Spatial and temporal patterns in sex-ratios of Atlantic cod (*Gadus morhua*) in the North Sea

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BIOcean5D

Co-funded by the European Union

DTU

Course: Topics in Aquatic Science and Technology

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1. Abstract

Commercial catches of fish species can be biased towards one sex due to fishing regulations combined to biological differences between the sexes, such as differences in growth, maturation, and spawning-related behaviour observed in Atlantic cod (*Gadus morhua*). Male cod have been found to arrive earlier than females to spawning areas, where fishing pressure is high. Consequently, they expose themselves to a greater risk of being caught. In this study, spatial and temporal trends in sex-ratios of North Sea cod were examined to establish whether this sex-ratio has changed during 5 decades of heavy exploitation, and whether its distribution could be linked to spawning behaviour. Sex-ratios were calculated as the relative proportion of females for each year, ICES Statistical Rectangle, and/or age group, using data from the ICES DATRAS database. A weak increasing trend in the sex-ratio of the entire North Sea, resulting in an increase from ~0.48 to ~0.52 over the period 1978-2021, was found. While this trend is too weak to impair fertilization success due to sperm limitation, it may lead to a decrease in sexual competition between males. In addition, the oldest age group (6+) showed consistently higher sex-ratios compared to all other age groups. This is consistent with the literature, which suggests that a higher proportion of older cod is female. Sex-ratios were found to be lower (~0.45) in the centre of the North Sea and higher in the southern, northern, and eastern areas of the North Sea (0.60). This pattern cannot be explained by the distribution of spawning grounds, which indicate that the central North Sea is unfavourable for spawning. It was concluded that temporal and spatial patterns in sex-ratios of North Sea cod are not large enough to be relevant for stock assessment models and management.

2. Introduction

The reproductive potential of a given fish stock is often determined based on the abundance of adult individuals assumed to be capable of spawning, which are collectively termed Spawning Stock Biomass (SSB). This leads to the assumption that there is a direct proportional correlation between SSB and egg production (Marshall et al., 2006). This assumption only holds true if the proportion of females, i.e. the sex-ratio of the stock, and their fecundity, i.e. egg production, does not change over time and space (Quinn and Deriso, 1999; Marshall et al., 2006). For sexually dimorphic species, in which the sexes exhibit different growth, mortalities, and maturation patterns the previous statements may not be valid (Ajiad et al. 1999; Lambert et al. 2003; Marshall et al., 2006). In addition, the fecundity of females (Kjesbu et al. 1998; Marteinsdottir and Begg, 2002), their physical condition, as well as the age-composition of the stock can also change through time (Marteinsdottir and Thorarinsson, 1998). Combined, these effects can have strong implications for the reproductive potential of the fish stock, due to egg/sperm limitation and/or changes in size/age at maturity, and ultimately affect recruitment (Smith et al., 2014). Consequently, skewness in the sex-ratio should be taken into account in stock assessment models for stocks, in which it can be observed (Smith et al., 2014).

Atlantic cod (*Gadus morhua*) is among the most economically and ecologically important fish species in the northern European waters, such as the North Sea and the Baltic Sea (ICES, 2015). In the North Sea, cod has experienced nearly a 90% decline in abundance between the 1970s and the early 2000s due to overexploitation, and the stock has not yet recovered (ICES, 2015; Rowe et al., 2004). Cod reaches sexual maturity between 2 and 7 years of age and is a broadcast spawner, meaning that the females release eggs in seawater (Rowe et al., 2004). The size, quantity, and quality of the eggs are dependent on the size and physical condition of the female, but they are usually between 1.25 and 1.75 mm in size and thousands or millions in numbers (Rowe et al., 2004). It follows, that a high number of healthy females is essential to ensure a successful recruitment. During mating, the male attaches to the female using its pelvic fin (ventral mount) and swims at the same speed of the female (Skjæraasen et al., 2006; Rowe et al., 2004). At this point, eggs and sperm are released directly in the seawater (Rowe et al., 2004). Satellite males quickly join the spawning event by releasing sperm in the immediate vicinity of the couple (Rowe et al., 2004). As a result, eggs released by a given female can be fertilized by multiple males (Rowe et al., 2004). The higher sperm concentration generated by this behaviour likely increases the fertilization of a given batch of eggs (Uusi-Heikkilä, 2020). Therefore, having a good male spawning stock can be crucial in ensuring a high fertilization success of the eggs (Butts et al., 2009).

In the North Sea, cod spawns in large aggregations from the start of January until the end of April (Rowe et al., 2004; ICES 2015; González-Irusta and Wright, 2015). Males tend to arrive at the spawning locations earlier than females (McKenzie, 1940; Chrzan, 1950; Morgan and Trippel, 1996) to hold territories for behavioural and acoustics displays aimed to attract females (Rowe et al., 2004; González-Irusta and Wright, 2015). This behaviour makes cod, especially male cod, vulnerable during the spawning season and at the spawning grounds, where fishing efforts and catches tend to be higher (Morgan and Trippel, 1996; Smith et al., 2014; González-Irusta and Wright, 2015). As a consequence, male cod tend to be fished out in higher proportions then females. In addition, the shoals of spawning cod can be broken up during fishing activities with negative repercussions to the reproductive success of the shoal (González-Irusta and Wright, 2015). Mating behaviours, such as courtship call and territoriality, can also be disrupted (González-Irusta and Wright, 2015). These stresses could also lead to lower reproductive success or affect the processes underlying mate choice and sexual competition.

While the observation discussed above suggest that fishing efforts may have affected the sex-ratio of North Sea cod via a male-biased exploitation, spatial and temporal patterns of the sex-ratio of cod have been largely disregarded. This study, which is conducted under the framework of the BIOcean5D project co-funded by the European Union (BIOcean5D, 2023), is aimed at investigating trends in sex-ratios of cod in the North Sea using data from scientific trawl surveys. The scientific surveys are expected to be more representative of the real population than commercial catch data. Since the literature suggests that males are more vulnerable to fishing pressure (Morgan and Trippel, 1996), it is hypothesized that the proportion of males has declined over the past decades, leading to an increase in the proportion of females. Moreover, it would be expected that the distribution of sex-ratios throughout the North Sea is determined by the distribution of spawning grounds. Specifically, it is hypothesized that the sex-ratio is biased towards male at or near spawning grounds during the 1st quarter of the year, since males generally arrive at the spawning locations earlier than females to defend spawning territories (González-Irusta and Wright, 2015).

3. Methods

3.1 Data extraction

Data was extracted from the DATRAS database (ICES DATRAS 2023), an online database managed by the International Council for the Exploration of the Sea ICES (ICES) that includes data from scientific and fishing surveys from the North Atlantic. The data found in this database is rigorously controlled and is provided in a standardized format. The survey of interest to this study is the North Sea International Bottom Trawl Survey (NS-IBTS), which is the oldest sampling effort conducted by ICES: the NS-IBTS was started in the early 1960s in the Greater North Sea. To this date, 7 countries, Netherlands, England, Scotland, Germany, France, Norway, and Sweden, participate yearly in the NS-IBTS. This survey is stratified into so-called ICES statistical rectangles (StatRecs), which have been in use since the 1970's and are spatial grid cells of 1° longitude and 0.5° latitude (Figure 1). Survey data is available for the period 1978-2021 for the 1st quarter of the year.

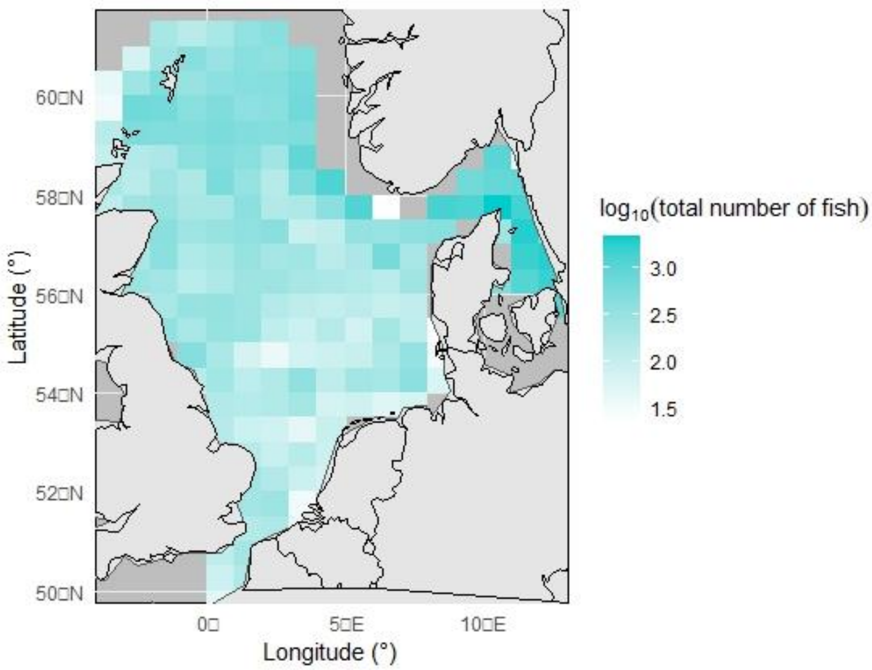

Figure 1: Sample size ($\log_{10}$ scale) of the ICES statistical rectangles in the North Sea for the study period 1978-2022**.** Grey cells contain no data from the IBTS survey.

Once the data was sourced and combined, the sex-ratio (S) and its standard error (SE) were calculated as follows:

$$S = \frac{n_{females}}{n_{males} + n_{females}}$$

$$SE = \sqrt{\frac{S(1-S)}{n_{males} + n_{females}}}$$

The sex-ratio, defined here as the relative proportion of female fish, was calculated for each ICES statistical rectangle, for each year, and for different age groups. Observations for a given year or ICES rectangle for which the total number of fish was considered to be too low were removed. For the temporal analyses, a minimum sample size of 50 was chosen, but for the spatial analyses a minimum sample size of 20 was chosen. The reasoning behind this choice is that if all the rectangle with less than 50 total fish were removed, there would have been too many holes in the data, and it would have been impossible to investigate temporal trends. It is important to mention that the geometric mean of the total number of fish for all ICES rectangles is 200 fish per rectangle. However, this value is mainly influenced by the high sample sizes in the Kattegat and Skagerrak. Over most of the central North Sea, sample sizes are around or below 100 (Figure 1).

3.2 Statistical analysis

All statistical analyses 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 DATRAS database was accessed using the "icesDatras" (Millar et al., 2022) and "icesVocab" (Millar and Magnusson, 2022) R packages. Linear models were constructed using the lm() function to investigate (i) temporal trends in sex-ratios and (ii) differences between age groups. Since the ratio calculated here is constrained between 0 and 1, and is therefore not a continuous variable, a *logit* transformation was necessary. The *logit* transformation applied here is the following:

$$S_{logit} = ln\left(\frac{S}{1 - S}\right)$$

This new variable was used in all the models as the response variable. The first model constructed was $S_{logit} \sim Year + tot$, where the covariate "tot" corresponds to the total number of fish, i.e. the sample size. A second model was then created to investigate the differences between age classes: $S_{logit} \sim Year + AgeGroup + tot$. For this analysis, the ages 1-11 where split into four age groups (Table 1). The glht() function from the "multcomp" R package (Hothorn et al., 2008) was then used to carry out a post-hoc Tukey test. During these analyses all observations with less than 50 total fish were removed.

Table 1: The four age groups defined and the associated age classes (in years of age).

Age Group 1	Age Group 2	Age Group 4	Age Group 6+
1	2-3	4-5	6+

Spatial patterns were investigated using General Additive Models (GAMs), in which smoothened terms of latitude and longitude were included. GAMs are Generalized Linear Models that create smooth functions of the predictor variables, so that these are linearly correlated with the response variable. GAMs were constructed in R using the gam() function from the "VGAM" package (Yee, 2015). These types of models are used here because the effects of latitude and longitude are not expected to be linear, and GAMs are able to model these non-linear effects.

The GAMs were defined as follows: $gam(S_{logit} \sim s(longitude) + s(latitude), weights{=}tot$. Here, the "weights" argument is used to correct for the differences in total number of fish between the ICES rectangles. This model structure was used to study spatial pattern of sex-ratios for all cod data, and 3+ year-old cod only.

3.3 Creation of maps

Spatial effects were illustrated in maps of the North Sea showing the relevant ICES statistical rectagles. The spatial data was plotted using the "simple feature" (sf) (Edzer

Pebesma, 2018) and the "ggplot2" (Wickham et al., 2020) R packages. In addition, the "rnaturalearthdata" and the "rnaturalearth" (Massicotte et al., 2023) R packages were used to load data of landmasses and countries around the North Sea. Predictions from the spatial GAMs were plotted using the same packages.

4. Results

4.1 Temporal trends

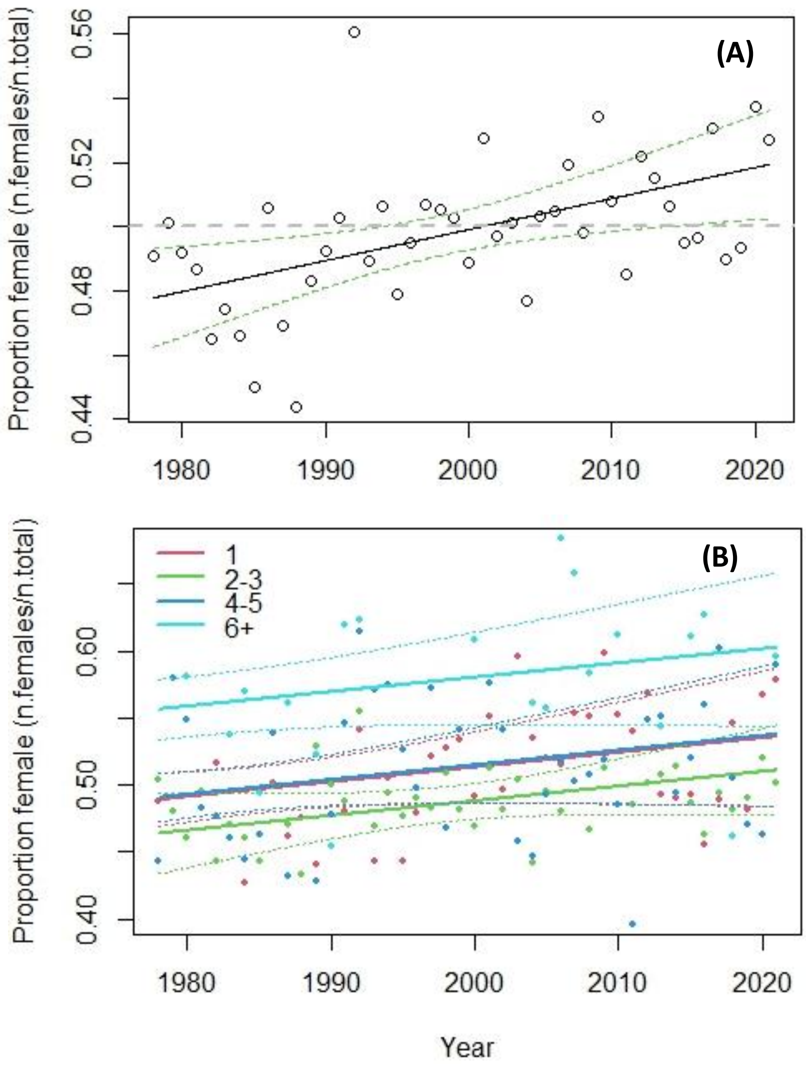

Figure 2: Sex ratio expressed as the proportion of female fish plotted against year for all cod **(A)** and for the four different age groups **(B)**. The grey dotted line **(A)** is a reference for equal number of female and male fish. The solid lines show the linear trend, while the dotted lines represent the 95% confidence intervals. The sex-ratio has significantly increased since the 1970s **(A)** and that the sex-ratio is generally higher for 6+ year-old cod **(B)**.

A weak but statistically significant increasing trend in sex-ratio of North Sea cod during the 1st quarter of the year was found during the period 1978-2021 ($S = 0.00097 \cdot year - 1.4$; $p = 0.003$; $F_{1,42} = 6.5$; $R^2 = 20$; Figure 2a). The covariate "tot", which was included in the model to correct for differences in sample sizes, was not statistically significant ($p = 0.644$), suggesting that the sex-ratio is not correlated to the sample size. This weakly increasing trend was found across all four age groups (Figure 2b). The slopes of the relationships of the individual age groups were not found to be statistically significant ($S = 0.0011 \cdot year – 1.7$; $p = 5.5 \cdot 10^{-11}$; $F_{5,141} = 13.8$; $R^2 = 31$; Figure 2b). However, the oldest age group, 6+, showed consistently higher sex-ratios than the other age groups (Figure 2b). In fact, the intercept of the line for the age group 6+ was significantly higher than that of all other age groups (Table 1). The covariate "tot" was also not significant in this model ($p = 0.746$). Diagnostic plots suggests that the models do not violate the assumptions of normality and Homoscedasticity of the residuals (Appendix, Figure 1,2).

Table 2: Results of the post-hoc Tukey test. The estimated differences are the differences between the intercepts of the trendlines for each pair of age groups. Age group 6, corresponding to 6+ year-old cod, had a higher intercept that all other age groups, and this difference was statistically significant.

Hypothesis	Difference	SE	t-value	p-value
AgeGroup2-AgeGroup1==0	-0.10	0.056	-1.8	0.27
AgeGroup3-AgeGroup1==0	0.0067	0.039	0.17	0.99
AgeGroup6-AgeGroup1==0	0.27	0.049	5.4	**<0.001**
AgeGroup3-AgeGroup2==0	0.11	0.059	1.8	0.25
AgeGroup6-AgeGroup2==0	0.37	0.072	5.2	**<0.001**
AgeGroup6-AgeGroup3==0	0.26	0.04	5.5	**<0.001**

4.2 Spatial patterns

Spatial patterns can be observed from the maps of the raw data without transformations (Figure 3). The proportion of females tends to be lower in the centre of the North Sea, and higher in the southern and north-western areas (Figure 3). The Skagerrak and Kattegat also seem to show higher proportions of females, compared to the centre of the North Sea (Figure 3). A similar pattern can be observed when looking only at 3+ year-old cod (Figure 3b). However, in this case the spatial patterns seem to be more pronounced (Figure 3b). The existence of such pattern was then confirmed by GAM models.

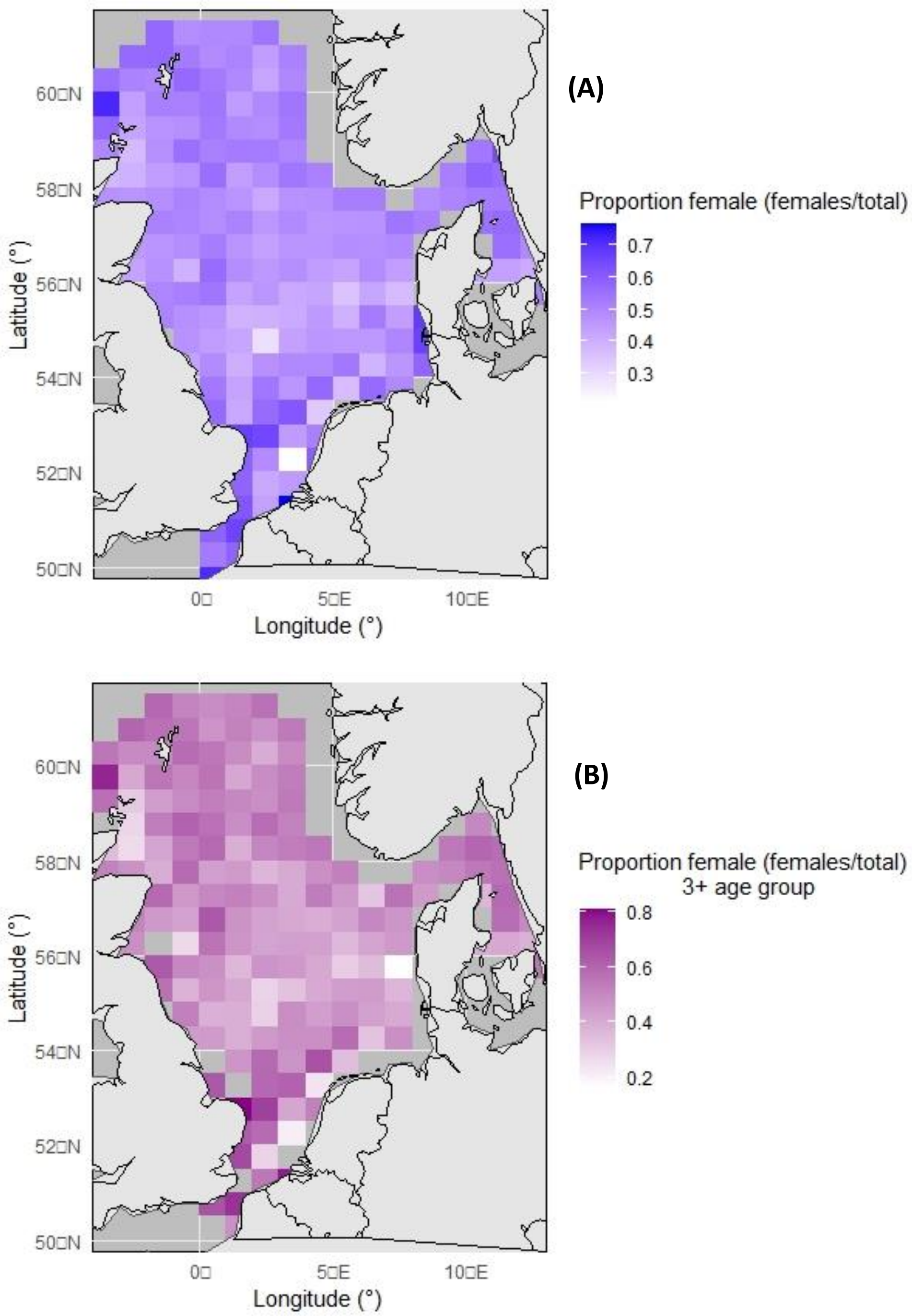

Figure 3: Sex ratio expressed as the proportion of female fish plotted for each ICES Statistical Rectangle in the North Sea for all cod **(A)** and for 3+ year old cod **(B)**.

The GAM model based on all age classes of cod was highly statistically significant, with both latitude and longitude having p-values lower than 0.0001, and explained 31.2% of the deviance over 188 ICES rectangles (df=185). The model predictions suggest that the proportion of females is significantly lower in the centre of the North Sea and higher in the south towards the English Channel, in the Kattegat, in the Skagerrak, and on a north-south line at longitude 0°. The exact same pattern can be observed for 3+ year-old cod (Figure 4b). In this case the GAM model explained 25% of the deviance over 172 ICES rectangles (df=169). Both latitude and longitude were found to be significant with p-values of 0.00037 and 0.014 respectively. It must be mentioned that these analyses were solely based on sex-ratios calculated during the 1st quarter of the year.

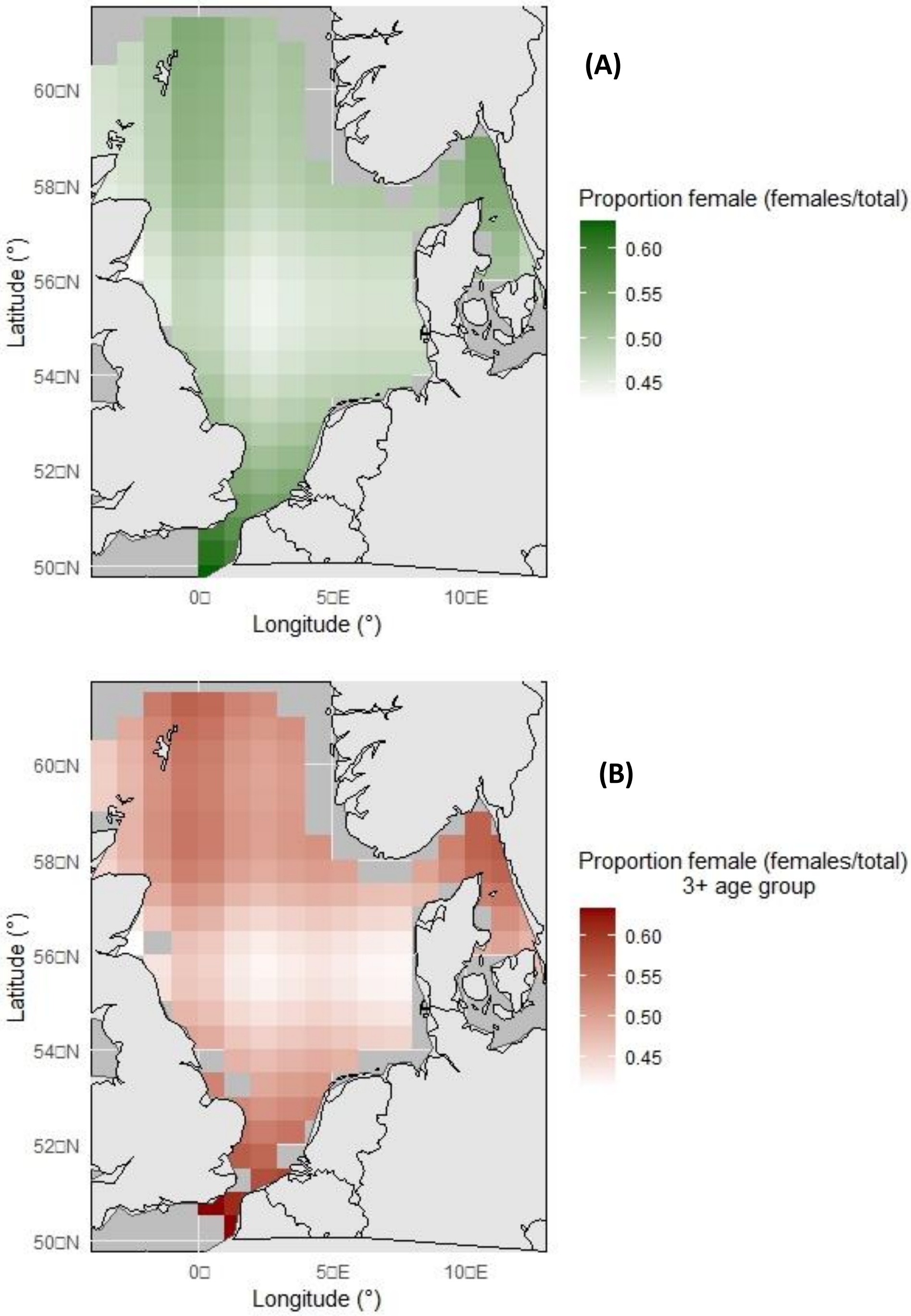

Figure 4: Sex-ratios predicted by GAM models for all age-classes of cod **(A)** and only for 3+ year-old cod **(B)**. The effect of longitude and latitude were in both cases highly significant ($p<0.01$) and the GAMs were able to explain >25% of the deviance.

5. Discussion

The goal of this study was to examine whether the sex-ratio of North Sea cod, calculated as the proportion of female fish, has (i) changed significantly since 1978 and (ii) whether it shows spatial patterns across the North Sea. It was hypothesized that, due to the high fishing pressures on the cod stock of the North Sea observed over the past 5 decades (ICES, 2015) combined to the fact that male cod are more vulnerable to fishing pressures than female cod (Smith et al., 2014; Morgan and Trippel, 1996), the proportion of female fish over the entire North Sea has increased since 1978. The linear regression analysis conducted here supports this hypothesis. When looking at the sex-ratio of cod in the North Sea, calculated across all age classes, this was found to have significantly increased since 1978 at a rate of ~0.001 y^{-1}, with an overall change of ~0.04. While during the start of the study period predicted by the model is ~0.48, for the end of the study period it is ~0.52. This observation could be explained by a male-biased exploitation over the study period combined to male spawning-related behaviour.

Numerous studies focussed on spawning shoals of cod have found skewed sex ratios (Morgan and Trippel, 1996). McKenzie (1940) observed that cod catches using gillnets and jiggers in Canadian waters where male-biased in autumn, which for that stock is within the spawning season. Similarly, Chrzan (1950) found that otter trawl catches in the bay of Gdansk during the spawning season were male-biased. The authors then suggested that this was caused by the fact that males were arriving earlier at the spawning ground and that this behaviour would expose them to a higher fishing mortality (Morgan and Trippel, 1996).

When the sex-ratios were calculated for four age groups separately, and the temporal trends were estimated for all age groups, it was determined that 6+ year-old cod are predominantly female (Figure 2b). This finding is consistent with the literature, since multiple studies have reported that older cod tend to be female (Parker 1992; Marshall et al., 2006). The authors determined that size-dependent exploitation can lead to changes in the size composition of cod stocks. Then they showed that when the average size in a cod stock decreases, the stock becomes more male-biased, while when the average size increases, the cod stock becomes more female-biased (Marshall et al., 2006). If fishing efforts are directed more towards the larger and older cod, which tend to be predominantly female, then the fishing pressure would be expected to be more female-biased (Marshall et al., 2006). This observation would contradict the previous hypothesis based on the spawning behaviour of males.

Since the observed change in sex-ratio over the study period is very small, it is unlikely that this influences the reproductive success or potential of the cod stock. However, if the sex ratio would continue to increase in the future, implications for cod management could arise. If the sex-ratio become considerably skewed towards either males or females, it will affect the reproductive potential of the stock (Marshall et al., 2006). In fact, if the proportion of females in the stock is lower than 50%, than the SSB will overestimate the actual reproductive potential, since females are often the limiting sex (Marshall et al., 2006). At these low relative proportions of females, more males will be attempting to fertilize eggs of a given females, leading to high sperm density and fertilization success (Uusi-Heikkilä, 2020). On the contrary, SSB underestimates the reproductive potential, when the stock is dominated by females (Marshall et al., 2006). Therefore, considering that the sex-ratio of cod in the North Sea is increasing, it would mean that the reproductive potential of the stock is increasing as well. This statement could only hold true until the sperm production by males would become the limiting factor. In fact, an excessively high relative proportion of females can lead to a decrease in egg fertilization rates as well as a high variance in fertilization success (Rowe et al., 2004). As previously mentioned, the observed increase in sex-ratios is very small and it is unlikely that this increase could negatively affect fertilization success. However, studies quantifying how changes in sex-ratio affect fertilization success are lacking, and therefore it is difficult to determine whether this change is entire negligible.

It is also unknown how many male cod are needed in a wild population to efficiently fertilize all eggs produced by the females. Studies on small populations or open net cages suggest that only very few males are needed to fertilize all eggs produced (Rowe et al., 2008; Rooney et al., 2018). A recent study investigating the differences in reproductive success between individuals of two adjacent cod populations, found that 3 out of 28 males fertilized >50% of the offspring (Rooney et al., 2018). Similarly, Rowe et al. (2008) found that 80% of the offspring was fertilized by 2 to 7 individuals in four different groups of 52 to 93 individuals (Rowe et al., 2008). One could generalize from these studies and hypothesize that just 20% of the population would have to be male to obtain a high fertilization success. Consequently, the small differences in relative proportion of males observed over the period 1978-2021 are not likely to negatively affect fertilization. However, it must be considered that studies assessing the reproductive success of marine fishes are scarce, due to the fact it is challenging to observed spawning behaviour of marine fish in the wild (Rowe et al., 2008).

While changes in the fertilization success might be unlikely, the observed changes in sex-ratios could affect other aspects of the reproduction of cod. In general, male fitness seems to be positively correlated with body length and with the length of pelvic and median fins (Skjæraasen et al., 2006; Rowe et al., 2008). The number of agonistic interactions initiated by male cod against competing males was also found to be positively correlated with fitness (Rowe et al., 2008). Similar trends were observed in other fish species (Uusi-Heikkilä, 2020). For example, in sand gobies populations with high relative proportions of males, in which the larger male were the ones buildings the nests (Kvarnemo et al., 1995). A reduction in the relative proportion of males in a given cod population, may lead to a less intense sexual competition between males. This could lead to changes in the selection towards larger and more aggressive males. It must be considered that, while the North Sea cod is managed as a single unit by ICES, it is constituted by distinct sub-stocks or sub-populations (ICES, 2015; González-Irusta and Wright, 2015). Therefore, different sub-populations could be impacted differently, and could show different behavioural responses.

Spatial patterns of sex-ratios of cod have been less studies and this study may be the first one to model the sex-ratio as a function of latitude and longitude with a decent resolution. In this study, the sex-ratio observed during the 1st quarter of the year was found to be male-biased in the centre of the North Sea (Figure 3,4). Considering that the males have been reported to migrate to the spawning areas earlier than females, it would be expected to find male-biased sex-ratios around the spawning areas and higher values elsewhere. Multiple spawning locations are known in the North Sea, primarily from plankton surveys and distributions of sexually mature cod (Fox et al., 2008; ICES, 2015): the southern and eastern edge of the Dogger Bank, the German Bights, the Moray Firth, and the eastern coast of the Shetlands. The spatial patterns presented in this study do not fully agree with this hypothesis. Male-biased sex ratios were found around the Dogger Bank, the German Bights, and to a lower degree in the Moray Firth (Figure 3,4). However, along the eastern coast of the Shetlands the sex-ratio was female-biased (Figure 3,4). This could indicate a difference in the spawning behaviour of the cod in this area, or that other factors, than the combination of fishing pressure and male behaviour, have affected the sex-ratio of cod in this area. Moreover, if we compare the map presented in this study, with a cod spawning habitat classification map from the literature (González-Irusta and Wright, 2015) it can be concluded that the sex-ratio tends to be male-biased in predominantly muddy areas that are unfavourable for spawning cod (González-Irusta and Wright, 2015). This observation is not consistent with the previously mentioned hypothesis that suggests that higher proportion of males should be observed at spawning grounds during the spawning season.

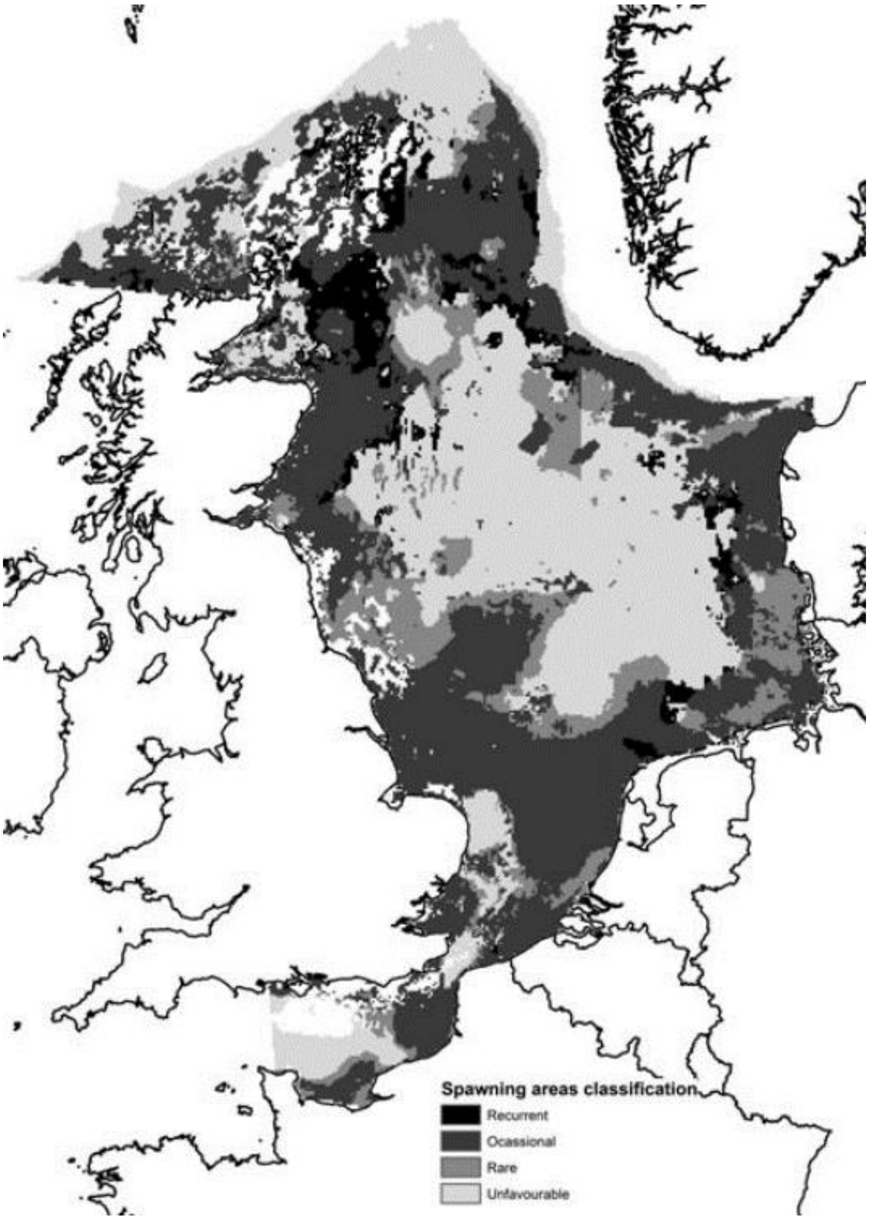

Figure 5: Map showing the classification of potential spawning habitat for cod in the North Sea. In the black areas cod spawning is recurrent, in the dark grey areas occasional, in the grey areas rare, and the light grey areas are classified as being unfavourable for cod reproduction. Taken from González-Irusta and Wright (2015).

5.1 Confounding effects of sample size

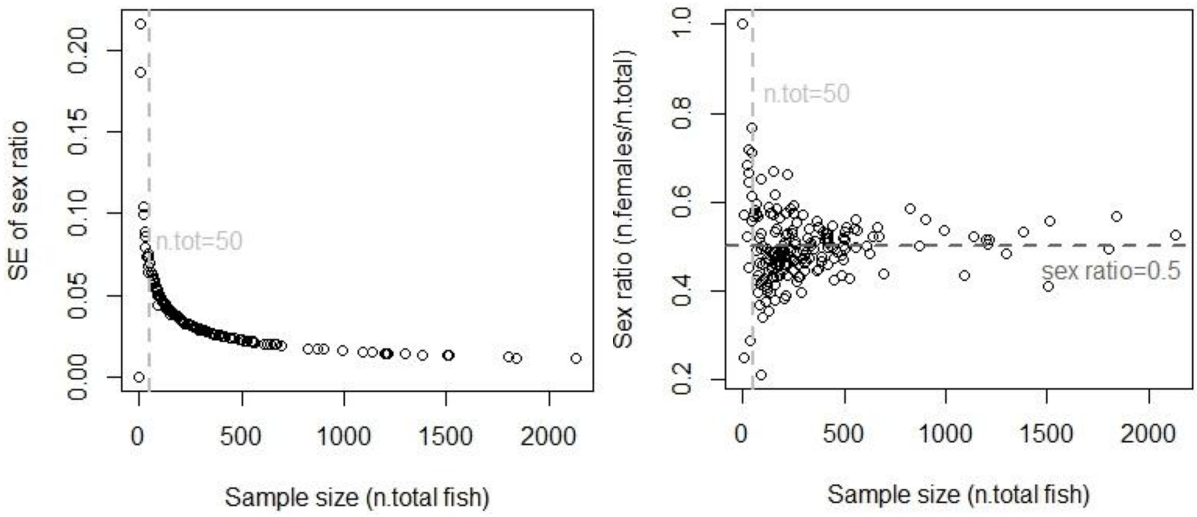

Figure 6: Illustration showing the stander error (SE) associated with the sex-ratio estimate and the corresponding number of total fish used **(A).** Plot showing the sex-ratio as a function of sample size **(B).** The vertical dashed line indicates the sample sizes of 50.

In this study, trends in sex-ratios of cod in the North Sea were explored. The first step in the conducted analyses was centred around the calculation of the sex-ratio. When the data was disaggregated by years, age groups, and/or ICES statistical rectangles, the number of total fish for which this ratio was calculated varied considerably. While for the calculation of the temporal trends, few years had less than 200 total fish, for the spatial models numerous ICES rectangles, mainly in the central and southern North Sea, had between 20 and 50 total fish. The SE associated with a sample size of 50 is around 0.07 (Figure 6a). Consequently, the variance in estimated sex-ratio is higher at low sample sizes compared to high sample sizes (Figure 6b). However, this variance is also due to spatial and temporal effects. Even though the number of total fish (“tot”) was included as a covariate or weight argument in all the models, the effect of sample size might not entirely be accounted for. Therefore, when interpreting the spatial analyses care must be taken as the degree of uncertainty is not provided here. It is suggested that the same analyses are repeated in the future, when a larger time-series will be available.

6. Conclusion

This study showed that the sex-ratio of North Sea cod is not constant over time and space. Both temporal and spatial trends were found. While none of these patterns were large enough to affect the reproductive success of the North Sea cod, they may lead to changes in spawning-related behaviour, particularly in males. Future work should aim to monitor the changes in sex-ratios of North Sea cod, since a further increase in the sex-ratio over the next decade might become relevant for the estimation of the reproductive potential of this stock. In addition, it would be interesting to investigate whether other species shows similar spatial and temporal trends.

7. Acknowledgements

I wish to thank my supervisor Dr Brian R. MacKenzie for his help and guidance throughout the entirety of this project. I would also like to thank Jonathan Stoundberg for teaching me how to access the ICES DATRAS database directly in R, which saved me time and effort.

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9. Appendix

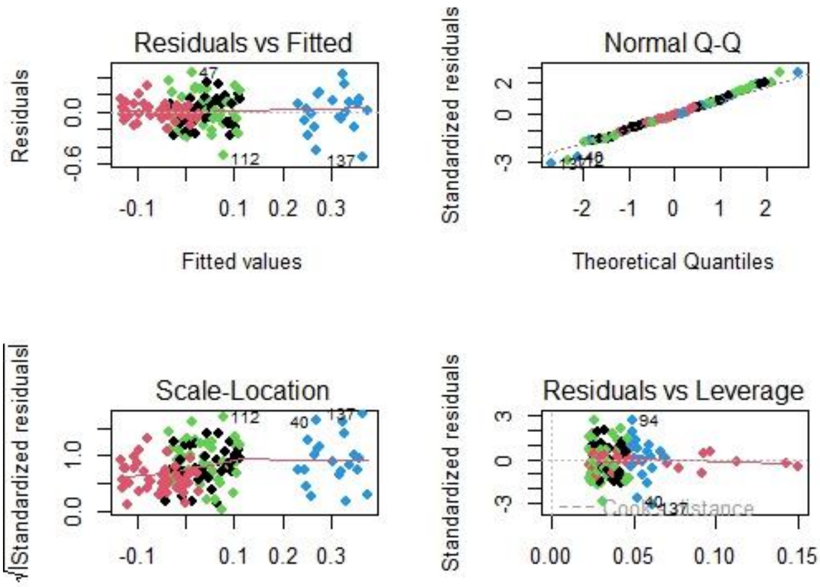

Figure 1: Diagnostic plots of the linear model examining the relationship between sex-ratio and year, for all 4 age classes. *Observations are coloured based on the group number (Group 1 in black, Group 2 in red, Group 3 in green, and Group 6+ in blue)*

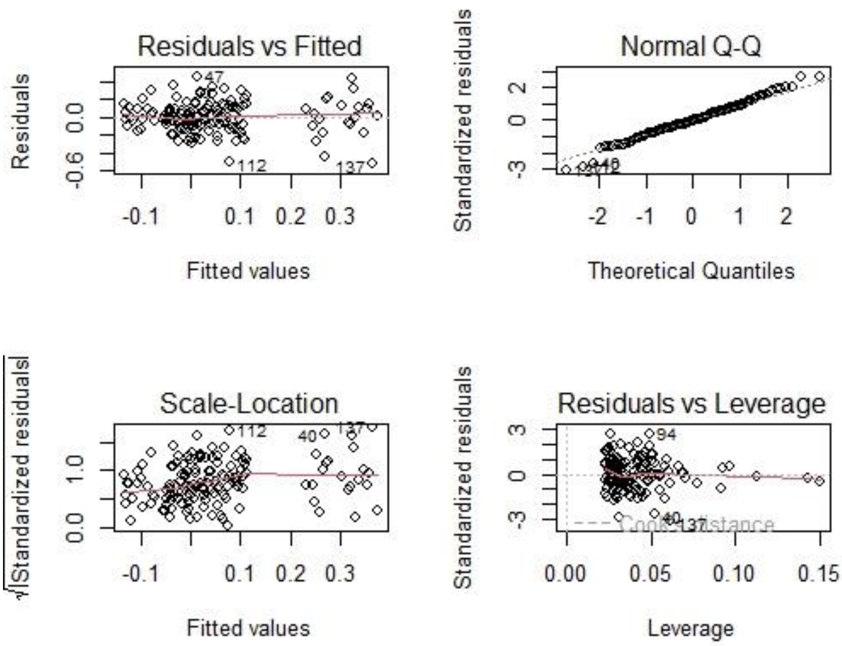

Figure 2: Diagnostic plots of the linear model examining the relationship between sex-ratio and year.

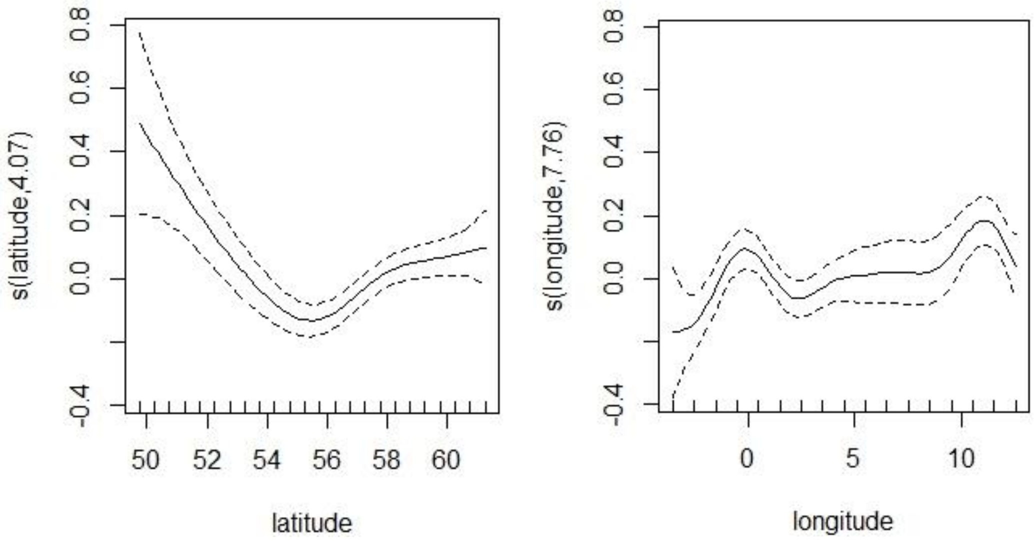

Figure 3: Illustration showing the smooth functions of latitude (left) and longitude (right) fitted by the GAM model having logit-transformed ratio as the response variable.

10. R code on github

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