Analysing historical Herring (*Clupea harengus*) monitoring data and the search for explanatory abiotic variables

Report internship project @ VLIZ – Research Department

Alexander Hooyberg

Tutors: *Gert Everaert* & *Ann-Katrien Lescrauwaet*

VLIZ

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2 Introduction: The bigger picture

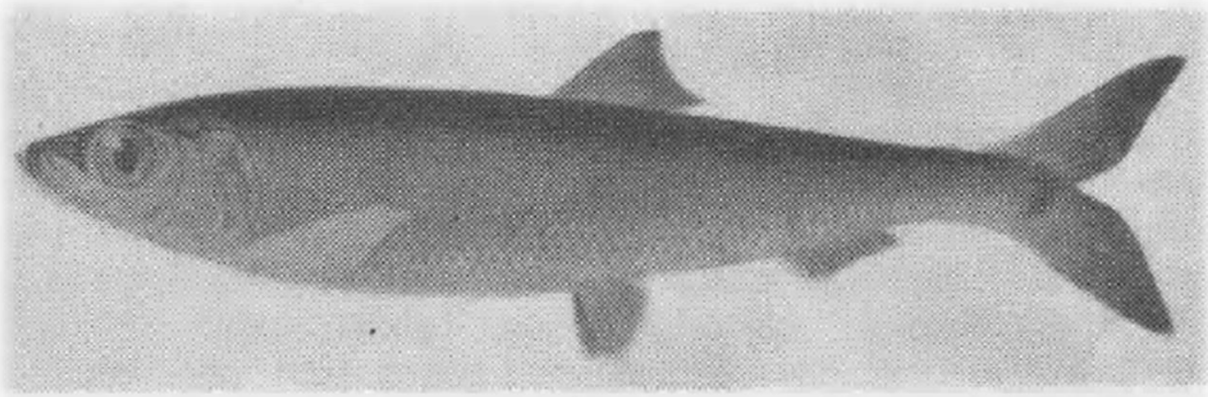

Fig. 1 — De Haring.

*Figure 1: Image of a herring (*Clupea harengus*) (Gilis, 1942).*

Atlantic herring (*Clupea harengus*) are found in the northern part of the Atlantic Ocean and have been one of the most important fish on European markets since the middle ages (Figure 1). Several forms and populations are present in the North Sea, which have long been studied for optimizing fishery activities. The populations can be classified into different North Sea herring 'spatial components' according to their different spawning grounds. Four herring components exist in the North Sea (Lescrauwaet et al. 2013):

- the Orkney-Shetland herring, which spawn off the Shetlands (August-September);
- the Buchan herring, which spawn off the eastern Scottish coasts;
- the Dogger or Bank herring, which spawn off the English Coasts in the central North Sea (September-October);
- and the Downs herring, which spawn in the English Channel and the southern bight of the North Sea (November-January).

They also show differences in vertebrae number and growth rate, which reflects salt concentrations of the seawater in which they live (Gilis, 1942). Gilis quotes: "*De gang van den groei verschilt van streek tot streek en men heeft vastgesteld, dat hoe hooger het zoutgehalte van het water hoe sneller de haring groeit*."

In this report, fisheries data from the Downs herring, which were caught in Belgian coastal waters, was investigated. They come there for spawning their 30000 eggs in the beginning of November at the age of three to four years, when they are in a relatively poor body condition. After spawning, these herring are called spent herring, and stay a few months in Belgian waters before heading back to their foraging grounds in central parts of North Sea (e.g. Dogger bank). Fishermen target these spent herring and move along with the spent herring population in an eastward direction (Lescrauwaet et al, 2013). Herring are also highly fished upon at their foraging grounds in the central parts of the North Sea. "*Hoe warmer het water, hoe sneller het ei ontkiemt",* or translated in English: "*The warmer the water, the faster the egg hatches*", is a quote from Gilis (1942). The new born larvae drift along with the northward currents along the Belgian, Dutch and Danish coasts, back to the feeding grounds (Gilis, 1942).

Besides these populations in the North Sea, there's also the Atlantic herring, which have a higher average number of vertebrae and a higher growth rate (Gilis, 1942). They migrate through the English Channel into the North Sea and do this at higher levels when the North Atlantic Oscillation (NAO) is high, due to more favourable water currents.

The NAO is a weather phenomenon in the North Atlantic Ocean of fluctuations in the difference of atmospheric pressure at sea level (SLP) between the Icelandic low and the Azores high (Wikipedia). During the negative NAO, the North Atlantic jet stream and storm track are shifted southwards, leading to more intense cold air outbreaks over Northern Europe and the Eastern United States (Peings and Magnusdottir, 2014).
The Atlantic Multidecadal Oscillation (AMO) is another climate phenomenon that is more related to ocean sea surface temperature than atmospheric pressure levels. It consists of an alternation between warm and cold sea surface temperature (SST) anomalies in the North Atlantic basin, with a period of 60–70 years (with the effect of climate warming cancelled out) (Peings and Magnusdottir, 2014).
The exact origin and effects of both phenomena are not fully understood yet, but a study demonstrated that the NAO is tied to the AMO, with an opposite signed relationship between the polarities of the AMO and the NAO, and a lag of the NAO by 10-15 years (Peings and Magnusdottir, 2014). This is probably because the AMO-related SST anomalies induce the atmospheric pressure differences seen in the NAO (Peings and Magnusdottir, 2014).

After World War I, the use of otter trawls instead of driftnets brought a huge increase in the amount of fish landed (Lescrauwaet et al. 2013). Right before World War II, approximately 40,000 tons of fish and other seafood per year was landed by Belgian fishers, of which a quarter consisted of herring (Lescrauwaet et al. 2013). During WWII, which started in Belgium in 1940 and ended in 1944, many fishermen fled to the UK or were set to service military purposes, so almost no fishing took place during that period. Also, in the rest of Europe, fishing activities were halted due to the war hazards (Baerends 1947 in Lescrauwaet et al. 2013, Gilis 1947, Lescrauwaet et al. 2013). However, from 1941 onwards, some fishermen were allowed to fish in front of Belgian and northern French coasts, under close surveillance of the occupying forces (De Mulder 1984). In that period, extraordinary high landings of North Sea herring were recorded, up to a tenfold the previous amounts. It is argued that these increased catches are explained by a combination of factors, including the sustained effect of a major increase in catch power, the effects of strong pre-WWII year classes, and the effects of decreased fishing mortality during the 6-year cessation in fishing on the herring feeding grounds in the central North Sea and in the English Channel.

Professor Gustave Gilson (1859-1944) and his collaborator Charles Gilis of the *Zeewetenschappelijk Instituut* made huge efforts to investigate the fauna in the Belgian part of the North Sea. They examined and reported the herring landings in Belgium from 1942 until 1950. They not only collected data about the landings itself (amount of kg, vessel names…), but also about individual fish characteristics (length, weight, vertebrae number, age…) of a subset of the landings. This data was stored at the VLIZ in paper forms and was recently analysed and put together into a large dataset, also by the VLIZ. This dataset was further analysed during this internship.

Besides the data from Gilson and Gilis, herring landing data from ICES (International Council for the Exploration of the Sea) was also made available for this project, as well as commercial fisheries data collected from local archives (HiFiData, VLIZ 2009). This comprised herring landing data from fishing areas in the Southern Bight of the North Sea (FAO area code IVc) from most years during the 20th century. The HiFidata contains commercial fisheries data (landings) that are earmarked for the specific geographic location of the 'Belgan coastal waters' (Lescrauwaet et al. 2013). Also, a lot of abiotic data collected during the 20th century (e.g. AMO index, Temperature anomalies, Salinity…) was incorporated in this study.

As fish quotas were only introduced in the 1970s, fish landing data from before this period offer unique opportunities for studying population dynamics, because landings were mainly related to the fish stocks present, and not to the quotas set by the government.

One of the main goals of this pilot study was to search for, and elucidate trends in individual fish characteristics during the (short) increase in herring catches in the 1940s (by means of the dataset from Gilson and Gilis). The individual fish characteristics were also linked to AMO and Temperature (T) anomalies data. Secondly, long term trends in the herring fishery data were investigated (by means of the ICES dataset), especially in relation to environmental variables. First, data exploration methods were used to give insights in the data and show possible correlations, after which we used correlation tests and modelling approaches to statistically test these relations (all analyses were conducted in RStudio, R Core Team, 2017). Our general research questions were:

1. Are the individual fish characteristics (condition, age, vertebrae number) related to each other, and do they vary over the years and during the season? (models 3.3.2.1, 3.3.2.2, 3.3.2.3)
2. How are AMO and T anomalies related to those fish characteristics? The AMO increases the number of Atlantic herring inflow in the North Sea, which show a higher number of vertebrae, but can we use the mean vertebrae number as a proxy for AMO intensity? (models 3.3.2.1, 3.3.2.2, 3.3.2.3).
3. Do the trends in herring landing data observed during the 1940s correlate with changes in individual fish characteristics? (model 3.3.2.4)
4. Do the trends in herring landing data observed during the 20th century, correlate with changes in abiotic variables of the water column? (model 4.3.2)

The information gathered during this pilot study will be used to give directions to future research conducted at the VLIZ. The entire project will provide essential understandings in the herring fish characteristics, population dynamics and factors influencing them in the Southern Bight of the North Sea. This is of vital importance to the sustainable management (e.g. Marine Strategy) of this important food source, as well as optimizing herring catches to ensure harmony between maintaining healthy fish stocks and sufficient income for the fisherman. With the Brexit coming close to reality (and the hypothetic situation that Belgian fisherman may not be allowed to fish in English waters anymore), the use of these ecosystem services might undergo changes, which can put the fisherman and the fish stocks under pressure. The development of economic alternatives are under study (ILVO, pers. Comm. 2017).

As a conclusion, it can be stated that the individual fish characteristics are related to each other, with Age correlated to the vertebrae number and the condition index BMI. BMI, Age and Vertebrae number showed differences over the years, the Vertebrae number also showed seasonal differences.
The changes in AMO and T anomalies were correlated with changes in BMI and Landings in the 1940s, while only the T anomalies were correlated with changes in the Vertebrae number.
The long term trends in herring landing data showed increases in Landings during the period 1920-1960.

Furthermore, a lot more questions were raised than were answered, which indicates the need for further research.

3 Analysing fish characteristics in relation to AMO and T anomalies

From December to March (and sometimes April and September), Gilson and Gilis collected landing data (ear, month, day, vessel name, fishing gear, fishing area and amount of kilograms landed that day), and data on individual herring characteristics of a subset (25 up to 119 individuals) of the landings. These latter include Length and Weight of the fish, gender, Maturity class, amount of fat, Vertebrae number (*Wervelgetal*), Age (as the amount of winter rings counted on the scales of the fish, *Winterringen*) and Stomach contents (see Table S 1 for explanation and units).

3.1 Data acquisition and processing

All herring landing datasets and abiotic datasets that were used in this study, are summarized into Table S 2, which shows all the datasets used for obtaining which variables, with the corresponding references.

3.1.1 The Gilson and Gilis dataset

The original dataset directly composed from the Gilson and Gilis reports (*Gilis*) contained more variables than were used in this study. From the original dataset, we made some adjustments and made a new subdataset dataset *Gilis1*:

- All variables and inconsistent elements were adjusted so that they were more easily handled in R (Table S 3);
- A selection of relevant variables was made to incorporate in *Gilis1* (Table 1);
- Only data with *fishing gear* values of '*bordentreil*' and '*haringtreil*' were incorporated.
- Gilson and Gilis sampled a different number of replicates (*individual number*) per catch series, which ranged from 25 to 119. We used a random sampling technique to reduce the number of replicates to the minimum (= 25). This resulted in a balanced design with 25 replicates per series, which was needed in the modelling procedures.
- A condition index was calculated based on Length and Weight according to Dourado and Davies (1987), and added this to *Gilis1*;

$$BMI = \frac{Weight(g)*1000}{\left(Length(cm)\right)^3}$$

- AMO and T anomalies data was incorporated into *Gilis1.* (see section 3.1.1)

The *Gilis* dataset was used for data exploration and correlation testing, while the subdataset (*Gilis1*) was used for modelling.

3.1.2 The AMO and T anomalies dataset

The original AMO and T anomalies dataset contained values for every month and year from before the 1900s until 2017. The values corresponding with the right year and month were added to the *Gilis1* dataset. As the *Gilis1* dataset does not cover all the months in a year, a separate dataset had to be made which spanned the same period as the *Gilis1* dataset (1942 – 1950), but which included all the months. As such, the data exploration was not biased.

Table 1: Explanation, units and values of all variables in the Gilis1 dataset.

Variables in Gilis1	Explanation	Units	Values
BMI	Condition index (calculated as Weight/Length^3)	.	3.3-13.6
Year	The year of landing	yyyy	1942 - 1950
Day.in.the.year	The day in the year of the landing	ddd	1-365
Amo	The Atlantic Multidecadal Oscillation index	.	-0.17 - +0.42
Temperature.anomalies	The Temperature anomalies	.	-0.4 - +0.32
Fishing.area.code	Code for which marine area the fish were caught	factor	0 - 12 (Table S 4)
fishing.gear	The fishing gear used to catch the fish	factor	bordentreil/haringtreil
Maturity.level	The level of maturity of the fish	factor	I-VIII
Maturity.numeric	The level of maturity of the fish	#	1 - 8
Winterringen	The amount of winterrings counted on the scales of the fish (= proxy for Age)	#	0 - 13
Wervelgetal	The Vertebrae number	#	54 - 61
amount.of.fish.caught.or.landed	The amount of fish landed that day	kg	300 -73 000

3.2 Data exploration

Data exploration comprised making boxplots to see certain patterns over the years and possible relations between the fish characteristics and the AMO and T anomalies data.

The patterns observed in Length were very similar to the patterns observed in the Weight of the herring, so in the next figures, only Length is plotted.

3.2.1 Differences in fish characteristics over the years

Length, Weight, age (*Winterringen*) and the Amount landed seemed to follow a cycle of 4-6 years, which may correspond with the cyclicity of the AMO cycle (see later) (Figure 2). Although BMI is based on Length and Weight, which both show these trends, we observe no trends in BMI (Figure 2).

The Vertebrae number (*Wervelgetal*), Maturity level and Fat content didn't show any trends over the years (not plotted).

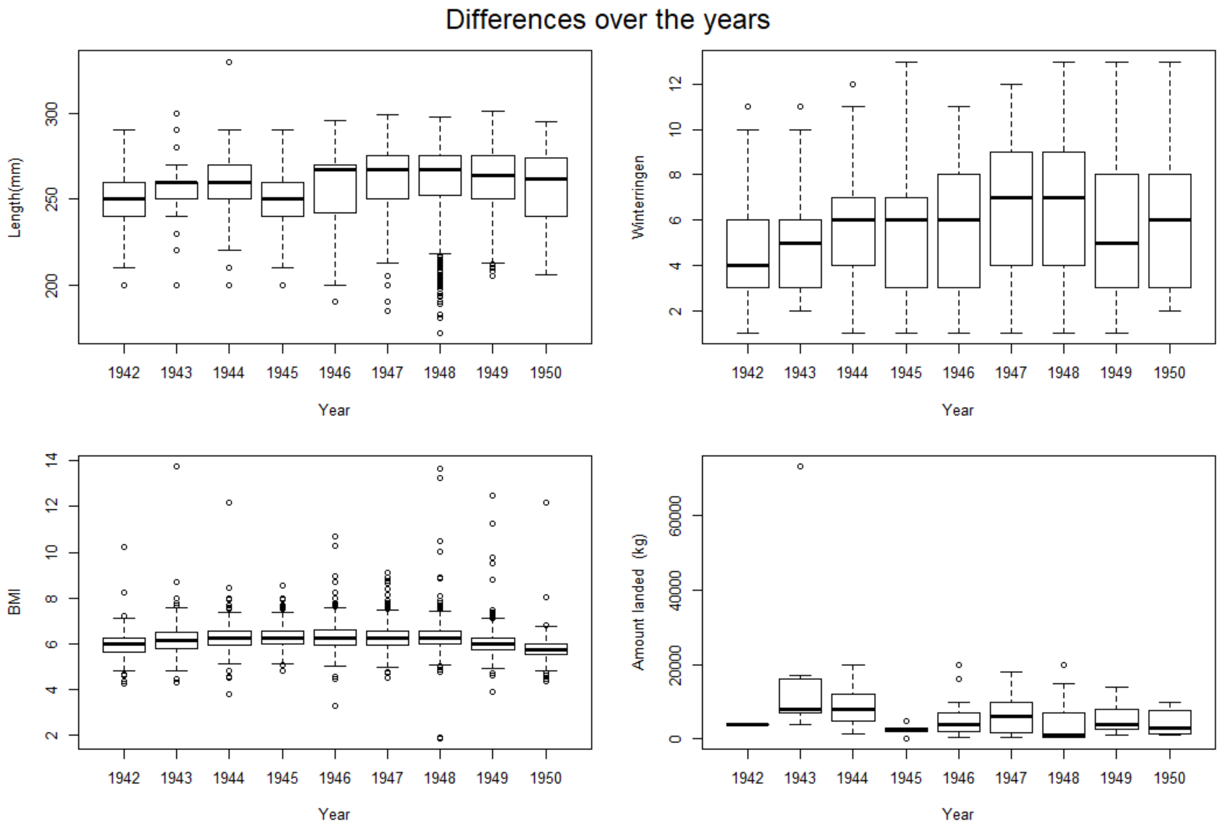

Figure 2: Differences over the years in Length, age (Winterringen), BMI and the amount of landed herring (Amount landed).

3.2.2 Seasonal differences in fish characteristics

During the fishing season (which starts in December), a decline in Length, Age (*Winterringen*) and BMI to a lesser extent was observed (Figure 3). Also, there's a peak in Amount landed in January (*januari*) (fig. 3). Mind that in fig. 3, April and September are underrepresented and having only 1 type of Fishing gear used (respectively *garnaalkor* and *no data*).

The Vertebrae number (*Wervelgetal*), Stomach contents (*Maaginhoud*), Vertebrae in the neck (*Halswervels*), Maturity level and Fat content didn't show any trends over the season (not plotted).

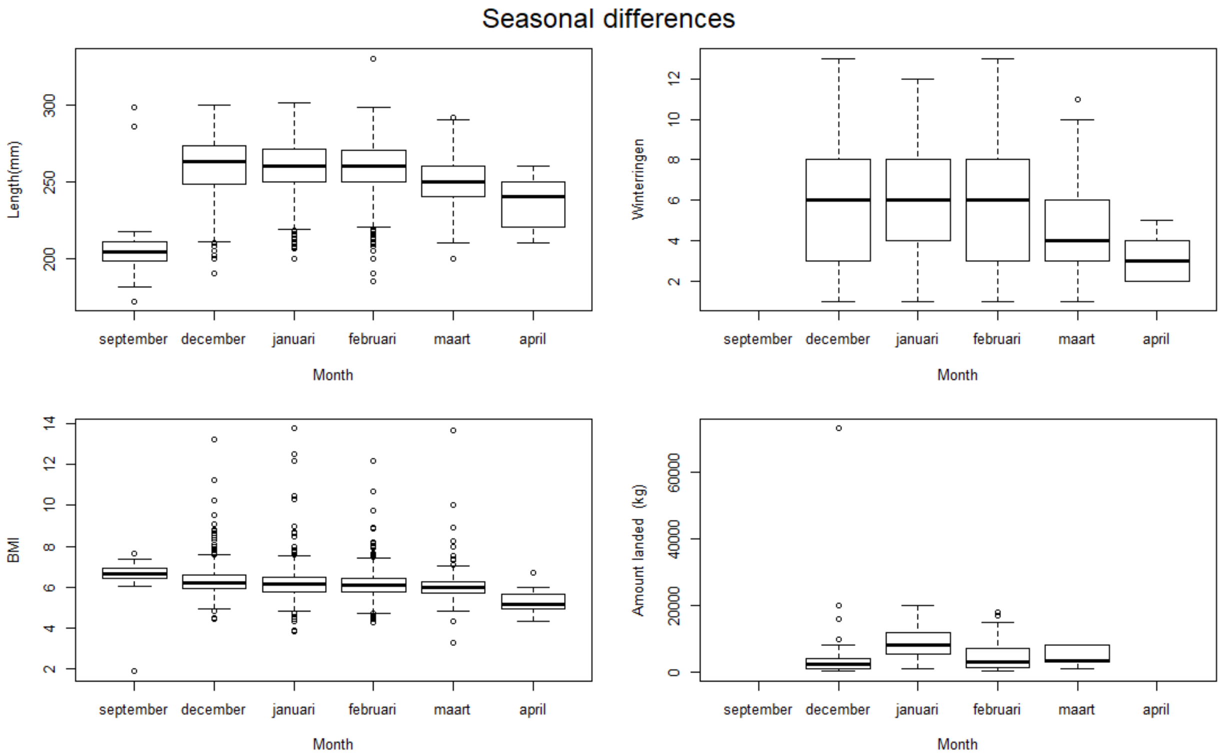

Figure 3: Seasonal differences in Length, age (Winterringen), BMI and the amount landed of landed herring (Amount landed.

3.2.3 Differences among fish characteristics

BMI has already shown not to follow the same trends as Length and Weight (Figure 2, Figure 3). This relation was further investigated in this section, together with the relationship between other fish characteristics. Importantly, Maturity level and Age (*Winterringen*) seem to be correlated (purely visual) with Length and Weight, but not with BMI (Figure 4). This means that the condition index (BMI) may not be a good representation of Length and the Weight. This is probably because we divided Weight by Length, which both show positive trends, as such resulting in an overall neutral trend.

No effect was found visually of the Vertebrae number (*Wervelgetal*, Figure 4), Stomach contents (*Maaginhoud*), Vertebrae in the neck (*Halswervels*) and Fat content (*Vet*) on Length and Weight (not plotted).

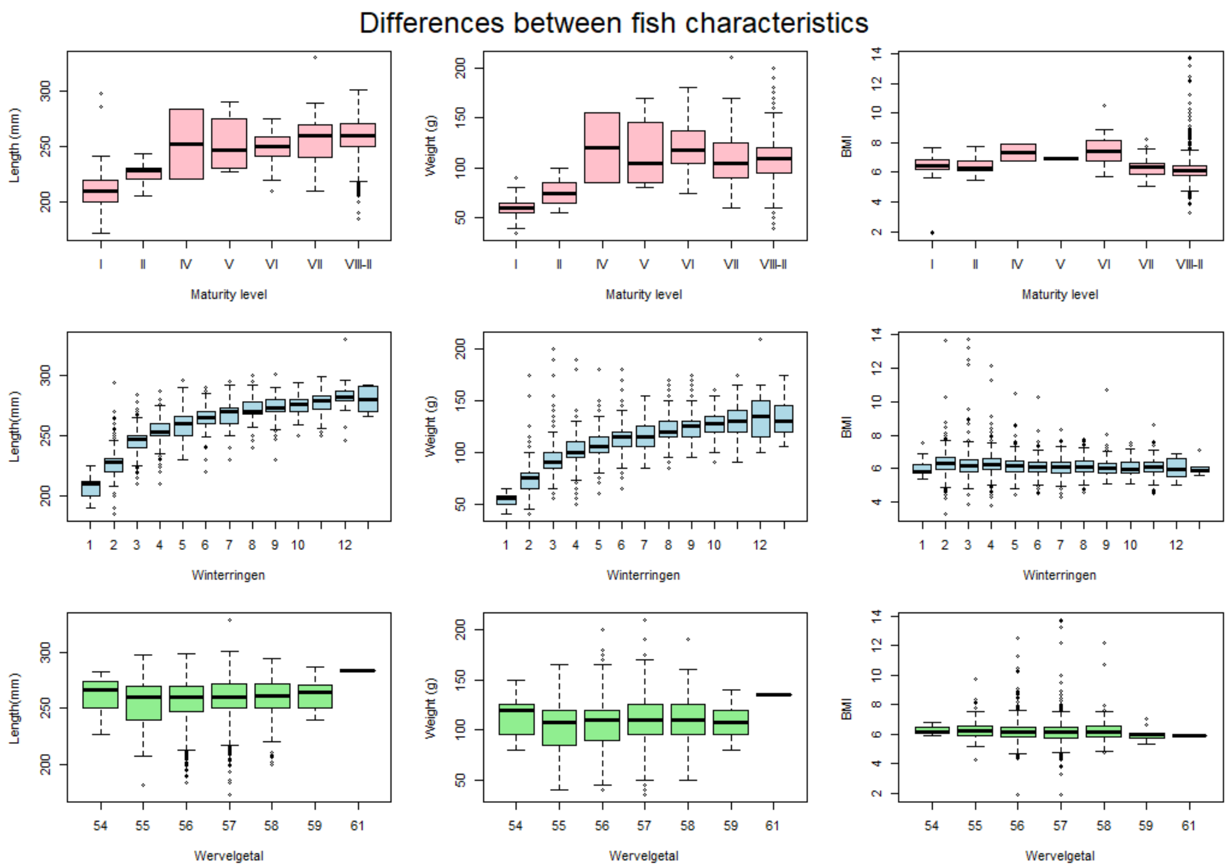

Figure 4: The relationships between the maturity level, age (Winterringen), amount of vertebrae (Wervelgetal) and Length, Weight and BMI.

The differences between males and females were investigated, and almost no differences were observed. However, the Vertebrae number (*Wervelgetal*) was positively related with Length in males, while a negative relation was observed in females (Figure 6).

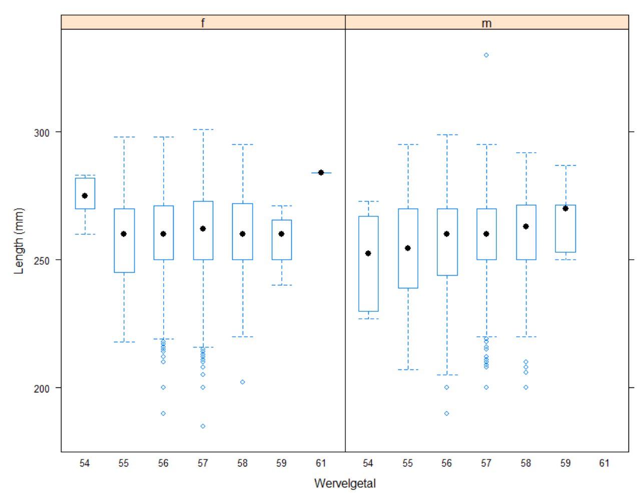

Figure 5: Boxplots showing length in function of the amount of vertebrae (Wervelgetal) for males and females.

3.2.4 Differences of fish characteristics between fishing gear and fishing area

Fishing area and Fishing gear showed variable effects on the fish characteristics, meaning that they should be incorporated as random effects into further models.

3.2.5 Trends in abiotic variables: AMO and T

As in Length, Weight, Age (*Winterringen*) and Amount landed, a more or less 4 to 6-year cycle can also be observed in the AMO data, and to a lesser extent in the T anomalies data (Figure 6).

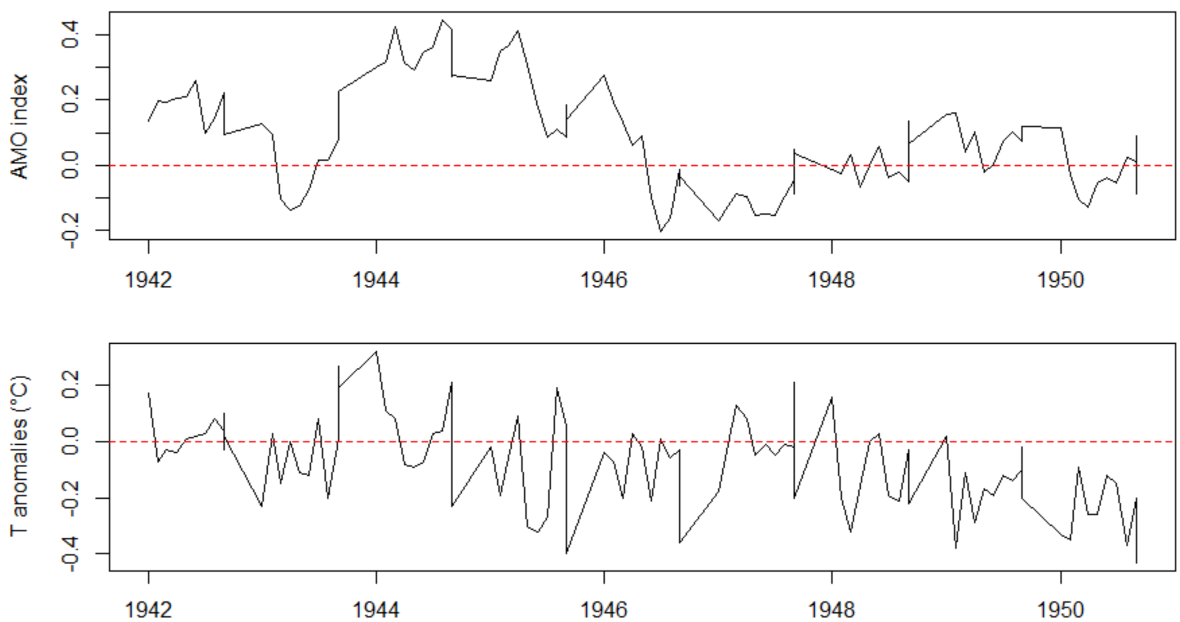

Figure 6: AMO indexes and Temperature (T) anomalies in the period 1942 to 1950. The red striped line indicates the border between positive and negative indexes/degrees difference.

3.3 Statistical tests

All data was not normal distributed, so all tests had to be non-parametric. A significance level of 0.05 was chosen.

3.3.1 Testing correlations and differences between groups

Pearson rank correlation coefficients were used to test the correlation between two numeric variables, while a Kruskal Wallis rank sum test and pairwise post-hoc Wilcoxon-rank-sum test with Bonferroni correction was performed when the data was grouped.

Data exploration showed that Stomach contents (*Maaginhoud*), Vertebrae in the neck (*Halswervels*) and Fat content (*Vet*) were not so interesting to include in our analysis. So, from here on, the focus was set testing relations between BMI, Length, Weight, Age (*Winterringen*), Amount landed, Maturity level and the Vertebrae number (*Wervelgetal*).

3.3.1.1 Differences in fish characteristics over the years

The correlation tests confirm what was seen in the graphs: most of the years differ significantly in the Length ($p < 2.2e-16$), Age (W*interringen*) ($p < 2.2e-16$), BMI ($p < 2.2e-16$) and Amount landed ($p < 2.2e-16$) (Table S 6). Most years didn't differ in the Vertebrae number ($p = 0.074$) (Table S 6).

3.3.1.2 Seasonal differences in fish characteristics

Seasonal differences occurred in Length ($p < 2.2e-16$) and BMI ($p < 2.2e-16$) (Table S 7). When testing the differences in Age (*Winterringen*) and Amount landed, an error was noticed because there were too much 'NA' values when comparing the groups. Overall, however, seasonal differences occurred in the Age (*Winterringen*) ($p < 2.2e-16$) and the Amount landed ($p < 2.2e-16$). The Vertebrae number (*Wervelgetal*) only differed in December, differing from January ($p = 4.50e-05$), February ($p = 7.80e-06$) and March ($p = 0.046$) (Table S 7).

3.3.1.3 Differences among fish characteristics

Fish characteristics were almost always highly significantly correlated among each other (Table S 8). Length was highly significantly and highly positively correlated with Weight (cor = 0.90, $p < 2.2e-16$). BMI was positively correlated with Weight (cor = 0.21, $p < 2.2e-16$), and negatively with Length (cor = -0.21, $p < 2.2e-16$) and Age (*winterringen*) (cor = -15, $p < 2.2e-16$). BMI was not correlated with the Vertebrae number (*Wervelgetal*) (cor = -0.02, $p = 0.056$) (Table S 8). BMI showed differences between certain groups of Maturity level ($p = 1.56e-14$)(Table S 8).

There was a slightly positive relationship between Length and the Vertebrae number (*Wervelgetal*) in females (cor = 0.05, $p = 0.008$) and in males (cor = 0.08, $p = 6.5e-6$). So, the opposite correlation observed in the data exploration (3.2.3: Figure 5) does not hold. Therefore, Gender was not included into further analyses.

3.3.1.4 Differences of fish characteristics between fishing gear and fishing area

Table S 9 shows that Fishing gear differs from each other in Length ($p = 6.144e-13$) and the BMI of the fish ($p = 2.2e-16$) that is caught with it. This matches the findings from the data exploration (3.2.4). The differences between Fishing areas were also investigated, but since there were 24 groups with each a pairwise comparison, those were not represented here. Most fishing areas were significantly different from one or several other fishing areas, both in terms of Length ($p < 2.2e-16$) and BMI ($p < 2.2e-16$) of the fish caught in the areas.

3.3.1.5 Trends in abiotic variables: AMO and T

AMO was positively correlated with the T anomalies (Table S 10) (cor = 0.28, $p < 2.2e-16$), as was to be expected. AMO was also positively correlated with BMI (cor = 0.03, $p = 0.010$) and the Amount landed (cor = 0.04, $p = 0.005$), and negatively with Length (makes sense, as Length is in the denominator in the formula of BMI) (cor = -0.09, $p = 3.67e-14$). The T anomalies were also positively correlated with BMI (cor = 0.13, $p < 2.2e-16$) and the Amount landed (cor = 0.32, $p < 2.2e-16$). No correlation between the T anomalies and Length was found (cor = -0.01, $p = 0.40$) (Table S 10).

3.3.2 Modelling statistical relationships

The correlation tests in the previous paragraph must be interpreted with caution, as they only covered the lumped data over the groups, and as such, hidden variables may play an important role in causing certain correlations. Therefore, several models were constructed, to entangle the variation caused by different variables. Four models were constructed to test the effects on BMI, the effects on the Age

(*Winterringen*), the effect on the Vertebrae number (*Wervegetal*) and the effect on the Amount landed. Those four models were chosen, because the data exploration and correlation testing showed that those were the most promising for having interesting relations with other variables. We didn't model Length nor Weight, because they were significantly correlated with the BMI, which is a more comprehensive indicator for the condition of the fish (although the trends of BMI in the data exploration were not the same as for Length and Weight).

First, several types of models were constructed: Linear Models (LM), Linear Mixed Effects Models (LMER) and Generalized Additive Models (GAM) (Zuur et al. 2009). In each type of model, the most interesting variables were included (BMI, Year, Day-in-the-year, Age (*Winterringen*), Vertebrae number (*Wervelgetal*), Maturity class, AMO and T anomalies), and the response variable was transformed (log10) when this resulted in a better model outcome. A manual stepwise selection procedure (both downwards and upwards) was conducted to filter the variables with a significant effect on the dependent variable. We did this using (type-III) ANOVA tests. As such, this resulted in a final model for each model type. These were then compared among each other by means of the Akaike Information Criterion (AIC). The best model would then have the lowest AIC, which means that it has the most variation in the data explained with the least amount of predictor variables. Mostly, the GAM models were chosen as final and best model, because these models allow easy representation of the effects of the response variables, and also non-linear trends were expected over the years. In the GAM models, k was always set to 5, to have a good balance between model simplicity and model fit. Also, Year was mostly set as cyclical, because we assumed trends over the years to show cyclical patterns (based from the data exploration). Furthermore, Fishing area was included as a random variable, as concluded in section 3.3.1.4. The four final models that resulted out of this procedure are discussed here.
Mind that, from here on, the *Gilis1* subdataset was used, because the models don't allow too much complexity and missing values in the dataset.

3.3.2.1 The BMI-model

In the development of the BMI-model, the four response variables Age (Winterringen), Year, AMO and T anomalies showed significant effects on the log10 of BMI. The effect of Maturity level on the BMI was significant but left out from the model as it was correlated with Age (*Winterringen*). This resulted in the final model, with the output represented in Figure S 1 and the representation in Figure 7:

$$log10(BMI) \sim Winterringen + Year + AMO + T\ anomalies + random(Fishing\ area)$$

In Figure 7a, the effect of Age (*Winterringen*) on BMI seems to decline when individuals get older ($p < 2e\text{-}16$). As the y-axes represent derivatives, this has to be interpreted as an optimum in BMI at the Age (*Winterringen*) of 5, with younger and older individuals having lower BMI values.
As in the data explorative plots, 2 optima are also seen in the effects on BMI over the study period: one just before the start of 1944, and one in 1947, which is much bigger and lies in the positive window (Figure 7c) thus increasing the BMI of the herring ($p = 6.57e\text{-}16$).
The effect of AMO on the BMI seemed to follow a logistic-shaped relationship, thus an increasing effect of AMO on BMI with higher AMO values (Figure 7d) ($p < 2e\text{-}16$). When AMO values diverge from 0.1, the BMI values of the fish increase.
Finally, extreme T anomalies showed positive effects on the BMI, whereas values closer to the mean (and slightly negative) have negative effects on the BMI ($p = 3.91e\text{-}9$) (Figure 7e).

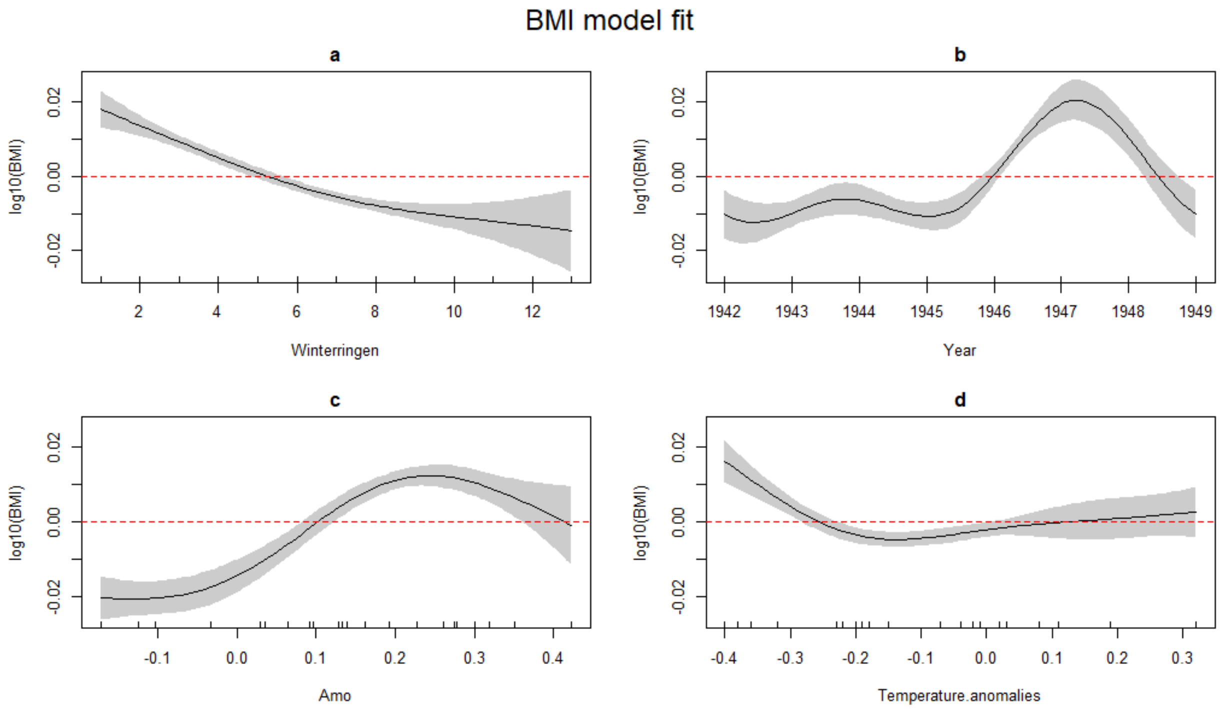

Figure 7: Representation of the BMI model. Y-axes represent derivatives, with the red dotted line indicating the line of 'no effect'. Positive Y values mean a positive effect of the response variable (X-axis) on the predictor variable (BMI), negative Y values mean negative effects on the predictor variable.

➔ Main conclusion: The BMI of the fish increases when individuals up till the age (*Winterringen*) of 5, in the years 1946 to 1948, when AMO values are high and when T anomalies are more extreme.

3.3.2.2 The Age-model (= The Winterringen-model)

Age (*Winterringen*) was significantly related to the time in the study period (Year), the BMI of the fish, the Maturity class and the Amount landed. The following model was obtained, with the output represented in Figure S 2 and the representation in Figure 8.

$$Winterringen \sim Year + BMI + Maturity + \ log10(Amount\ landed) + random(Fishing\ area)$$

In that period 1946 to 1947, there was an increase in Amount landed, whereas in other years in the study period there was a decrease (Figure 8a) ($p = 1.69e\text{-}12$).
The effect of BMI on the Age (*Winterringen*) in Figure 8b, is only significant around a BMI of 5.5 to 9 ($p < 2e\text{-}16$). In that range of BMI, the effect on the age declines from being positive up to BMI values of 6.5 to negative with higher BMI values. This means that oldest individuals are found with a BMI of 6.5.
There is a rising effect (however always negative) of Maturity level on Age (*Winterringen*) (Figure 8c), meaning that the Age (*Winterringen*) declines most when individuals are the least mature (*Maturity level*) ($p = 2.1e\text{-}4$).
The final graph (Figure 8d) indicates that the relation between the Amount landed and the Age (*Winterringen*) is negative with medium log values of Amount landed, and higher with increasing values of Amount landed ($p = 3.4e\text{-}4$). When the fish stocks are high, more older aged individuals were caught.

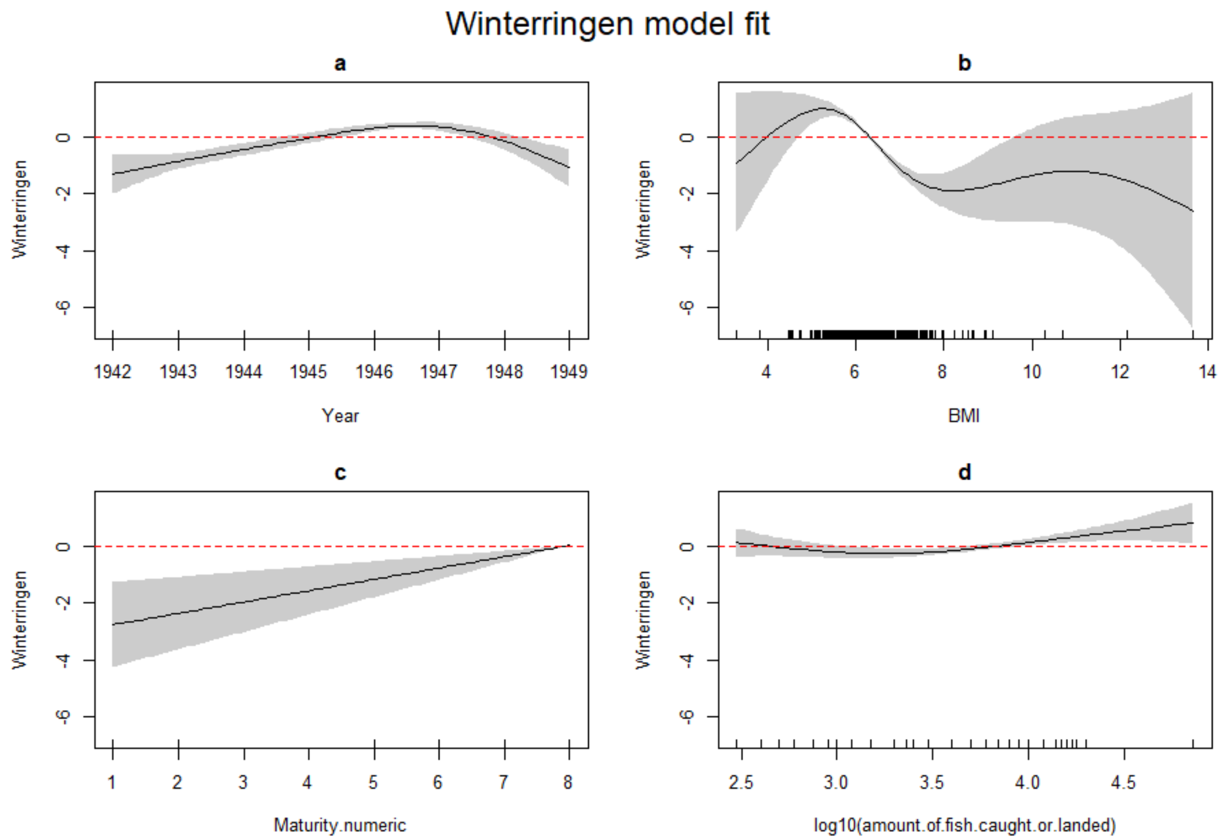

Figure 8: Representation of the Age-model. Y-axes represent derivatives, with the red dotted line indicating the line of 'no effect'. Positive Y values mean a positive effect of the response variable (X-axis) on the predictor variable (Age = Winterringen), negative Y values mean negative effects on the predictor variable.

➔ Main conclusion: There was a strong increase in Age (*Winterringen*) in the period 1946-1947. The effect of BMI on Age (*Winterringen*) declined, while the highest decrease in Age (*Winterringen*) occurred in low Maturity levels. Higher Amount landed values also resulted in an increase of the average Age (*Winterringen*).

3.3.2.3 The Amount-of-vertebrae-model (= The Wervelgetal-model)

For modelling the Vertebrae number (*Wervelgetal*), a model selection procedure was performed on three separate datasets: one with the individuals with a relatively high vertebrae number (>= median), one with the individuals with a relatively low vertebrae number (< median) and one with all the individuals. The calculated median Vertebrae number was 57. We made this subdivision because we were interested in how the herring with a high vertebrae number (with a high fraction of herring that streamed in through the English Channel from the Atlantic Ocean) behaves in relation to the other variables, and if they behave differently than the ones with a low vertebrae number (with a low fraction of herring from the Atlantic Ocean). They were also modelled together with the full dataset. When modelling only those individuals with a relatively low Vertebrae number, no significant explanatory variables were found, so this resulted in only two models.

For the individuals with a high Vertebrae number (*Wervelgetal*) we found the following model, with output and representation respectively in Figure S 3 and Figure 10:

$$Wervelgetal \sim Year + Day.in.the.year + T\ anomalies + Winterringen + Amount\ landed + random(Fishing\ area)$$

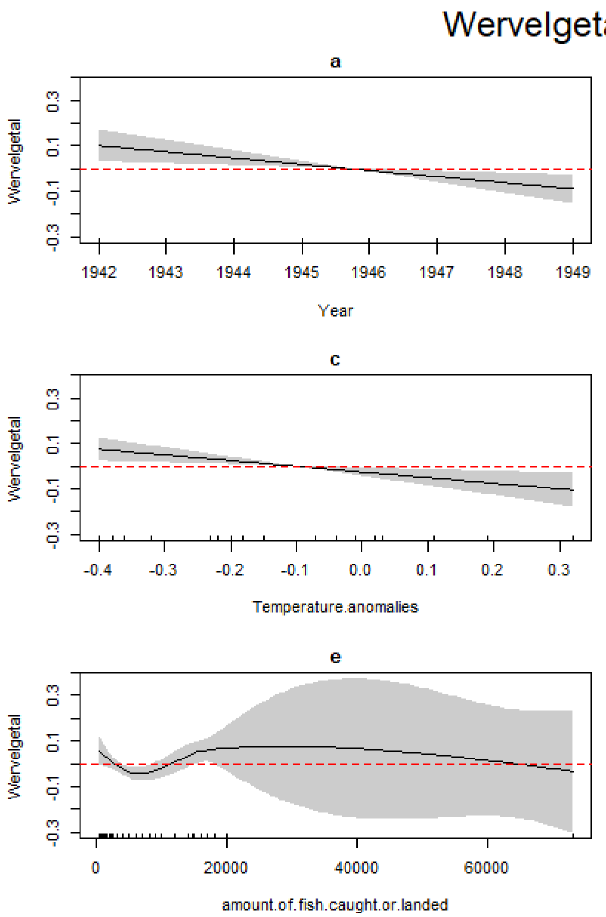

Figure 9: Representation of the Amount of vertebrae-model (= Wervelmodel). With only the individuals with a high amount of vertebrae included. Y-axes represent derivatives, with the red dotted line indicating the line of 'no effect'. Positive Y values mean a positive effect of the response variable (X-axis) on the predictor variable (Amount of vertebrae = Wervelgetal), negative Y values mean negative effects on the predictor variable.

The effect of Year on the Vertebrae number (*Wervelgetal*) declined linearly over the years, crossing the line of zero effect just before 1946 ($p = 0.004$). Then there was the highest amount of inflow of individuals with a high Vertebrae number from the Atlantic Ocean through the English Channel (Figure 9a).
The same trend was observed during the season (Figure 9b), with the highest average Vertebrae number (*Wervelgetal*) around day 80 (somewhere around March) ($p = 0.0001$).
An overall linear declining effect of T anomalies on the Vertebrae number (*Wervelgetal*) is observed when T anomalies increase ($p = 0.005$). The mean Vertebrae number (*Wervelgetal*) number was highest when T anomalies values were slightly before the 0-baseline, meaning that at that moment the highest amount of inflow of individuals from the Atlantic is observed. The declining trend also indicates the negative effect of global warming on the Vertebrae number (*Wervelgetal*).

During the model selection, Age (Winterringen) didn't have a significant effect on the variation explained in the model (p = 0.13). But the AIC of the models with and without Age (*Winterringen*) indicated that we should keep the variable in the model, so it was kept in the model. However, interpreting this term is not appropriate (Figure 9d).
The relation between Amount landed and the Vertebrae number (*Wervelgetal*) declines when Amount landings are low, and not significant when Amount landed increased (probably due to the 1 extremely high values 73000, Figure 9e).

The following model was obtained with including all the individuals (high and low Vertebrae number (*Wervelgetal*). The output and representation are presented in respectively in and Figure 10:

$$Wervelgetal \sim Winterringen + Day.in.the.year + T\ anomalies + random(Fishing\ area)$$

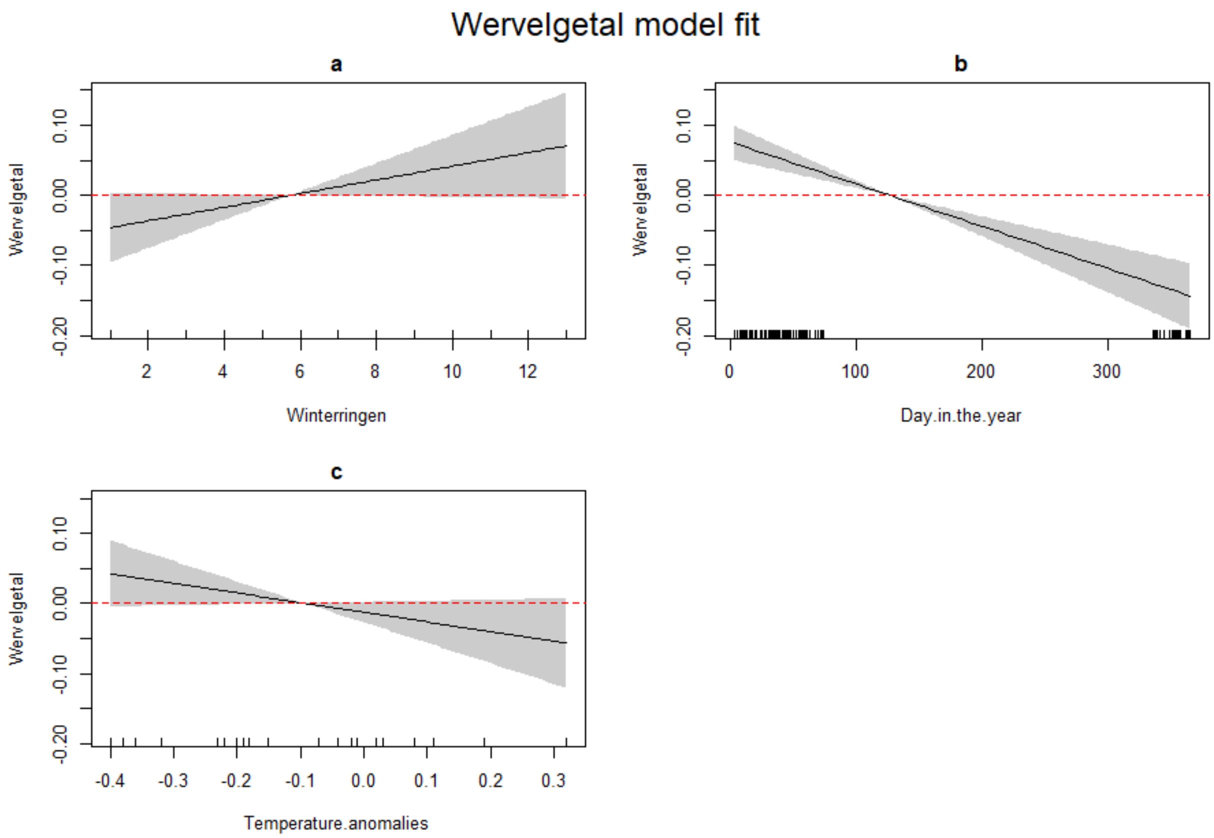

Figure 10: Representation of the Amount of vertebrae-model (= Wervelmodel). With all the individuals included. Y-axes represent derivatives, with the red dotted line indicating the line of 'no effect'. Positive Y values mean a positive effect of the response variable (X-axis) on the predictor variable (Amount of vertebrae = Wervelgetal), negative Y values mean negative effects on the predictor variable.

The effects of Age (*Winterringen*) (Figure 10a, Figure S 4, p = 0.061) and T anomalies (Figure 10c, Figure S 4, p = 0.074) on the Vertebrae number (*Wervelgetal*) were not significant, but still had to be included in the model. No inferences can be made about their relation. As in the model with only individuals with high Vertebrae number (*Wervelgetal*) included, we also see the same seasonal effects when all individuals were included: a lower average Vertebrae number (*Wervelgetal*) in the end of the year (Figure 10b, p = 1.27e-9).

➔ Main conclusion: Individuals with a low Vertebrae number (*Wervelgetal*) were not related to any other investigated variable. Average Vertebrae number (Wervelgetal) values were highest just before 1946, and in the beginning of the year. Lowest average Vertebrae number (Wervelgetal) values were observed when T anomalies were more extreme and in individuals with medium Age (*Winterringen*) (6 *Winterringen*).

3.3.2.4 The Amount-Landed-model

The final model tried to relate Amount landed to the fish characteristics. Bear in mind that Gilson and Gilis presumably noted this landing data arbitrarily, for example, only when catches were extraordinary high. The results of this sort of data should therefore be interpreted with caution. The model with the corresponding output and representation is respectively shown below and in Figure S 5 and Figure 11.

$$log10(Amount\ Landed) \sim Year + Day.in.the.year + AMO + T\ anomalies + random(Fishing\ area)$$

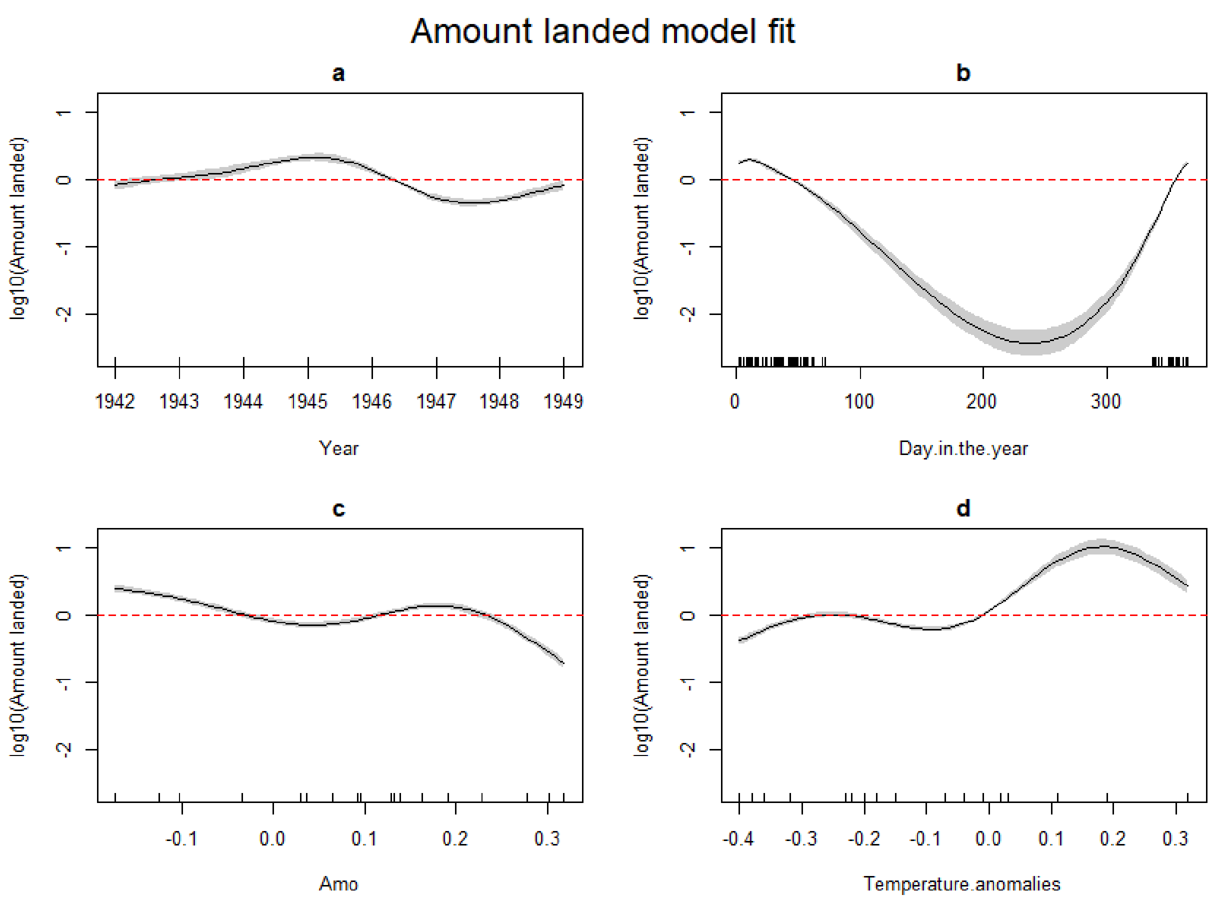

Figure 11: Representation of the Amount landed-model. With all the individuals included. Y-axes represent derivatives, with the red dotted line indicating the line of 'no effect'. Positive Y values mean a positive effect of the response variable (X-axis) on the predictor variable (amount landed), negative Y values mean negative effects on the predictor variable.

All explanatory variables in the model were significant. The Amount landed model showed better outcomes when the predictor variable was log10 transformed. An optimum effect on the Amount landed was observed around year 1945 (Figure 11a, $p = 2.8e-5$). This doesn't correspond with the explorative plot (Figure 2) which showed 2 optima in the study period. This may be due to the fact that other variables fluctuate over the years, with different effects on the amount of fish landed (for example AMO or T anomalies are chanceful). The observed wave-formed trend can indicate cyclicity.
Seasonal differences were also significant (Figure 11b, $p < 2e-16$), but need to be interpreted with caution, because no data is available throughout spring, summer and fall. We do see positive effects on the Amount landed in the fishing season, with an optimum in January. This corresponds nicely with the data explorative plots (Figure 3), where January had the highest landings.
More extreme and negative AMO values have a positive effect on Amount landed. Positive values have negative effects on Amount landed, except between AMO values of 0.1 and 0.2, the effect is positive again (Figure 11c, $p < 2e-16$).
Overall, higher T anomalies have a higher effect on Amount landed, with a negative effect when T anomalies drop below the zero baseline (Figure 11d, $p < 2e-16$).

➔ Main conclusion: According to the model, highest increases in Amount landed occurred in 1945 and in January of each year. The effects of AMO and T anomalies on the Amount landed are rather complicated, with increases in landings when AMO values are negative or in the range of 0.1 to 0.2, and when T anomalies are positive.

4 Analysing the long-term trends from ICES data and influencing factors in herring landing data

After analysing the dataset from Gilson and Gilis, curiosity rose about the long-term trends in herring landings data. How does the story of the 1940s fits in the bigger picture of the 20th century? Long term trends in herring landings data were analysed, together with some abiotic variables (including AMO and T, which were also tested directly against the Gilis landings data, but also Salinity, pH…) which might explain variation in the herring landings data.

As a hypothesis, it's stated that the North Atlantic Oscillation and the Temperature anomalies, which significantly influenced the short-term landings data from Gilson, are also responsible for the long-term trends in herring landings data. Furthermore, we expect some abiotic variables to coincide with the AMO and T data (e.g. salinity changes due to differential inflow of water from the Atlantic Ocean) and as such also explain variability in the herring landing data.

4.1 Data acquisition and processing

First, different datasets of herring landing data were visualized to see which one was the most complete. Later on, several other datasets with environmental variables were also visualized to get an idea about data availability and to see already some extra trends. All the variables which could explain some variation in the herring landings data were merged into one data frame. This data frame was then used to generate a model (with the landings as predictor variable), on which ANOVA-tests could be applied.

Three sources of herring landings data were analysed: landings data from ICES, landings data from Belgium (HiFi data, VLIZ 2009) and the detailed dataset with all the information collected by Gilson and Gilis in the period 1942 - 1950. Only data from the Southern Bight of the North Sea, and Northern parts of the English Channel were selected. For the ICES landings data, this was equal to the FAO area IVc. FAO area IV (including all subdivisions, also IVc) was also included, but only when landings happened in Belgian harbours.

For the abiotic variables, Table S 1 shows which datasets were used, where the data was located in a specific map on the S-drive of the VLIZ (if needed, contact tutors), a reference code to the online data and which variables were used out of the dataset.

All these datasets consisted of the physical or chemical variable(s) with the correspondent dates and map coordinates. All map coordinates were approximately in the same range as of the herring landing data, so no selection was made on that. For each variable, the mean was calculated per year. As such resulting in the same resolution as the herring landing data.

There was also a dataset available with zooplankton data, but this study only focused in modelling the abiotic response variables on the Landing data.

4.2 Data exploration

The only data exploration performed was visualising the data over entire study period (20th century). Figure 12 shows that the ICES landing data was the most complete, so analyses were based on that dataset. The Gilis landings data nicely fits in the ICES landings data (Figure 12), with having also two clear peaks in the 1940's, but with lower amounts of kilograms (mind that the units on the graph are not the same, see legend).
The abiotic data was also visually presented, showing the lack of data of most variables over most of the study period (Figure S 6, Figure S 7, Figure S 8).

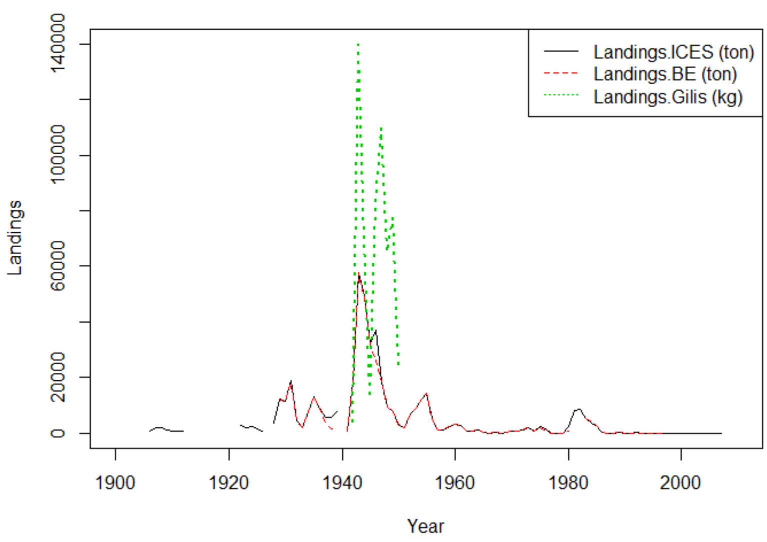

Figure 12: Comparison between the different landing datasets. Mind the legend, and that the units of the Gilson dataset are different than the others.

The ICES landings data was the most complete (Figure 12), so analyses were based on that dataset. The Gilis landings data nicely fits in the ICES landings data, with having also two clear peaks in the 1940's, but with lower amounts of kilograms (mind that the units on the graph are not the same, see legend).

4.3 Statistical tests

4.3.1 Testing correlations

A Pearson Correlation Test, which tested if the Gilson and Gilis data fits in the long-term data of the 20th Century by ICES, showed that they were not correlated (cor = 0.4629, p = 0.2095).

The correlation between Alkalinity and Salinity was also tested, because this was necessary to understand the model outputs (see 4.3.2). They proved to be significantly correlated (cor = -0.5392, p = 0.03806).

4.3.2 Modelling statistical relationships

Also here, different kinds of models were constructed in trying to explain the most variation in the long term herring landing data: Linear Models (LM) and Generalized Additive Models (GAM) (Zuur et al. 2009). No Linear Mixed Effects Models were chosen here, because we had no variables to include as random variables. Also, here, a manual model selection procedure was conducted for both types of models, which resulted in 2 best models, with lowest AIC criteria for each type of model. Then, they were compared in how much variation they explained, and which variables showed significant influences on the herring landing data. Logically, Salinity and Alkalinity were correlated, but if they were modelled separately in two GAMs, none were significant. If modelled together, only Salinity was significant, but this model was not valid because it included 2 correlated variables. Eventually, only the effect of Year was significant.

The output and representation of the final model is respectively presented in Figure S 9 and Figure 13.

$$ICES\ Landings \sim Year$$

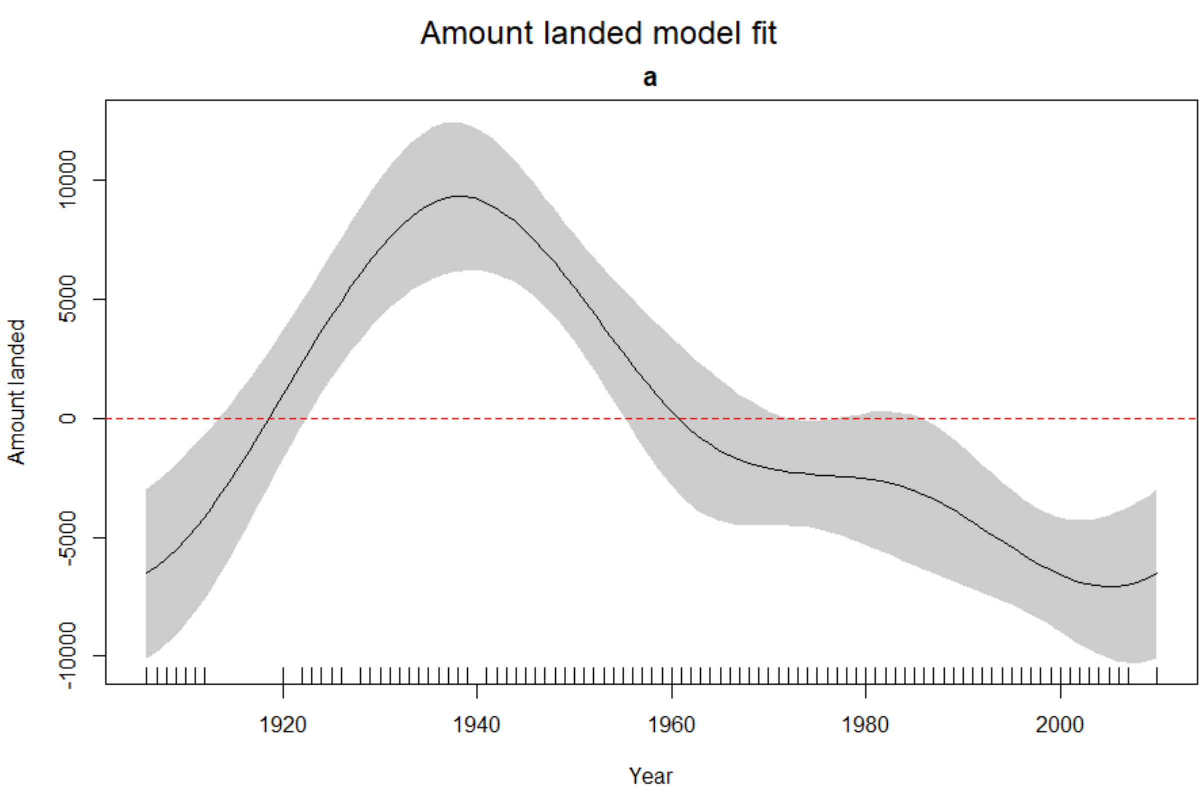

Figure 13: Representation of the Amount landed-model. With all the individuals included. Y-axes represent derivatives, with the red dotted line indicating the line of 'no effect'. Positive Y values mean a positive effect of the response variable (X-axis) on the predictor variable (amount landed), negative Y values mean negative effects on the predictor variable.

Remarkably, not the AMO nor the Temperature anomalies had a significant effect on the long-term ICES landing data of the herring.

Increases in the Amount landed were observed in the period 1920 to 1960, with an optimum in 1940 (Figure 13, Figure S 9, p = 5.11e-8). Before 1920 and after 1960, the Amount landed decreased.

5 General conclusions and recommendations for future research

Analysing population dynamics in historical settings proved to be quite complex. The following answers may be given to our research questions.

1. The individual fish characteristics were related to each other, with Age correlated to the Vertebrae number (model 3.3.2.3) and the condition index BMI (models 3.3.2.1, 3.3.2.2). BMI, Age and Vertebrae number showed differences over the years. The Vertebrae number also showed seasonal differences.
2. The changes in AMO and T anomalies were correlated with changes and BMI (model 3.3.2.1), while only the T anomalies were correlated with changes in the Vertebrae number (model 3.3.2.3).
3. The herring landing data in the 1940s showed to be correlated with AMO indices and T anomalies, but not with individual fish characteristics (model 3.3.2.4). However, the variation in Age seemed to be explained by the Amount landed (model 3.3.2.2).
4. The long-term trends in herring landing data showed increases during the period 1920-1960. Effects of Salinity and Alkalinity were not clear and should be further investigated in the future, also in relationship with AMO and T anomalies.

Furthermore, the correlation test showed that the Landing data from Gilson and Gilis doesn't correlate with the landing data from ICES, so the conclusions made about landing data in the Gilson and Gilis dataset cannot be scaled up or vice versa.

Some interesting conclusions could be formulated, but a lot more questions were raised than were answered, which is matter for further research. These questions include:

a) How is the herring population before the Belgian coasts influenced by activities in other part of the North Sea? For example, to which extent resulted the decrease in fishing activities in the entire North Sea during WW2 in elevated herring catches before Belgian coasts?
b) This study linked landing data and biotic data from the herring, only with abiotic data (AMO, T, Salinity…). The niche of the herring obviously doesn't stop there, and for a complete understanding of the population dynamics of the herring, biotic interactions with other species (especially zooplankton as their main food source, and also the predators of herring larvae and adults) should be incorporated.
c) Another question is what the precise relation is between the AMO and NAO, and how this affects the water column and movements in the North Sea and the inflow of water from the North Atlantic Ocean. And does this water bring along a lot of herring from the Atlantic? How

can we distinct those individuals from 'native' herring of the North Sea? The division in this study was quite arbitrarily, based on the median, and this was possibly not the best way.

d) Gilis (1942) noted that herring especially feed on zooplankton, and that phytoplankton can obscure their ability to feed by forming slimy substances in the gills. With phytoplankton blooms occurring more and more, this should be investigated too. Investigating the effect of phytoplankton blooms per se should not be the only goal. Also, the effect of lower concentrations of phytoplankton bloom should be considered.

When reading the notes from Gilson and Gilis, it was clear that he discovered already a lot. Although we have made considerable advances up to today, there's still a lot of work to be done, especially in a changing marine environment as it is happening in the 21st century (global warming, aquaculture, introduction of artificial hard substrates, altered water quality, Marine Spatial plans…). The use of new techniques such as the rapidly developing monitoring and DNA extraction techniques will allow researchers to improve current knowledge at an accelerated rate in the future. Thanks to the open data sources from the VLIZ and the ICES, this project was made possible, and highlights the importance of open data sources in general. Finally, a lot of the highlighted research questions are probably being investigated now (this project didn't allow time for an extensive literature study), but only the integrated approach of all of the research groups working together will allow the fast gaining of knowledge, which is necessary for the sustainable use of the ecosystem services provided by *Clupea harengus*.

6 Acknowledgements

I'd like to thank Michiel Vandeguchte (VLIZ – Director research department) for the great opportunity for allowing me to participate in this project. Also, many thanks to my tutors Gert Everaert and Ann-Katrien Lescrauwaet, who taught me new experiences in the scientific thinking and the execution of the analyses in R.

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8 Supplementary material

8.1 Tables

Table S 1: Variables in the original dataset from Gilson and Gilis (called 'Gilis') with corresponding meaning (explanation) and units and values

Variables in Gilis original	Explanation	Units	Values
Year	The year of landing	yyyy	1942 - 1950
month	The month of landing	mm	9,12,1,2,3,4
data	The specific date of landing	dd-mm-yyyy	1-31
species	Clupea harengus		Clupea harengus
series	Several series were landed on a day, this indicates which one	#	1-29
Fishing area code	Code for which marine area the fish were caught	factor	0-12 (See Table S2)
vessel name	Code name of the vessel which caught the fish	factor	…
fishing gear	The fishing gear used to catch the fish	factor	bordentreil/haringtreil/garnaalkor/kor
amount of fish caught or landed	The amount of fish landed that day	kg	300 -73 000
individual number	In each series, they selected a couple of individuals min. 25, this number gives a specific number to each of the fish sampled	#	1 - 25 or more up to 119
Length	The length of the fish	mm	172 - 330
Weight	The weight of the fish	g	35 - 210
gender	The gender of the fish	factor	m/f
Maturity level	The level of maturity of the fish	factor	I-VIII
vet 1/2	Fat content of the individuals	factor	0 = without fat, 1 = some fat, + = a lot of fat, M = highest fat
Wervelgetal	The amount of vertebrae	#	54 - 61
Winterringen	The amount of winterrings counted on the scales of the fish (= proxy for age)	#	0 - 13; + = >9, ill. = illegible
Maaginhoud vereenvoudigd	The contents of the stomach	factor	0-12 (See Table S3)
Percentage maaginhoud gevuld	The percentage filled in the stomach scaled to 1	#	0-1
Halswervels	Amount of vertebrae in the neck	#	22-28

K2	Unknown and excluded	?	13-19
L1	Unknown and excluded	?	64-168

Table S 2: Summary of all datasets used in this study with reference to the map in the S-drive of the VLIZ, file names, correspondent time spans and the variables used. Values in red proved to have no data, or were overlapping with other data (e.g. T, DOXY), and were thus excluded from the analysis.

Map on S-drive	File name	Download link	Timespan	Variables
Ijle haring data	Copy of ijleharing_databank_Definitief	?	1942-1950 (year + month + day)	See Table S 1Table S 1: Variables in the original dataset from Gilson and Gilis (called 'Gilis') with corresponding meaning (explanation) and units and values
ICES data on landings in europe	1903-1949_Landings ICES_1950-2010	Link	1903-2010 (year + month)	Landings (tons) + a lot more…
Dissolved Oxygen data	DATA_4wzml5u44pkpdztywtwyslcx	Link	1903-2016 (year + month)	DOXY (ml/l)
NAO	AMO data	?	1856-2017 (year + month)	AMO
Nitrate data	DATA_4wzml5u44pkpdztywtwyslcx2_nitra	Link	1960-2016 (year + month)	NITR (µmol/l)
pH data	DATA_4wzml5u44pkpdztywtwyslcx_pH	Link	1925 + 1968-2016 (year + month)	pH
Temperature and salinity data	BelgianHistTemp&Sal_merged T & Sal & many more	Link	1903-1965 (year + month)	T, Sal (PSU), Chlor, DOXY (ml/l), Alkalinity, Turbidity,

				Temp Air (°C), Si (mg/m^3), N-NO2 (mg/m^3), Ptot (mg/m^3)
Temperature anomalies	Global temperature anomolies as from data_giss_nasa_govgistemp	?	1880-2017	T anomalies

Table S 3: Showing the inconsistent values in the Gilis dataset and in which values they were replaced.

Variable	**Value**	**Replacement**
Amount of fish caught or landed	samen 10000 kg	10000
	3000 - 5000 kg	4000
	6000 en 1800	7800
	2000-2500 kg	2250
	72 vaartuigen	NA
	2500 - 3000 - 4000	3250
	no data	NA
Winterringen	ill.	NA
	0	NA
	+ (means more than 9)	11
Wervelgetal	0	NA

Table S 4: Explanation of the fishing area codes mentioned in the Gilis dataset

Fishing area code - Value	**Explanation**
no data	no data
1	Knokke - Zeebrugge
2	Wandelaarbank
3	Zeebrugge - De Haan
4	De Haan - Bredene - Oostende
5	Stroombank
6	Wenduine bank
7	Ravelingenbank
8	oostende bank
9	Mariakerke - Middelkerke
10	Middelkerke - Nieuwpoort
11	Nieuwpoort - De Panne
12	Broersbank
13	De Panne - Duinkerke

14	Westhinder zandbank
15	Traepegeer zandbank
16	Duinkerken - Calais
17	Boei HK. 2
18	Boei HK.1
19	Boei NF. 9
20	Boei NF. 7
21	Oost Dyck
22	O.D.4
23	O.D.2
24	Belgische kust, niet gedefinieerd waar precies

Table S 5: Explanation of the stomach content values (Maaginhoud vereenvoudigd) mentioned in the Gilis dataset

Maaginhoud vereenvoudigd - Value	**Explanation**
0	leeg
1	gevuld, onbekend waarmee
2	copepoden
3	Gobius minutus
4	Visei
5	Vislarve
6	copepoden + vislarve
7	garnaal
8	schubben
9	schizopoden
10	jonge haring
11	copepoden + visei
12	garnaal + zoetemondjes
no data	no data

Table S 6: Yearly differences in Length, age (Winterringen), BMI, amount landed and wervelgetal

Differences over the years									
Length	Kruskal-Wallis chi-squared = 362.15, df = 8, p-value < 2.2e-16								
	Pairwise comparisons using Wilcoxon rank sum test								
		1942	1943	1944	1945	1946	1947	1948	1949
	1943	**0.0196**	-	-	-	-	-	-	-
	1944	**5.70E-06**	0.407	-	-	-	-	-	-
	1945	1	0.3208	**9.00E-05**	-	-	-	-	-
	1946	**5.30E-13**	**2.20E-09**	**2.00E-06**	**6.80E-15**	-	-	-	-
	1947	**2.00E-16**	**2.00E-16**	**8.00E-14**	**2.00E-16**	0.6163	-	-	-

	1948	**2.00E-16**	**2.00E-16**	**2.00E-16**	**2.00E-16**	**0.0176**	1	-	-
	1949	**2.00E-16**	**1.70E-15**	**2.30E-10**	**2.00E-16**	1	1	0.3148	-
	1950	**6.40E-06**	**0.0285**	0.9443	**1.90E-06**	1	**0.0041**	**7.00E-05**	0.0977
Winterringen	Kruskal-Wallis chi-squared = 238.11, df = 8, p-value < 2.2e-16								
	Pairwise comparisons using Wilcoxon rank sum test								
		1942	1943	1944	1945	1946	1947	1948	1949
	1943	**9.00E-05**	-	-	-	-	-	-	-
	1944	**2.00E-16**	**1.30E-10**	-	-	-	-	-	-
	1945	**1.90E-14**	**8.70E-07**	1	-	-	-	-	-
	1946	**1.40E-09**	**0.00056**	1	1	-	-	-	-
	1947	**2.00E-16**	**3.40E-13**	**0.00061**	**0.00486**	**0.00349**	-	-	-
	1948	**2.00E-16**	**2.00E-16**	**1.90E-10**	**4.00E-09**	**9.50E-10**	0.26986	-	-
	1949	**1.50E-11**	**0.00028**	1	1	1	0.23891	**2.90E-07**	-
	1950	**0.0007**	1	1	1	1	**0.00378**	**8.60E-08**	1
BMI	Kruskal-Wallis chi-squared = 807.92, df = 8, p-value < 2.2e-16								
	Pairwise comparisons using Wilcoxon rank sum test								
		1942	1943	1944	1945	1946	1947	1948	1949
	1943	**2.80E-09**	-	-	-	-	-	-	-
	1944	**1.30E-15**	0.305	-	-	-	-	-	-
	1945	**2.00E-16**	**0.0092**	1	-	-	-	-	-
	1946	**2.00E-16**	**0.0078**	1	1	-	-	-	-
	1947	**2.00E-16**	0.0876	1	1	1	-	-	-
	1948	**2.00E-16**	**9.80E-05**	1	1	1	1	-	-
	1949	0.3324	**1.60E-10**	**2.00E-16**	**2.00E-16**	**2.00E-16**	**2.00E-16**	**2.00E-16**	-
	1950	**1.20E-06**	**2.00E-16**	**2.00E-16**	**2.00E-16**	**2.00E-16**	**2.00E-16**	**2.00E-16**	**2.00E-16**
Amount landed	Kruskal-Wallis chi-squared = 561.13, df = 8, p-value < 2.2e-16								
	Pairwise comparisons using Wilcoxon rank sum test								
		1942	1943	1944	1945	1946	1947	1948	1949
	1943	**0.00015**	-	-	-	-	-	-	-
	1944	**0.00016**	**5.90E-05**	-	-	-	-	-	-
	1945	**1.40E-07**	**2.00E-16**	**2.00E-16**	-	-	-	-	-
	1946	1	**2.00E-16**	**2.00E-16**	**2.00E-16**	-	-	-	-
	1947	1	**5.10E-15**	**0.00278**	**3.10E-13**	**0.00019**	-	-	-
	1948	**0.00909**	**2.00E-16**	**2.00E-16**	1	**9.10E-13**	**2.00E-16**	-	-
	1949	1	**2.00E-16**	**2.10E-12**	**2.00E-16**	**0.00111**	1	**2.00E-16**	-
	1950	1	**2.00E-16**	**2.00E-16**	**0.00676**	1	**3.40E-05**	**2.00E-16**	**5.90E-07**
Wervelgetal	Kruskal-Wallis chi-squared = 14.314, df = 8, p-value = 0.07395								

	Pairwise comparisons using Wilcoxon rank sum test								
		1942	1943	1944	1945	1946	1947	1948	1949
	1943	1	-	-	-	-	-	-	-
	1944	1	1	-	-	-	-	-	-
	1945	1	1	1	-	-	-	-	-
	1946	1	1	0.171	1	-	-	-	-
	1947	1	1	1	1	1	-	-	-
	1948	1	1	1	1	1	1	-	-
	1949	1	1	1	1	1	1	1	-
	1950	1	1	**0.028**	1	1	1	1	1

Table S 7: Seasonal differences in length, age (Winterringen), BMI, amount landed and wervelgetal

Seasonal differences						
Length	Kruskal-Wallis chi-squared = 243.11, df = 5, p-value < 2.2e-16					
	Pairwise comparisons using Wilcoxon rank sum test					
		1	2	3	4	9
	2	0.71682	-	-	-	-
	3	**2.00E-16**	**2.80E-12**	-	-	-
	4	**1.60E-07**	**1.50E-06**	**0.00097**	-	-
	9	**2.00E-16**	**2.00E-16**	**2.00E-16**	**8.80E-09**	-
	12	1	0.05005	**2.00E-16**	**1.50E-06**	**2.00E-16**
Winterringen	Kruskal-Wallis chi-squared = 142.85, df = 4, p-value < 2.2e-16					
	Pairwise comparisons using Wilcoxon rank sum test					
	ERROR: NOT ENOUGH OBSERVATIONS					
BMI	Kruskal-Wallis chi-squared = 216.89, df = 5, p-value < 2.2e-16					
	Pairwise comparisons using Wilcoxon rank sum test					
		1	2	3	4	9
	2	**0.045**	-	-	-	-
	3	**3.00E-13**	**1.60E-07**	-	-	-
	4	**2.20E-10**	**1.10E-09**	**1.20E-07**	-	-
	9	**3.00E-10**	**2.90E-12**	**1.40E-15**	**9.80E-09**	-
	12	**9.80E-05**	**6.30E-12**	**2.00E-16**	**1.70E-11**	**2.40E-08**
Amount landed	Kruskal-Wallis chi-squared = 821.72, df = 3, p-value < 2.2e-16					
	Pairwise comparisons using Wilcoxon rank sum test					
	ERROR: NOT ENOUGH OBSERVATIONS					
Wervelgetal	Kruskal-Wallis chi-squared = 35.248, df = 5, p-value = 1.342e-06					

	Pairwise comparisons using Wilcoxon rank sum test					
		1	2	3	4	9
	2	1	-	-	-	-
	3	1	1	-	-	-
	4	1	1	1	-	-
	9	1	0.763	1	1	-
	12	**4.50E-05**	**7.80E-06**	**0.046**	1	1

Table S 8: Differences in fish characteristics: correlation tests

Differences in fish characteristics						
Comparison	**Test**				**Correlation**	**p-value**
Length - Weight	Pearson's product-moment correlation				0.9045509	**2.20E-16**
BMI - Weight	Pearson's product-moment correlation				0.2058998	**2.20E-16**
BMI - Length	Pearson's product-moment correlation				-0.2147512	**2.20E-16**
BMI - Winterringen	Pearson's product-moment correlation				-0.1463491	**2.20E-16**
BMI - Wervelgetal	Pearson's product-moment correlation				-0.02350544	0.05588
BMI - Maturity level	Kruskal-Wallis chi-squared				77.201	**1.351E-14**
	Pairwise comparisons using Wilcoxon rank sum test					
		I	II	IV	V	VI	VII
	II	1	-	-	-	-	-
	IV	1	1	-	-	-	-
	V	0.89527	1	1	-	-	-
	VI	**0.00038**	**0.00578**	1	1	-	-
	VII	1	1	1	0.68436	**0.000037**	-
	VIII-II	**0.001**	0.44813	0.62433	0.06502	**2.1E-07**	**0.02983**
Comparison	**Test**				**Correlation**	**p-value**
Length - Wervelgetal (females)	Pearson's product-moment correlation				0.04637479	**0.00813**
Length - Wervelgetal (males)	Pearson's product-moment correlation				0.07826414	**6.53E-06**

Table S 9: Kruskal-wallis and Wilcoxon rank sum test comparing groups of fishing gear in values of length and BMI

Length - Fishing Gear	Kruskal-Wallis chi-squared = 59.91, df = 3, p-value = 6.144e-13			
	Pairwise comparisons using Wilcoxon rank sum test			
		bordentreil	garnaalkor	haringtreil
	garnaalkor	**6.90E-06**	-	-
	haringtreil	**3.30E-06**	**9.70E-07**	-
	kor	**0.00018**	**1.30E-05**	**0.03948**
BMI - Fishing Gear	Kruskal-Wallis chi-squared = 81.668, df = 3, p-value < 2.2e-16			
	Pairwise comparisons using Wilcoxon rank sum test			
		bordentreil	garnaalkor	haringtreil
	garnaalkor	**1.40E-09**	-	-

	haringtreil	**9.10E-07**	**5.10E-12**	-
	kor	1	**1.50E-08**	0.16

Table S 10: Correlations between AMO, T and BMI, Length

Correlations between AMO, T and BMI, Length			
Comparison	**Test**	**Correlation**	**p-value**
AMO - T	Pearson's product-moment correlation	0.2824387	**2.2E-16**
AMO - BMI	Pearson's product-moment correlation	0.03184853	**0.009502**
AMO - Length	Pearson's product-moment correlation	-0.092813	**3.669E-14**
AMO - Amount landed	Pearson's product-moment correlation	0.04370141	**0.004665**
T - BMI	Pearson's product-moment correlation	0.1328232	**2.2E-16**
T - Length	Pearson's product-moment correlation	-0.01042152	0.3962
T- Amount landed	Pearson's product-moment correlation	0.3162682	**2.2E-16**

8.2 Figures

```
> summary(bmimodel_Final)

Family: gaussian
Link function: identity

Formula:
log10(BMI) ~ s(Winterringen, k = 5) + s(Year, k = 5, bs = "cc") +
    s(Amo, k = 5) + s(Temperature.anomalies, k = 5)

Parametric coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.7945719  0.0007109    1118   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                          edf Ref.df     F  p-value
s(Winterringen)         2.180  2.636 50.31  < 2e-16 ***
s(Year)                 2.994  3.000 23.58 6.57e-16 ***
s(Amo)                  3.629  3.924 24.24  < 2e-16 ***
s(Temperature.anomalies) 3.307  3.705 12.36 3.91e-09 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.0976   Deviance explained = 10.2%
GCV = 0.0013246  Scale est. = 0.0013179  n = 2608
```

Figure S 1: R output from the BMI-model.

```
> summary(wrmodel_Final)

Family: gaussian
Link function: identity

Formula:
Winterringen ~ s(Year, k = 5) + s(BMI, k = 5) + s(Maturity.numeric,
    k = 5) + s(log10(amount.of.fish.caught.or.landed), k = 5)

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  5.72753    0.05861   97.73   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                          edf Ref.df     F  p-value
s(Year)                                 3.284  3.728 18.38 1.69e-12 ***
s(BMI)                                  3.819  3.982 35.44  < 2e-16 ***
s(Maturity.numeric)                     1.000  1.000 13.79 0.000211 ***
s(log10(amount.of.fish.caught.or.landed)) 2.384  2.911  4.43 0.003471 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.118   Deviance explained = 12.3%
GCV = 6.1157  Scale est. = 6.076     n = 1769
```

Figure S 2: R output from the Age model (=Winterringen model)

```
> summary(wervelmodelH_Final);plot(wervelmodelH_Final)

Family: gaussian
Link function: identity

Formula:
Wervelgetal ~ s(Year, k = 5) + s(Day.in.the.year, k = 5) + s(Temperature.anomalies,
    k = 5) + s(Winterringen, k = 5) + s(amount.of.fish.caught.or.landed,
    k = 5)

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) 57.13741    0.01159    4931   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                    edf Ref.df      F  p-value
s(Year)                           1.000  1.000  8.261 0.004136 **
s(Day.in.the.year)                1.000  1.000 13.971 0.000196 ***
s(Temperature.anomalies)          1.000  1.000  8.061 0.004614 **
s(Winterringen)                   1.000  1.000  2.349 0.125693
s(amount.of.fish.caught.or.landed) 3.511  3.832  2.457 0.029578 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.0208   Deviance explained = 2.82%
GCV = 0.13503  Scale est. = 0.13387   n = 997
```

Figure S 3: R output from the Amount of vertebrae model (= Wervelgetal model). With only individuals with high amount of vertebrae included.

```
> summary(wervelmodel_Final);AIC(wervelmodel_Final);plot(wervelmodel_Final)

Family: gaussian
Link function: identity

Formula:
Wervelgetal ~ s(Winterringen, k = 5) + s(Day.in.the.year, k = 5) +
    s(Temperature.anomalies, k = 5)

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) 56.59202    0.01316    4301   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                         edf Ref.df      F  p-value
s(Winterringen)            1      1  3.514   0.0610 .
s(Day.in.the.year)         1      1 37.113 1.27e-09 ***
s(Temperature.anomalies)   1      1  3.204   0.0736 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.0141   Deviance explained = 1.52%
GCV = 0.45222  Scale est. = 0.45153   n = 2608
[1] 5333.508
```

Figure S 4: R output from the Amount of vertebrae model (= Wervelgetal model). All individuals are included.

```
> summary(landedmodel_Final);anova(landedmodel_Final)

Family: gaussian
Link function: identity

Formula:
log10(amount.of.fish.caught.or.landed) ~ s(Year, k = 5, bs = "cc") +
    s(Day.in.the.year, k = 5, bs = "cc") + s(Amo, k = 5) + s(Temperature.anomalies,
    k = 5) + fishing.gear + Fishing.area.code

Parametric coefficients:
                        Estimate Std. Error t value Pr(>|t|)
(Intercept)              5.07753    0.16770  30.277  < 2e-16 ***
fishing.gearharingtreil -0.88773    0.17589  -5.047 4.96e-07 ***
Fishing.area.code4      -0.71410    0.06725 -10.618  < 2e-16 ***
Fishing.area.code5      -0.75746    0.07501 -10.098  < 2e-16 ***
Fishing.area.code6      -0.74407    0.09829  -7.570 6.05e-14 ***
Fishing.area.code7      -0.75641    0.08558  -8.839  < 2e-16 ***
Fishing.area.code8      -0.14813    0.07423  -1.996  0.04613 *
Fishing.area.code9      -0.53731    0.08462  -6.350 2.75e-10 ***
Fishing.area.code10     -0.61153    0.07199  -8.495  < 2e-16 ***
Fishing.area.code11     -0.57881    0.06602  -8.767  < 2e-16 ***
Fishing.area.code12     -0.14665    0.09141  -1.604  0.10885
Fishing.area.code13     -0.59179    0.07544  -7.844 7.59e-15 ***
Fishing.area.code14     -0.82534    0.08261  -9.991  < 2e-16 ***
Fishing.area.code15     -0.73547    0.09514  -7.730 1.81e-14 ***
Fishing.area.code16     -1.04826    0.09004 -11.642  < 2e-16 ***
Fishing.area.code17     -0.59644    0.07734  -7.712 2.08e-14 ***
Fishing.area.code21     -0.68259    0.09189  -7.428 1.72e-13 ***
Fishing.area.code22     -0.46104    0.12758  -3.614  0.00031 ***
Fishing.area.code24     -0.70462    0.23050  -3.057  0.00227 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
Approximate significance of smooth terms:
                          edf Ref.df       F p-value
s(Year)                 2.271      3   6.411 2.8e-05 ***
s(Day.in.the.year)      2.933      3 159.976 < 2e-16 ***
s(Amo)                  4.000      4  88.295 < 2e-16 ***
s(Temperature.anomalies) 4.000     4  40.667 < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.695   Deviance explained = 70.1%
GCV = 0.069661  Scale est. = 0.068379  n = 1750

Family: gaussian
Link function: identity

Formula:
log10(amount.of.fish.caught.or.landed) ~ s(Year, k = 5, bs = "cc") +
    s(Day.in.the.year, k = 5, bs = "cc") + s(Amo, k = 5) + s(Temperature.anomalies,
    k = 5) + fishing.gear + Fishing.area.code

Parametric Terms:
                  df     F  p-value
fishing.gear       1 25.47 4.96e-07
Fishing.area.code 17 34.87  < 2e-16

Approximate significance of smooth terms:
                          edf Ref.df       F p-value
s(Year)                 2.271  3.000   6.411 2.8e-05
s(Day.in.the.year)      2.933  3.000 159.976 < 2e-16
s(Amo)                  4.000  4.000  88.295 < 2e-16
s(Temperature.anomalies) 4.000 4.000  40.667 < 2e-16
```

Figure S 5: R output from the Amount landed model.

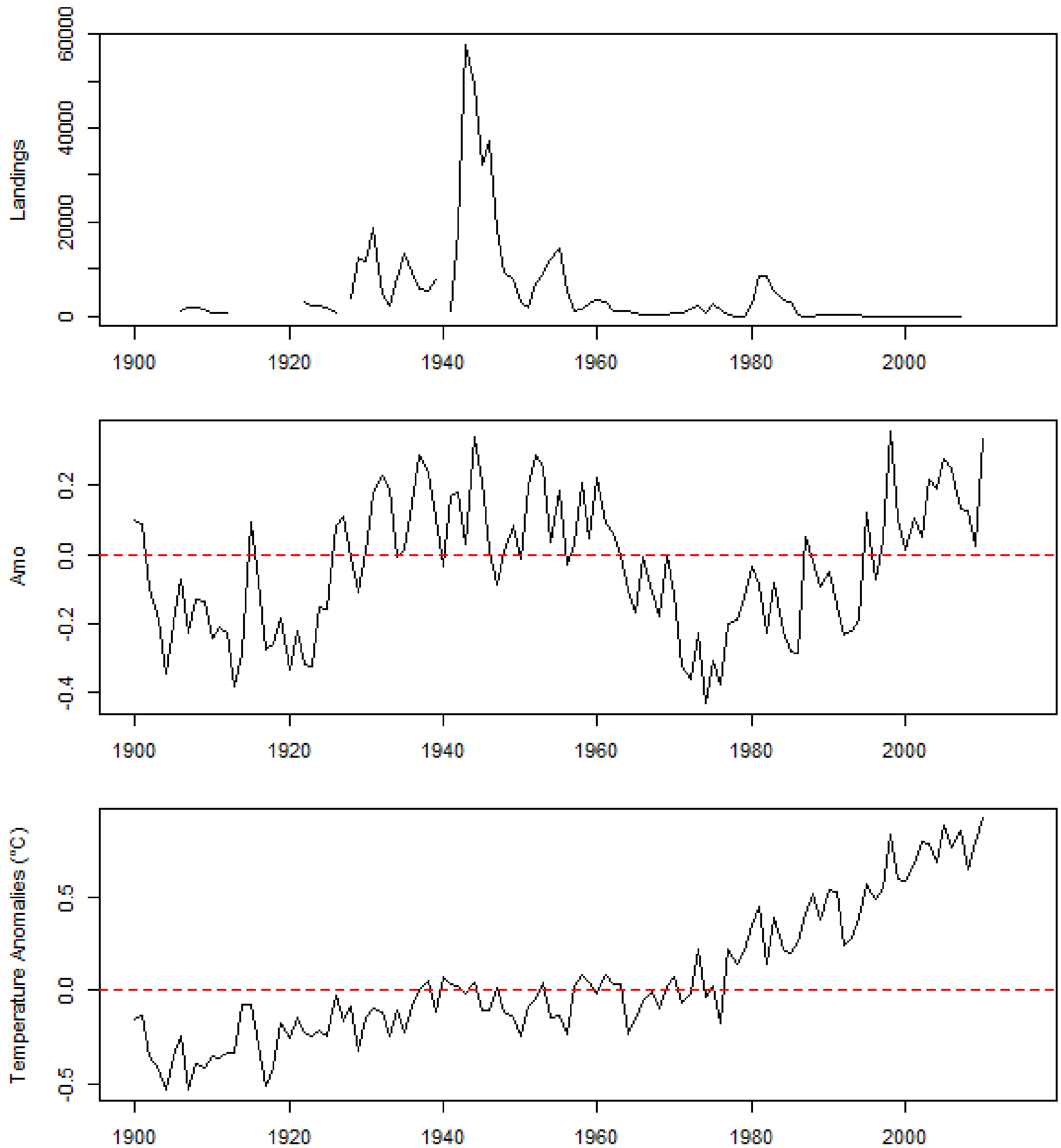

Figure S 6: Trends in the 20th century in the ICES landings data, AMO, and T anomalies.

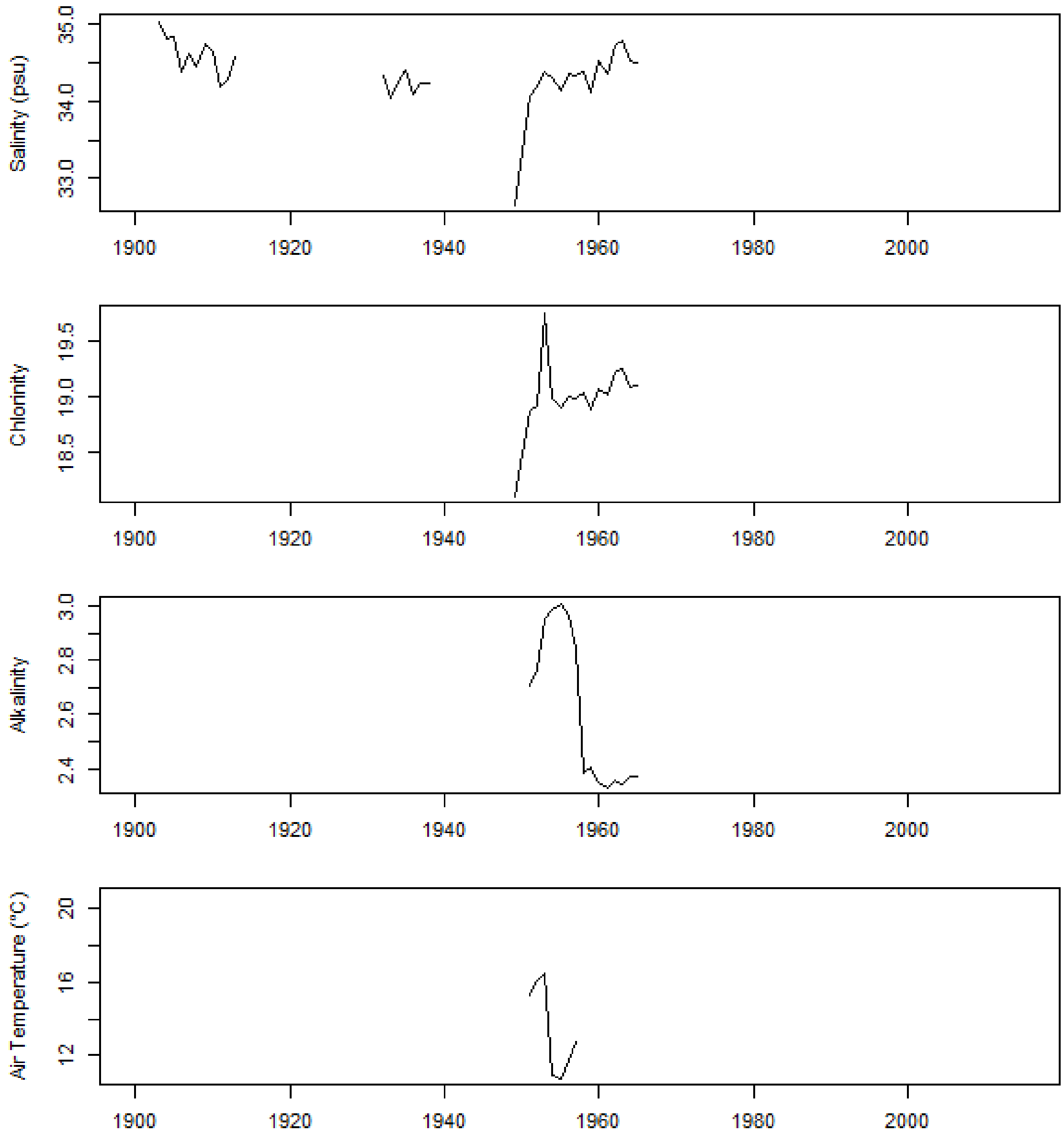

Figure S 7: Trends in the 20th century in the Salinity, Chlorinity, Alkalinity and Air Temperature.

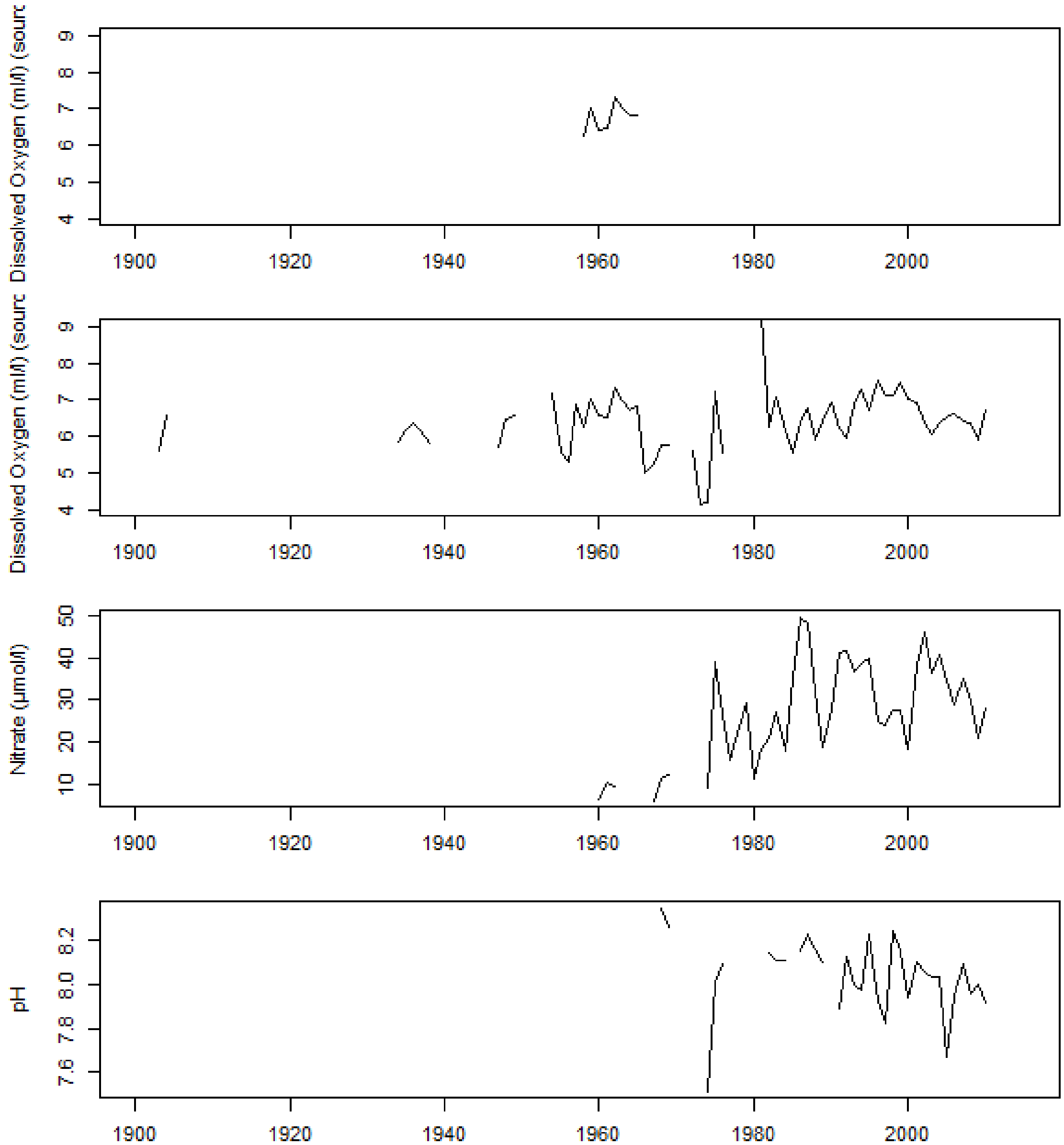

Figure S 8: Trends in the 20th century in the Dissolved Oxygen (from source 1), Dissolved Oxygen (from source 2), Nitrate and pH.

```
> summary(herringmodel_Final)

Family: gaussian
Link function: identity

Formula:
Landings.ICES ~ s(Year, k = 5, bs = "cc")

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   5003.1      838.4   5.968 4.79e-08 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
          edf Ref.df     F  p-value
s(Year) 2.83      3 13.91 5.11e-08 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.304   Deviance explained = 32.6%
GCV = 6.8174e+07  Scale est. = 6.5366e+07  n = 93
```

Figure S 9: R output from the Amount landed model on the long term ICES dataset with abiotic response variables.