELAS
ANGUANG
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COTTIDAX
SPONCAN
LOLIGINX
MULLSUR
RAJASPP
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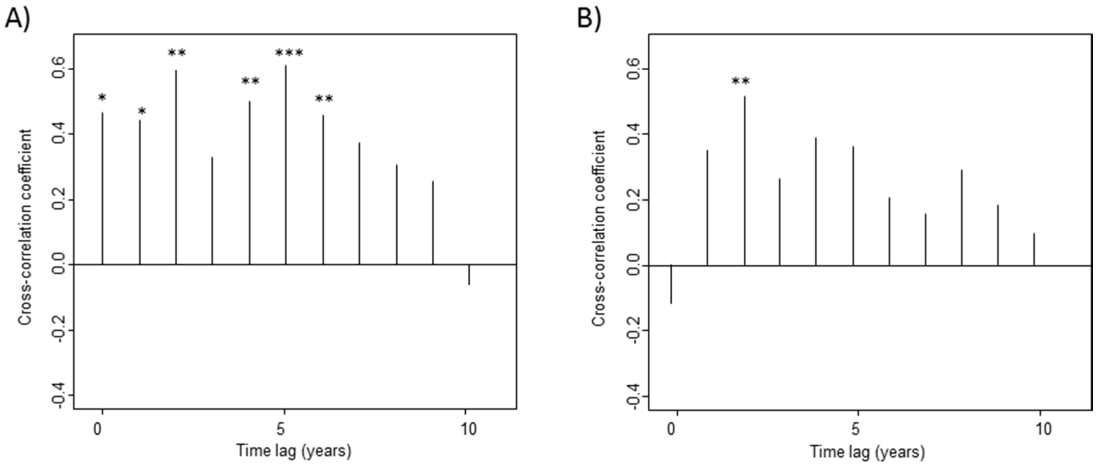
Figure 3.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Cross-correlation coefficient
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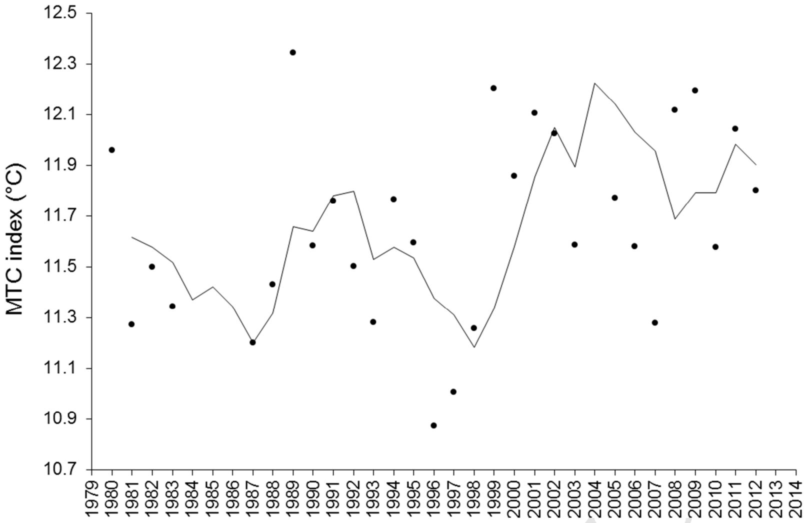
Time lag (years)

Figure 4.

1122 

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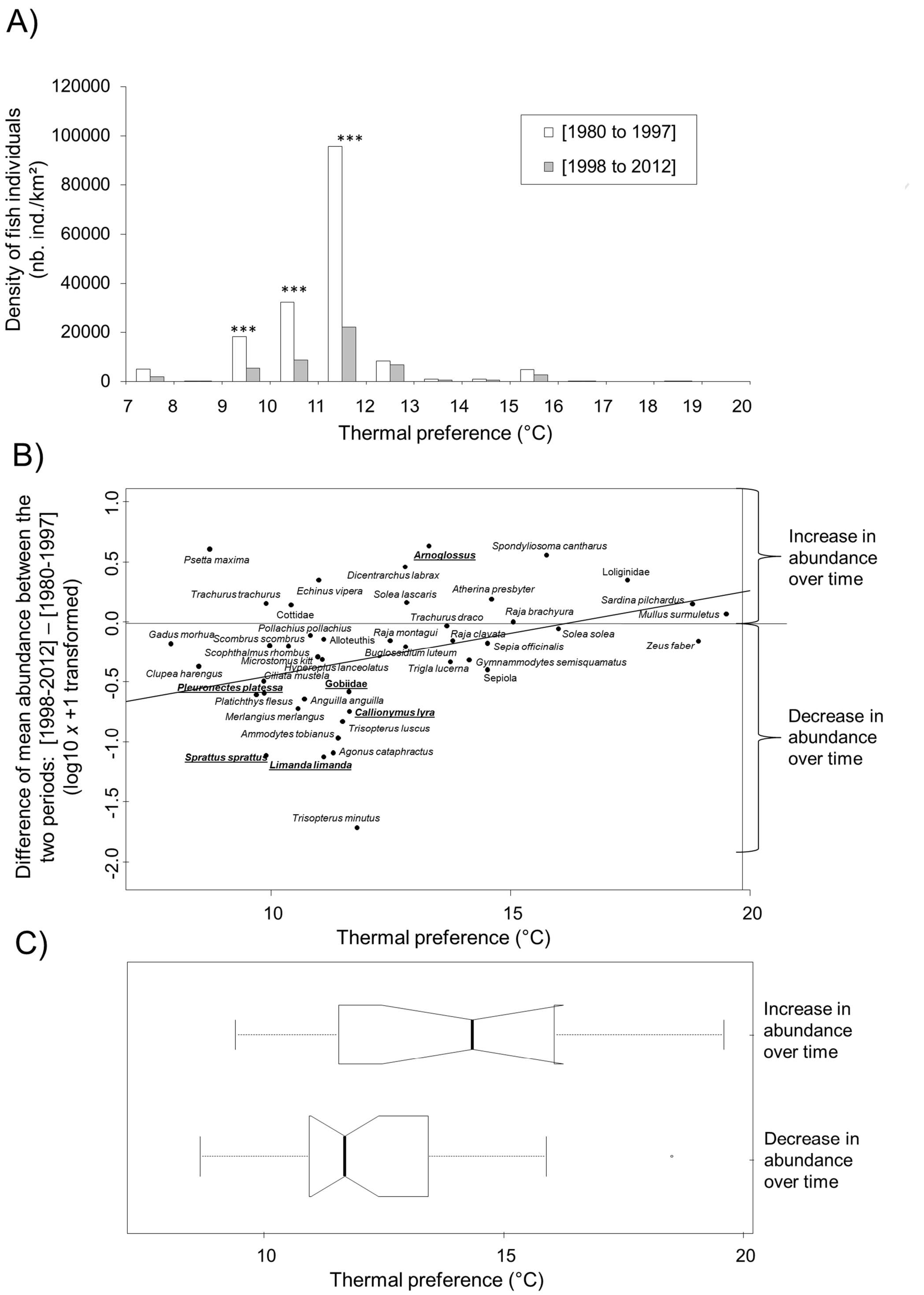

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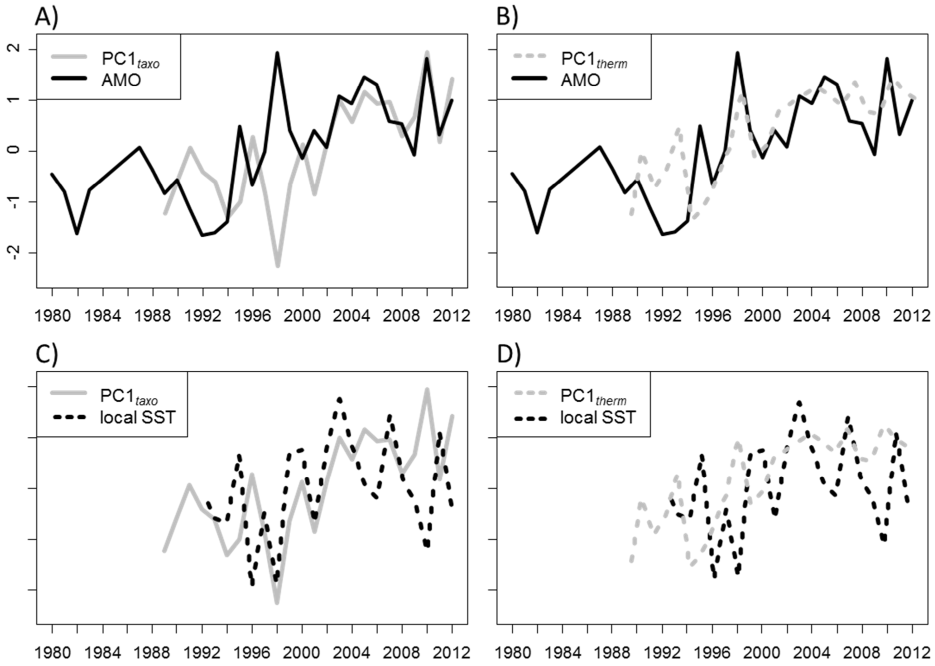

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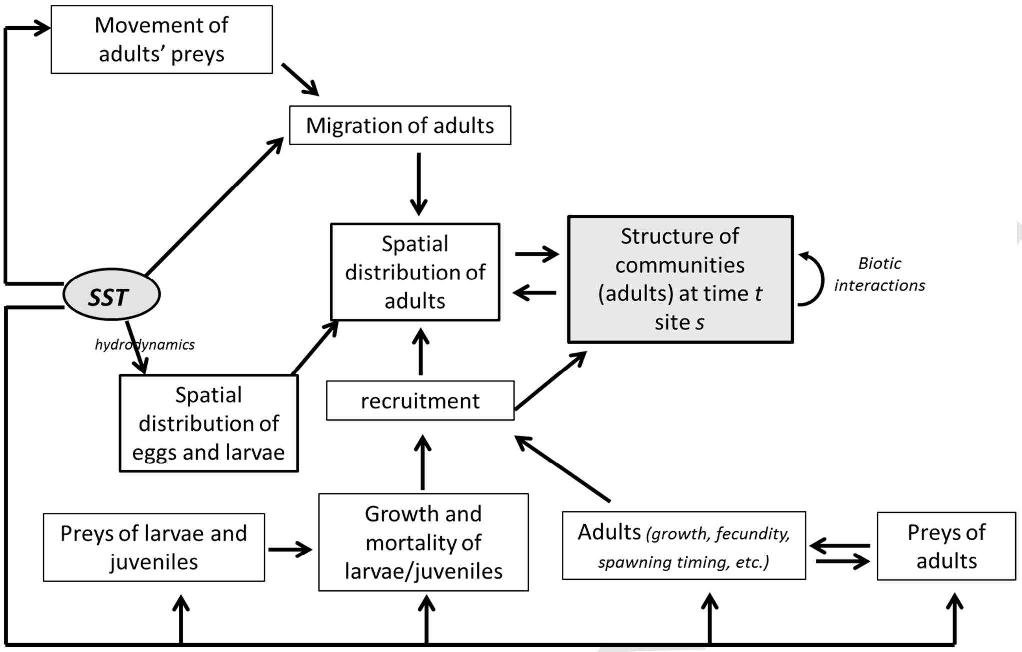
1127 Figure 7.

1128 

1129 Figure 8.

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