

MODELLING THE DISTRIBUTION OF NORWEGIAN
COASTAL COD (*GADUS MORHUA*)

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ABSTRACT

Knowledge about a species' distribution, and the factors driving the distribution, is important in both fishery management and conservation. It can help explain distributional shifts and variations in abundance as a response to environmental changes. But spatial dynamics are complex and not easy to analyse, and a flexible model is therefore necessary. Atlantic cod (*Gadus morhua*) is a commercially important species and includes two stocks present on the northern coast of Norway, one of which is the Norwegian coastal cod. The distribution of coastal cod has not yet been analysed using spatial modelling, which is the focus of this thesis. Using Generalized Additive Models (GAM), we investigated if the distribution of coastal cod in northern Norway changed during the period 2003-2021, and if the distribution could be explained by both density-dependent and density-independent factors. We also investigated if there were any differences in the environmental conditions experienced by different-sized cod by modelling the density of three selected length groups: 25cm, 55cm, and 85cm. The results showed that the distribution has not changed significantly during the time period, although the local densities have varied. Temperature and spawning stock biomass had both an effect on the spatial variations in density and an increase in these factors could result in an expanded distribution. The temperature could have a negative effect on the abundance of the local populations in some areas and a positive effect in other areas. Increased spawning stock biomass could result in a wider distribution, but some local populations could also contribute to the increased spawning stock biomass. When studying different-sized cod, the results showed that temperature and depth alone could not explain the spatial variations observed between the length groups, although the cod seem to experience different habitats during ontogeny.

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1 INTRODUCTION

Knowledge about the spatial dynamics of a population is an important part of fishery management and also of conservation (Bartolino et al., 2017). A better understanding of a species' distribution, including the factors driving the distribution, will attribute to the understanding of distributional shifts as a response to environmental changes (Ciannelli et al., 2008). The knowledge can also help understand migration patterns and variations observed in abundance. But the distribution is very complex and is driven by several different factors. The distribution can be affected by density-dependent and density-independent factors and fishing pressure caused by humans (Bartolino et al., 2017). The density-dependent factors can be both inter- and interspecific, like competition or predation, while the density-independent factors are environmental (Ciannelli et al., 2008).

The complexity of a species distribution makes it difficult to analyse, even with a large amount of data on both the spatial distribution and environmental data. The relationships between fish abundance or occurrence and environmental parameters are often nonlinear, causing some challenges in statistical analysis, and abundance data often display features like for example patchiness and an overabundance of zero or low catches. The use of regression analysis is one of the approaches that can be used for spatial modelling. Nonlinearities in the data put some restraint on which statistical models can be used. One of the statistical model types used for this kind of data is Generalized Additive Models (GAM) (Ciannelli et al., 2008; Murase et al., 2009). As with a Generalized Linear Model (GLM), the GAM allows for modelling different error distributions such as the binomial, Poisson and normal. In contrast to the GLM, a GAM can handle smooth functions for the covariates. This means that the model allows for a non-linear relationship between the covariates and response, resulting in a flexible model that can be used for modelling distribution (Wood, 2017).

In fisheries management, fish populations are divided into units called stocks. A stock is a group of individuals of the same species, where the individuals are somewhat isolated from other groups of the same species. The stock is self-reproducing and shares the same geographical distribution and migratory patterns (Jennings et al., 2009). The demersal fish species Atlantic cod (*Gadus morhua*) is divided into about 20 stocks in the North Atlantic, where two of them are found along the coast of northern Norway; Northeast Arctic cod (NEAC) and Norwegian

coastal cod (NCC) (Berg & Albert, 2003). The Atlantic cod is found in a large variety of habitats, ranging from open oceans to fjords, habitats that are found along the coast of Norway.

There are some physical differences between individuals of the NEAC and NCC, with NEAC generally found to be longer and thinner than the NCC (Stransky et al., 2008; Svåsand et al., 2005). However, the otoliths are analysed to reliably distinguish the two stocks in fishery management. The two stocks are distinguished by the variations in the shape and the distance between the two translucent zones closest to the centre of the otolith (Berg et al., 2005). This method for separating the two stocks is relatively fast and cheap but it is also subjective to the reader of the otoliths (Berg & Albert, 2003; Stransky et al., 2008).

There are also several differences in the life history of the NCC and the NEAC. The Northeast Arctic cod performs long-distance migrations from their feeding areas in the Barents Sea, to the spawning areas along the coast of Norway (Bergstad et al., 1987; Stransky et al., 2008). The coastal cod is typically found inside the fjords and does not migrate long distances. Since the NCC is more stationary and has been shown to display a genetic difference along the coast of Norway, it is more vulnerable than the NEAC and a concentrated fishing effort could potentially take a large proportion of one population (Dahle et al., 2018). The two stocks have an overlap in distribution during the spawning migration of NEAC since the coastal cod are generally distributed in the coastal areas (Berg & Albert, 2003). Because of this overlap, mostly during spawning season, the coastal cod is a part of a mixed fishery (Michalsen et al., 2014; Stransky et al., 2008). NCC does not have a quota of its own but is part of the total quota for cod, where the catch of NEAC makes up the largest portion (Aglen et al., 2020). There are regulations in place so that the fishery is directed away from the NCC and towards the NEAC. These regulations include gear regulations, time restrictions or area restrictions (ICES, 2023b). For further analysis, the focus will be on the distribution of NCC, which has not been analysed in detail using spatial statistical methods.

Before 2021, the NCC was divided into two stocks, one respectively south and north of 62°N. Genetic studies show that the population structure is more complex than this division and that there is a genetic gradient from north to south (Dahle et al., 2018). The coastal cod furthest north has some gene flow with Northeast Arctic cod, and the gene flow decreases further south (Dahle et al., 2018). The local differences in the coastal cod and more consistently sampled data in the northern region were the basis of why the coastal cod stock north of 62°N was divided

into two management units, 62°N–67°N and 67°N– the Russian border (ICES, 2021). North of 67°N the coastal cod is more abundant than in the south, but the proportion of coastal cod among all cod increases southwards since the abundance of NEAC decreases (Berg & Albert, 2003).

As previously mentioned, changes in distribution can be caused by both density-dependent and density-independent factors. Density-independent factors like temperature and depth have been shown to influence the distribution of a great number of species, including cod (Zemeckis et al., 2017). Different sizes of fish can have different depth preferences. The preferred depth could be correlated to preferences for both temperature and salinity or could be due to prey availability and predator avoidance (Swain, 1993). For juvenile fish, shallow waters with cover from macroalgae might be preferable, decreasing the risk of predation (Berg & Albert, 2003). There have been studies showing that smaller individuals occupy shallower depths than bigger individuals, a phenomenon called Heincke's law (Macpherson & Duarte, 1991).

The temperature has also been shown to affect spatial distribution. As for all organisms, cod has a temperature range that is optimal for growth and reproduction, and the temperature can drive migrations and changes in distribution (Spotowitz et al., 2022). The optimum temperature for an individual can vary over the life span. For cod, the optimum temperature for larger individuals is lower than for smaller individuals (Berg & Albert, 2003), but studies show that the optimum temperature for growth ranges between 11°C and 16°C even though cod can survive in a much broader temperature range (Rose, 2019). Temperature changes can result in an expanded or contracted distribution range, as seen for some of the North Atlantic fish that expands towards the north during warmer periods (Andrade et al., 2020). Boreal fish species like cod and haddock have exhibited a northward expansion as a result of favourable conditions in terms of increased temperature in the Barents Sea (Fossheim et al., 2015).

Density-dependent factors affecting the distribution of a population can be, for example, predation and competition. The theory of ideal free distribution for a population refers to a scenario in which the distribution of individuals results in the highest possible fitness for all individuals (Fretwell & Lucas, 1969; Shepherd & Litvak, 2004). This is not only based on food availability but also the density of individuals existing in the habitat. A higher abundance of individuals in a habitat will cause competition and could drive the fish into habitats that have

less optimal environmental conditions but with more food available (Bartolino et al., 2017). The prey available in the suboptimal habitat could potentially be less preferable, but the competition is lower.

In most cases, both density-dependent and density-independent factors affect the distribution of a population, but there is some difficulty in analysing these interactions all at once and how they can drive changes in distribution. This is why spatial modelling is a valuable tool for studying distribution. Spatial modelling allows us to see if multiple different interactions can help explain the observed variations in distribution. In this thesis spatial modelling is used to analyse the distribution of Norwegian coastal cod between the years 2003–2021 to answer the question: Has the distribution of coastal cod changed over time? If yes, how does this display in the distribution of different coastal cod length groups? If the distribution has changed, how can this be explained by environmental factors?

Based on the findings above I hypothesize that the distribution of Norwegian coastal cod depends on both temperature and spawning stock biomass. Specifically, I hypothesize that increasing either one of these drivers will result in an increased depth range and wider spatial distribution. Regarding the distribution of different length groups of coastal cod, I hypothesize that larger individuals, compared to smaller individuals, will occupy 1) cooler waters and 2) deeper waters.

2 MATERIALS AND METHODS

2.1 DATA COLLECTION

2.1.1 Survey Area

The Institute of Marine Research (IMR) conducts an annual coastal survey along the coast of Norway, north of 62°N, during the autumn months of October and November. The primary objective of this survey is to obtain information about the abundance of several important commercial species, including coastal cod (Staby et al., 2020). The coastal survey combines the areas that have been covered for saithe since 1985 and covered for coastal cod since 1995 and have since 2003 been conducted as one coastal survey. The survey covers the coastal banks, fjords, and coastal areas between Stad in central Norway and Varanger in northern Norway.

The coastal survey has been standardized since 2003 in relation to acoustic transects, trawl hauls and CTD stations. The trawl sampling includes both fixed trawl stations and opportunistic acoustic target identification hauls. Since 2017, there have been additional hauls to monitor deep-sea shrimp and redfish species. CTD casts are taken at a selection of the fixed trawl stations.

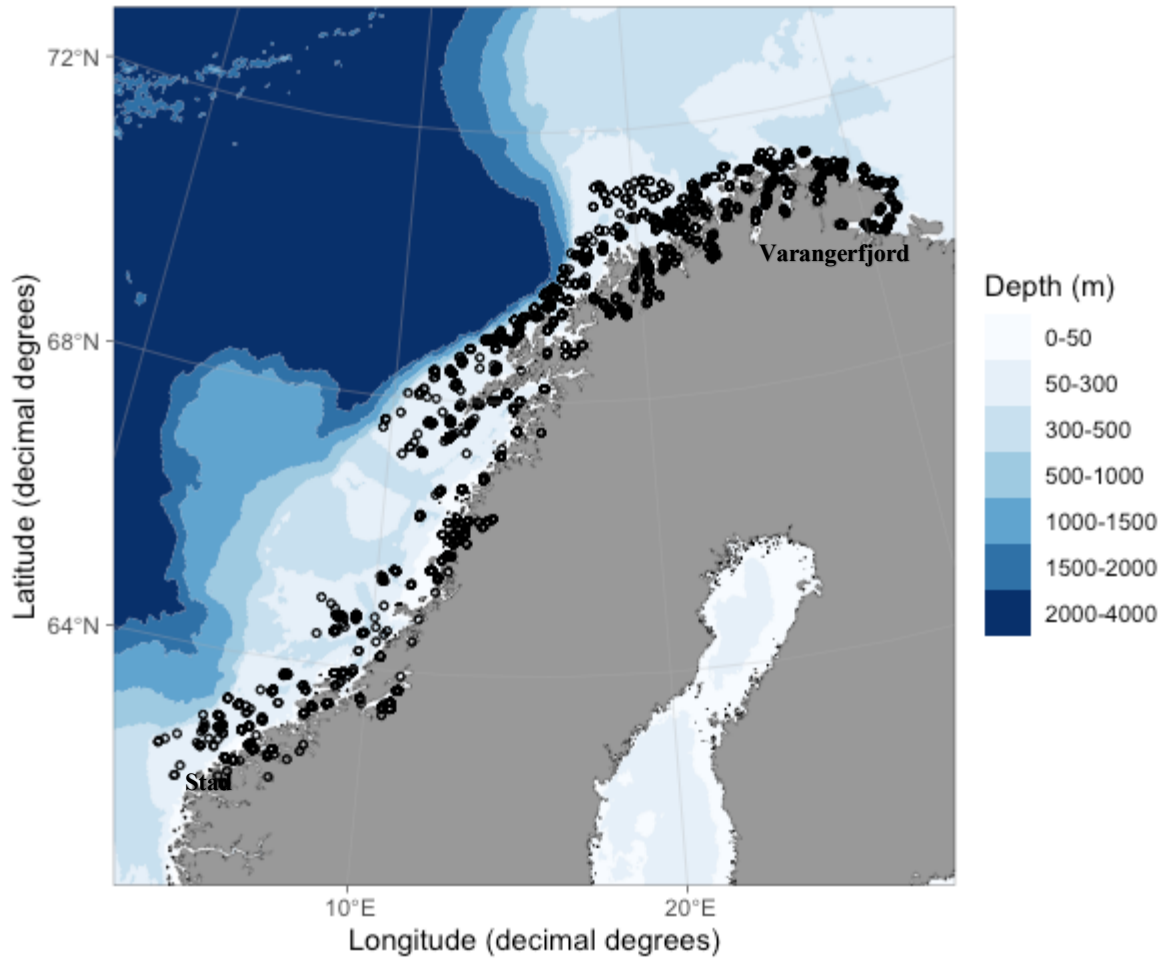


Figure 1: Map of bottom trawl stations on the coastal survey from 2003–2021

2.1.2 Biological Sampling

The bottom trawl used is a Campelen 1800 standard shrimp trawl with 20mm mesh size in the cod end. The trawl is rigged with rock hopper gear, trawl doors and Scanmar trawl and door sensors to provide information about the door spread, trawl opening and bottom contact. The standard vessel speed for the hauls ranges between 3–4 knots, and the general trawl duration is 30 minutes, though some trawls are as short as 10 minutes due to unsuitable bottom. Vertical trawl opening is between 3.5–4.5m and door spread (distance between trawl doors) generally varies between 47–53m, though this can be higher in shallower water.

The catches are sorted and weighed by species, and length measurements are taken for both commercially important and less important species. In instances when the trawl catch is too big to be sorted as a whole, length measurements are taken from a representative subsample. For commercially important fish species, including cod, extended biological measurements are done for a subsample of individuals selected through stratified sampling in which up to 5

individuals for each 5cm length group are selected. The extended biological data recorded includes individual weight, sex, gonad maturity stage and otoliths. Otolith sampling is used for determining age, and for cod used to distinguish between NEAC and coastal cod.

2.1.3 Covariates

The low number of CTD stations and the large distance between them made it difficult to describe the physical parameters at each trawl station. Instead, the physical variables used were retrieved from the modelling system NorKyst800 (Albretsen et al., 2011). The temperature from the model is a calculated mean of the two-week window centred around the date of the trawl at the specific location. The modelled depth was in some cases different from the depth trawled due to model resolution (800 m polygons, within which depth may also vary), and the temperature may differ somewhat from that experienced by the caught cod. The depth used as a covariate in the analysis was the bottom depth recorded at the start of trawling.

The spawning stock biomass estimates (SSB) from the time period were retrieved from ICES 2022 stock assessment (ICES, 2023a).

2.2 DATA PROCESSING

2.2.1 Swept area estimate

The software StoX (Johnsen et al., 2019) was used to produce survey indices of coastal cod. The abundance indices are calculated using swept area fish density estimates. The density estimates are calculated per 5 cm length group per station by the equation (1):

$$\rho = \frac{f}{a} \quad (1)$$

where ρ is the number of fish per length group per nautical mile squared at each trawl station, f is the estimated frequency of length l , and a is the swept area (nm^2). The swept area is calculated with equation (2):

$$a = d * \frac{EW}{1852} \quad (2)$$

where d is the towed distance (nm), and EW (m) is the length-dependent fishing width. The fishing width for cod is dependent on cod length. According to Dickson (1993), the effective fishing width increases linearly with size for individuals between 15 and 62cm. The efficiency is lower for small individuals than for larger ones, because they can escape over or beneath the sweeps of the net.

The swept area data was exported from StoX and R version 4.2.1 (R Core Team, 2022) was used for further data manipulation and analysis.

2.2.2 Calculating the Proportion of Coastal Cod

To distinguish between NCC and NEAC, the morphological structure of the otoliths is used, thus providing a proportion of coastal cod in the catch (figure 2). The proportion of NCC for each length group and station was then used to find the swept area density of coastal cod per length group in the abundance of cod from each trawl station. It was assumed that the proportion of coastal cod by length group among the smaller subsample with typed otoliths was representative for the proportions in the total catch. In some cases, mostly for smaller length groups, it is difficult to distinguish between the two stocks of cod, and consequently, the proportion of coastal cod is unknown. For cod < 2 years, 43% of age samples were not typed as either coastal or NEA cod. However, of the cod that had been typed, most had been typed as coastal cod and it was therefore assumed that the swept area density of all length groups < 30 cm (approximately 2 years old) with missing information were coastal cod (figure 3). In a few cases, the proportion of coastal cod was unknown for larger length groups; a total of 64 individual cod > 1 year were missing otolith type due to sampling error. For length group-station combinations that were consequently missing a proportion of coastal cod, the mean proportion of coastal cod for the specific length group in the survey area north of 67°N was used to find the swept area density.

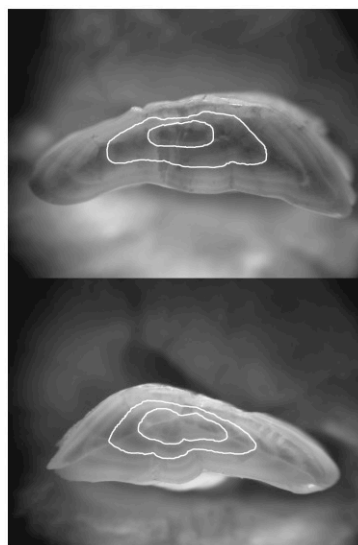


Figure 2: An image of a coastal cod otolith (top) and a Northeast Arctic cod otolith (bottom). The two first translucent zones, used to distinguish between the two stocks are highlighted (Berg et al., 2005)

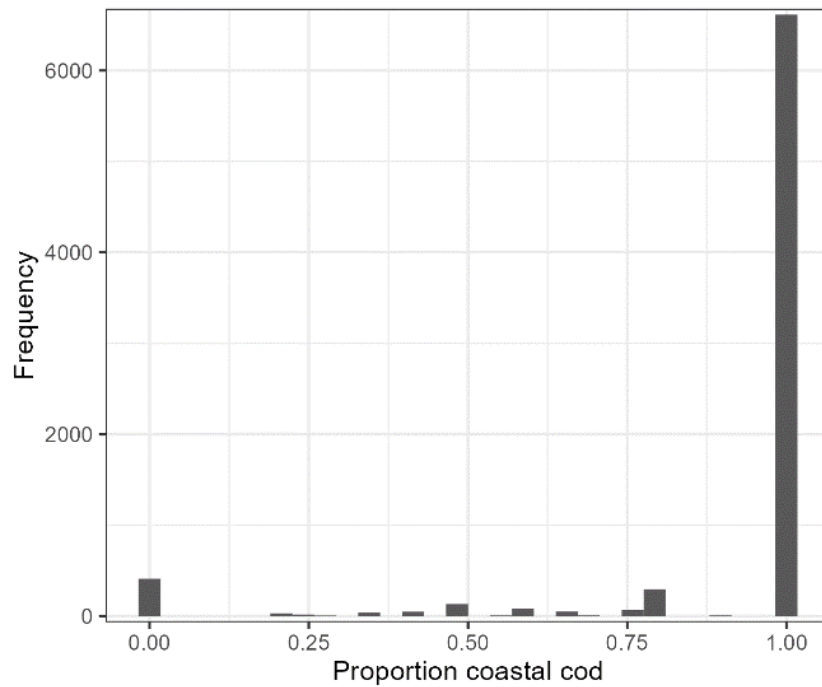


Figure 3: The proportion of coastal cod among all cod < 30cm that has been typed in the total dataset.

2.2.3 Data Selection

Only data from the bottom trawls from the coastal survey was used in this analysis. We chose to only include the catch data north of 67°N since the coverage of the trawl stations in this area compared to south of 67°N is much better (figure 4a and 4b). The smallest length groups are difficult to sample representatively, and there were not many observations of coastal cod >105cm, so the length groups included in the analysis range from 15 cm–105 cm (figure 5). For the analysis, the 5cm length groups were further aggregated into 10cm length groups to reduce data volume. The length group 15cm includes cod in the range 15–25cm, 25cm includes 25–35cm and so on.

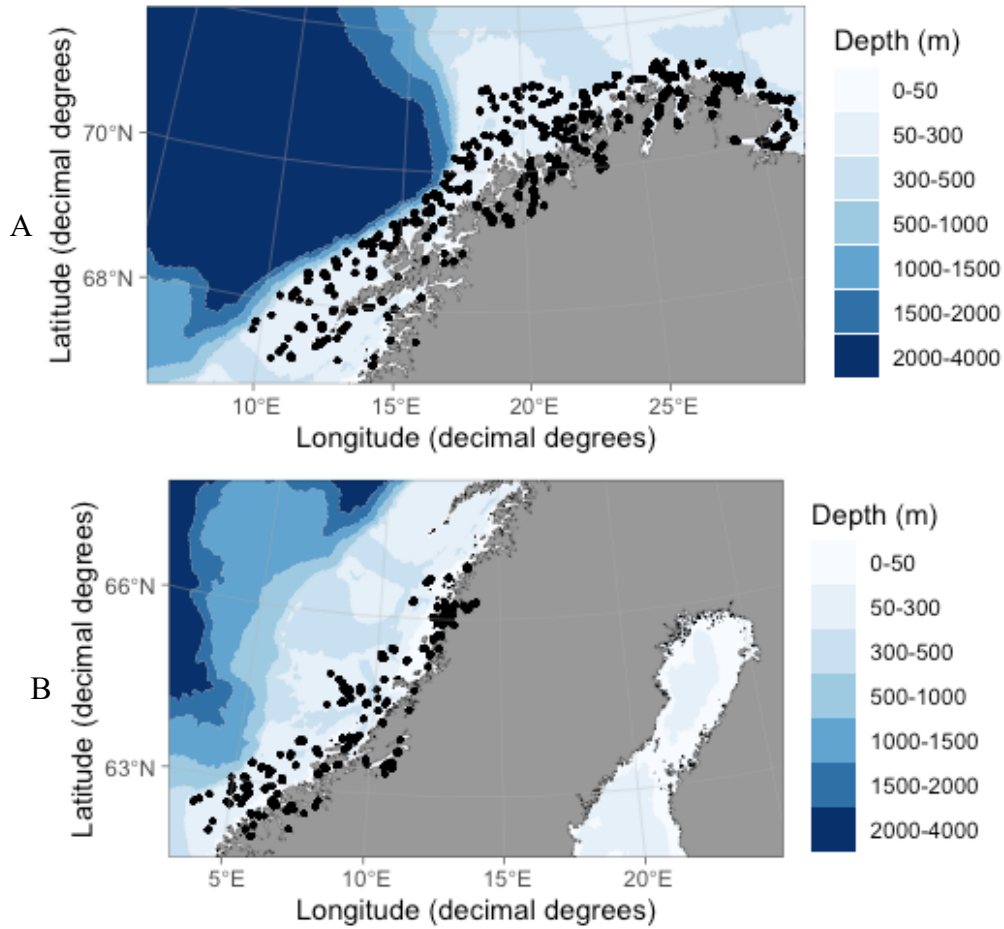


Figure 4: Trawl stations from all years divided into regions a) north of 67°N and b) 62–67°N.

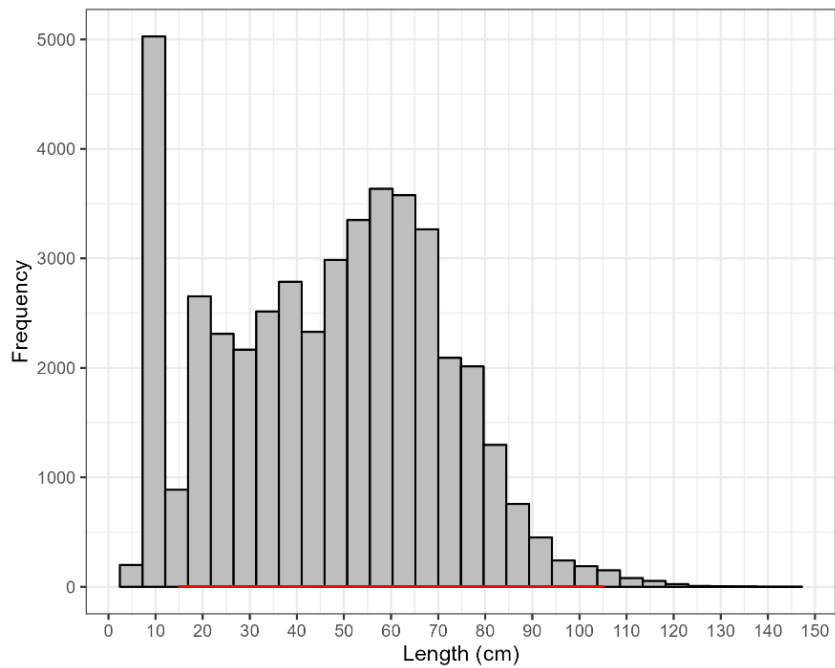


Figure 5: Frequency distribution of all length groups from all years, with the length groups included in further analysis marked with a red line.

2.3 DATA ANALYSIS

To analyse the distribution, Generalized Additive Models (GAM) were fitted to the data. The response in all models was the density of coastal cod per station; this density was either the total density or the density of a particular length group, depending on the analysis. The smooth function for longitude and latitude $s(x, y)$ was included in all models to account for spatial distribution. All models were fitted using a Tweedie distribution since the data included both zeroes and continuous positive values.

To investigate the change in distribution over time, the first model included a spatially varying coefficient, and had the formula:

Total density $\sim s(x,y) + s(x, y, \text{by} = \text{year})$ (Appendix A).

The by-term year was used as both factor and numeric variables. By using a spatially varying coefficient, the changes in distributional patterns over time could be studied. The variable year was used as a factor to create a local linear regression between density and year per year, allowing us to study the changes in distributional patterns every year. With year as a numeric variable, we could analyse the total change in distributional patterns in the time period studied. To constrain how much wiggleness the smooths could have, a k-value was set for the terms. Since the result of this part was not as expected, and it was not included in the main part of the analysis.

The next step was to establish how the density of coastal cod was distributed and how the total density varied over the time series (model 1, table 1). The covariates used were formulated as shown in Table 1 with a smoother for year to see how the density has changed over time regardless of location.

To see if there was any size-dependent change in local density, the density of 3 chosen length groups: 25cm (model 2a, table 1), 55cm (model 2b, table 1) and 85cm (model 2c, table 1) was filtered out and used as a response in three different models using the smooth terms for longitude and latitude, and year.

For further analysis of what drives the change in distribution, the next step was to look at the local changes in total density with changes in temperature and spawning stock biomass using a

by-term in the smooth functions for (x, y) (model 3, table 1). The by-term allows for an interaction between the smooth and a parametric term, creating local linear regressions between density and SSB and between density and temperature.

In the final section of the modelling, more covariates were added to the GAMs of the three chosen length groups (model 4a-c, table 1). This was done to investigate if the density of different-sized coastal cod could be explained by environmental factors. The covariates used in the models were temperature, bottom depth, and height of the sun at the time of the trawl. All covariates were added as smooths. The sun height was added to account for how the light levels influence the availability of different sizes of cod to the trawl and were calculated using the date of the trawl, time of day and geographical position.

All analysis was done in R version 4.2.1 (R Core Team, 2022) using the packages *mgcv* (Wood, 2017) for GAM, and *tidyverse* (Wickham H et al., 2019) and *mgcViz* (Fasiolo M., 2018) for visualisation.

For model validation, the function *gam.check* was used to investigate model fit. The diagnostic plots were visually inspected to see how well the model predicted the observations, and how the residuals were distributed. The deviance explained and the Akaike information criterion (AIC) was used to evaluate the different covariates used.

Table 1: The model formulas used in the analysis with the corresponding model ID.

<i>Model ID</i>	<i>Response (density)</i>	<i>Formula</i>
1	Total density	density ~ s(longitude, latitude) + s(year)
2a	Density of lgr 25 cm	density ~ s(longitude, latitude) + s(year)
2b	Density of lgr 55 cm	density ~ s(longitude, latitude) + s(year)
2c	Density of lgr 85 cm	density ~ s(longitude, latitude) + s(year)
3	Total density	density ~ s(longitude, latitude) + s(year) + s(longitude, latitude, by = ssb(tonn)) + s(longitude, latitude, by = temperature)
4a	Density of lgr 25 cm	density ~ s(year) + s(longitude, latitude) + s(temp) + s(depth) + s(sunheight)
4b	Density of lgr 55 cm	density ~ s(year) + s(longitude, latitude) + s(temp) + s(depth) + s(sunheight)
4c	Density of lgr 85 cm	density ~ s(year) + s(longitude, latitude) + s(temp) + s(depth) + s(sunheight)

3 RESULTS

3.1 CATCH DATA

Over the time series from 2003 to 2021, there were a total of 2192 stations (figure 6). 2021 was the year with the most stations with a total of 177 stations. 1894 of the stations had coastal cod present in the catch.

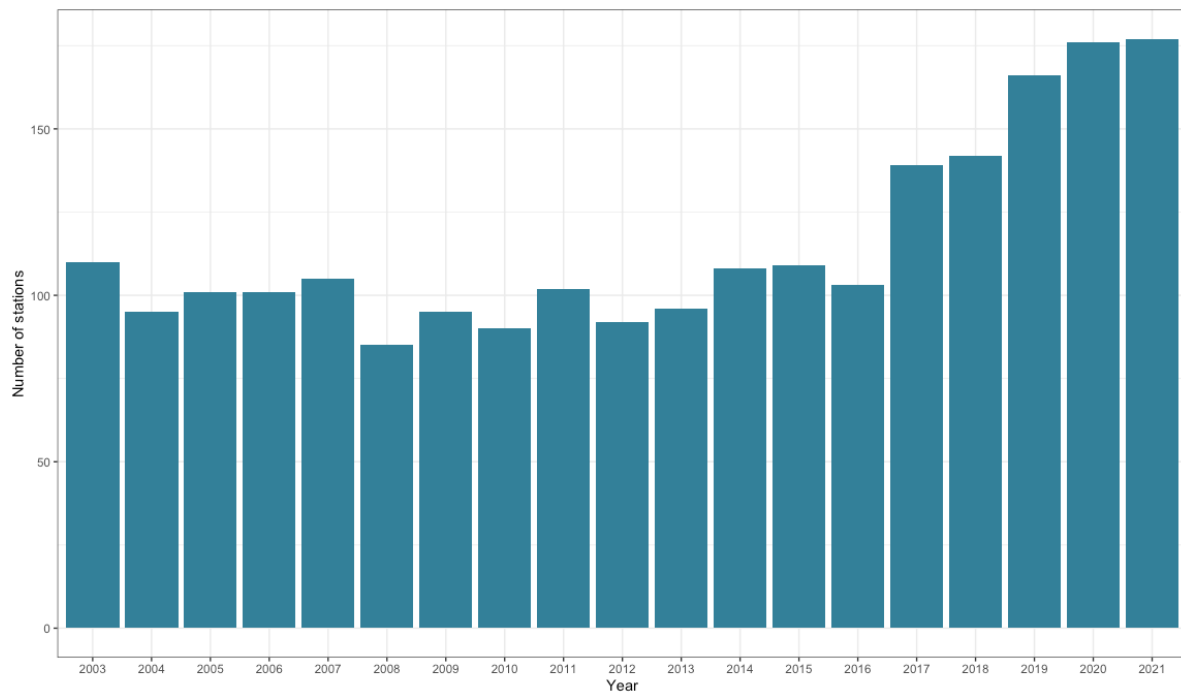


Figure 6: Number of stations (each corresponding to a trawl haul) per year.

Figure 7 shows the proportion of trawls containing coastal cod per length group. The figure shows that for the smaller length groups, the proportion of coastal cod was larger. Within each length group, there was more observations with 100% coastal cod than any smaller proportion.

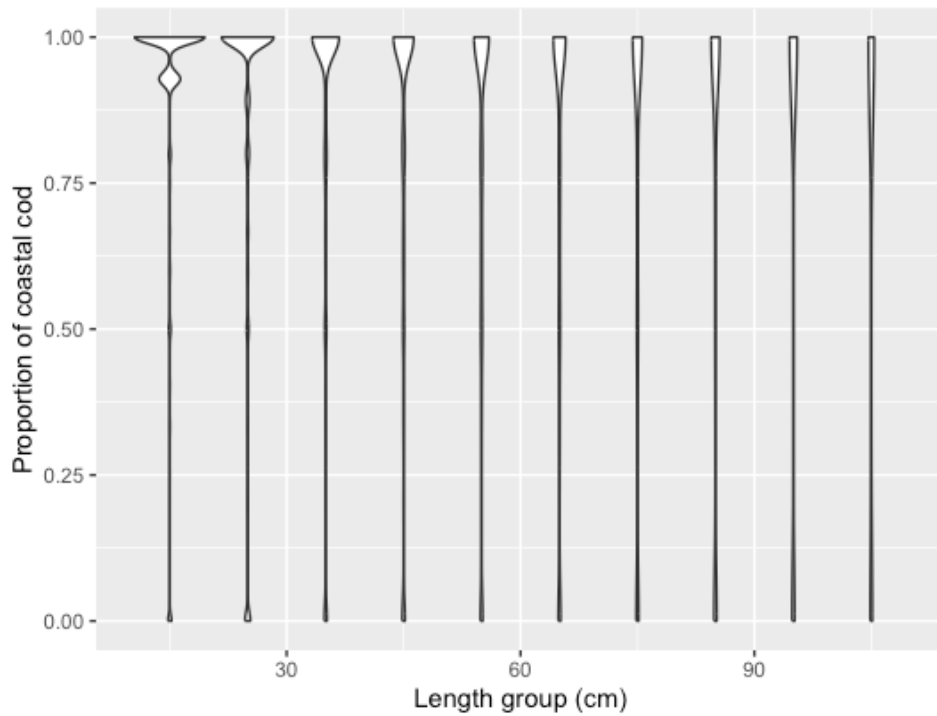


Figure 7: Proportion of trawls with coastal cod present per length group (cm) for all years.

The spawning stock biomass of coastal cod has fluctuated during the time period studied (figure 8). The highest estimated SSB was in 2014, after which it has generally decreased, possibly showing a small increase in later years.

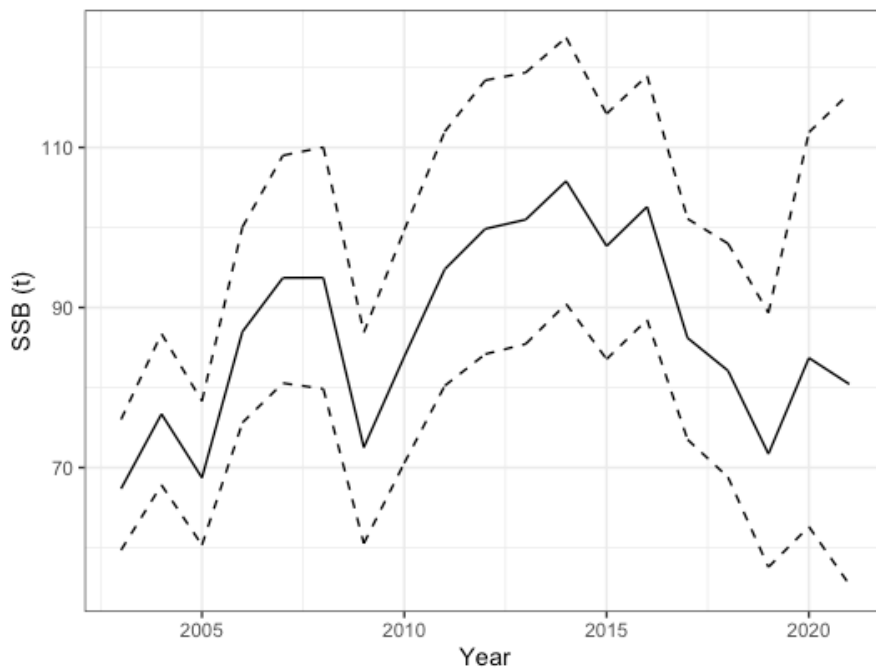


Figure 8: Spawning Stock Biomass (t) in the period 2003 to 2021 from the 2022 stock assessment of coastal cod north of 67°N (ICES, 2023a). The dashed lines show the 95% confidence interval.

The temperature has fluctuated some in the years 2003–2021 (figure 9). The station with the lowest temperature is from 2006 at between 1–2°C, while the highest temperature observed was in 2016 at approximately 12°C. The median from each year is somewhere in the interval 6–9 °C. The warmest temperatures were recorded around Lofoten and generally in the southern region of the study area. The coldest temperatures were observed in Varangerfjorden and the northernmost part of the study area (Appendix B, figures 1 and 2).

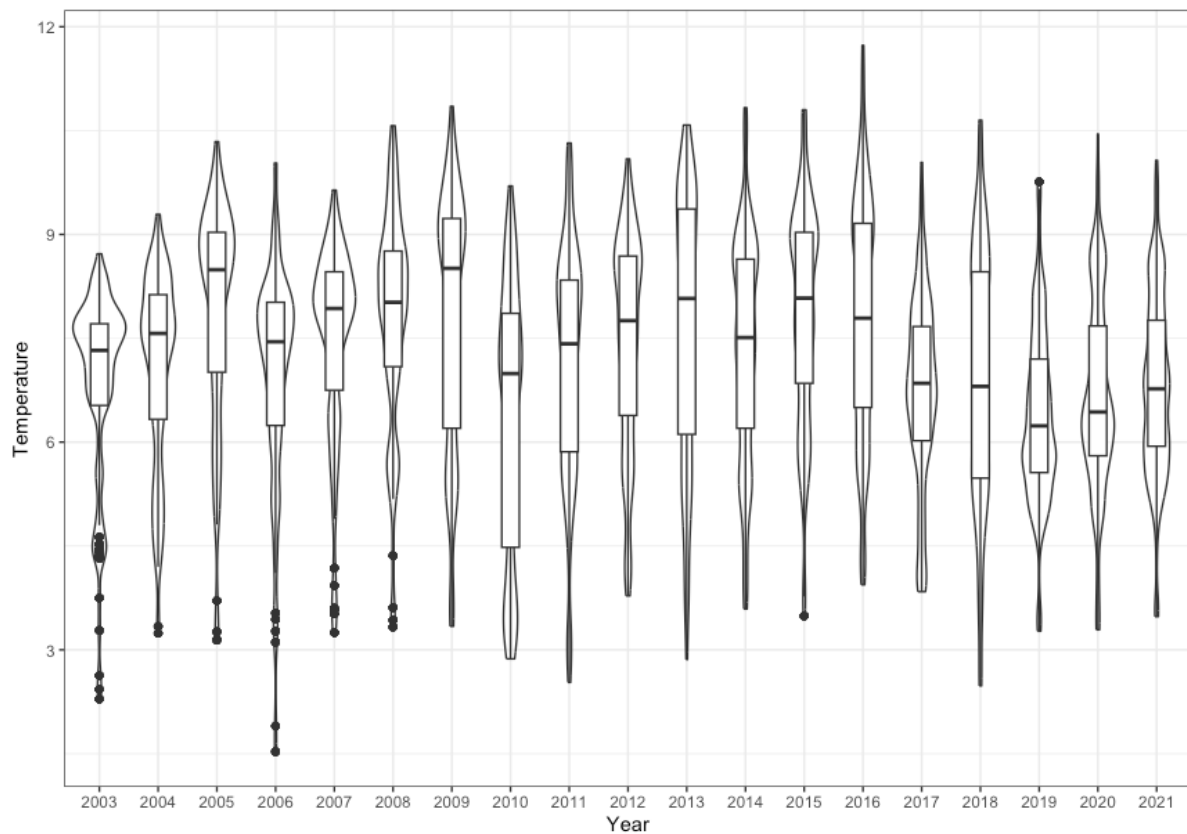


Figure 9: Change in temperature (°C) over time per station. From 2003–2021. The boxplots show the median (bold line) and the 1st and 3rd quantiles of the observed temperature each year. The violins show how the observations are distributed, with high densities where the violin is wide.

The bottom depth at which it was trawled does not vary much from year to year (figure 10), as expected with most stations being placed at fixed locations. The deepest station recorded was in 2011 at approximately 560m deep. At least one station below 500 meters was sampled in all but 2 years since 2007. The median bottom depth sampled is between 150-200 meters for all years except 2018 when it was just below 200m. The density of observations at each depth is higher at shallower depths (<300m) and decreases with increasing depth.

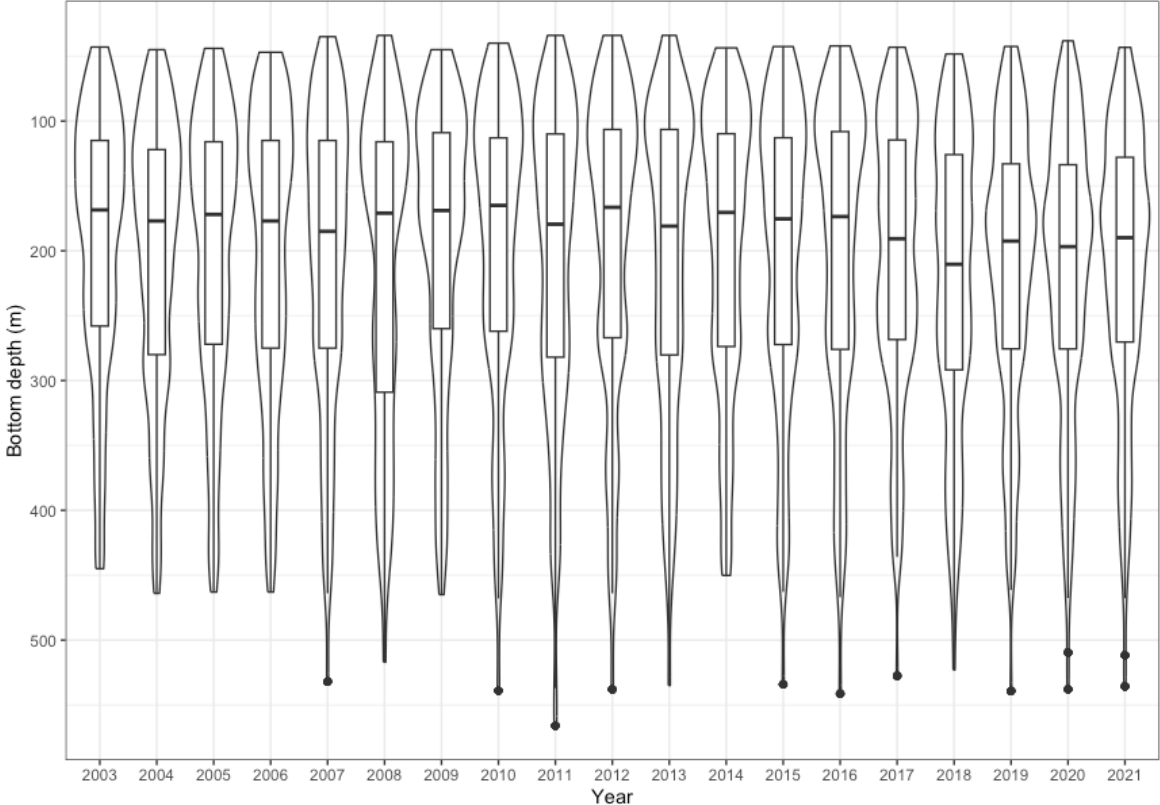


Figure 10: The sampled bottom depths recorded over the years 2003–2021: Boxplots show the median (bold line) and 1st and 3rd quantiles of the observations. The violins show how the observations are distributed, with high densities where the violin is wide.

3.2 SPATIAL AND TEMPORAL VARIATIONS IN DENSITY

Appendix A shows the result of the analysis with year as a spatial variable coefficient, investigating if there have been any changes in distribution over time. It was used in two separate formulations: year as a factor and as a numeric variable. When using year as a factor, the model made a distribution pattern for each year (appendix A, figure 1). The spatial pattern varied very little. When including the spatial variable coefficient as a numeric variable, the model tests a local linear regression between density and year (appendix A, figure 2). The term spatial smooth term $s(x,y)$ was included to represent the average density distribution but was not significant in this model. The results of this showed that it was difficult to separate the average distribution pattern from the small changes over time. When limiting how much the smooth functions could vary, by changing the k-value, for both the spatial smooth term including a spatial variable coefficient $s(x, y, by = year)$ (appendix A, figure 3) and for both smooths $(s(x,y) + s(x,y, by = year))$ (appendix A, figure 4) it resulted in a significant p-value for the spatial smooth term but not for the spatial variable coefficient. The term $s(x,y)$ was then removed from the model (appendix A, figure 5) and the results showed that there is a small increase in density over time close to the coast, but the slopes of the regression between density and year are small.

Figure 11 shows the modelled distribution of coastal cod along the coast of Norway. The model shows that the density of coastal cod is higher along the coast than out towards the Norwegian Sea and Barents Sea, and the density was highest within the fjords. The density has fluctuated over time (figure 12), with a decrease from 2003 to 2006, an increase from 2006 to 2014, and a decrease from 2014 to 2018. In later years, 2018-2021 the total density was somewhat stable. The figure indicates that the response is not linear with year. Both smoothers in this model were significant ($p < 0.001$, table 2). The model explained 42.9% of the deviance.

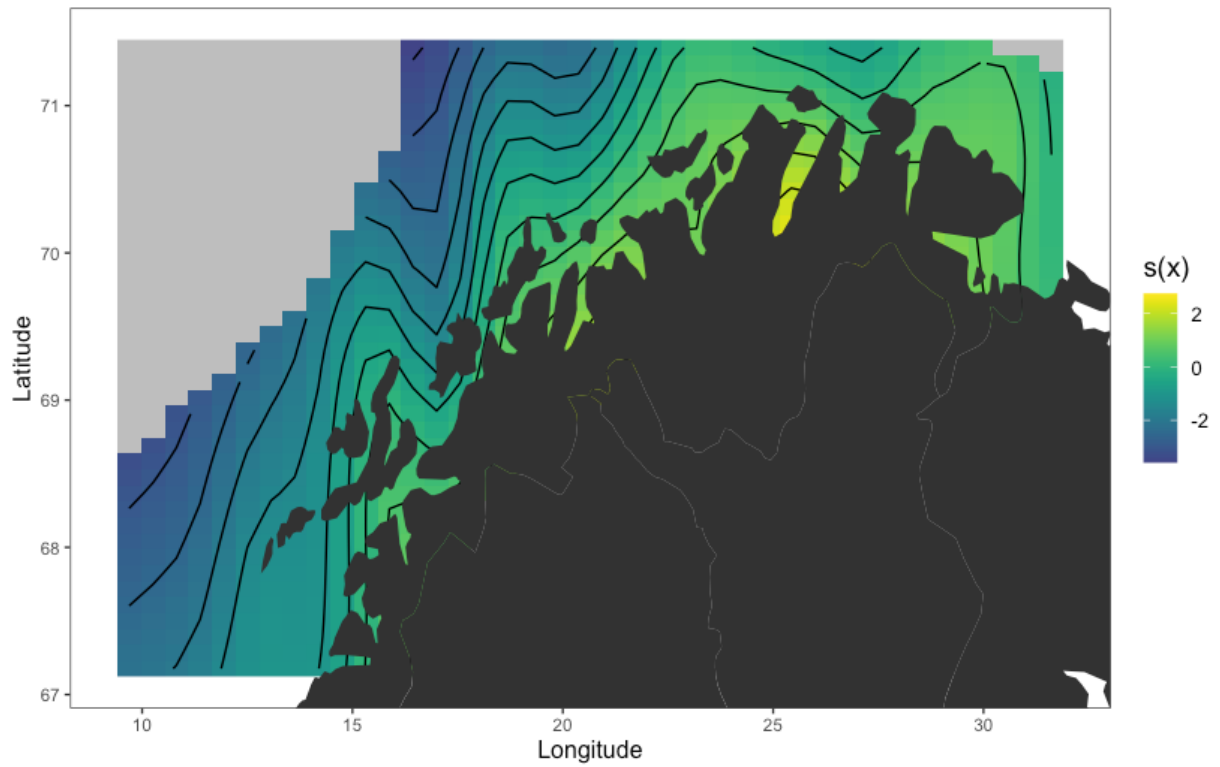


Figure 11: Model 1. Density of coastal cod along the coast of Norway (north of 67°N). The colours indicate the geographical pattern of density, with yellow indicating the highest density, and blue indicate lowest density. Numbers on the legend represent the deviation from the average density (0) on a log link scale.

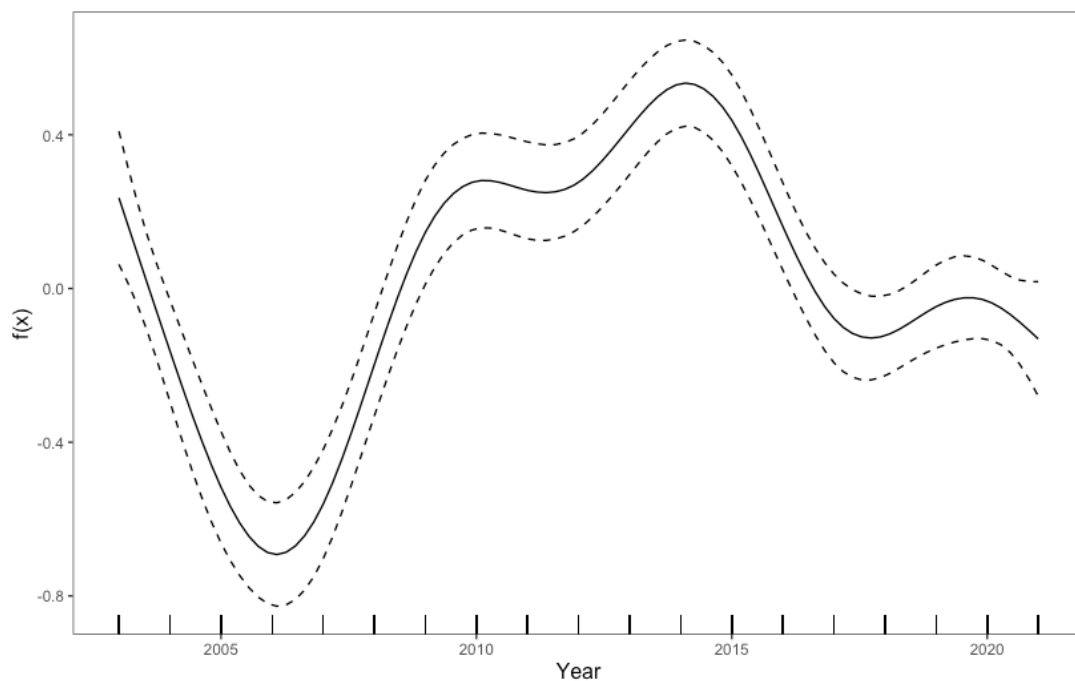


Figure 12: Smooth function of changes in local density over time. The y-axis shows deviations from the average density (0 on the y-axis) on a log link scale for changing values on the x-axis. The dotted line shows the 95% confidence interval of the smooth estimate.

The density for the three length groups chosen (figure 13) showed some similar spatial trends with higher-than-average density closer to the shore and a decrease outwards to the Norwegian Sea. For length groups 25 cm (figure 13A) and 55 cm (figure 13B), the density was high around Lofoten, Langøya and Andøya. The 55 cm length group also occurred in higher density in the coastal areas stretching towards the Barents Sea. The same was observed for the 85 cm length group (figure 13C), but with a smaller deviation from the average density for the length group. The spatial smooth term was significant for all three models (p -value < 0.001 , table 2).

The overall density over time (figure 14) had the greatest fluctuations for length groups 25 cm (figure 14A) and 85 cm (figure 14C), whereas the length group 55 cm (figure 14B) showed a relatively more stable variation in density. The length groups 25 cm and 85 cm showed similar trends with a decrease from 2003 to approximately 2006, followed by an increase to approximately 2014. The smallest length group in the latest years of the time period had an increase from 2019–2021, whereas the largest length group had a decrease over the years starting in the year 2014. 55 cm cod shared some of the same fluctuations seen for the largest length group but with smaller amplitude variations. The covariate year was in all three models significant (p -value < 0.001 , table 2).

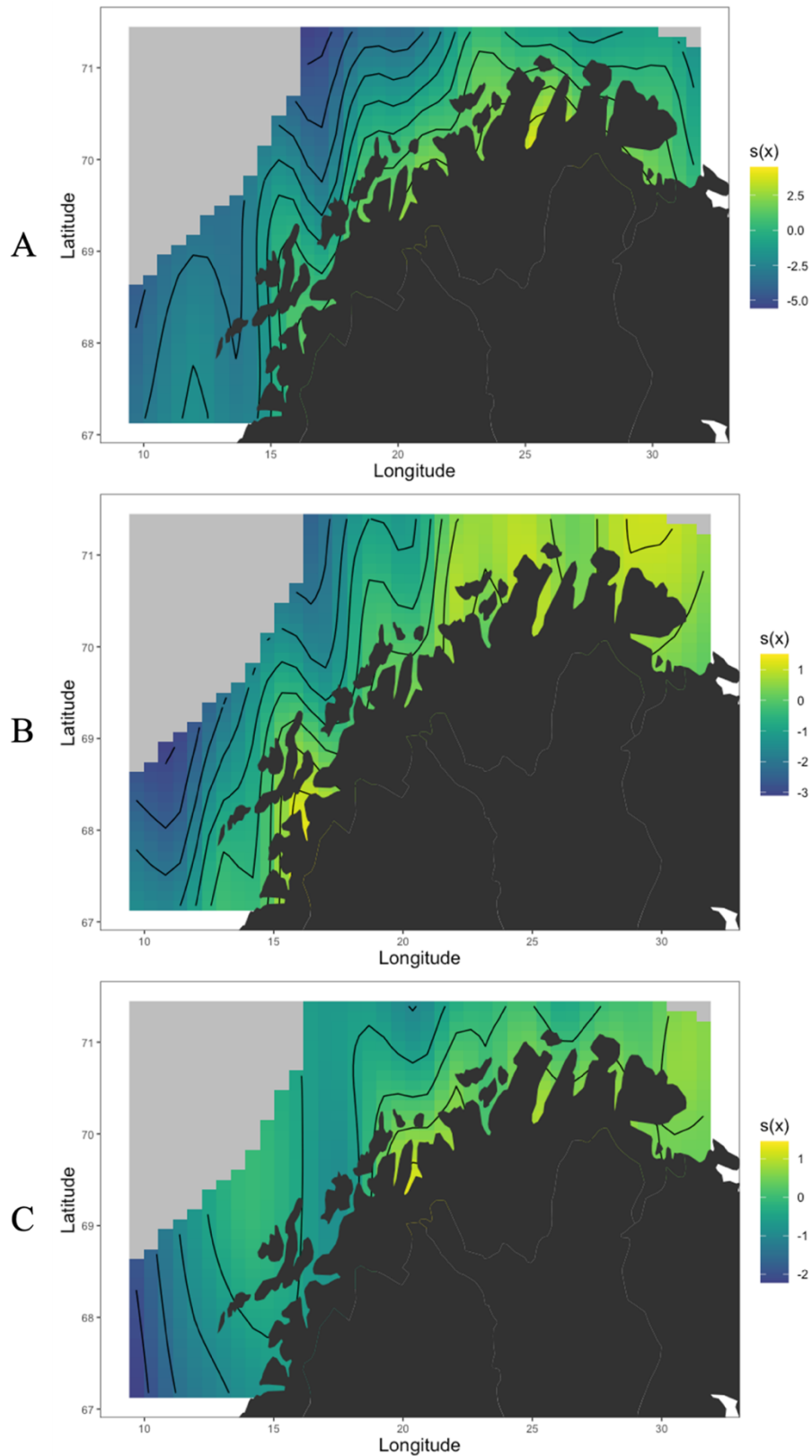


Figure 13: Model 2. Total density for length groups a) 25cm, b) 55cm and c) 85cm. The colours indicate the geographical pattern of density, with yellow indicating the highest density, and blue indicating the lowest density. Numbers on the legend represent the deviation from the average density (0) on a log link scale.

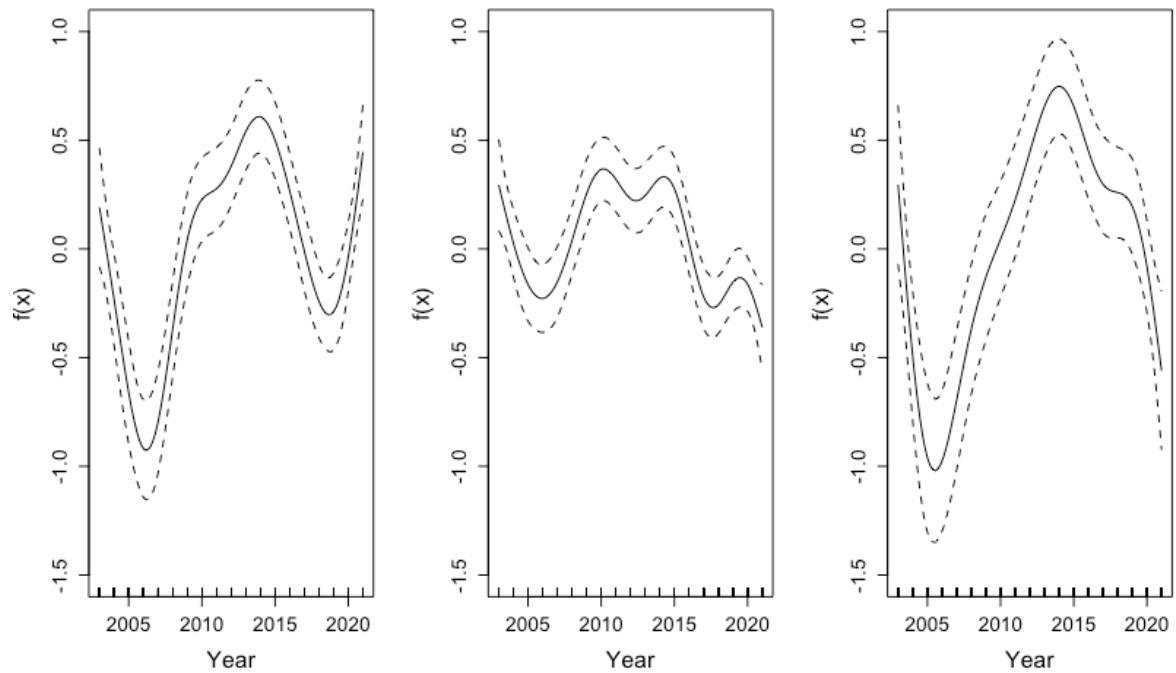


Figure 14: Smooth functions for the density of length groups a) 25cm, b) 55cm and c) 85cm as a function of year. The y-axis shows deviations from the average density (0 on the y-axis) on a log link scale for changing values on the x-axis. The dotted line displays the 95% confidence interval of the function.

3.3 INVESTIGATING WHAT DRIVES A CHANGE IN DISTRIBUTION

Figure 15 illustrates the impact of spawning stock biomass (SSB) and temperature on the distribution of coastal cod. Areas where the increased SSB results in an increase in density (figure 15a) are roughly the same areas in which a similar density response is associated with reduced temperature (figure 15b). With increased spawning stock biomass, the density increases in areas stretching out towards the Norwegian Sea in the west. The model also shows an increase in density in Porsangerfjorden and the adjacent area. With increasing temperature, the model shows an increase in density in the coastal area as far south as Bodø, but a decrease in density in the northern fjords such as Porsangerfjorden and Laksefjorden. The smooth terms for both temperature and SSB had a significant effect (p -value < 0.001), and the model explained 49.8% of the deviance.

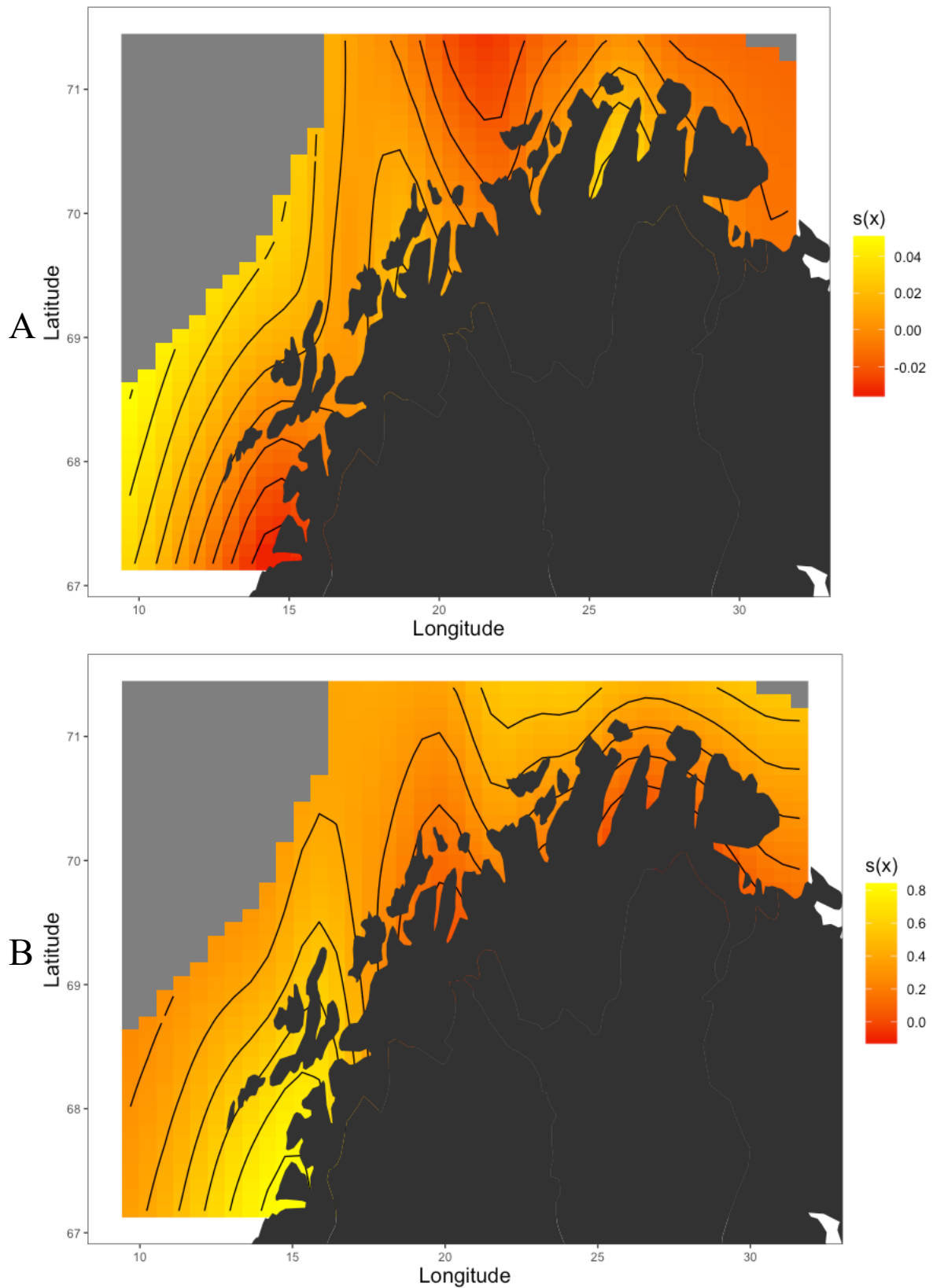


Figure 15: Model 3. GAM smooth showing the change in total density with changing a) spawning stock biomass and b) temperature. The colours and values indicate the magnitude of the slope of the linear regression between a) SSB and b) temperature with yellow being a positive slope and red showing a negative slope.

The three models including environmental covariates for the three length groups 25cm and 55cm and 85cm showed a decrease in deviance explained with increasing size, with the model for the smallest length group having the highest deviance explained (table 2). For all 3 length groups, the overall density increased with increased temperature (figure 16). The 55 cm length group has the steepest increase in density with increased temperature (16b). All three length groups showed a decrease in density with temperatures $<8^{\circ}\text{C}$. Temperature had a significant effect for the 55cm and 85 cm groups with a p-value of <0.001 and <0.01 respectively. The temperature did not have a significant effect for the smallest length group (25cm).

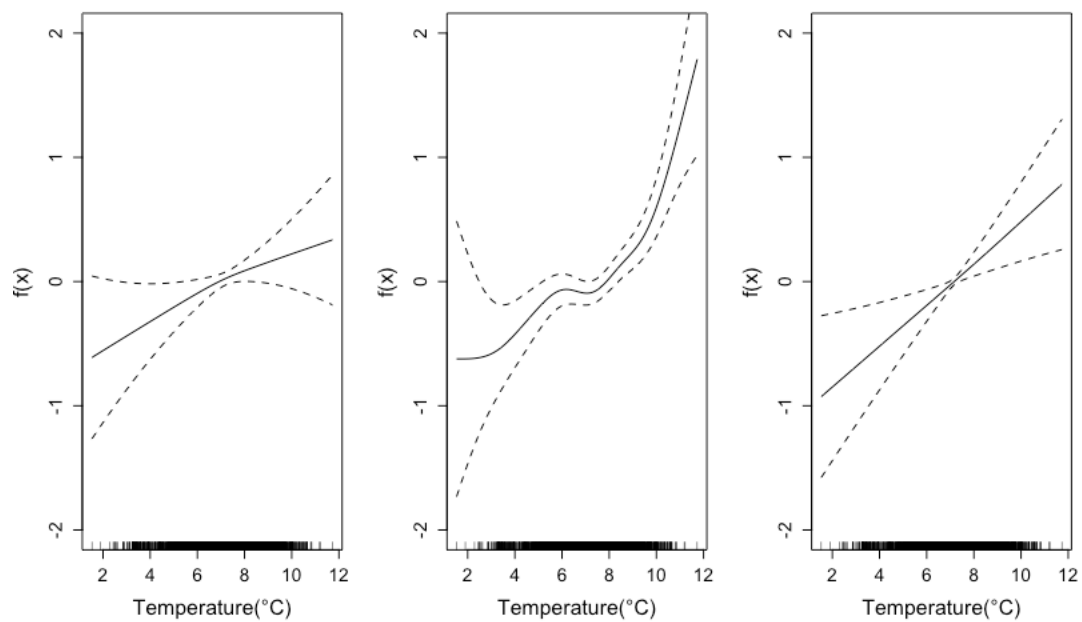


Figure 16: Model 4. Estimated smoother for temperature, for length groups a) 25cm, b) 55cm and c) 85cm. The y-axis shows deviations from the average density (0 on the y-axis) on a log link scale for changing values on the x-axis. The dotted lines display the 95% confidence interval.

All three length groups exhibited a decrease in density with increasing depth (figure 17). The depth-effect was significant for all three length groups with a p-value <0.001 for 25cm and 55cm. The 85cm length group had a p-value of <0.01 , which is less significant than the two others. The two smallest length groups had a greater decrease in density with increasing depth below approximately 300m than the largest length group, which showed a more stable decrease with increasing depth.

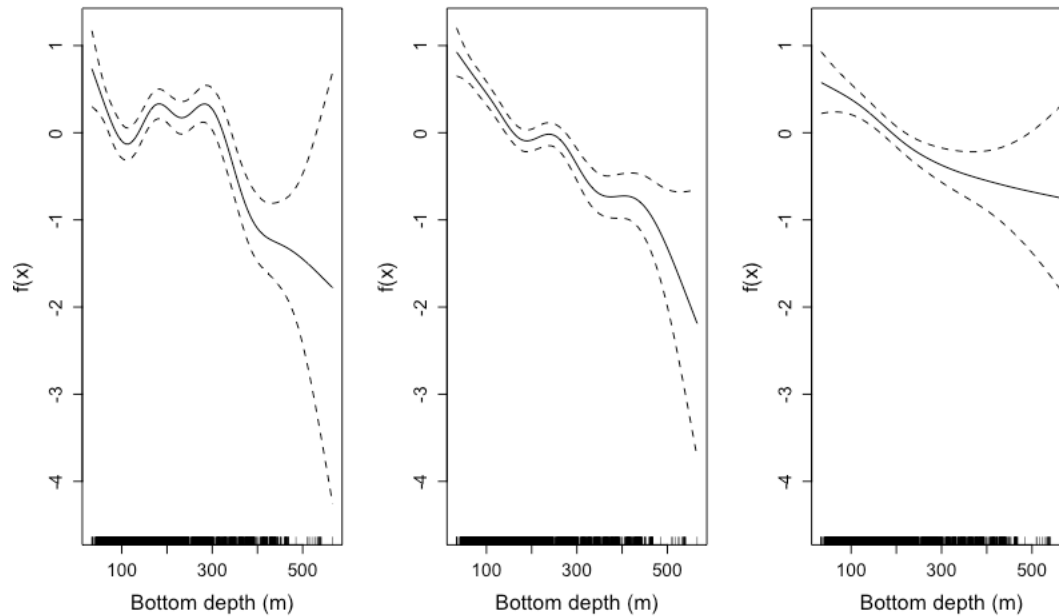


Figure 17: Model 4. Estimated smoother for bottom depth for length group a) 25cm, b) 55cm and c) 85cm. The y-axis shows deviations from the average density (0 on the y-axis) on a log link scale for changing values on the x-axis. The dotted lines display the 95% confidence interval.

Figure 18 shows the effect the light has on the density of cod caught. The effect for the smallest length groups (figure 18a) is less clear than for the bigger length groups, showing an increase in density at both day and night and a decrease around sun height at 0 (sun at the horizon). The length groups 55cm (figure 18b) and 85cm (figure 18c), show an increase in density with increasing light. All three models showed that sun height had a significant effect on the density (p -value < 0.001 for the 55 cm and 85 cm length groups, 0.0433 for the 25cm length group).

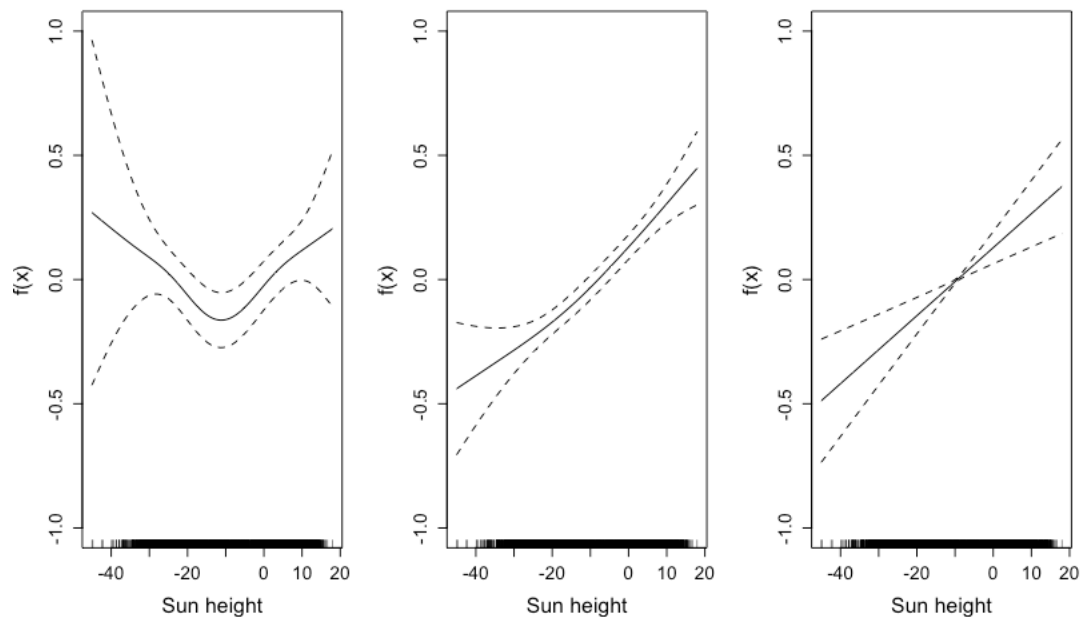


Figure 18: Model 4. Estimated smoothers for sun height for length group a) 25cm, b) 55cm and c) 85cm. The y-axis shows deviations from the average density (0 on the y-axis) on a log link scale for changing values on the x-axis. The dotted line displays the 95% confidence interval.

3.4 MODEL COMPARISON

Model 1 included only the spatial smoother $s(x,y)$ as a covariate for the response total density. Model 3 included SSB and temperature as a by-term in the smoother. The results show that they have a difference in deviance explained, where model 3 explains approximately 11% more than the model without the two covariates (table 2). Model 3 has a lower AIC than model 1 (table 2).

Model 2a and 4a, studying the length group 25cm, shows a small increase in deviance explained and a lower AIC when including more covariates (table 2). For the 55cm length group, model 4b explains approximately 14% more of the deviance than what is observed in model 2b (table 2). The AIC is also lower. In the model used for the largest cod, 85cm, the deviance explained

increased from 16% in the initial model to 22.8% when including covariates; the AIC was also lower for the more complicated model (table 2).

When examining the diagnostic plots, the quantile-quantile plots look ok, with some more skew observed for models 1, 3, 2b and 4b compared to the other models (Appendix B). The histogram of residuals looks ok, with a normal distribution centered around 0 for all models. The observed line in the residuals vs linear predictor represents the zero values in the data. The models have some difficulty predicting the highest values, which is seen in the response vs. fitted values for all model diagnostic plots.

When comparing the model fit for models 1 and 3, the diagnostic plots show no evident change. The model fit for the 85cm length group improved when including covariates (models 2c and 4c, Appendix B, figures 4 and 8), but the other two length groups did not show any change in model fit (Appendix B).

Table 2: Summary of model output with the corresponding model ID. Different colours indicate different responses, and the models with corresponding colours are comparable.

Model ID	Deviance (%)	AIC	Longitude, latitude	Longitude, latitude	Year		Temperature		Bottom depth		Sun height		Longitude, Latitude, by = SSB		Longitude, Latitude, by = Temperature	
			p-value	df	p-value	df	p-value	df	p-value	df	p-value	df	p-value	df	p-value	df
1	42.9	31515	<0.001	26.649	<0.001	8.051										
2a	48.2	15130	<0.001	26.263	<0.001	7.599										
2b	22.3	20043	<0.001	25.261	<0.001	7.486										
2c	16	7601	<0.001	19.450	<0.001	7.008										
3	53.3	31066	<0.001	12.23	<0.001	8.07							<0.001	20.91	<0.001	19.26
4a	51.6	14943	<0.001	25.33	<0.001	7.47	0.0935	1.45	<0.001	6.86	0.0433	2.97				
4b	36.7	19526	<0.001	21.80	<0.001	7.53	<0.001	4.9	<0.001	6.14	<0.001	1.62				
4c	22.8	7467	<0.001	16.69	<0.001	6.90	<0.01	1.07	<0.01	2.27	<0.001	1.00				

4 DISCUSSION

The aim of this study was to investigate if the distribution of coastal cod has changed over time and see if the change could be explained by different environmental factors. I also looked at how the environment affected different length groups' distribution. My working hypothesis was that there will be a change in distribution with increasing temperature and increasing spawning stock biomass which would result in an increased depth range and wider spatial distribution. I also hypothesized that larger individuals, compared to smaller individuals, would occupy 1) cooler waters and 2) deeper waters.

The results showed that there has not been a significant change in distribution and that the density has changed over time, but not between areas. The density was higher along the coast and decreased outwards to the Norwegian Sea, and the density fluctuated over the period studied. As expected, increasing spawning stock biomass seems to result in a wider distribution. An increased temperature also seems to result in a wider overall distribution, with the smallest increase in density in the fjords and, surprisingly, the highest increase in the area around Bodø.

In analysing the distribution of different length groups, the models showed some of the same trends as the model for total density, where the smallest length group showed the highest density towards the fjords, and the two larger length groups showed a wider distribution with density around average for the length group stretching out towards the Norwegian Sea.

4.1 CHANGES IN DENSITY FOR ALL COD

Our results showed that the relative distribution of density has not changed significantly during the time period studied. Even though there have been changes in density, there is only a small change in distribution close to the coast (Appendix A).

The distribution pattern was as expected, with higher density in fjords and the coastal areas, with decreasing density out towards the Norwegian Sea. The NCC is adapted to the coast and is more stationary than for example the NEAC which is shown to perform long-distance migrations (Michalsen et al., 2014). In contrast, the NCC can have restricted ranges even within the same fjord system, which have been shown for fjords like Ullsfjord and Sørffjord and further south in Norway (Berg & Pedersen, 2001).

Temperature increases seem to increase density in areas stretching from the coast to the Barents Sea. This is according to the working hypothesis that the coastal cod will experience a northward shift in distribution with increased temperature. There is, however, a limit to how far north the population can distribute before it no longer is in a coastal area. This gives reason to believe that instead of the NCC leaving its coastal habitat entirely, could result in a shift to colder coastal habitats or have more severe consequences such as poor recruitment and higher mortality rates. According to Righton et al. (2010), the cod are able to sustain large changes in temperatures, and the hypothesized northward shift in distribution might be a combination of several factors like prey availability. However, it is worth noting that even though the cod could survive and grow in a wide temperature range, an increased sea temperature could potentially influence the recruitment success (Brander, 2000). The temperature can affect recruitment success in several ways. Examples of this could be the effects on mortality, growth, and metabolic rates in larval stages. Temperature can also affect prey availability such as the abundance of zooplankton, which is crucial for the survival of larvae (Fouzai et al., 2015). The results also showed a decline in density with increasing temperature in some of the fjords found in the northern area. This could be due to high temperatures registered in years of low density in this area, or that the local population is more affected by an increase in temperatures. The results also show an increase in density with temperature in the most southern coastal area, which is unexpected. This could be a result of increased stock biomass in years with high temperatures in these areas. There are generally warmer temperatures recorded in this area (Appendix C, figures 1 and 2), which could result in this positive effect.

The spawning stock biomass seems to have the opposite effect on density, compared to temperature (figure 15). The distribution seems to extend further out from the coast towards the Norwegian Sea in the west, along with in some of the northern fjords when SSB increases. The extended distribution towards the west is probably due to density dependence. Increased competition may drive the coastal cod to habitats that are less favourable in terms of environmental factors (Swain & Kramer, 1995). Demersal fish like cod are found in an environment that is heterogeneous, like for example the coastal area of Norway. It is therefore difficult to predict what kind of habitat they will migrate to in the case of increased biomass and increased competition. But given the results, increased competition could potentially explain an expansion in distribution. It is also worth noting that competition is not the only density-dependent factor that plays a role in the distribution, but also predation. When the abundance of cod is high, there is more foraging on the young cod, which could explain

variations in the density (Rose, 2019). The increased density in the northern fjords and the area west of Lofoten is probably due to high densities recorded in years with high SSB. These areas could therefore contribute a lot to an increase in stock biomass.

When comparing model 1, using only the spatial term as a smoother, and model 3 which also has spatially varying effects of SSB and temperature, model 3 has a better fit. The model has both lower AIC and explains 11% more of the deviance in the observations, and both spatially varying effects were significant in the model. This suggests that changes in both temperature and SSB could contribute to a change in distribution for coastal cod.

4.2 CHANGES IN DENSITY FOR DIFFERENT-SIZED COD

4.2.1 Trends in density over time

The changes for overall density for the different-sized cod showed for both the smallest and biggest cod similar trends we saw in total density and some of the similar trends for SSB. It appears that the changes in density over time are mostly connected to the changes in density for these two length groups. The 55 cm length group is more stable throughout the year but followed similar curvature as the total density. The density of the smallest and largest individuals used in this analysis is both important for the total density of cod. Recruitment relies on the abundance of small individuals, whereas the largest individuals are important for reproduction. The length at which 50% of the cod north of 67°N mature is 60cm (ICES, 2023a; Staby et al., 2020), so many of the individuals in the 55cm length group and all in the 85cm length group have matured. The 85cm length group and a big portion of the 55cm length group make up the spawning stock biomass. This could be why the 85cm length group is so strongly connected to the trends we see in the total density, and the 55cm length group is not as strongly connected but follows similar trends.

4.2.2 Temperature

The temperature did not have the expected effect on density. I hypothesized that different-sized cod would occupy different temperature ranges, with lower temperatures for larger cod. The results show that the density of all three length groups increases with increasing temperature, with both the smallest and biggest cod showing a similar trend in the smoother visualized for temperature. The uncertainty is relatively high for both length groups for both ends of the temperature scale, and the temperature does not have a significant effect on the density of the

25cm length group. The 55cm length group has the largest increase in density with increased temperature.

When studying the different temperatures observed at the trawl stations (Appendix C, figures 1 and 2) there is a difference in the range of temperatures measured between different fjords, in addition to a difference between the north and south of the area. The local populations of cod seem therefore to experience different temperature ranges during the time period studied. The temperature has an influence on the growth rate, where higher temperatures result in higher growth rates for cod (Berg & Albert, 2003), and studies have shown that larger cod has better growth rates at lower temperatures than small cod (Pedersen & Jobling, 1989). There are other factors that decide which temperature ranges the cod resides in because growth rates alone do not determine the habitat choice. For example, during ontogeny, when the cod leaves its nursing habitat for deeper, cooler water, the benefit of increased growth at optimal temperatures may increase predation risk (Jordaan & Kling, 2003).

Righton et al. (2010) found that Atlantic cod did not seem to reside in temperatures that are optimal for growth, but that the temperature preference could be a result of competition at high densities, or food availability (Righton et al., 2010). In our analysis, we found that temperature was not significant for the smallest length group, which means that there is something other than temperature that can explain how the small fish are distributed. This could be, for example, shelter from predation (further discussed later). The largest cod used in the analysis did not show a clear effect of temperature, even though the temperature was significant. It could be an indication that this length group is found in a large range of temperatures. The temperature had the largest effect on the 55cm length group, which had the largest increase in density with increasing temperature. The uncertainty was high in the lower part of the temperature scale, which is probably due to a small number of observations at $<3^{\circ}\text{C}$, but it seems as if the temperature is an important factor for explaining the distribution of this length group.

4.2.3 Depth

All length groups depicted a decrease in density with increasing depth, but the largest cod had a smaller decrease than the two other length groups. There was a relatively small difference between the 25cm length group and the 55cm length group in terms of smooth functions for density by depth, but they both showed lower relative densities at large depths like 500m, in comparison to the largest length group. There was however a small number of stations at this

depth. The density of the smallest cod was stable from 50m to 300m and then exhibits a large decrease, which could indicate that the preferred depth for cod of this size prefers depths <300m. The 55cm length group showed the largest decrease in density around 400m, which could indicate that they have a wider depth range than the small fish. The largest cod, 85cm length group, exhibited the largest depth range of the three, with a relatively stable density down to 550m depth.

There are several things that can explain the difference we observe in depth ranges. As discussed earlier, temperature is an important factor, and the water temperature varies at different depths. In a study by Carla et al. (2015), they found that smaller cod could withstand higher temperatures than larger cod because larger fish could experience issues with oxygen at high water temperatures (Carla et al., 2015). This could help explain the differences in depth ranges for the smallest and biggest cod in this thesis. The differences in depth could also be a result of the different kinds of habitats the cod resides in during its lifetime. Cod is not the only fish that uses coastal areas as nurseries, and this could be due to the vegetation that is found here. The vegetation and sand bottom provides shelter from predation and is particularly important for cod during their early years (Borg et al., 1997). During the ontogeny, the cod moves to greater depths with lower temperatures. The greater depths have, in comparison to shallow waters, lower food supplies, but the colder temperature lowers metabolic costs (Macpherson & Duarte, 1991).

It seems evident that both temperature and depth are density-independent factors that explain how the different-sized cod are distributed. Even though the results did not show a clear difference in temperature ranges, there was a clear difference in depth preference. It seems as if the migration from shallow waters with greater food supplies, warmer temperatures, and shelter from predation into deeper waters with lower temperatures and lower metabolic costs is a trade-off (Swain, 1993).

The deviance explained increased for all three length groups when temperature, depth and light were included in the models, but the increase was largest for the 55cm length group. The smallest cod had relatively high deviance explained compared to the other two length groups, with approximately 50%, but the difference from model 2a to 4a was small suggesting that the location plays a role in the spatial variations in density, but the temperature, depth and light do not contribute so much. Which can be associated with the habitat choice of the smaller cod. As

mentioned earlier, the smaller cod has been associated with habitats containing vegetative cover used for protection against predation (Dunlop et al., 2022). Even though Dunlop et al. (2022) sampled at shallower depths than what was done in this thesis, it could provide some answers as to why the location explains more of the spatial variations for the 25cm length group. The models for the largest cod do not provide a good fit, with low deviance explained for both models 2c and 4c. This suggests that the chosen covariates and location do not help explain the spatial variations in density very well. As mentioned, the model for the 55cm length group was much better when more covariates were included, which could mean that the environmental covariates do provide some explanation for the spatial variations in density for this length group.

4.3 LIMITATIONS

The models were used as a means to explain spatial variations in density, and some of the models did provide a good fit. The diagnostic plots showed that the models have some difficulty in predicting very high values, and if the models were to be used in predicting how the density would change with a changing environment, they would need some improvements.

Sun height was included as a covariate to account for the differences in the availability of cod during different times of the day. The two largest length groups both showed an increase with increasing sun height, which means that the density of those length groups was higher when the sun was above the horizon. This could mean that when there was limited light, the density on the sea floor is lower because the cod is located higher up in the water column due to vertical migrations. The same results have been shown by other studies on cod (Kotwicki et al., 2009; Ono et al., 2017). Kotwicki et al. (2009) investigated how light affected the availability of walleye pollock (*Gadus chalcogrammus*) to the bottom trawl and discussed how the pollock performed vertical migrations with a decrease in light levels to optimize their feeding. This could explain the lower densities we observe with low levels of light. The smallest length group show no such clear effect from light levels, which might suggest that the light is not affecting how available the smallest fish are to the trawl. An explanation of this could be that smaller fish is situated in shallower areas and feed on smaller prey like benthic crustaceans that occupy the sea bed, in comparison to larger cod that also feed on mobile prey, like fish (Rose, 2019).

We chose to exclude length groups smaller than 15 cm because they occupy areas that are difficult to sample. The sampling was better for cod larger than 15cm north of 67°N than south

of 67°N. As suggested by Berg and Albert (2003) the smaller cod is situated closer to the shore in areas where trawling is impossible, and there are more unavailable areas south of 67°N. In their study, they proposed that this affected cod under the size of 25cm (Berg & Albert, 2003), and cod ranging from 15–25 cm were included in this analysis.

The temperature used in the models was extracted from the NorKyst-800 model since there was a large distance between the CTD stations compared to the trawl stations. There were some deviations when comparing the modelled depth with the bottom at which the trawl was submerged. Given the complexity of the bathymetry and the resolution of the model, the modelled depth was expected to deviate from the trawled depth in some cases, especially in areas like the fjords. In cases with big differences in modelled depth and trawled depth, the modelled depth was usually shallower than the trawled depth. In areas with a strong thermocline, this means that the temperature used in the analysis could potentially be higher than that experienced by the cod at the sea floor.

4.4 FUTURE RESEARCH

This study contributes some knowledge about what drives changes in distribution in Norwegian coastal cod, but our models do not provide a full understanding of the spatial variations in density. It would be interesting to include other environmental factors in the model, to see if anything else drives the variations, such as fishing activity and seabed substrate. It would also be interesting to see if the distribution could be explained by using the ocean currents present along the coast of Norway. Including other variables in the models could contribute to an improved fit, and the models could be used for predictions.

It is worth noting that the data used in this study were all collected during the same months every year. Including samples taken at different times of the year could account for seasonal variations in distribution, which would also be interesting.

4.5 CONCLUDING REMARKS

It has already been established how important spatial ecology is for the management of cod, and for understanding changes in abundance and behaviour in context with changes in the environment. The use of spatial modelling provides a method that can deal with the complexity of spatial and nonlinear data and allows us to understand how both density-dependent and density-independent influence the abundance or occurrence of fish.

In this study, we found that the distribution of coastal cod in northern Norway has not changed significantly during the period 2003–2021, but that both density-dependent and density-independent factors explain the distribution of the cod. When studying the different-sized cod, the results showed that the cod experience different habitats during its ontogeny, but temperature and depth alone cannot explain the spatial variations observed.

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APPENDICES

APPENDIX A – MODELLING THE CHANGE IN DISTRIBUTION OVER TIME

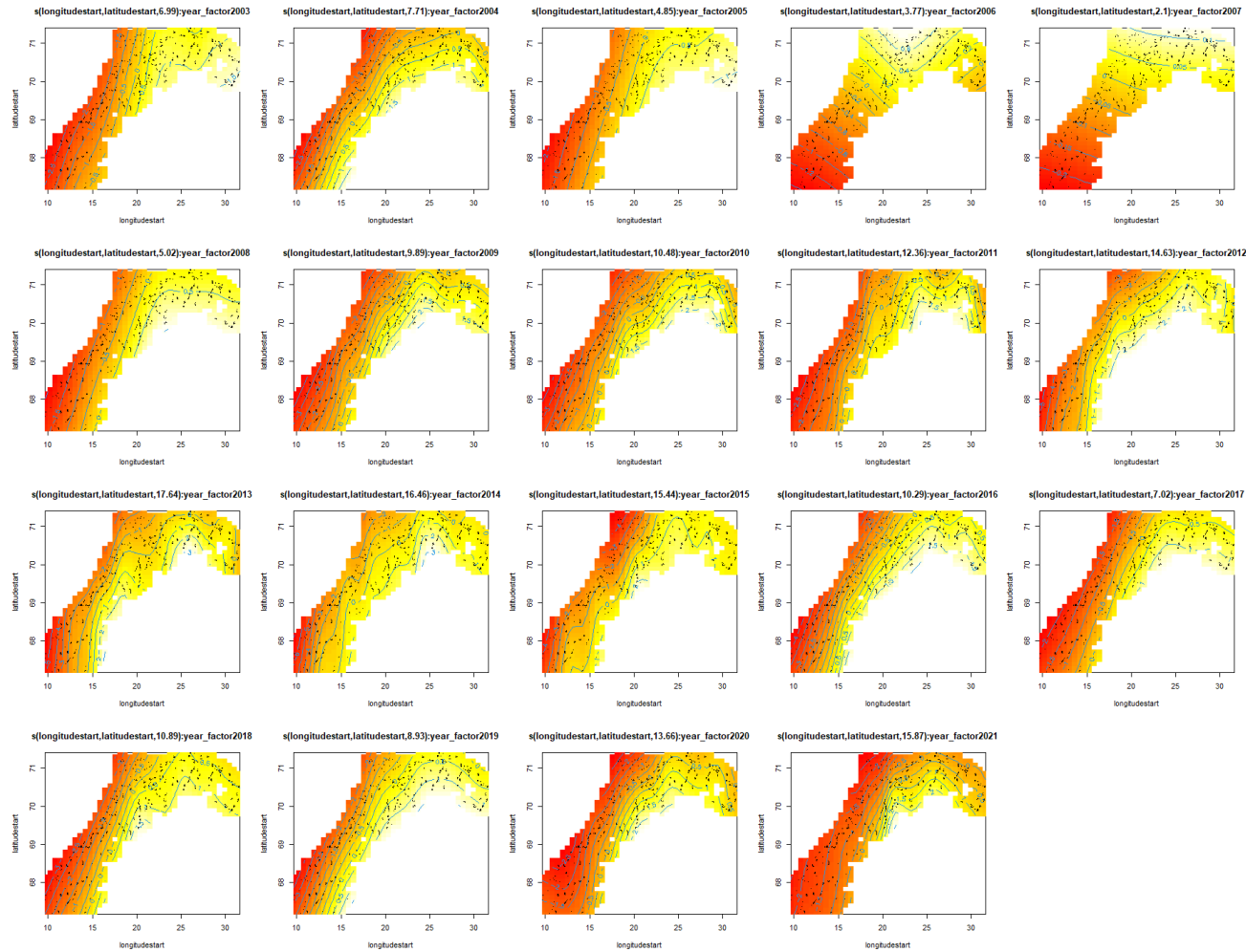


Figure 1: GAM smooth showing the change in total density with year. The colours indicate the slope of the local linear regression between year and density, with yellow showing the highest increase.

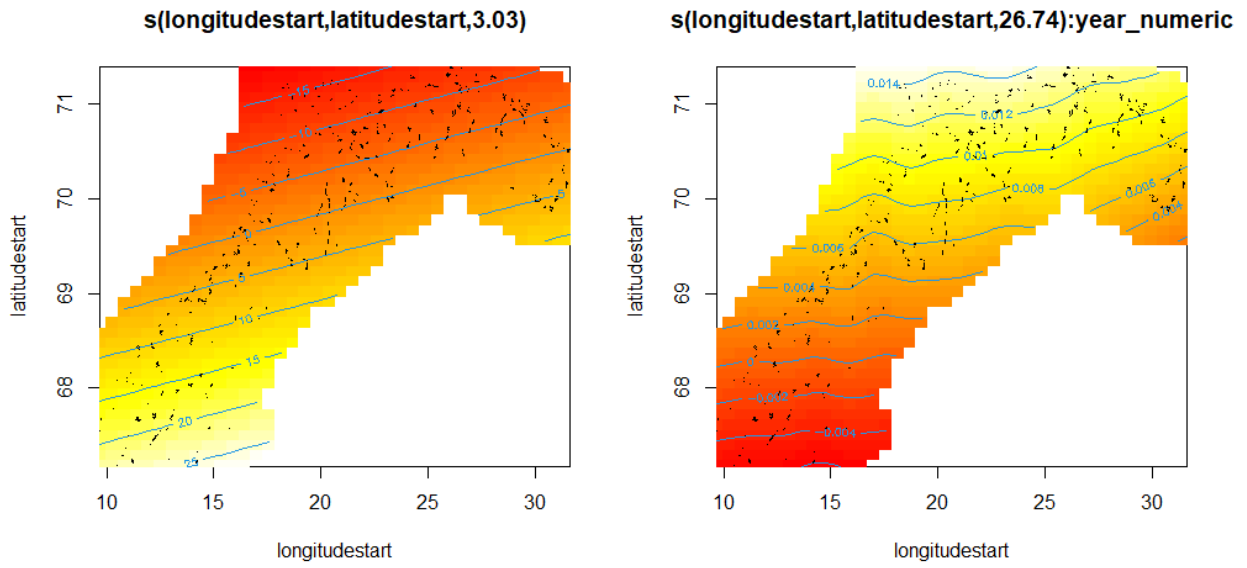


Figure 2: The change in distribution by year on the right, and the spatial pattern on the left, with total density as the response. The term $s(x,y)$ is not significant.

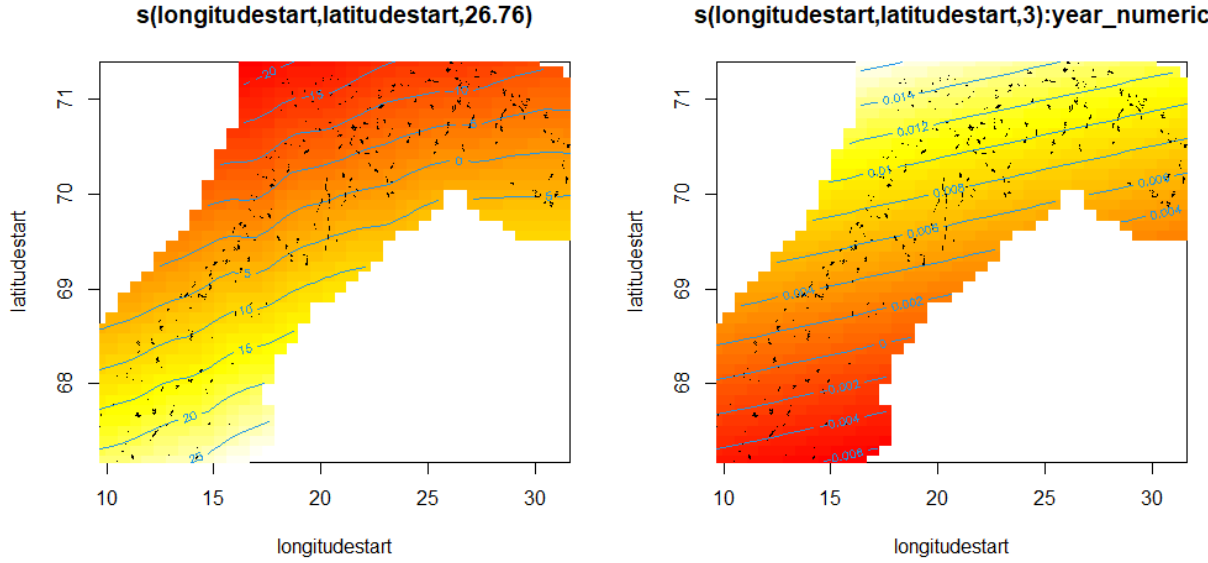


Figure 3: The change in distribution by year on the right, and the spatial pattern on the left, with total density as response. The model includes a k -value for the term $s(x,y, by = year)$ (left). The term $s(x,y, by = year)$ is not significant.

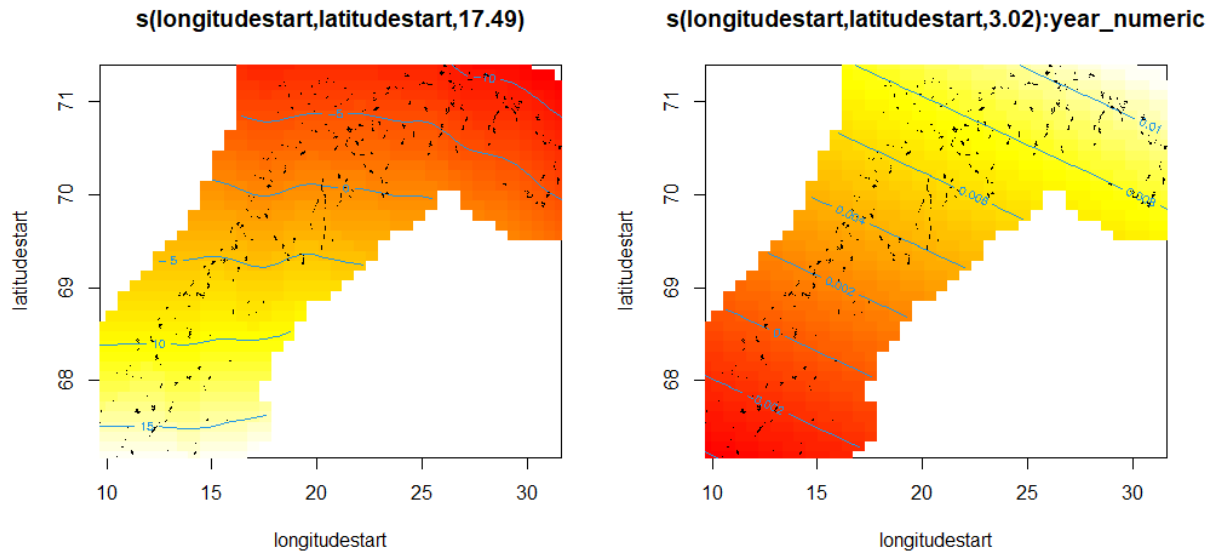


Figure 4: The change in distribution by year on the right, and the spatial pattern on the left, both for total density. The model includes a k -value for both the term $s(x,y, by = year)$ (right) and $s(x,y)$ (left). The P -value for the term $s(x,y, by = year)$ was 0.426, and <0.001 for $s(x,y)$.

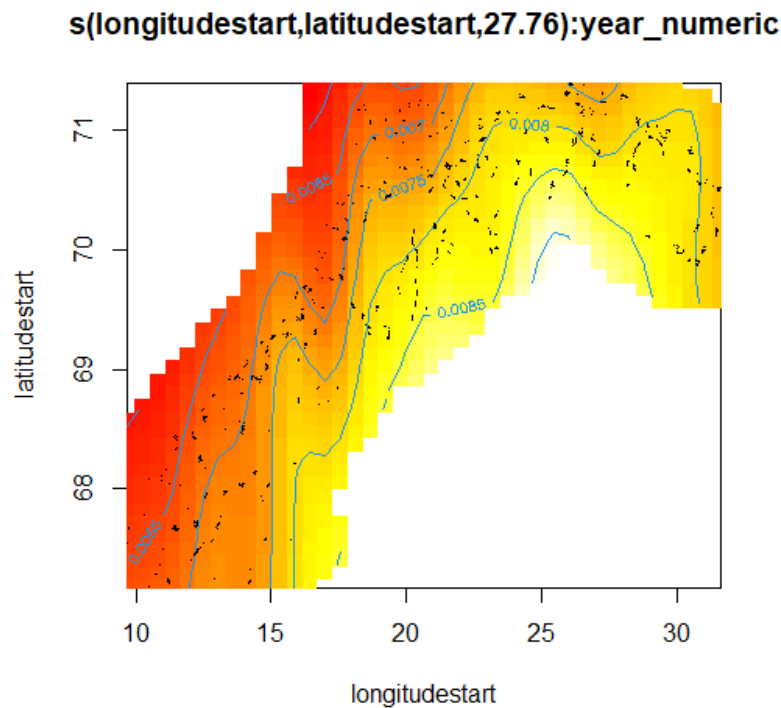


Figure 5: The change in distribution over time for total density.

APPENDIX B – DIAGNOSTIC PLOTS

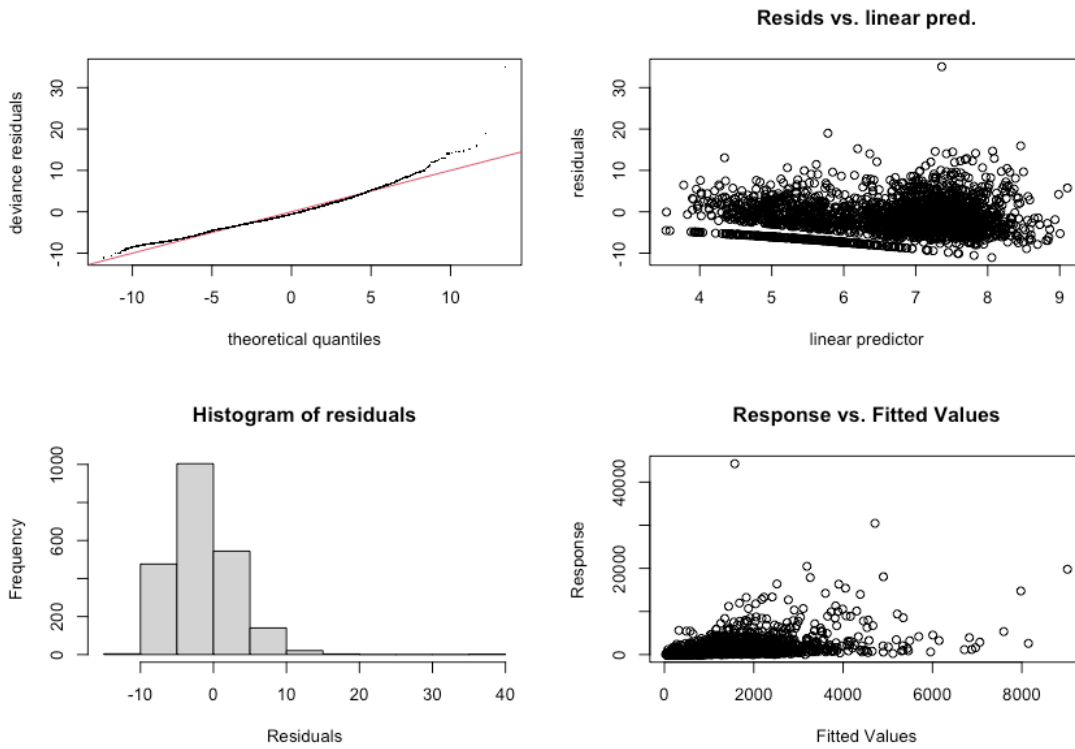


Figure 1: diagnostic plots for model 1. A quantile-quantile plot is shown in the upper left. The lower left is a histogram of model residuals, the upper right shows residuals vs. linear predictor and the lower right shows the response vs. fitted values.

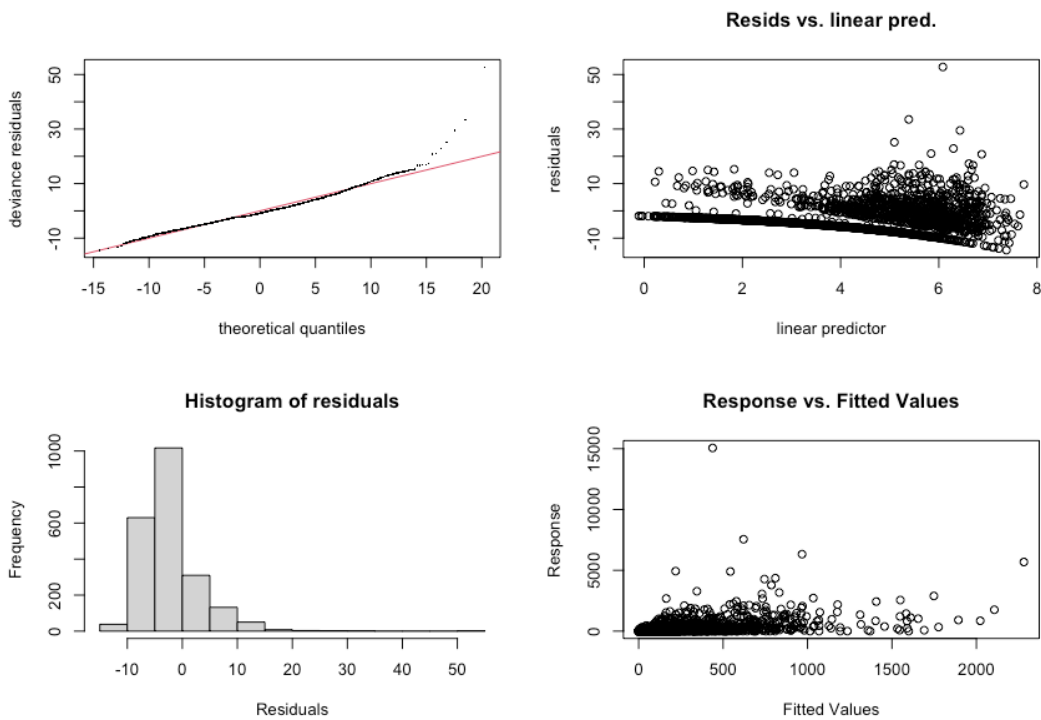


Figure 2: diagnostic plots for model 2a. A quantile-quantile plot is shown in the upper left. The lower left is a histogram of model residuals, the upper right shows residuals vs. linear predictor and the lower right shows the response vs. fitted values.

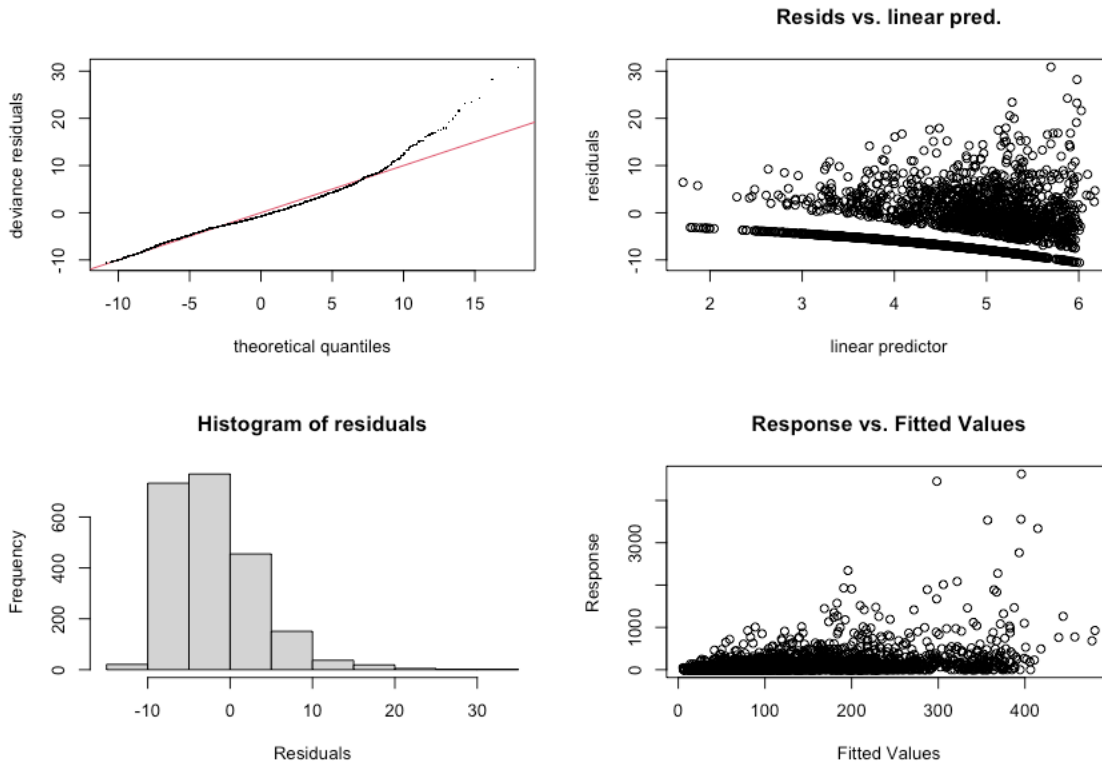


Figure 3: diagnostic plots for model 2b. A quantile-quantile plot is shown in the upper left. The lower left is a histogram of model residuals, the upper right shows residuals vs. linear predictor and the lower right shows the response vs. fitted values.

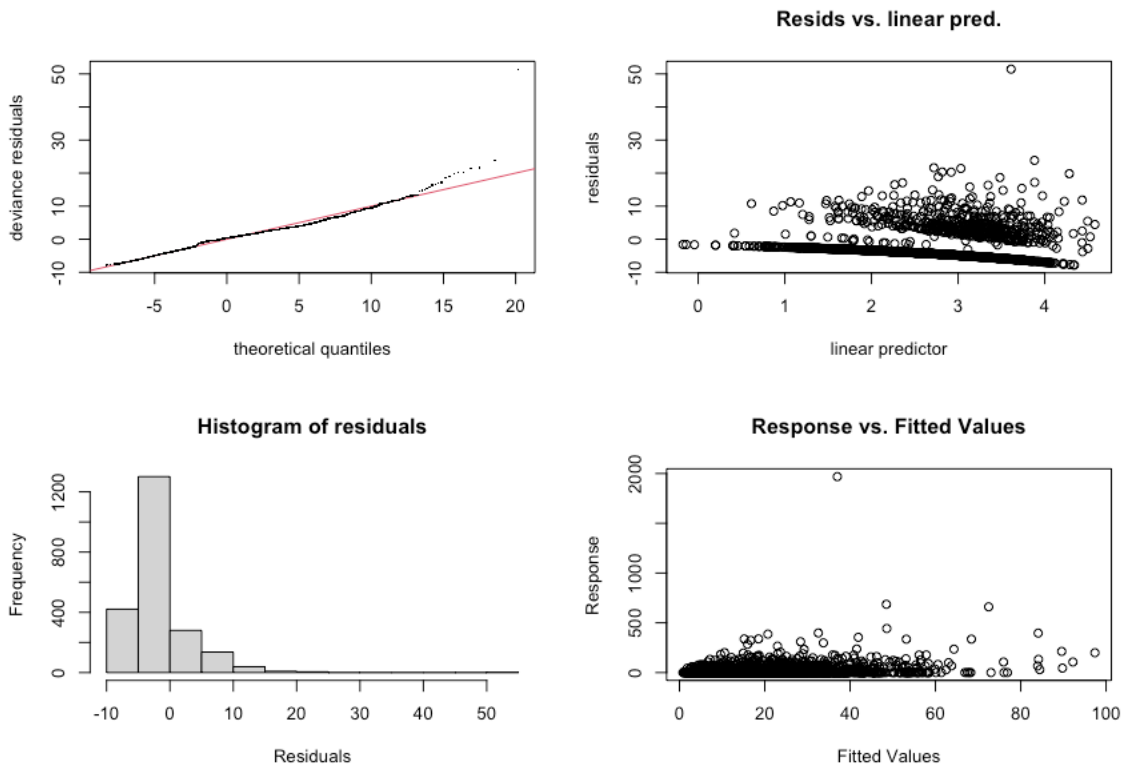


Figure 4: diagnostic plots for model 2c. A quantile-quantile plot is shown in the upper left. The lower left is a histogram of model residuals, the upper right shows residuals vs. linear predictor and the lower right shows the response vs. fitted values.

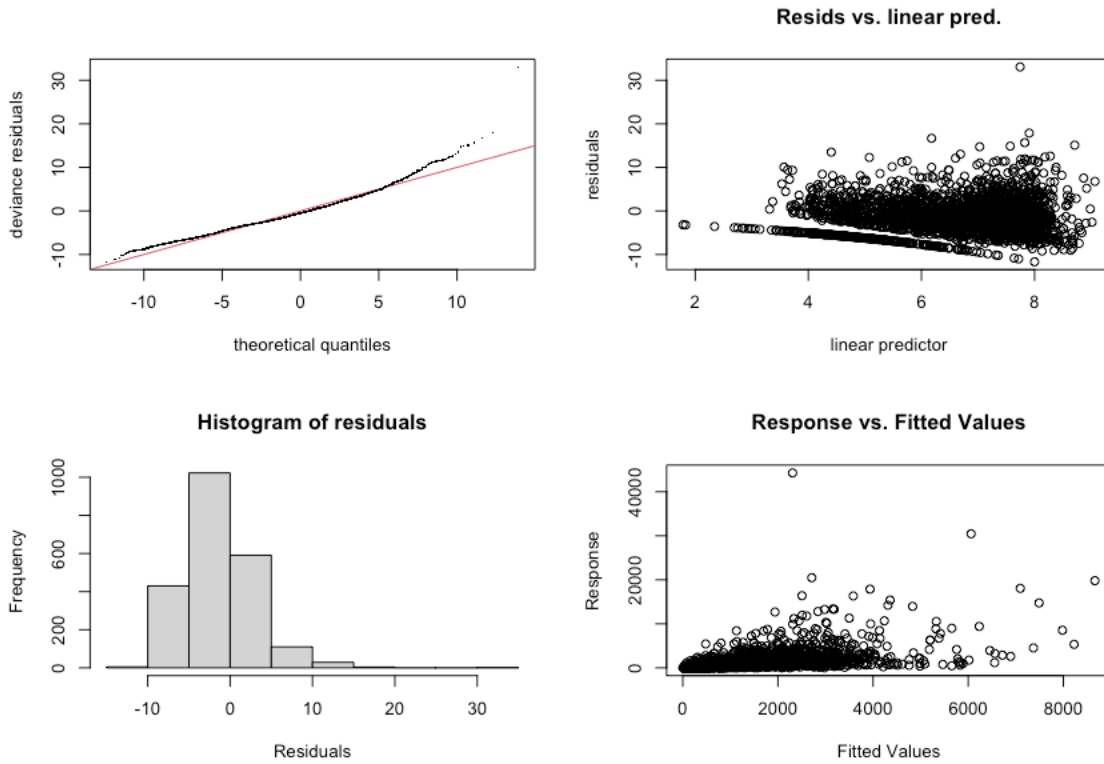


Figure 5: Diagnostic plots for model 3. A quantile-quantile plot is shown in the upper left. The lower left is a histogram of model residuals, the upper right shows residuals vs. linear predictor and the lower right shows the response vs. fitted values.

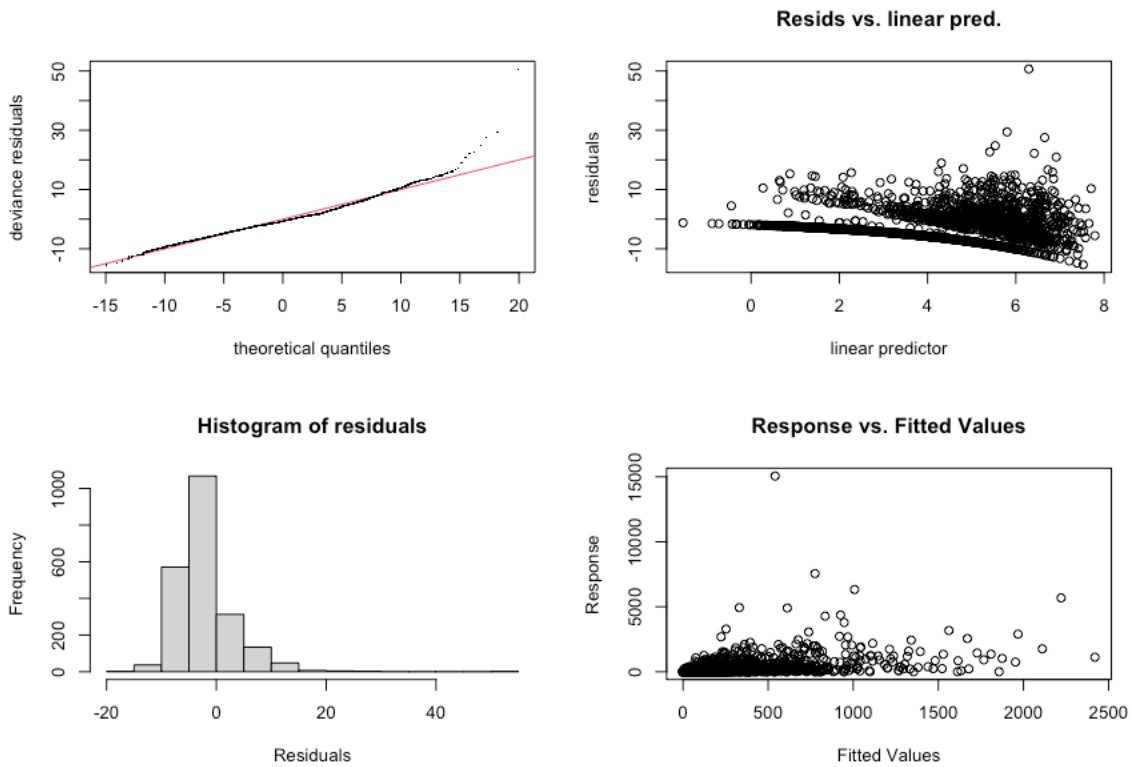


Figure 6: diagnostic plots for model 4a. A quantile-quantile plot is shown in the upper left. The lower left is a histogram of model residuals, the upper right shows residuals vs. linear predictor and the lower right shows the response vs. fitted values.

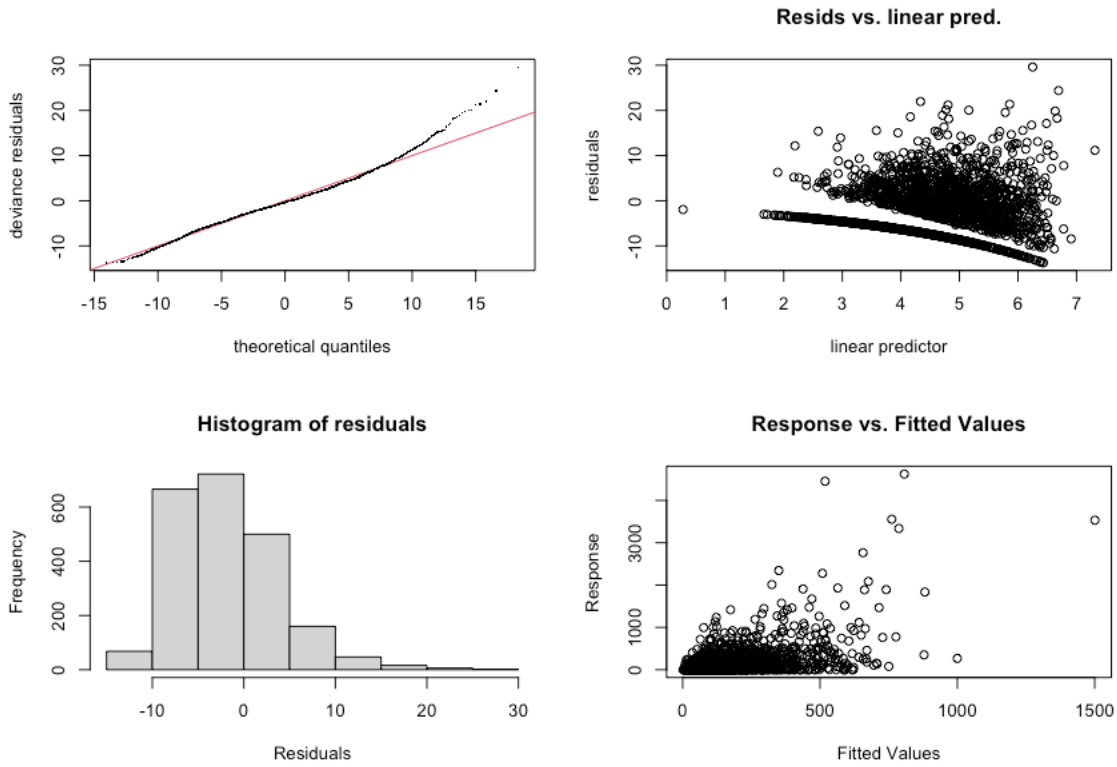


Figure 7: diagnostic plots for model 4b, A quantile-quantile plot is shown in the upper left. The lower left is a histogram of model residuals, the upper right shows residuals vs. linear predictor and the lower right shows the response vs. fitted values.

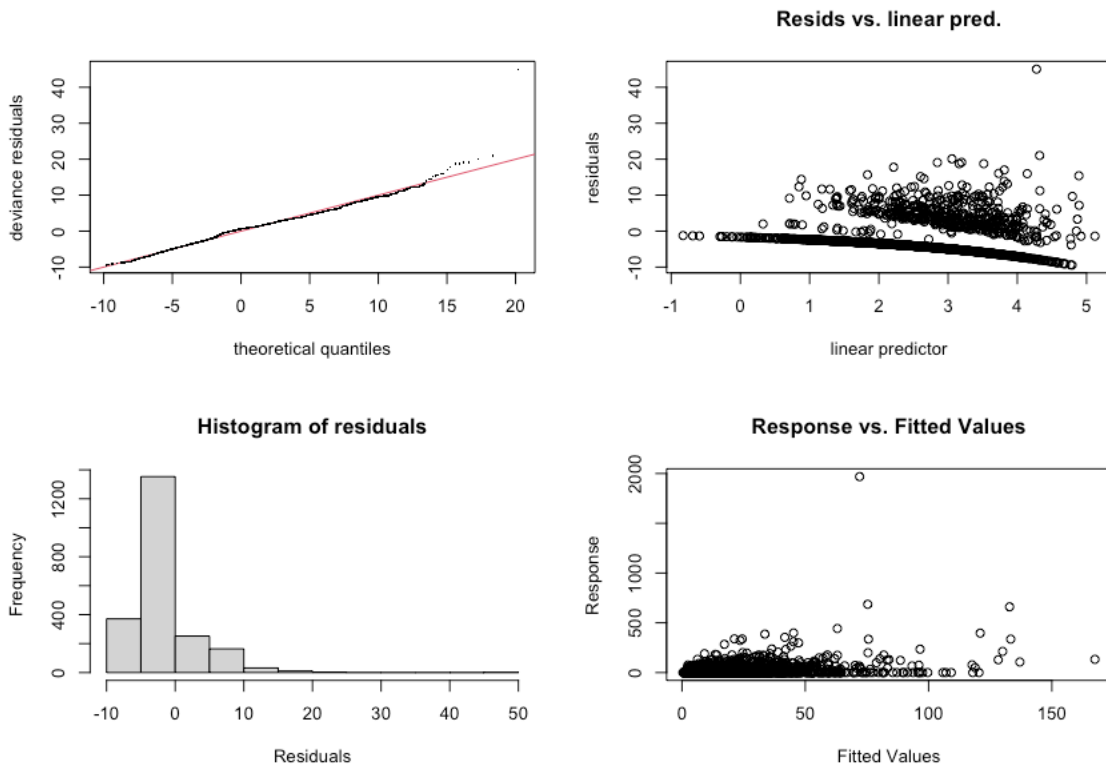


Figure 8: diagnostic plots for model 4c. A quantile-quantile plot is shown in the upper left. The lower left is a histogram of model residuals, the upper right shows residuals vs. linear predictor and the lower right shows the response vs. fitted values.

APPENDIX C – MAPS WITH TEMPERATURE OBSERVATIONS

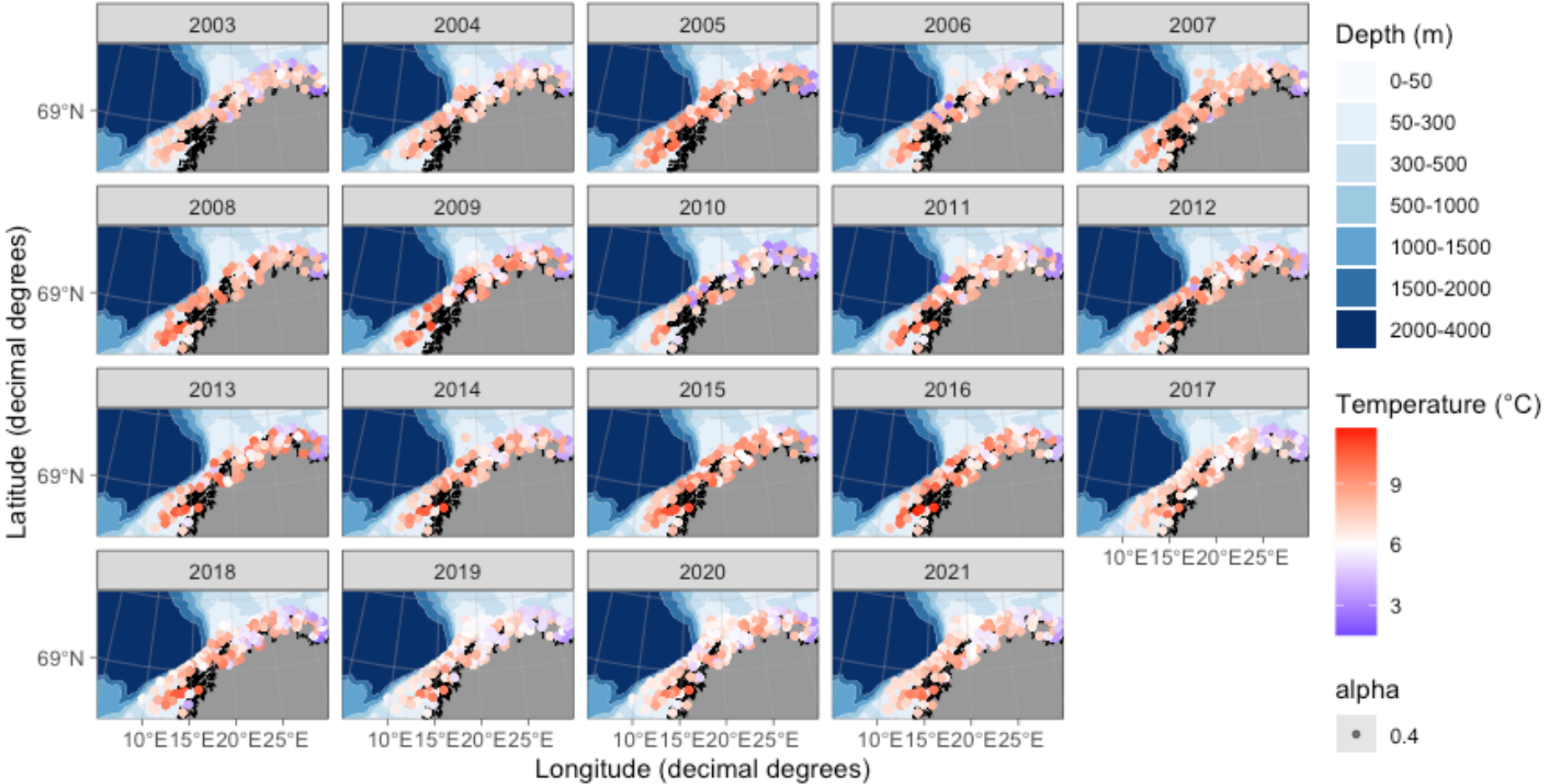


Figure 1: map showing the distribution of temperature observations per year. Each point represents an observation.

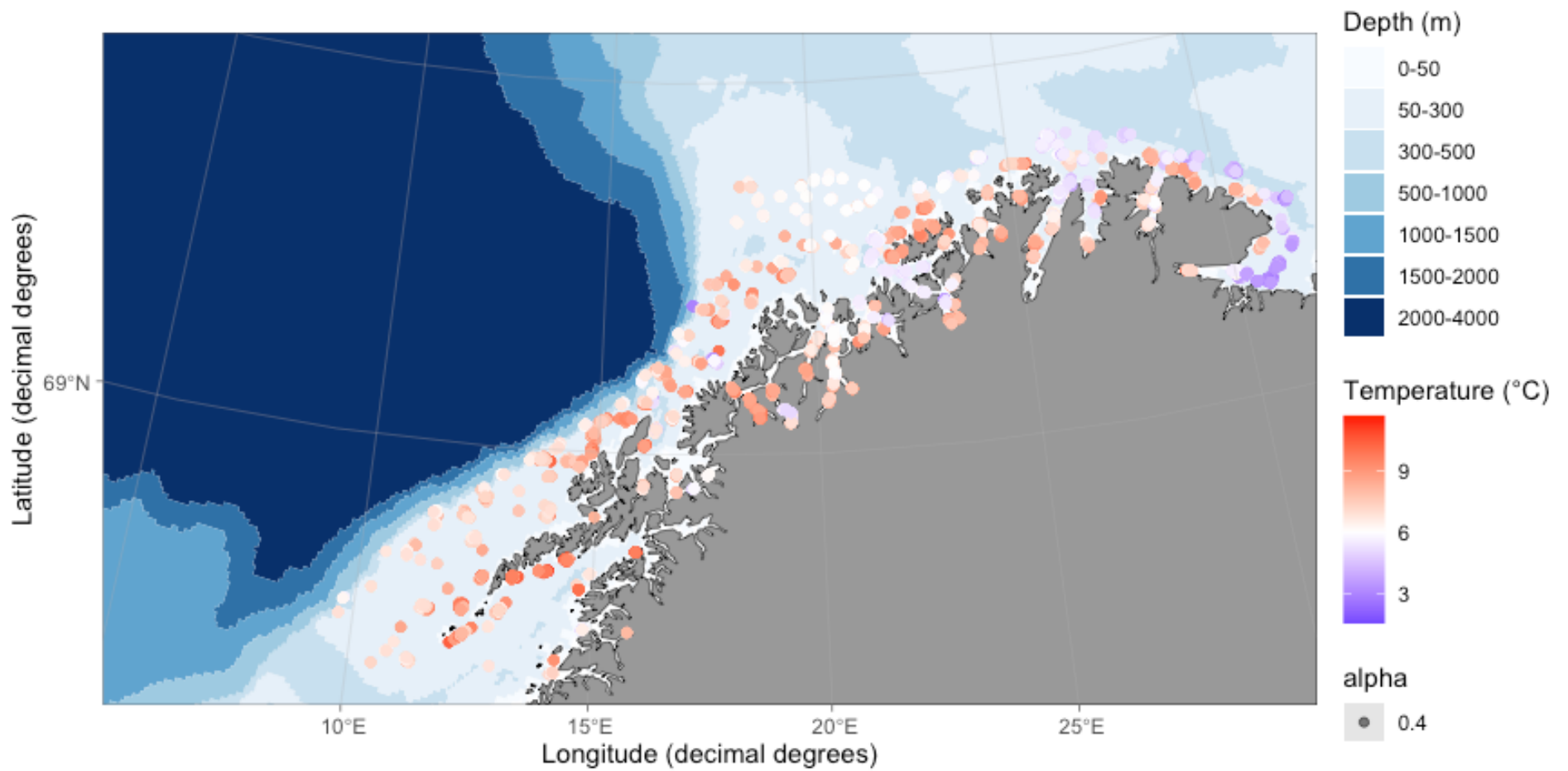


Figure 2: Map showing all temperature observations. Each point represents an observation.