Linking recruitment of autumn-spawning North Sea herring (*Clupea harengus*) to fall phytoplankton bloom phenology

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1. Abstract

Reliable estimates of recruitment are necessary to derive robust estimates of maximum sustainable yields for fish stocks around the globe. Accurately predicting recruitment would ultimately reduce the risk of bad fisheries management and following ecological and economic damages. The autumn-spawning North Sea herring (*Clupea harengus*) stock has fluctuated strongly over last century, and almost collapsed at the end of the 1970s. Prey availability, which is expected to be related to the autumn phytoplankton bloom, is regarded as one of the major factors determining herring larvae survivorship and recruitment. If certain characteristics of this bloom can be used to predict herring recruitment, these could be used to improve recruitment prediction models. In this study, chlorophyll a concentrations of the North Sea obtained from satellite imagery were used to investigate the link between herring recruitment and autumn phytoplankton bloom. A reliable relationship between these two variables could be used to predict herring recruitment up to one year in advance. While no relationships between indices of fall phytoplankton bloom timing, intensity, and initiation and recruitment were found, changes in the phenology of this bloom over the period 1998-2021 have been detected. The timing of the autumn bloom has shifted by approximately 5 weeks, from the end of November to the end of December. This change could have led to a trophic mismatch in other marine organisms of the North Sea.

2. Introduction

Predicting recruitment of fish stocks in an accurate and reliable way has been a primary research field in fisheries research for over a century (e.g. Hjort, 1994). Recruitment is one of the key variables used to derive the maximum sustainable yield (MSY) of fish stocks, which is used for the management of numerous fish stock around the globe (Thornson, 2022). Due to the vast number of biotic and abiotic factors that influence recruitment, and its extremely variable nature, unravelling which of these processes are the most relevant and could improve existing recruitment prediction models is extremely challenging. Furthermore, data on larval abundances and distributions, environmental variables, and recruitment time series are often insufficient and of low spatial and temporal resolution (Thornson, 2022). Luckily, technological advances, such as ocean colour remote sensing (OCRS), are continuously providing novel and more efficient ways of gathering environmental and hydrographic data, including chlorophyll concentrations (Platt et al., 2007; Zheng and DiGiacomo, 2017).

Autumn-spawning North Sea herring (*Clupea harengus*) is a highly ecologically and economically important species in the North Sea (ICES, 2022). Historically, it has been among the largest commercial fish stock in the world, with yearly catches surpassing 1 million tonnes (ICES, 2015). Primarily due to overfishing and changes in the hydrography of the North Sea (Corten et al., 1990) the stock has collapsed between the 1970s and 1980s (ICES, 2022). From a spawning stock biomass (SSB) approaching 4.5 million tonnes in the 1940s, it plummeted to merely 0.1 million tonnes in the 1970s (ICES, 2022). While the spawning stock has recovered, the recruitment continues to be low (Payne et al., 2009; ICES, 2022). Over the last 5 decades, numerous research efforts have aimed at identifying the most important drivers of herring recruitment (Ile and Sinclair, 1982; Cushing, 1990).

One of the leading recruitment hypotheses that has been extensively discussed and criticized is the Match-Mismatch Hypothesis (MMH) postulated by Cushing (1975, 1990). Cushing suggested that prey-availability during early life stages is crucial for a high larval survival and eventually for a successful recruitment (Cushing, 1975; Cushing, 1990). Therefore, a good spatial and temporal overlap between prey and fish larvae is expected to yield a strong recruitment and year class (Cushing, 1990). Since then, multiple research groups have tried to provide additional evidence supporting this hypothesis (Ferreira et al., 2023) or arguing against this hypothesis (Leggett and DeBlois, 1994). More recently, Ferreira et al. (2023) explored whether predator-prey spatio-temporal overlap explains variability in pelagic fish recruitment. They developed an overlap index to quantify the spatio-temporal overlap in prey and predator abundance and found that for North Sea autumn-spawning herring the MMH could explain over 20% of the variability in 1 year-olds (Ferreira et al., 2023). The authors explained that phytoplankton blooms can be linked to herring recruitment both directly and indirectly. Certain larger phytoplankton groups, such as diatoms, can be directly consumed by herring (Denis et al., 2016; Bils et al., 2022). While these prey items are generally not the food of choice of larval herring, they can significantly improve nutrition and survival of the larvae (Illing et al. 2015; Bils et al., 2022). On the contrary, numerous areas of the North Sea, including herring spawning ground such as the Dogger Bank (ICES, 1977), are dominated by small flagellates of <10 um, which can constitute >80% of the phytoplankton biomass (Nielsen et al., 1993). These are too small to be consumed by herring larvae which are mm long and can consume prey of and in size (Nielsen et al., 1993). However, these organisms can be consumed by microzooplankton, which in turn can be consumed by copepods (Bils et al., 2022). These small crustaceans constitute arguably the best source of food for fish larvae as their high lipid content (Jackson and Lenz, 2016). Following these observations, it would therefore be logical to assume that a high availability of these groups of phytoplankton would positively benefit larval survival by reducing risk of starvation.

In this project, ocean colour data from sentinel missions of the European Space Agency (ESA) has been used to test whether the phenological characteristics of the autumn phytoplankton bloom of the North Sea are significantly correlated to herring recruitment. The remote sensing data has been used to derive chlorophyll a concentration time-series (ESA, 2022). From this data, indices of initiation, intensity, and timing of the autumn phytoplankton bloom of the North Sea were calculated. Temporal trends in these indices were examined and discussed. Lastly, these indices were assessed as potential predictors of North Sea herring recruitment.

3. Methods

3.1 Satellite data

Satellite images taken by the sentinel expedition (sentinel-3) from the European Space Agency (ESA). This expedition has been conducted by for the GlobColour project and is available online through the Copernicus Marine Service (EU, 2023). The resolution of the data is approximately 4 km^2 grid cells of 0.0417° latitude and 0.0417° longitude. Since satellite imagery is heavily affected by cloud cover and other environmental variables, a vast number of missing datapoints were missing in the dataset. To reduce this problem, the Chl-a concentration was averaged for every 7-day week of the year (52 weeks during each year). Furthermore, the data was divided to derive a dataset for the western part of the North Sea, which was defined here as the area of the North Sea west of longitude 3° (Appendix, Figure 4). Time-series of average Chl-a values over the entire North Sea were then computed, from which the following phytoplankton phenology indices were derived and analysed as predictors of herring recruitment:

Table 1: Indices describing the intensity, initiation, and timing of the autumn phytoplankton bloom of the North Sea used in this study.

Index Description	Index of	Source
1st week above 5% above yearly median	Start of bloom	Ferreira et al. 2014
Autumn max Chl-a	Intensity	Ferreira et al. 2014
Autumn max Chl-a western NS	Intensity	Ferreira et al. 2014
Week at which autumn max is reached	Timing	Ferreira et al. 2014
Week at which autumn max is reached in western NS	Timing	Ferreira et al. 2014
Max weekly increment in Chl-a (autumn)	Productivity	Ferreira et al. 2014
Mean autumn Chl-a	Intensity	-
Mean autumn Chl-a western NS	Intensity	-
Week at which max weekly increment in Chl-a (autumn) is observed	Start of bloom	-

It is important to note that term "autumn" is defined here as the period from the start of August to the end of the year. While the index of the start of the bloom was taken from Ferreira et al. (2014), it was modified. Here, it is defined as the 1st week at which a value above 5% above the yearly median Chl-a is observed, without considering following weeks. The weekly increment in Chl-a was calculated as the difference between the value from week *i+1* and the value from week *i*, and corresponds to the weekly growth rate of the bloom.

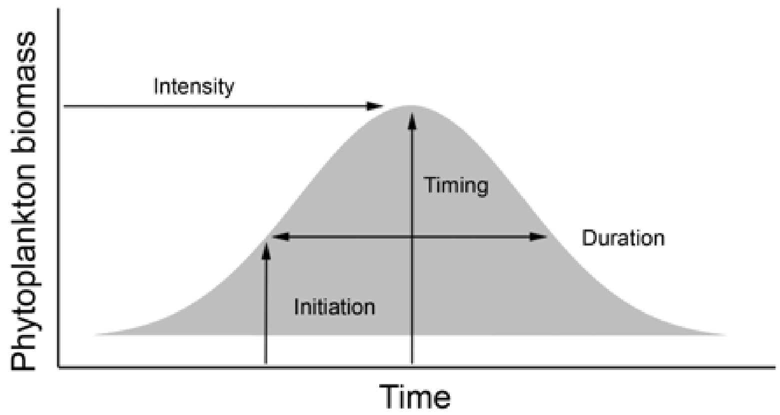

Figure 1: Major phenological characteristics of a phytoplankton bloom: initiation, intensity, timing, and duration. Taken from Platt et al. (2007).

3.2 Herring recruitment time-series

Time series of herring recruitment were downloaded from the ICES Stock Information Database (ICES, 2023). These herring recruitment estimates are given by ICES in thousands of year-olds. Therefore, to match the recruitment estimates with the corresponding SSB values that produced that recruitment, all recruitment values were shifted one year backwards to the year in which they were born. The natural logarithm of the recruitment index (Platt et al., 2007) was finally calculated as follows:

$$S = \ln\left(\frac{R}{SSB}\right)$$

, where R is the recruitment (thousands) and SSB (tonnes) is the spawning stock biomass.

3.3 Statistical analysis

Statistical analyses and data processing were carried out in the software R x64 version 4.2.2 from 31.10.2022 (Copyright (C) 2022 The R Foundation for Statistical Computing). The phytoplankton development throughout the individual years was modelled using General Additive Models (GAMs), constructed using the gam() function from the "VGAM" package (Yee, 2015), with a smoothened term of time (s(week)) as the only predictor variable. The resulting splined were used to re-calculate some of the previously described phytoplankton bloom indices which are particularly affected by small fluctuations (Appendix). This typology of statistical models was chosen here because development of Chl-a over the year is not linear, and GAMs are generally used to model non-linear effects.

Linear models were constructed using the lm() function to explore whether (i) the phytoplankton bloom indices have changed significantly though time and whether (ii) these indices are significantly correlated to the recruitment index of herring.

North Sea maps showing the distribution of Chl-a were created using the "simple feature" (sf) (Edzer Pebesma, 2018) and the "ggplot2" (Wickham et al., 2020) R packages. Landmass and countries were added using the "rnaturalearthdata" and the "rnaturalearth" (Massicotte et al., 2023) R packages.

4. Results

4.1 Distribution of phytoplankton

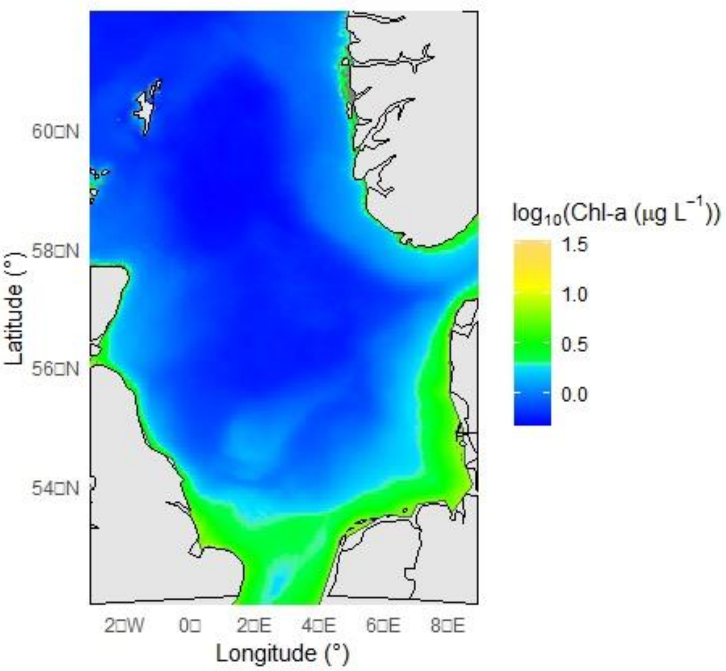

Figure 2: Logarithm of base 10 of the average Chla concentration (µg L-1) over the study period 1998-2021 plotted against latitude (x axis) and longitude (y axis).

The highest production in the North Sea is observed in the southern and south-western areas (Figure 1). A hotspot of primary production can be observed in the central North Sea, around the Dogger Bank. In addition, all coastal areas have very high chlorophyll concentrations, that tend to increase towards the coast.

4.2 Temporal trends in phytoplankton phenology

The mean Chl-a concentration averaged over the entire North Sea was found to have significantly increased over the period 1998-2021 for the months of August, September, October, November December (Figure 2; $F_{5,114}$=25.35, $p < 2.2 \cdot 10^{-16}$, $R^2 = 0.51$). This trend was relatively weak ($0.0083 \pm 0.0031\ y^{-1}$, $F_{5,114}$=25.35, $p = 0.01$), and the coefficient of this trend was not significantly different across the five months (Figure 3). While the Chl-a concentration was not different between the months of August, September, October, and November, the month of December showed consistently higher concentrations ($p = 1.5 \cdot 10^{-14}$, $F_{5,114}$=25.35).

The year 1999 stands out for having a very intense and early autumn phytoplankton bloom, compared to all other years (Figure 3b).

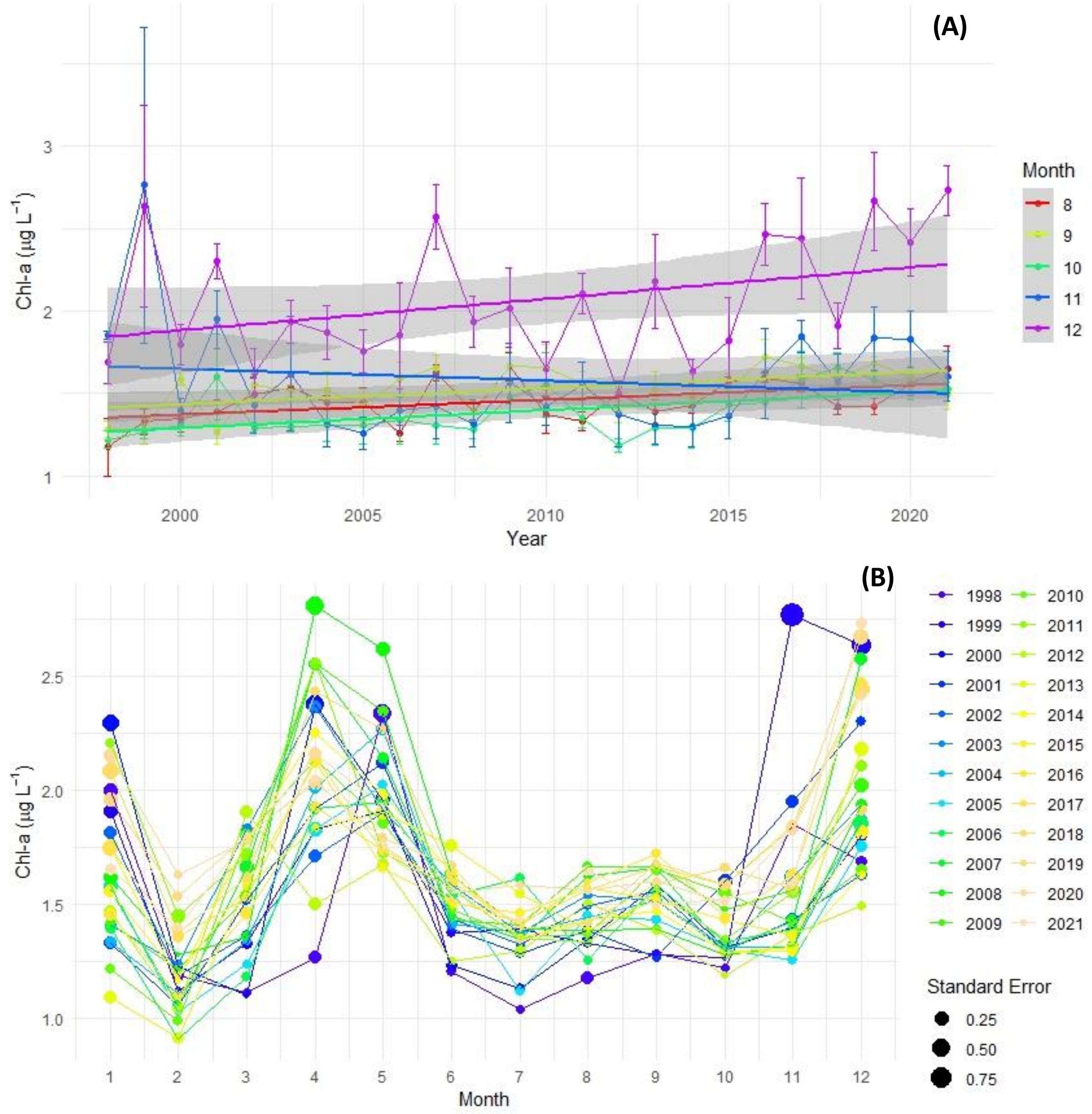

Figure 3: Chl-a concentration plotted as a function of time **(A)** for the 5 autumn months. Development of Chl-a over the course of the year for the 24 years of the time-series.

The timing of the North Sea autumn phytoplankton bloom was found to be significantly delayed over the period 1998-2021 by approximately 5 weeks (Figure 4; $F_{1,22}$=11.58, p-value=0.0026, R^2=0.32). The week number at which the fall maximum Chl-a concentration occurs has increased since 1998 at a rate of 0.2 ± 0.06 weeks y^{-1} (Figure 4a). The same trend was found when using the week number at which the autumn maximum modelled Chl-a is reached (Figure

3). I found a significant temporal trend. This indicator is observed about 5 weeks later compared to the end of the 20th century (Figure 4b). This trend was weakly significant ($F_{1,22}$=5.4, p-value=0.03, R^2=0.16). It is important to mention that the fall blooms probably progress during the start of the following year, since this indicator of the start of the bloom is often found right at the end of the year. In the graph of the measured Chl-a concentration, year 2002 stands out for having occurred particularly early in the year (Figure 4a). If this year is removed from the data, the relationship remains significant. On the other hand, for the plot of modelled Chl-a, year 2001 stands out for having an extremely early bloom (Figure 4b). In this case, if the year 2001 is removed from the data the relationship becomes not statistically significant. In fact, during 2002, no intense Chl-a peak is observed during the entire autumn (Appendix, Figure 1). No other indices of the start or timing of the bloom were not found to have changed significantly.

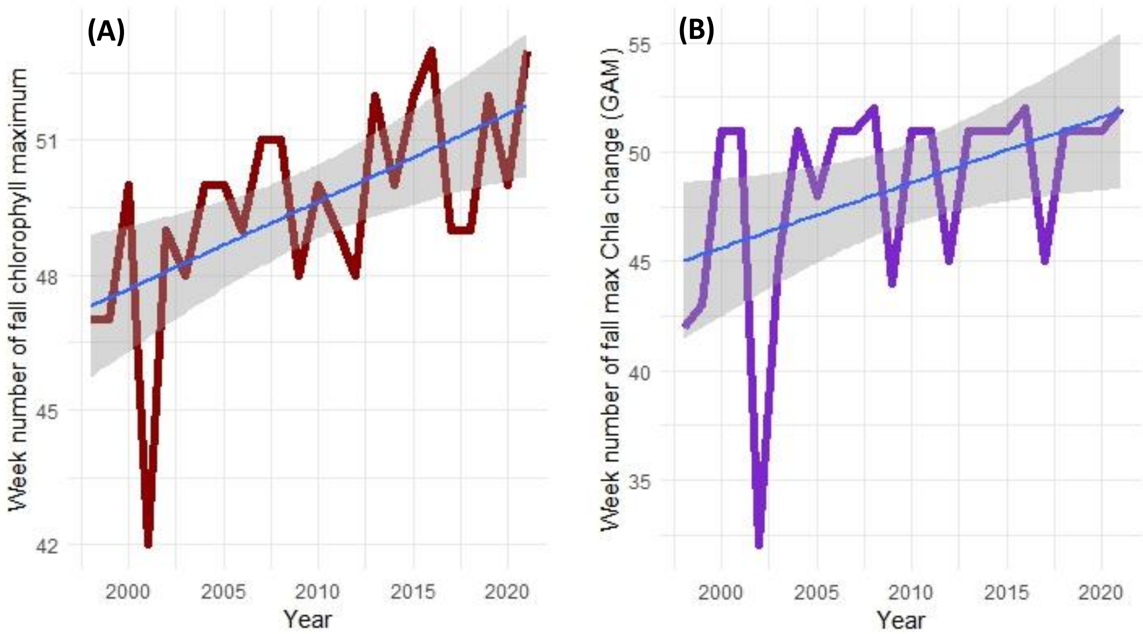

Figure 4: Week number at which the fall maximum chlorophyll a concentration of North Sea is observed **(A)**. Week number at which the modelled fall maximum chlorophyll a concentration of North Sea is observed **(B)**. The solid line indicates the trend over the study period 1998-2021 and the green lines indicate the 95% confidence interval.

4.3 Link to herring recruitment

Unfortunately, none of the examined bloom start, timing, and intensity indices were found to be significantly correlated with the herring recruitment index. Nevertheless, some important considerations can be made. Firstly, the year 1999 stands out, as it has a high value across all indices used and has a high associated recruitment index (Figure 5). Secondly, all indices have increased over the last 7 years, although no increase in the herring recruitment index is observed (Figure 5).

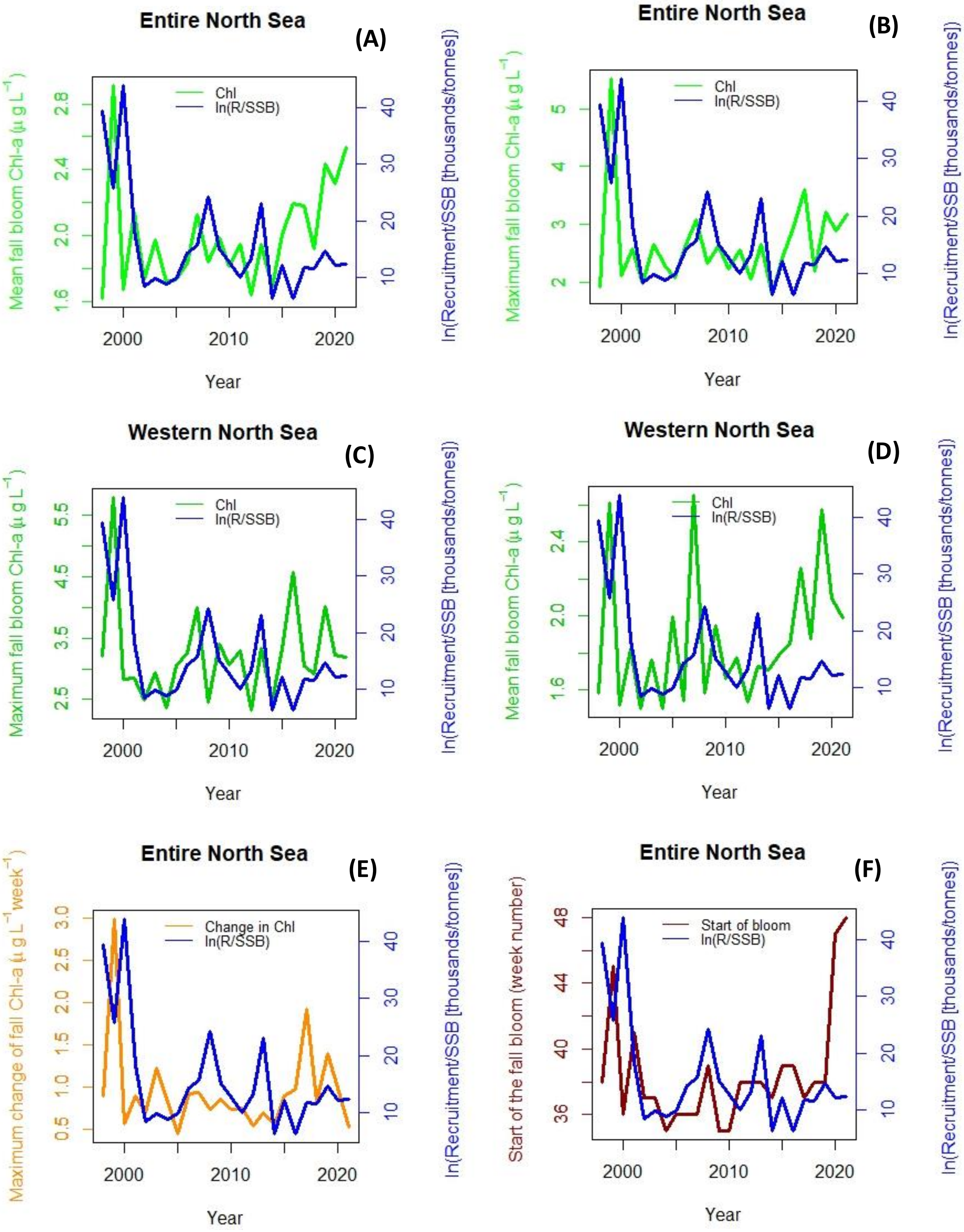

Figure 5: Time-series plots of the herring recruitment index for the entire North Sea and of examined phytoplankton bloom phenology indices.

5. Discussion

The goal of this study was to determine whether the phenological characteristics of the autumn phytoplankton bloom estimated from remote sensing methods, can be used to predict the recruitment of autumn-spawning North Sea herring. During the first part of this study, indices describing the timing and intensity of the North Sea autumn phytoplankton bloom where computed and temporal trends were examined. It was shown that over the study period 1998-2021, the timing of the bloom peak has shifted by over a month. In the last years of the time-series, the autumn Chl-a max was observed during the last week of the year (week 52). It could even be possible that this concentration was still increasing, and that the true bloom maximum occurred at the start of the following year (Appendix, Figure 1). Over the entire study period, Chl-a was consistently higher during the month of December compared to all other autumn months, and it was shown that monthly-average Chl-a has increased over time for the autumn months. Considering that this is a fairly large change in the timing of the autumn bloom, it is expected to have a string impact in the seasonality of zooplankton species, and eventually on the survival of fish larvae (Cushing, 1990). However, contrary to our expectations, no correlation to the herring recruitment index was found.

This was unexpected since there is a large body of evidence suggesting that many herring stocks, including the North Sea stock (Ferreira et al., 2023) are affected my match-mismatch dynamics. For example, recruitment of Baltic Sea herring has been suggested to be strongly driven by copepods availability during vulnerable larval stages (Illing et al., 2018). For this stock, high abundance of copepods at the right time can generate strong year classes (Illing et al., 2018). Vikebø et al. (2012) proposed that the Norwegian spring-spawning herring can also be affected by this mechanism. This stock follows a peculiar southwards and upstream migration pattern during the spawning season (Vikebø et al., 2012). It was shown that in these areas, a better overlap in herring larvae hatch time and phytoplankton bloom is possible, making it worth for the adults to invest energy and time to migrate to these areas and ensure a high larval survival (Vikebø et al., 2012). The authors therefore concluded that this behaviour originated due to this match-mismatch dynamics. Batten et al. (2016) found that diatoms and ciliates explained, respectively, 75% and 45% of the yearly variability in Pacific herring recruitment (Batten et al. 2016). It follows, that this stock is likely strongly dependent on match-mismatch dynamics. More recently, Ferreira et al. (2023) examined the spatio-temporal overlap of zooplankton, phytoplankton, and herring larvae in the North Sea and found that an index describing this overlap could explain 23% of the variability in herring recruitment. Considering these findings, it should have been expected to find a similar correlation in the present study.

On the contrary, evidence indicates recruitment of fish stock, even stocks belonging to the same species, can be driven by different dynamics, including predation (Bishop and Green, 2001; Kotterba et al., 2014), larval transport via currents to nurseries (Corten et al., 2013), temperature (Kristiansen et al., 2011; Corten et al., 2013), oxygen availability and salinity (Köster et al., 2005; Heikinheimo, 2008).

Early life stages are often more vulnerable to predation than adult life stages due to their size and limited physical abilities (Arula et al., 2022). In general, smaller organism have more potential predators than larger organism. Since North Sea herring spawn in shallow coastal and estuarine waters, where they lay their eggs on gravel or eelgrass, their eggs and larvae can be cannibalized (Corten et al., 2013) or consumed by other fishes (Kotterba et al., 2014), birds (Bishop and Green, 2001), and other animals. It was suggested that for some herring stocks, predation on early life stages can have strong implications. For example, glaucous-winged gulls (*Larus glaucescens*), may eat over a fourth of the total spawning deposition (Bishop and Green, 2001) and three-spine sticklebacks (*Gasterosteus aculeatus*) can consume up to 10% of the deposition (Kotterba et al., 2014). Stomach content analyses of multiple potential herring eggs and larvae predators could reveal important predator-prey interactions in the North Sea that could potentially explain the observed fluctuations in recruitment.

Another important factor affecting the survivorship of herring larvae is temperature. In fact, early life stages are thought to be more vulnerable to changes in environmental factors compared to adult life stages (Arula et al., 2022). Corten et al. (2013) suggested that temperature may be responsible for the low North Sea herring recruitments observed at the start of this century. Temperature and light regimes can determine the importance of match-mismatch dynamics across different latitudes, as a study focussed on Atlantic cod has concluded (Kristiansen et al., 2011). Since the rate at which ocean have been warming has increased over the last decades, it is reasonable to assume that it could have impacted herring recruitment dynamics. Furthermore, increasing temperatures have enabled species such as anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) to invade the North Sea (Payne et al., 2009). These new species may have impacted herring recruitment by feeding on herring larvae and eggs (Payne et al., 2009) or by competing against herring for food. If this this is the case, then further warming of the North Sea may exacerbate the poor conditions for herring recruitment.

Changes in hydrography can also affect herring recruitment. North Sea herring spawn mainly along the western coast of the North Sea, and in deeper locations such as around the Dogger Bank (ICES, 1977). The recruits are then transported by currents to the nursery areas in the German Bight Skagerrak, and Kattegat (Corten, 1990). This transport is crucial for their survival, and changes in the hydrography of the North Sea that influence this eastern current can have serious implications for the North Sea herring recruitment. In the 1970s a reduced inflow of Atlantic water from the northern end of the North Sea caused a weakening of this eastward transport. As a matter of fact, this event led to a low herring recruitment (Corten, 1990). Small-scale changes in current patters could thus be a possible explanation of a reduced recruitment success of the North Sea herring.

It must also be mentioned that the herring recruitment has been relatively low and constant over the last 20 years (Payne et al., 2009; ICES, 2015). This has resulted in a lack of stronger year classes over more recent years (Appendix, Figure 5). Without a large variance in the recruitment time-series, it is considerably more difficulty to unravel significant trends. Moreover, while a clear mismatch always leads to a poor recruitment, a good match can lead to both good and bad outcomes, as other factors can play an important role (Leggett and DeBlois, 1994). These two problems can make studies like the one presented here extremely challenging.

Another disregarded source of variability can come from spatial and population effects. In this study, the autumn-spawning North Sea herring was considered as one unit, since ICES provides only a singular recruitment estimate for the whole North Sea (ICES, 2015; ICES, 2022). However, this stock is constituted of distinct populations that spawn at different times and that contribute in different proportions to the total recruitment (ICES, 2022). In addition, the relative contribution of each of these sub-populations to the total recruitment is not constant over time (ICES, 2022). These subpopulations could be driven by affected differently by match-mismatch dynamics as well as other factors affecting recruitment. If this was the case, in order to unravel the effect of phytoplankton phenology on herring recruitment, it would be necessary to account for differences between the subpopulations.

Finally, it must be considered that remote sensing can have limitations (Zheng and DiGiacomo, 2017). Satellites can only measure what happens at the very surface of the oceans (Zheng and DiGiacomo, 2017). Depending on the turbidity, the water layer measured may only be few meters or less. It follows that if the vertical phytoplankton distribution in the water column is centred around Deep Chlorophyll Maxima (DCM) then it would be out of reach for remote sensing methods. This could lead to a underestimation of chlorophyll concentrations.

6. Conclusion

It is logical to assume that there is a link to some degree at some level between phytoplankton phenology and herring recruitment. However, disentangling all the factors affecting fish recruitment and determining the relative effect of each of them can be extremely challenging. This study failed at discovering a useful relationship between the fall phytoplankton bloom and herring recruitment and highlights the difficulty of relating environmental variables to fish recruitment.

While this study failed it primary goals, it provided interesting evidence suggesting that the timing of the fall bloom in the North Sea has significantly shifted towards the end of the year by 5 weeks over the study period 1998-2021. Future efforts should investigate whether this change has negatively affected other marine species in the North Sea.

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8. Appendix

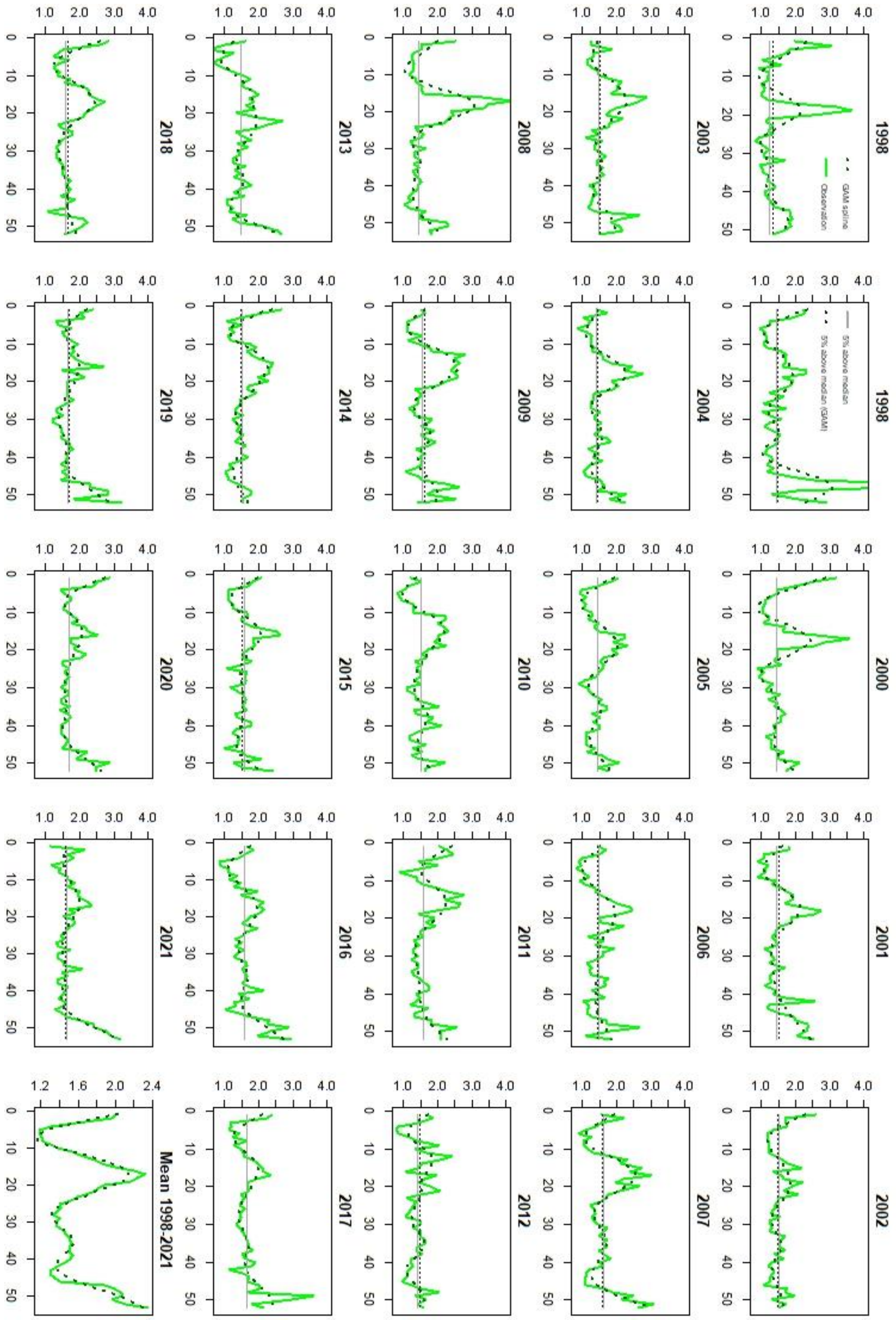

Figure 1: Chl-a and GAM modelled Chl-a development over the year for all 24 years of the time-series. The last plot shows the Chl-a concentrations averaged over the entire study period.

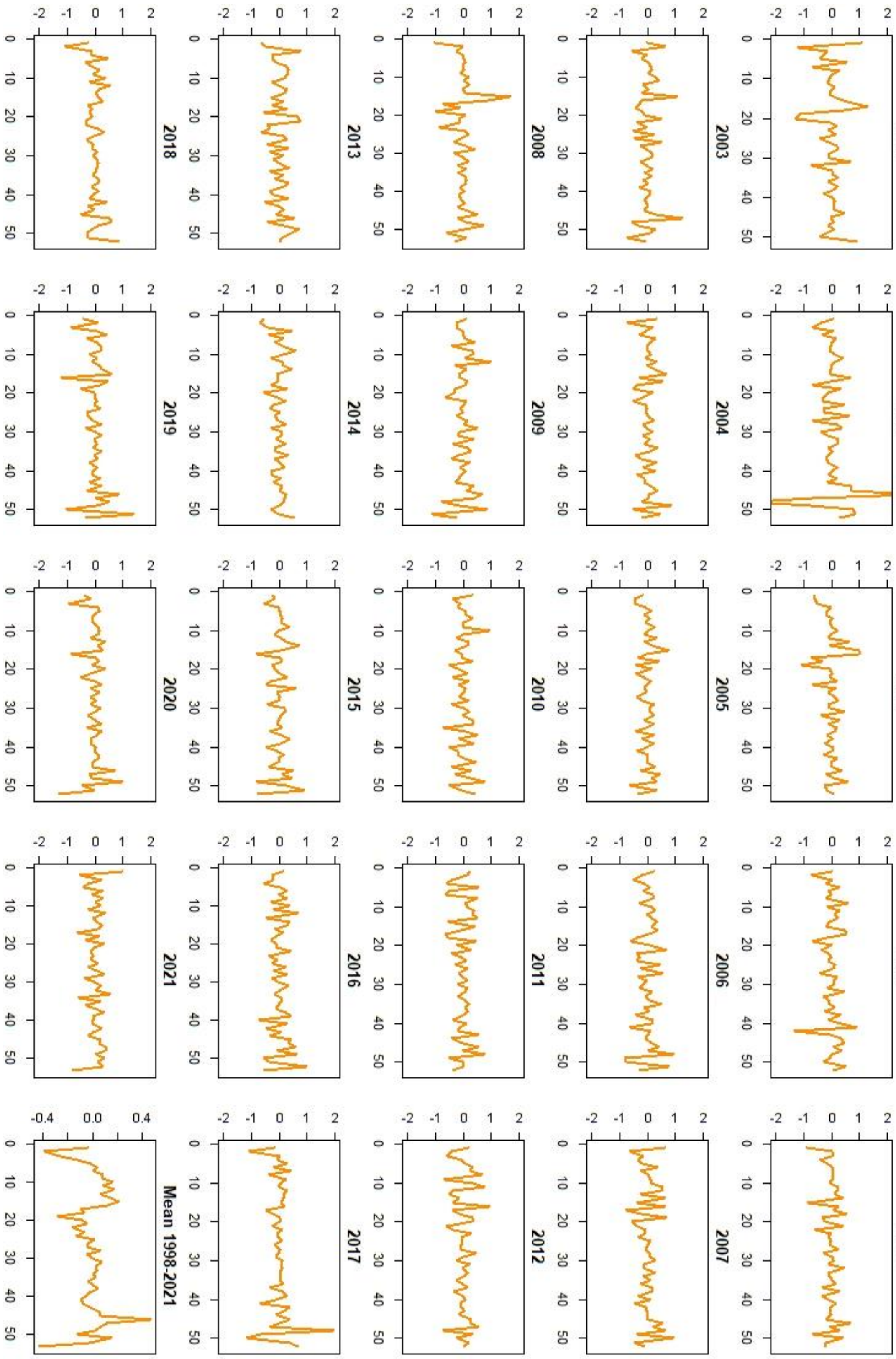

Figure 2: Change in Chl-a concentration plotted as a function of week number for all 24 years of the time-series and averaged over the entire study period.

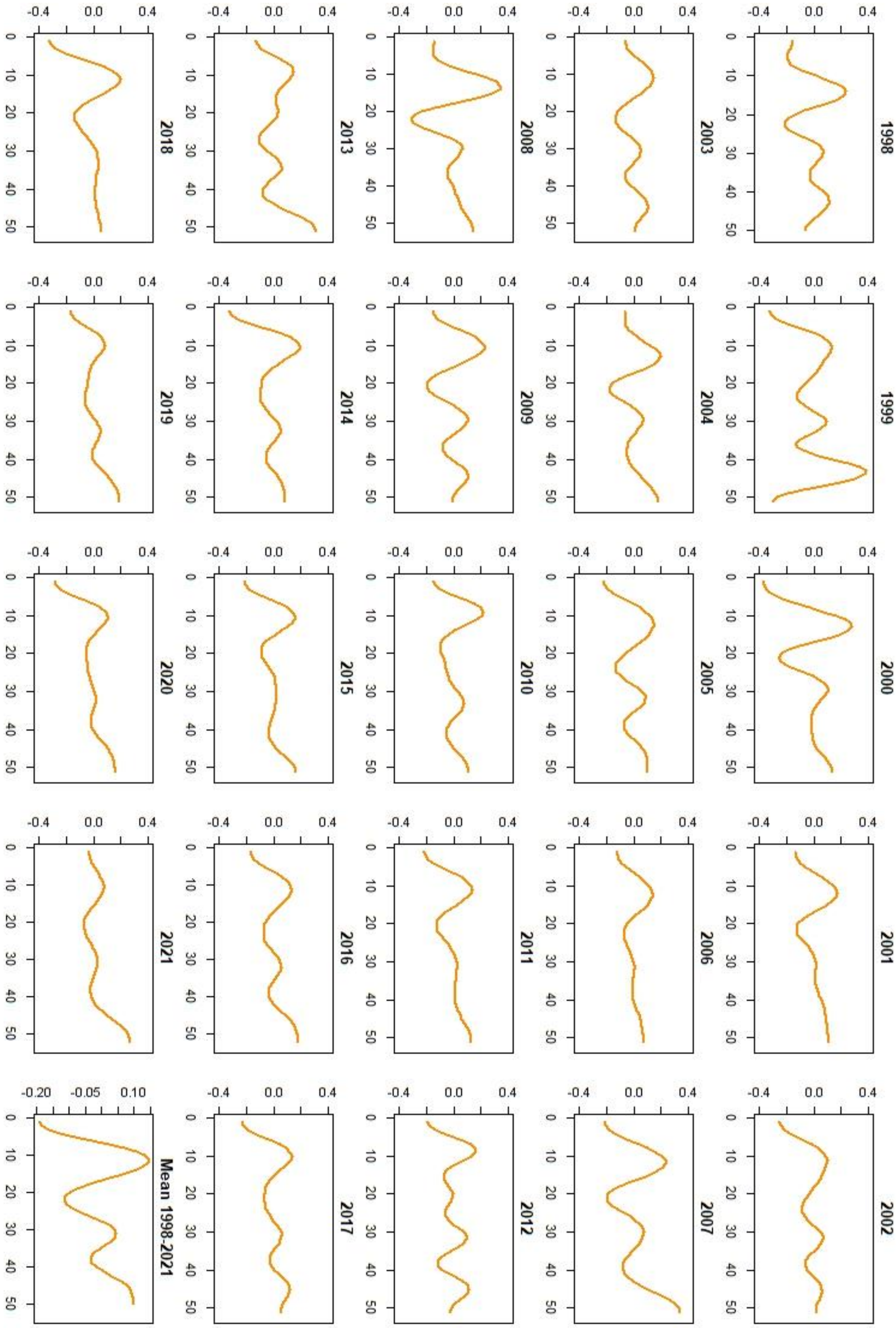

Figure 3: Change in Chl-a concentration predicted by the GAM models plotted as a function of week number for all 24 years of the time-series and averaged over the entire study period.

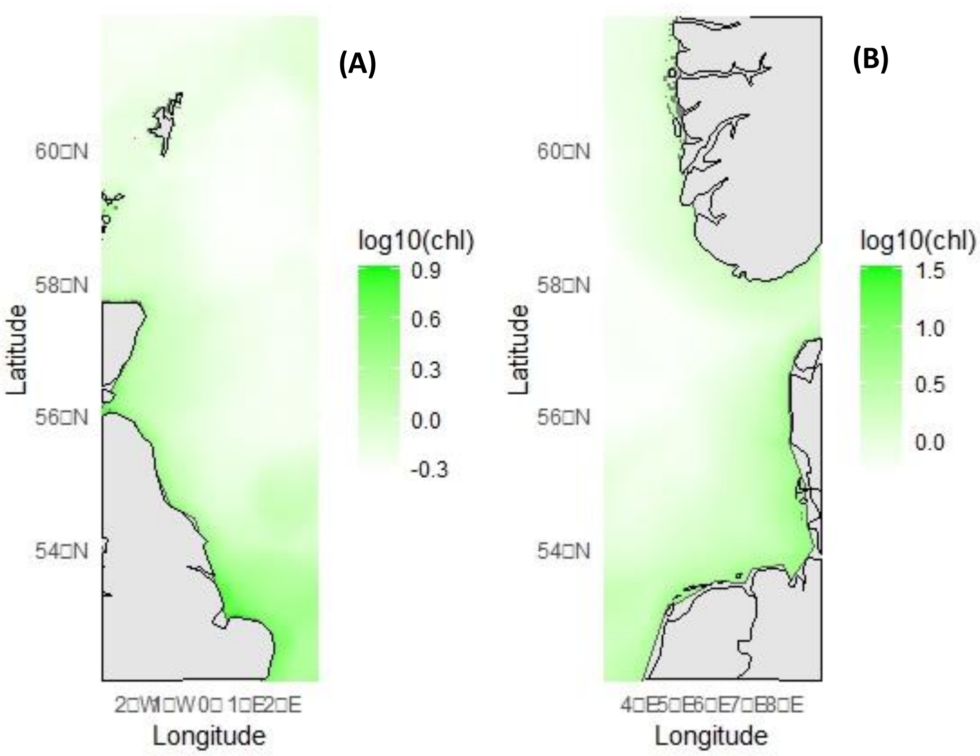

Figure 4: Maps of the western **(A)** and eastern **(B)** North Sea.

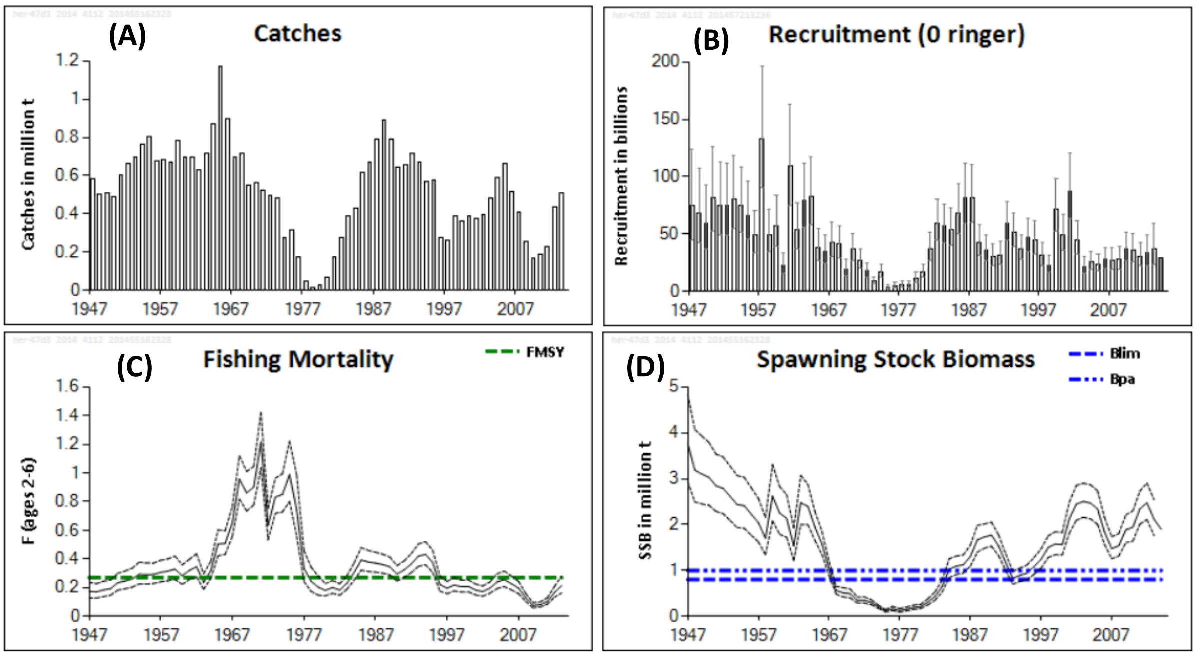

Figure 5: Summary plots of the 2015 catch advice report published by ICES.

9. R code on github

Link for the repository: https://github.com/Giacks/NPD.git (Herring_Satellites.R)