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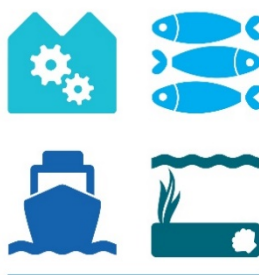
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Preface

This present report is based on the project "Kystfisk 3 – vigtige faktorer for udbredelse af torsk og rødspætter i de danske kystområder" funded by the European Maritime and Fisheries Fund and the Danish Fisheries Agency.

DTU Aqua, Kgs. Lyngby
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Executive summary

Danish fishermen have experienced a decline in coastal fishing resources and have called for an explanation of these changes. For example, cod and plaice appear to have changed their distributions with less fish present in coastal areas. The project aims at explaining this apparent strong decline in cod and plaice in coastal waters by using a range of approaches including genetic analyses of juvenile and adult individuals, statistical models of suitable habitats, numerical models linking hydrography and life history to resolve population connectivity over several years. The results produced in the project can improve our understanding of the factors driving changes in distribution and abundance of coastal fish populations and can inform assessment working groups on those species targeting the adequate management of the different stocks.

Observations on hydrography and fish catches obtained from standard research cruises and monitoring stations in the Kattegat confirm the tendency of a reduction of adult cod in coastal areas in the investigated period (1995-2015). In details, while the relative abundances of the younger 1-year old cod in shallow areas (<25 m) increase, the other age groups (2 and 3 year olds) show a decline. For plaice all age groups show some increase, most prominent for the 1-year olds, which were relatively under-represented in shallow areas before 2008. Changes for plaice abundance can likely be explained by the general increase in the stocks across the entire region and adjacent areas.

The detected trends in relative abundance appear to follow closely the changes in hydrography, namely an increase in temperature and a reduced salinity in the Kattegat. Hydrography variability is linked to the general circulation of the North Sea – Danish Straits – Baltic Sea system and detailed cluster analyses show the key role of the Kattegat in regulating exchanges between North Sea and Baltic. Additionally, the Skagerrak-Kattegat region has experienced significant increase in temperature (>1.5 $^{\circ}$C since 1990) and a reduction in surface salinity, regulated by the freshening of the Baltic Sea in the same period. These results indicate substantial changes of the surface layers in the Kattegat while the deeper parts appear less affected.

Since the relative changes occurring in surface and deeper layers in the Kattegat, we can infer that coastal habitats for cod and plaice are now significantly different than in the past (e.g., conditions before the 1990). We can hypothesize that changes in hydrography could elicit a behavioural response in adult fish, which could move into deeper parts and away from shallow coastal areas. The hypothesis is consistent with genetic data on juvenile cod. Indeed, the Kattegat region is composed by a mixed population of cod with North Sea origin and local Kattegat cod, while juvenile plaice appear to be predominantly locally recruited. Although the region is characterized by large year-to-year variability we detect the tendency of North Sea cod to use deeper areas than those from the Kattegat, possibly indicating different levels of adaptation and plasticity as well as differential exposure to observed environmental changes.

Results from the modelling of transport of eggs and larvae of both cod and plaice are in agreement with the genetic results of local recruitment for plaice and large year-to-year fluctuations in the mixing of cod individuals. Detailed analyses of the connectivity patterns in the period 1990-2012 show no major changes in the transport of juveniles between different regions. For cod major exchanges within the Baltic sea regions support the management of this population as a

single stock. On the other hand, exchanges between North Sea and Kattegat are more variable and largely correlated with inflow and outflow events in the Baltic.

We conclude that changes in distributions of commercial fish stocks, such as the decrease in fish abundances especially in coastal areas observed in Danish waters, could potentially bias the estimate of stock abundance obtained through research surveys. Hence, given the complicated interactions between topographical changes, hydrography, food web and individual behaviour we recommend that better monitoring strategies for the entire stock distribution range, including coastal areas, should be developed possibly making use of modern observation technologies for autonomous habitat mapping. Overall, it is clear that the stock assessment and management challenges in such complex transition areas cannot simply be solved by adjusting boundaries for stock assessment, as movement and mixing occurs across the entire transition zone from the North Sea into the Baltic. Merging a larger area would solve the issue of movements between smaller areas, however would lose track of the dynamics and status of individual populations, which is important for understanding the stock dynamics of the species in an area, and develop appropriate management solutions. Thus, a remaining challenge is to find an optimal way to take into account the biological knowledge of stock mixing and connectivity in stock assessment and management.

This challenge could be faced by supporting a holistic integrated ecosystem approach. Indeed, there is a need for integrated knowledge of connectivity across areas, focussing on stock mixing and the major drivers at fine spatial scales. A pilot study on Integrated Ecosystem Assessment (IEA) in the Skagerrak-Kattegat region could be developed through five steps: (1) Scoping management objectives and available data (2) Identify and score all drivers and pressures acting on the system (3) Define indicators for ecosystem state and track their dynamics in time and space (4) Assess ecosystem status and vulnerabilities (5) Inform fishery management and policy makers on the boundaries for the sustainable development of the area under future scenarios.

Contents

1. Introduction

Identifying the spatial and temporal distributions in marine fishes and understanding the cues for this structuring is important for fisheries management and species conservation (Reiss et al., 2009; Cianelli et al., 2013). Fish exhibit both ontogenetic and seasonal shifts in distribution patterns (Rijnsdorp & Van Beek, 1991; van Keeken et al., 2007; Seitz et al., 2014; Brown et al., 2018). In addition, fish respond differently to environmental conditions and pressures from human activities. Changes in pressures may affect habitat and fish species productivity, but these changes may not be easy to predict. While some species may alter their distribution patterns in time and space (Støttrup et al., 2017), others may adapt given consistent and gradual changes. Productivity in some species may decrease/increase due to habitat compression/expansion, or changes in the phenology of important life-history events such as spawning and migration. Thus, changes in spatial or temporal distributions alter local abundance of the different fish stocks, affecting local or coastal fisheries and local communities that depend on these fisheries.

For most species, fish spawning takes place in spatially well-defined areas that offer environmental conditions that favour reproductive success (Planque et al., 2011). For example, Baltic cod in the Bornholm basin are restricted to a water mass delineated by the lower salinity for successful fertilization, temperature tolerance range and minimum oxygen level requirements (Hinrichsen et al., 2002). In the North Sea, spawning areas for cod and plaice were generally near frontal areas that are highly productive habitats for early stage fish larvae (Munk et al., 2002, 2009). Similarly, many marine species have early-life stages that are highly restricted in their spatial distribution. For example, post-metamorphosed juvenile flounder and turbot are restricted to the < 4m depth during their first year (Gibson, 1994; Andersen et al., 2005).

Figure 1.1. Topography of the study area with indication of the Danish straits and main regional seas.

The association of these environmental conditions with species presence or abundance is used to derive species-specific and life-stage specific habitat models. Depth, temperature and oxygen are among the environmental parameters that best could describe spawning, feeding and juvenile habitats for cod and plaice (Støttrup et al. 2014). For demersal spawning species (e.g. herring), sediment type may be an important environmental variable. Human activities such as aggregate extraction, coastal protection or dumping may cause changes in depth or sediment type. Similarly, the consequences of climate change may affect depth or salinity. Temperature and oxygen levels may be affected by climate change and/or eutrophication. These changes in depth, sediment, temperature, oxygen or salinity may affect the habitat quality or magnitude of available favourable habitat for fish species.

1.1 Methods for data analyses

Earlier studies point to changes distribution of fish and the nearshore areas, and parallel changes in the environmental conditions. We present here an overview of the changes in environmental conditions, as derived from observations on temperature and salinity at the sea bottom, and illustrate the changes in the abundance for two important commercial species: plaice and cod. The description of decadal changes in hydrography is based on standard CTD observations from the target area and we will focus on the abundances of cod and plaice measured by standard trawl surveys (IBTS) in the Kattegat and the inner Danish waters from the 1990s until today. Parts of this analysis will be divided into age groups to see if there are differences in changes of juvenile and adult distributions.

1.2 Hydrographic changes, described by the bottom layer temperature and salinity

Water temperature and salinity are considered key environmental parameters for a range of marine animals and it is then important to analyse possible long-term changes of these variables. As cod and plaice are demersal fish species (meaning that from the juvenile stage they preferably stay near the seabed) we expect that those populations are particularly dependent on environmental conditions at the bottom. Hence, we analyse temperature and salinity data in shallow areas as separate from those in deeper layers.

For the analysis, we use hydrographic data from the ICES database, using temperature and salinity in the period 1975-2018. We use data from the Kattegat and inner Danish waters (areas 21 and 22), and distinguish these into four depth layers: 1-5 m, 5-10 m, 10-25 m and >25 m. and we further separate information into quarters of the year (Q1-Q4).

The decadal changes in temperature and salinity at sea bottom are illustrated in Figure 1.2. The bottom temperature increased during the period in all seasons and at all bottom depths (Figure 1.2). The level of increase was 1-2 °C during the four decades. Salinity changes showed more diverse trends during the period. The salinity at bottom depths below 5 m could show either a slight increase or decrease, dependent on the season, when the shallowest areas above 5 m showed a marked decline of about 2 per mille salinity for all seasons.

To inspect the geographical variation in hydrographic changes, we calculated the rate of change for specific sub-areas of the Kattegat and inner Danish waters (for the period 1994-2015). We divide the area in rectangles of ¼ latitude and ½ longitude, and calculate the incremental coefficient of the annual change in temperature and salinity for these sub-areas (Figure 1.3). The rate

of change shows an increase for temperature; greatest in central areas of the Kattegat mainly around Anholt. On the other hand, salinity appears to decrease in shallow areas in inner Danish waters and around Læsø and Skagen, while in more central areas of the Kattegat salinity tends to increase. This could possibly be related to the inflow/outflow patterns in the region: the decreasing salinity of the upper water layers (and thus in shallow areas) is probably linked to a larger surface outflow from the Baltic, which would lead to enhanced inflow of saltier bottom water from the Skagerrak.
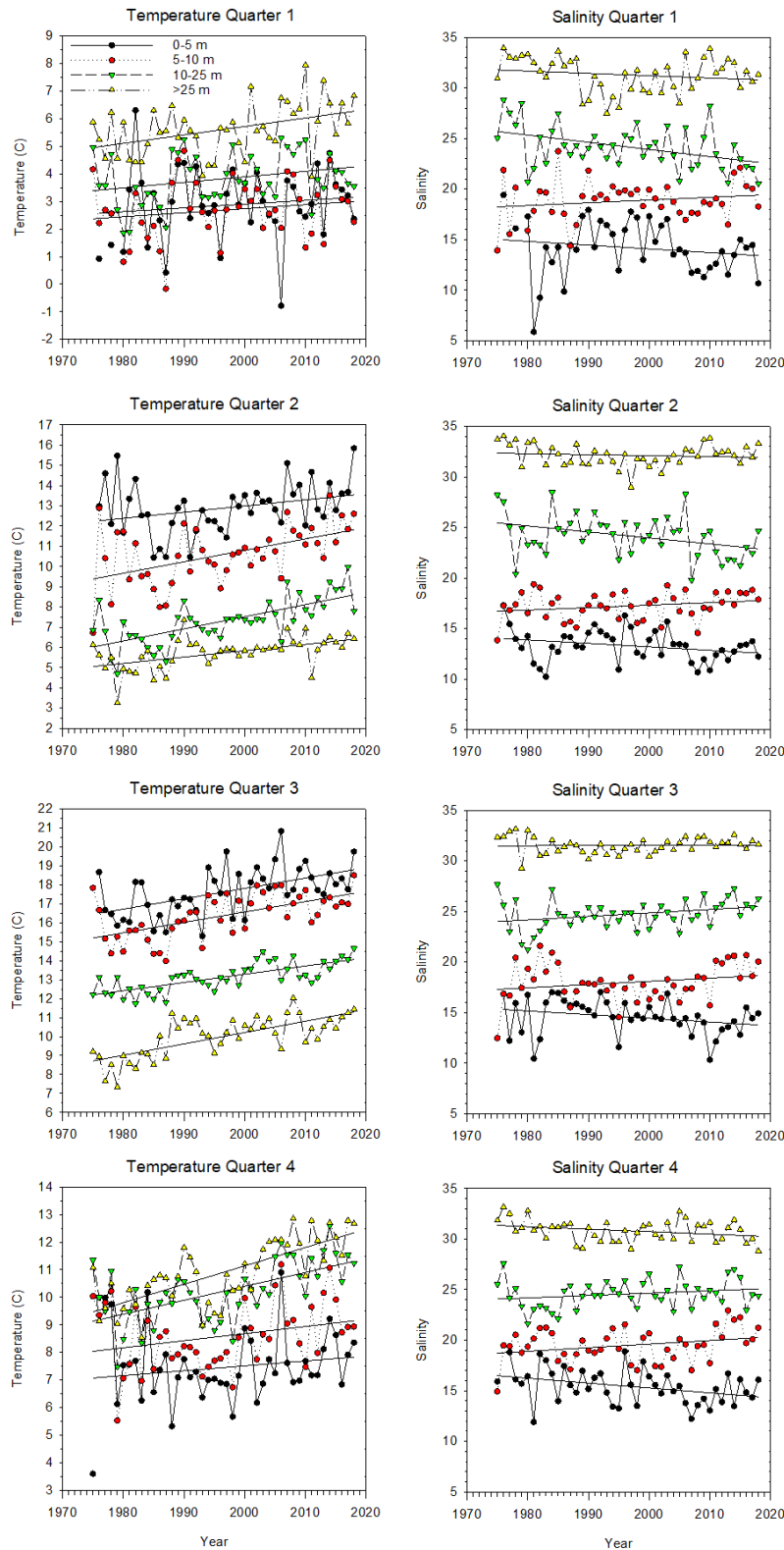
Figure 1.2. Changes in bottom temperature (left) and salinities (right) from 1975-2018. Average values for the Kattegat and inner Danish waters, subdivided into quarters of the year, and bottom depth strata as indicated in legend.
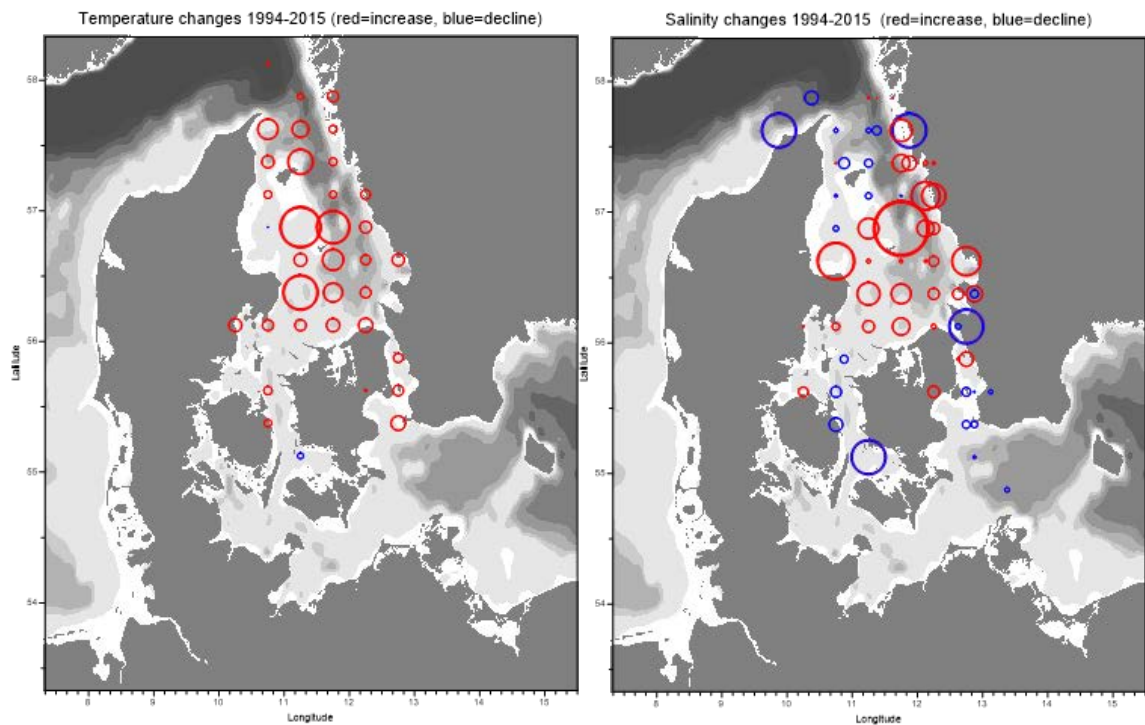
Figure 1.3. Changes in temperature and salinity in Quarter 4 during the period 1994-2015. The size of circles illustrates relative magnitude of the increase (red) or decline (blue) in values during the period.

1.3   Temporal and spatial variability in abundances of cod and plaice

For a description of the general abundances of cod and plaice, we use data from the so-called IBTS surveys. These standard surveys of research vessels are carried out twice a year, in March (Q1) and in November (Q4). During the surveys about 1-2 hauls are made with bottom trawls within areas of size ¼ latitude times ½ longitude. We calculate an index of general occurrence of the fish species (for the 1 year, and older "1+", groups) by first finding the average amount of cod within these smaller areas, and then averaging them for the whole area. This index is shown in Figure 1.4 for cod and plaice and for the November cruise and March cruise, respectively

There is great year-to-year variation, with some years of particularly large or small abundances. That said, the indices indicate a decline for cod abundance to around the year 2010, and a levelling out thereafter, when for plaice there was a slight increase until around year 2010, and a more pronounced increase thereafter.

We investigate whether the apparent decline in cod and increase in plaice abundances has differed among areas of Kattegat and inner Danish waters. We calculate the incremental coefficient for abundances in sub-areas for the period of investigation, and relate this to the average abundance within the sub-area, thus express the relative change for each species (Figure 1.5). Some spatial tendency is apparent for both species. The relative decline in abundances of cod appear to be largest in the shallow (often coastal) areas. The relative increase in abundances of

plaice is highest in – some of – the shallower areas, however, specific shallow areas south of Læsø and around Samsø have experienced decline in plaice during the period of investigation abundances.
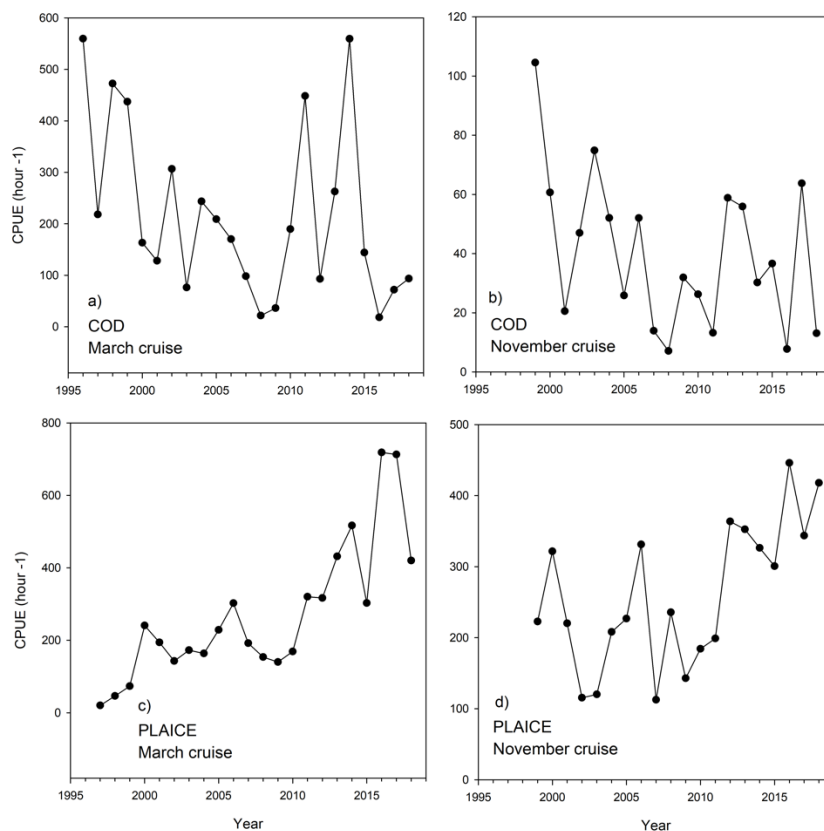
Figure 1.4. Average abundances of cod (a-b) and plaice (c-d) in Kattegat and the inner Danish waters, based on standard survey hauls for march (a-c) and November (b-d) cruises.

1.4 Changes in distributional patterns of ages groups of cod and plaice

Here we investigate whether there have been apparent changes in the relative abundances of different age groups in shallow areas of the Kattegat. We use data for the three most common age groups: 1-, 2- and 3-year-olds for both cod and plaice and abundances in areas of a water depth below 25 m water depth are related to abundances estimated for the entire area (Figure 1.6). For cod there is a tendency that the younger 1-year old during the period increase in relative abundance in shallow (<25 m) areas, while both the other age groups (2 and 3 year olds) tend to decline in their relative abundances in shallow areas. For plaice all age groups show some increase in shallow areas, however the increase in relative abundance are most prominent for the 1- year olds, which were relatively under-represented in shallow areas before 2008.
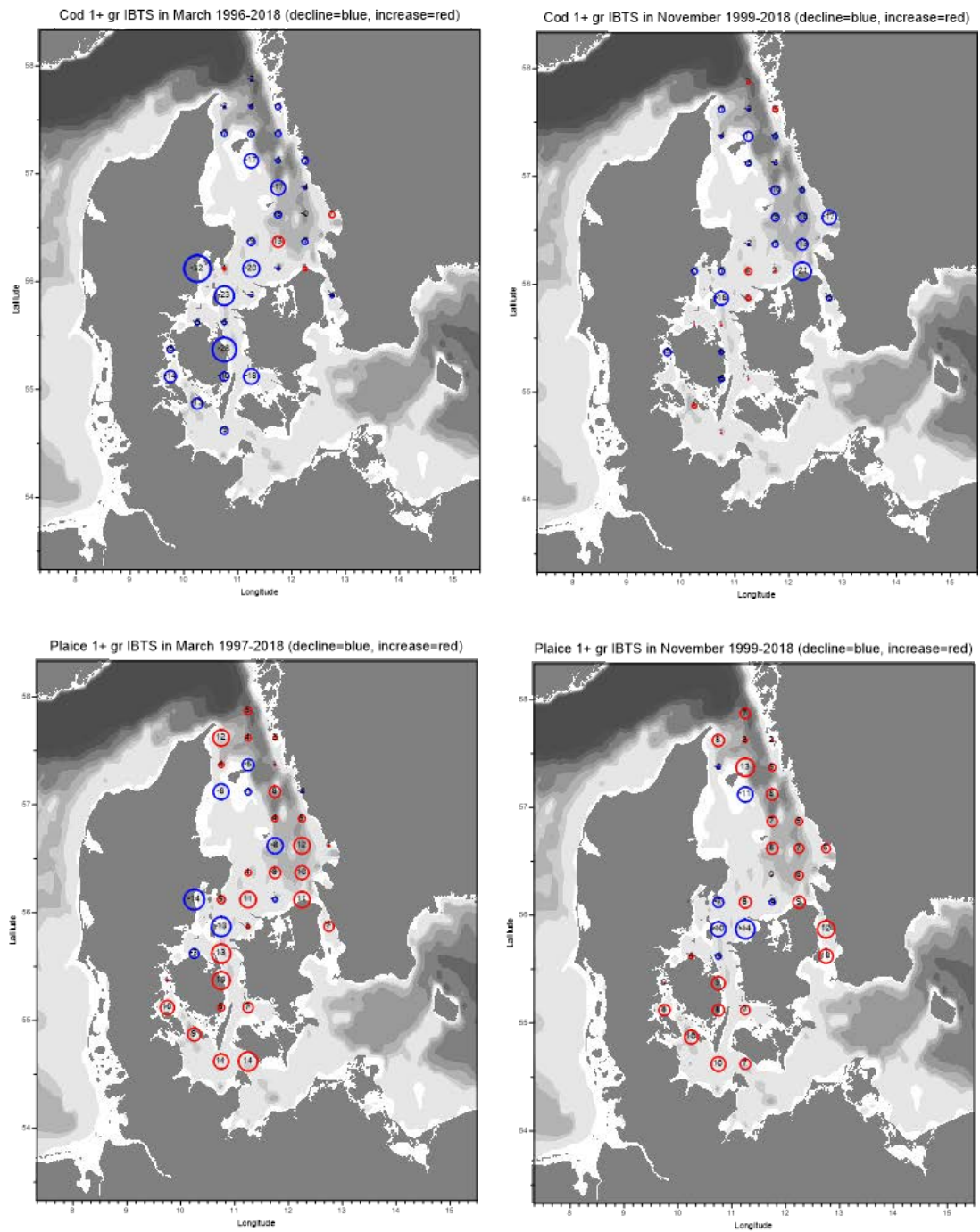
Figure 1.5. Relative decline (blue) and increase (red) in abundances of cod and plaice within sub-areas. Charts to the left illustrate patters as apparent from the March survey, when right charts illustrate patterns for the November survey.

1.5   Summary

The present investigation of historical information on hydrography and fish abundances in Katte-gat shows that major physical and ecological changes have taken place during the last three decades. It further illustrates that changes are most prominent for the shallowest areas. There has been a marked increase in temperature of about 2°C, and for the shallowest areas there has been a parallel decline of 1-2 per mille salinity. Respective abundances of plaice and cod showed significant changes during the period; an increase was seen for plaice, while cod tended to decline in abundance. The diminishing cod abundances was most apparent in shallow, nearshore areas, and for the ages of two and more years.
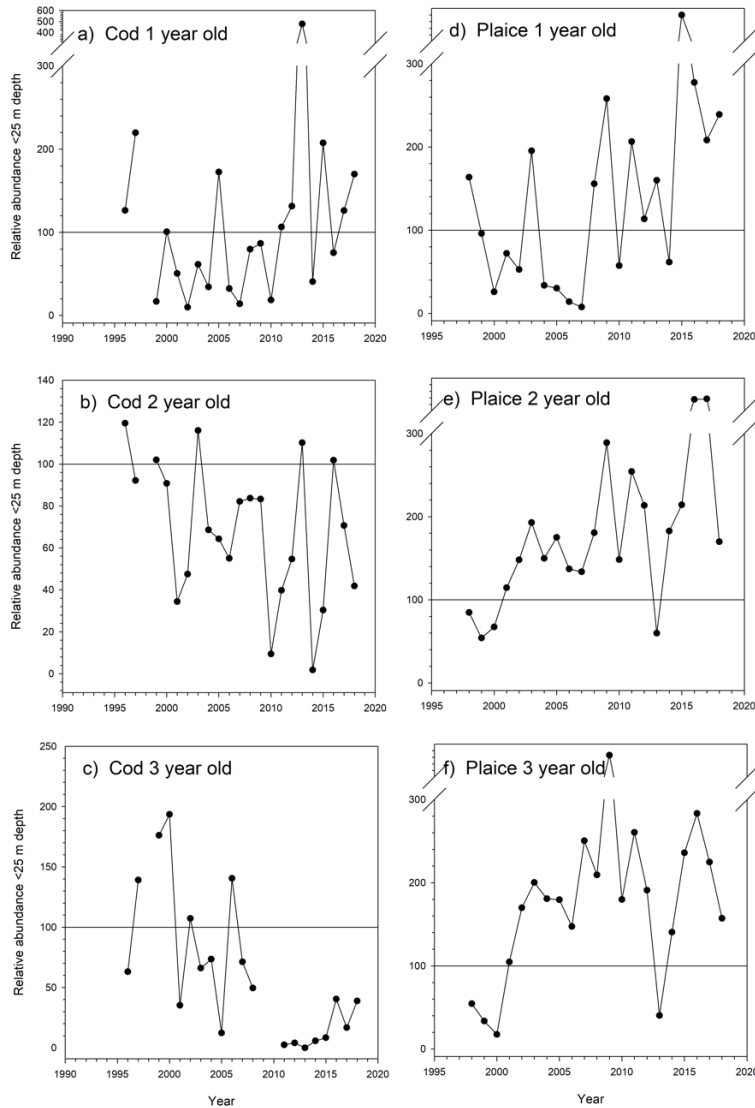
Figure 1.6. Relative predominance in shallow areas (<25 m) for age groups (1, 2 and 3) of cod and plaice.

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2. Analyses of the hydrographic changes

North Sea and Baltic Sea are interconnected by a system of shallow passages located all around Denmark. This system includes Skagerrak, Kattegat and the so called Danish Straits (Grand Belt, Little belt, and the Øresund). Hydrographic processes in the area are regulated by a combination of wind-driven and tidal-driven circulations as well as topographical effects. Distinct water masses occur in the region: North Sea water flowing from the German Bight along the western coast of Denmark (Jutland current); Baltic Sea water flowing northwards through the Danish Straits; subsurface Atlantic water branching off from the Atlantic current and moving south along the coast of Norway (Fig. 2.1, Christensen et al 2018). The circulation is well described by estuarine-like conditions characterized by a two-layer density structure generally present all year around and in most of the region, where low salinity waters of Baltic origins flows at the surface above bottom saltier waters (Stigebrandt & Gustafsson 2003).
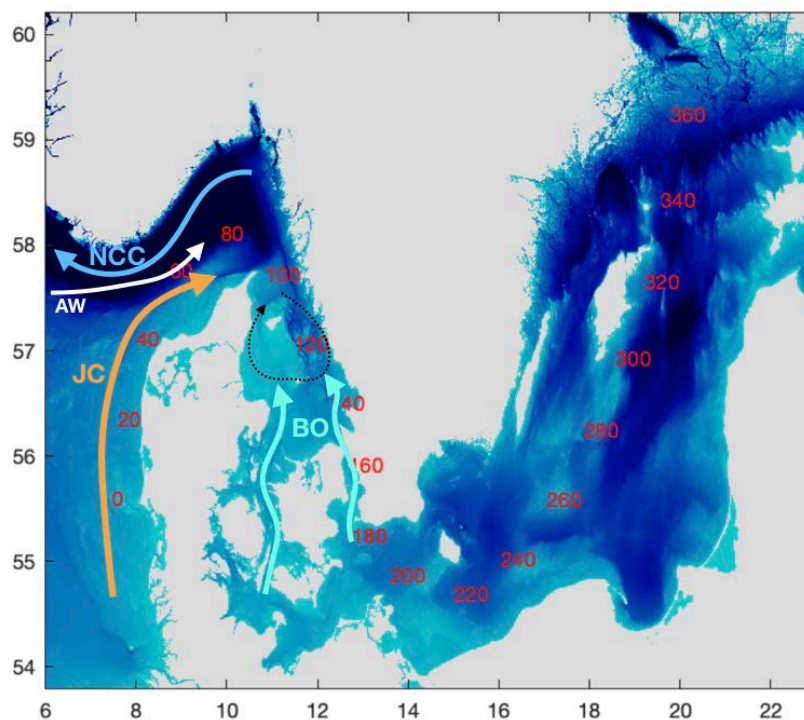
Figure 2.1. Locations of the transect used for the characterization of the distribution of water masses. Every 10th station is listed and the in-between stations are omitted for graphical purposes. Major currents are shown: (JC) Jutland Current, (AW) Atlantic Water, (NCC) Norwegian coastal current, (BO) Baltic outflow.

Modelling studies have shown that exchanges in the region are critically dependent on large-scale wind regimes, topographic features and rapid horizontal and vertical mixing processes occurring in the Kattegat (e.g., Zhang et al 2016, She et al. 2007 and references therein). Barotropic forcing is the major driver for inflow or outflow dynamics throughout the Danish straits and is ultimately regulated by wind stress across the Skagerrak (Christensen et al 2018). The

Kattegat circulation is predominately anticyclonic and influence by the presence of a permanent front (i.e., the Kattegat-Skagerrak front) and a strong salinity stratification. Inflow and outflow dynamics between Baltic Sea and North Sea contributes to the mixing in the area and the formation of an intermediate water. In case of inflow events (from the North Sea into the Baltic) mixing processes are prevalent, while the vertical stratification is maintained in presence of outflow events from the Baltic Sea into the North Sea (Stanev et al. 2015). The Kattegat plays a central role in regulating the factors driving flow partitioning among the different passages of the Danish straits (Stanev et al. 2015).
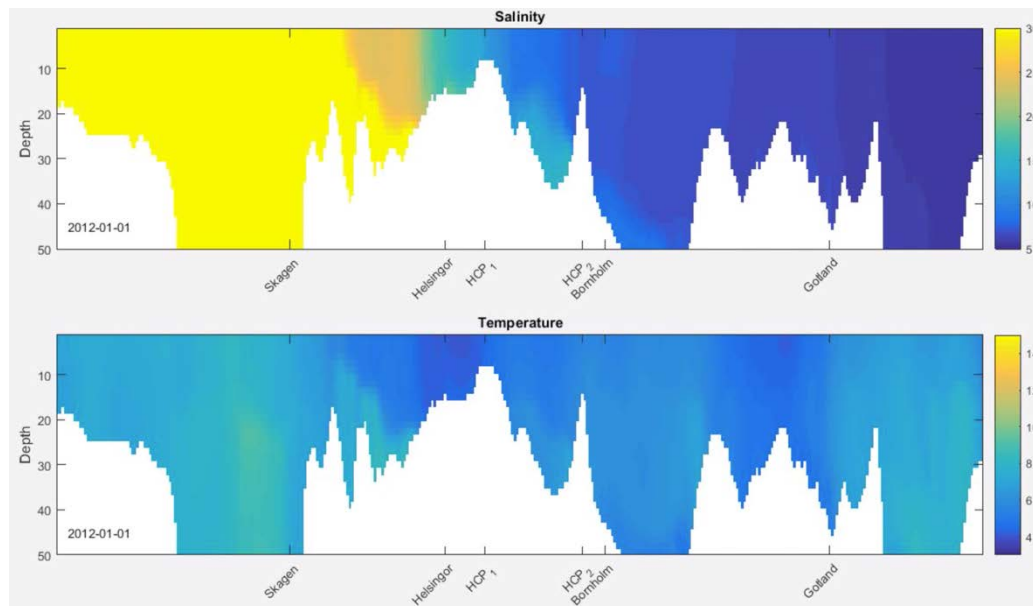
Figure 2.2. Example of values of salinity (upper panel) and temperature (lower panel) along the transect in 2012.

To understand the exchanges between Baltic Sea and North Sea and the factors affecting eggs and larval distribution in those areas, it is then important to analyse the dynamics of these water masses over extended time period. We use here output from 1960 to 2012 from the operational HBM model operated by the Danish Meteorological Institute (DMI) at 10 km horizontal resolution and up to 77 vertical z-layers covering the entire study area. We extract a transect (Figure 2.1) covering North Sea, Øresund, western and eastern Baltic.

Temperature and salinity data are extracted on the transect at 1 day time resolution. Clear distinction between the Baltic brackish waters and North Sea waters is obtained (Figure 2.2). A large region of mixing from the Kattegat to the Øresund and wester Baltic Sea is also appearing although largely varying in space and time. Focussing on the Kattegat as a transition between the North Sea and the Baltic Sea and extracting winter-period data for specific stations, we can detect a general increase in temperature and the significant freshening of the Baltic Sea water (Fig. 2.3). Water temperature increased in the entire region with a ca. 1 degree gained in the Kattegat bottom layers between 1985 and 2009 (Figure 2.3).

Salinity decreased, more evidently in the surface layer with a decrease from ca. 22 psu to 21 psu. The Kattegat then shows similar trends to the Baltic Sea although mainly in the surface and with different timing respect to the Baltic: warming starting later (ca. 1990 instead of 1980 in

the Baltic) and salinity decrease (from ca. 1985). Salinity in deeper layers are changing only very little. This indicate substantial changes in the surface ocean as well as in the general vertical structure of the water column after 2000. Thus, todays fish habitats in the region are substantially different from conditions found in the 70ies.
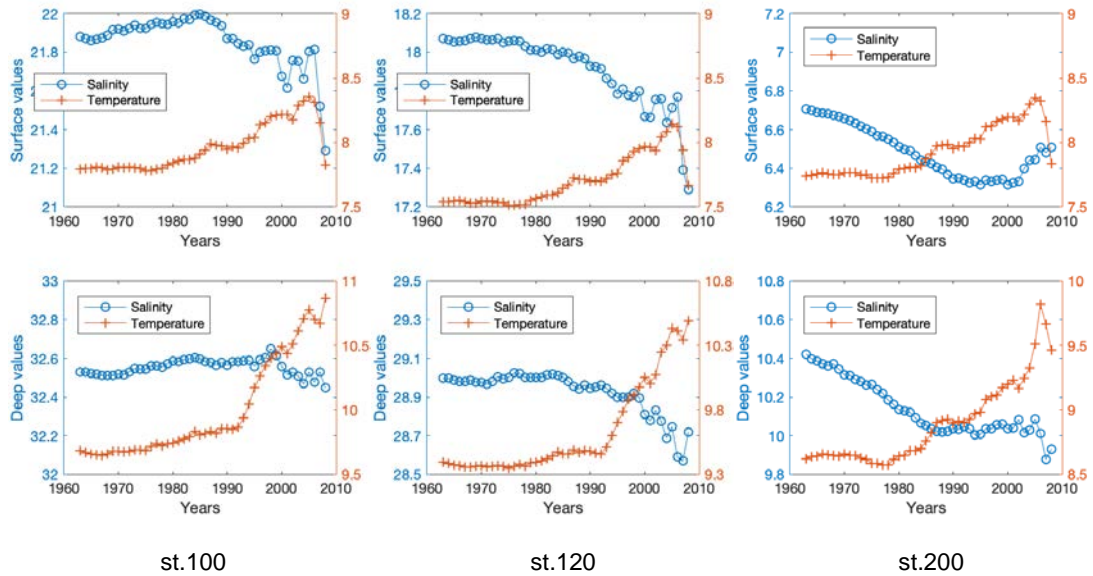
Figure 2.3. Time series of salinity (upper panels) and temperature (lower panels) at different stations across the Kattegat, Baltic Sea regions and at different depths. St.100 entrance of the Skagerrak-Kattegat, st.120 Kattegat, st.200 western Baltic.

2.1 Clustering method

A new clustering algorithm has been developed to quantify and categorize water masses based on temperature and salinity values as well as to establish relationships and links between those features and abundance of cod and plaice populations. As oceanic data usually include a multitude of parameters both in space and time, we aim at developing methods that are flexible and able to efficiently scale with data availability. This is achieved using state-of-the-art libraries with GPU acceleration such as Tensor flow and the convenient use of the Time Series toolbox. To optimize memory usage in handling the big data set, the data have been split into time intervals of a one-year duration. Every processed year can be used as a precondition for the new year analysed.

Bayesian Gaussian Mixture models using two different inference models have been developed (see details in Appendix A). Application of them over the entire transect for the full-time series (1960-2012) shows details of the evolution of the different water masses over time, with identification of both seasonal and multi-decadal variations. Generally, three to five water masses are recognized with the major groups being Baltic Sea; North Sea; and intermediate waters (Fig. 2.3).
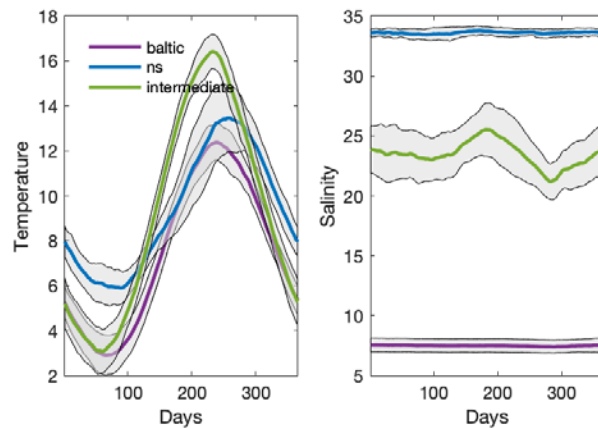
Figure 2.4. Average seasonal dynamics of temperature and salinity in the period 1960-2012. The values are the centroid of the three major clusters in our data: Baltic Sea; North Sea; Intermediate water.

2.2 Distribution of water masses

The dynamics of centroids and variance of the clusters indicate trends and variability in water masses composition. Following the dynamic of the centroids for the different clusters we can then explore large-scale changes occurring across different regions. Anomalies (reference period 1960-1975) in salinity and temperature are presented in Figure 2.5 across different years and seasons. Salinity of the Baltic cluster decreases sharply around ca. 1990 with a reduction of ~1 psu in the period 1980-1990. A further sharp decrease is recorded around 2009. These recent freshening events of the Baltic sea are affecting all seasons and are not in contrast with results from other analyses (Gorger et al. 2019; Schimanke & Markus Meier, 2016; Girjatowicz & Świątek 2016; Helcom 2018) although the magnitude of freshening detected here are much larger (total ca. 2 psu reduction relative to the 1960-1975 reference period).

The analyses of the salinity trends in the Baltic Sea cluster deserves further investigations. On the other hand, the salinity of the North Sea cluster does not show major trends, while intermediate cluster salinity shows repeated large changes overs years and seasons with a major decrease in salinity in recent periods and during summer. This is likely related to an increased outflow from the Baltic, which is known to affect salinity of surface water in the Kattegat.

Intermediate waters also show a marked increase in temperature conditions (mainly summer) likely driven by summer water temperature increases in the North Sea cluster (Figure 2.5).
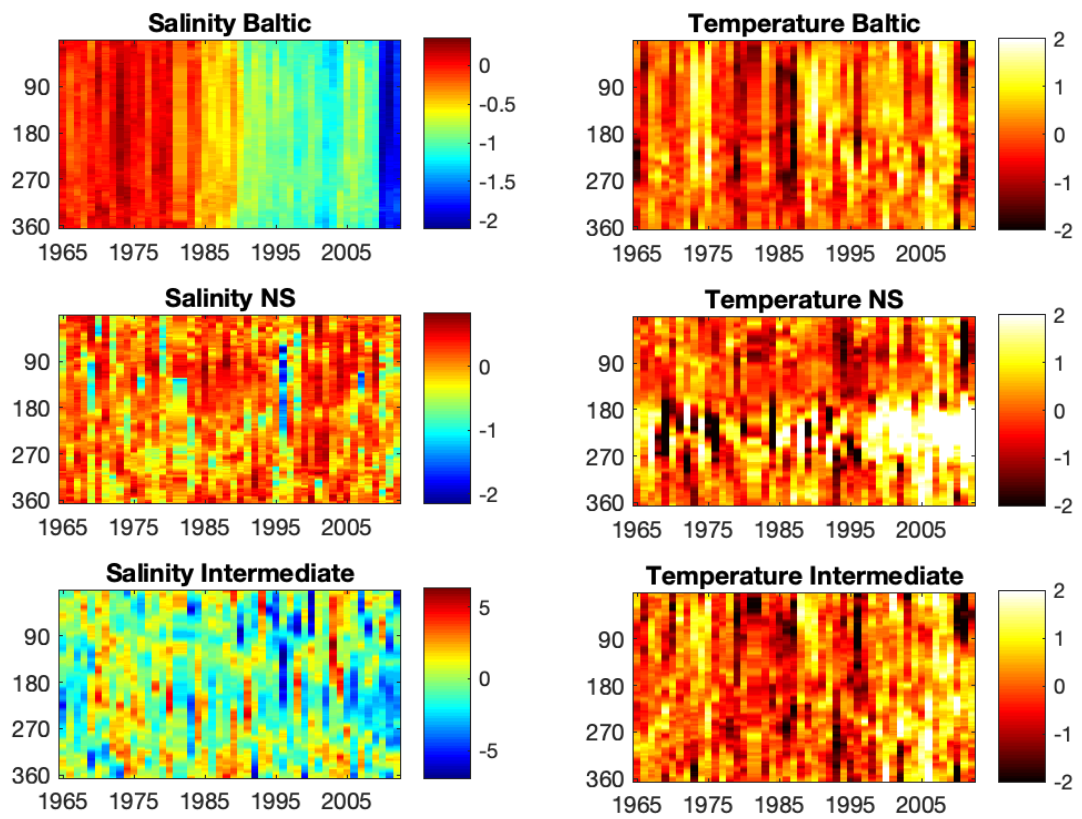
Figure 2.5. Anomalies in salinity (left panels) and temperature (right panels) for the different water masses. Anomalies are calculated over the average cluster values in the period 1960-1975.

The dynamic of the different water masses is analysed using the average spatial coverage of the clusters in the Danish straits (Figure 6). Year-to-year variability appears to be quite high but with a ca. 10-year cycle of the presence of North Sea water. This cycle appears to be well explained by averaged values of the NAO index (Figure 2.6).

(a)   (b)
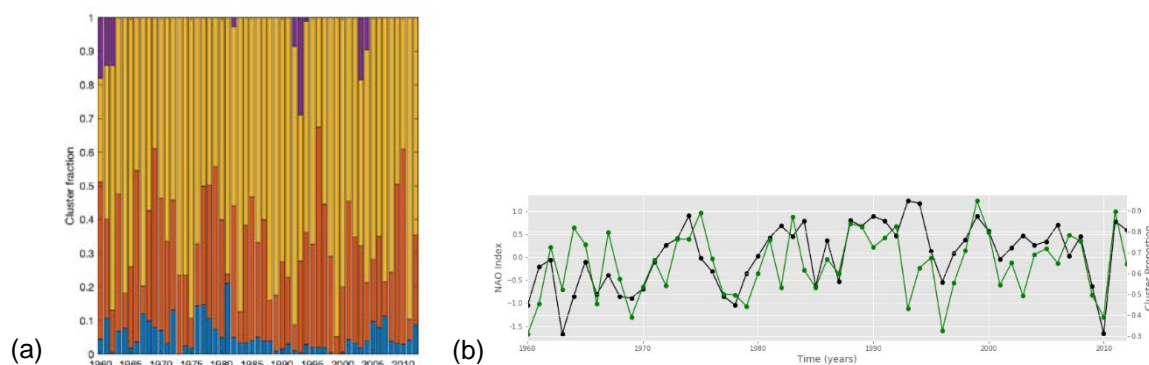
Figure 2.6. (a) Distribution of clusters in the Kattegat in different years (average over the year). Clusters are: Baltic Sea (blue), North Sea (red), Intermediate (orange), low salinity intermediate (purple). Region considered: st140 and st170 (Kattegat-Øresund). (b) correlation between intermediate water cluster and NAO index.

2.3   Summary

Hydrodynamic properties of Skagerrak Kattegat system have changed since 1990 with a general increase in temperature and a reduction in salinity, which is more evident in the surface layers and likely linked to the general freshening of the Baltic Sea. Large year-to-year variability in the exchanges between North Sea and Baltic is observed but with no major trends over the period 1960 -2012. Correlation between presence of different water masses and large-scale oceanographic oscillations (i.e. NAO index) is recorded. Generally, the clustering method develop performs well in detecting water masses and their trend over time. Further research is needed for classification of outliers (i.e. extreme events).

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3. Habitat mapping

This chapter is dealing with the development of statistical spatial distribution models for cod and plaice in the North Sea and the inner Danish waters. Available information from scientific bottom trawl surveys is combined with information from hydrodynamic models to identify important correlations of species distribution and environment. Main results are distribution maps of the two species for adults and juveniles. The study area for the habitat mapping includes the central part of the North Sea, Skagerrak, Kattegat, the Belt Seas, the Sound, and the western Baltic Sea (longitude: 3°W - 16°E, latitude: 54°N - 59°N). Data availability restricts the time period of the modelling and predictive habitat mapping. The scientific surveys were not standardized until 1991 and the hydro dynamical model that is used in this study is only available until 2012. Therefore, the period from 1991 to 2012 is used to fit the statistical models and produce habitat maps for cod and plaice.

3.1 Data and modelling

3.1.1 Bottom trawl surveys

The study area is covered by two biannual international scientific bottom trawl surveys. Each survey is conducted in a period of several weeks; for the analysis we aggregate the data to quarters of the year where each station was sampled, i.e. Q1 (January - March), Q2 (April - June), Q3 (July - September), and Q4 (October - December). Two surveys that are covering the study area are used in the analysis, the Baltic International Trawl Survey (BITS), which is conducted in the first and fourth quarter of the year and the North Sea International Bottom Trawl Survey (NS-IBTS), which takes place in the first and third quarter. The stations for both surveys are shown in Figure 3.1. During the surveys, information is gathered on the haul level, i.e. for each station there is recorded, (i) haul information (starting position, starting time, haul duration), (ii) species information (numbers at length per species), and (iii) biological information based on subsample of the catch for some target species (weight, maturation). ICES makes all bottom trawl survey data available through the DATRAS data portal (ICES, 2018). The data was downloaded and pre-processed using the R package DATRAS (Kristensen and Berg, 2018).
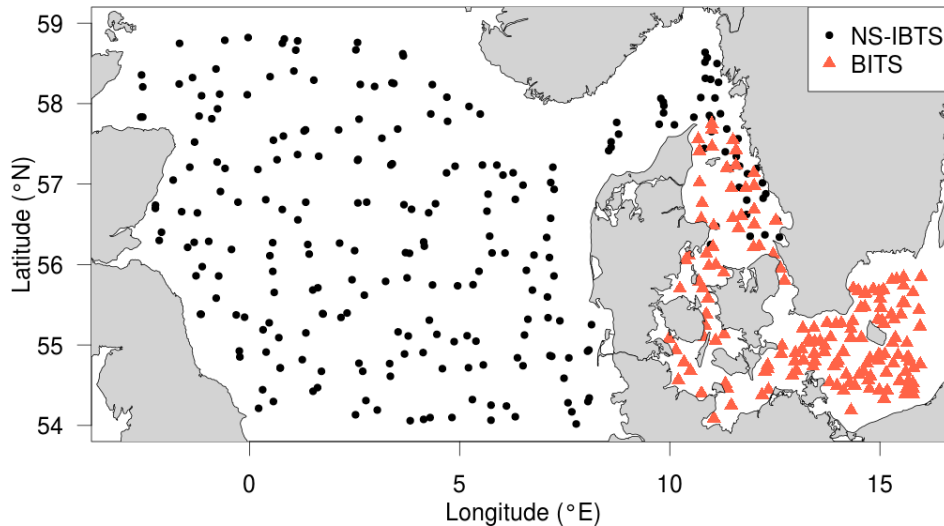
Figure 3.1. Stations of the North Sea International Bottom Trawl Survey (NS-IBTS, black dots) and the Baltic International Trawl Survey (BITS, orange triangles). Only stations inside the study are shown.

Two important life stages are of interest and their corresponding habitats are investigated: the spawning areas and the nursery areas. We assume that the spawning areas are the areas with higher aggregations of mature individuals during the first quarter of the year. Further, we assume that nursery areas are areas with the highest aggregations of immature individuals during the third quarter of the year. Maturity stage and length are recorded for a subsample of the individuals during the survey and maturity ogives are fitted using logistic regression, i.e. Generalised Linear model with binomial response and logit link function. The length at 50% maturation (L_{50}) is calculated using the linear predictors, as the absolute value of the ratio of the intercept to the slope (Figure 3.2).
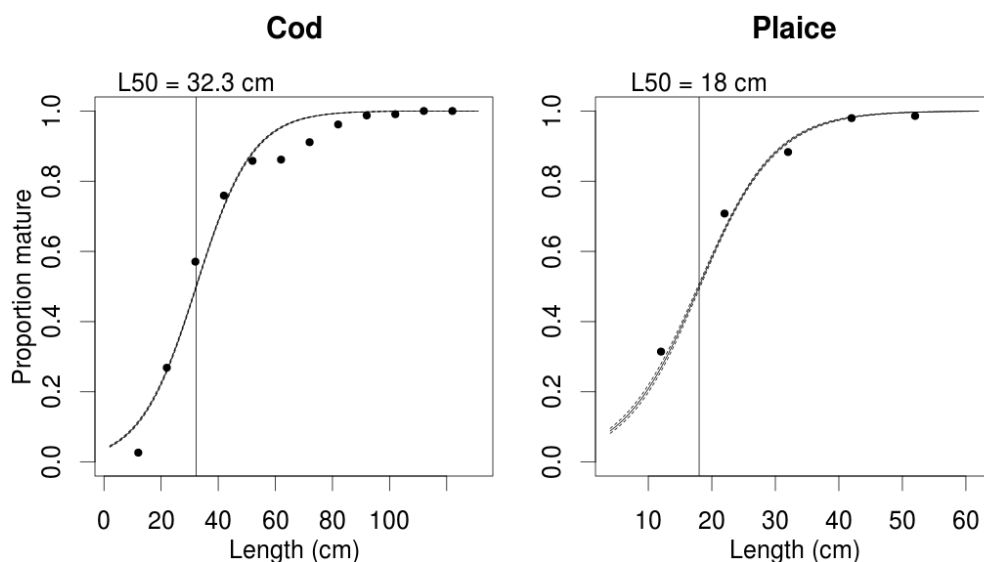
Figure 3.2. Fitted maturation ogives (solid lines) for cod (left) and plaice (right). The input data are shown as black points.

3.1.2 Hydrodynamic model output

In order to correlate environmental conditions to the observations of each survey haul, we use predictions from the HBM model operated by the Danish Meteorological Institute (DMI) at 10 km horizontal resolution and up to 77 depth layers. Specifically, we considered bottom estimates of temperature (°C), salinity (PSU), oxygen (mmol/m^3), current strength and nutrient concentration. The IBMlib software (Christensen et al., 2018) was used to extract environmental information at half meter above sea bottom for each survey station. Additionally, model predictions of the same environmental parameters are extracted at each model grid point for the first and third quarter of all the years.

3.1.3 Statistical models

Generalised Additive Models (GAMs, Wood, 2006) are used to model survey catch data using the available environmental parameters as explanatory variables. GAMs are often used to model species distributions and fisheries catch rates based on hydrographic and ecosystem variables (Grüss et al., 2018). The abundance used as response variable and hydrographical conditions at the sampling locations and depth as explanatory variables. The logarithm of trawling duration was used as offset to allow for variations in effort. The Tweedie distribution was used due to its flexibility compared to the negative binomial and the quasi-Poisson distributions, especially with respect to zero inflation (Miller et al., 2013). The logarithmic link function is used to assure non-negative predictions. The effect of the explanatory variables was modelled using smooth function and in particular thin-plate regression splines. The final models are selected using a selection process based on the minimization of the corrected Akaike Information Criterion (AICc), i.e. the AIC corrected for small sample sizes (Akaike, 1974; Burnham et al., 2011). The AICc converges to the AIC with large sample size. The modelling was done using the 'mgcv' package (Wood, 2006) in the R statistical language (R core team, 2019).

3.2 Potential spawning areas

3.2.1 Cod

The final model for mature cod includes depth, temperature, salinity and oxygen as statistically significant. The predictive maps for cod are presented separately for the North Sea and the inner Danish waters, as the predicted values are in different magnitude in the two areas and the interest is in the spawning areas in each area. The spatial patterns do not appear to be very different between years, Figure 3.3 shows as an example the first and last years in the analysis, i.e. 1991 and 2012, in North Sea. Figure 3.4 shows the same years for the inner Danish waters.
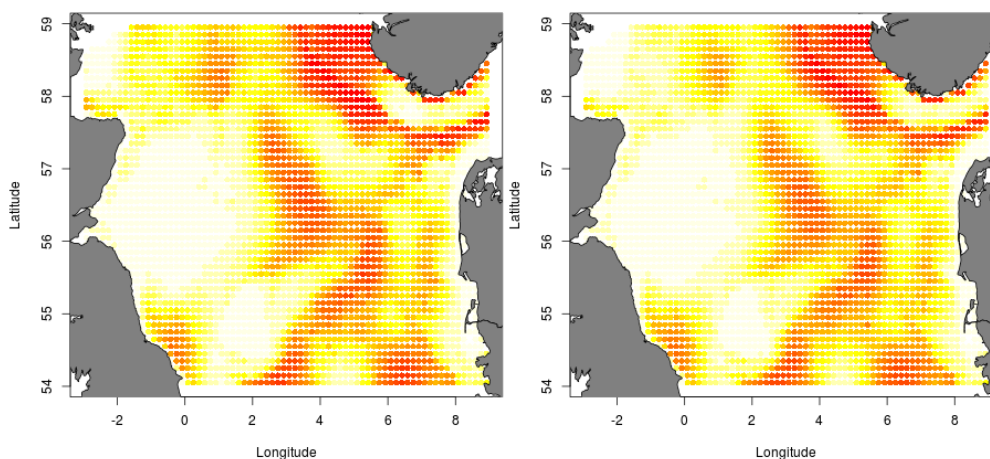
Figure 3.3. Habitat maps that correspond to potential spawning areas in the North Sea, for 1991 (left) and 2012 (right). The density is shown as a gradient from yellow (middle density) to red (high density).
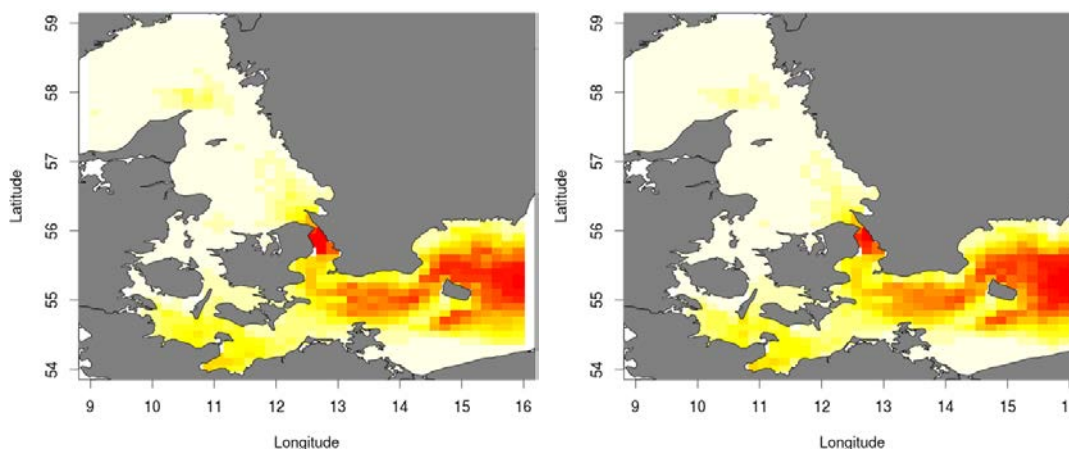
Figure 3.4. Habitat maps that correspond to potential spawning areas for cod in the inner Danish waters and western Baltic Sea, for 1991 (left) and 2012 (right). The density is shown as a gradient from yellow (middle density) to red (high density).

3.2.2 Plaice

The final model for mature plaice includes depth, temperature, bottom current strength and time of day of the haul. The differences between years are relatively small. The predictive map of potential spawning areas for 2012, i.e. the last year of the analysis, is shown in Figure 3.5.
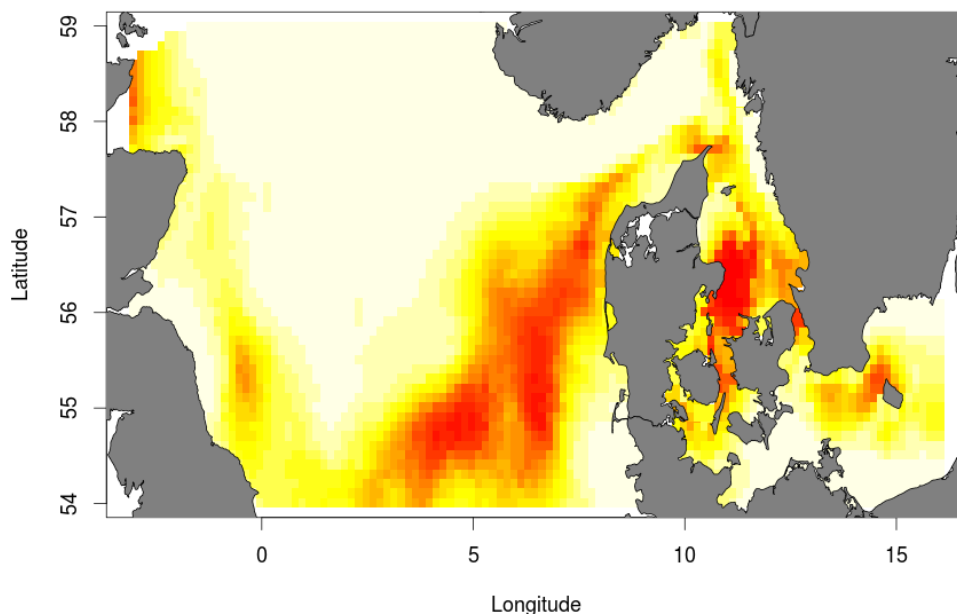
Figure 3.5. Habitat maps that correspond to potential spawning areas for plaice in 2012. The density is shown as a gradient from yellow (middle density) to red (high density).

3.3 Potential nursery areas

3.3.1 Cod

The selected model for the immature part of the cod population included depth, temperature, salinity, oxygen, bottom current strength and nutrients. The predictive map for 2012 provides an indication of important habitats for immature cod population (Figure 3.6).
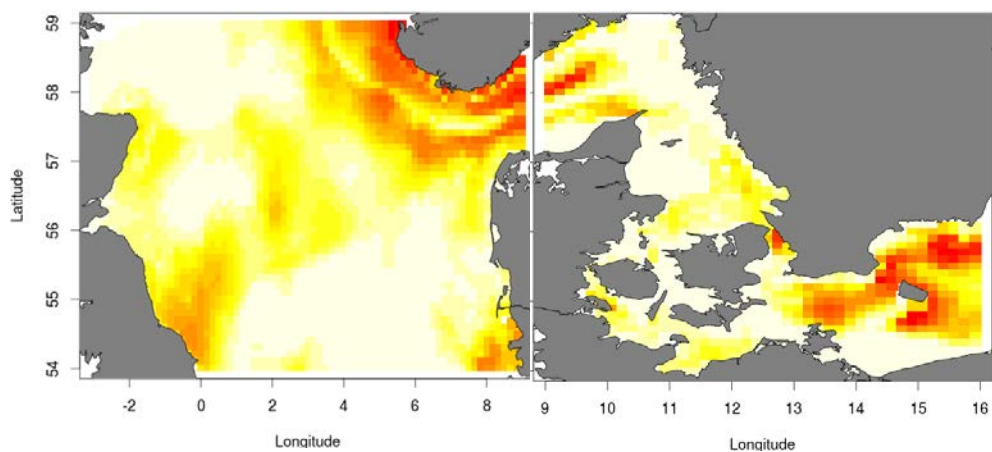
Figure 3.6. Habitat map of potential important areas for immature cod in 2012 for North Sea (left) and inner Danish waters and western Baltic Sea (right). The density is shown as a gradient from yellow (middle density) to red (high density).

3.3.2 Plaice

The selected model for immature plaice included depth, temperature, salinity, oxygen, bottom current strength and nutrients. The predictive map for 2012 with potentially important areas for immature plaice is shown in Figure 3.7.
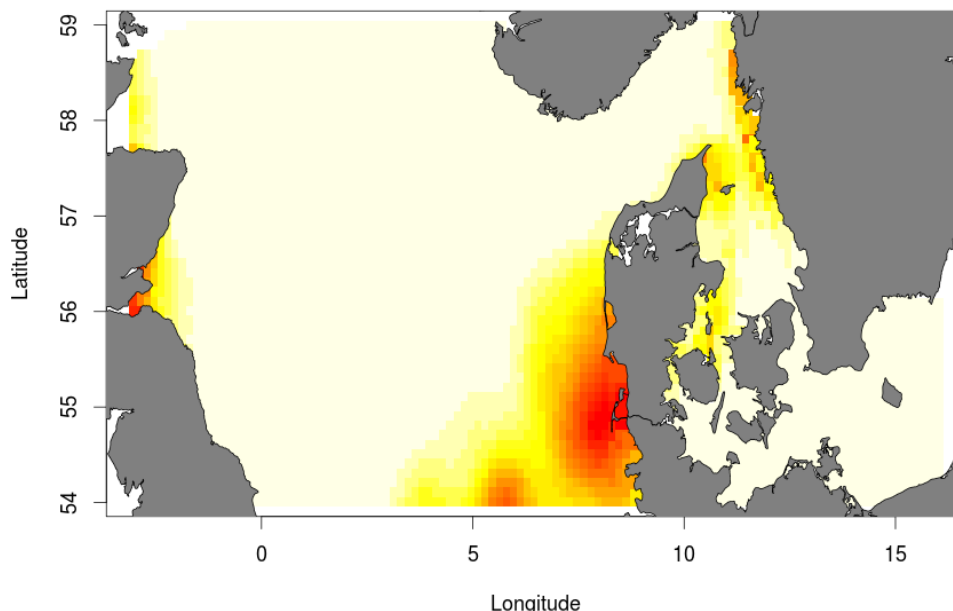
Figure 3.7. Habitat map of potential important areas for immature plaice in 2012 for the North Sea, the inner Danish waters, and western Baltic Sea. The density is shown as a gradient from yellow (middle density) to red (high density).

3.4 Summary

We investigated potential habitats for two life stages of cod and plaice, we modelled adult cod and plaice in the first quarter and immature cod in the third quarter as proxies for spawning areas and nursery areas, respectively. The models related abundance per trawling duration of the two species with depth and environmental conditions at the time of capture. Potential spawning areas for cod include the Sound, most of Western Baltic, and a large part of the North Sea (especially Eastern part with highest densities estimated in Southern Viking). For plaice the potential spawning areas include the German Bight and Fisher areas in the North Sea, and the area from Kattegat to the Greater Belt.

Potential nursery areas were very different for the two species. Immature cod densities were higher off the Norwegian coast in the North Sea and Skagerrak, the Sound, and in the Arkona and Bornholm basins. Highest densities of immature plaice were observed in the German Bight and close to the Swedish coast in Kattegat.

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4. Genetics

The purpose of the genetic work was to investigate the population of origin of European plaice and Atlantic cod juveniles in coastal regions. We have focused the work on the transitional region between the North Sea and Baltic Sea as the highly dynamic environmental conditions in this region could potentially affect the distribution and dynamics of fish populations. Several earlier studies have mapped the distribution of spawning populations of plaice and cod with the use of genetic data. Such work usually focuses on adult spawning fish as these are the basis for local populations.

In the European plaice, a recent study applied thousands of genetic markers and identified important genetic differences between populations in the transition zone between the North Sea and Baltic Sea (Le Moan et al. 2019). The genetic differences were particularly pronounced for specific regions in the plaice genome. In the current project, we have used this information to study the relationship between genetic signatures in adults and juveniles collected within the same geographical regions.

Atlantic cod in the transition zone has been studied intensively with use of genetic markers and tagging data. Studies have found clear genetic differences between North Sea and transition zone populations (Nielsen et al. 2003; Berg et al. 2015). Genetic analyses of juveniles and adults collected outside main spawning periods have shown that the Kattegat is characterized by highly dynamic patterns of population mixing (ICES 2017). The genetic data and data from otolith microchemical signatures have indicated that North Sea juveniles enter the Kattegat at early life stages and return to the North Sea when they reach maturity. Consequently, very few spawning cod of North Sea origin are found in the Kattegat (ICES 2017). These results are further supported by tagging data that have suggested that cod migrate between the Kattegat and the North Sea (Svedäng et al. 2007). In this project, we have focused on characterizing the mixing for the juvenile cod in order to relate these data to potential drivers of mixing.
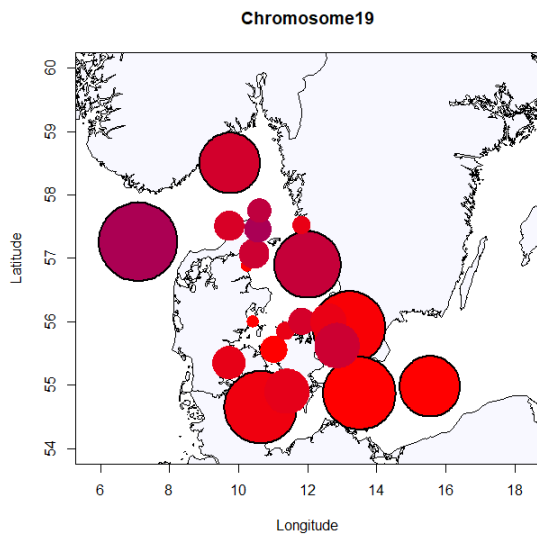
Figure 4.1. Comparison of genetic profiles in adults (large circles) and juveniles (small circles) for genetic variation on chromosome 19.
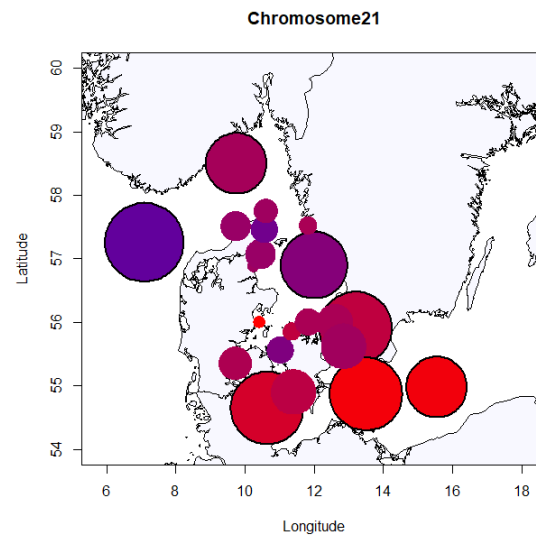
Figure 4.2. Comparison of genetic profiles in adults (large circles) and juveniles (small circles) for genetic variation on chromosome 21.

4.1 Plaice juveniles

Samples of approximately 150 juvenile plaice collected in 2016 by DTU Aqua on a coastal survey were compared to adults collected at spawning time during 2016 and 2017 (see Le Moan et al. 2019). We used the double-digest RAD sequencing (ddRAD; Poland and Rife 2012) approach to analyze thousands of genetic markers in each individual (see Le Moan et al. 2019 for details). This information was used to compare the genetic profiles for adults and juveniles for the specific genomic regions showing high divergence within the geographical region. These highly differentiated genomic regions are likely so-called inversions located on chromosomes 19 and 21 in the plaice genome. We estimated the frequencies of the two variants of the inversions at each sampling site, and then used the frequencies to represent the genetic profiles through a unique blending of red/blue colors for each sampling site. The reasoning for this approach was that similar genetic profiles (i.e. here similar colours) for juveniles and adults within a geographical region would indicate local origin of juveniles and that juveniles recruit to local coastal nurseries.

Results showed similarity of genetic profiles obtained from adult spawning populations and juveniles collected in nearby nursery areas (Figures 4.1, 4.2). These results suggest that juveniles originate from locally spawning parents, although it should be kept in mind that these data represent only one snapshot in time (i.e. for juveniles from 2016).

4.2 Cod, spawning adults from the Skagerrak

Cod in the North Sea and Kattegat/Øresund/Western Baltic Sea show clear genetic differences, which can be used to identify the population of origin of individuals collected in areas where populations mix, as for example observed in the Kattegat (ICES 2017). However, the genetic profile of spawning cod in the Skagerrak is not well known. Samples of cod in spawning condi-

tion were therefore collected from the Skagerrak on the Swedish IBTS, Q1 2019. Only six individuals in spawning condition were obtained from the cruise, however this number was still sufficient to provide an overall assessment of the origin of fish spawning in the area.

Results showed that five of the six spawning cod collected in the Skagerrak assigned genetically to the North Sea baseline, while one individual assigned to the Kattegat baseline. These results suggest that cod juveniles spawned in the Skagerrak are most likely to have a North Sea genetic signature. The results are also in line with other data, which suggest that the majority of spawning activity of the local Kattegat population takes place in the southernmost parts of the Kattegat (ICES 2017).

4.3 Cod, juveniles collected by the key fishers

Samples of juvenile cod from coastal regions were targeted for sampling in collaboration with key fishers in spring 2019. The purpose of the collections was to identify the population of origin of juvenile cod in the coastal regions in the Kattegat. Priority was given to areas 8, 9, 10, 15, 19 and 20 in Figure 4.3, aiming for 50-75 fish per area. Unfortunately, the sampling program resulted in the collection of very few fish (<10 individuals in total), which prevented any further analyses of this part of the data.
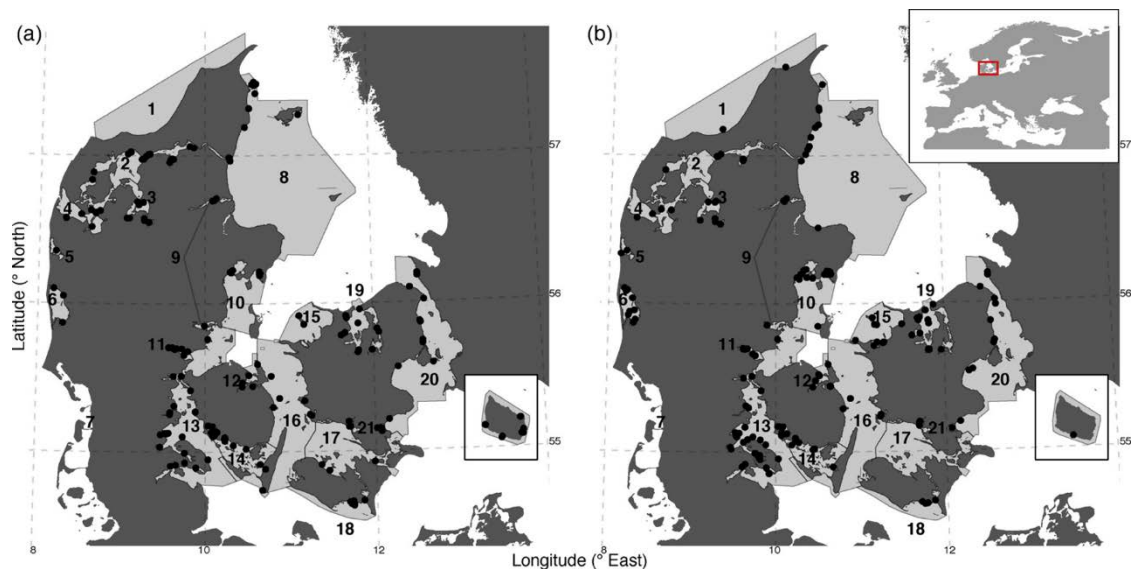
Figure 4.3. Location of key fishers fishing with fyke nets in a) and gill nets in b) (from Støttrup *et al.* 2018).

4.4 Cod, time series of juvenile otoliths

Otoliths from juvenile cod from the Kattegat were available for 1998, 2001, 2003, 2004, 2005, 2010, 2011, 2012 and 2014. Most of these individuals were likely collected offshore (at least compared to locations for juveniles collected by key fishers). For these historical samples, we followed laboratory protocols developed for working with sensitive samples (Bonanomi et al. 2015, Hemmer-Hansen et al. 2019). Briefly, each otolith was first evaluated for evidence of cross-sample contamination, and samples displaying evidence for contamination were excluded for further analyses. Samples with sufficient quality and quantity of DNA and without signs of contamination were analyzed for population of origin, following the procedure applied to fresh tissue samples of cod in the Kattegat (ICES 2017). Here, 187 genetic markers that provide high sensitivity for discriminating between North Sea, local Kattegat/Øresund/Western Baltic and

Eastern Baltic populations were analyzed and each fish was allocated to the most likely population of origin based on its unique genetic profile (see ICES 2017 for further detail on the methodology).

1998-2015 otoliths (n=325)
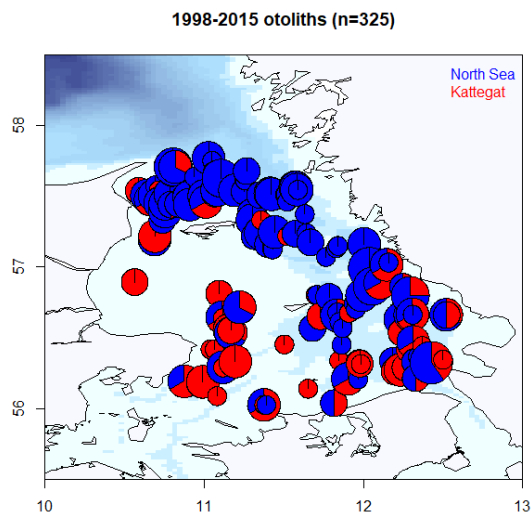
Figure 4.4. Proportions of North Sea (blue) and Kattegat (red) for all analyzed otoliths. Size of pie charts is proportional to sample size.

A total of 464 otoliths were analyzed. Of these, sufficient quantities of DNA could not be extracted from 122 of the otoliths while 11 otoliths were discarded due to the detection of contamination (i.e. the presence of DNA from more than one individual). The remaining fish were assigned to the most likely population of origin in a baseline consisting of "North Sea", "Kattegat" (Kattegat, Øresund and western Baltic combined) and "Eastern Baltic". Results confirmed the north-south gradient in mixing proportions between North Sea and Kattegat that has also been observed for adults and early life stages, but also confirmed the absence of data from very coastal regions within the Kattegat (Figure 4.4). In addition, considerable variation between cohorts was found (Figure 4.5). A very pronounced North Sea "inflow" was found for the 2011 year class (also confirmed when analyzing the same cohort collected as older fish after 2011; see ICES 2017). The 2003 and 2004 year classes also showed a dominance of juveniles of North Sea origin, although the patterns were less pronounced than for 2011.
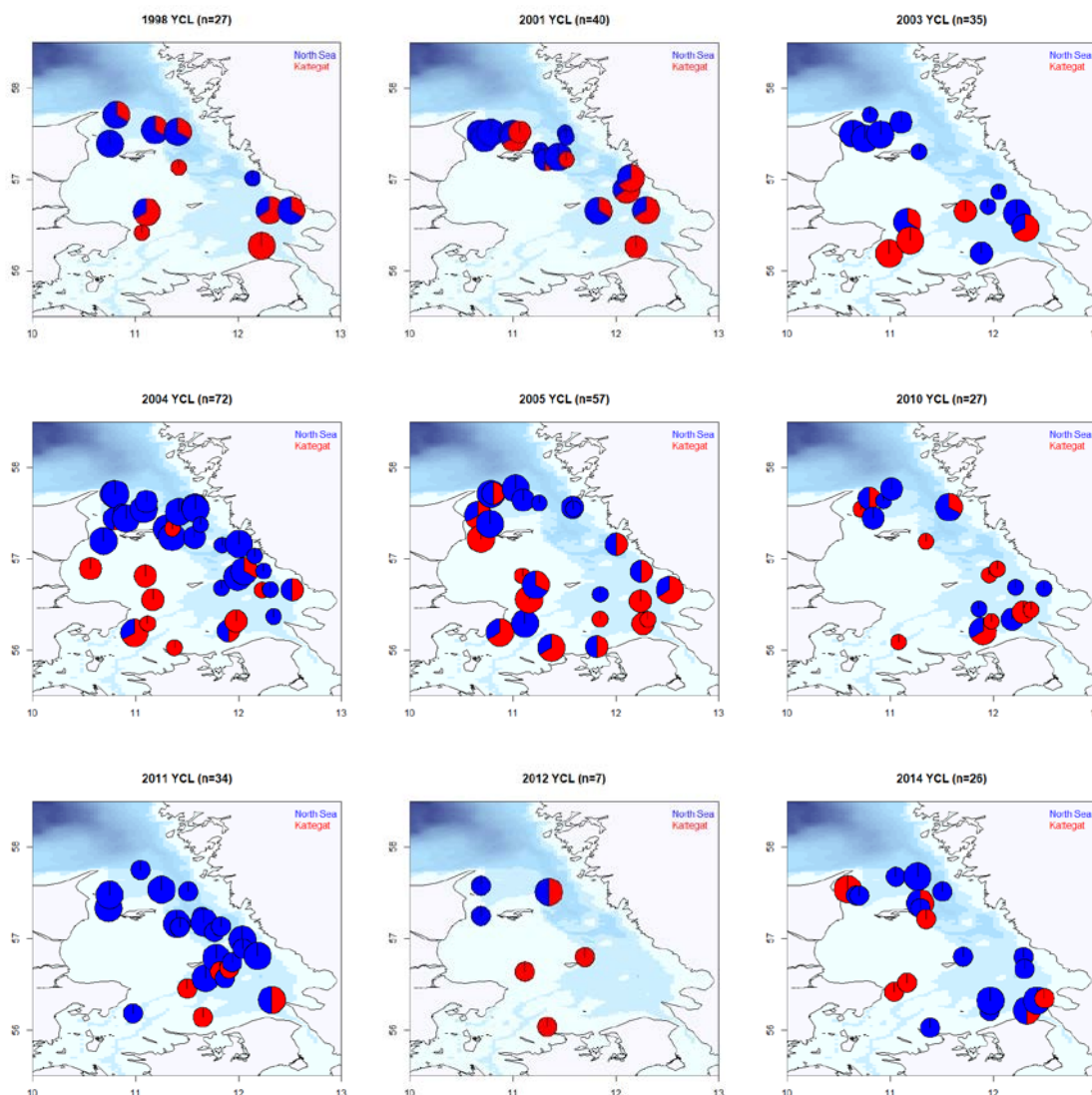
Figure 4.5. Proportions of North Sea (blue) and Kattegat (red) juveniles in different year classes. Size of pie charts is proportional to sample size.

4.4.1 Effects of latitude and depth

We investigated the spatial distribution of mixing through generalized additive modelling (gam), using the proportion of North Sea fish as a response variable and different combinations of explanatory variables in the models (Table 4.1). When evaluating models through the Akaike Information Criterion (AIC), we found the best fit for the model including effects from both latitude and depth (model m2, Table 4.1). The model showed the overall tendency for local Kattegat fish to be distributed mainly in the shallower water depths and in the southern parts of the Kattegat (Figure 4.6), as also indicated by the distribution of population components in Figures 4.4 and 4.5. In contrast, the North Sea fish were observed in both deeper and more shallow areas (Figure 4.6). It should be noted that the data did not permit the inclusion of temporal effects in the models and hence the temporal dynamics indicated in the observations of mixing in Figure 4.5 cannot be modelled with the present data sets. Consequently, these analyses should be viewed as a first attempt to explain overall geographical patterns in the data.
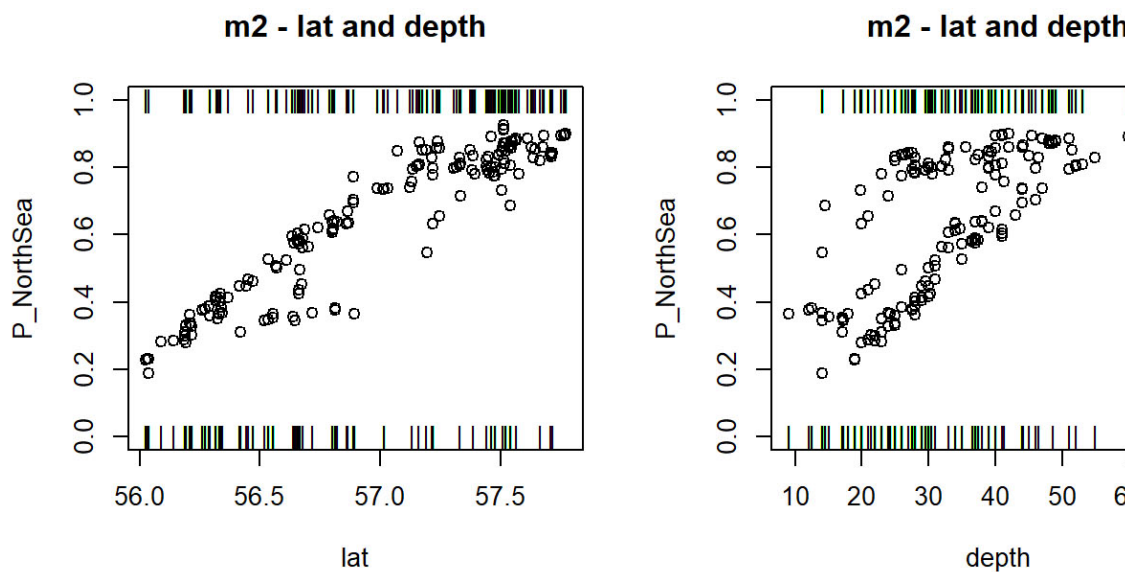
Figure 4.6. Best model fit to the data (proportion of North Sea fish per station), including effects from latitude (left) and depth (right).

4.4.2 Effects on stock-recruitment relationship

To investigate possible effects of stock mixing of juveniles on stock assessments, we extracted data on spawning stock biomass and recruitment from the latest ICES advice (ICES 2019). These data are currently aggregated across the entire Kattegat without taking stock mixing into account. However, the data may provide an incorrect relationship between spawning stock biomass and recruitment the following year if a significant part of the juveniles is in fact not spawned within the Kattegat but originate from spawning in the North Sea.

To evaluate such effects, we compared the stock-recruitment relationship for the raw data with the relationship corrected for stock mixing by assuming that the spawning stock biomass reflected fish of only local Kattegat origin (see also ICES 2017) while the recruitment consisted of a mix of fish of North Sea and local origin. To obtain a "mixing-corrected" estimate of recruitment we simply excluded the proportion of North Sea juveniles from the raw recruitment data. The mixing-corrected recruitment data showed a clearer relationship between spawning stock biomass and recruitment the following year (Figure 4.7), indicating that information about stock mixing may be important for improving the stock assessment of cod in the Kattegat. It should be noted that data material is still limited and that these analyses should mainly be viewed as a qualitative evaluation of potential effects. More data will be needed to get a full understanding of the quantitative effects of mixing.
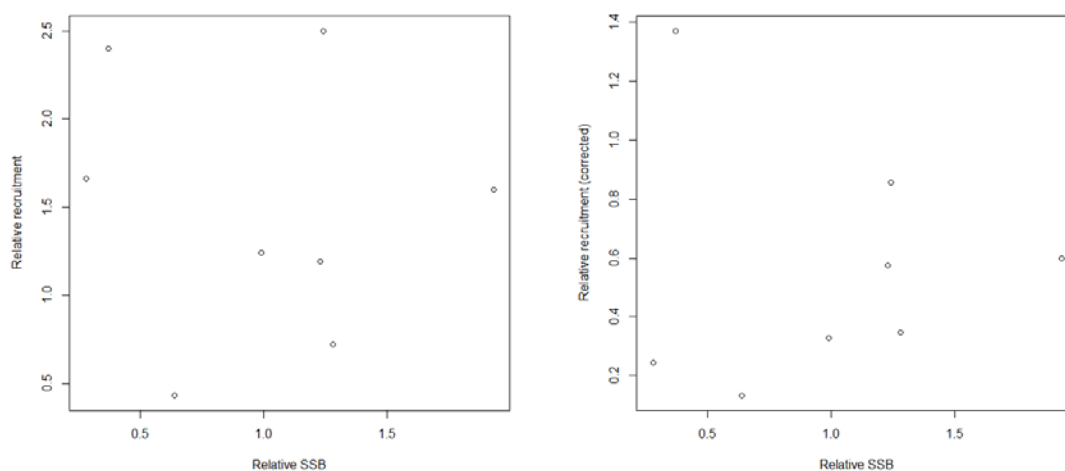
Figure 4.7. Relationship between spawning stock biomass (SSB) and recruitment (fish of age 1) the following year for raw data (left) and data with the proportion of North Sea juvenile fish excluded (right). One data point with relative recruitment above 1.2 in the panel to the right was for 2012 where only seven fish were available to estimate mixing proportions (see also Figure 4.5), hence this estimate should be interpreted with caution.

Table 4.1. Summaries for the different gam models. The best model was chosen based on the AIC criterion.

Model	df	AIC
m1 - latitude	2.000090	365.0974
m2 – latitude and depth	3.935383	359.5149
m3 – latitude and longitude	4.947483	363.9645
m4 – latitude, longitude and depth	5.393826	362.2345

4.5 Summary

We found support for a hypothesis of recruitment to local nursery grounds for plaice juveniles collected in 2016. This does not exclude mixing of juveniles from different spawning grounds in particular nursery areas, but mainly suggests that local recruitment is at least possible in plaice. However, data is so far limited to a single year of juvenile sampling and time series analyses would be important to get a better understanding of temporal patterns of recruitment in the species. Since there are relatively clear genetic differences between North Sea and transition zone plaice populations, genetic data could be used to track temporal patterns of mixing, for example related to similar time series from connectivity matrices available through this project.

For cod, we have confirmed that mixing of fish of North Sea and local origin occurs at the juvenile life stages and have now obtained an improved understanding of temporal dynamics of mixing. This is important for improving future stock assessment, and our very preliminary analyses of stock-recruitment relationships suggest that genetic data may provide a very valuable tool to achieve this. We found a tendency for local juvenile cod in the Kattegat to be distributed in more shallow waters. Consequently, it is possible that the two stock components are impacted differently by environmental changes in the region.

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5. Modelling connectivity

5.1 Cod

Four cod stocks inhabit Danish waters according to ICES: the eastern Baltic cod (ICES, 2019a), western Baltic cod (ICES, 2019b), Kattegat cod (ICES, 2019c) and North Sea cod (ICES, 2019d). Those different stocks might present different spawning time, egg´s neutral buoyancy density and environmental thresholds for survival of eggs and larvae. These differences should be taken into account when studying cod in this area. However, most information is available for only one stock. For example, Bestriding et al. (2014) studied North Sea cod larvae settlement length, and there is no information for cod larvae settlement length for the other stocks. In this case, we assumed that all the larvae followed North Sea´s cod settlement length.

The connectivity between spawning areas and settling areas is simulated using IBMlib (Christensen et al., 2018) coupled with output from the operational HBM model operated by the Danish Meteorological Institute (DMI) at 10 km horizontal resolution and up to 77 vertical z-layers. The period considered for the analyses is from 1990 to 2012. Recruitment probability (T_{ij}) from a spawning habitat i to settlement habitat j is calculated as:

$$T_{ji} = \frac{1}{R_i} N_{ji}$$

Where Ri is the number of released eggs from spawning habitat i and N_{ji} is the number of larvae settling in the habitat j which came from $i,$ weighted by their survival change along the transport.

In the individual-based modelling context, there are two types of connectivity analysis: downstream and upstream. Downstream connectivity refers to the probability that a particle with an initial position corresponding to a selected grid cell will disperse and end up in any of the other grid cells in the connectivity grid, while the upstream connectivity refers to the probability that agents that settled in the specified grid cell originated from any of the other grid cells (Hansen & Christensen, 2008). In this study, downstream connectivity analysis was conducted. Two examples of connectivity matrix are shown in Figure 5.1. With a visual comparison of these two years, we can appreciate that particles released in the 1995 settled in more areas than in 1992.
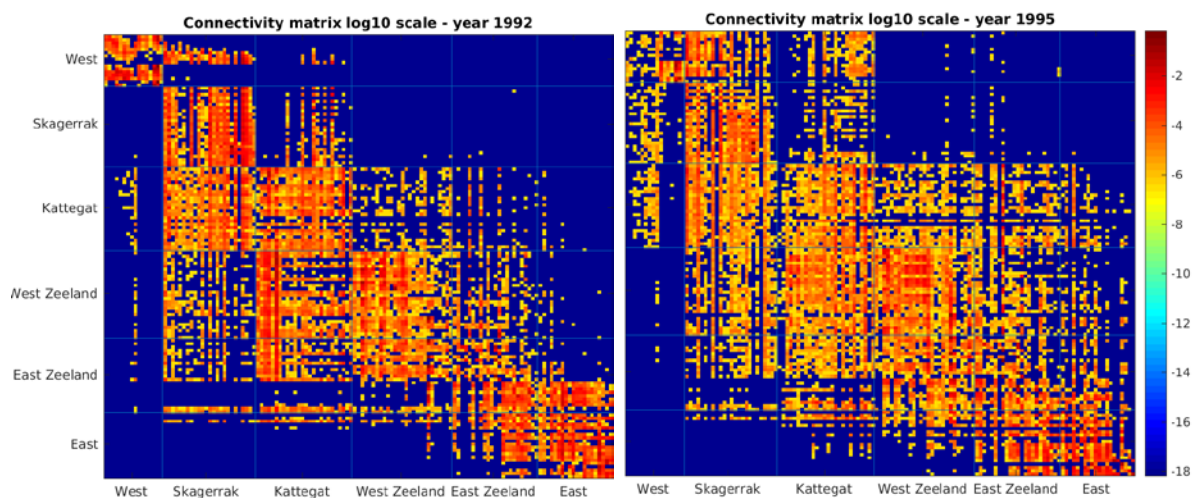
Figure 5.1. Connectivity matrix in log10 scale for 1992 (left) and 1995 (right). The y-axis is spawning regions while the x-axis are regions where the particles settled.

5.1.1 Proportion of particle end positions

Based on the connectivity matrix results, a time series of the proportion of particle drifted and retained in each release area was produced (Figure 5.2).
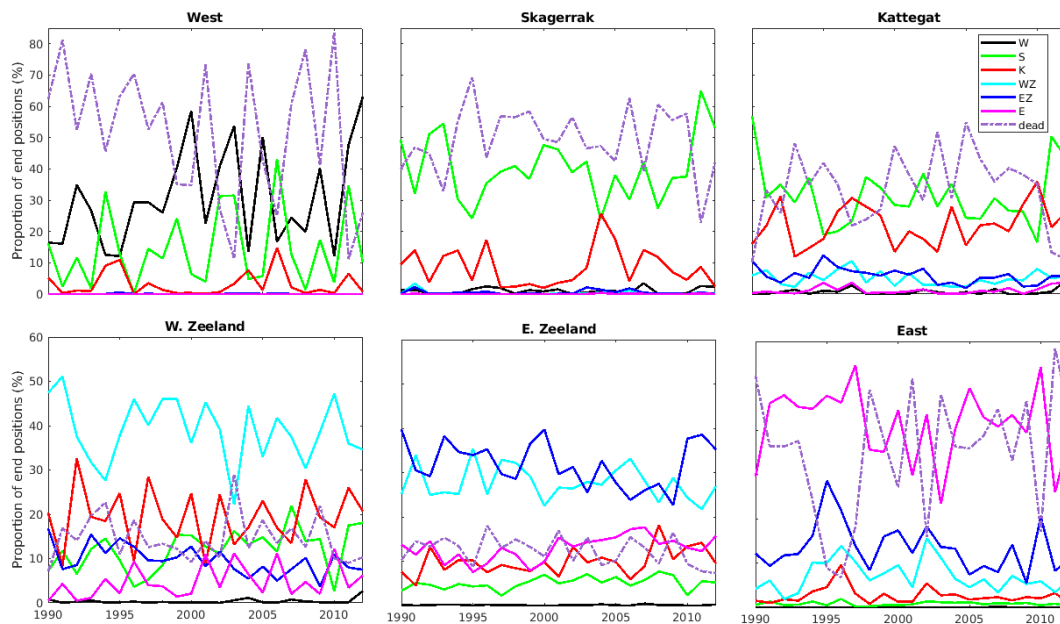
Figure 5.2. Time series of proportions of particles end position. Each box represents a different release area and lines corresponds to the proportion settled in each region or not settled ("dead").

Generally, population connectivity across regions shows large year-to-year variability. However, on average most of the particles released near the west coast stayed in the west coast or died, with few been able to settle in Skagerrak. The majority of the particles released in the Skagerrak stayed in this area or died, and some were able to settle in the Kattegat. Particles released in the Kattegat settled in Skagerrak, remained in the same area, died, and less than 10% settled in the West Zeeland, East Zeeland and East. Particles released in the West Zeeland remained in the region, settled in Kattegat or in the Skagerrak, East Zeeland and East or died. Particles released in East Zeeland stayed in the region, settled in West Zeeland, East, Kattegat or Skagerrak and between 10 to 20% were not able to settle. The majority of particles released in the East remained in the area or died.

Table 5.1. Mean ± standard deviation of connectivity between regions. W stands for West, S for Skagerrak, K for Kattegat, WZ for West Zeeland, EZ for East Zeeland and E for East. The rows represent where the particles were released and the columns where the particles settled.

Decade 1990						
	W	S	K	WZ	EZ	E
W	24.4 ± 9.7	12.8 ± 10.2	3.3 ± 3.9	0.0 ± 0.1	0.1 ± 0.2	0.0 ± 0.0
S	1.0 ± 0.9	39.4 ± 9.7	8.3 ± 5.7	0.4 ± 1.0	0.4 ± 0.7	0.0 ± 0.0
K	0.7 ± 0.9	32.3 ± 11.0	22.3 ± 6.9	6.0 ± 2.6	7.3 ± 2.6	1.2 ± 1.3
WZ	0.2 ± 0.2	9.4 ± 3.9	19.5 ± 7.7	41.1 ± 7.5	11.6 ± 3.1	3.2 ± 2.8
EZ	0.1 ± 0.1	4.2 ± 1.0	8.7 ± 2.3	28.9 ± 4.3	33.6 ± 4.0	11.0 ± 2.4
E	0.0 ± 0.0	0.7 ± 0.6	3.0 ± 2.6	7.3 ± 3.7	15.0 ± 6.1	43.2 ± 7.5
Decade 2000						
	W	S	K	WZ	EZ	E
W	34.1 ± 16.6	15.8 ± 14.6	3.2 ± 4.7	0.0 ± 0.0	0.0 ± 0.1	0.0 ± 0.0
S	0.8 ± 1.0	37.4 ± 7.9	9.9 ± 7.5	0.3 ± 0.3	0.7 ± 0.8	0.1 ± 0.1
K	0.5 ± 0.6	29.0 ± 4.6	20.1 ± 5.3	3.7 ± 1.4	5.0 ± 2.2	0.7 ± 0.6
WZ	0.3 ± 0.4	14.5 ± 3.0	18.9 ± 6.1	36.8 ± 7.0	8.0 ± 2.9	5.6 ± 4.0
EZ	0.1 ± 0.1	6.1 ± 1.1	10.3 ± 3.4	27.5 ± 3.1	28.6 ± 5.0	14.6 ± 2.1
E	0.0 ± 0.0	0.9 ± 0.3	2.3 ± 1.2	7.4 ± 3.7	11.9 ± 4.3	39.7 ± 7.6

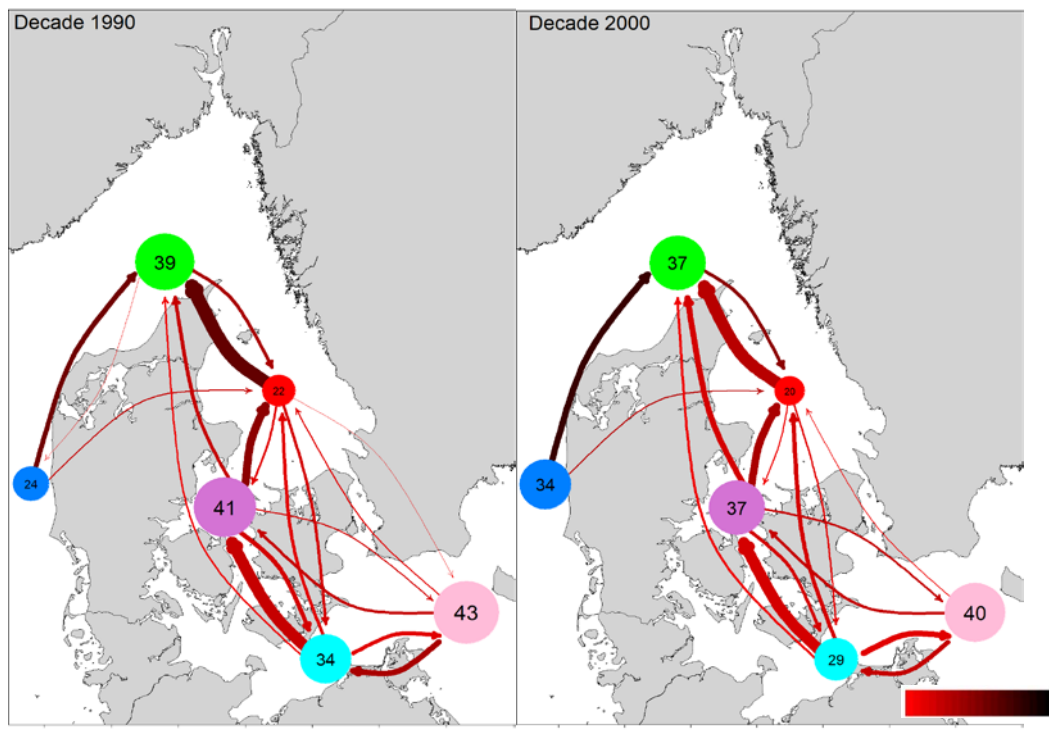**Figure 5.3. Proportion of particles retained and transferred: left represents average for the 1990-1999 and right for the 2000-2009. The number in the circle represents the proportion retained in each area, the arrow width represents the proportion going to the other region, and the arrows´ colour represents the standard deviation (from red (0%) to black (18%)). Only transfers with more than 1% are represented.**

Long-term averages of this quantities for the different decades included in the analyses shows persistent connectivity patterns in the region (Figure 5.3, Table 5.1). Comparing the connectivity between regions in 1990 and 2000 decade and between years, connectivity between regions seems to vary annually, but between decades seems not vary greatly, except by the particles retained in the West, which in decade 2000 were 9.7% greater than in 1990´s. Besides this area, difference between decades were less than 5% in average. Comparing these two decades, in 2000s particles had greater chance to remain in the West, and less chance to remain in all the other areas. The Skagerrak and Kattegat were important regions of recipients. Overall, the exchange between regions for both decades follow same trends (Figure 5.3).

5.2 Plaice

Drift experiments on plaice were conducted with the IBMlib framework (IBMlib, 2016) for the period 1994-2013 to better understand the importance of local and offshore spawning of European plaice. We studied four spawning grounds: Dogger Bank, German Bight, Skagerrak and Kattegat, and four nursery grounds: Jammer Bay, Jutland, Zealand and Swedish Coast.

Based on the connectivity matrix, time series of the proportion of particles drifted and retained in each release area were produced (Figure 5.4).
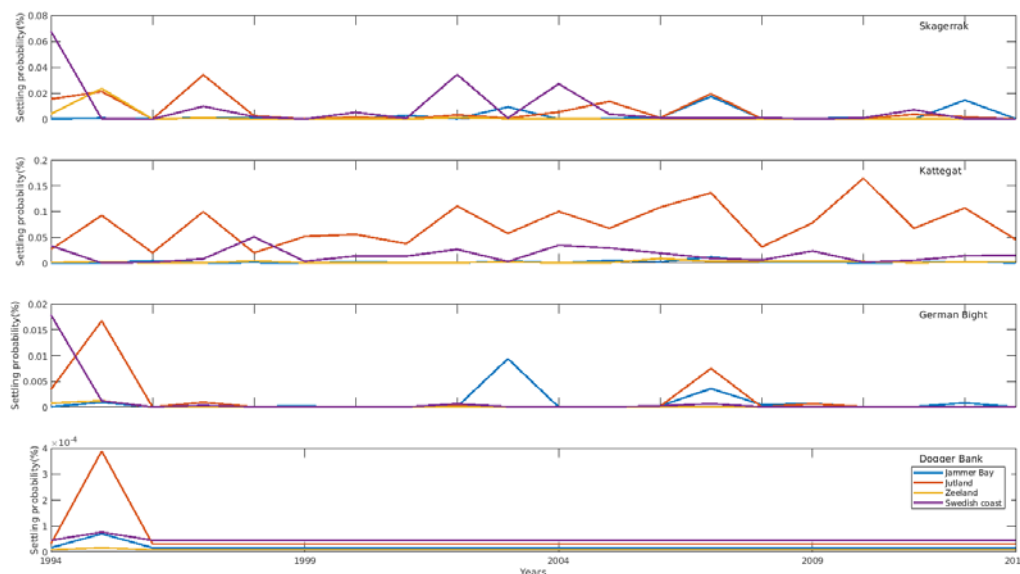
Figure 5.4. Time series of recruitment probability. Each box represents a release area and lines corresponds to the settling probability for each area.

Connectivity values for the area show that Kattegat is the most important spawning ground for European plaice settling in Jutland and Swedish coast, followed by Skagerrak and German Bight. Retention in regions nearby the spawning areas is always important for plaice (e.g. 2003 and 2012), although in some years drifting to other areas can be relevant too (e.g. 1995 and 1997). The inflow from German Bight to Skagerrak and Kattegat is very variable, there were four years with more than 0.005% probability of settling in the area, some years with very low probability (e.g. 1997 and 2009), and years with almost no probability to settle in the area (e.g. 1998). Besides the unusual year 1995, the probability that Dogger Bank can support local populations in the Skagerrak and Kattegat is very low (Figure 5.4). It is important to underline that

while for cod the analyses was on the potential connectivity (meaning that mortality was not explicitly included), here for plaice survival probability is considered as connectivity values, including the effect of suitable settling habitat and predation and natural mortality.

The average and standard deviation of connectivity between the regions for the whole period was calculated and plotted (Figure 5.5).
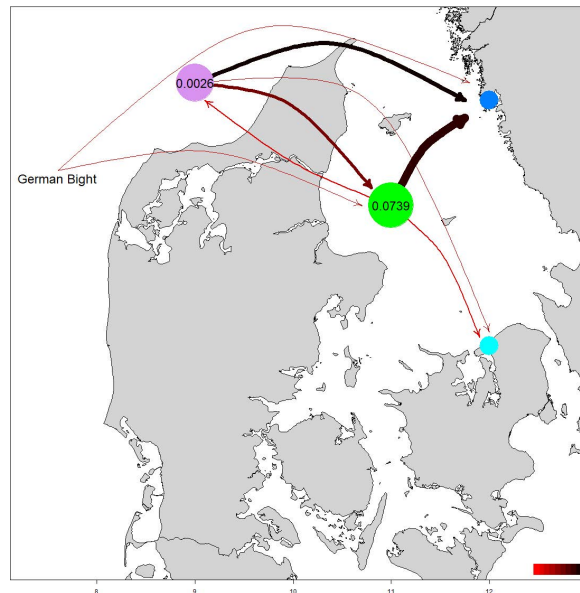
Figure 5.5. Proportion of particles retained and transferred between regions for the whole period (1994-2013). The number inside the circle represents the proportion retained, the arrow width represents the proportion drifted to other regions (from 0.0011% to 0.0158%), and the arrows´ colour represents the standard deviation (from red (0%) to black (0.0017%)). Only transfers greater than 0.001% are represented.

Overall, Kattegat has a greater retention than in Skagerrak. Juvenile plaice in the Skagerrak is mainly from retained eggs from the Kattegat. Retention for the Jutland area is important too and eggs originated from German Bight and Skagerrak significantly contribute to the recruitment. High connectivity between Zealand and Kattegat suggest retention in the area, but in some fraction often originate from the Skagerrak. Swedish coast receives primarily from Kattegat (again suggesting retention), and followed by Skagerrak and German Bight.

The simulations had the same concentration of eggs in all spawning areas for all years. Meaning we focused on understanding the transportation variability for settlement of juvenile plaice. However, recruitment is dependent not only on that but also on spawning intensity. Therefore, it might be that due to a stronger spawning in German Bight, German Bight can contribute with more juvenile plaice in Kattegat than the own local spawning in Kattegat. Nevertheless, with this study it was possible to observe the great interannual variability in plaice settling based in the currents, support the hypothesis of a local recruitment in Kattegat and demonstrating that the probability of Dogger Bank been a relevant spawning ground to plaice settling in Skagerrak and Kattegat is very low.

5.3 Model description

We conducted drift experiments with the 3D physical circulation model HBM. Horizontal and vertical diffusivity were applied in the simulations, 100 m²/s horizontally (based in Gurney et al., 2001) and 0.01 m²/s vertically.

We defined Dogger Bank and German Bight as spawning grounds for plaice based in Hufnagl et al. (2013), while Kattegat and Skagerrak based in Cardinale et al. (2011), with Skagerrak expanded to include all the areas where more than 50% were at least 10 to 40 m deep. We defined the settlement areas based in the topography – areas shallower than 10 meters (from IOWtopo2, 2008) – and in the substratum (from GEUS, 1999) – where it is considered soft (Figure 5.6). Every year it was released 966,000 particles, distributed as 10 egg/larvae per km² over the spawning areas.

We considered three life stages: pelagic egg, pelagic larvae and demersal larvae. Horizontally, all stages were passive. Vertically, eggs were positive buoyant to ρ=1020 kg/m³ (Coombs et al., 1990; Petereit et al., 2014), pelagic larvae passive and demersal larvae swam with average downward speed of 4 mm/s. The spawning date was on March 1 as Nielsen et al. (2004) indicates its spawning period as "late February and early March". The duration of each life stage was determined by the temperature, following Bolle et al. (2000) and Hufnagl et al. (2013). Mortality rate was included for each life stage (33.4/year, 16.5/year and 5.86/year) based in Wennhage (1999). We considered larvae dead if they did not find a suitable habitat to settle.
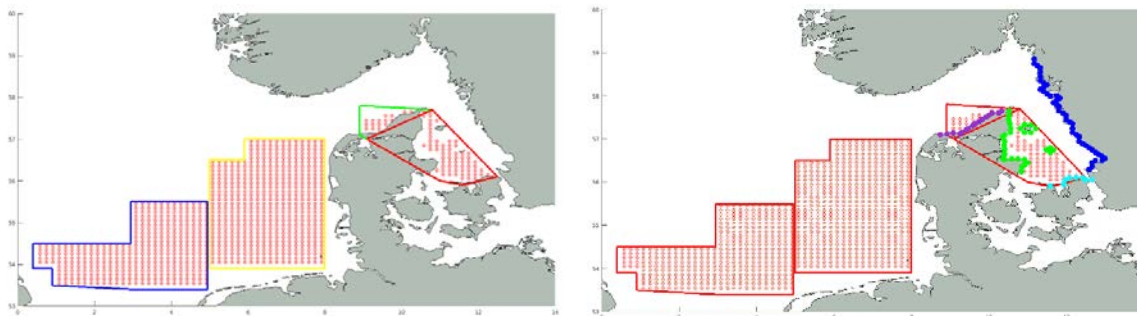
Figure 5.6. Left: Spawning grounds: Dogger Bank (blue line), German Bight (yellow line), Skagerrak (green line) and Kattegat (red line). Right: Spawning grounds in red with the coastal settlement habitats: Jammer Bay (in purple), Jutland (in green), Zealand (in cyan), Swedish coast (in blue).

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6. Synthesis

6.1 Environmental factors driving distributions and fish exchanges

6.1.1 Cod

Cod exhibits demographically delineated habitat occupation (Figure 6.1). Genetic studies reveal two distinct types; resident groups and seasonal migrants and can represent isolated groups of fish (Knutsen et al. 2003). Resident populations appear to be most common in coastal areas as documented from Norway, Iceland and the Canadian eastern seaboard (Knutsen et al. 2003; Pampoulie et al 2006; Jónsdóttir et al. 2001). Spatial memory seems to play a role in the distinct spawning migrations that cod undertake during winter (Tupper & Boutilier, 1995; Svedäng et al., 2007). Cod tagged in Skagerrak were observed to migrate toward the North Sea during the spawning season to return to the eastern Skagerrak later in spring. The migration route to the North Sea is apparently along the northern coast of Jutland and spawning site believed to the Fisher Bank (Svedäng et al., 2007) or near the edge of the Dogger bank (Munk et al., 2009). In the North Sea, the preferred temperature for spawning is around 5-7 °C (González-Irusta & Wright, 2016) with a preference for high salinity waters. Possibly mature cod residing in deeper waters migrate to shallower banks for spawning, preferably in salinity frontal systems that are highly productive areas and serve to retain the eggs and larvae and transport them to suitable nursery habitats (Munk et al., 2002, 2009). Management distinguishes between North Sea and Skagerrak, Kattegat, western and eastern Baltic cod stocks. However, no distinctions are made between offshore and coastal groups.
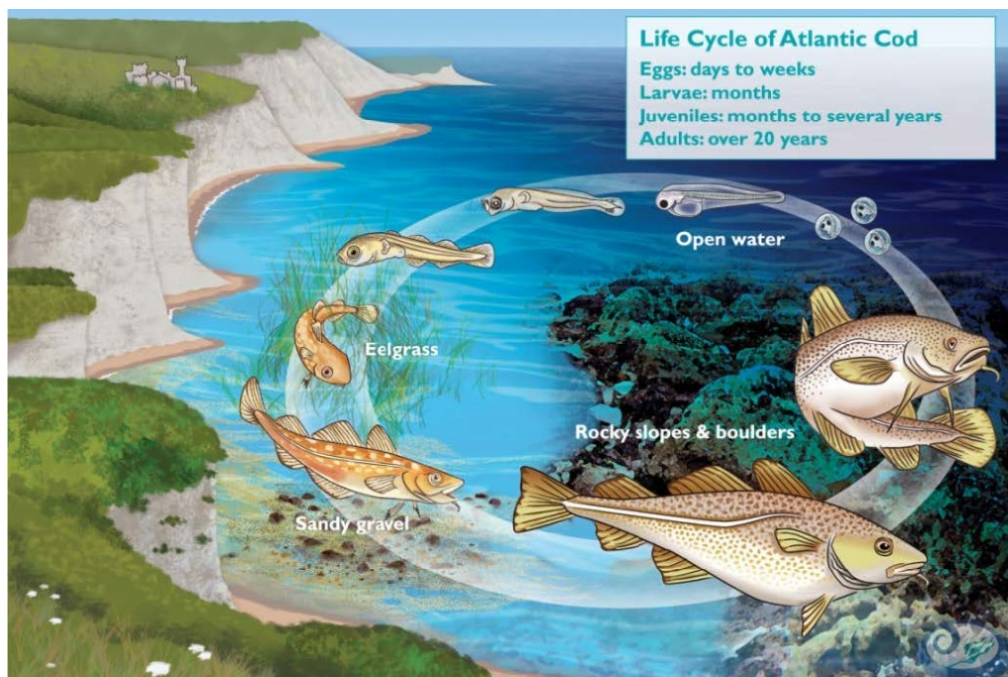

Figure 6.1 Illustration of the life cycle of cod.

In Lelievre, (2014) North Sea cod eggs mainly distributed near Dutch, German and Danish coasts and along the edge of the Dogger Bank (some studies NW, other south and eastern of the bank). The spawned eggs and hatched larvae are pelagic, but when reaching a size of ~5

cm at around 3 months of age, they transfer to a demersal lifestyle, close to the bottom and exhibit a preference to complex habitats such as vegetated areas that provide protection from predators (Lough & Bolz, 1989). They occupy the shallow areas until around 12-15 cm, after which they seek towards deeper waters. Cod may migrate to the shallow waters to feed during summer but seek deeper waters during winter.

The cod spawning grounds in the Kattegat and inner Danish waters have been mapped in Støttrup et al. (2019). Cod spawning in the Kattegat occurs during January to the end of April and take place mainly off Falkenberg and southward along the Swedish coast, the south-eastern part of Kattegat and the area around the entrance to the Sound and the northern part of the sound (Støttrup et al 2019). The summer feeding grounds are significantly different and located along the Swedish west coast. Salinity and depth best described the habitat for adult cod. The juvenile cod habitat overlaps with the spawning areas in the south-eastern part of Kattegat and northern part of the Sound (Støttrup et al. 2019). Salinity, temperature, oxygen levels and depth best described the habitat for juvenile cod.

In this project, the modelling of mature and immature cod was redone using the extended study area. Therefore, the environmental parameters that are identified as more important to describe the population density of cod are not the same as in the previous study. For example, in this study temperature, salinity and oxygen are identified as important parameters that could explain adult cod distribution, additional to depth (e.g., Støttrup et al. 2019).

6.1.2   Plaice

Plaice also exhibits demographically delineated habitat occupation (Figure 6.2). Plaice spawns from December to March all over the North Sea at depths > 30 m but also exhibit homing behaviour to distinct offshore spawning grounds (De Veen, 1978). This observation is confirmed by the analysis done in this project; the partial effect of depth to the abundance of mature plaice is highest for depths between 30 and 80 m (Figure 6.3). The mature plaice migrate between feeding grounds in the summer and the winter spawning grounds (De Veen, 1978). Highest densities of fish abundance during the spawning season were observed around and south of Fisher Bank (Munk et al., 2009). The observed homing behaviour with high site fidelity of up to 100% (Hunter et al. 2003) led to the hypothesis of distinct sub populations, with evidence of mixing during feeding and on the nursery grounds (Hufnagl et al., 2013). The presence of distinct populations in the Skagerrak and in the Kattegat was confirmed in a study by Ulrich et al. (2017). These stocks are separate from the neighbouring areas in the North Sea and the Baltic Sea, with strong natal spawning regions and mixing on the feeding and nursery grounds. The results indicated that a large proportion of the plaice caught in Skagerrak may be of the North Sea stock. Within ICES, management changed the stock delineation in 2015 and now distinguishes among stocks of the English Channel, the North Sea including since 2015 Skagerrak, the Kattegat including the Belt Sea and Sound, and the Baltic Sea. The implications of this new management, and assuming separate Skagerrak and North Sea stocks, is that the Skagerrak stock risks depletion due to the increasing North Sea plaice stock and increasing fishing pressure.

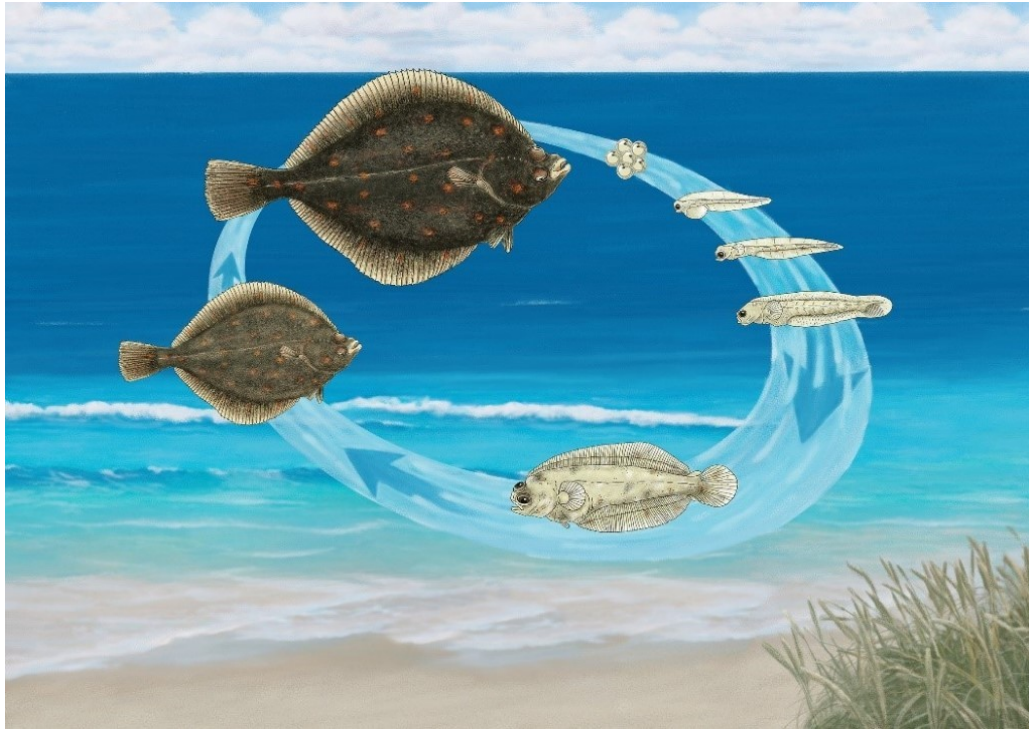**Figure 6.2. Illustration of the life cycle of plaice.**
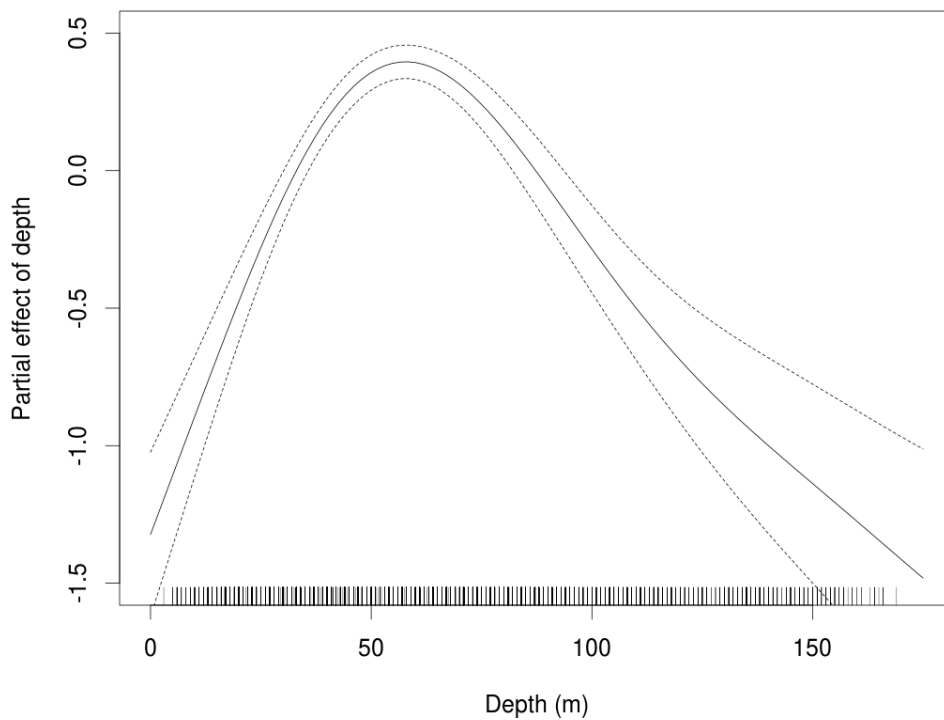

Depth (m)

Figure 6.3. Partial effect of depth on the abundance of mature plaice in the selected GAM model.

6.1.3   Drivers of distribution shifts

Dutz et al. (2016) reviewed trends found in the abundance of cod *Gadus morhua* and plaice *Pleuronectes platessa* showing declines in abundance in coastal areas of different regions and

impacting the fisheries (e.g. coastal commercial fisheries in Denmark: Statue et al. report). Declines in abundance can be accompanied by large-scale changes in the spatial distribution (Fisher & Frank, 2004). While the effects of climate change (i.e. Increasing water temperature) is the main hypothesis for the observed changes in coastal versus off-shore distribution (Ditz et al., 2016), other factors may be involved such as nutrient loading, primary productivity or food availability (Støttrup et al., 2017) or the interaction between increasing sea water temperatures and energetic demands (Teal et al., 2012). Benefits of a more offshore dispersal of juvenile plaice may be the decreased risk of predation or decreased intra/inter-specific competitive interactions (Van De Wolfshaar et al., 2015). This may explain the increase in the North Sea plaice population during the period when juvenile presence had shifted towards deeper waters.

6.1.4 Climate change

Climate change is reported to be a significant driver of changes in fish distribution. Latitudinal shifts due to sea temperature warming was observed for cod in the central part of the North Sea (Perry et al., 2005). Temperature affects growth, which in turn affects spawning times or timing of migration to spawning areas (Drinkwater, 2005). Cod spawning areas are closely associated with frontal features (Munk et al., 2009; Lelièvre et al., 2014), which are highly productive areas that ensure sufficient food for the early life stages. These frontal areas are influenced by meteorological conditions, which may alter with climate change. Since the persistence of cod spawning grounds in the North Sea is related to the interannual stability in temperature, climate change may affect the magnitude or location of these grounds. Furthermore, spawning cod were shown to prefer coarse sand areas (González-Irusta & Wright, 2016) and thus impacts that alter the nature of the spawning ground, such as aggregate extraction and marine developments may pose a permanent threat to cod spawning areas. Climate change affects cod distribution during spawning season due to shrinkage of suitable habitat caused by increased temperatures (Lelièvre et al., 2014; González-Irusta & Wright, 2016) as well as their distribution in other seasons (Freitas et al., 2015). Since, these changes may occur rapidly (Drinkwater, 2005) and may drive environmental conditions to as yet unchartered levels, it may be difficult to predict how these changes will affect the North Sea cod population and the fisheries.

Coastal fisheries targeting demersal species such as cod and plaice have declined in recent decades (Støttrup et al. report). As a result, the fleet of small, often family-owned vessels have been reduced impacting coastal fishing communities (Dinesen et al. 2018). Climate change was shown to be one driver of the decline in coastal fishery after cod (Dinesen 2019). This was supported by a) the significant correlation between the spatio-temporal distribution of thermally suitable habitat for adult cod and the cod catches in coastal areas; and b) the increase in the area of unsuitable habitat for adult cod due to the rise in water temperature. This shrinkage of suitable habitat for cod caused a change in distribution toward offshore, colder, deeper waters rendering the stock inaccessible to coastal fisheries and affecting a sector of the fisheries as well as management in that it called for changes in the existing vessel-based ITQ system (Dinesen et al. 2019).

Climatic extremes occur in the oceans in the form of marine heatwaves, warm water events that can last many weeks to months and extend over large areas. Marine heatwaves have been observed to redistribute marine species and lead to a range of ecological impacts (Oliver et al 2017). It is believed these events will occur more frequently and for prolonged periods due to

climate change. Marine heat waves are monitored in the North Sea: http://www.fishfore-casts.dtu.dk/heatwaves/north_sea. During the past 12 months, strong heatwave events have been observed along the southwest coast of Denmark, from the Wadden Sea up to Blåvands Huk Rev and a blob offshore west of Ringkøbing Fjord.

6.1.5 Fishery

Fishery causes changes in spatial patterns, demography or stock structure (van Beek 1990; Rijnsdorp and Pastoors 1995). The loss of larger individuals and decrease in size at age may result in localized depletions (Berkeley et al. 2004). Localized depletions can also result from a mismatch between management and population units (Heath et al.). The North Sea cod, managed as one stock consists of two populations, a localized North Sea unit (Viking) and a more widespread Dogger unit. Based on a spatial and temporal discrete model, it was predicted that under certain spatial fishery patterns, there was a risk of the severe decline or extinction of the Viking unit. The same may be true for the Skagerrak plaice stock, possibly a distinct stock, but managed as one stock with the North Sea plaice stock, which is at an historic high level and increasing. Management aims to deliver maximum sustainable yields for the combined stock. Since the North Sea plaice stock is at its historic highest level, management may impose higher than sustainable fishing effort on the Skagerrak stock. There is, however, strong indication that the North Sea plaice stock has already peaked, and the assessment advice will be for lower quotas in the coming years. This new situation may again change the relative impacts on the sub-populations.

The effects of fishery interact closely with climate change and directly or indirectly cause changes in fish communities and ecosystems. The removal of biomass through fishery may affect distribution. Relying on survey data, a modelling study showed that cod at low stock size were caught primarily in regions of near-optimal temperatures, while at high stock size increased their spatial extent to include suboptimal temperatures (Blanchard et al., 2005). Shrinkage of suitable habitat may cause cod to congregate and increase their vulnerability to fishing mortality (Rindorf and Lewy 2102). Cod aggregating in a surveyed habitat may result in higher population estimates in stock assessment (Rindorf and Lewy 2102) whereas if they congregate near wreck and reefs not covered in surveys, the resulting population estimates may be too low (Wieland et al., 2009). These discrepancies in population estimates may be cause for concern in management and frustration in the fisheries.

6.1.6 Predation

Predation by inflating avian and marine mammal populations has increased mortality of fish in coastal areas (Leopold et al. 1998; Konigson et al. 2009). It is unclear if the predation pressure is sufficient to cause permanent spatial distribution shifts. In the literature, it is shown that there are shifts in other systems, e.g. Fauchald et.al (2016) observed effects on seabird foraging on capelin.

6.1.7 Other factors

Shifts to deeper waters were also observed for plaice in the central North Sea, although without indications of latitudinal shifts Perry et al., 2005). An offshore shift in distribution off the Danish west coast of the larger North Sea plaice (>20 cm) was already evident around the 1980s, followed a decade later by a similar shift in distribution of juvenile plaice (van Keeken et al. 2006).

However, this shift in plaice distribution was only partially attributed to increasing sea temperatures in coastal waters and more likely attributable to multiple factors. Changes in the relative distribution of the smaller size classes (age 1-3) of plaice was correlated to changes in the nutrient loading along the Danish west coast (Støttrup et al. 2019). Nutrient loading (both P and N), which had increased dramatically during the last century up to the 1980s, resulted in a switch in the benthic community to highly productive species. During the latest three decades, P and more recently N loading declined significantly due to successful water quality management resulting in decreases in benthic productivity and believed to be the primary cause of the observed changes in distribution (Teal et al. 2008; Støttrup et al 2019).

6.2 Implications for monitoring data used in stock assessments

Changes in distributions of commercial fish stocks, such as the decrease in fish abundances especially in coastal areas observed in Danish waters, could potentially bias the estimate of stock abundance obtained through research surveys. Standard research surveys targeting demersal species, such as cod and plaice, in Danish waters are conducted at relatively fixed stations, mostly in areas with water depth more than 20m. Thus, if the fraction of a fish stock distributed in near-shore areas, i.e. out of the range of good survey coverage is changing between years, this could potentially bias the survey indices. Also, in case of mixed stocks, the representation of different stock components in survey indices for a given area could vary, as some might be distributed relatively more in coastal areas than others (as shown for Kattegat and North Sea cod in this project).

Therefore, monitoring and documentation of distribution changes of fish stocks is important to account for such changes in survey data, used as input to stock assessments. Survey coverage is generally considered adequate in more offshore areas, being poorer in shallow waters in inshore areas. Thus, with the distribution change of the fish to more offshore waters, the main area of stock distribution is probably better covered in surveys in later years. Monitoring the entire stock distribution range, including coastal areas, is recommended for future also by developing new monitoring technologies. Linking fish distributions to their suitable habitat in terms on environmental conditions, as demonstrated in this project (Section 3), can contribute to appropriate survey design and survey modelling in future, to obtain representative picture of stock trends for stock assessment purposes. Furthermore, understanding the causes for distribution change (e.g. linked to changes in hydrographic variables, described in Section 2) will help to be able to foresee near future developments and adapt data collection for stock assessment purposes, where necessary. For example, if the distribution change is related to warmer temperatures (Section 2), it is unlikely that this development would reverse in near future.

6.2.1 Implications for stock definitions

One of the key questions in stock assessment and management context is to what extent the recruits found in a given location is a result of the adult biomass in the same area. The results showed for plaice, that recruitment is in many cases relatively local, however mixing between Kattegat and Skagerrak occurs as well in some years (Section 4). For cod, the picture is more diverse. Cod in the Kattegat has earlier been documented to include a substantial proportion of individuals of North Sea origin (EMFF 33113-B-16-034). In the present project, this was further confirmed, with attempts to improve the understanding of the mechanisms driving this stock mixing (Section 4). Importantly, the extent of stock mixing can depend on year-class strength in different areas and/or hydrographic conditions. Connectivity analyses demonstrated a lot of

movement of cod early life stages in Danish waters (Section 5). The main large connectivity patterns seem relatively stable, however associated with variability around it. Thus, the recruitment of cod found in the Kattegat includes a large North Sea component and is possibly also affected by drift and movements from further south, i.e. western Baltic, with varying proportions between years. Knowledge is so far lacking on potential mixing and movements of cod between Kattegat and Western Baltic and to what extent these are genetically different populations. This question is in focus in a new EMFF project "Forvaltning af blandende torskebestande i overgangzonen mellem Nordsø og Østersø: Hvordan kan det gøres mest effektivt?".

Overall, it is clear that the stock assessment and management challenges in such complex transition areas cannot simply be solved by adjusting boundaries for stock assessment, as movement and mixing occurs across the entire transition zone from the North Sea into the Baltic. Merging a larger area would solve the issue of movements between smaller areas, however would lose track of the dynamics and status of individual populations, which is important for understanding the stock dynamics of the species in an area, and develop appropriate management solutions. Thus, a remaining challenge is to find an optimal way to take into account the biological knowledge of stock mixing and connectivity in stock assessment and management.

6.2.2 Implications for stock assessment modelling

Potential gains to link assessments of different stocks, i.e. use information for one stock in the assessment of another stock, have been investigated in EMFF project 33113-B-15-003. "Bestandsvurdering og forvaltning af forbundne bestande". The presently operational stock assessment framework developed in that project, which allows to take into account connections between stocks is well suited for situations, where several stocks are dependent on the same external conditions (for example temperature), compete for the same prey or are connected through predator prey interactions.

The changes in hydrographic conditions, that the present project has demonstrated (Section 2), can be expected to impact on productivity of a number of fish stocks. Thus, the assessment framework developed in EMFF 33113-B-15-003 can be used to test hypothesis on similar impacts of hydrographic conditions expected on neighbouring populations or different species in an area. The analyses conducted in EMFF 33113-B-15-003 showed several examples, where more robust stock assessment results could be obtained by taking into account correlations between developments of different stocks (Albertson et al. 2017). However, for cod stocks around Kattegat, no clear correlations could be demonstrated that would have improved the assessment. The results of the present project suggest that this could be because of the complex processes in this transition area, where the abundances in one area are, in addition to external drivers, affected by movements between areas, with extensive inter-annual variation. This adds additional complexity, where further development in stock assessment and management models is needed.

The present project provides increased understanding of the mechanisms and processes that affect fish abundances in different locations, and connectivity between the areas. This provides input to further work towards optimal assessment and management models in this complex area, subject to extensive movements, where patterns are associated with high variability. Further development of such tools is conducted in EMFF project 33113-B-17-092 and planned

in "Forvaltning af blandende torskebestande i overgangzonen mellem Nordsø og Østersø: Hvordan kan det gøres mest effektivt?".

6.2.3 Implications for management

Improved information on connectivity between areas, produced in this project can be used to identify sensitive areas (e.g. spawning, nursery areas) that could require extra protection, for example in the context of marine spatial planning. Also, information on spatial distribution of individual stock components and their movement patterns allows for their more appropriate protection and management. For example, the results of this project showed that different stock components may be affected differently by climate change (due to differences in their distribution), which is important information in the context of conservation of these populations. Improved information on the origin of recruitment in relation to adult stock can also improve the knowledge on stock-recruitment relationships that inform fisheries management reference points, to ensure maximum sustainable yields.

Changes in fish distributions, such as the reduced abundances in coastal areas, have implication for local fishing opportunities, especially for smaller vessels. The results of this project demonstrate that the perception of fish stock dynamics can be locally different, when fish are disappearing from some areas while abundances may increase in other areas. Documentation of spatial distributions of stocks and their suitable habitats is therefore useful to communicate the changes occurring in fish stocks in Danish waters and clarify the reasons for possible locally different perceptions. The new knowledge produced in this project helps to understand and explain the observed dynamics, which is a prerequisite for identifying what could be achieved by different management measures.

The reasons for fish distribution changes are not fully understood. These seem to be associated with declining salinity in shallow waters and temperature increase, as shown in this project (Section 2). However, these hydrographic changes are not fully explaining the observed spatial dynamics of fish stocks, and other human activities affecting fish habitats near the coast (e.g. gravel and sand extraction) as well as areas with oxygen depletion may play important roles as well. Thus, an integrated approach to include all relevant human and natural pressures is needed, to gain further understanding of the reasons for changes in fish stocks, and develop appropriate management in the region. Importantly, the future management needs to adapt to climate related changes in the ecosystems. The results of this project have demonstrated pronounced changes in climate related hydrographic conditions, and identified connections to local fish availability. This suggests that more pronounced consequences for fisheries can be expected in future, when climate change continues, that management as well as fisheries would need to be prepared for.

6.3 Conclusions

It is recognized that the transition zone from North Sea to the Baltic is an area with complex fish population structures, involving mixing and migrations of different stocks and species. This challenge the definition of meaningful units for stock assessment purposes that in standard approaches assume closed populations. This project has provided new understanding of the mechanisms and processes involved in determining stock structures in different areas, including the extent of mixing, and connectivity between different areas (Sections 4.5), which can help to

develop better solutions to assessment and management of the important fish stocks in such complex areas.

We have identified important temporal and spatial patterns of environmental drivers that could potentially affect the distribution and connectivity of cod and plaice populations. For coastal regions, it is possible that different populations are differentially affected by changes in environmental conditions. This knowledge is important for future management of vulnerable populations and we recommend that future work focus on obtaining a more detailed understanding of the distribution of populations in coastal regions and link this knowledge to potential drivers of change on finer geographical scales.

Hence, given the complicated interactions between topographical changes, hydrography, food web and individual behaviour we recommend that better monitoring strategies for the entire stock distribution range, including coastal areas, should be developed possibly making use of modern observation technologies for autonomous habitat mapping. Overall, it is clear that the stock assessment and management challenges in such complex transition areas cannot simply be solved by adjusting boundaries for stock assessment, as movement and mixing occurs across the entire transition zone from the North Sea into the Baltic. Merging a larger area would solve the issue of movements between smaller areas, however would lose track of the dynamics and status of individual populations, which is important for understanding the stock dynamics of the species in an area, and develop appropriate management solutions. Thus, a remaining challenge is to find an optimal way to take into account the biological knowledge of stock mixing and connectivity in stock assessment and management.

This challenge could be faced by supporting a holistic integrated ecosystem approach in the Skagerrak-Kattegat region developed through five steps: (1) Scope management objectives and available data, (2) Identify and score all drivers and pressures acting on the system, (3) Define indicators for ecosystem state and track their dynamics in time and space, (4) Assess ecosystem status and vulnerabilities, and (5) Inform fishery management and policy makers on the boundaries for the sustainable development of the area under future scenarios.

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Supplementary material

Appendix A. Cluster analyses

A tensor is constructed as illustrated in Figure A.1 to efficiently process the data. Notice, that the geospatial dimension is lost, however, the model findings can be unrolled and mapped back to geolocation of each data point. A downside of having structured the data set as a tensor is that data along the seabed must be omitted. However, this is a requirement when using Tensorflow libraries. If one cannot do this compromise, the probabilistic language STAN can be used, although it does not scale well with large sets of data.
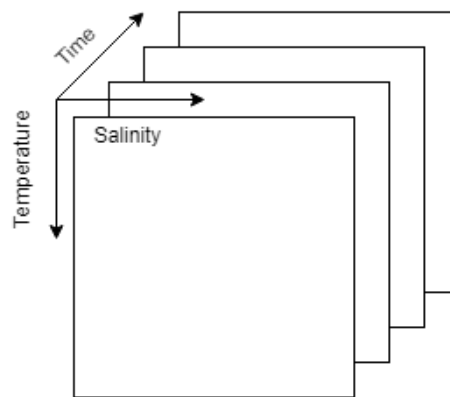

Figure A.1. Illustration of the dimensionality of the data wrapped as a tensor.
A Gaussian Mixture Time Series model is proposed as a model for the set of data. The probabilistic Bayesian model is visualized by means of a probabilistic graphical model (PGM).
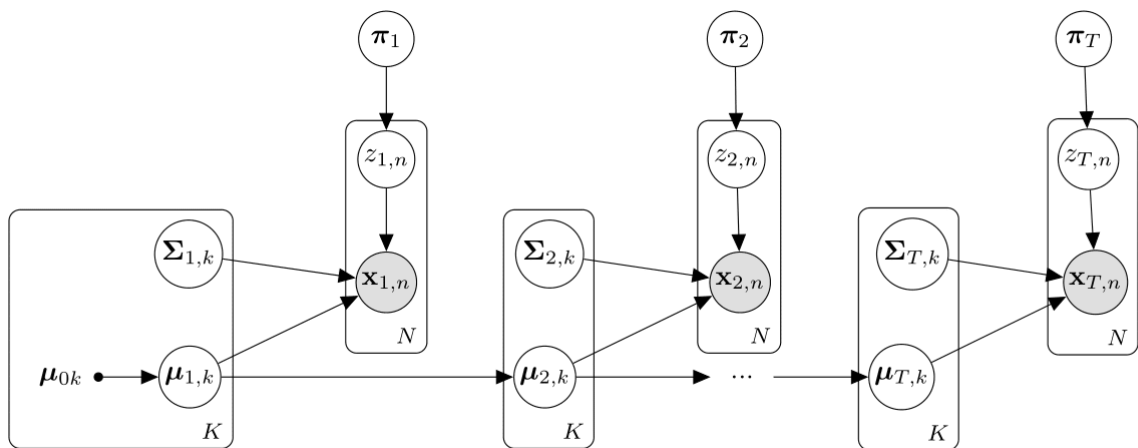

Figure A.2. PGM.

It is illustrated that for each point of observed data $\mathbf{x}_{t,n}$ there is a latent variable $z_{t,n} \in \{1,\dots,K\}$ indicating which of the K clusters $\mathbf{x}_{t,n}$ will be assigned to. We have that $\boldsymbol{\pi}_t = (\pi_{t,1},\dots,\pi_{t,K})$ where $\pi_{t,k} = P(z_{t,n} = k)$ is the prior probability that $\mathbf{x}_{t,n}$ belongs to the cluster k. Thus, $\mathbf{x}_{t,n}$ will be of the kth Gaussian mixture component with a mean $\boldsymbol{\mu}_{t,k}$ and covariance $\boldsymbol{\Sigma}_{t,k}$ given that $z_{t,n} =$

k in the time instant t. We will use a Dirichlet distribution for the mixture weights parametrized by $\mathbf{v_t} = \mathbf{1}$ so that is it is uniform over the simplexes.

The set of data is assumed to arise from a maximum of $K = 10$ clusters, however, it is far from obvious how to determine a priori what this number should be. For an *infinite* mixture, we simply have that $K \to \infty$. This is in our case achieved from experience by, if, in our simulations, all components contribute non-negligible mass to the mixture, we add to the previous number K. We get that doubling our $K = 10$ will not contribute to any significant change in our model posterior as the additional cluster components will be of a proportion many orders of magnitude lower than the previously dominant clusters.

To infer the latent states of our model, we tested with two different approaches. To do Bayesian inference prior distributions needs to be assigned to all unknowns in the model. The computational preferable priors with respect to the libraries have been chosen as conjugate base distributions quicken the processing time. There exist inference algorithms fir non-conjugate base distribution but none at this time scale with data sets as large as the one involved in this paper. According to literature, Gibbs sampling should perform best as we are proposing a sample in a high-dimensional space, however, the acceptance ratio for our Hamiltonian Monte Carlo inference is quite good and in the range of $[0.58, 0.81]$. In addition, out of the inference methods Tensorflow Probability offers Hamiltonian Monte Carlo is a fine choice as it can converge rapidly, samples the state space jointly (as opposed to coordinatewise), and is computationally faster.

GMTS with Gibbs inference

For $t \in \{1, \dots, T\}$ time steps, we would like to model $k \in \{1, \dots, K\}$ clusters on $n \in \{1, \dots, N\}$ samples each with a dimension of D using the following Bayesian Gaussian Mixture Time Series model using Gibbs inference:

$$
\begin{aligned}
\boldsymbol{\pi}_t &\sim \text{Dirichlet}(\mathbf{v}_t) \\
\boldsymbol{\mu}_{t,k} &\sim \text{Normal}(\boldsymbol{\mu}_{t-1,k}, c_1 \mathbf{I}) \\
\boldsymbol{\Sigma}_{t,k} &\sim \text{InverseGamma}(\alpha, \beta) \\
z_{t,n} &\sim \text{Categorical}(\boldsymbol{\pi}_t) \\
\mathbf{x}_{t,n} &\sim \text{Normal}(\boldsymbol{\mu}_{z_{t,n}}, \boldsymbol{\Sigma}_{z_{t,n}})
\end{aligned}
$$

where $\boldsymbol{\mu}_{1,k} \sim \text{Normal}(\boldsymbol{\mu}_{0k}, c_0 \mathbf{I})$.

We utilize Gibbs sampling iterations which, if done enough times, will by the fundamental theorem of Markov chain yield samples from the posterior $p(\boldsymbol{\pi}, \mathbf{z}, \{\boldsymbol{\mu}_k, \boldsymbol{\Sigma}_k\}_{k=1}^K | \boldsymbol{\chi})$.

For every point in time $t \in \{1, \dots, T\}$, the Gibbs sampling algorithm below is called using the Edward probabilistic library:

- randomly generate $\left(\boldsymbol{\pi}^{(1)}, \mathbf{z}^{(1)}, \boldsymbol{\mu}^{(1)}, \boldsymbol{\Sigma}^{(1)}\right)$
- for $s = 1$ to S do following iterations:
  a. draw $\mathbf{z}^{(s+1)} \sim p(\mathbf{z} | \mathbf{z}_{\setminus n}^{(s)}, \boldsymbol{\mu}^{(s)}, \boldsymbol{\Sigma}^{(s)}, \boldsymbol{\pi}^{(s)}, \mathbf{x}_n)$
  b. draw $\boldsymbol{\pi}^{(s+1)} \sim p(\boldsymbol{\pi} | \mathbf{z}^{(s+1)}, \boldsymbol{\mu}^{(s)}, \boldsymbol{\Sigma}^{(s)}, \boldsymbol{\chi})$
  c. draw $\boldsymbol{\mu}^{(s+1)} \sim p(\boldsymbol{\mu} | \mathbf{z}^{(s+1)}, \boldsymbol{\Sigma}^{(s)}, \boldsymbol{\pi}^{(s)}, \boldsymbol{\chi})$
  d. draw $\boldsymbol{\Sigma}^{(s+1)} \sim p(\boldsymbol{\Sigma} | \mathbf{z}^{(s+1)}, \boldsymbol{\mu}^{(s+1)}, \boldsymbol{\pi}^{(s+1)}, \boldsymbol{\chi})$

where $\setminus n$ subscript indicates all indexes except n and where we have omitted the k and t subscript for simplicity. In addition, rather than update all parameters one at a time, we also update the block of parameters $\boldsymbol{\pi}$ and $\boldsymbol{\mu}$ one at a time as putting correlated parameters in a block can improve convergence and mixing.

The Edward probabilistic library will sample from the above listed conditionals provided that conjugate relationships exist. This is a downside when proposing the model of the Gaussian Mixture as the conjugate prior of the variance of the Multivariate Normal distribution is an Inverse Gamma distribution.
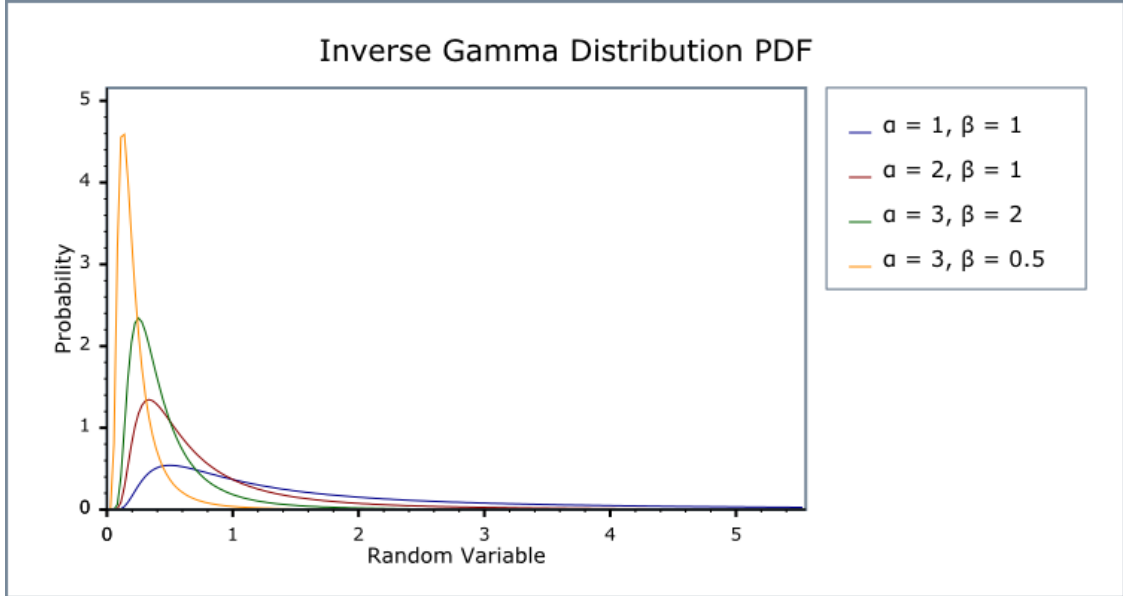

Figure A.3. Probability Density Functions of Inverse Gamma distributions.

The Inverse Gamma distribution is parameterized such that variance prior will take on smaller values as this is the deciding factor of the number of clusters formed. To avoid exploding variances and thus the ability of the cluster to model more of the data than intended the Inverse Gamma has been set to $\alpha = 3$ and $\beta = 0.5$ as can be seen on the orange curve in Figure A.3. The degree of detailed dynamics exhibited of the data set can be controlled in this manner. Therefore, if one wishes to split larger clusters into smaller clusters and go from a macro level to a micro level it is possible.

GMTS with Hamiltonian Monte Carlo inference
For $t \in \{1, \dots, T\}$ time steps, we would like to model $k \in \{1, \dots, K\}$ clusters on $n \in \{1, \dots, N\}$ samples each with a dimension of D using the following Bayesian Gaussian Mixture Time Series model using Hamiltonian Monte Carlo inference:

$$
\begin{aligned}
\boldsymbol{\pi}_t &\sim \text{Dirichlet}(\mathbf{v}_t) \\
\boldsymbol{\mu}_{t,k} &\sim \text{Normal}(\boldsymbol{\mu}_{t-1,k}, c_1 \mathbf{I}) \\
\boldsymbol{\Sigma}_{t,k} &\sim \text{Wishart}(c_2 \mathbf{I}, \rho) \\
z_{t,n} &\sim \text{Categorical}(\boldsymbol{\pi}_t) \\
\mathbf{x}_{t,n} &\sim \text{Normal}(\boldsymbol{\mu}_{z_{t,n}}, \boldsymbol{\Sigma}_{z_{t,n}}^{-\frac{1}{2}})
\end{aligned}
$$

where $\boldsymbol{\mu}_{1,k} \sim \text{Normal}(\boldsymbol{\mu}_{0k}, c_0 \mathbf{I})$ and $\boldsymbol{\Sigma}_{1,k} \sim \text{Wishart}(\alpha, \mathbf{I})$. Notice, the Cholesky semantics as we model the covariance matrix parameter for the multivariate normal as a precision matrix. This is computationally advantageous as we use the Tensorflow Probability library for inferencing and since it is natural choice for the precision as it is a conjugate. The prior distributions are chosen such that there is conjugacy between the joint prior distribution and the likelihood so that the distribution of the mean depend on the precision.

We wish to sample from the posterior $p(\boldsymbol{\pi}, \{\boldsymbol{\mu}_k, \boldsymbol{\Sigma}_k\}_{k=1}^K | \boldsymbol{\chi})$. Fortunately, we are able to marginalize out z using the Tensorflow library. To properly do inference, Hamiltonian Monte Carlo requires the log-likelihood function to be differentiable with respect to the states. In addition, we can obtain significantly higher statistical efficiency if the state space is unconstrained. To overcome these hurdles, we must make sure that $\sum_{k=1}^K \pi_{t,k} = 1$ as well as $\pi_{t,k} > 0$. Furthermore, we must have that $\boldsymbol{\Sigma}_{t,k}$ is positive definite as it is an inverse covariance matrix.

Thus, for every point in time $t \in \{1, .., T\}$, the Hamiltonian Monte Carlo algorithm will perform following operations:
1. transform the constrained variables to an unconstrained space
2. perform the Markov chain Monte Carlo
3. transform the previously transformed variables back to constrained space

We use an adaptive step size in the gradient-informed steps of the Hamiltonian Monte Carlo algorithm that simply increases or decreases based on the average of exp(min(0,log-acceptance ratio)). Furthermore, we can improve convergence to the (local) maximum likelihood by the nature of a time series. The acceptance ratio will improve and stabilize rather quickly around at e.g. $t = 3$ as we can make an informed choice on the first state of the Hamiltonian Monte Carlo algorithm as we simply just use the previously last found state, in this case at $t = 2$.

Appendix B. Connectivity analyses: Model description

The particles were released near the coast of Denmark, west coast of Sweden and South coast of Norway (Figure 1). In this study, the settlement area is the same as the release area, meaning the result of connectivity analysis is a square matrix. The trajectories of the simulated particles were computed using forward Euler scheme (Press et al., 2009).

Hydrographic data

The hydrodynamic model used in this study is HBM, which provides temperature, salinity and ocean currents with temporal resolution of 15 minutes, spatial resolution of 3 nautical miles in the North sea – Baltic Sea with 50 vertical layers (Huess & Nielsen, 2019).

Biological description

The spawning time varies between the stocks (Table 1). In this study, we opted for releasing the particles only during the peak.

Table B.1. Duration of the peak of the spawning season in different areas and the dates used in this study to release particles.

Area	Peak timing	References	This study spawning time
Danish West coast and Skagerrak	February - March	Brander (1994)	15/02 - 15/03
Kattegat and Sound	January - February	Vitale et al. (2005)	15/01 - 15/02
Kiel and Mecklenburg bay	March - April	Bleil et al. (2009)	15/03 - 15/04
Arkona	June - July	Bleil et al. (2009)	15/06 - 15/07

Each year we released 750 particles in each emission box (Figure B.1), totalling 102750 particles. The simulations were conducted from January 15th to October 31st, from 1990 to 2012, with time step of one hour. Natural mortality rate was not included. The results were divided in six regions: West, Skagerrak, Kattegat, West Zeeland, East Zeeland and East (Figure B.1).
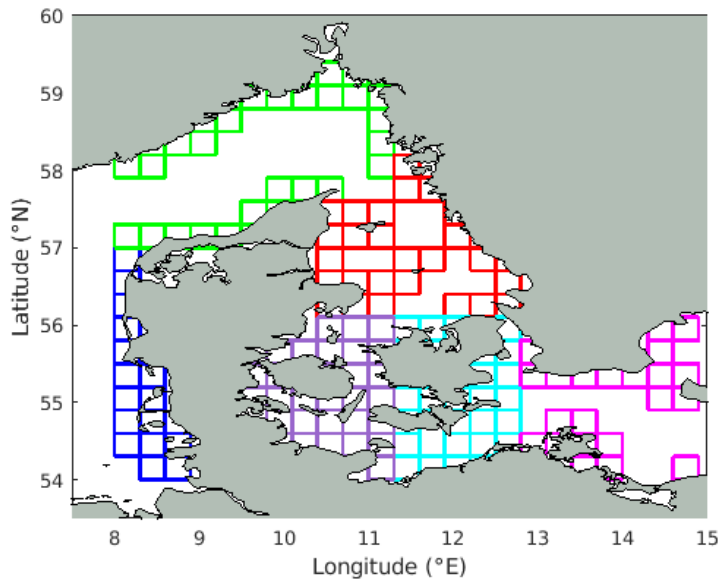
Figure B.1. Study area regions: West (blue), Skagerrak (green), Kattegat (red), West Zeeland (purple), East Zeeland (cyan) and East (magenta). The squares represents both the emit boxes and settlement boxes.

Cod eggs were released in the peak season, from 1 meter above the sea bottom, up to 40% of the sea depth. The duration of the all the eggs stages followed the Thompson and Riley (1981) equation

$$\log_e D = -0.1T + 3.46$$

Where D is the duration in days and T is the temperature in degrees Celsius.

All eggs had vertical velocity based in the stokes terminal velocity. The neutral buoyancy for all eggs was determined as 1011.33 kg/cm^3, which is the neutral buoyancy of Baltic cod (Nissling & Westin, 1991). Wieland et al. (1994) identified that at oxygen concentrations below 2 ml O_2 l^{1-} the development of Baltic eggs ceased. Oxygen dissolved concentration is not one of the outputs of HBM, therefore a threshold for survival of cod eggs based in its requirements could not be incorporated in this model.

Nissling (2004) found that the Baltic cod larval length at hatching is dependent of the temperature. In this study, we gave the average length, which is 3.71 mm, to all newly hatched larvae, independent of the temperature. The growth rate of cod larvae in the model based in Nielsen and Munk (2004), which identified an age depend growth for cod larvae, from 3.2% d^{1-} at age 20 days to 1.9% d^{1-} at age 90 days.

Vertical migration patterns of North Sea or Baltic cod larvae are unknown (Huwer et al., 2016). In this study, larvae had diel vertical migration from 0 to 30 meters, which is the depth range where cod larvae were found in western Baltic Sea (Westerberg, 1994), with vertical swimming speed proportional to the body length (1 body length per second). Larvae smaller than 4.01 mm were considered yolk sac larvae (Nissling, 2004) and passive drifters.

Bastrikin et al. (2014) based in the dietary analysis of North Sea cod, found that settlement was a gradual process that started when the larvae had 34 (±2) mm until 49 (±3) mm. Based on that,

larvae were able to settle when reached 32 mm. If larvae reached 52 mm and it did not find the suitable settlement area, then the particle would be considered dead. It is important to note that other areas can be suitable for cod settling which were not included in this study, for example the eastern Baltic, therefore the result showing dead particles includes particles that would settle in a different geographical area which was not considered in this study.

Particles Trajectories

The connectivity analysis does not inform where particles ended if they were not inside the settlement grid. Therefore, it is advantageous when there are many particles not settling to observe some of the particles trajectories. As the West was the region in which more particles have not settled, some of the particles trajectories are shown in Figure B.2.
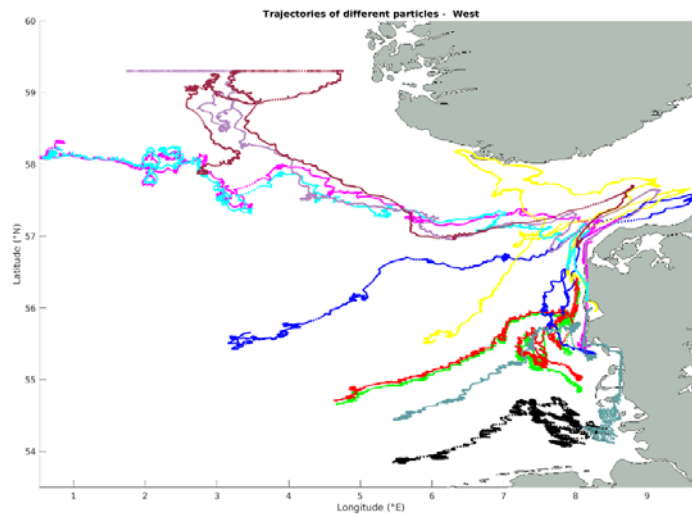

Figure B.2. Example of trajectories of 10 particles released in the West.

Most of the particles that were not able to settle were carried away to the North Sea (Figure B.2). The Norwegian coast seems to be destination of some of the cod larvae released in the West (Figure B.2).