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Long-term variability of ichthyoplankton in relation to environmental fluctuations and recruitment

Par : Camille BOURGEOIS

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Devant le jury composé de :

Président : Etienne RIVOT (Enseignant-chercheur Institut Agro Rennes-Angers)

Maître de stage : Christophe LOOTS, Paul MARCHAL (Chercheurs IFREMER Boulogne-sur-Mer)

Enseignant référent : Pablo BROSSET (Enseignant-chercheur Institut Agro Rennes-Angers)

Autres membres du jury :

Jean-Baptiste ROMAGNAN (Chercheur IFREMER Nantes)

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Table of contents

List of figures:

List of tables:

List of appendices:

I. Introduction

In fisheries, recruitment is the process in which young fish enter the exploited area and become liable to contact with the fishing gear (FAO, 1971). Variability in recruitment, the drivers of which are largely unknown, is the main cause of fluctuations in catches (Hjort, 1914). Increasing knowledge on the mechanisms underlying recruitment, and being able to predict it, would improve the scientific basis supporting fisheries management. Recruitment is the result of egg production and larval survival processes (Brosset et al., 2020; Yang and Yamakawa, 2022). In fish stock assessments, predictive models of recruitment dynamics usually consider spawners biomass (and resulting egg production) as the main driver of recruitment. Examples of such stock-recruitment models include the Ricker (1954) or the Beverton & Holt (1957) equations. However, a large majority of exploited stocks do not have a well-defined stock-recruitment relationship (Szuwalski et al., 2015). Numerous studies have shown that recruitment is linked to the survival of the developmental stages influenced by environmental factors (Hjort, 1914; Brunel, 2006; Yang and Yamakawa, 2022).

Ichthyoplankton represents « the eggs and larvae of fish and forms part of the plankton assemblages during their development » (Borja et al., 2019). The planktonic phase forms the basis of fish stocks, and its ability to survival will determine year class strength and eventually recruitment (Borja et al., 2019). There are three main processes that can affect the survival rate of ichthyoplankton : advective transport (determined by winds, sea temperature and currents), the timely availability of planktonic prey to fish larvae (Brunel, 2006), and top-down predation (Bailey and Houde, 1989; Houde, 2008). The influence of bottom-up processes on larvae survival is particularly acute during their first feeding period, which Hjort (1914) referred to as the critical period. Cushing (1975) also put forward the « match-mismatch » hypothesis between the peak of abundance of zooplankton prey and that of the larvae as a mechanism for larvae not finding their food in a timely manner and deceasing as a result of it. Other processes such as density-dependence and predation can also affect these stages (Brunel, 2006). Hence, considering spawning biomass and egg production only is insufficient to predict recruitment (Hjort, 1914; Houde, 2008; Cury et al., 2015).

This study investigates the link between the dynamics of ichthyoplankton, considering both eggs and larvae, in relation to environmental factors, spawning stock biomass, and the extent to which these could contribute to recruitment. Two species and two stocks for each specie will be considered in this study: sprat (*Sprattus sprattus*) in the English Channel (ICES Divisions 7d and 7e), spr.27.7de; sprat in the Skagerrak, Kattegat and North Sea (ICES Division 3a and Subarea 4), spr.27.3a4; sole (*Solea solea*) in the Eastern English Channel (ICES Division 7d), sol.27.7d; and sole in the North Sea (Subarea 4), sol.27.4. For the sake of simplicity, spr.27.7de, spr.27.3a4, sol.7d and sol.4 will from now on be referred to as English Channel sprat, North Sea sprat, Eastern English Channel sole and North Sea sole, respectively. While both sprat and sole are spring-spawning in the English Channel and the North Sea, they also have different physiological and biogeographical characteristics as well as contrasted commercial values. Sprat is a small pelagic fish of little economic importance in the English Channel, but the North Sea stock is targeted by the Danish and Norwegian industrial fisheries for fish reduction. In addition, sprat is a key prey for many economically important fish such as sea bass and whiting (Quéro, 1984). Moreover, sprat is a cold-water specie mainly distributed in Northern Europe coastal areas (*figure 1*), although it is also found in lower quantities in the Mediterranean and the Black Sea. Sprat spawning begins in January in the English Channel and from April until July in the North Sea (Quéro, 1984; Schlaich et al., 2023).

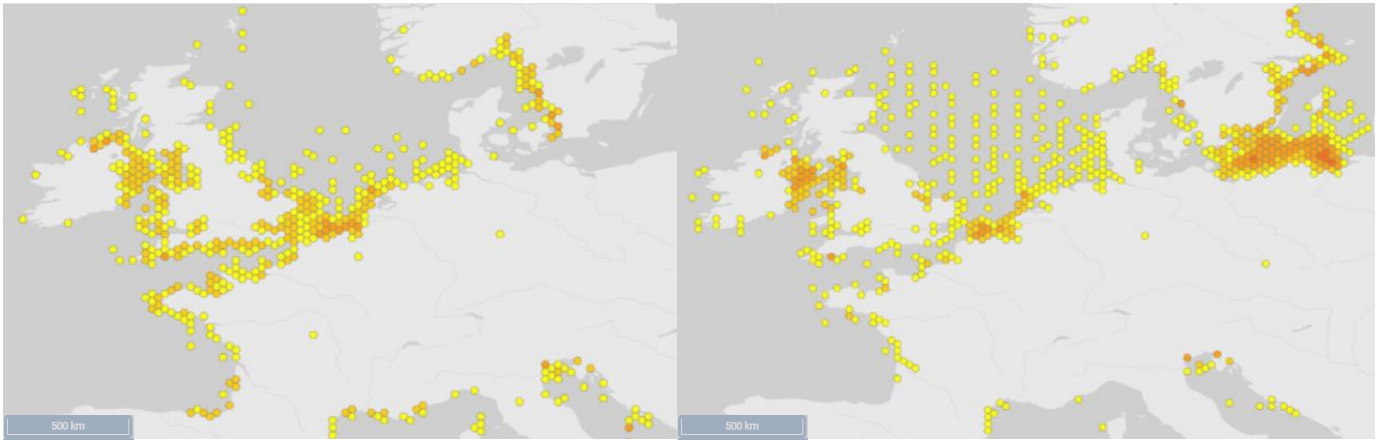

Figure 1 : Distribution area of sole (left) and sprat (right) from 1924 to 2023 in the North Sea and English Channel region © (GBIF Secretariat, 2023; GBIF Secretariat, 2023). *The colour intensity of the dots correlates with the presence of individuals.*

Sole is a demersal flatfish species of very high economic value in all areas where it is caught, particularly the English Channel and the North Sea. Compared to sprat, sole has a more southerly distribution (Baudron et al., 2020) and it is acquainted to warmer waters *(figure 1)*. Due to their different life history traits and habitats, changes in environmental conditions could affect sole and sprat in different ways. Sole spawning begins in the English Channel from February to June and from March to July in the North Sea (Woehrling and Le Fèvre-Lehoërff, 1998). Both stocks have their spawning peaks in April-May, which explains why the larvae and eggs of sole and sprat are most abundant in spring. Eggs and larvae can be found in both offshore and inshore areas, with a higher density on the coast (Grioche, 1998). Larvae also migrate during their development to reach nurseries. Depending on their size, the abundance of large larvae will be greater towards the coast and greater off-shore for small larvae.

Catches of sole in both the Eastern English Channel and the North Sea have declined in recent years *(figure 2)*, mainly due to sustained low recruitments (ICES, 2024a; ICES, 2024b). Fishing pressure on the stock is below the fishing pressure to ensure MSY[1] (Maximum sustainable yield) management for both stocks, and spawning-stock size is above spawning-stock size for North Sea sole and below spawning-stock size for Eastern English Channel sole to ensure MSY management (*Appendix I*, ICES, 2024a; ICES, 2024b).

[1] MSY is the largest quantity of biomass that can be extracted on average over the long term from a fish stock under existing environmental conditions without affecting the reproductive process (Caddy, J.F. and Mahon, R., 1995)

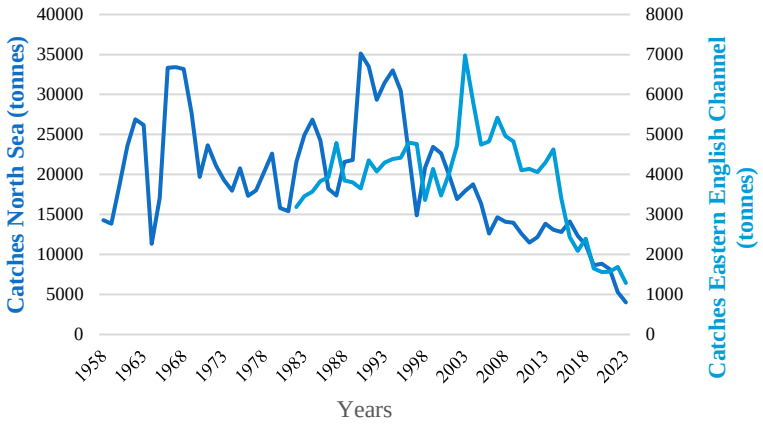

Figure 2 : Catches of sole in the Eastern English Channel and the North Sea (ICES, 2024a; ICES, 2024b).

English Channel sprat fishing pressure has steeply decreased and it is below the MSY fishing pressure while biomass has overall increased in recent years *(Appendix II)*. No biomass reference points have been defined for this stock and no recruitment could be estimated from the ICES stock assessment (ICES, 2024c). North Sea sprat recruitment has been subject to strong variability since the 80's, and the 2023 value was below historical average (ICES, 2024d; ICES, 2024c). The biomass of North Sea sprat stock is consistent with MSY management. No reference points for fishing pressure have been defined for this stock (ICES, 2024d).

Investigating the dynamics of ichthyoplankton (eggs, larvae and their interactions) is a decisive step to understanding year class fluctuations, including the decline in sole recruitment.

The aim of this study is to determine the impact of environmental changes on the dynamics of eggs and larvae of sole and sprat. First, species and areas were considered and analysed separately and then, when possible, compared in the context of contrasted hydrological characteristics. I analysed to that purpose several time series derived from the environmental, ecological and fisheries monitoring at the Gravelines Nuclear Power Plant, in the North Sea (since 1976), and at the Penly Nuclear Power Plant in the Eastern English Channel (since 1988). These data were supplied by EDF as part of the Impact des Grands Aménagements (IGA) project. A long-term temporal analysis of the data was carried out to highlight i) links between egg abundance, environmental changes and spawning biomass, ii) links between larval abundance, egg abundance, environmental changes and recruitment.

II. Materials and methods:

1. Data:
    a. *Presentation of available data*

The data are provided by the environmental, ecological and fisheries monitoring from the IGA project. Five nuclear power plants (CNPE) are monitored in France, including Gravelines (Nord department) and Penly (Seine Maritime department), both located in northern France *(figure 3)*.

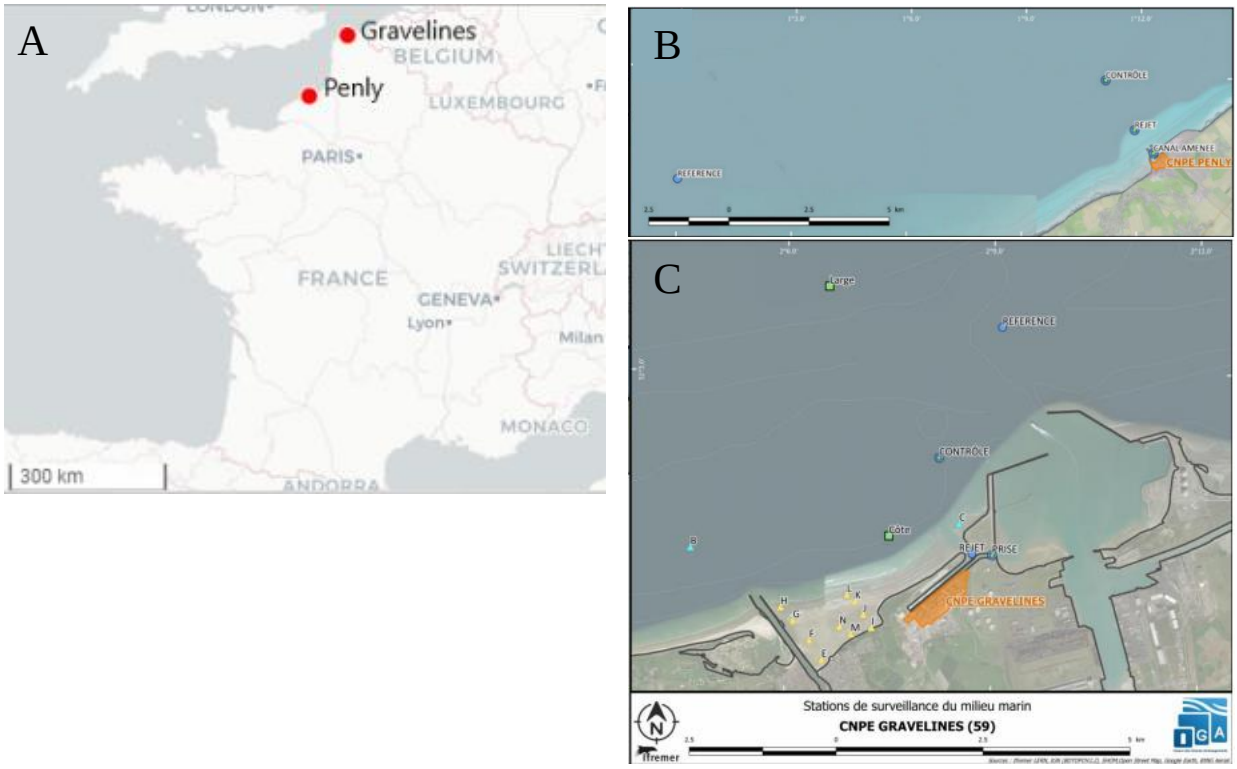

Figure 3: Maps of sampling points: Geographical position of the Gravelines and Penly CNPE (A) and sampling points at Penly (B, Schlaich et al., 2023) and Gravelines (C, Wacquet et al., 2023).

There are environmental similarities between Gravelines and Penly areas. Both locations are subject to north-north-easterly currents and are influenced by continental inputs from Aa (Gravelines), Arques and Saâne (Penly) rivers. The Gravelines area is subject to a temperate oceanic climate (slight seasonal variations, cold winters, little sunshine) and Penly to a predominantly continental climate (contrasted seasons), even though this area is also influenced by a maritime climate (mild and humid) and a southern climate (Schlaich et al., 2023; Wacquet et al., 2023). In addition, the Gravelines area is subject to stronger hydrodynamics than the Penly area (Schlaich et al., 2023; Wacquet et al., 2023).

The CNPE monitoring program (IGA project) has started at Gravelines and Penly since 1976 and 1988, respectively. The aim of the IGA project is to monitor the influence nuclear power plants may have on the marine environment and also to assess whether and the extent to which these changes could affect the functioning of these nuclear power plants. To achieve this, numerous surveys are carried out each year to sample different parameters including hydrology characteristics, as well as abundances of phytoplankton, zooplankton and ichthyoplankton. Four sampling points are monitored at Gravelines: « Prise », « Cote », « Controle » (renamed « ControleG ») and « Large », and three at Penly: « Rejet », « Canal » and « Controle » *(figure 3).* Nevertheless, only data from the « Controle» and « Canal » points at the Penly CNPE and the « ControleG », « Large » and « Cote » points at the Gravelines CNPE could be used in the context of this study.

Stock indicators such as spawning biomass and recruitment were also considered in the present study. Recruitment and spawning biomass data for North Sea and English Channel sole

and North Sea sprat were drawn from ICES stock assessments (ICES, 2024b; ICES, 2024a; ICES, 2024d). For English Channel sprat, the ICES assessment is essentially based on information from the Western English Channel, and it was therefore not considered representative of stock dynamics around the Penly area. In addition, this assessment does not estimate recruitment or spawning biomass. Instead, abundance indices from the Channel Groundfish Survey (CGFS), restricted to ICES statistical rectangles 28F0, 29F0 and 29F1 surrounding the Penly area, were used. As a first proxy, sprat individuals smaller and larger than 10 cm were considered to represent recruits and spawners, respectively (FishBase, 2015).

Numerous variables were used in this study:

Ichthyoplankton abundance:

The ichthyoplankton abundances of sole and sprat are collected for all the sampling points. All ichthyoplankton samples taken in the vicinity of the Penly and Gravelines CNPE are taken using a bongo net made up of two cyclindro-conical nets. Each net represents a replica. These nets are well-designed to sample ichthyoplankton (Schlaich et al., 2023; Wacquet et al., 2023). Monitoring of sole and sprat communities is carried out between April and May. These months correspond to the peak of ichthyoplanktonic abundances for the two species under investigation. Once collected, the samples are preserved in bottles pre-filled with a preservative sauce composed of formaldehyde. The eggs and larvae are then sorted, identified using Russel's identification key and counted. The number of individuals counted is related to the total volume of the sample. Eggs are divided into two stages of development: a « non-Embryonated » stage and an « Embryonated » stage. The development stages of larvae are not recorded. Fish eggs and larvae abundances in April and May were the explained variables in our analyses. However, fish egg abundancess were also used as a potential explanatory variable contributing to the dynamics of fish larvae abundance. When fish egg abundances was the explained variable, only « non-Embryonated » eggs were considered, since this stage was expected to be more closely related to spawning biomass (Trippel, 1999). When fish egg abundances was an explanatory variable, all eggs stages were retained.

Chlorophyll-a:

Phytoplankton is composed of planktonic microalgae and represents the primary production. Since 1989, chlorophyll-a was measured at the « Prise » point at Gravelines CNPE on a weekly basis, and it was here considered as a proxy of phytoplankton concentration. In order to obtain a monthly value, weekly data were averaged for each of the two months.

Zooplankton:

The « Zooplankton » dataset gathers zooplankton counts of all zooplankton taxa found at the « Prise » point of Gravelines CNPE. Based on Potignon (2022), only zooplanktonic species corresponding to the « spring-summer » class was retained: *T. longicornis*, *P. elongatus*, *C. hamatus* and *O. dioica.* Abundance of these species were summed to derive an abundance index of zooplankton available for sole larvae. For sprat, only abundances of *T. longicornis*, *P. elongatus* and *C. hamatus* were used and summed since *O. dioica* did not appear to be part of the sprat diet (Arrhenius and Hansson, 1993; Dickmann and Alheit, 2004; Möllmann et al., 2004; Carpentier et al., 2009; Voss et al., 2009).

Although only available at the Gravelines « Prise » point, data on zooplankton abundance and chlorophyll-a concentration were also used to depict phytoplankton and zooplankton dynamics at the three other points (« ControleG », « Cote », « Large »).

Temperature:

Temperature is a parameter that has a major influence on species biological activities. Temperature was collected at each point during each sampling survey using a temperature probe (± 0.01°) (Schlaich et al., 2023; Wacquet et al., 2023).

Salinity:

Like temperature, salinity (°/∘∘) is also a key variable influencing biological activities in the marine environment. Salinity was measured using a conductivity probe (± 0.01) at each point during each sampling survey (Schlaich et al., 2023; Wacquet et al., 2023).

The available datasets and variables are summarized in *Table 1*.

Table 1: All available variables and associated datasets.

Source	Area	Variables	Time
IGA	Gravelines – Penly (All the points)	Years – Month – Species – Stage of development (eggs or larvae) – Abundance – Temperature – Salinity	1976-2023 (Gravelines) 1988-2023 (Penly)
	Gravelines: « Prise » Point	Years – Month – Abundance of zooplanktonic species	1979-2022
		Years – Month – Chlorophyll-a concentration	1978-2023
ICES	Gravelines – North Sea (area 4) (ICES, 2024d; ICES, 2024a)	Years – Spawning biomass – Recruitment (sole et sprat)	1976-2023
	Penly – Eastern Channel (area 7d) (ICES, 2024b)	Years – Spawning biomass – Recruitment (sole)	1988-2023
CGFS	Penly – Eastern Channel	Years – Indices of spawning abundance (>10cm individuals) and recruitment (<10cm individuals) (sprat)	1988-2023

b. *Data transformation*

The exploration of the different datasets resulted in an initial filtering of the data used in subsequent analyses.
First, high spatial variability in ichthyoplankton distribution can result in an overly large amount of false absences (and of false zeroes), despite the actual presence of ichthyoplankton in the sampling zone. To limit the number of false zeroes, the maximum abundance of the two replicas from each sampling operation was retained for analysis.

In addition, all datasets were prone to missing values, the proportion of which varied between 3% and 32% *(Appendix III)*. Time autocorrelation were examined and sometimes included explicitly in the models implemented in this study, which required to not have any

missing values in the time series. A linear interpolation of the data was carried out using the *pastecs* package. A sensitivity analysis was performed to evaluate the extent to which this interpolation procedure affected modelling output *(see Section II.2.b).*

Finally, the correlation between the variables was shown on a correlation graph *(Appendix IV)*. No obvious patterns could be identified except an overall positive correlation between salinity and temperature. Salinity was therefore removed from the explanatory variables. All other variables were retained in subsequent modelling.

c. *Exploratory approach*

An initial principal component analyses (PCA) was carried out on the qualitative variables available (Month, Sampling points, CNPE, Species, Stage of development) in an attempt to identify global patterns *(Appendix V).* This PCA enabled us to visualise that the ichthyoplankton abundances varied overall between months and across sampling points for the two species. As a result, the series have been analysed separately for each combination of month and sampling point.

In a second step, the cumulative sums (CumSums) were calculated for all the time series of ichthyoplankton abundances and explanatory variables to graphically observe whether the variables followed similar trends (Ibanez et al., 1993 ; Le Fevre-Lehoerff et al., 1995 ; *Appendix VI*). For each value $x_{i,j}$ with $i \in [1; n]$ of a time series j, the mean m_j used as reference value was subtracted, and the difference obtained was summed over all the time series:

$$\sum_{i=1}^{n} (x_{i,j} - m_j)$$

Thus, the ichthyoplankton abundance datasets were separated into 40 time series corresponding to the combinations of life stages (egg, larva), species (sole, sprat), months (April, May) and sampling points (« ContrôleG », « Côte », « Large » for Gravelines and « Contrôle » and « Canal » for Penly). Each time series gathers data from 1979 to 2022 for Gravelines and 1988 to 2022 for Penly. We can see from the cumulative sum of ichthyoplankton abundance (*figure 4)* that the time series do not show a single trend. In April, sprat larvae and eggs showed negative cumulative sums for all the sampling points. The abundance of these communities is lower than the average value. This decrease in abundance compared with the average has been observed since the 2000s. For sole, we have also observed a lower abundance of eggs in April compared with the mean value for all the sampling points since 2000. The observations for sole larval abundance are more complex. However, the sole larval abundance has been higher than the average value for all sampling points since 2010 for Gravelines, and since 2015 for Penly in April. As for the abundance of ichthyoplankton in May, the observations are the same as those described in April for the two stages of both species, i.e., a negative cumulative sum for all the sampling point for sprat eggs and larvae and for sole eggs observed since the 2000s and a positive cumulative sum for all the sampling points since 2010 and 2015 for sole larvae at Gravelines and Penly respectively *(figure 4)*.

One point that can be added is the fact that April sprat eggs and May sprat larvae seem to follow similar patterns for all sampling points. This is most apparent at the « Canal » point at Penly. This pattern could not be observed for sole. However, the behaviour of the cumulative sums seems to be the same for the larvae in both months and also for the eggs in both months.

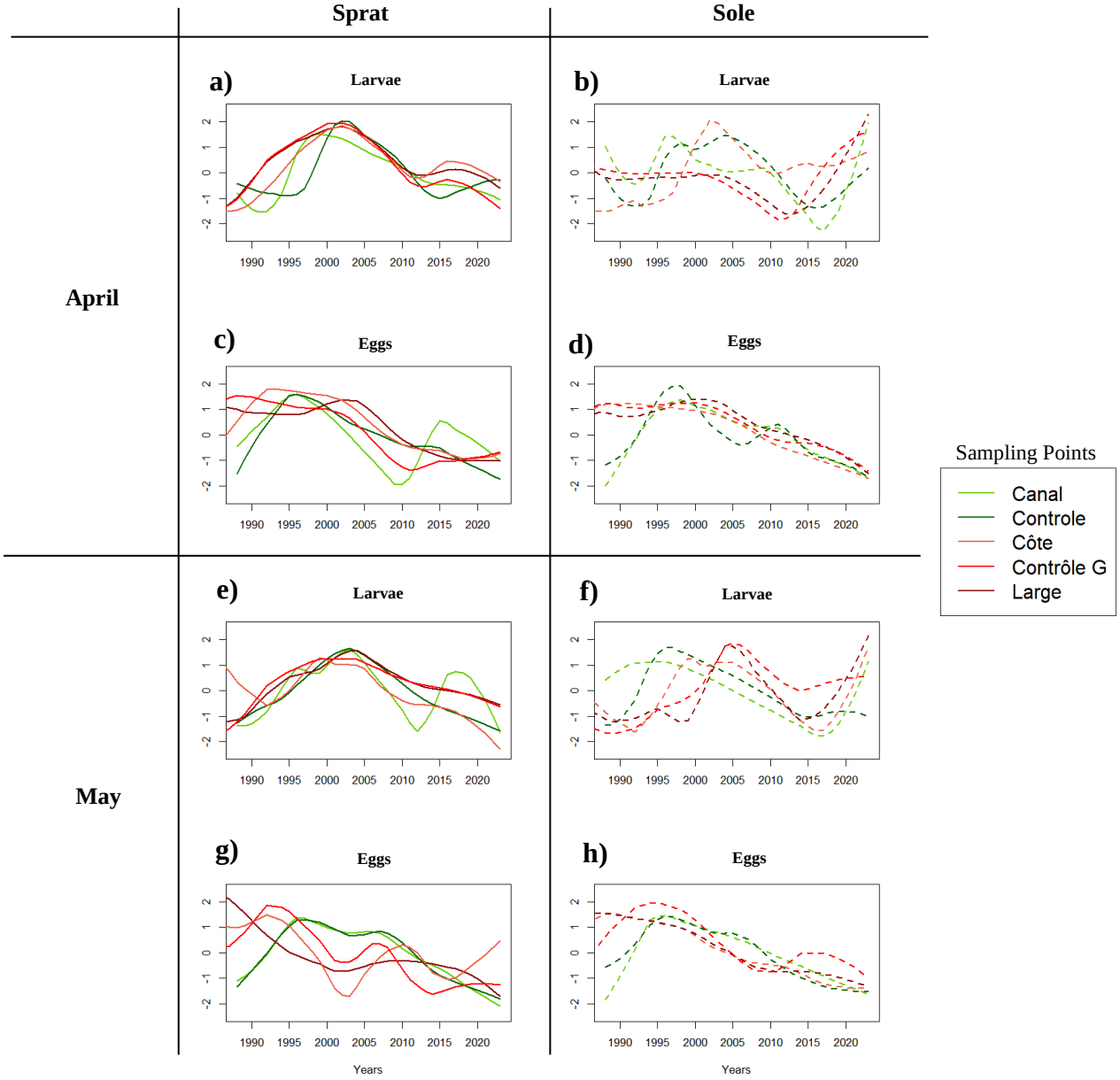

Figure 4: Time series of cumulative sums of abundances of (a, c, e, g) sprat and (b, d, f, h) sole (e, f, g, h) eggs and (a, b, c, d) larvae in (a, b, e, f) April and (c, d, g, h) May, based on five sampling points.

2. Modelling approach

Links between environment, spawning biomass, ichthyoplankton and recruitment were investigated using a statistical modelling approach.

a. *Methodology for analysing time series*

The analyses were carried out using R statistical software. Models of varying complexity were used in this study. Firstly, all the time series were analysed using simple generalised linear models (GLM) using the *glmmtmb* package:

$$Y = a + bX_i + \varepsilon \qquad \varepsilon \sim N(0, \sigma^2)$$

with Y the modelled response, a the intercept, X_i the explanatory variables, b the regression coefficients associated to each explanatory variable and ε the residuals.

Table 2 shows which explanatory variables were considered in relation to the different explained variables (eggs, larvae) for the different CNPEs and months. The selection varied depending on data available (e.g., zooplankton and chlorophyll-a abundances were only available in Gravelines) and ecological sense (e.g., April egg abundance could potentially infer May larvae abundance, but May egg abundance could not have any causal link with April larvae abundance).

Table 2: Model parameterization

CNPE	**Y**	**Equation**
Gravelines & Penly	Egg Abundance (April and May)	Y ~ Temperature + Spawning biomass
Gravelines	Larval Abundance April	Y ~ Temperature + Zooplankton + Chlorophyll-a + April eggs
	Larval Abundance May	Y ~ Temperature + Zooplankton + Chlorophyll-a + April eggs + may eggs
Penly	Larval Abundance April	Y ~ Temperature + April eggs
	Larval Abundance May	Y ~ Temperature + April eggs + may eggs
Gravelines & Penly	Recruitment	Y ~ Larval abundance

Model performance was first assessed based on an analysis of residuals, testing for normality, absence of correlation with the explanatory variables, homoscedasticity (homogeneity and independence) and absence of temporal autocorrelation. When deviating from the above assumptions, further analyses were performed using different types of models of increasing complexity following a protocol described in *figure 5*. The best model was chosen to reduce the structure of residuals as much as possible, starting with the absence of temporal autocorrelation. When the residual analysis did not allow for choosing between different models, the model with the minimum value of the Akaike information criterion (AIC, Crawley (2007)) and being the least complex (according to the principle of parsimony) was selected.

Presence of time autocorrelation in the residuals. The autocorrelation of the residuals was calculated using the « acf » function from the *stats* package. Only autocorrelations with a lag of 1 or 2 years were considered as relevant from an ecological point of view given the span of the time series. In this case, a generalised linear mixed model (GLMM, Crawley (2007), Zuur et al. (2008)) was used and a mixed effect on the year was added as a first attempt to account for the autocorrelation in the residuals. If this was not sufficient to remove the autocorrelation in the residuals, a first-order autoregressive process (AR1) was added to the GLMM. This process captures the time dependence of the series between year N and N+1. However, the AR1 process was sometimes not sufficient to fully capture the time dependency in the residuals. A generalised additive model (GAM, Crawley (2007), Zuur et al. (2008)) was then built with the package *mgcv*

$$Y = a + f(X_i) + \varepsilon \qquad \varepsilon \sim N(0, \sigma^2)$$

Using a smoother was sometimes sufficient to account for temporal autocorrelation in the residuals. Otherwise, more complex mixed generalised additive models (GAMM, Crawley (2007), Zuur et al. (2008)) were used in combination with an AR1 process. Finally, when all the generalised models failed to remove this autocorrelation from the data, we moved on to ARIMAX models (Autoregressive Integrated Moving Average with eXogenous factors). ARIMAX models allow for modelling the dependence between an observation and observations from previous years using an autoregressive (AR) process, and also the dependence between an observation and the forecast errors of previous observations through a moving average (MA) process.

Non-respect of linearity and homogeneity of residuals: When the residuals did not exhibit temporal autocorrelation but when the other residual assumptions were not valid, generalised additive models were used.

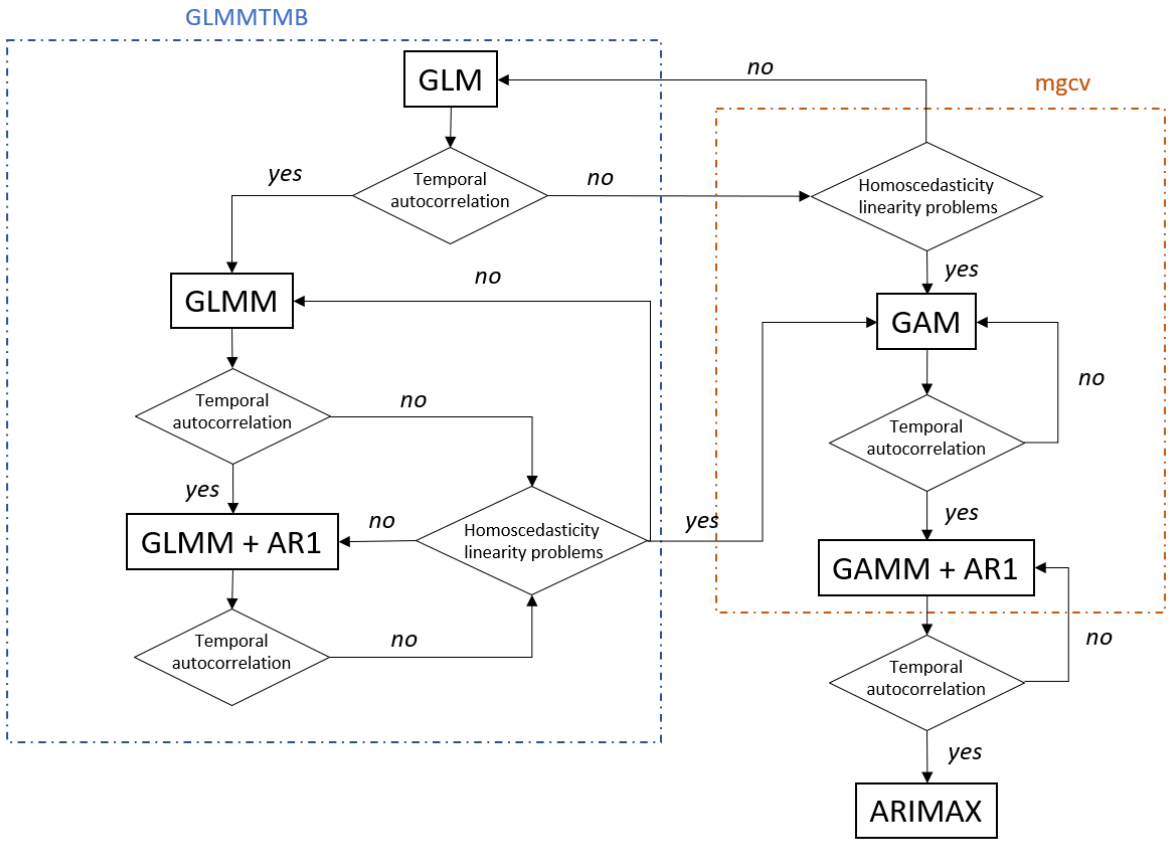

Figure 5: Protocol for model building and selection for the analysis of ichthyoplankton series in relation to environmental variables and spawning biomass.

A decisive step in the modelling was to choose an appropriate family distribution. A Tweedie distribution was here used to model the impact of environmental variables and spawning biomass on ichthyoplankton abundance. The Tweedie distribution is suitable for positive continuous values with a large number of zeroes.

A similar methodology was used to model recruitment as a function of larval abundance. However, in the case of recruitment modelling, ARIMAX models were extensively used *(Appendix XI)*. ARIMAX models, however, do not handle a variety of probability distributions, and normal distributions have to be assumed, so recruitments were log-transformed. A gamma distribution (with a logarithm link) was used when GLMs were applied to model recruitment

variations in relation to larval abundance. This distribution was appropriate since recruitment values are continuous and strictly positive.

Details of the models retained for each time series are presented in the *appendix VII.*

b. *Sensitivity analysis for interpolation method*

The interpolation method used to complete the time series may influence modelling results, especially in cases where the number of missing data was large. A sensitivity analysis was therefore carried out on all sprat and sole eggs and larvae time series, using 5 different interpolation methods:

- The linear interpolation method (baseline)
- The spline interpolation method
- The « random » interpolation method. Each missing value was randomly replaced by a value from the time series.
- The « min-max » interpolation method. Each missing value was randomly replaced by the minimum or the maximum values in the time series.
- The median method. Each missing value was replaced by the median value of the time series.

The « random » and « min-max » interpolation methods were based on 500 runs, from which the probabilities of each explanatory variable being significant ($p < 0.05$) were obtained. The random interpolation method was considered more realistic as it drew from historical values and variability and it was used in subsequent analyses. The other interpolation methods were more exploratory and their results are provided for comparison purposes only.

The results of the sensitivity analysis are presented in *appendix VIII*. Only the results of the sensitivity analysis building on the random interpolation method have been considered to help interpreting modelling outputs. With the random interpolation method, I defined for each pair of explanatory and explained variables a « sensitivity to missing values score » (SMVS) as the percentage of runs (i.e., the number of runs divided by 500) for which the probability that the explanatory variable significantly ($p < 0.05$) contributed to the explained variable.

III. Results

The time trends of the different variables and the modelling results are presented below. Sensitivity analyses determined the robustness of statistical correlation (p-values) to missing values. The choice was made to detail only those results for which the SMVS was greater than 50%. Below this threshold, the results were considered too sensitive to the interpolation method to draw any meaningful conclusions regarding possible links between the variables.

1. Time trends

Egg abundances

For all sampling points at Gravelines and Penly, we can see that the sole and sprat egg abundances have been declining since the 1980s and 1990s for all months, with the exception of sprat eggs in May at Gravelines, which have varied without trend over time *(figure 6)*.

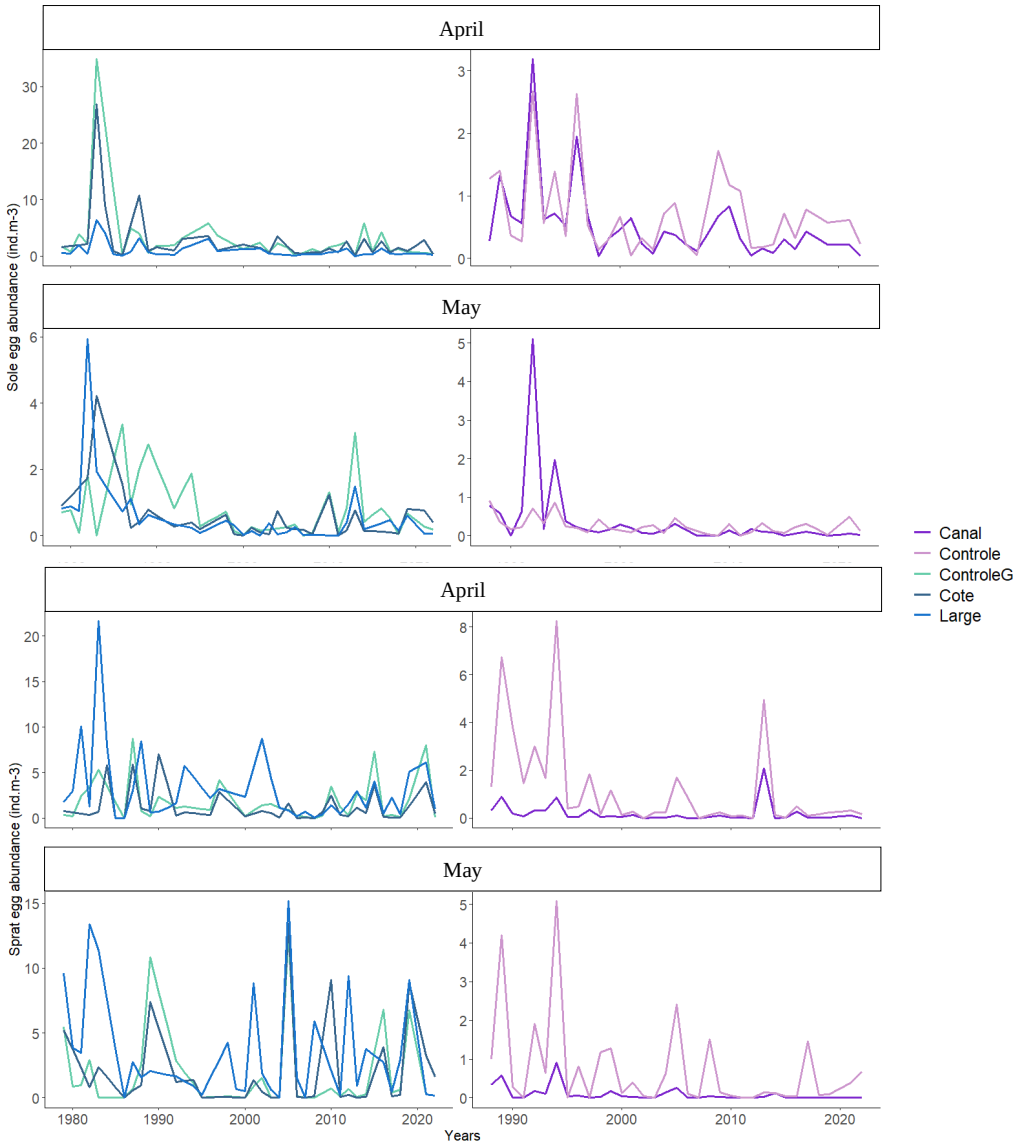

Figure 6: Annual variations in sole (top) and sprat (bottom) egg abundances (ind.m^{-3}) time on the different sampling stations at Gravelines (left) and Penly (right) in April and in May.

Larval abundances

For both sampling sites, sole larval abundance in April and May seems to have increased slightly since the 1980s and 1990s *(figure 7)*. In contrast, sprat larval abundance has declined since the 1980s (Gravelines) and 1990s (Penly) for both months *(figure 7)*.

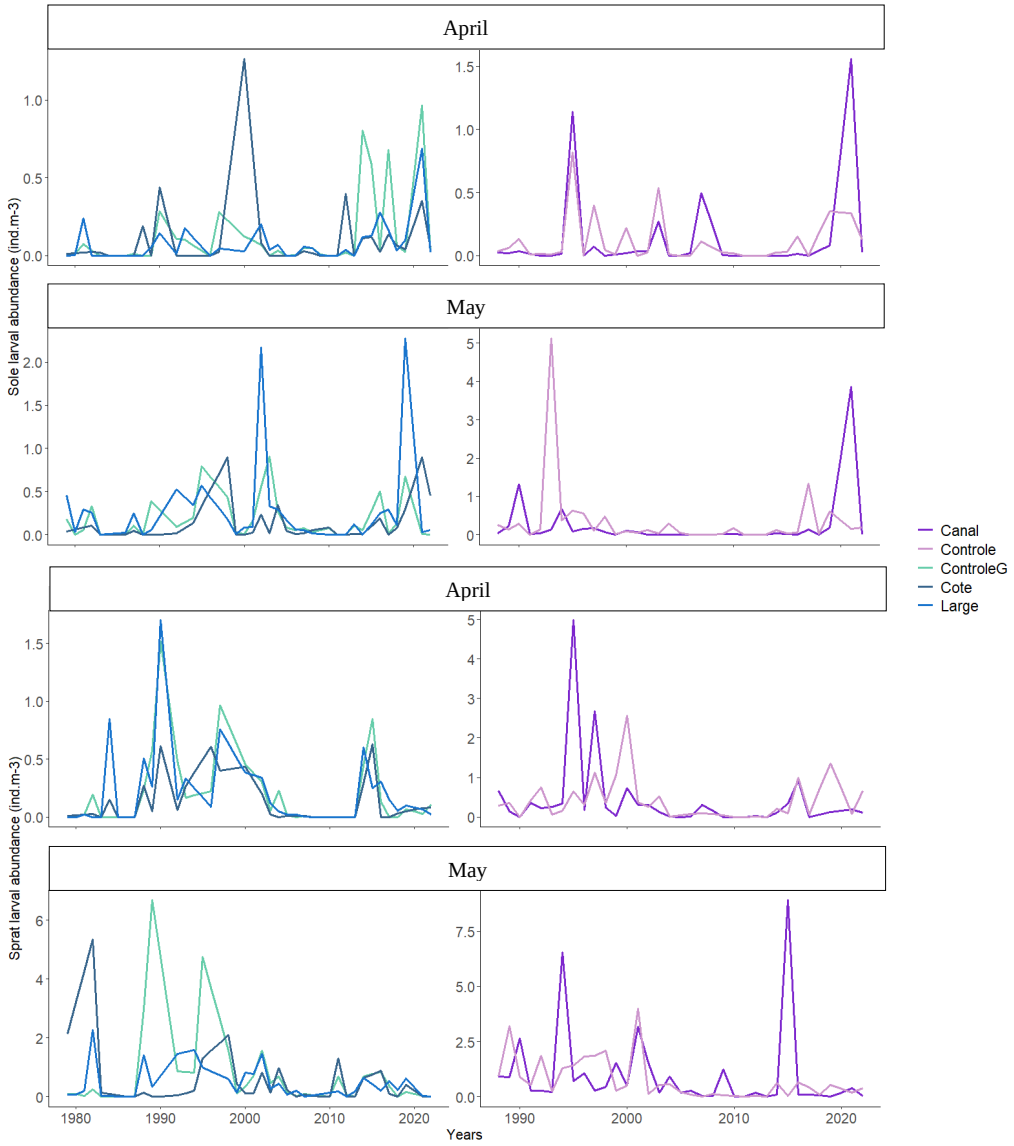

Figure 7: Annual variations in sole (top) and sprat (bottom) larval abundances (ind.m^{-3}) on the different sampling stations at Gravelines (left) and Penly (right) in April and in May

Temperature

Sea temperatures at both Gravelines (North Sea) and Penly (Eastern English Channel) have increased by 1-2°C on average since 1980 *(figure 8)*.

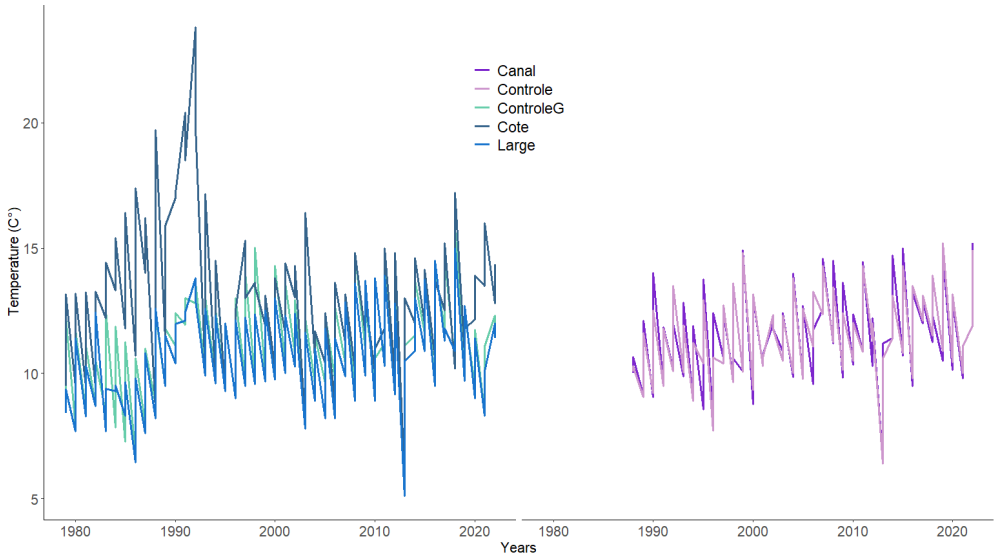

Figure 8: Annual variations in sea temperatures (°C) at Gravelines (left) and Penly (right).

Zooplankton abundance

To better visualise changes in zooplankton abundance, the data were log-transformed *(figure 9)*. Without taking into account abundance values equal to zero, the average zooplankton abundance for the two months in the Gravelines site has overall decreased since the 1980s.

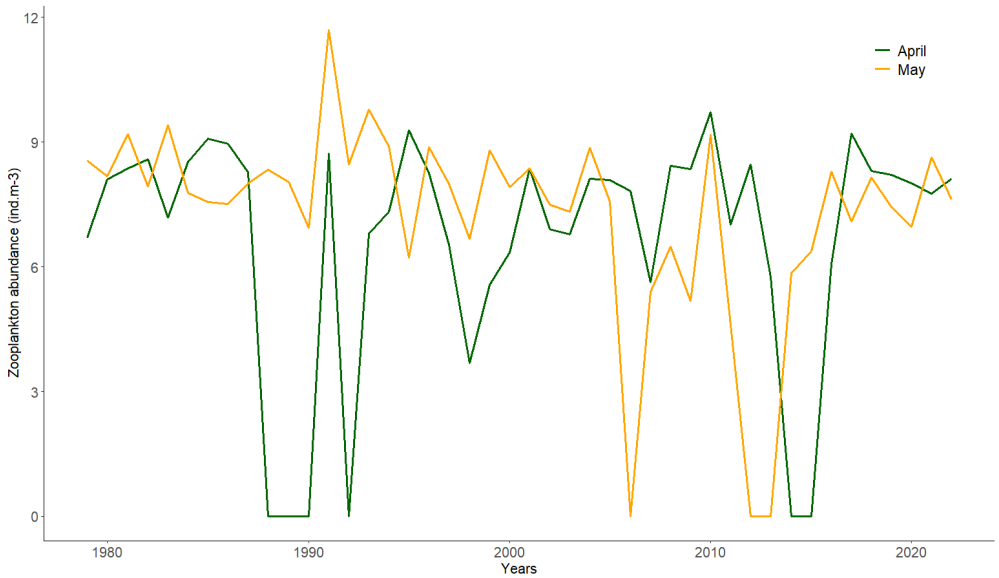

Figure 9: Annual variations in zooplankton abundance (ind.m^{-3}) at Gravelines in April and in May. Data are log-transformed (log(y+1)).

Chlorophyll-a Concentration

Figure 10 shows that the annual series concentration of chlorophyll-a concentration is dome-shaped in April and May. Chlorophyll-a concentration increased until the 2000s, then decreased until 2022, reaching values similar to those observed in the 1980s.

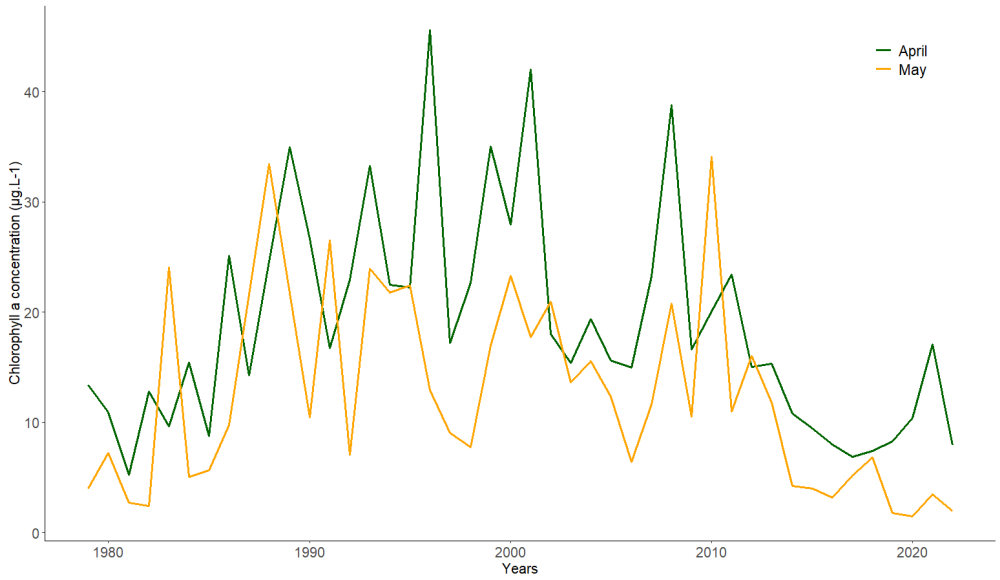

Figure 10: Annual variations in chlorophyll-a concentration (µg.L^{-1}) at Gravelines in April and in May.

Recruitment

In both areas, sole recruitment has declined steeply since the 1990s in the North Sea and since the 2010s in the Eastern English Channel. As for sprat, recruitment has increased slightly since the 1980s in North Sea, but it remained considerably below values observed in the 1970s. In the Eastern English Channel, recruitment (represented by CGFS data) appears to have been stable since the 1990s despite two peaks *(figure 11)*.

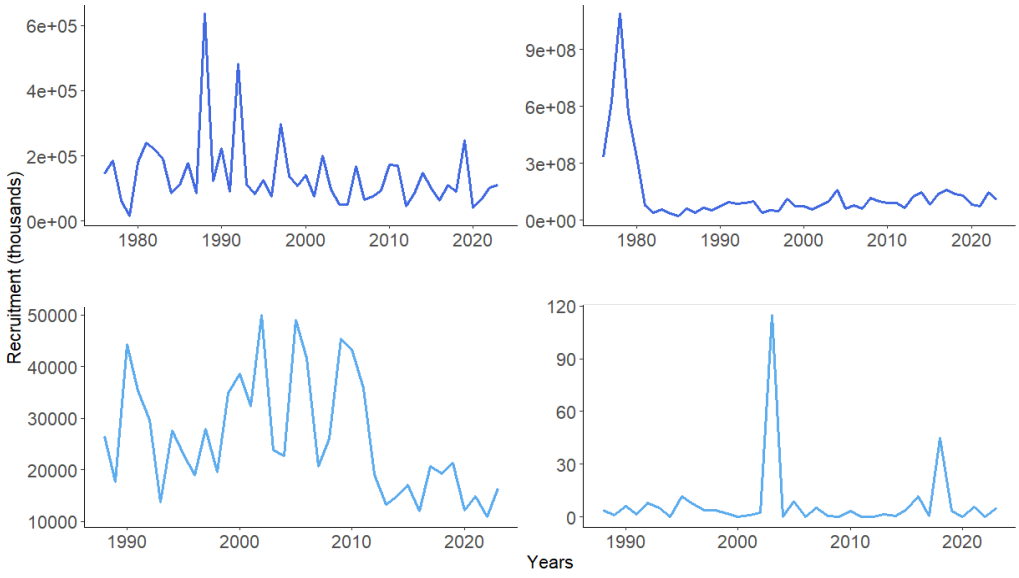

Figure 11: Annual variations in sole (left) and sprat (right) recruitment in the North Sea (top) and the Eastern English Channel (bottom).

Spawning Biomass

Like recruitment, the sole spawning biomass of sole in both areas has decreased since 1990

(North Sea) and 2014 (Eastern English Channel). The spawning biomass of North Sea sprat has increased since the 1980s, while the CGFS indices suggest an increase since the 1990s in in the Eastern English Channel *(figure 12)*.

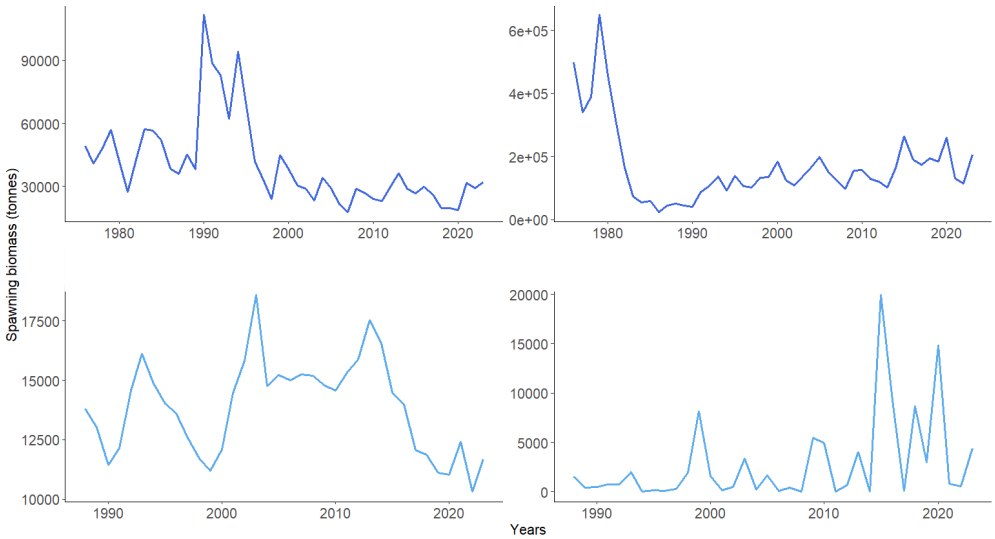

Figure 12: Annual variations in sole (left) and sprat (right) spawning biomass in the North Sea (top) and the Eastern English Channel (bottom).

2. Links between the egg abundance, temperature and spawning biomass
    a. *Sole eggs*

Link with temperature

At Gravelines, the modelling results show a non-linear relationship between temperature and sole egg abundances *(figure 13)*. This result was robust to the replacement of missing values for the « ControleG » point (with SMVS of 96% and 82% in April and May, respectively), but not for the other sampling points (with SMVS lower than 50%).

In April, the relationship was significant ($p < 0.05$) for « ControleG », with a maximum abundance of sole eggs observed between 8 and 10°C. In May, an overall negative relationship was found for the « ControleG » point.

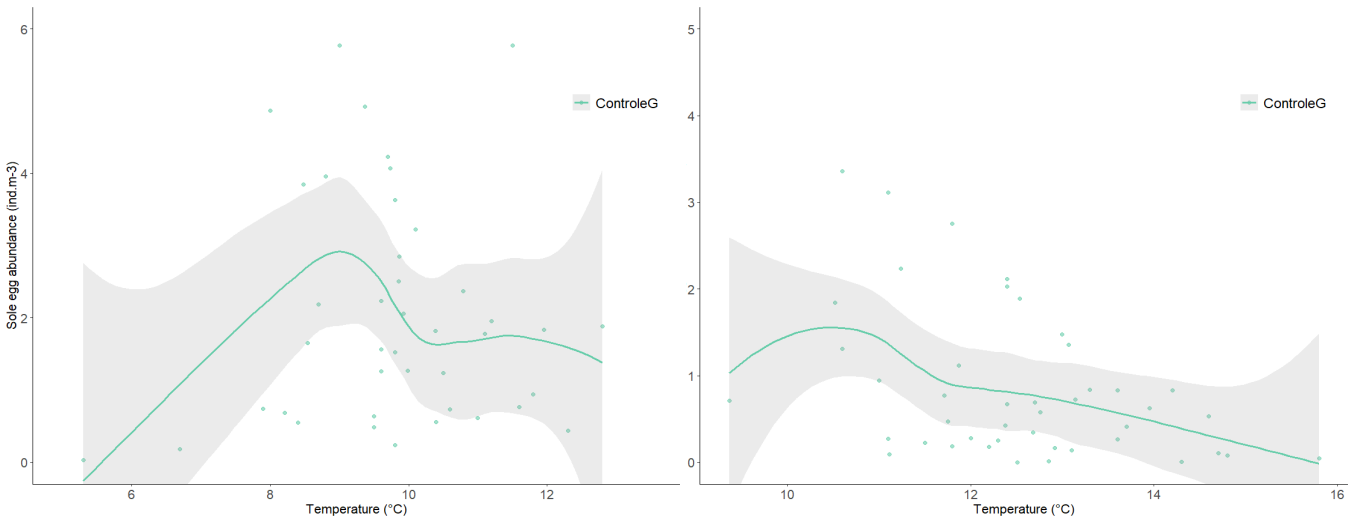

Figure 13: Relation between sole egg abundance and temperature at Gravelines in April (left) and May (right).

At Penly, the relationship was significant only at the « Canal » point in April and at the « Controle » point in May ($p<0.05$), with SMVS of 59% and 99%, respectively. Sole egg abundances decreased with temperature in April and May *(figure 14)*. In April, the maximal abundance of sole eggs was found around 8°C. There were, however, too few points in the neighbourhood of the presumed optimum value to strongly support this finding.

In May, no optimal temperature value could be found in relation to sole egg abundances within the current data range (10-16°C) *(figure 15)*.

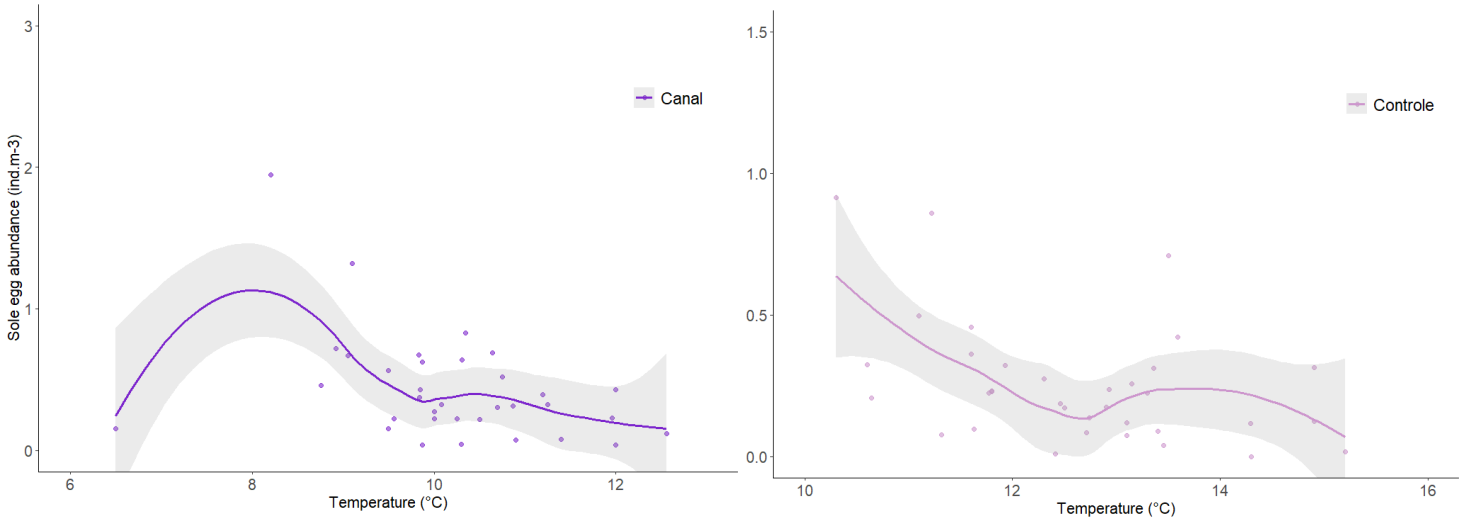

Figure 14: Relation between sole egg abundances and temperature at Penly in April (left) and May (right).

Link with spawning biomass

At Gravelines, a significantly ($p<0.05$) non-linear relationship was found between the spawning stock biomass (SSB) and the abundance of sole eggs in April for « ControleG » and « Large » sampling points, with SMVS of 68% and 65%, respectively. The correlation between sole egg abundances and SSB at the « Cote » point was not significant.

Graphically, an optimum of sole egg abundances can be observed with the spawning biomass at around 60,000t *(figure 15)*. However, most of the points are located before this optimum and only 4 points contribute to the decreasing part of the curve. Values observed after this optimum correspond to high spawning biomass values observed in the 1980s. This means that the relationship obtained is overall positive over the last three decades.

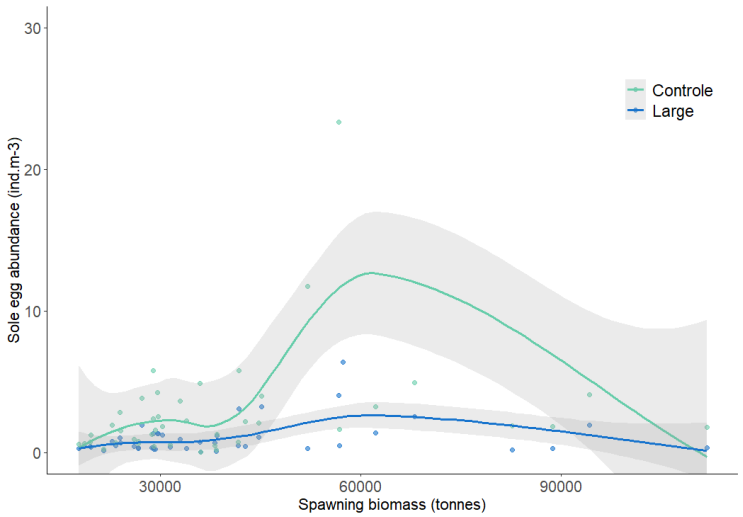

Figure 15: Relation between sole egg abundances and spawning biomass at Gravelines in April

In May, the contribution of sole SSB to egg abundances at Gravelines were either not significant ($p<0.05$), or could not be interpreted as the SMVS was lower than 50%.

At Penly, in April, the relationship between the spawning biomass and the abundance of sole eggs in April was significant ($p < 0.05$) and non-linear for the two sampling points *(figure 16)*. A maximum of eggs was observed with a spawning biomass of 13,000-14,000t. This relationship was very robust for both points (with SMVS of 99% and 98% for « Canal » and « Controle », respectively).

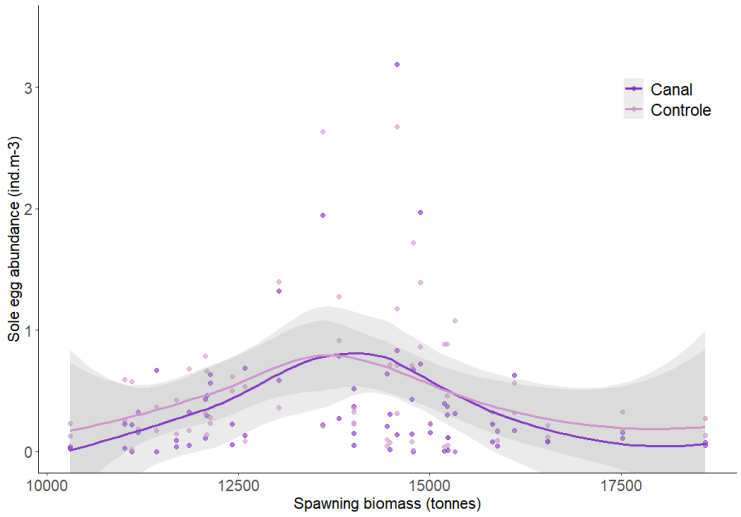

Figure 16: Relation between sole egg abundances and spawning biomass in Penly in April

In May, the contribution of sole SSB to egg abundances at Penly were either not significant ($p < 0.05$), or could not be interpreted as the SMVS was lower than 50%.

b. Sprat eggs

Link with temperature

At Gravelines, temperature was found to be significantly ($p < 0.05$) correlated to sprat egg abundances in April for the « Cote » point *(figure 17)*, with a SMVS of 69%. An optimum could be found graphically around 16°C. However, this optimum value was supported by few data points (temperatures exceeded 15°C in only 4 sampling points). No significant relationships between sprat egg abundances and temperature were found in May.

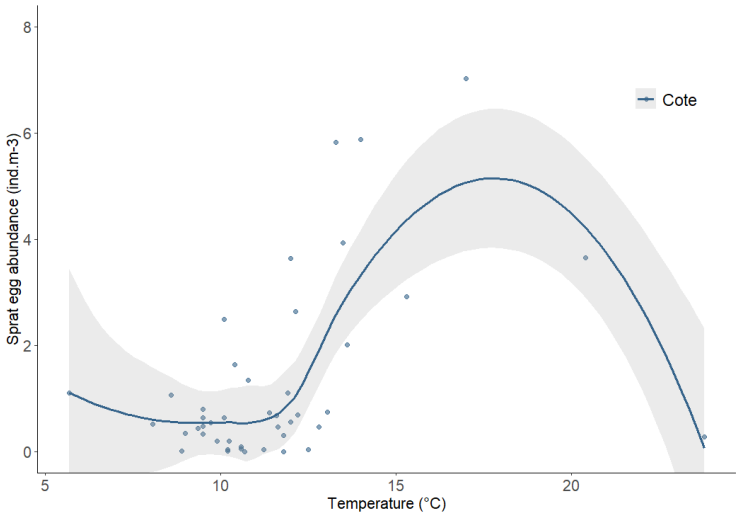

Figure 17: Relation between sprat egg abundance and temperature at Gravelines in April.

At Penly, a negative relationship between temperature and sprat egg abundance in April was observed for the two sampling points *(figure 18)*. The overall effect of temperature on sprat egg abundance was negative over the data range, and no optimum value could be found. In addition, the relationship in May between temperature and sprat egg abundance was extremely robust, with SMVS of 99% for both the « Controle » and the « Canal » points.

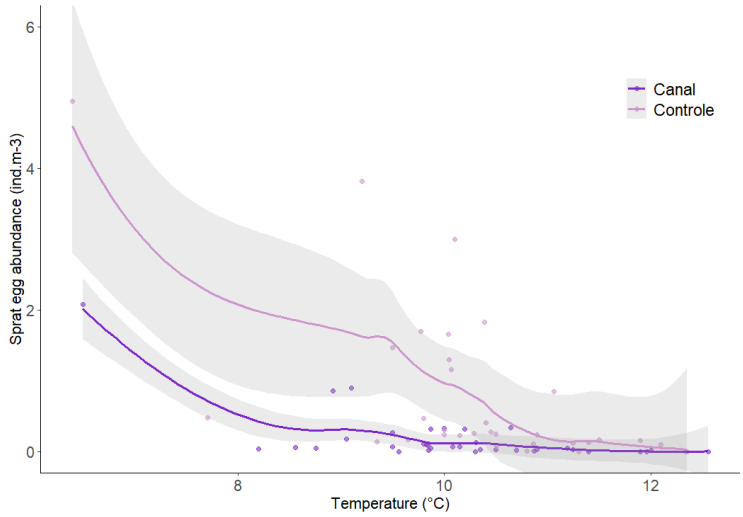

Figure 18: Relation between sprat egg abundances and temperature at Penly in April.

Link with spawning biomass

No significant relationship was detected between sprat egg abundances and spawning biomass.

3. Links between larval abundance, environment and egg abundances
    a. *Sole larvae*

At Gravelines, several explanatory variables (temperature, chlorophyll a, sole egg abundances) were found significantly ($p < 0.05$) related to sole larval abundances for different months and stations. However, the estimated parameters and their associated p-value were highly sensitive to the replacement of missing values (with a maximum SMVS of 38%, *appendix VIII).*

Link with egg abundances:

At Penly, only a significant non-linear relationship ($p<0.05$) was found between the abundance of sole larvae and sole eggs in May at the « Controle » point, with a very high SMVS of 96%. Although the relationship was rather complex *(figure 19)*, sole larval abundances increased overall until the abundance of sole eggs in May was of 0.5 ind.m^{-3}, and it stabilized afterwards.

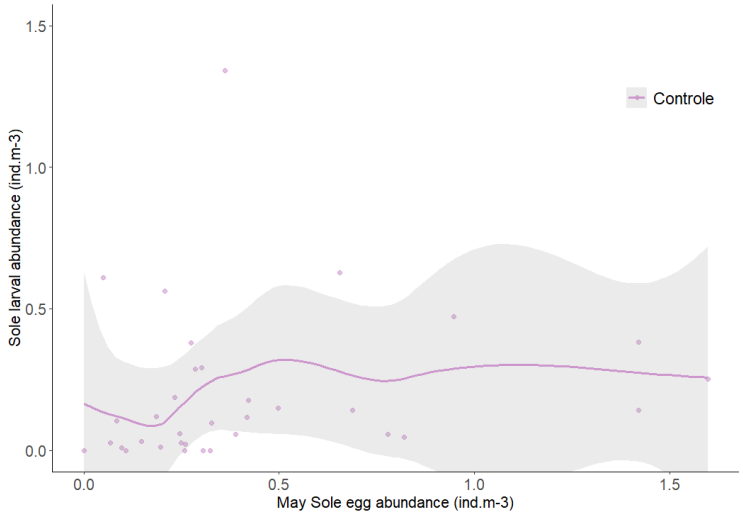

Figure 19: Relation between sole larval abundance and May sole egg abundance in Penly in May.

    b. *Sprat larvae*

Significant and robust (according to SMVS) relationships between sprat larvae and explanatory variables were only found at Gravelines and only those are presented below. For the Penly site, no variable showed a significant relationship with the sprat larval abundance for any combination of sampling points and months.

Link with temperature:

At the Gravelines site, a significant relationship ($p<0.05$) was obtained with temperature only for two points in April: a non-linear relationship for the « Large » point and a positive relationship for the « Controle » point, with SMVS of 68% and 71%, respectively. Graphically,

the non-linear relationship obtained for the « Large » point was overall positive *(figure 20)*. Indeed, the part of the curve located after the « optimum » is made up of only 6 points.

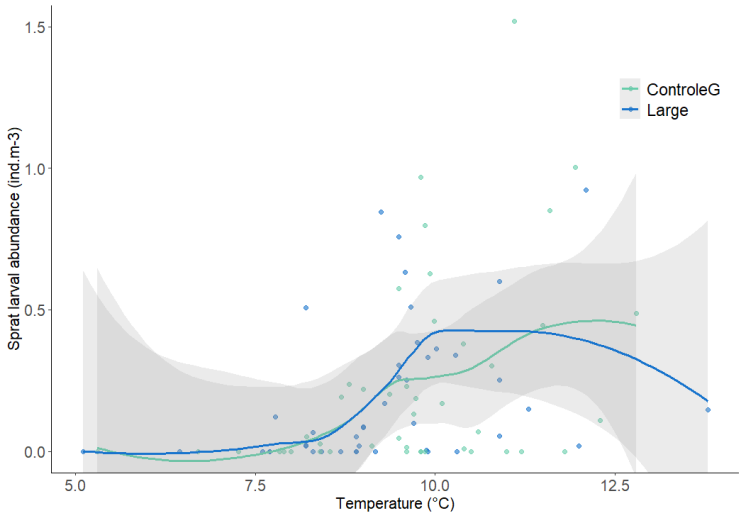

Figure 20: Relation between sprat larval abundance and temperature at Gravelines in April.

Despite the significant relationships with temperature obtained in May for the « Large » and « Cote » points, the p-value were highly sensitive to the choice of interpolation method (with SMVS of 40% and 44%, respectively).

Link with Zooplankton abundance:

At Gravelines, a significant non-linear relationship ($p < 0.05$) was obtained with zooplankton abundance for the « Large » point in April only, with a SMVS of 80%. No clear patterns could be identified *(figure 21)*. No significant relationship was found in May.

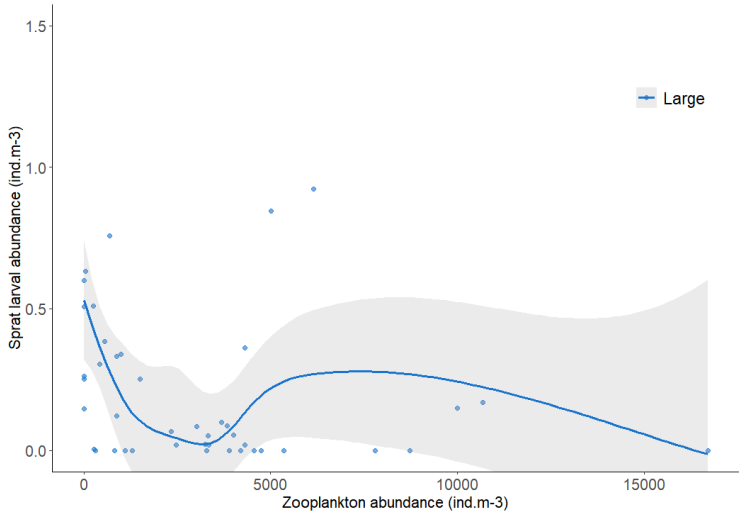

Figure 21: Relation between sprat larval abundance and zooplankton abundance in April at Gravelines.

Link with April egg abundances:

At Gravelines, a significant ($p<0.05$) and robust (SMVS=68%) relationship between sprat larval abundance in April and the abundance of sprat eggs for the same month was found for the

« Controle » point. We can see graphically that sprat larval abundance overall increased with sprat egg abundance in April for the « Controle » point *(figure 22).*

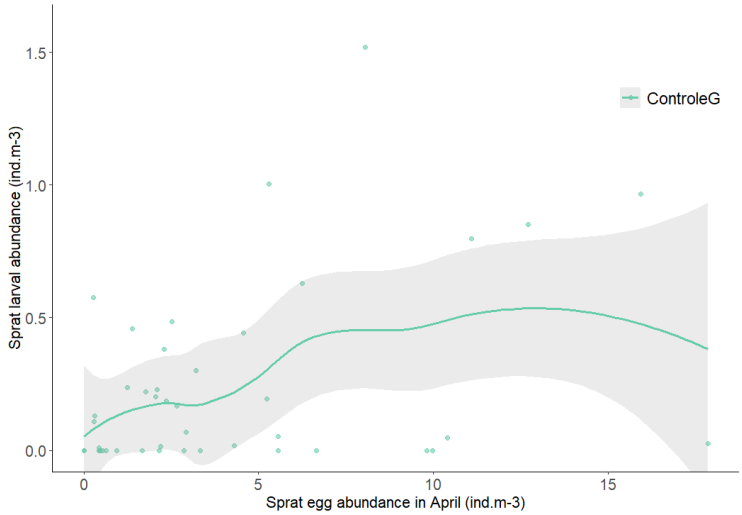

Figure 22: Relation between sprat larval abundance and sprat egg abundance at Gravelines in April.

Link with Chlorophyll-a:

Although chlorophyll-a was found to be significant when analysing the time series of sprat larval abundance using linear interpolation, the significance of the relationship was very sensitive to the interpolation method. A maximum score of 52% was obtained with chlorophyll a for the « Cote » point in May.

4. Link between recruitment and larval abundance

The abundance of sole or sprat larvae did not appear to contribute significantly ($p < 0.05$) to the variability in recruitment for any area (Gravelines and Penly) and month (April or May).

IV. Discussion:

1. Link between egg abundance, temperature and spawning biomass

Meaningful relationships have been found between temperature, spawning biomass and egg abundances. For sprat, temperature was determined to be significant only in April at Gravelines and Penly. At Gravelines the maximum sprat egg abundances was observed around 16°C at the « Cote » point. However, this point is located close to the plant's discharge water (Cf II.1) which can explain higher observed temperatures. High abundances above 12°C may be the result of eggs drifting from spawning further offshore and carried by currents towards the coast where temperatures are higher. Except for several values, most of the observed abundances were found where temperatures were below 12°C and similarly for Penly. This range of temperature is in accordance with the spawning optimum for sprat between 8 and 11°C and up to 13°C in the North Sea (Quéro, 1984; Peck et al., 2012; Archambault et al., 2018). However, unlike Gravelines, the relationship at Penly is strictly negative. Another hypothesis for this negative relationship is that in the Eastern English Channel, spawning may start in January (Quéro, 1984; Schlaich et al., 2023). Additional sampling in January-March, when sea temperatures are lower than in April-May, would be needed to better evaluate the relationship

between sprat egg abundancess and temperature (Schlaich et al., 2023).

At both Gravelines and Penly, we observe a negative relationship between sole egg abundances and temperature, when temperatures exceed 8-10°C. Graphically, we can even observe a temperature optimum at around these temperatures. This optimum temperature bears out results from other studies investigating sole spawning in relation to sea temperature. In fact, sole starts spawning at around 7-8°C (Fonds, 1979; Quéro, 1984), and the optimal temperature is between 8 and 12°C. Above these temperature values, spawning remains possible but is less effective and leads to lower egg abundances (Fonds, 1979 ; Devauchelle et al., 1987; Sardi et al., 2021).

These optimal temperatures would be linked to better egg survival and development for both species. Indeed, in sole, increasing temperature beyond the optimal range of temperature (8-12°C) may result in smaller and poorer quality eggs, smaller-sized yolk sacs, lower energy reserves, increased egg deformation, and decreased survival (Devauchelle et al., 1987; Silve, 2023). The same applies to sprat, where too high temperatures would result in premature hatching with individuals the development of which is not complete (Thompson et al., 1981; Petereit et al., 2008; Peck et al., 2012). Additionally, Petereit et al. (2008) showed that the survival rate was highest for temperatures between 8 and 10°C in contrast to the study by Peck et al. (2012), who found a similar survival rate for North Sea sprat eggs between 5 and 16°C. Our results cannot confirm or refute these two studies. Indeed, the majority of our non-zero abundances are in the 8-12°C range, but we have observed a positive relationship between sprat egg abundance and temperature. This may suggest a higher survival rate at higher temperatures given that eggs in the English Channel are heat-adapted (high thermal sensitivity, Petereit et al., 2008). Moreover, these optimal spawning temperatures could also reflect an adaptation to match-mismatch dynamics (Cushing 1975). Laying eggs at these temperatures would allow the eggs to hatch and first-feeding larvae to emerge in a period of high zooplanktonic prey abundance (Sardi et al., 2021; Sardi et al., 2023). However, in the optimal window of temperature, a high variability in the egg abundance levels were observed. This may be due to sampling bias or to other explanatory factors that were not included in our analyses. For instance, eggs can be exported passively outside the sampling area according to currents and wind intensity (Grioche, 1998). Moreover, the variability can be explained by spawning biomass too.

The abundance of eggs is strongly linked to the female spawners. The older and larger the females, the more eggs they will lay (Green, 2008) : this is the maternal effect. In addition, the proportion of eggs is also linked to their condition (Green, 2008; Takasuka et al., 2019; Koenigbauer and Höök, 2023). For North Sea sole, in Gravelines, the spawning biomass was overall positively related to the abundance of sole eggs in April and May, i.e., the greater the spawning biomass, the greater the abundance of sole eggs. A similar relationship was found for plaice, another flatfish, in the Baltic Sea (Ustups et al., 2013). Gravelines belongs to a major North Sea sole spawning ground (van de Wolfshaar et al., 2022; Wacquet et al., 2023), which may explain the strong relationship between egg abundances and spawning biomass. In Penly, Eastern English Channel sole spawning biomass and the sole egg abundance have a dome-shaped relationship in April and less so in May. This might be a sign of density-dependence in the area which was not observed in Gravelines for the North Sea stock. The mechanisms of density-dependence on eggs production are of two kinds. The first is predation, which is the primary cause of eggs mortality (Leggett and Deblois, 1994; Brunel, 2006). The second is directly linked to the abundance of spawners (Green, 2008) and the ability of the habitat to accommodate spawners (Brunel, 2006).

Our results suggest that the temporal dynamics of sole egg abundances in this area may reflect a more global dynamic of sole spawning stock biomass at the larger scale of the southern

North Sea. This finding could be a valuable contribution to fisheries advice, as sole egg abundances could be integrated into stock assessment as an independent index of spawning stock biomass.

For sprat, no significant relationship was observed between spawning biomass and egg abundances. For the North Sea stock, this may be due to the large distance between Gravelines and the spawning grounds, which are located mainly inside the German Bight, off the coast of Jutland and close to the western and northern coasts of Scotland (Munk, 1991). The main spawning grounds of the English Channel sprat stock are generally unknown. In addition, we used CGFS information to derive a sprat spawning index and not ICES stock assessment outputs as for sole. The CGFS, however, is better designed to sample demersal rather than pelagic fish like sprat, which could have adversely affected the reliability of the English Channel sprat spawning index used in this study.

2. Link between larval abundance, temperature and plankton

As with eggs, we obtained several significant relationships between larval abundance and environmental variables (temperature, chlorophyll-a, zooplankton abundance, egg abundances). However, the sensitivity of larvae to environmental parameters depends on these developmental stages, which could not be identified. As a result, relationships obtained between larval abundance and environmental factors should be treated with caution.

For instance, larval temperature tolerance changes with larval development (Irvin, 1974). Temperature also has an influence on the duration of the stages. Larval development stages last longer or shorter depending on the temperature, and therefore affect the different abundances of the different life stages (Yin and Blaxter, 1987) and lead to different larval survival rates (Nissling, 2004). This may explain why no relationship was obtained between sole larval abundance and temperature for the two zones. Nevertheless, a positive relationship between larvae abundance and temperature was found at Gravelines for sprat. Sprat eggs have a wide temperature tolerance (2-20°C, (Peck et al., 2012; Di Pane et al., 2020), which may explain why sprat larvae may be encountered at various temperatures. However, the optimum temperature for the growth and survival of sprat larvae in the North Sea was found between 7 and 12°C (Peck et al., 2012). This corresponds to the temperature range at which sprat larvae were sampled in this study. Above 12°C, abundance seems to decrease. This would confirm the observations of Frisk et al. (2015) that high temperatures lead to poor physiological state, increased energy requirements, andmore rapid starvation.

The stage of development is also an important factor in determining the diet and condition of individuals. The prey composition of sole and sprat larvae depends on the size of the mouth (Houde, 2001; Voss et al., 2009). Sole and sprat larvae can be separated into several developmental stages characterised by the yolk sac (Russell, 1976). Once the yolk sac has been absorbed, the larvae switch from an endogenous diet (stage 1) to an exogenous diet (stage 2) (Russell, 1976). This makes them more susceptible to starvation : the critical period (Hjort, 1914). The abundance of zooplankton prey is important for the survival of the larvae. The diet of sole larvae consists of a wide range of prey, including planktonic and epi-benthic prey, until metamorphosis. Larval sole consume a variety of prey including copepods, cladocerans, nauplii, polychaetes, harpacticoid copepods, invertebrate eggs, small bivalves and gastropods, and appendicularians. (Ryland, 1964; Wyatt, 1974; Grioche, 1998; Lagardere et al., 1998; Amara et al., 2000). Grioche (1998) and Grioche et al. (2001) found that the diet of sole larvae varies according to the larval developmental stage and that the link with plankton abundance is more intense during early larval stages and decreased with later stages.

Similarly, sprat larvae feed on a wide variety of planktonic prey such as copepods,

nauplii (*Acartia spp.* ; *T. longicornis* ; *C. hamatus*), cladocerans, microplankton, etc. (Arrhenius and Hansson, 1993; Dickmann and Alheit, 2004; Möllmann et al., 2004; Carpentier et al., 2009; Voss et al., 2009). The difficulty to find a relationship between larval abundance and zooplankton abundance may be the result of several modelling choices. In fact, the « Zooplankton » variable from all the sampling points in Gravelines were considered to be identical to those from the « Prise » point. However, this assumption could be at fault, due to the heterogeneity of zooplankton spatial distribution (Grioche and Koubbi, 1997). In addition, zooplankton abundance was calculated as the sum of several zooplankton species characteristic of the spring period, which could have blurred the relationship with sprat larval abundance.

For both sole and sprat, we were able to find a significantly positive or non-linear relationship between egg abundances and larval abundance. The graphs showed a plateau for high egg abundances. These plateaus may be the result of density-dependent processes such as predation or environmental carrying capacity (space, trophic), which could regulate the development of populations (Brunel, 2006; May, 1977)).

However, other processes may explain the absence of relationship in some cases for larvae of both species. Firstly, larvae are mobile animals despite their limited swimming capacity (Houde, 2016). Sprat and sole larvae are capable of migrating, which challenges their sampling on fixed stations with limited spatial extent (Grioche, 1998; Lagardere et al., 1998; Voss et al., 2007; Di Pane et al., 2020). They can migrate in several ways. Firstly, they can carry out nychthemeral migrations guided by light as part of their feeding (Grioche, 1998; Voss et al., 2007). But they are also capable of ontogenic migrations to move from offshore areas to coastal areas close to feeding grounds (Grioche, 1998; Voss et al., 2007). Young larvae are more likely to make nocturnal migrations and older larvae ontogenic migrations (Grioche, 1998). In addition, larvae can be carried away by currents. There is a continuity of larval assemblages from the English Channel to the North Sea; water masses flow northwards with north-easterly currents (Grioche, 1998). This continuity may explain why larval abundance is greater in the North Sea than in the English Channel (Grioche, 1998). Finally, larvae may not be well sampled due to occasional clogging of the nets by the proliferating algae *Phaeocystis globosa* (Schlaich et al., 2023; Wacquet et al., 2023), or due to active net avoidance (Grioche, 1998).

3. Link between larval abundance and recruitment

Recruitment is controlled by multiple tropho- and hydrodynamic processes affecting early life stages of fish from spawning to juvenile stage (Houde, 2008; Savina et al., 2016). Many processes can therefore influence recruitment. Link between recruitment and fish larvae can be stage- and species-dependent (Houde, 2016). No significant relationship was observed between larval abundances and recruitment indices used in the present study. Several explanations are possible. First, as discussed in the introduction, larval survival is a major process explaining recruitment variability. Brosset et al. (2020) showed for Northwest Atlantic mackerel that recruitment peaks were linked to high larval survival rate and a spatio-temporal match between larvae and available food. The spatio-temporal shift influencing low recruitment in Brosset et al. (2020) could also be a cause of our low recruitment. However, the approximation made for the « Zooplankton » and « Chlorophyll-a » variables may have prevented us from being able to test this hypothesis. In addition, our results showed that it was difficult to find a relationship between larval abundance and environmental variables by taking into account only our data, in particular due to larval migrations and the lack of determination of developmental stages. Indeed, in the critical period hypothesis formulated by Hjort (1914), stage 2 larvae representing the critical stage would be the main contributor to recruitment

variability. Leggett and Deblois (1994) and Houde (2016), on the other hand, suggested that recruitment variability could be linked to later stages larvae. For plaice, another flatfish, recruitment can be predicted from young stage abundances while for clupeids such as sprat, recruitment can be explained by later stage abundance (Houde, 2008).

Secondly, the variability in recruitment could be linked to the spawning date because this influences the environmental conditions experienced by the ichthyoplankton and therefore the survival rate of the larvae (Savina et al., 2016). Our results showed an increase in temperature in the North Sea and the Eastern English Channel. This could have an influence on the start date of spawning and thus on the environmental conditions encountered by ichthyoplankton. Moreover, wind systems and climate strongly control recruitment variability (Houde, 2016).

Overall, it appears that the link between recruitment and larval abundance remains often difficult to demonstrate because of other upstream factors affecting recruitment variability at other developmental stage (Ustups et al., 2013). For instance, for sole, recruitment would also be linked to metamorphosis (Leggett and Deblois, 1994; Post et al., 2017) and juveniles settlement success. Recruitment of sole is also strongly linked to the quality and size of the area and the density of juveniles (Gibson, 1994; Le Pape et al., 2003b; Le Pape et al., 2003a). Poor habitat quality will reduce the survival of juveniles and therefore limit recruitment (Gibson, 1994). For sprat, recruitment may also be linked to temperature experienced during eggs and larval phases so that recruitment could be predicted before spawning period in the Baltic Sea (MacKenzie and Köster, 2004).

V. Conclusion:

The present study provided highlights on the effect of environmental and population dynamic variations on the long-term spatio-temporal variability of ichthyoplankton stages for sole and sprat. In particular, a strong relationship was found between egg abundances and temperature for both species as well as with the spawning stock biomass for sole. On the contrary, no clear relationship was found for the larval stage regarding environmental variables. Also, no link between larval abundances and recruitment was found.

Following this long-term study, we can envisage several perspectives. the first, an egg abundances index derived from data collected at the Gravelines power plant could thus be integrated in the assessment of North Sea sole as an index of spawning biomass.

The second would be an improvement in the interpolation method. Missing data are a real problem in statistical analysis. In addition, it would be interesting to be able to quantify the sampling bias (blocked nets, handling problems, etc.) in order to estimate the real abundance of plankton for all communities (ichthyoplankton, zooplankton, phytoplankton).

Finally, the reliability of the SMVS threshold chosen (50%) during our sensitivity analysis to qualify the robustness of our results to the replacement of missing values could be further investigated building on simulated data sets.

Apart from the methodological perspectives, this study confirmed the difficulties to explain recruitment variability. However, improving our knowledge of larvae could provide a better understanding of recruitment variability. In particular, knowledge of the nutritional status of the larvae would help quantifying their potential survival and subsequent recruitment. In fact, it would be interesting to be able to start building a long-term database on larval condition from IGA samples. As the samples are currently preserved in a formaldehyde solution, it is impossible to carry out condition analyses. However, new samples could be collected and preserved in a way such analyses could be carried out. For example, we could calculate the

histological indices of the larvae according to their stage of development, as was done by Grioche (1998) and Di Pane (2019). It would also be possible to measure lipids contents, as was done by Di Pane (2019), in order to determine the larvae's energy reserves. This would allow to determine whether the proportion of larvae are in poor or good condition, and linking to variations in recruitment.

Furthermore, one limitation of this study in analysing the link between larval abundance and zooplankton abundance was the simplifications made to derive this variable. Larvae stomach contents could be investigated, as was done by Denis (2016), to find out whether the diet of our larvae has changed over time in relation to zooplankton abundance in the area. This would make it possible to better determine the link between zooplankton and larval abundances and condition.

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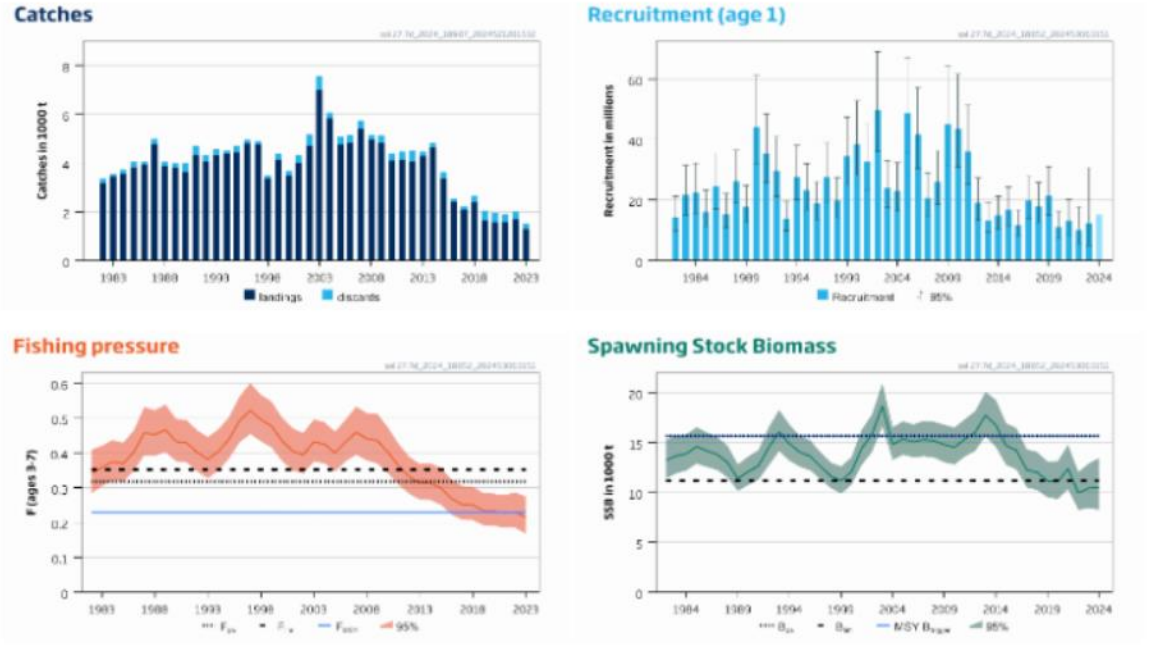
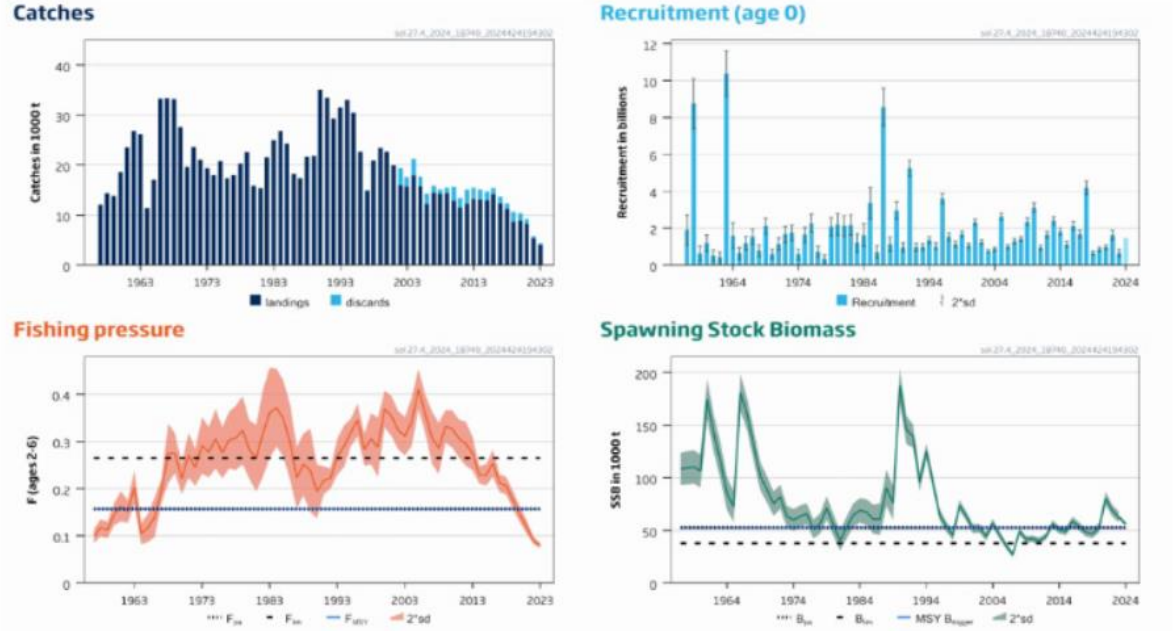
VII. Appendix:

Appendix I: Stock indicator for sole Eastern English Channel stock and sole North Sea stock (Catches, Recruitment, Fishing pressure, Spawning stock Biomass)

1) Eastern English Channel

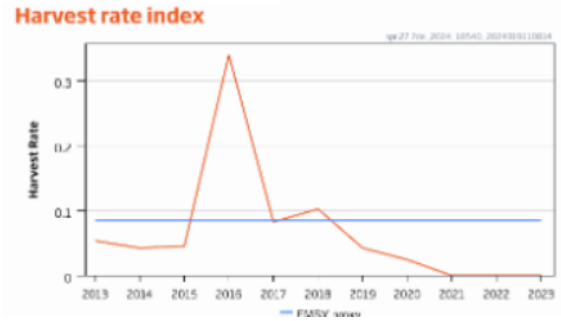


2) North Sea

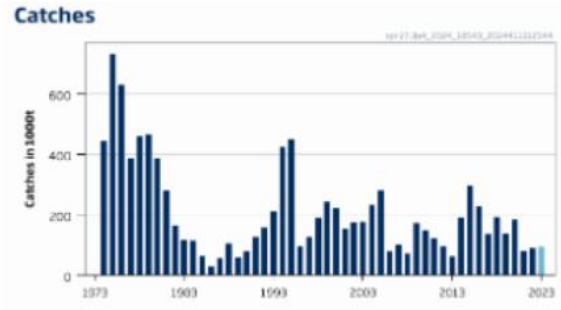


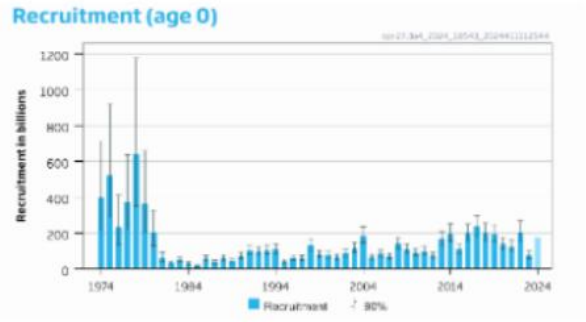
Appendix II: Stock indicator for sprat Eastern English Channel stock (catches, Harvest rate index and stock size indicator) and sprat North Sea stock (Catches, Recruitment, Fishing pressure, Spawning stock Biomass)

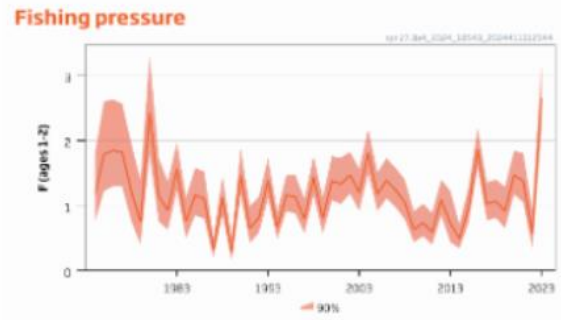
1) Eastern English Channel

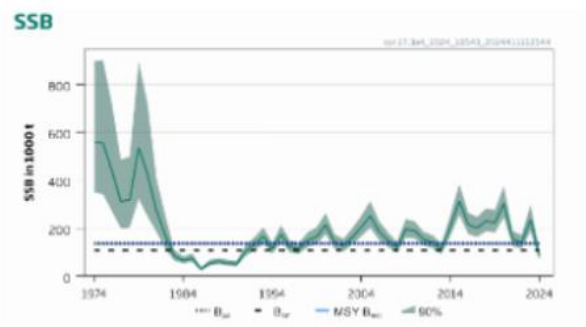


2) North Sea





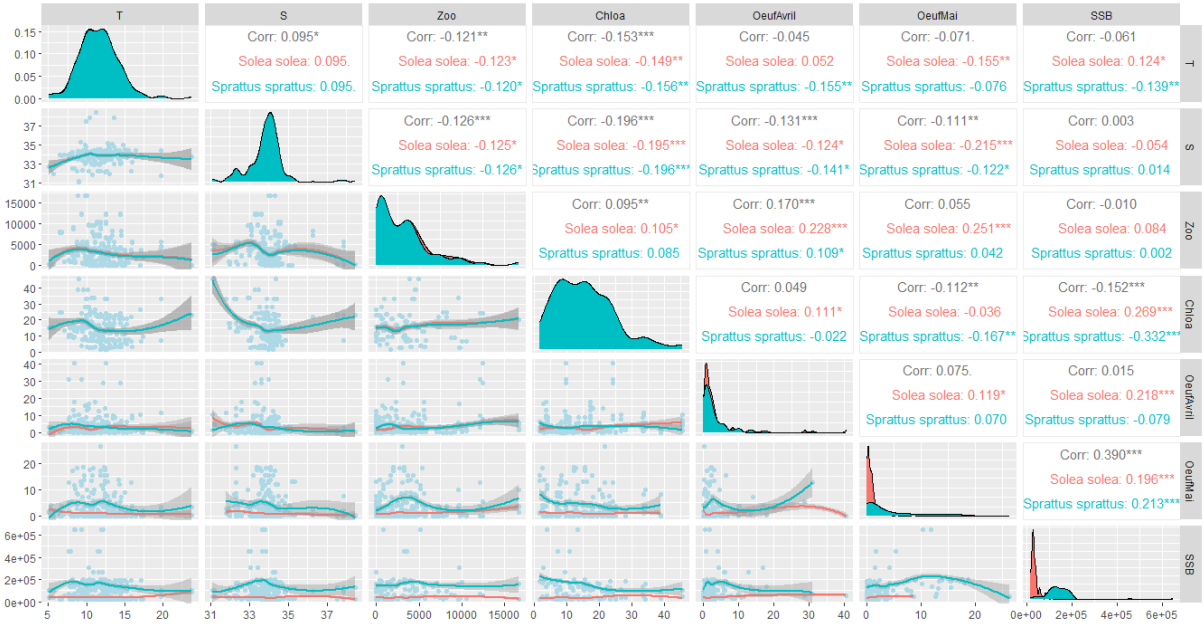




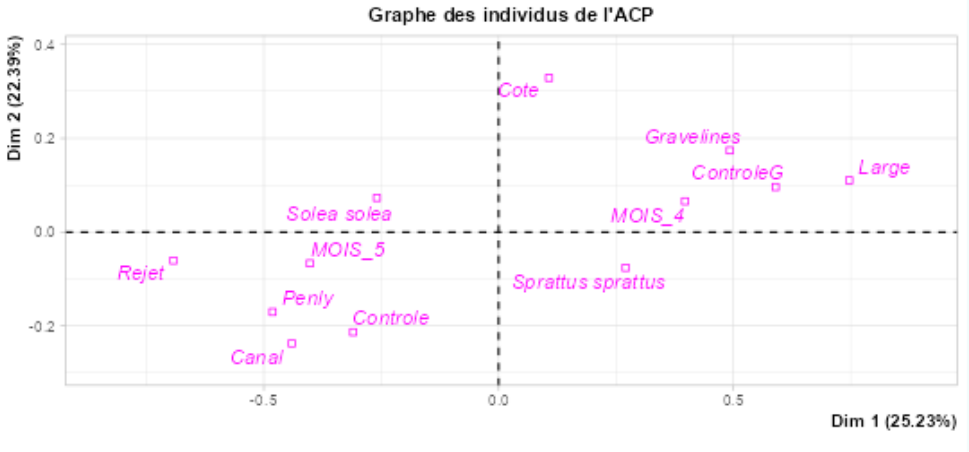
<u>Appendix III:</u> percentage of missing data for each time series. *The proportion of missing data is identical for the different stages and species in the same sampling zone at a given time.*

		% Missing data
Gravelines (44 years)	Large April	15,9%
	Large May	27,2%
	Controle April	20,4%
	Controle May	25%
	Cote April	22,7%
	Cote May	31,8%
Penly (35 years)	Canal April	8,5%
	Canal May	2,8%
	Controle April	8,5%
	Controle May	2,8%

Appendix IV: Variable correlation graph

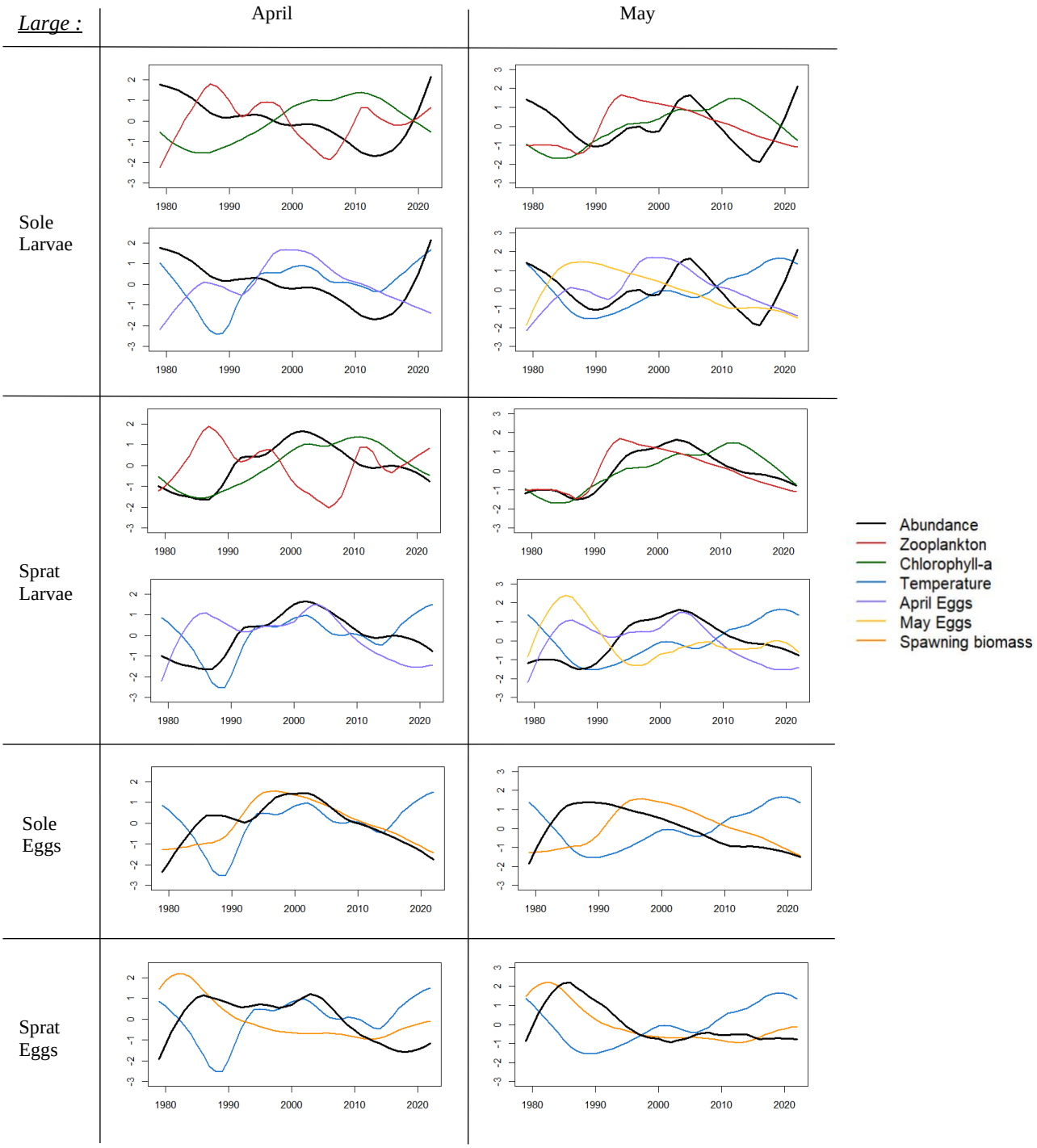


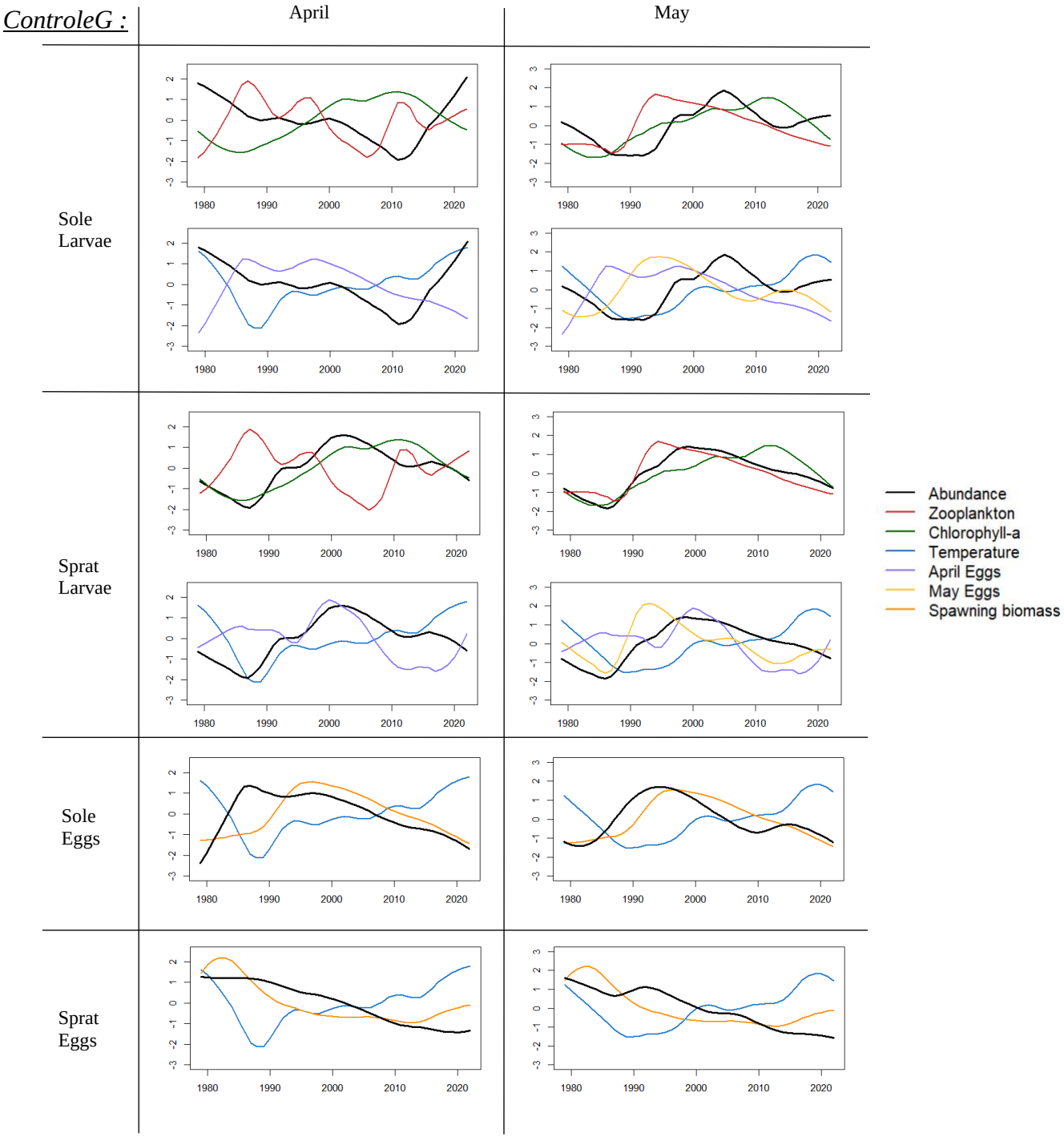
Appendix V: PCA of qualitative factors

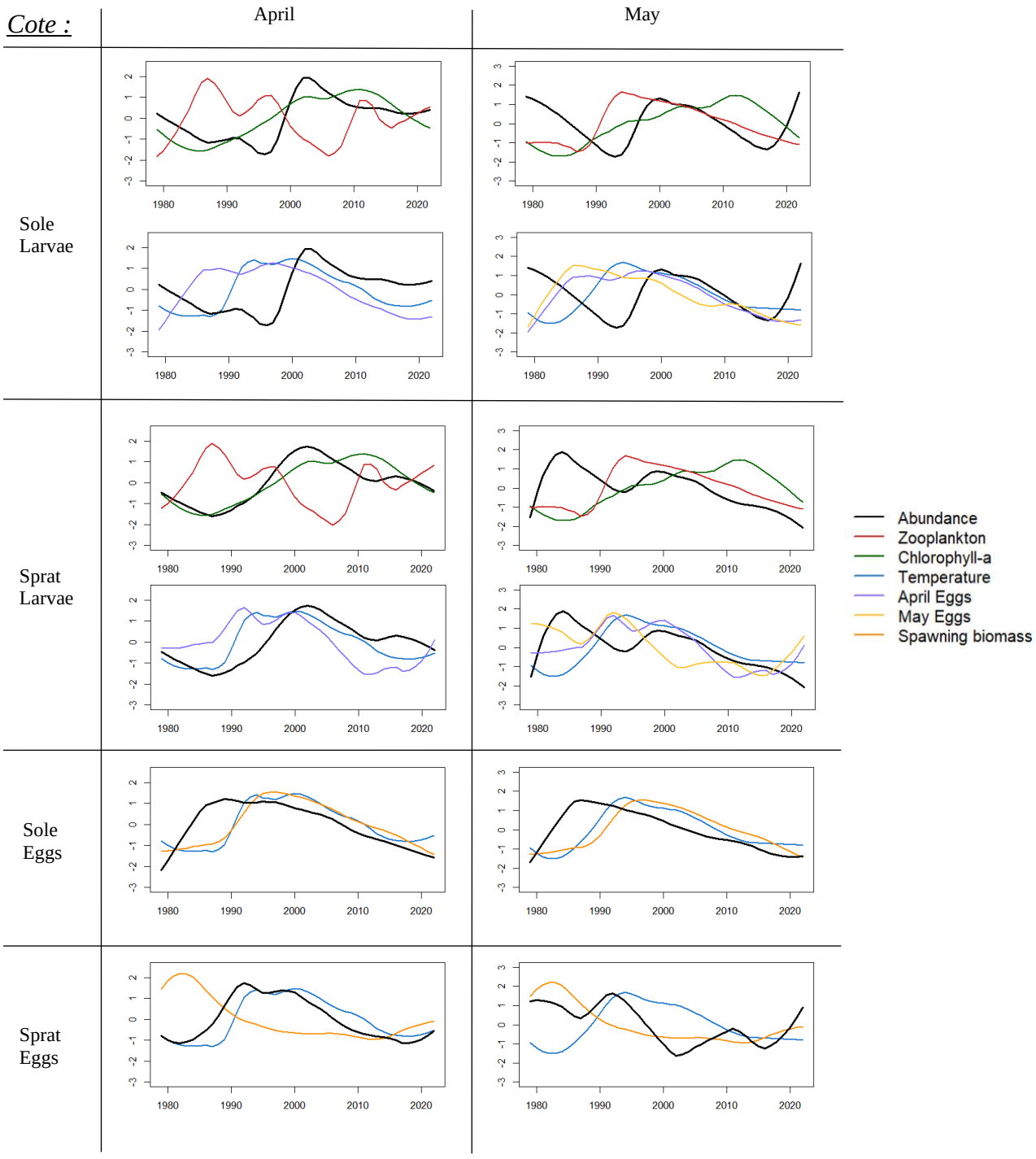


Appendix VI: Cumulative sums reduced centred of time series (abundance, environmental and population factors).

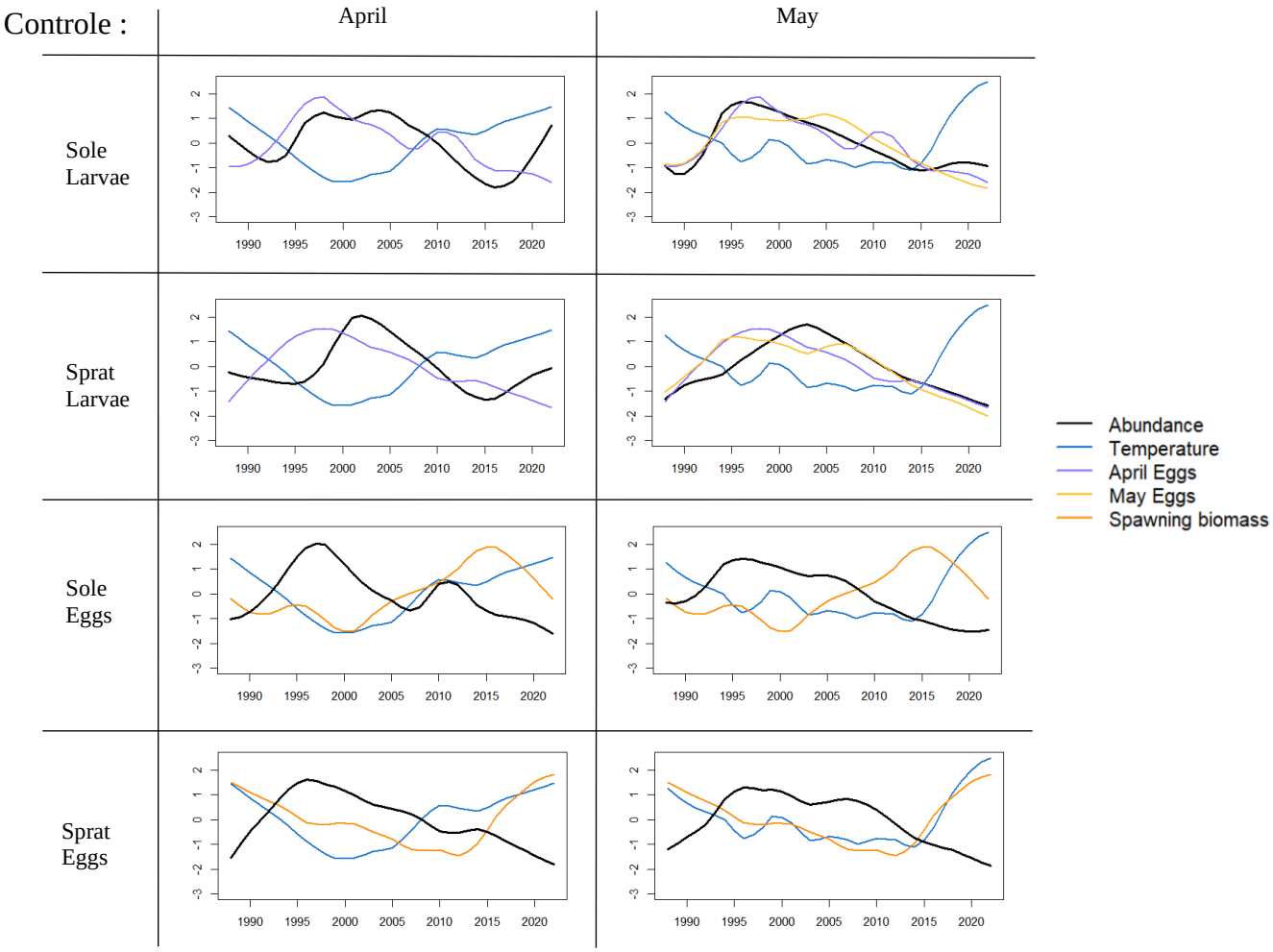
1. Ichthyoplankton and environmental factors



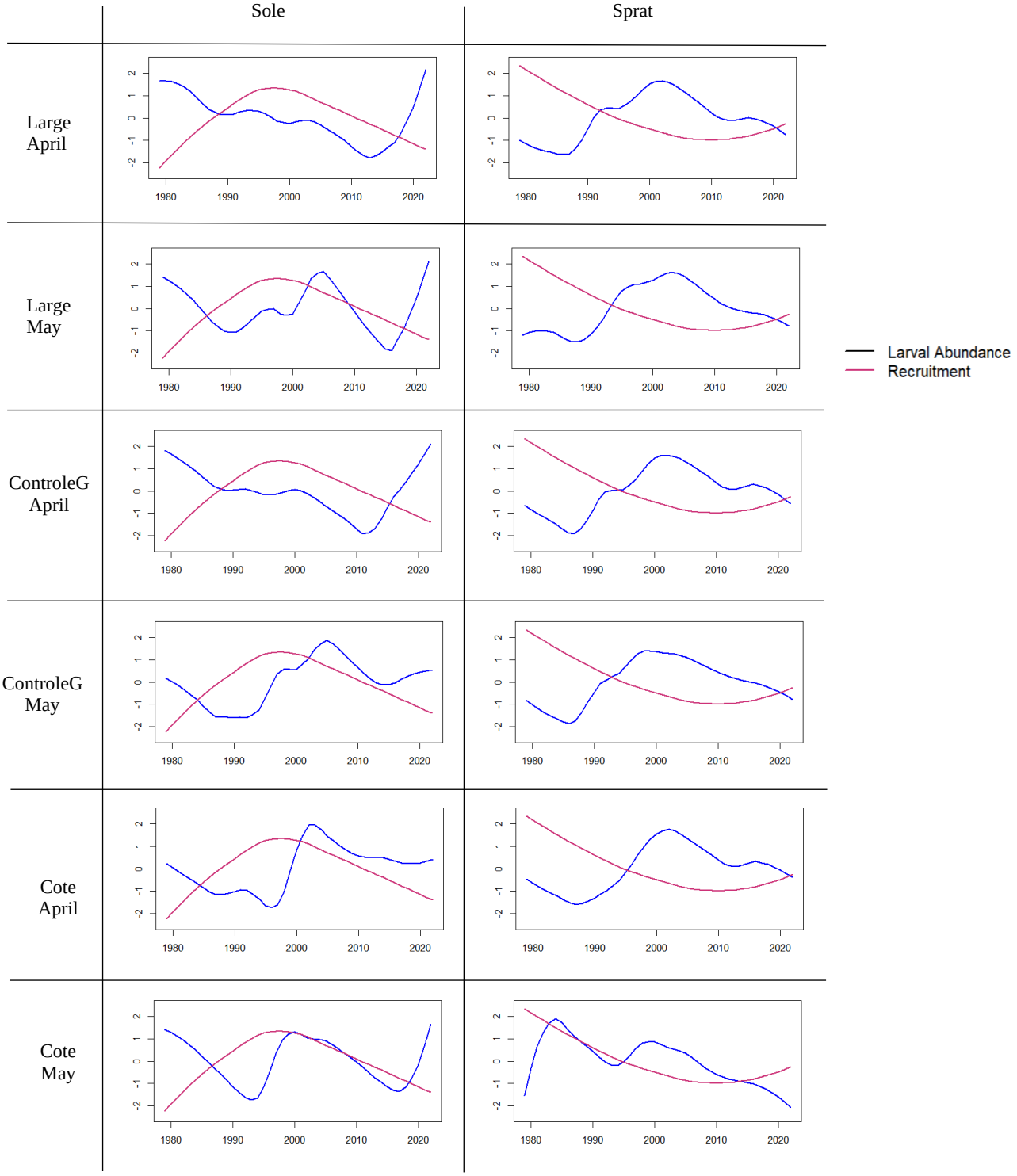

ControleG :
April
May
Sole Larvae
Sprat Larvae
Sole Eggs
Sprat Eggs
Abundance
Zooplankton
Chlorophyll-a
Temperature
April Eggs
May Eggs
Spawning biomass

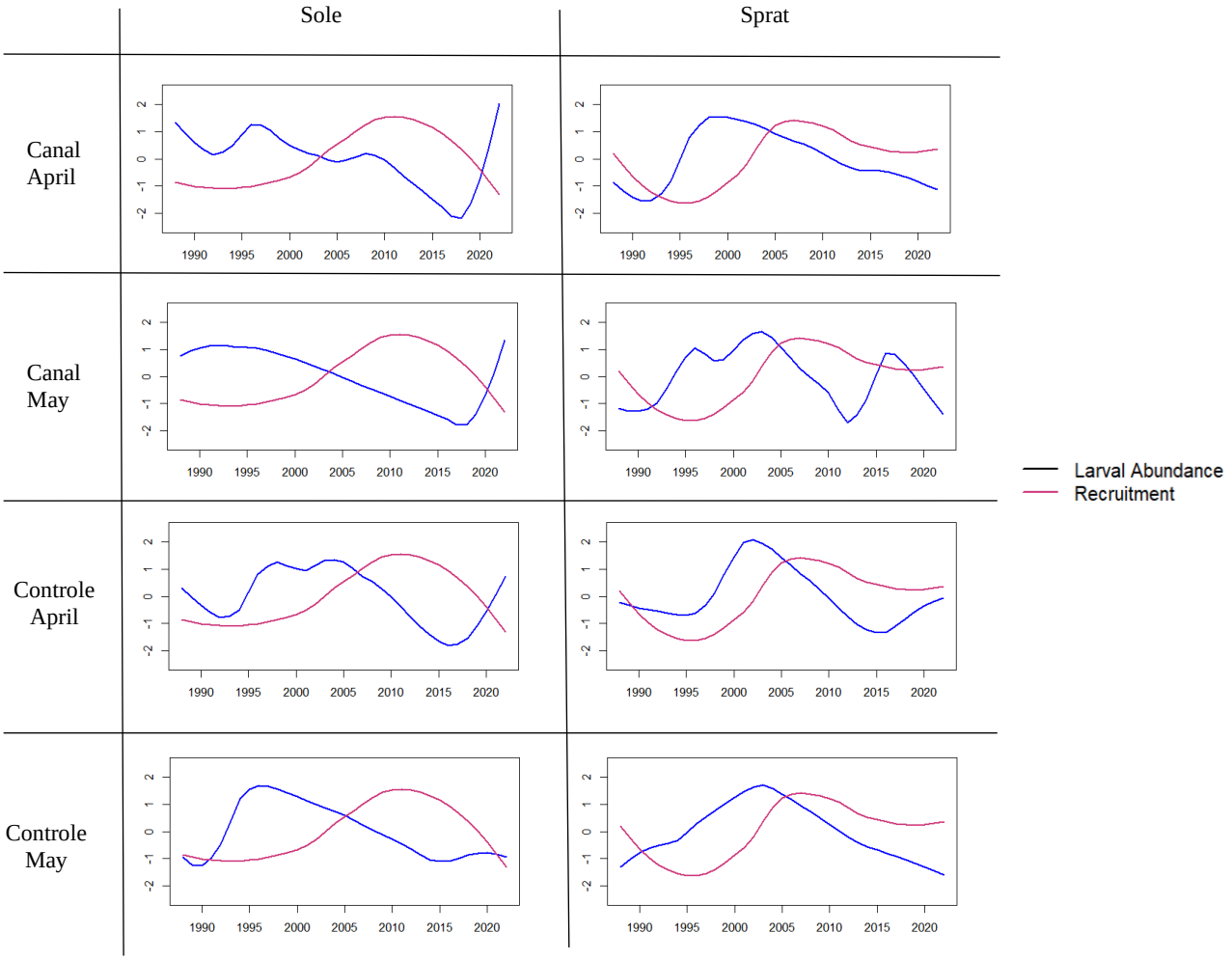

Cote :
April
May
Sole Larvae
Sprat Larvae
Sole Eggs
Sprat Eggs
Abundance
Zooplankton
Chlorophyll-a
Temperature
April Eggs
May Eggs
Spawning biomass


Canal :
April
May
Sole Larvae
Sprat Larvae
Sole Eggs
Sprat Eggs
-3 -2 -1 0 1 2
1990 1995 2000 2005 2010 2015 2020
Abundance
Temperature
April Eggs
May Eggs
Spawning biomass



2. <u>Larval abundance and recruitment</u>


Sole
Sprat
Large April
Large May
ControleG April
ControleG May
Cote April
Cote May
Larval Abundance
Recruitment
1980
1990
2000
2010
2020
-2
-1
0
1
2


Sole
Sprat
Canal April
Canal May
Controle April
Controle May
-2 -1 0 1 2
1990 1995 2000 2005 2010 2015 2020
Larval Abundance
Recruitment

Appendix VII: Summary of models used for ichthyoplankton modelling

	Gravelines			**Penly**	
	Large	Controle	Cote	Canal	Controle
Sole larvae April	ARIMAX	GAM	ARIMAX	GAM	GAM
Sprat larvae April	GAM	GLM	ARIMAX	GAM	GLM
Sole larvae May	GAM	GAM	GAM	GLMM + AR1	GAM
Sprat larvae May	GAM	ARIMAX	GLMM + AR1	GAM	GAM
Sole eggs April	GAM	GAM	GAMM	GAM	GAM
Sole eggs May	GLM	GLM	GLMM + AR1	GAM	GLM
Sprat eggs April	GLM	GLM	GAM	GAM	GAM
Sprat eggs May	GLM	ARIMAX	ARIMAX	GLM	GLM

Appendix VIII: Sensitivity analysis

1. For Sole Larvae

	Sole Large April	Sole Large May	Sole ControleG April	Sole ControleG May	Sole Cote April	Sole Cote May	Sole Canal April	Sole Canal May	Sole Controle April	Sole Controle May
Linear	x	May Eggs (-)	a-Chlorophyll (-)	x	X	A-Chlorophyll (-) May eggs	X	X	x	May eggs
Random	x	x	x	x	X	X	X	Temperature	x	May eggs April eggs ~
Min-max	April eggs	x	x	x	X	X	X	Temperature	x	May eggs April eggs
Median	April eggs	x	Temperature	x	X	April eggs May eggs	X	X	x	May eggs
Spline	x	x	April eggs (-)	x	X	A-Chlorophyll (-) April eggs	X	X	x	April eggs May eggs

Method	Factor	Sole Large April	Sole Large May	Sole ControleG April	Sole ControleG May	Sole Cote April	Sole Cote May	Sole Canal April	Sole Canal May	Sole Controle April	Sole Controle May
Minmax	Temperature	0.532	0	0.158	0	0,184	0,1	0,17	0,884	0.152	0,012
	A-Chlorophyll	0.008	0	0.132	0	0,058	0,310	X	X	X	X
	Zooplankton	0.102	0	0.022	0	0,192	0,088	X	X	X	X
	April eggs	0.812	0	0.324	0	0,280	0,064	0,12	0,098	0.252	0,838
	May eggs	X	0	X	0	X	0,148	X	0,086	X	0,814
Random	Temperature	0.018	0.138	0.376	0.002	0,004	0,090	0,006	0,976	0.040	0,006
	A-Chlorophyll	0.000	0.090	0.120	0.000	0,062	0,194	X	X	X	X
	Zooplankton	0.030	0.058	0.018	0.022	0,012	0,052	X	X	X	X
	April eggs	0.004	0.144	0.004	0.120	0,062	0,082	0	0,002	0.012	0,584
	May eggs	X	0.004	X	0.000	X	0,028	X	0,002	X	0,96

2. For sprat Larvae

	Sole Large April	Sole Large May	Sole ControleG April	Sole ControleG May	Sole Cote April	Sole Cote May	Sole Canal April	Sole Canal May	Sole Controle April	Sole Controle May
Linear	Zooplankton Temperature	temperature April eggs (+)	Temperature (+) April eggs (+) a-Chlorophyll (+)	X	April eggs (+)	Temperature (-) a-Chlorophyll (-) April eggs	x	X	X	X
Random	Zooplankton Temperature	x	temperature	A-Chlorophyll	Zooplankton ~	x	x	X	X	X
Min-max	x	x	x	May eggs	X	x	x	May eggs	X	X
Median	Zooplankton (-) Temperature (+)	temperature (+) May eggs	Temperature (+) April eggs (+) Zooplankton (-) a-Chlorophyll (+)	A-Chlorophyll (+) Temperature May eggs (+)	April eggs A-Chlorophyll (+) Zooplankton (-)	Temperature (-)	x	X	X	X
Spline	Zooplankton (-) Temperature (+)	Temperature April eggs (+)	Temperature (+) April eggs (+) a-Chlorophyll +	May eggs (+) Zooplankton	April eggs (+)	Temperature (-) a-Chlorophyll (-) May eggs (-)	x	May eggs	X	X

Method	Factor	Sole Large April	Sole Large May	Sole ControleG April	Sole ControleG May	Sole Cote April	Sole Cote May	Sole Canal April	Sole Canal May	Sole Controle April	Sole Controle May
Minmax	Temperature	0.536	0.130	0.200	0,3	0,178	0.088	0.272	0,092	0,106	0,088
	A-Chlorophyll	0.134	0.034	0.250	0,340	0,354	0.520	X	0	0	0
	Zooplankton	0.172	0.228	0.136	0,186	0,356	0.216	X	0	0	0
	April eggs	0.178	0.002	0.474	0,3	0,476	0.070	0.272	0,334	0,052	0,032
	May eggs	X	0.126	X	0,606	0	0.136	X	0,626	0	0,230
Random	Temperature	0.676	0.406	0.712	0,0548	0,004	0.444	0.022	0,976	0	0,106
	A-Chlorophyll	0.060	0.106	0.526	0,748	0,062	0.452	X	X	X	X
	Zooplankton	0.802	0.056	0.372	0,296	0,012	0.086	X	X	X	X
	April eggs	0.140	0.026	0.682	0,19	0,062	0.152	0.022	0,002	0	0,038
	May eggs	X	0.332	X	0,286	X	0.228	X	0,002	X	0,002

3. For Sole Eggs

	Sole Large April	Sole Large May	Sole ControleG April	Sole ControleG May	Sole Cote April	Sole Cote May	Sole Canal April	Sole Canal May	Sole Contrôle April	Sole Controle May
Linear	Temperature SSB (+)	Temperature (-)	Temperature (-) SSB (+)	Temperature (-) SSB (+)	SSB	Temperature (-)	Temperature (-) SSB	SSB	SSB	Temperature (-)
Random	Temperature SSB	X	SSB	Temperature	SSB	X	SSB	X	SSB	Temperature
Minmax	x	X	SSB ~	X	SBB Temperature	X	x	X	SSB	Temperature ~
Median	Temperature SSB	Temperature (-)	Temperature (-) SSB (+)	Temperature (-)	SSB	X	Temperature (-) SSB	X	SSB	Temperature (-)
Spline	Temperature SSB (+)	X	Temperature (-) SSB (+)	Temperature (-)	SSB	Temperature (-)	Temperature (-) SSB	SSB	SSB	Temperature (-)

Method	Factor	Sole Large April	Sole Large May	Sole ControleG April	Sole ControleG May	Sole Cote April	Sole Cote May	Sole Canal April	Sole Canal May	Sole Contrôle April	Sole Controle May
Random	Temperature	0.964	0,170	0,214	0,824	0,060	0,020	0.594	0,086	0,170	0,994
	SSB	0.648	0,098	0,682	0,156	0,908	0,214	0.998	0,416	0,978	0
Minmax	Temperature	0.320	0,518	0,384	0,222	0,764	0,126	0.300	0,384	0,238	0,618
	SSB	0.522	0,284	0,634	0,198	0,708	0,272	0.208	0,354	0,806	0

4. For Sprat eggs

	Sprat Large April	Sprat Large May	Sprat ControleG April	Sprat ControleG May	Sprat Cote April	Sprat Cote May	Sprat Canal April	Sprat Canal May	Sprat Contrôle April	Sprat Controle May
Linear	X	X	X	X	Temperature (+)	X	Temperature	X	Temperature	X
Random	X	X	X	X	Temperature	X	Temperature	X	Temperature	X
Minmax	X	X	X	X	Temperature	X	x	X	Temperature	X
Median	X	X	X	X	Temperature	Temperature (-)	Temperature (-)	X	Temperature SSB (-)	X
Spline	X	X	X	X	Temperature	Temperature (-)	Temperature (-)	X	Temperature SSB (-)	X

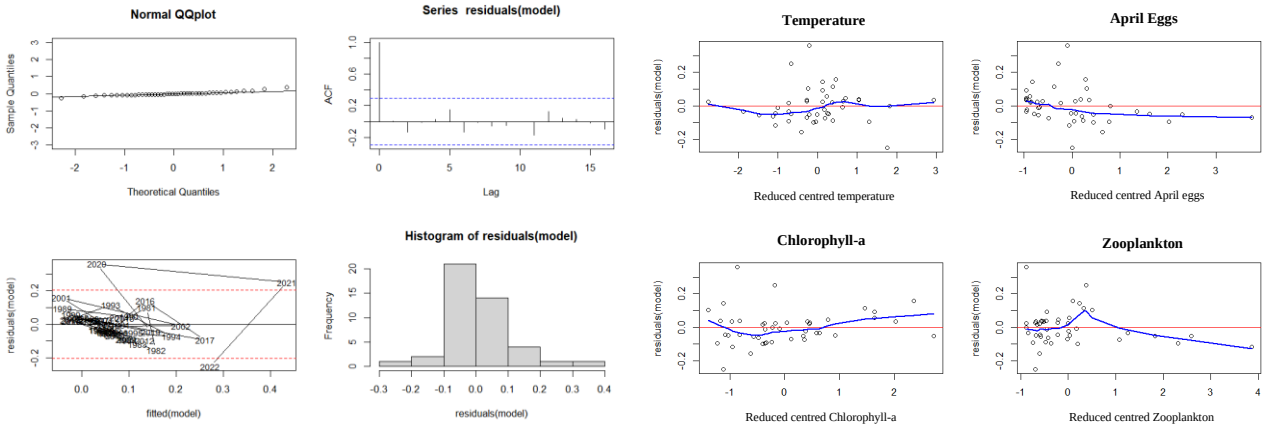
Method	Factor	Sprat Large April	Sprat Large May	Sprat ControleG April	Sprat ControleG May	Sprat Cote April	Sprat Cote May	Sprat Canal April	Sprat Canal May	Sprat Contrôle April	Sprat Controle May
Random	Temperature	0,098	0	0,004	0,022	0.690	0,017	0.998	0	0,994	0
	SSB	0	0,01	0	0	0.088	0,08	0.040	0	0,402	0,328
Minmax	Temperature	0,438	0,052	0,092	0,07	0.874	0,40	0.568	0	0,840	0
	SSB	0	0,016	0,018	0	0.134	0,07	0.272	0	0,384	0,232

Appendix IX: Summary of results obtained after modelling with a linear interpolation for ichthyoplankton modelling

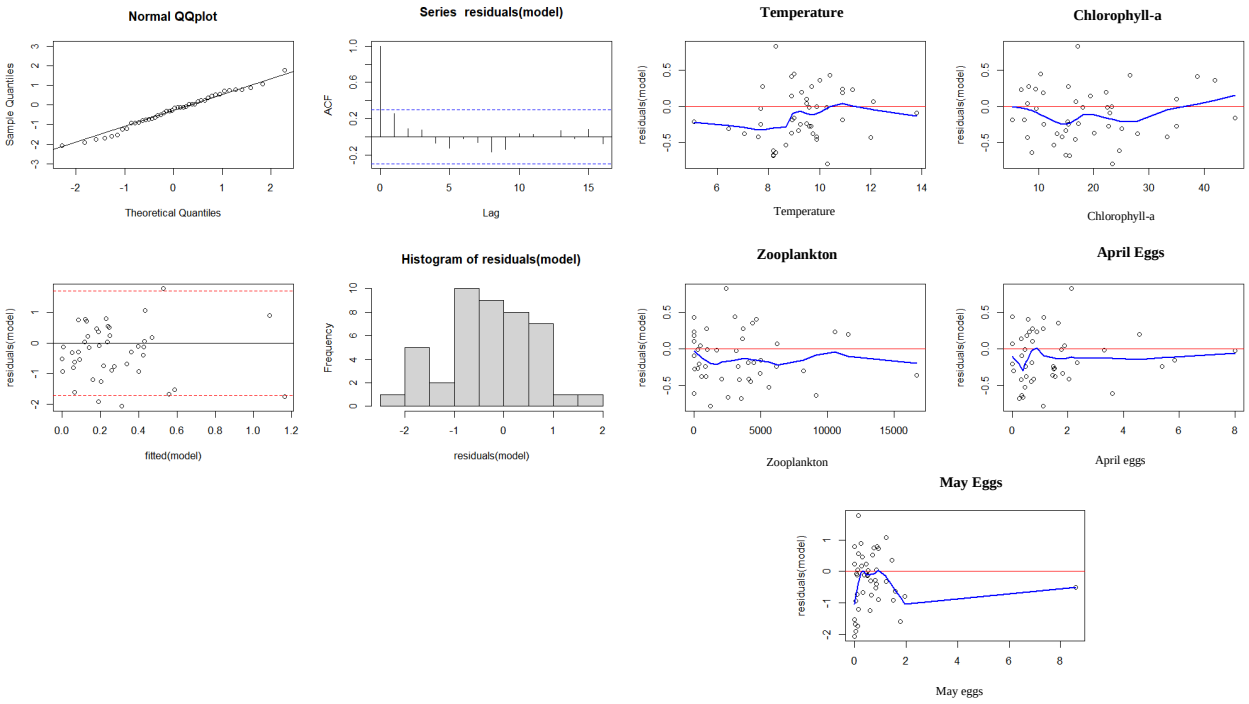
	Gravelines			**Penly**	
	Large	Controle	Cote	Canal	Controle
Sole larvae April	April Eggs a-Chlorophyll (+) Zooplankton (-)	a-Chlorophyll (-)	X	X	X
Sprat larvae April	Temperature Zooplankton	Temperature (+) April Eggs (+) a-Chlorophyll (+)	Temperature (-) April Eggs a-Chlorophyll (+)	X	X
Sole larvae May	May Eggs (-) a-Chlorophyll	X	May Eggs a-Chlorophyll (-)	X	May Eggs (+)
Sprat larvae May	Temperature April Eggs (+)	X	Temperature (-) April Eggs a-Chlorophyll (-)	X	X
Sole eggs April	Temperature SSB (+)	Temperature SSB	X	Temperature (-) SSB	SSB
Sole eggs May	Temperature (-)	Temperature (-) SSB (+)	Temperature (-) SSB	SSB	Temperature (-)
Sprat eggs April	Temperature (+)	X	X	Temperature	Temperature
Sprat eggs May	X	X	X	X	X

Appendix X: Residuals from ichthyoplankton modelling:

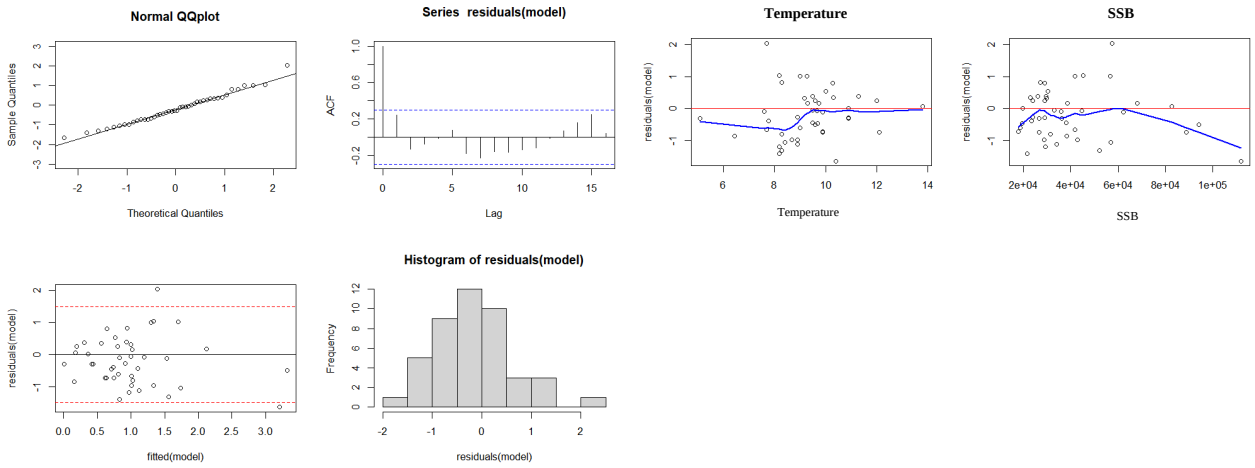
Sole larval abundance April "Large":



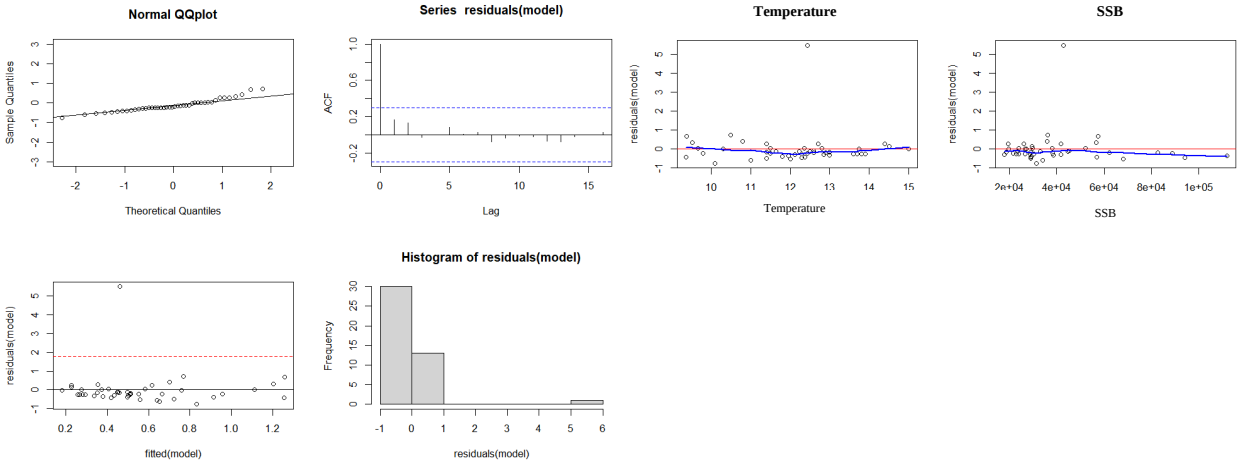
Sole larval abundance May "Large":



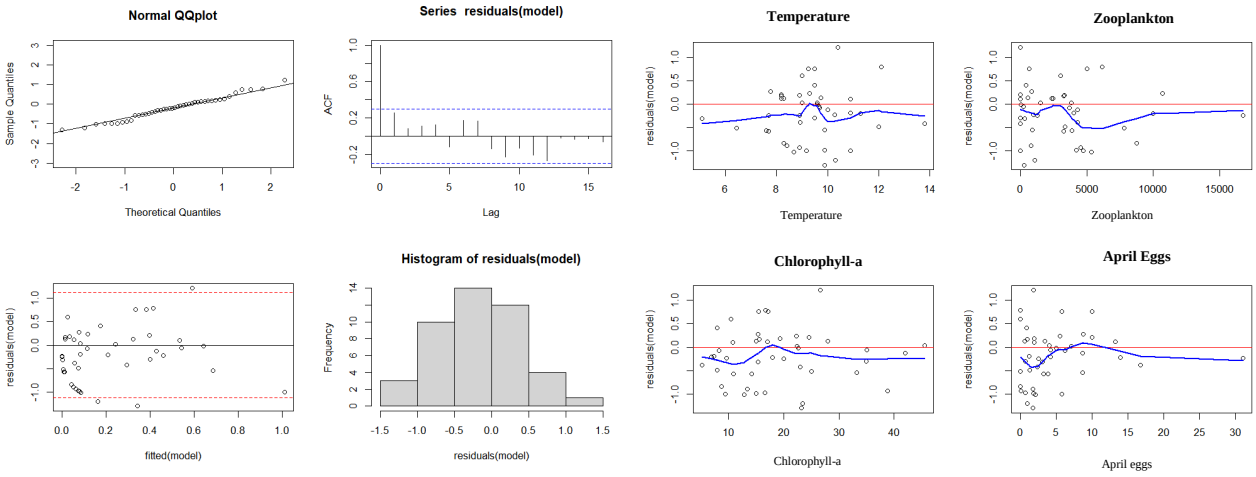
Sole egg abundance April "Large":



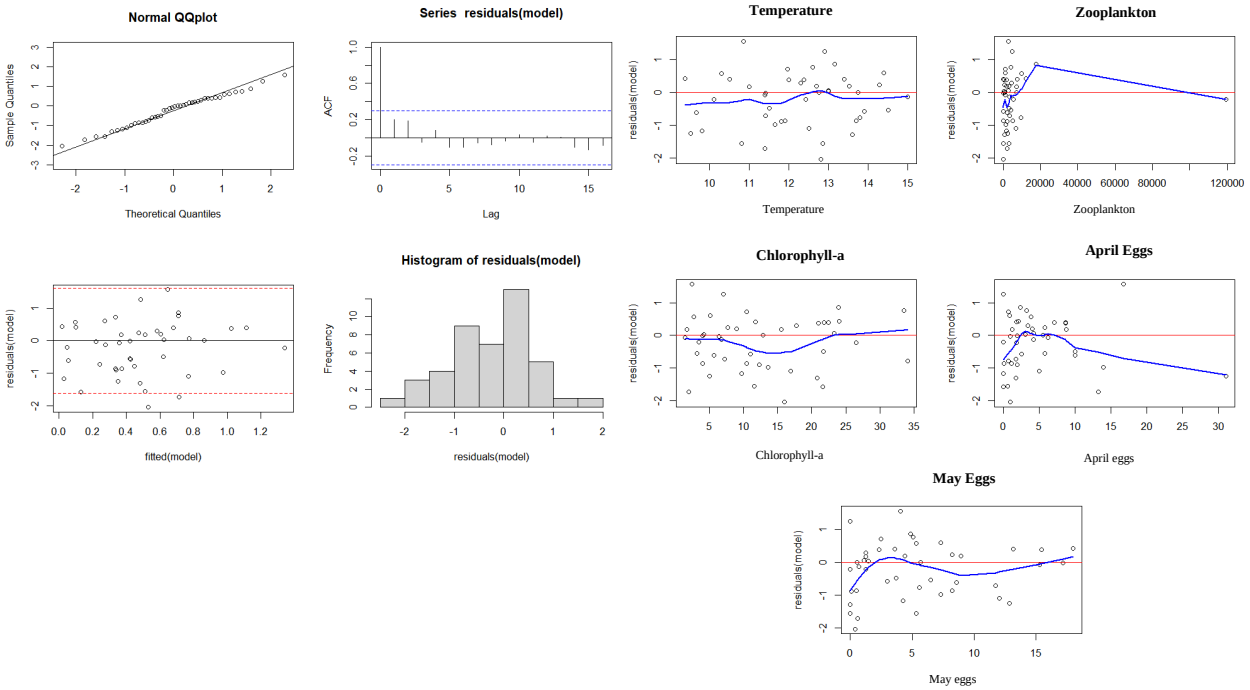
Sole egg abundance May "Large":



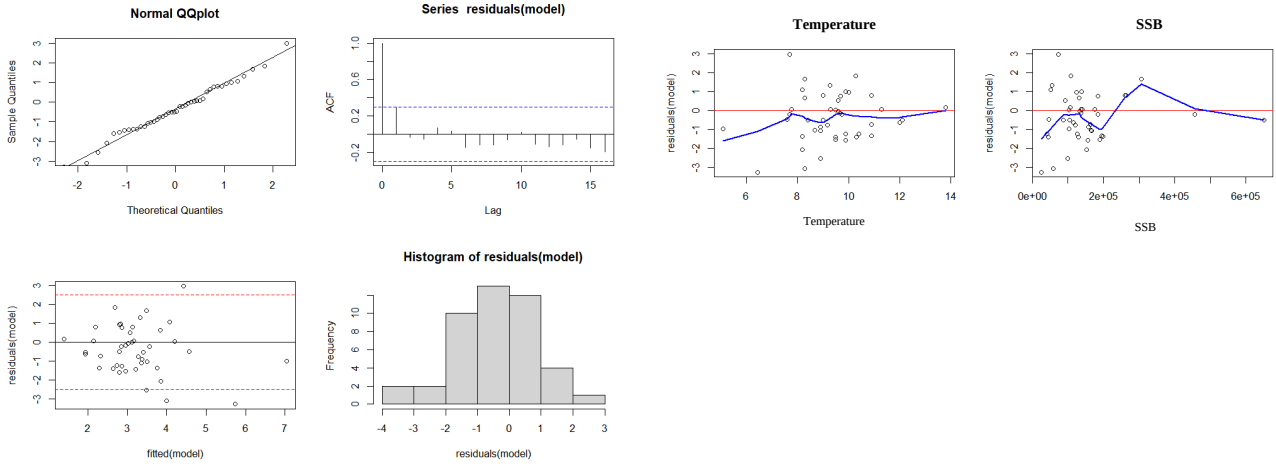
Sprat larval abundance April "Large":



Sprat larval abundance May "Large":



Sprat egg abundance April "Large":



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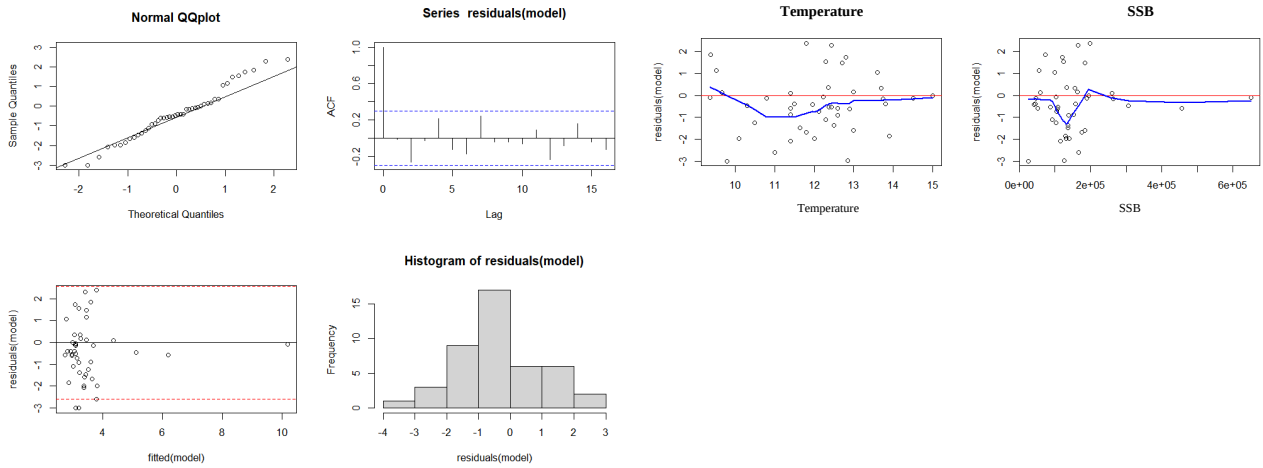
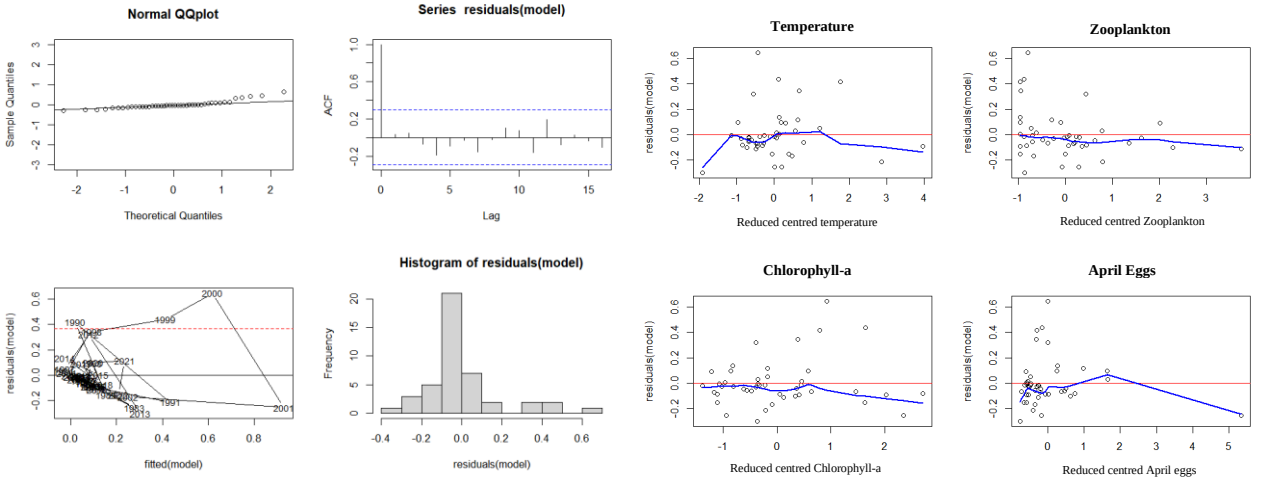


Sole larval abundance April "Cote":



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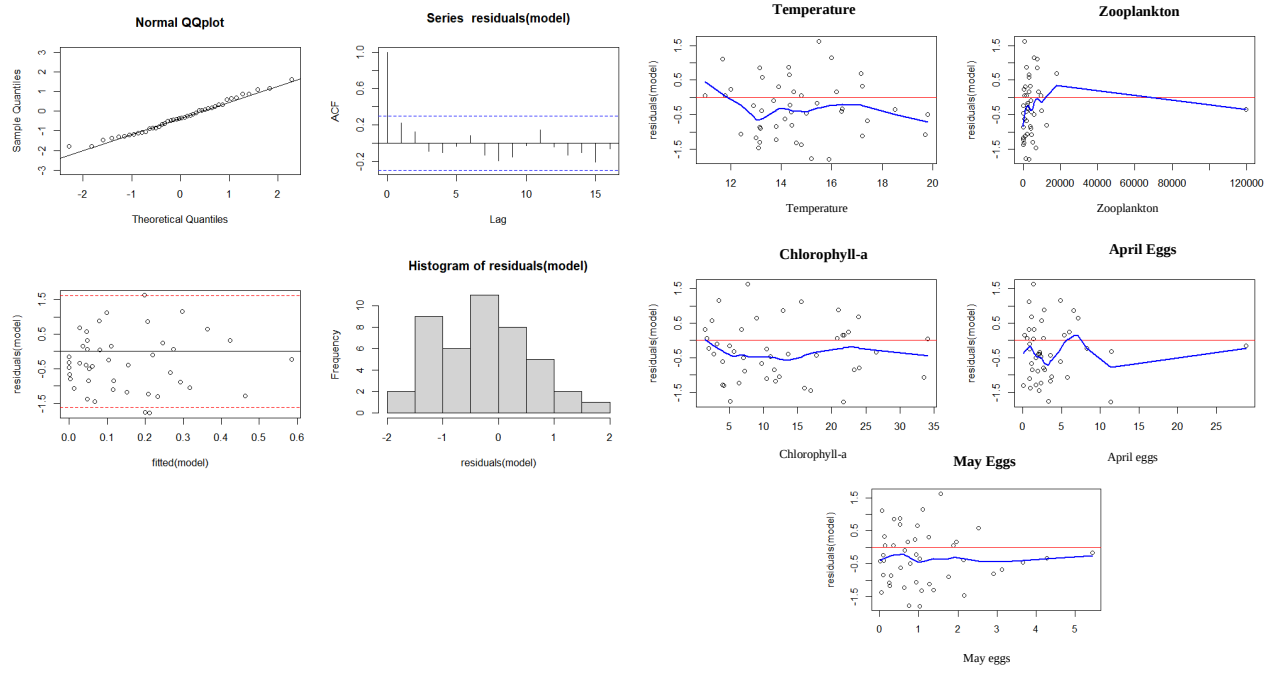
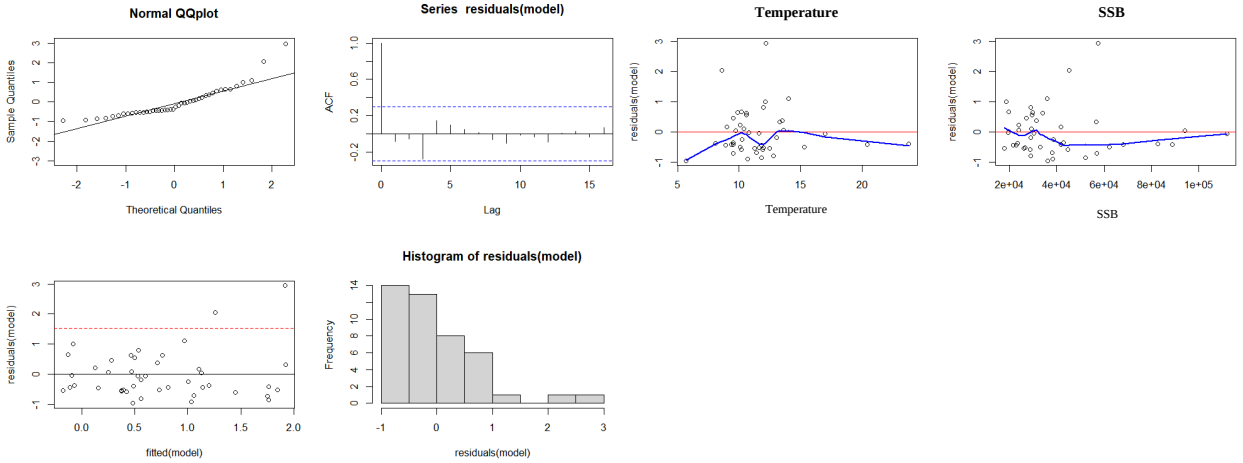
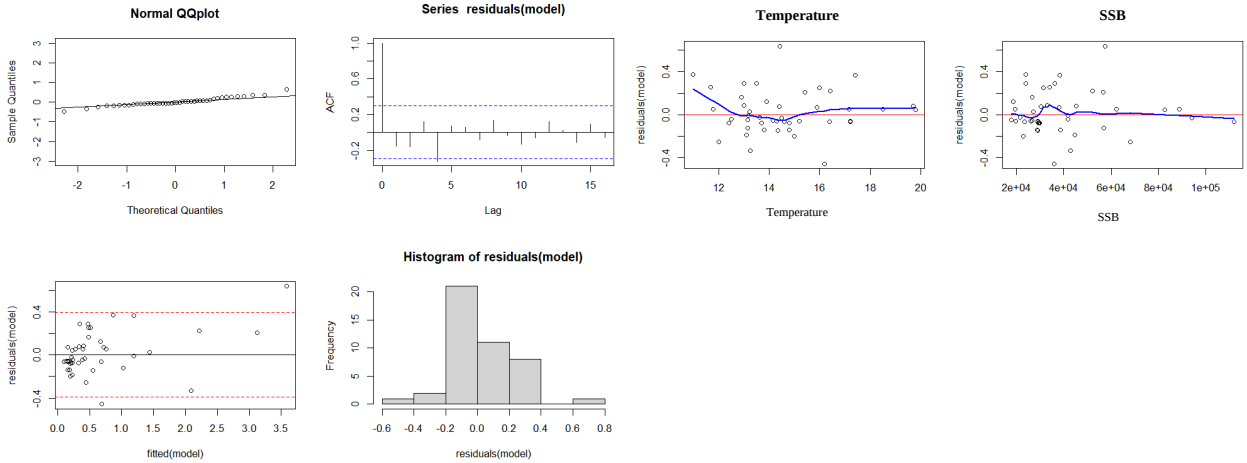


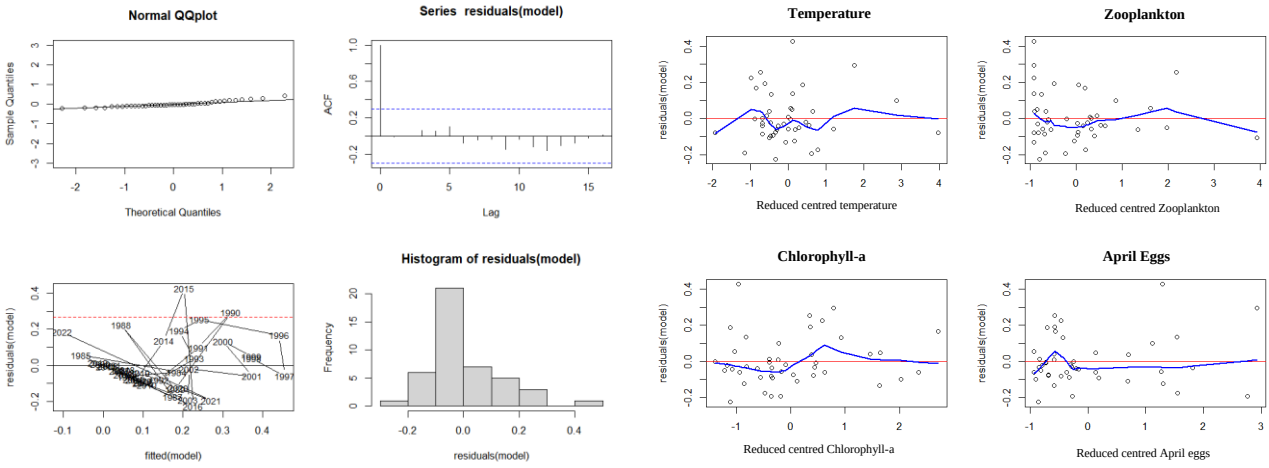
Sole egg abundance April "Cote":



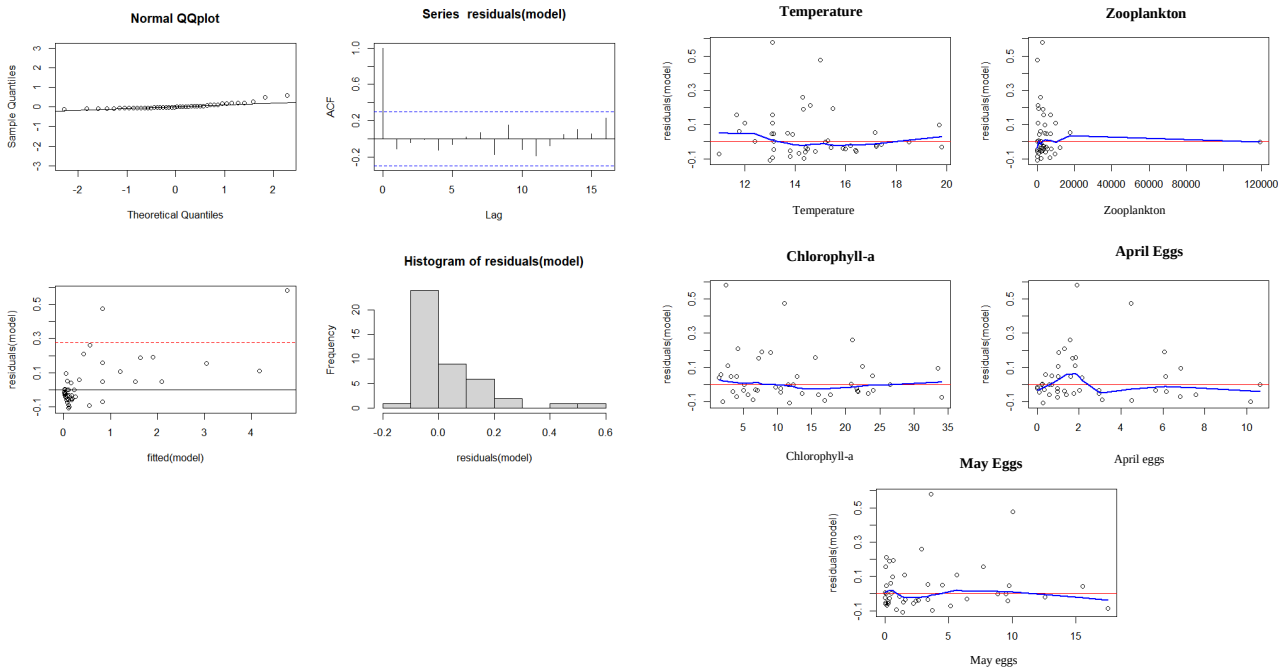
Sole egg abundance May "Cote":



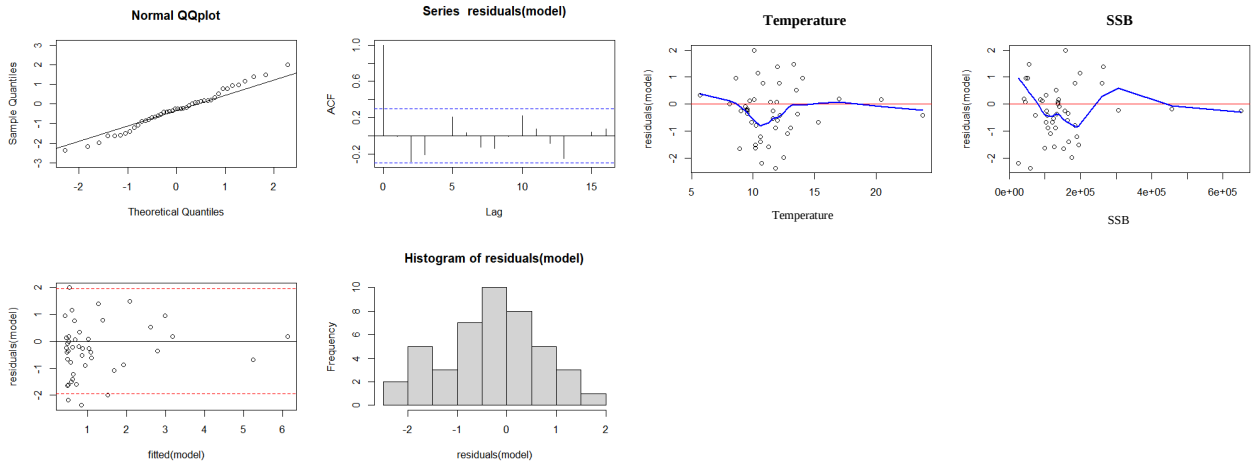
Sprat larval abundance April "Cote":



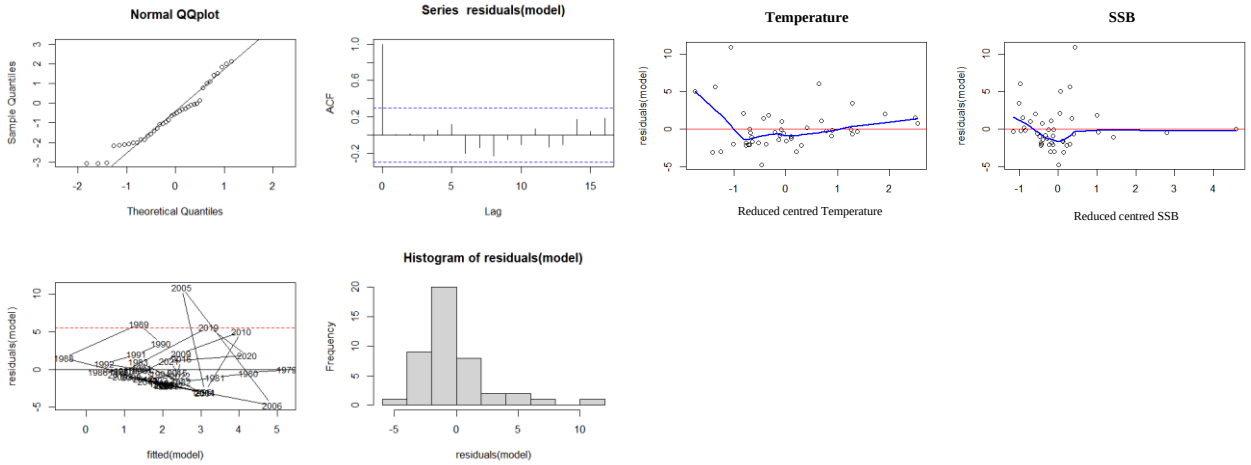
Sprat larval abundance May "Cote":



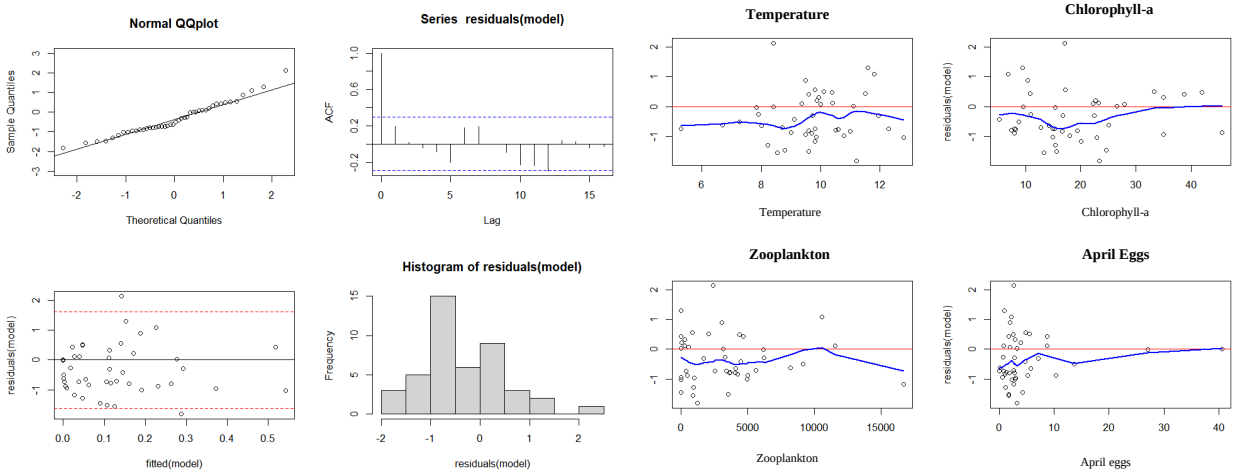
Sprat egg abundance April "Cote":



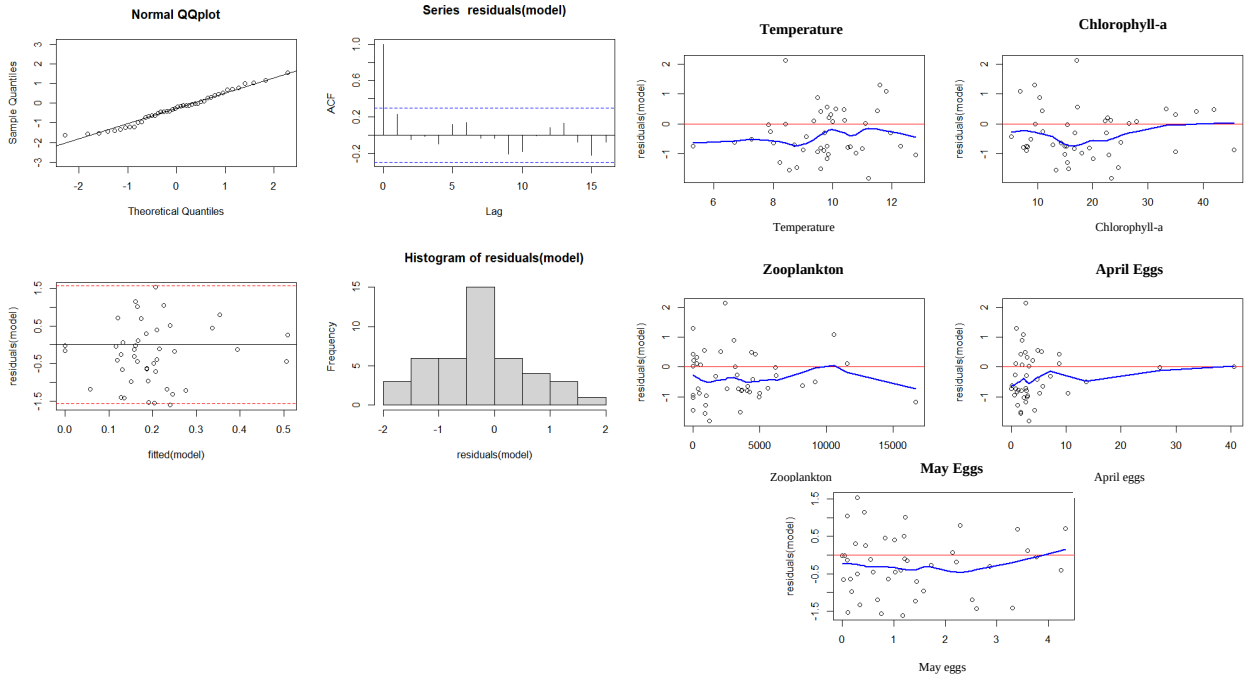
Sprat egg abundance May "Cote":



Sole larval abundance April "ControleG":



Sole larval abundance May "ControleG":



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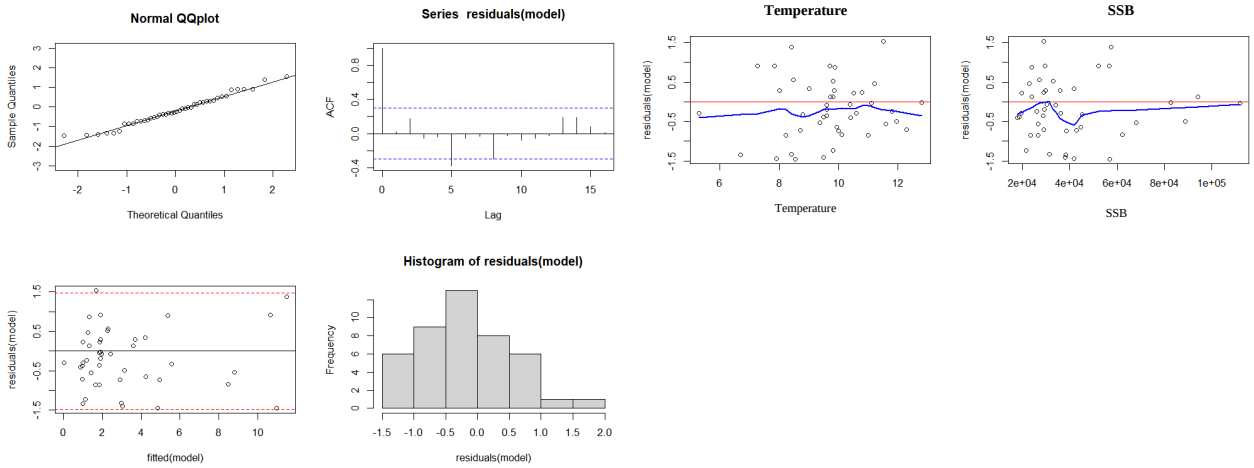

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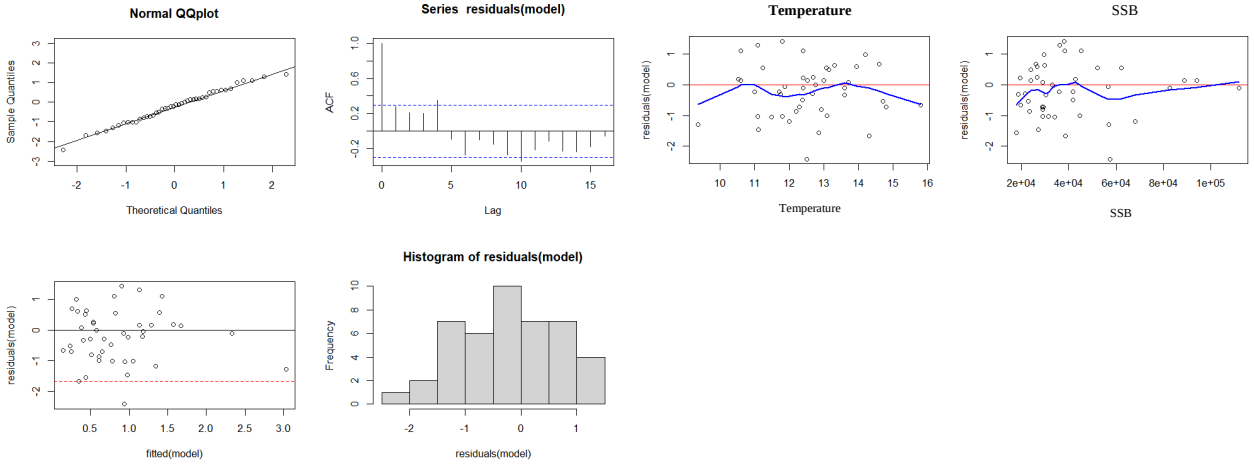
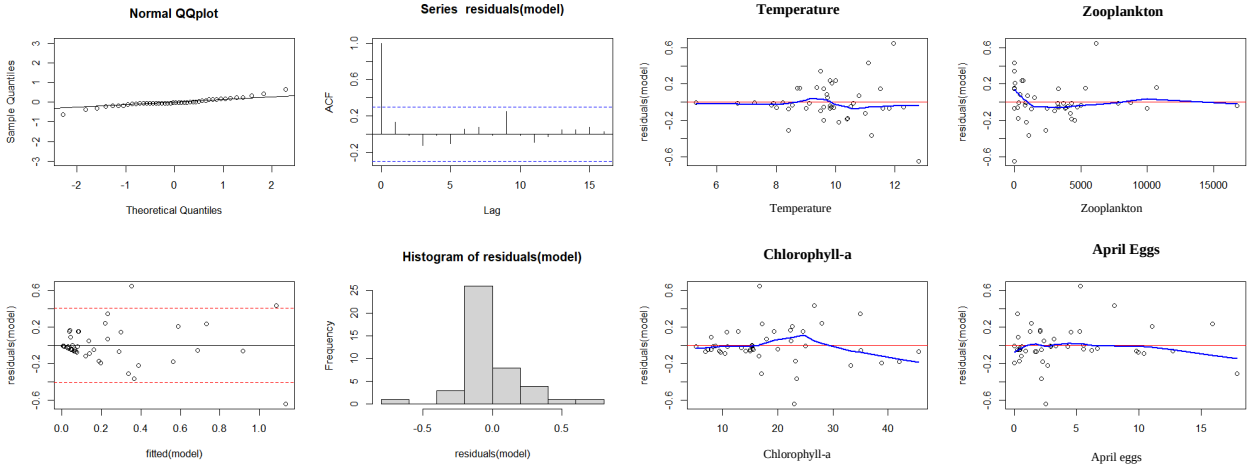


Sprat larval abundance April "ControleG":



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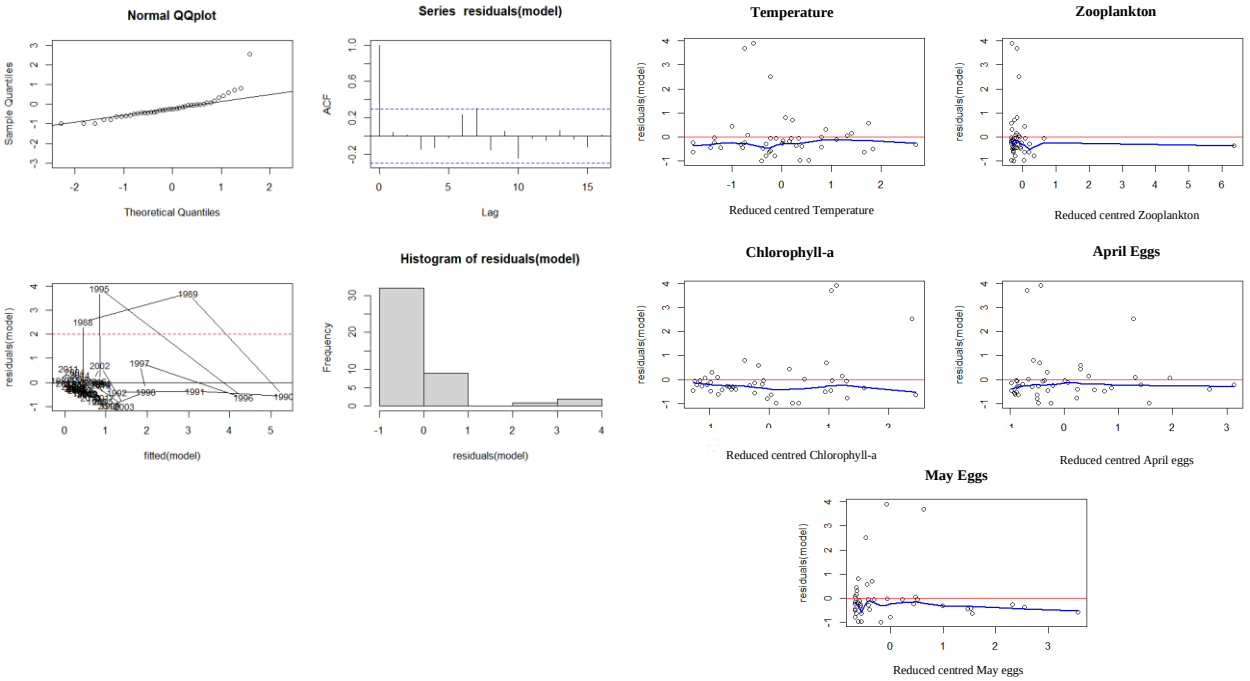
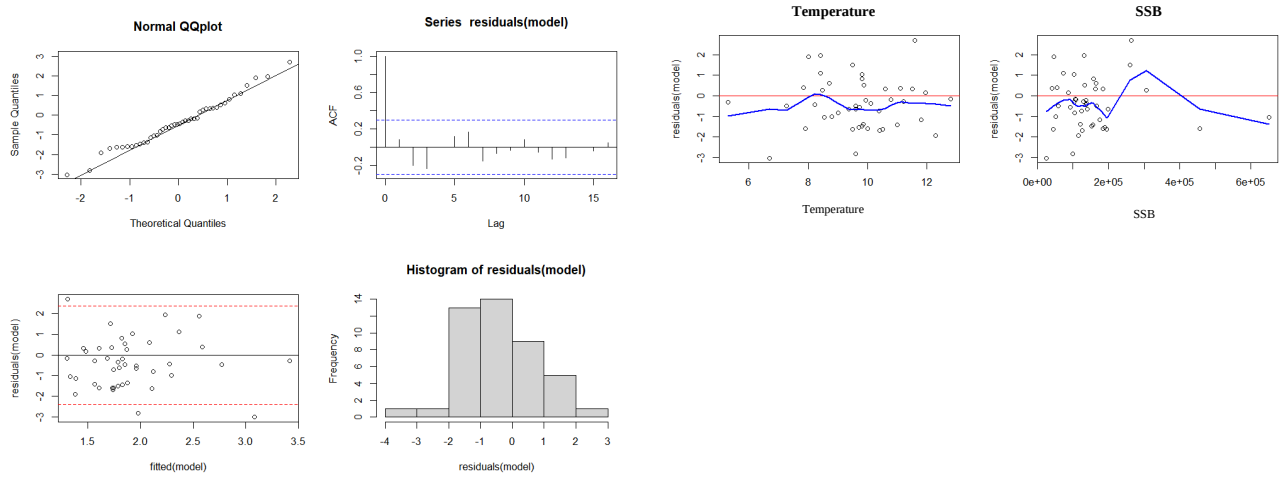


Sprat egg abundance April "ControleG":



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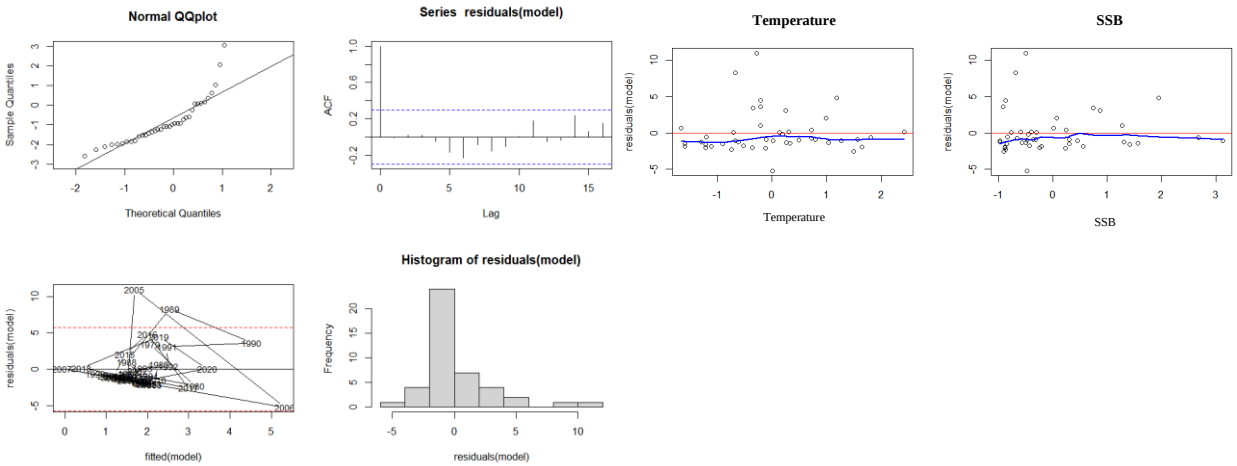

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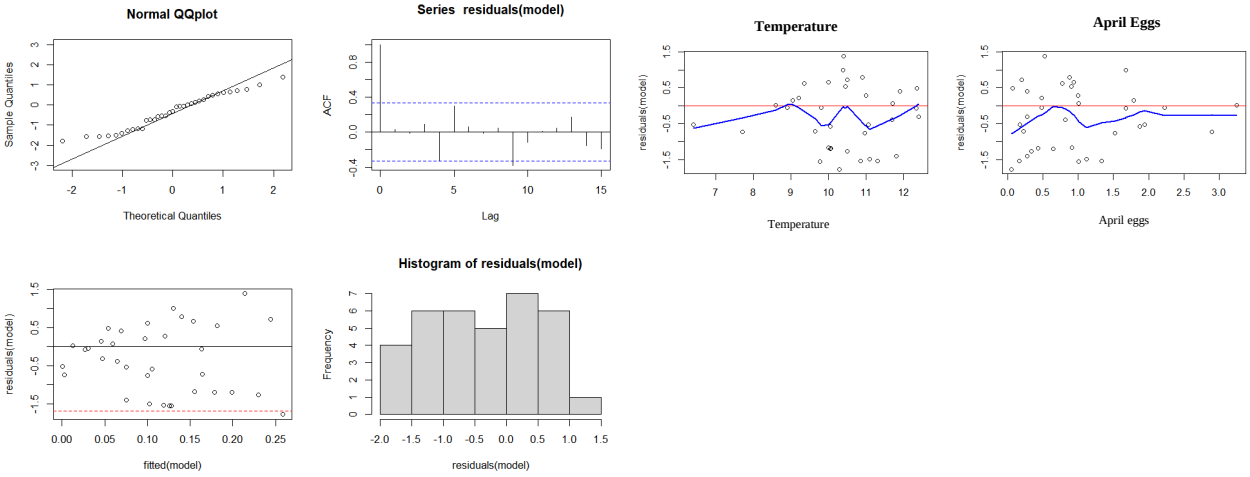

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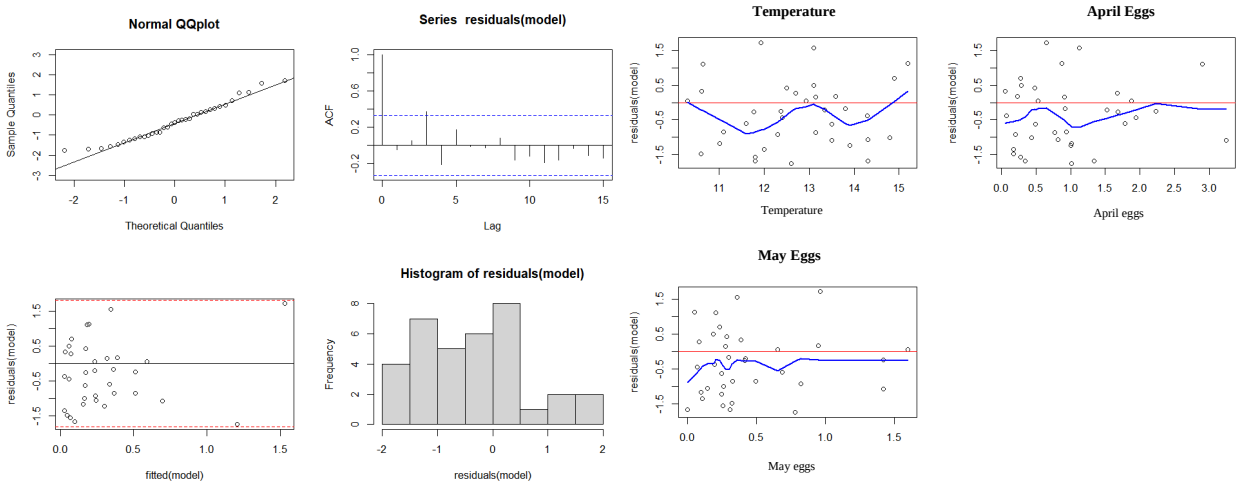
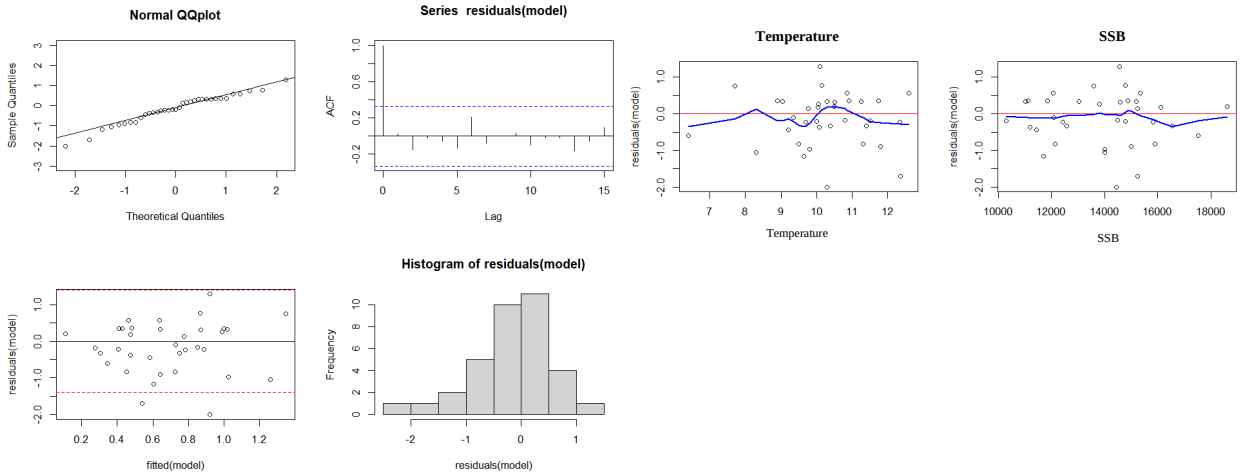


Sole egg abundance April "Controle":



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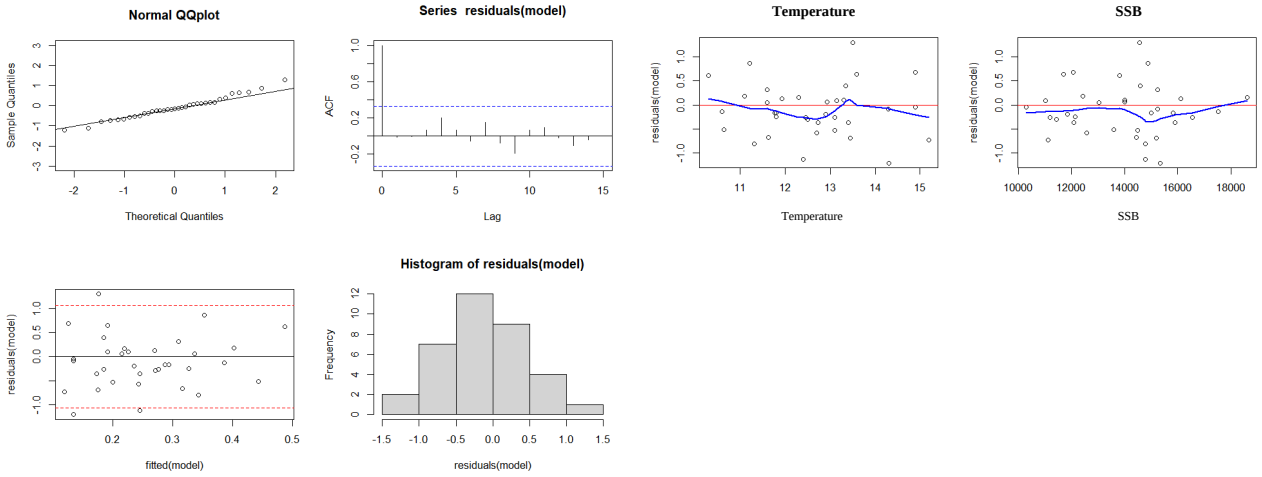

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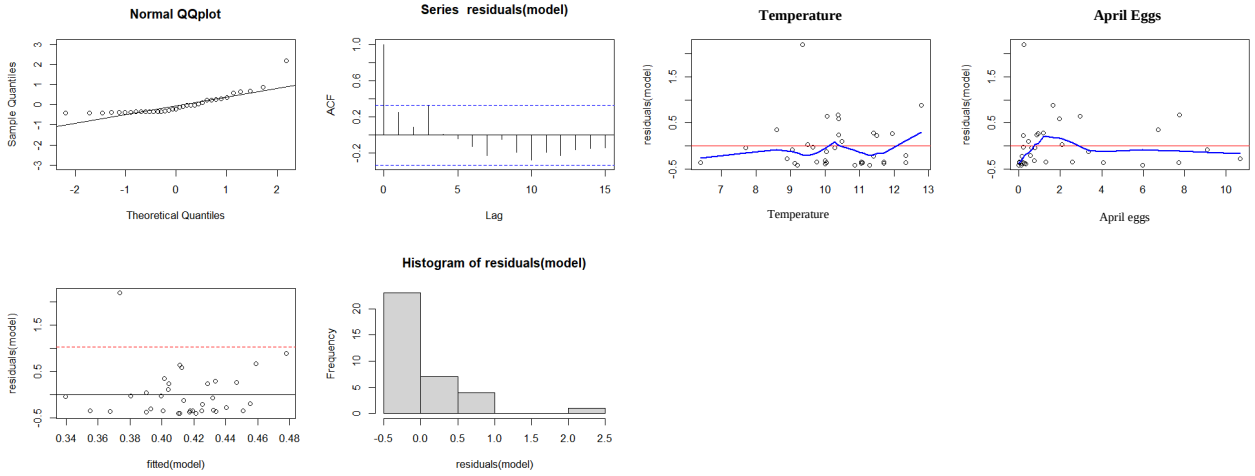
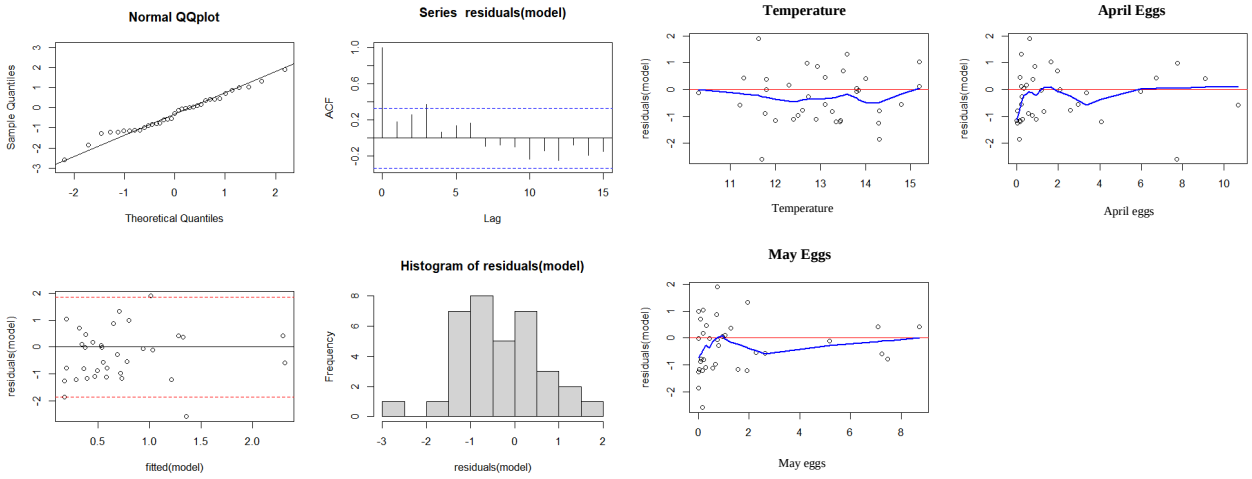


Sprat larval abundance May "Controle":



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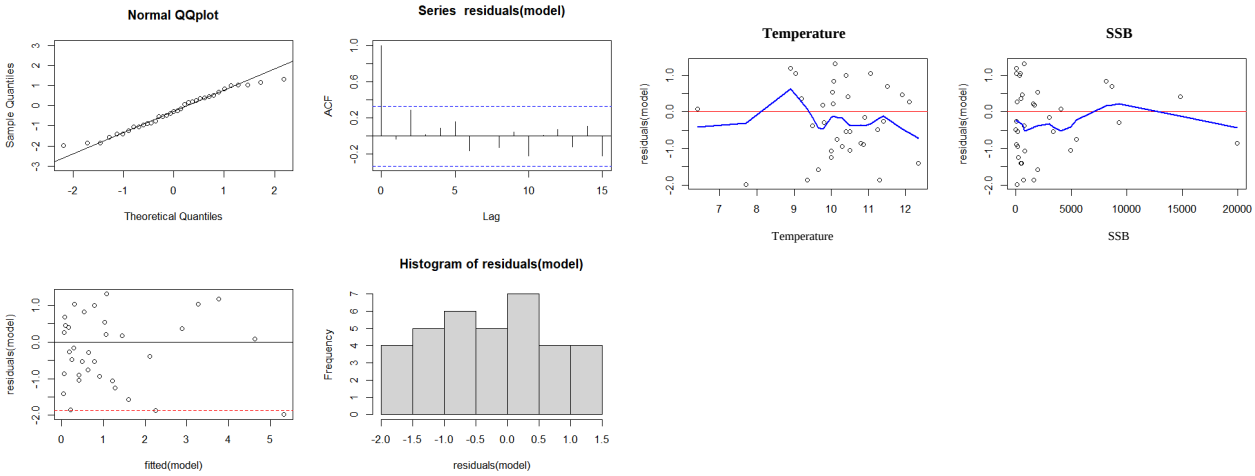
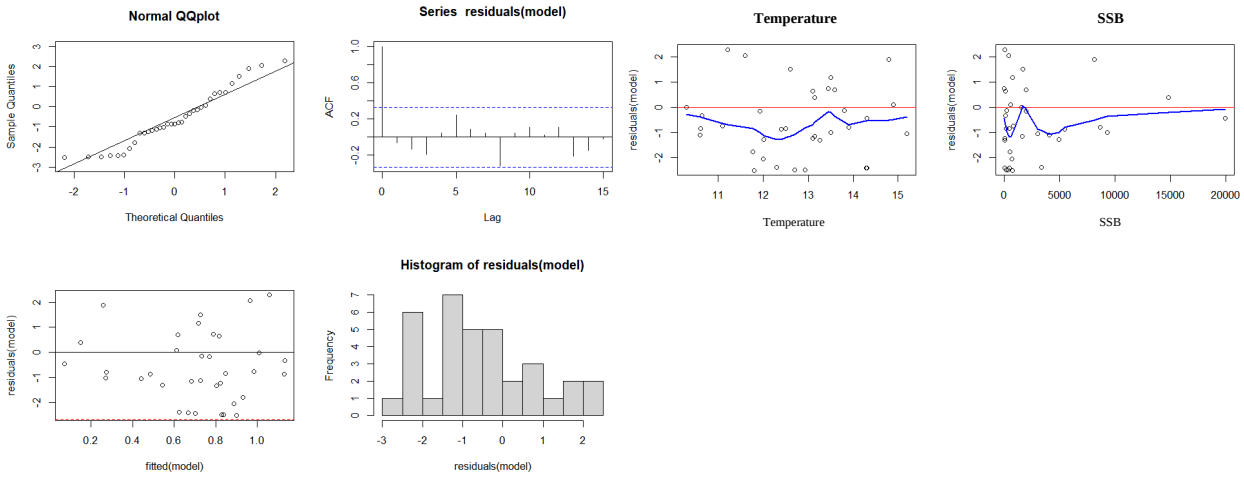
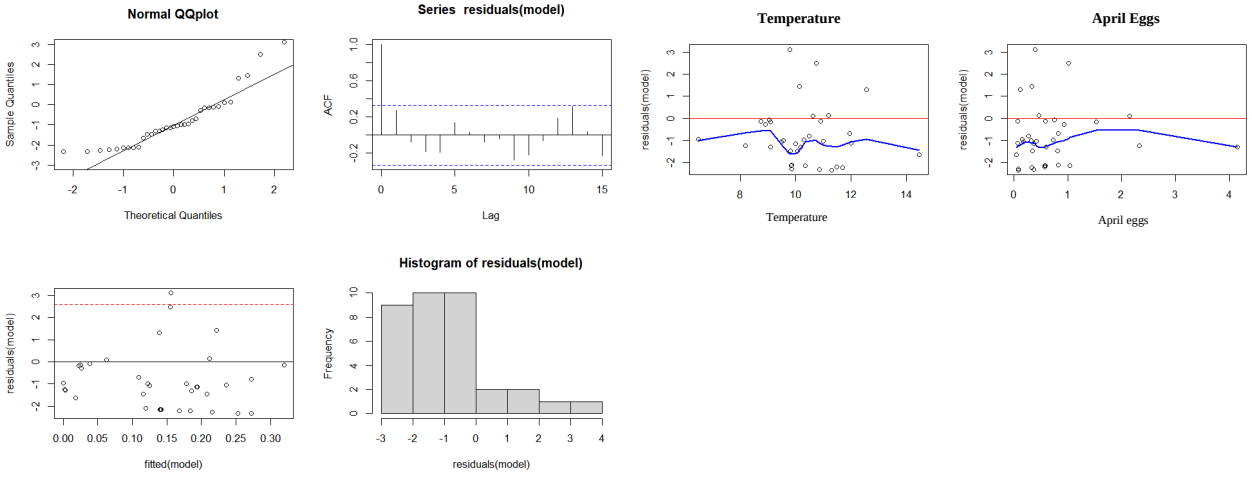


Sprat egg abundance May "Controle":



Sole larval abundance April "Canal":



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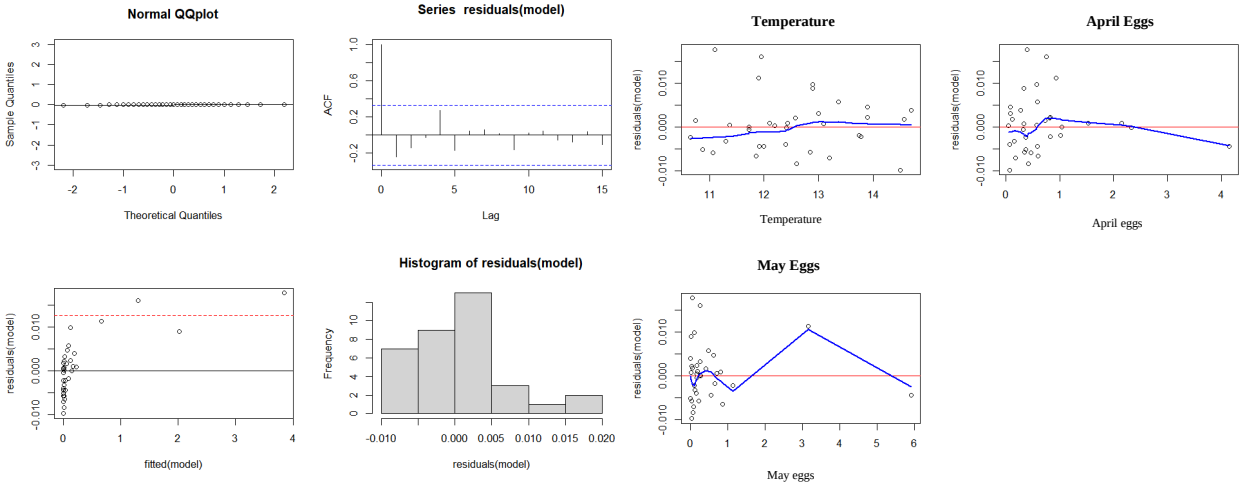

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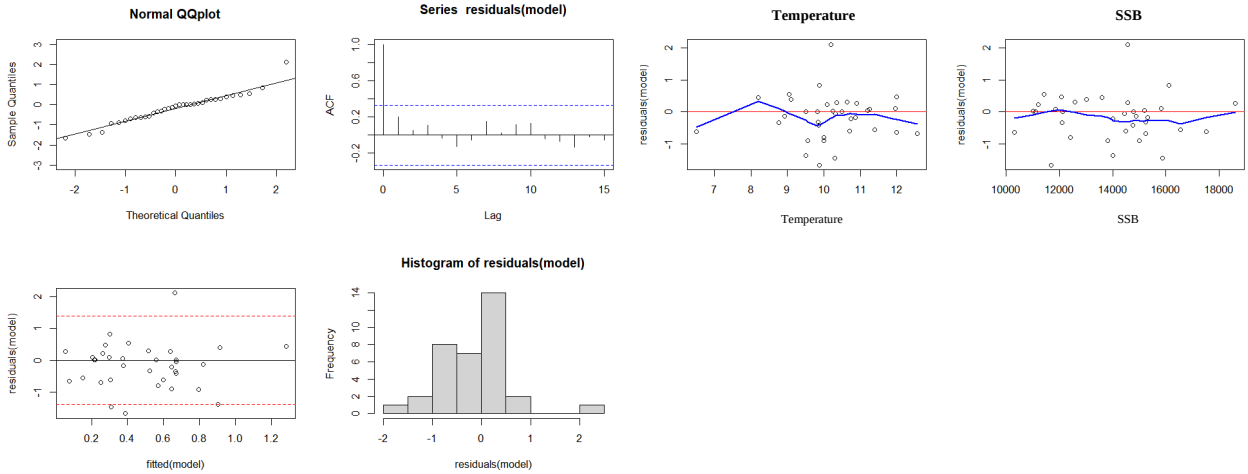

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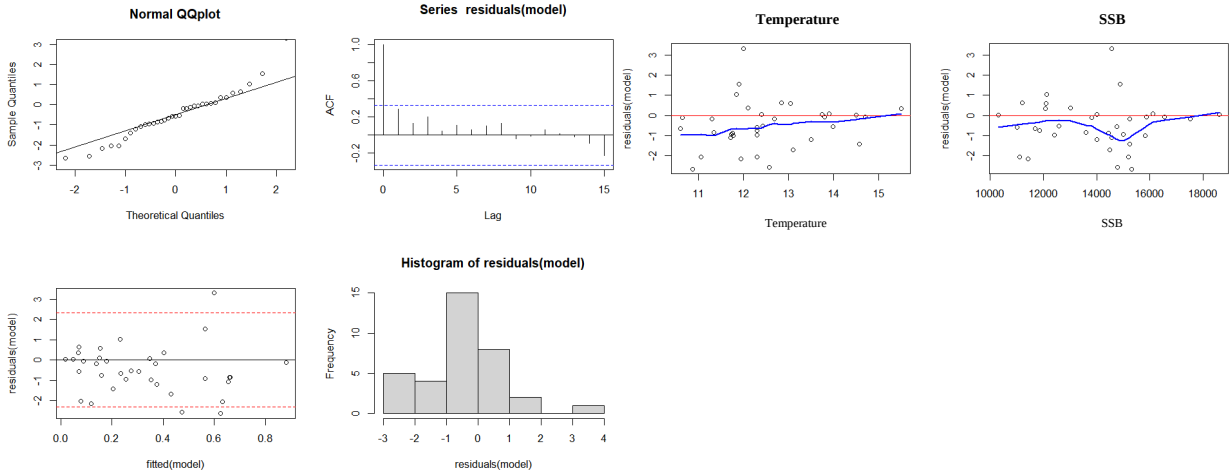

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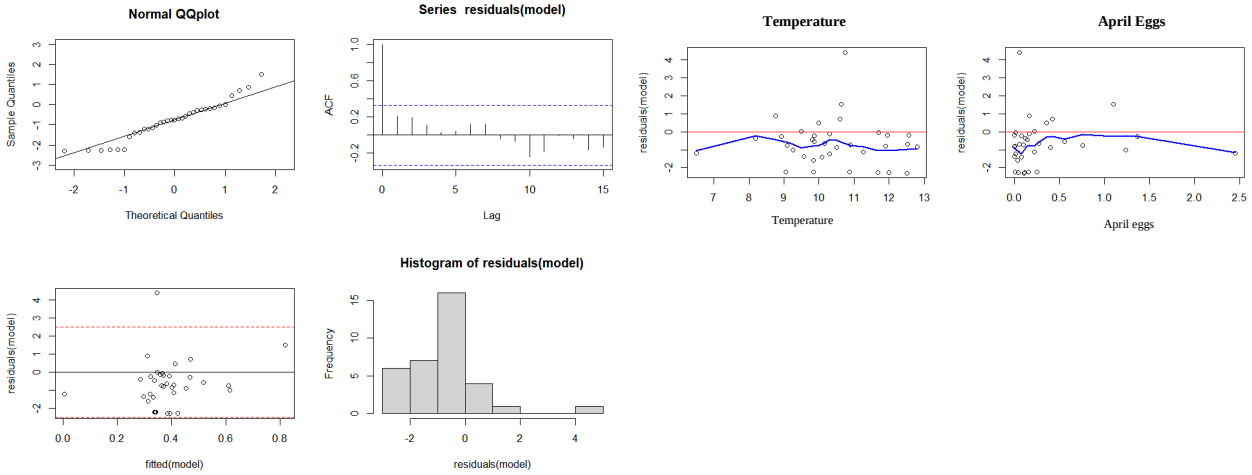

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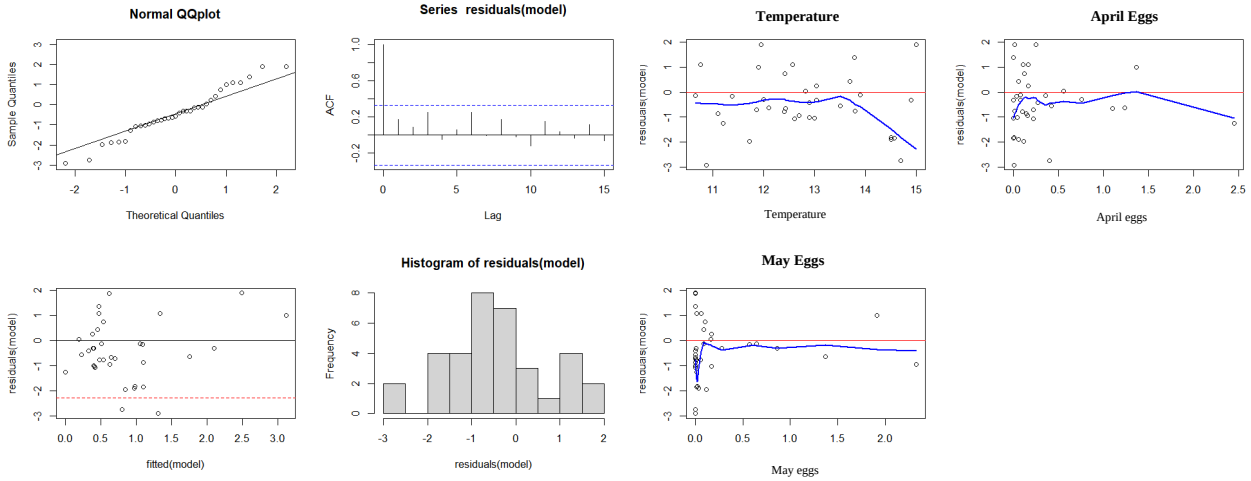

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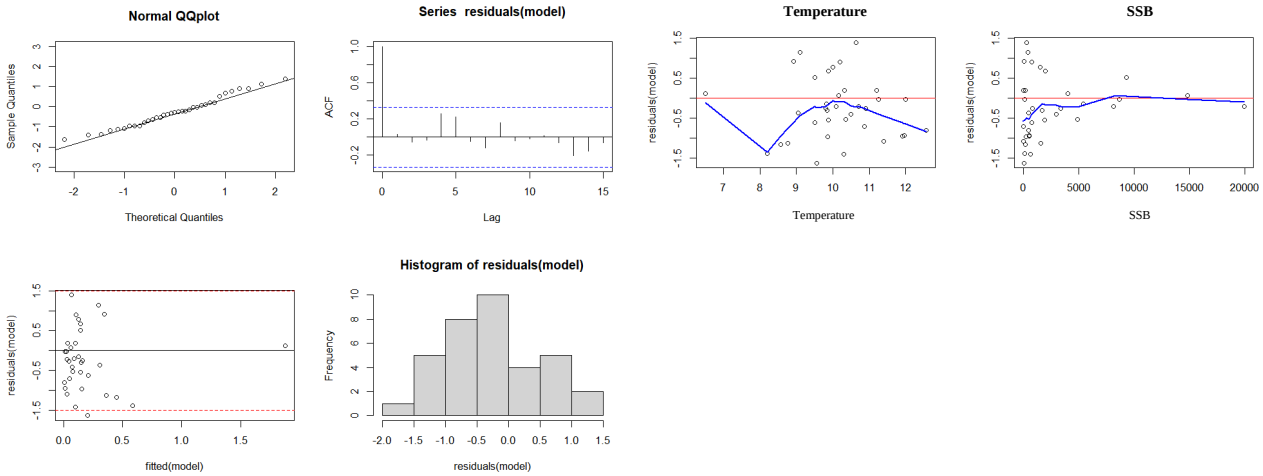

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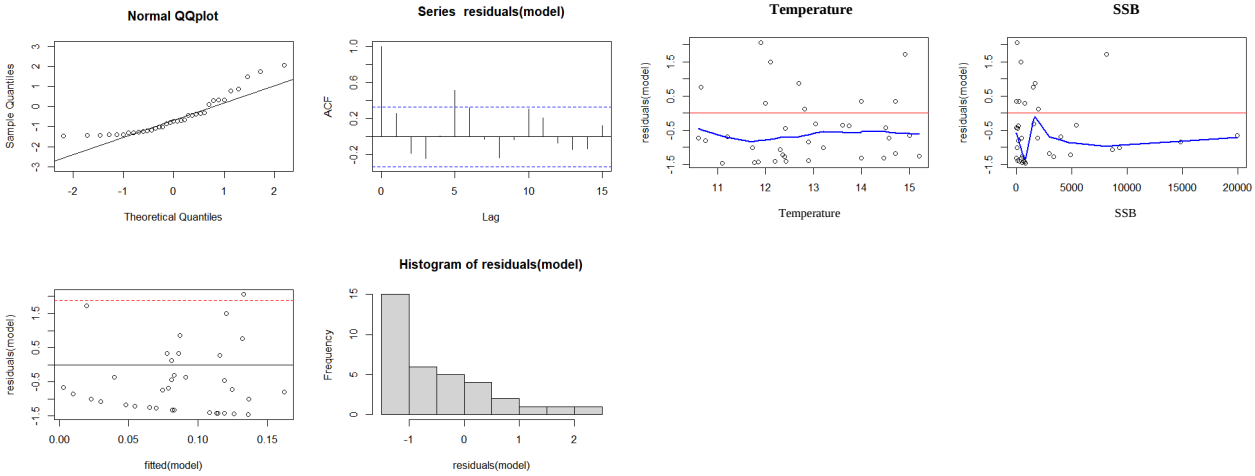
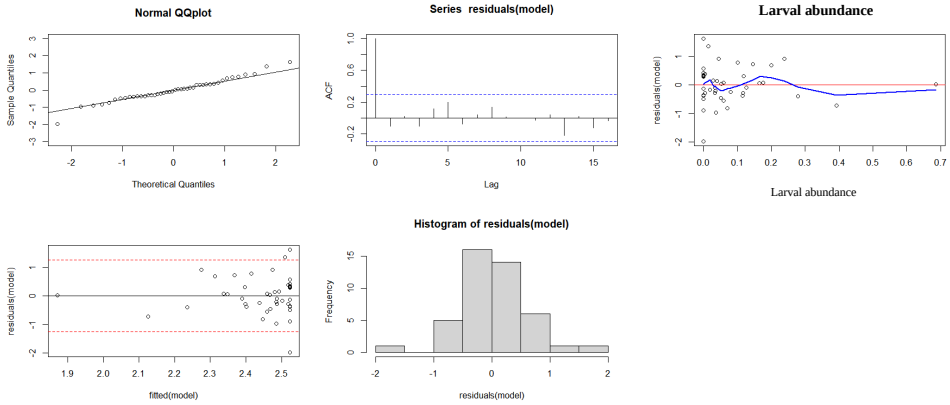


Appendix XI: Summary of models used for recruitment modelling

	Gravelines			**Penly**	
	Large	Controle	Cote	Canal	Controle
Sole larvae April	GLM	GLM	GLM	ARIMAX	ARIMAX
Sprat larvae April	ARIMAX	ARIMAX	ARIMAX	ARIMAX	ARIMAX
Sole larvae May	GLM	GLM	GLM	ARIMAX	ARIMAX
Sprat larvae May	ARIMAX	ARIMAX	ARIMAX	ARIMAX	ARIMAX

Appendix XII: Residuals from recruitment modelling

Sole April "Large":



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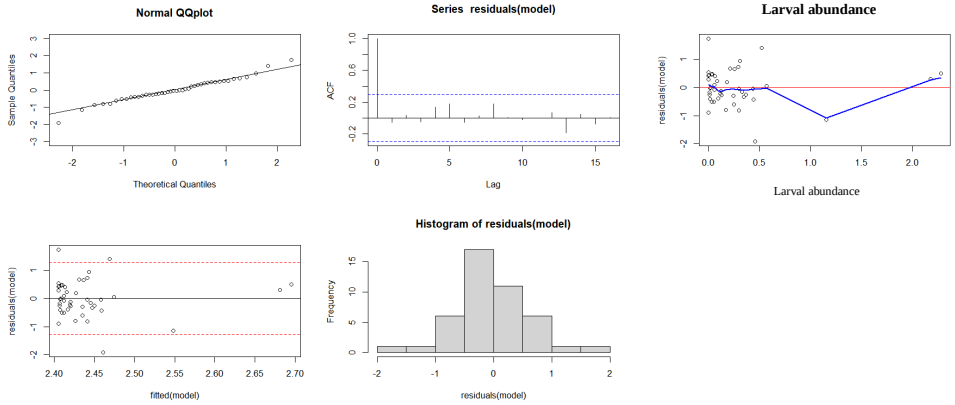

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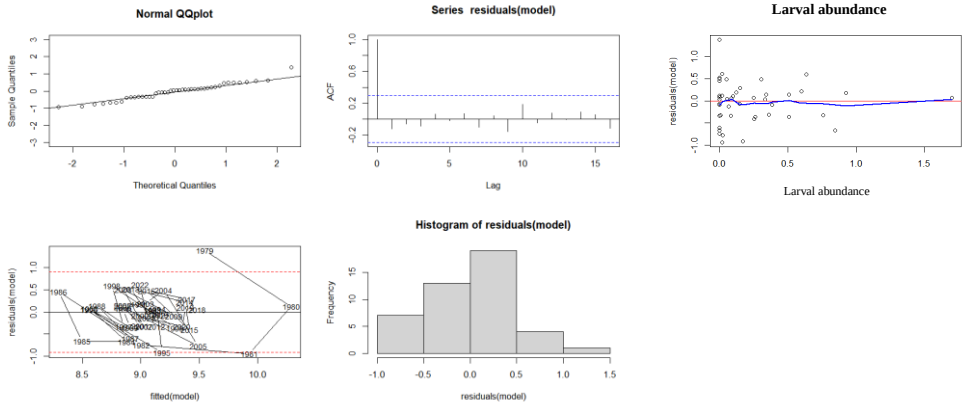

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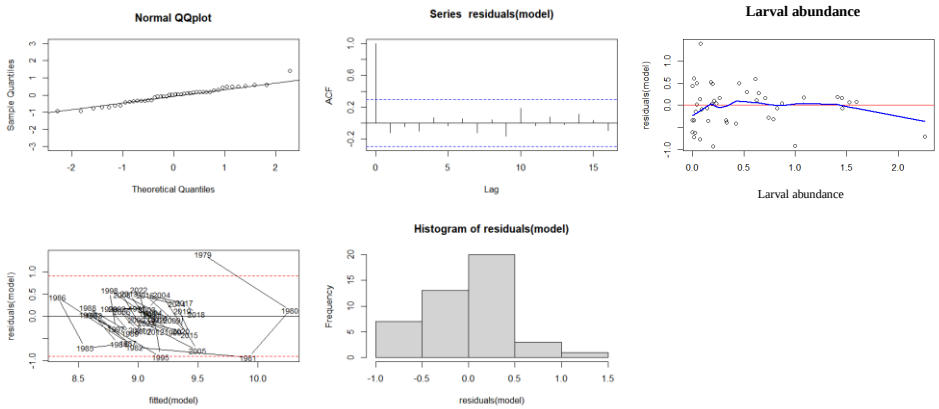

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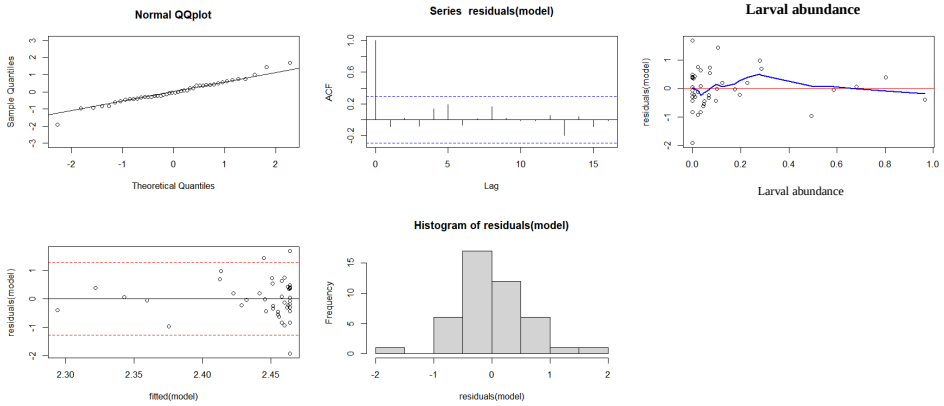

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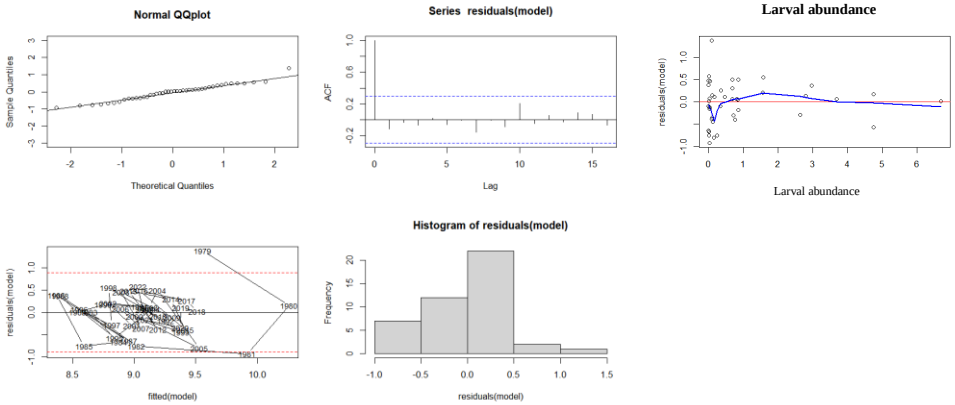

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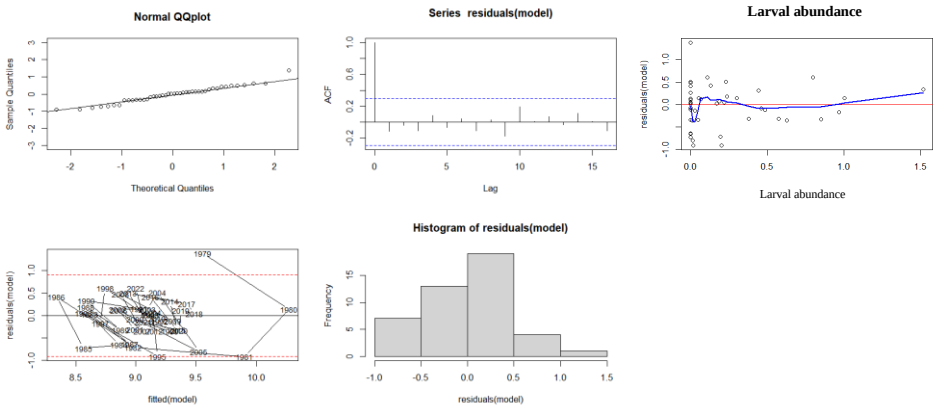

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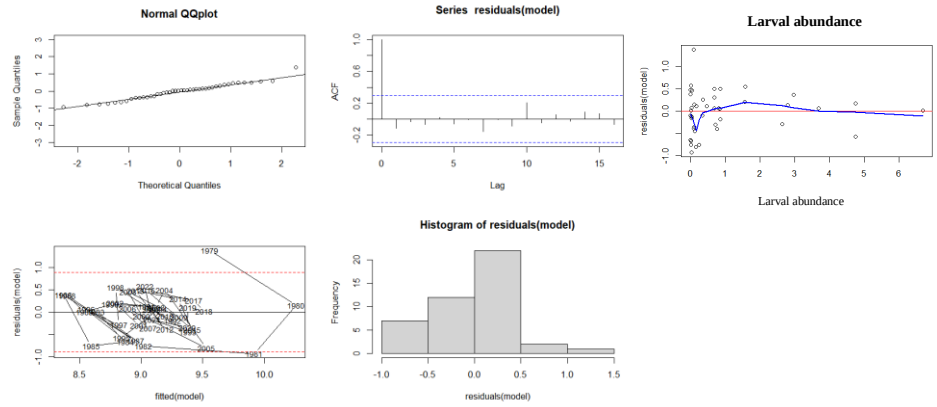

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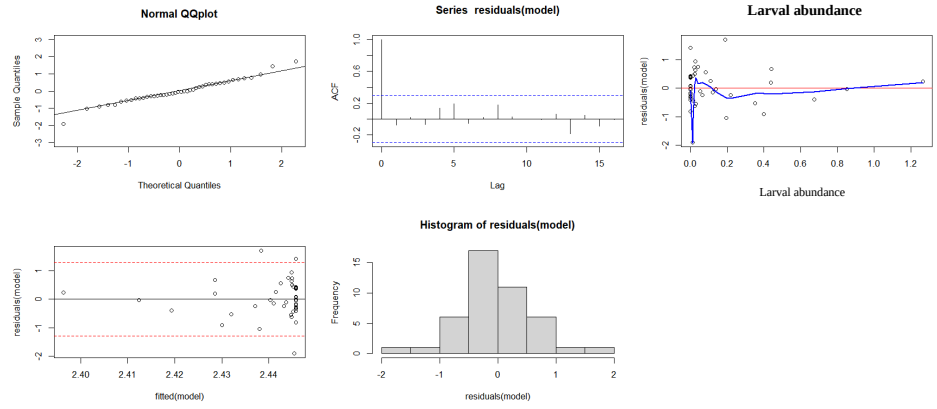

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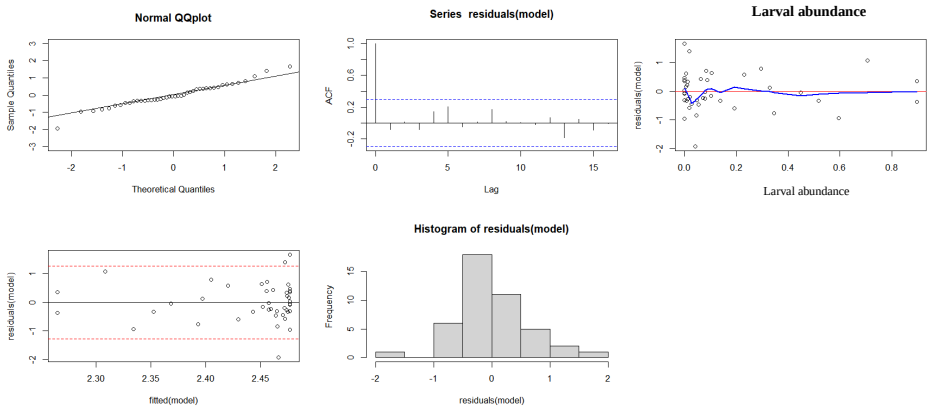

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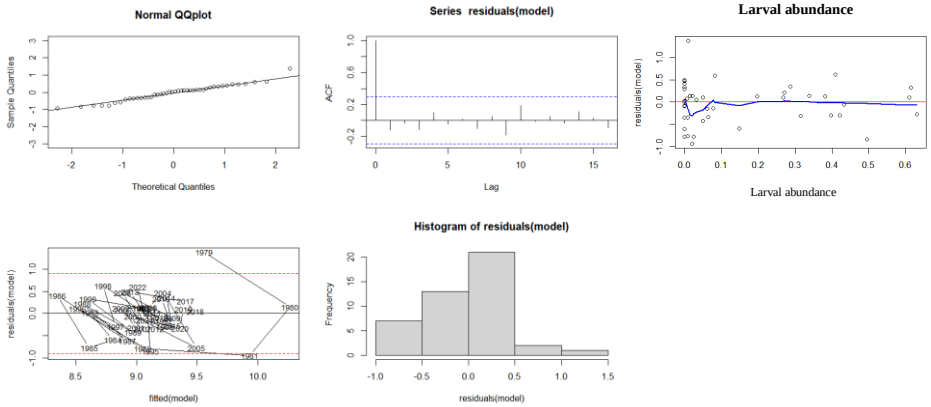

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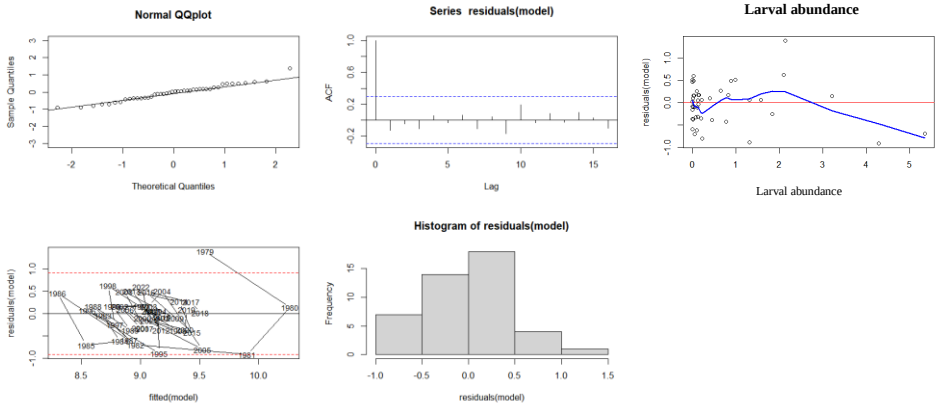

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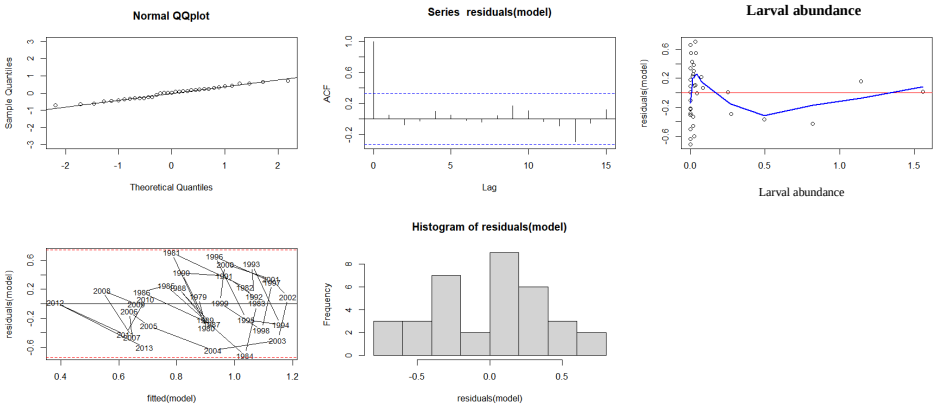

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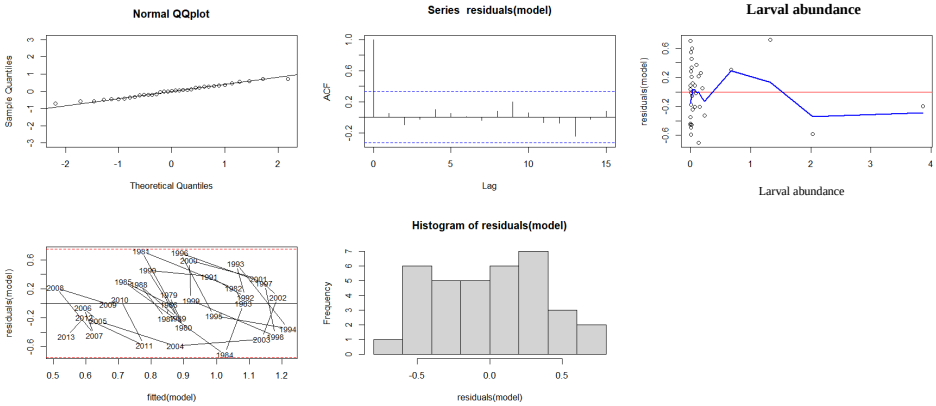

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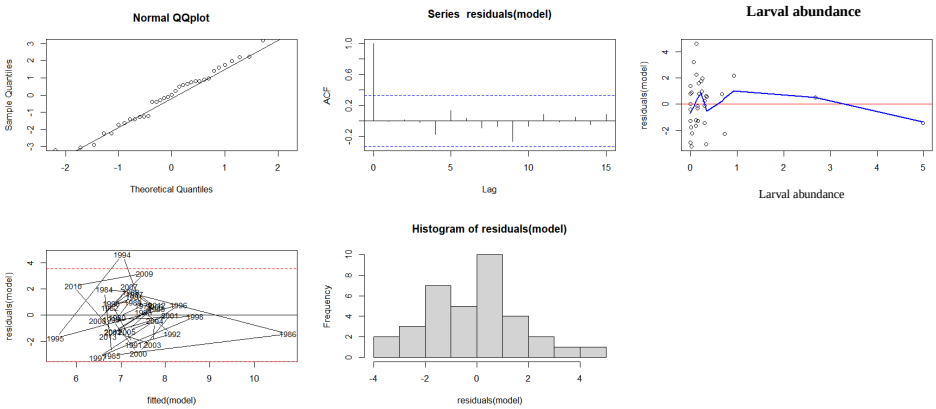

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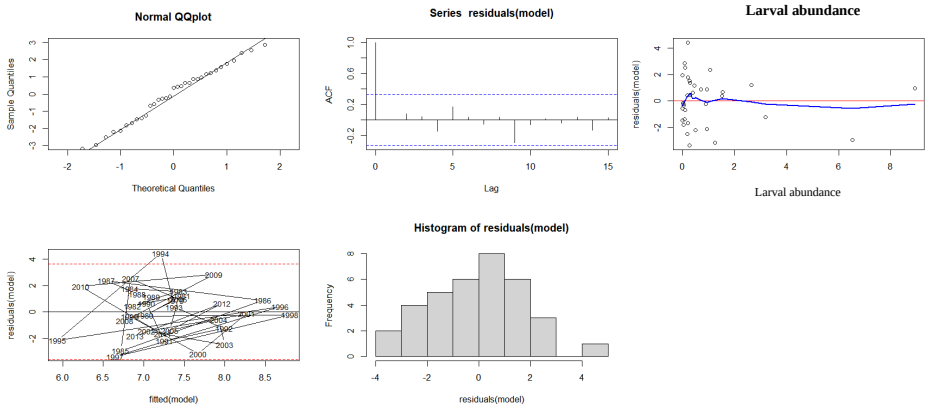

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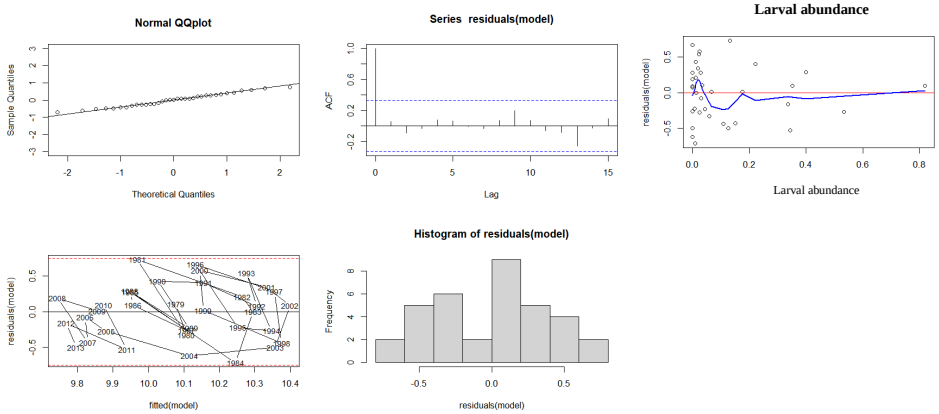

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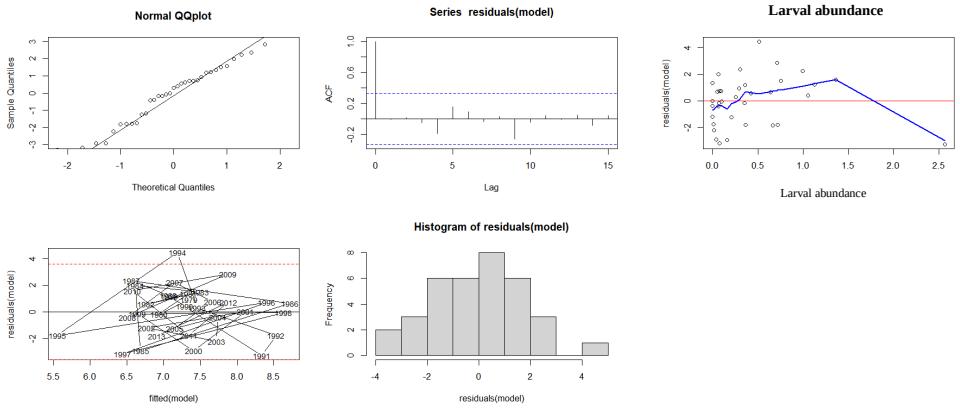

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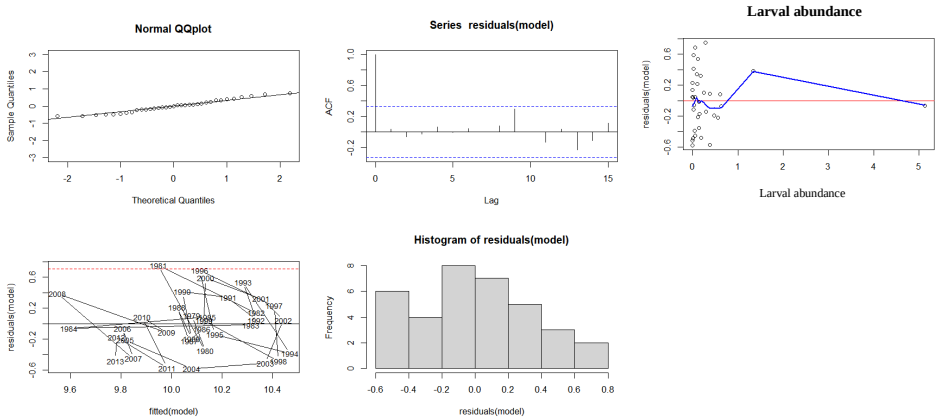

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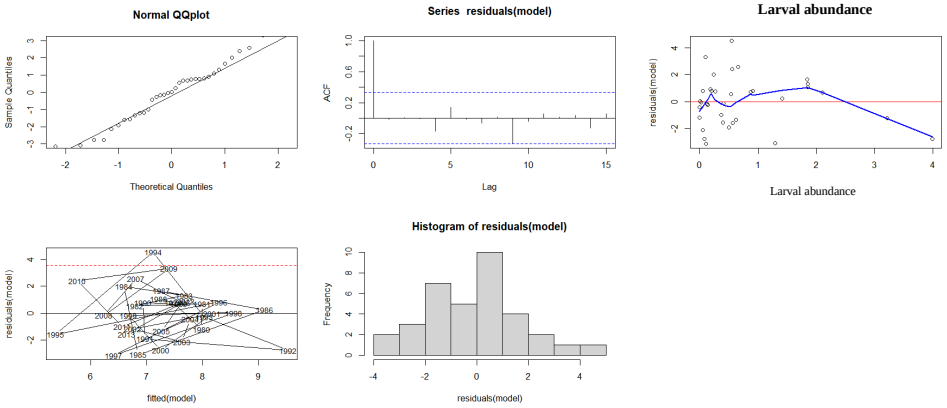

L'INSTITUT agro Rennes Angers	Diplôme : Ingénieur Agronome Spécialité : Sciences Halieutiques et Aquacoles Spécialisation / option : Ressources et Ecosystèmes Aquatiques Enseignant référent : Etienne RIVOT

Auteur(s) : Camille BOURGEOIS Date de naissance* : 07/11/2000	Organisme d'accueil : IFREMER Boulogne-sur-Mer, unité halieutique Manche Mer du Nord Adresse : 150 quai Gambetta, 62200 Boulogne-sur-Mer Maître de stage : Christophe LOOTS, Paul MARCHAL
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Titre français : Variabilité à long terme de l'ichtyoplancton en lien avec les fluctuations environnementales et le recrutement

Titre anglais : Long-term variability of ichthyoplankton in relation to environmental fluctuations and recruitment

Résumé (1600 caractères maximum) :

L'étude de l'ichtyoplancton est essentielle afin de mieux comprendre la variabilité du recrutement. La majorité des processus qui affectent le recrutement se situent pendant la phase planctonique. La survie des larves résulte d'une combinaison de facteurs abiotiques et biotiques. Cette étude vise à identifier les impacts des variables environnementales sur l'abondance de l'ichtyoplancton (œufs et larves) afin de comprendre la variabilité du recrutement en Manche orientale et en Mer du Nord. Deux espèces sont étudiées : la sole (*Solea solea*) et le sprat (*Sprattus sprattus*). C'est deux espèces sont caractéristiques du printemps et constituent la majorité des espèces trouvées lors des échantillonnages. La série de données d'IGA (Impact des Grands Aménagements) des centrales nucléaires de Gravelines et de Penly est une des rares séries à long terme (~50 ans) disponible en Manche et en mer du Nord. Des modèles généralisés (linéaires et additifs) ainsi que des modèles ARIMAX sont utilisés. La robustesse des résultats au remplacement des valeurs manquantes des séries temporelles a été testée. L'étude a révélé que l'abondance des œufs était corrélée à la température ainsi qu'à la biomasse féconde pour la sole et uniquement à la température pour le sprat. Quant aux larves, aucun lien robuste n'a été obtenu entre l'abondance larvaire et les variables environnementales testées. Enfin, aucun lien entre l'abondance larvaire et le recrutement n'a été obtenu dans les zones échantillonnées.

Abstract (1600 characters maximum) :

The study of ichthyoplankton is essential in order to better understand the variability of recruitment. Most of the processes that affect recruitment occur during the planktonic phase. Larval survival is the result of a combination of abiotic and biotic factors. This study aims to identify the impact of environmental variables on the abundance of ichthyoplankton (eggs and larvae) in order to understand the variability of recruitment in the Eastern English Channel and the North Sea. Two species have been investigated: sole (*Solea solea*) and sprat (*Sprattus sprattus*). These two species are characteristic of the spring season and represent the majority of species found during sampling. The IGA (Impact des Grands Aménagements) data series for the Gravelines and Penly nuclear power plants is one of the few long-term series (~50 years) available in the Eastern English Channel and the Southern North Sea. Generalised models (linear and additive) as well as ARIMAX models are used. The robustness of the results to the replacement of missing values in the time series were tested. The study revealed that egg abundance was correlated with temperature and spawning biomass for sole and only with temperature for sprat. As for larvae, no robust link was obtained between larval abundance and the environmental variables tested. Finally, no link was found between larval abundance and recruitment in the areas sampled.

Mots-clés : Ichtyoplancton ; Recrutement ; Variables environnementales ; Modèles généralisés ; Analyse long-terme

Key Words : Ichthyoplankton ; Recruitment; Environmental variables ; Generalised models; Long-term analysis