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Colophon

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DTU Aqua Report no.:	357-2020
Year:	The project period was January 2016 to January 2019. The report was published in March 2020.
Reference:	Hemmer-Hansen, J., Hüssy, K., Vinther, M., Albertsen, C. M., Storr-Paulsen, M., Eero, M. (2020) Sustainable management of Kattegat cod; better knowledge of stock components and migration. DTU Aqua Report no. 357-2020. National Institute of Aquatic Resources, Technical University of Denmark. 42 pp.
Cover photo:	xxxxx
Published by:	National Institute of Aquatic Resources (DTU Aqua), Vejlsøvej 39, 8600 Silkeborg
Download:	www.aqua.dtu.dk/publikationer
ISSN:	1395-8216
ISBN:	978-87-7481-281-4

Preface

The present report is based on the project “Bæredygtig forvaltning af Kattegat-torsk: bedre viden om bestandskomponenter og migration” funded with 3.1 million DKK by the European Maritime and Fisheries Fund and the Danish Fisheries Agency.

European Union
European Maritime and Fisheries Fund

HAV & FISK

DTU Aqua, Denmark, March 2020

Indhold

Summary

This report describes the main findings from the EMFF project "Bæredygtig forvaltning af Kattegat-torsk; bedre viden om bestandskomponenter og migration" (J. nr. 33113-B-16-034) which was initiated to improve our understanding of stock mixing and migration in Atlantic cod in the Kattegat in order to improve the data for stock assessment and management. The stock assessment of the Kattegat cod has recently been challenged due to a large "unallocated mortality", i.e. a large fraction of fish that disappears from the area, but cannot be explained by mortality due to fishing or natural causes. It has been hypothesized that migration between the Kattegat and the North Sea could explain some of the unallocated mortality.

The major scientific questions we aimed at answering in the project were:

1. Do cod from the North Sea and Kattegat mix within the Kattegat stock assessment and management area?

If they do, then

2. During which time of their life do North Sea cod enter the Kattegat?
3. Are there any spatial patterns of mixing and are there indications of different magnitudes of mixing for different age classes?
4. Do cod migrate between the Kattegat and North Sea?

The project had three main components: Genetic analyses to identify population of origin of fish, chemical analyses to identify individual fish migration histories and finally integration of results with stock assessment and the development of future procedures for data collection and stock assessment in Kattegat cod. We used a unique combination of methodology that allowed us to both identify the population of origin, and hence mixing of populations, with high spatial and temporal resolution, and the migration trajectories of individual fish.

Genetic data revealed that North Sea and local Kattegat/transition zone cod indeed co-occur (mix) within the Kattegat, and that there is a gradient in mixing proportion from high proportion of North Sea cod in the northern parts of the Kattegat to lower proportions in the south. We also found variation between ages and sizes of fish with higher proportions of North Sea fish among the younger/smaller fish. Chemical signatures in the cod otoliths also suggested that North Sea and Kattegat early juvenile stages have different environmental, and thus geographic, origins, and that the North Sea fish enter the Kattegat as larvae or juveniles and leave at approximately age 4, presumably for spawning. Collectively, the results indicate that North Sea cod enter the Kattegat as early life stages and migrate back to the North Sea when they reach sexual maturity. Analyses of spawning fish confirmed that spawning activity in the southern Kattegat is dominated by fish of local origin. Results from our study have improved our understanding of the complex interaction of different biological populations with the Kattegat stock assessment and management area. The project has thus contributed directly to improving the basis for sustainable management of cod in the Kattegat, in particular through the identification of future data collection and stock assessment strategies that are able to take migration into account. The project results have been communicated to the scientific community, including the ICES advisory working group, as well as stakeholders from industry and management at several occasions in Denmark and abroad.

1. Project background

Under the current fisheries management regime, Atlantic cod (*Gadus morhua*) are treated as separate stocks in the North Sea and Kattegat. Consequently, stock assessment and management is conducted separately for the two areas (ICES 2017; see also Figure 1-MAP).

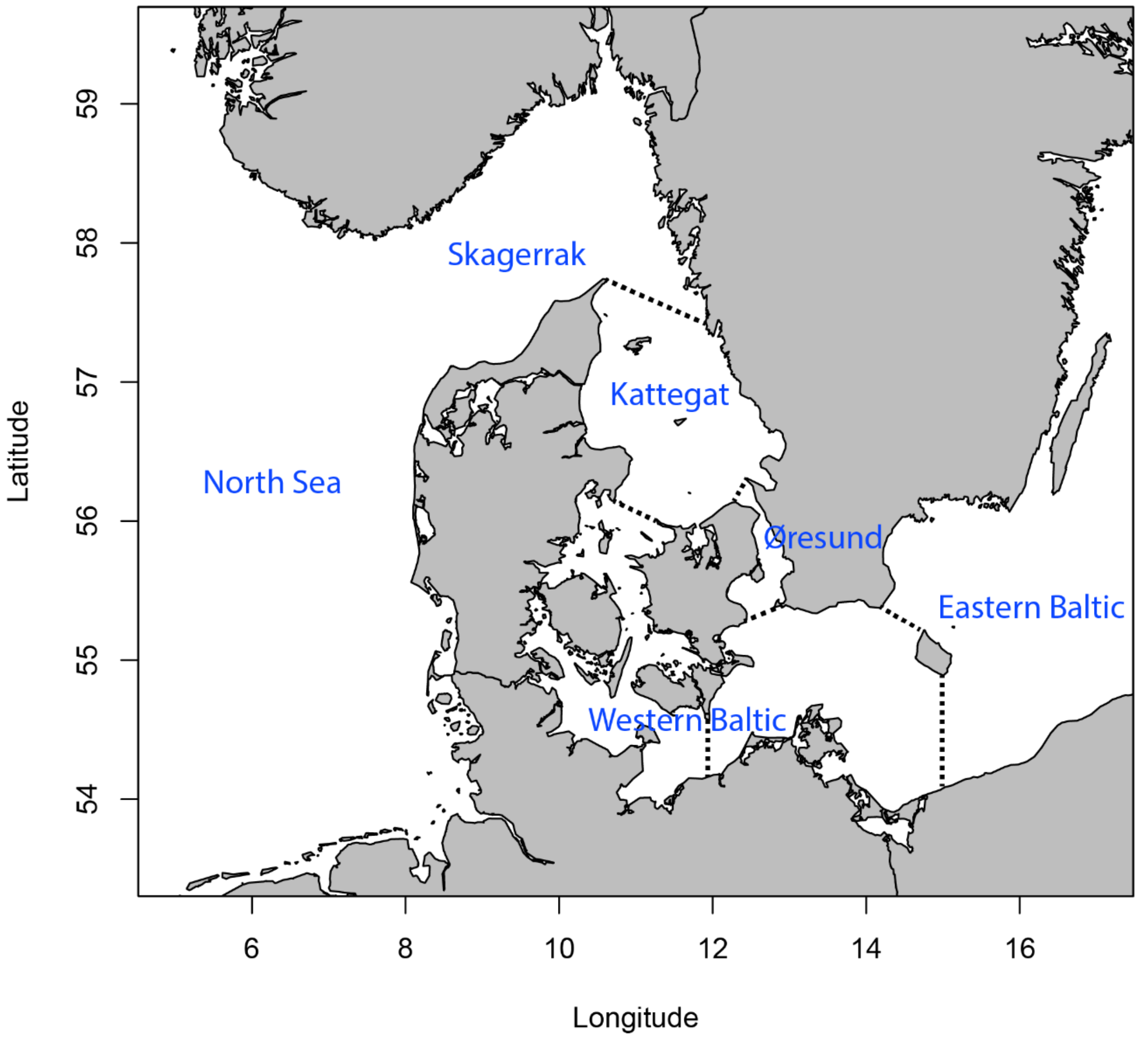

Figure 1. Map of the study area with approximate locations of ICES stock assessment and management areas indicated by dashed lines.

The stock assessment of cod in the Kattegat has been challenged due to a large “unallocated” mortality, i.e. fish that are disappearing from the area but cannot be explained by fishing and natural mortality (ICES 2017). This has represented a challenge to stock assessment and resulted in the categorization of cod in the Kattegat as a “data limited stock”, which automatically affects harvesting under a precautionary fisheries management approach. Recent data suggested that migration of cod between the Kattegat and neighbouring areas may partly explain the “unallocated” mortality, and this project was initiated to provide data to support a more robust stock assessment of cod in the Kattegat.

The North Sea-Baltic Sea transition zone is a highly dynamic region characterized by an environmental gradient between the fully marine North Sea and the brackish Baltic Sea. Several fish species show population structure, i.e. the presence of genetically and ecologically unique populations or stocks, in the region (e.g. Atlantic herring, Bekkevold *et al.* 2011; Atlantic cod, Nielsen *et al.* 2009, Berg *et al.* 2015; turbot, Nielsen *et al.* 2003; sprat Limborg *et al.* 2009). However, in marine fishes management areas may not full account for the geographical distribution of populations (Reiss *et al.* 2009; Bonanomi *et al.* 2013; Heath *et al.* 2014; Hemmer-Hansen *et al.* 2019; Bernatchez *et al.* 2018; Kerr *et al.* 2017). The true distribution of resources should be taken into account to secure sustainable management, including an ability to protect weaker populations from overexploitation (Heath *et al.* 2014),

In Atlantic cod, mixing of genetically unique populations has been described in the western Baltic Sea (Sick 1965; Hussy *et al.* 2016, Hemmer-Hansen *et al.* 2019), and this dynamic has been taken into account in the stock assessment to secure sustainable management of both populations when they are harvested together (ICES 2015). In the Kattegat, mapping of spawning areas based on the distribution of eggs and spawning adults have shown that in particular the southern parts of the region is a centre for spawning cod (Vitale *et al.* 2008; Börjesson *et al.* 2013). Genetic data suggest that these spawning fish in the Kattegat are genetically different from the North Sea cod (Berg *et al.* 2015; André *et al.* 2016), supporting the presence of genetically unique populations in the two areas.

Despite a presumed concentration of spawning in the southern parts of the Kattegat, the distribution of young fish (recruits) have shown trends towards increased densities in the northern parts of the Kattegat (north of 57 °N; ICES WKROUND 2009), suggesting that there is a link between recruitment in the Kattegat and spawning outside the Kattegat. Kattegat cod spawn predominantly in January/February in the south-eastern part of the Kattegat (Börjesson *et al.*, 2013; Vitale *et al.*, 2008). Early life stages of this stock have in recent years largely been retained in the Kattegat (Jonsson *et al.*, 2016). North Sea cod spawn in February/March along the southern and eastern edges of the Dogger Bank, in the German Bight, the Moray Firth and to the east of the Shetlands (Brander, 1994; Fox *et al.*, 2008; Munk *et al.*, 2009). Drift simulations have shown that cod eggs, larvae and early juveniles spawned in the North Sea may be advected for more than 600 km during their drift period (Eero *et al.*, 2016). In particular individuals spawned in the German Bight are frequently transported into the Skagerrak (Eero *et al.*, 2016). The early life stages are entrained by the Jutland current running north along the west coast of Denmark into the eastern part of Skagerrak (Dyrssen, 1993; Jakobsen, 1997; Svansson, 1975). During westerly conditions, strong currents prevail from the Skagerrak towards the Baltic Sea along the coast of Sweden. An inflow of North Sea cod into the Kattegat during their early life stages is thus highly likely, where drift durations from the North Sea to the Kattegat may range from days to months (Eero *et al.*, 2016). Genetic studies of juvenile cod from the fjords on the Norwegian Skagerrak coast to the central Kattegat support this, in that they are genetically similar to cod from offshore spawning areas in the eastern North Sea, with substantial temporal variation in advection (André *et al.*, 2016; Knutsen *et al.*, 2004; Stenseth *et al.*, 2006). Owing to the low stock size of Kattegat cod and the influx of individuals from other areas, Jonsson *et al.* (2016) estimated that only 35% of the juveniles in Kattegat are from locally retained spawning areas.

Information of juvenile and adult cod's migrations is available from several Swedish tagging experiments from the 1950's, 1990's and 2000's. These studies found that cod tagged as 1-year old juveniles in Kattegat only undertook limited migrations until the age of 2 years and 30 - 50 cm in length, when they moved offshore towards the south and west – towards the spawning grounds in the southern Kattegat and the eastern North Sea (Pihl and Ulmestrand, 1993). Adult cod tagged at offshore and in coastal locations in the Skagerrak undertook far-reaching migrations ranging from the southern North Sea to the central Kattegat (Danielssen, 1969). Migrations of adult cod tagged along the Swedish Kattegat coast were directed both south and north towards the Øresund and the eastern North Sea, with some coherence between tagging location and migration direction (Righton *et al.*, 2010; Svedäng *et al.*, 2010). Of the cod tagged in the northern Kattegat, 12% were recaptured in the Skagerrak or eastern North Sea, while cod tagged in the Øresund and the southern/central Kattegat were primarily resident (Svedäng *et al.*, 2010). Geolocation of individuals based on electronic tags (DST's) documented that the migrations of cod tagged in the northern Kattegat and Skagerrak are directional movements towards the North Sea that coincide with known spawning times (Svedäng *et al.*, 2007). Subsequent returns to the areas where the cod were tagged also occurred, but quantification thereof was not possible (Svedäng *et al.*, 2007). Linking genetics with tagging-based migration patterns, André *et al.* (André *et al.*, 2016) suggested a strong correspondence between genotype and philopatric migrations towards natal spawning grounds in cod from the Skagerrak/Kattegat area.

Collectively, available data from a range of sources suggest a high degree of connectivity between the North Sea and the Kattegat, and that migration between the two areas may at least partly explain the substantial unallocated mortality observed in stock assessment models in the Kattegat. In this project, we applied a combination of genetic analyses to identify population of origin, and chemical signatures in otoliths to infer individual fish migration histories, to provide data for a better understanding of the migration and mixing patterns of cod in the Kattegat. These data were subsequently used as a basis for improving stock assessment and future data collection so that management can be aligned with the variation in the distribution of the resource.

2. Project results

In the following section, we describe the main findings from the project. We have divided the presentation of results into two main sections focusing on the description of the baseline and analyses of fish from the Kattegat, respectively. Results are presented separately for genetics and microchemistry and before they are collated in the following synthesis section.

2.1 Baseline, genetics

With still decreasing costs and increasing throughput, genetic analyses have recently emerged as a practical tool for marine fisheries management and monitoring (Martinsohn *et al.* 2019, Hemmer-Hansen *et al.* 2019, Bernatchez *et al.* 2018). In particular, the methodology has been refined to develop targeted sets of genetic markers that provide high statistical power for identifying the population of origin of individual fish, based on matching individual fish genetic profiles to a baseline consisting of known populations in the study area (Nielsen *et al.* 2012, Bekkevold *et al.* 2015, Hemmer-Hansen *et al.* 2019).

The environmental transition zone between the North Sea and Baltic Sea is also characterized as a genetic transition zone in several species (Johanneson and André 2006; Limborg *et al.* 2009), including Atlantic cod (Nielsen *et al.* 2003). These differences are believed to be linked to the colonization and adaptation processes associated with the colonization of the Baltic Sea (Nielsen *et al.* 2003, 2009). On a local scale, new genetic data have also shown that populations in the North Sea and Kattegat are genetically unique (Berg *et al.* 2015; Andre *et al.* 2016; Barth *et al.* 2017), although differences are smaller than those observed between the North Sea and eastern Baltic Sea. Here, we used the information from previous work to select a number of genetic markers that show high levels of genetic differentiation between the North Sea and Kattegat/transition zone and use these genetic markers to determine the population of origin for a large number of cod collected from the Kattegat.

2.1.1 Materials and methods

Samples for the baseline consisted of 586 cod collected at spawning time in the North Sea, Kattegat/transition zone and eastern Baltic Sea populations (Figure 1, Table 1). Samples were collected over several years to obtain a sufficient representation of genetic variation in the baseline populations.

Table 1. Baseline individuals collected for genetic analyses

Sample	Sample size
North Sea	*213*
2002 North Sea ”Viking”	98
2003 North Sea ”Dogger”	45
2014 Q01 North Sea ”Dogger” (DK IBTS)	18
2016 Q01 North Sea ”Viking” (DE IBTS)	3
2016 Q01 North Sea ”Viking” (NO IBTS)	49
Kattegat/transition zone	*293*
2004 Kattegat (SE)	48
2015 Kattegat (DK)	75
1997 Oresund (DK)	45
2003 Oresund (DK)	45
1996 Western Baltic (DK)	45
2012 Western Baltic (DK)	35
Eastern Baltic	*80*
1997 Eastern Baltic (DK)	40
2007 Eastern Baltic (DK)	40

The selection of specific genetic markers (single nucleotide polymorphism, SNPs) was based on screening data sets from published work (Heath *et al.* 2014, Barth *et al.* 2017; Nielsen *et al.* 2012). Here, we selected genetic markers that displayed high levels of population differentiation in comparisons involving North Sea and transition zone samples.

DNA was extracted by Chelex resin (Estoup *et al.* 2996) and genetic markers (single nucleotide polymorphisms, SNPs) were genotyped on a Fluidigm Biomark HD system and individual genotypes determined from genotype clustering on proprietary software.

Genetic marker independence was assessed by calculating levels of linkage disequilibrium (essentially correlation between patterns for individual genetic markers) between individual genetic markers in the baseline samples, using the R package LDheatmap (Shin *et al.* 2006). Assignment to most likely baseline sample was conducted by calculating genotype likelihoods using the programme GeneClass2 (Piry *et al.* 2004), following the method by Rannala and Mountain (1997). Assignment was based on the highest assignment score, which is the likelihood of the most likely population divided by the sum of all likelihoods. The assignment score ranges between 0 and 100. Initial screening identified high genetic similarity between samples collected within the North Sea and transition zone, respectively. Hence, these samples were grouped into reporting groups for assignment purposes, i.e. the “Kattegat” reporting group consisted of baseline fish collected in the Kattegat, Øresund and western Baltic Sea within the transition zone between the North Sea and Baltic Sea.

Statistical power for population assignment to reporting groups was evaluated by self-assignment with the leave-one-out procedure following the principles described in Ogden and Linacre

(2015). Here, likelihood ratios (likelihood of “home” vs likelihood of “away”) were calculated for all pairwise scenarios. A clear separation of likelihood ratio distributions indicates high statistical power for individual assignment to the reporting groups (Ogden and Linacre 2015).

2.1.2 Results and discussion

Among 192 targeted genetic markers, 187 could be reliably be genotyped. These markers were assessed in all individuals and used for individual assignment.

Estimates of linkage disequilibrium between markers in baseline samples showed overall low levels of correlation between markers (Figure 2), demonstrating that markers can be considered independent for population assignment purposes.

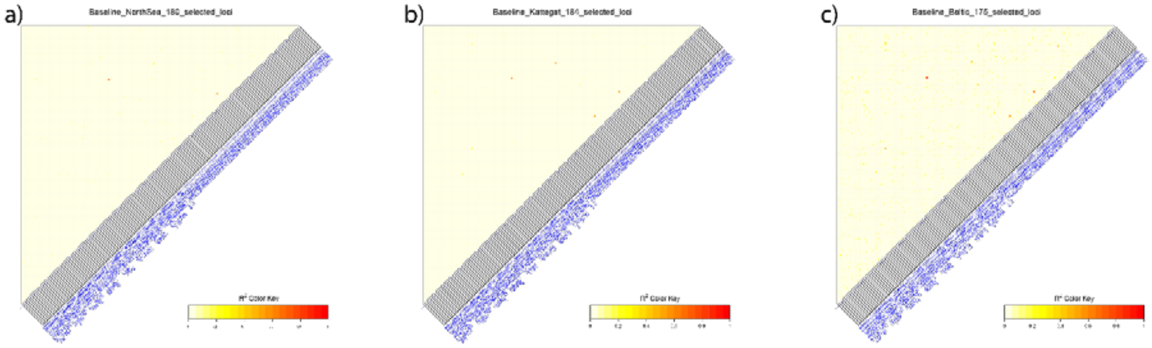

Figure 2. Linkage disequilibrium heatmaps in baseline samples collected in the North Sea in a), Kattegat/transition zone in b) and Eastern Baltic in c).

The distribution of likelihood ratios for all three pairwise comparisons of reporting groups were clearly separated for all comparisons (Figure 3).

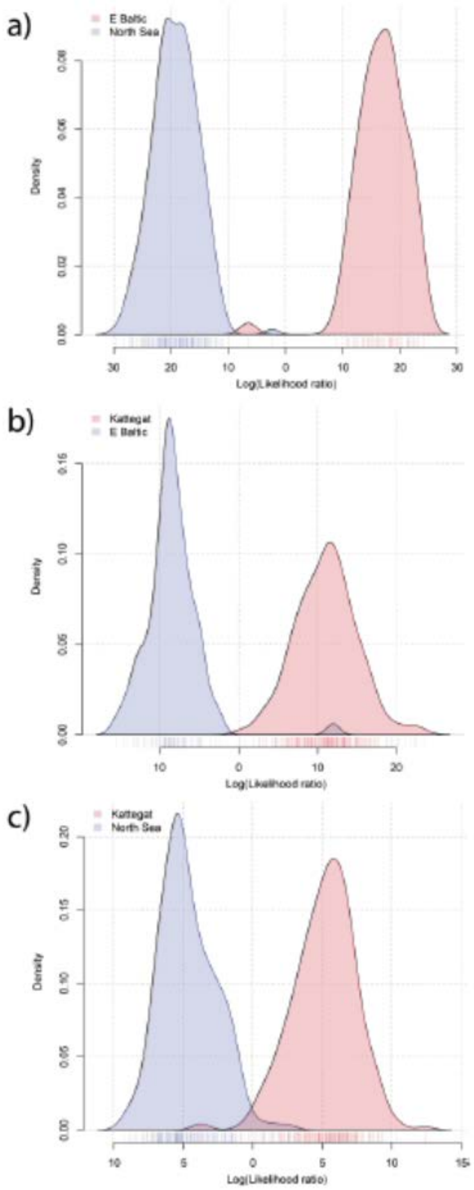

Figure 3. Distribution of likelihood ratios for assignment to baseline reporting groups. Assignment to Eastern Baltic and North Sea in a), Eastern Baltic and Kattegat in b) and North Sea and Kattegat in c).

Overall, the initial screening of baseline samples showed that the identified set of genetic markers were highly efficient for identifying population of origin when comparing the three reporting groups (“North Sea”, “Kattegat/transition zone” and “Eastern Baltic Sea”), which was the main purpose of the study. Identification of populations on finer geographical scales within reporting groups (e.g. separating Kattegat from western Baltic Sea) was not possible with this method.

2.2 Baseline, microchemistry

The Kattegat, together with the Øresund and the Belt Sea, lies in the transition area between the marine North Sea and the brakish Baltic Sea. The topography in this area becomes successively more shallow from > 120 m in North Sea and Skagerrak, to 40 – 80 m in the northern Kattegat, to depths of 20 – 40 m in the southern Kattegat. The hydrography is characterized by deep-water inflow of saline water from the North Sea and outflow of freshwater from river runoff in the surface. These topographic and hydrographic conditions lead to a salinity gradient ranging from fully marine saltwater in the North Sea to brackish water of very low salinity in the eastern Baltic Sea (Figure 4). This salinity gradient provides an ideal setup for studying fish migrations based on chronological analyses of the chemical composition of their otoliths.

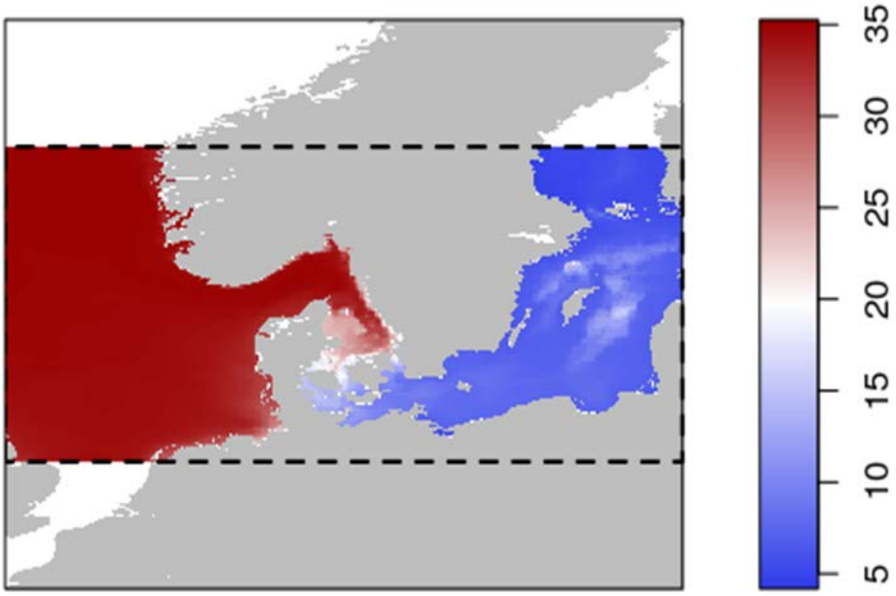

Figure 4. Map of average bottom salinity over the period January 17 2016 to December 17 2018 based on daily means from the Copernicus Marine Environment Monitoring Service Global Ocean 1/12^∘ Physics Analysis and Forecast (GLOBAL_ANALYSIS_FORECAST_PHY_001_024).

Otoliths consist of calcium carbonate (~98%) and organic matrix (~2 %) and small quantities of trace elements. The biomineralization of the otolith is regulated by physiological processes resulting in both daily growth increments and distinct annual growth zones reflecting seasonally fluctuating conditions in temperature and food availability (Beckman and Wilson, 1995; Høie and Folkvord, 2006; Weidman and Millner, 2000). Trace elements are absorbed primarily from the water across the gill surface and therefore provide a record of environmental conditions experienced by the fish (Campana, 1999; Milton and Chenery, 2001; Watanabe et al., 1997). The chemical composition of the water depends on the geo-chemistry of the surrounding catchment and therefore provides an area-specific fingerprint which is reflected in the fish’s otoliths (Walther and Limburg, 2012). Otolith chemistry has over the last three decades gained increasing attention as a tool for analyzing for example fish stock dynamics, migration patterns, pollution exposure and connectivity between habitats, and plays an increasingly important role as a fisheries management tool (Campana, 1999; Campana and Thorrold, 2001; Carlson et al., 2017; Elsdon et al., 2008).

In the present study, we made use of the combination of environmental gradients occurring in the area and the otolith’s chronological record of environments experienced by the fish to study early life stage drift and migration patterns of cod in the Kattegat. More specifically, we tested whether 1) North Sea cod are spawned in the same spawning areas as Kattegat cod, and 2) Adult cod in the Kattegat perform return-migrations between the Skagerrak/North Sea and the Kattegat.

2.2.1 Materials and methods

Baseline samples were selected from survey samples of spawning individuals from existing samples covering the North Sea (IBTS1 1996), the western and eastern Baltic Sea (BITS2 1996) as well as the new samples collected for this project in the southern and northern Kattegat (KASU2 2016). See Table 2 and Figure 1 for overview of otolith samples.

Otoliths were embedded in Epoxy resin (Struers®) and sectioned through the core using an Accutom-100 multi-cut sectioning machine to obtain a 1 cm wide block containing the rostral part of the otolith with the nucleus exposed at the sectioned surface. The Laser Ablation Inductively Coupled Mass Spectrometry (LA ICP-MS) facility at the Geological Survey of Denmark (GEUS) was used to analyze the chemical composition of the otolith from nucleus to edge of the otlith. The data thus represent elemental signatures spanning the period from hatch to death of each individual. Further details of the analytical setup may be found in Hansen *et al.* (2018). This study focused on magnesium (^{24}Mg), calcium (^{43}Ca), manganese (^{55}Mn), copper (^{65}Cu), zink (^{66}Zn), strontium (^{88}Sr) and barium (^{138}Ba), which are elements that are known to have discriminatory power in cod from this area. Only the measurements at the edge of the otolith, representative of the environmental signal prior to capture, were used for deriving the baseline signature.

Table 2. Overview over baseline samples used in this study

Age	North Sea	Kattegat north	Kattegat south	Western Baltic	Eastern Baltic	TOTAL
0		66	36			102
1	4	21	13			38
2	8	37	38			83
3	2	8	13	1	5	29
4	2	18	41	14	12	87
5		1	5		18	24
6		2	5		1	8
8			1		1	2
TOTAL	16	135	152	15	37	355

For the identification of spawning origin, elemental fingerprints from the pelagic juvenile stage were analyzed using standard analyses protocols based on single element analysis of variance (ANOVA), comparison of multi-element fingerprints (MANOVA) and Linear Discriminant Analysis (LDA) to assess classification success based on the multi-element fingerprints (Campana, 2005, Kerr and Campana, 2013).

The assignment of measured otolith strontium values to salinity levels experienced is based on a multi-step approach:

1. Collation of published values of the relationship between otolith Sr and salinity
   The collation of published otolith Sr – salinity relationship from published laboratory experiment values covers 8 studies of a diverse range of species from different taxa and habitats around the world (Barnes and Gillanders, 2013; Elsdon and Gillanders, 2002; Hicks et al., 2010; Lin et al., 2007; Martin and Wuenschel, 2006; Miller, 2011; Oeberst et al., 2009; Secor et al., 1995; Stanley et al., 2015) which are shown in Figure 5.
2. Establishment of a baseline collection of cod otoliths
   An overview of the baseline samples covering the North Sea, Kattegat, western Baltic and eastern Baltic Sea is given in Table 2. From these samples, the elemental composition of the measurements at the edge of the otolith, representative of the time and environment occupied prior to catch, was used.
3. Salinity data from the cod habitat
   From the hydrographic database Copernicus Marine Environment Monitoring Service Global Ocean 1/12° Physics Analysis and Forecast (GLOBAL_ANALYSIS_FORECAST_PHY_001_024), bottom salinity values covering the entire study area were extracted to derive habitat-specific values (Figure 4). Additionally, salinity values were extracted for the catch location of each fish.
4. Establishment of a salinity-strontium calibration curve
   The combined datasets (literature and measured) were then used to estimate the calibration curve to be used for translating otolith strontium values to experienced salinities (Figure 5).
5. A state-space-migration model
   Mass spectrometry data have inherent measurement errors. Therefore, a regime-switching state-space model was developed to filter the signal from the noise. The model included three layers. The first layer modelled areas of attraction, reflecting the different salinity levels in the four areas: the North Sea, Kattegat, western Baltic, and eastern Baltic (Figure 6). The second layer modelled the true strontium level in an otolith, given the attraction area, by an AR(1) process on log-scale from the core to the edge. Finally, the third layer modelled observed strontium levels, given the true level, by a log-normal distribution.

Migration patterns of adult cod were derived by assigning habitat use based on this state-space migration model. Thereafter habitat use from hatch to capture was calculated for each genotype separately as the percentage of individuals with a specific habitat assignment within each time interval.

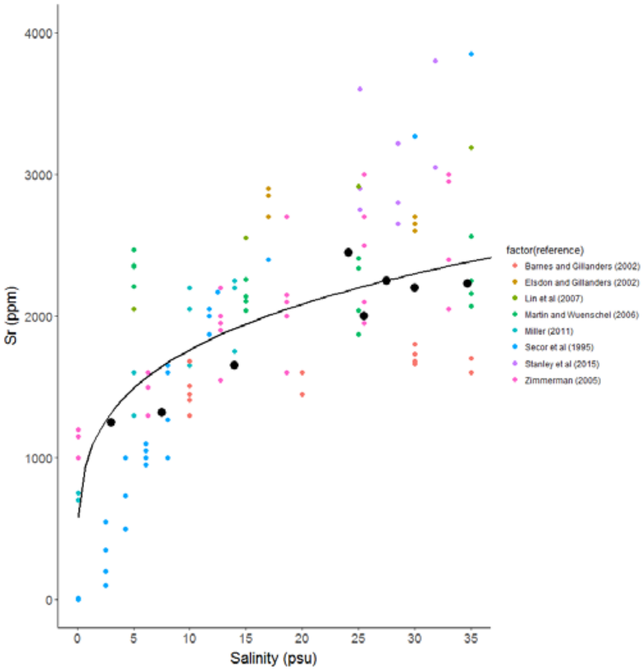

Figure 5. Salinity-strontium calibration curve derived from literature values and this study (black line). Points show individual observations from the literature. Observations from the present project are black dots.

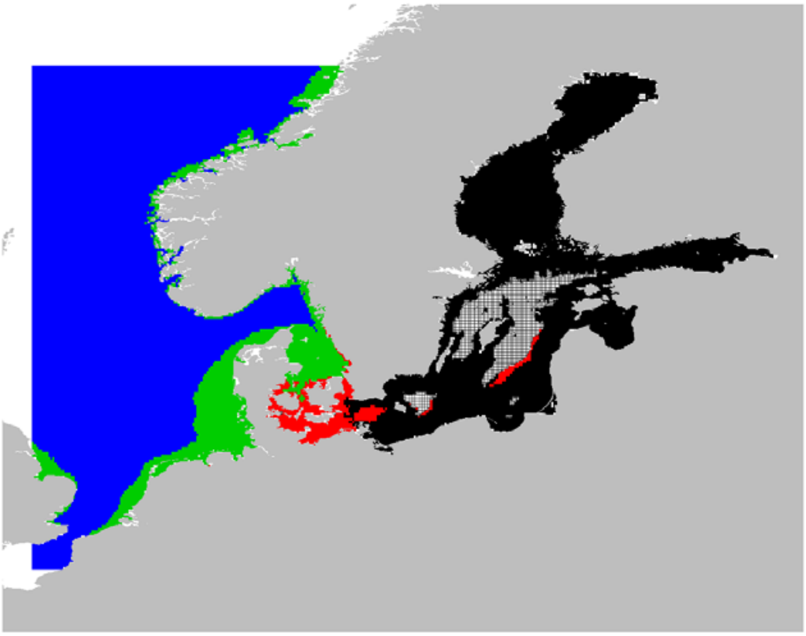

Figure 6. Map of the study area, where the colours represent attraction areas based on near-bottom salinity. It should be noted that because this map is based on bottom salinities it looks as if e.g. cod from Kattegat could be confounded with cod from coastal waters of the Danish North Sea or western Baltic cod with cod from the Gotland basin. However, these alternative areas are either too shallow (North Sea) or too deep (Gotland) for cod to occur, and there is therefore no risk of mis-assigning individuals.

2.3 Samples from the Kattegat, genetics

2.3.1 Materials and Methods

We collected 2370 cod from different geographical areas with the Kattegat (Table 3) from a combination of Danish and Swedish cruises, harbor sampling and discard sampling. Biological data was collected for all fish.

DNA extraction and genotyping followed the procedure described for the baseline samples. Assignment procedure followed those developed for the baseline assignment power procedure, i.e. assignment to reporting groups with the highest genotype likelihood.

Table 3. Samples collected from the Kattegat for genetic analyses

Year	Quarter	Source	Sample size
1996	3	DK cruise	146
1998	3	DK cruise	91
2008	4	DK cod survey	92
2013	4	SE cod survey	252
2014	4	DK cod survey	100
2015	1	SE IBTS	208
2015	4	SE cod survey	282
2015	3	DK sole survey	115
2015	3	SE IBTS	159
2016	1	SE IBTS	83
2016	4	DK discard sampling	22
2016	4	DK harbour sampling	17
2016	4	DK cruise	62
2016	3	DK cruise	156
2016	4	DK sole survey	202
2017	1	SE IBTS	141
2017	4	SE cod survey	242

2.3.2 Results and discussion

The full genetic data set until 2016 was used to calculate predicted probabilities of local Kattegat origin, integrated through the entire Kattegat assessment area (see section “Implications to stock assessment and management” below) and to link “origin” to estimates of biomass. Here, we will highlight the main findings and provide examples of the results from the genetic analyses in this section.

Results from genetic assignment confirmed the presence of both North Sea and local Kattegat cod in the Kattegat. (Figures 7 and 8). The presence of North Sea fish was most prominent for younger/smaller fish and for the northernmost parts of the Kattegat (Figures 7-9). Among cod older than four years only few individuals were of North Sea origin. The age and size at which 50% of the population is mature in North Sea cod is approximately 3 years and 48 cm (Yoneda and Wright, 2004). This supports the hypothesis that North Sea cod show natal homing for spawning and do not subsequently return to the Kattegat.

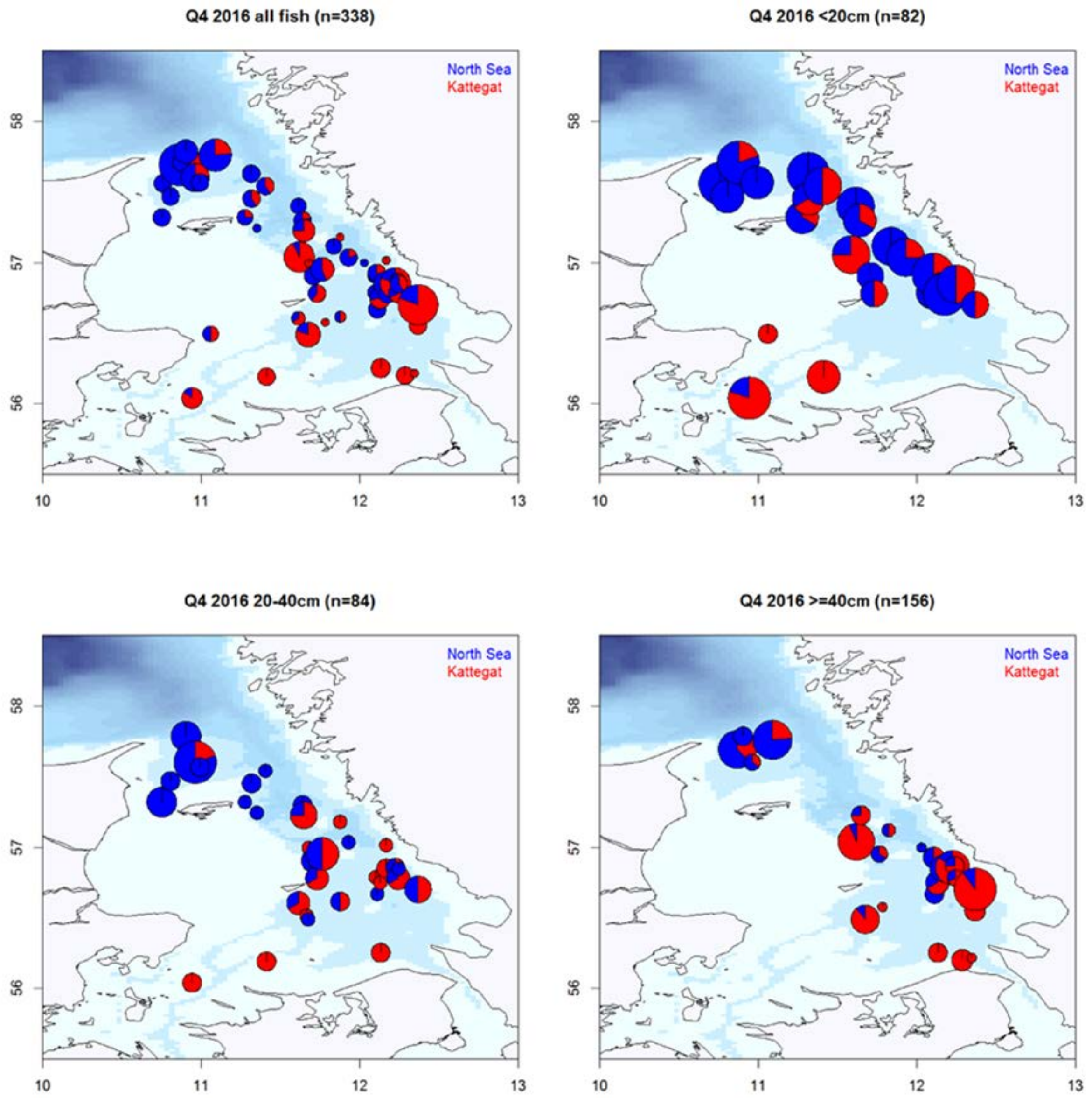

Figure 7. Proportion of North Sea (blue) and Kattegat/transition zone (red) cod in quarter 4, 2016. Data are represented by different lengths groups, with all fish (top left), fish < 20 cm (top right), fish between 20 and 40 cm (bottom left) and fish > 40 cm (bottom right). Size of pie is proportional to sample size and total number of fish (n) is shown in brackets above each map.

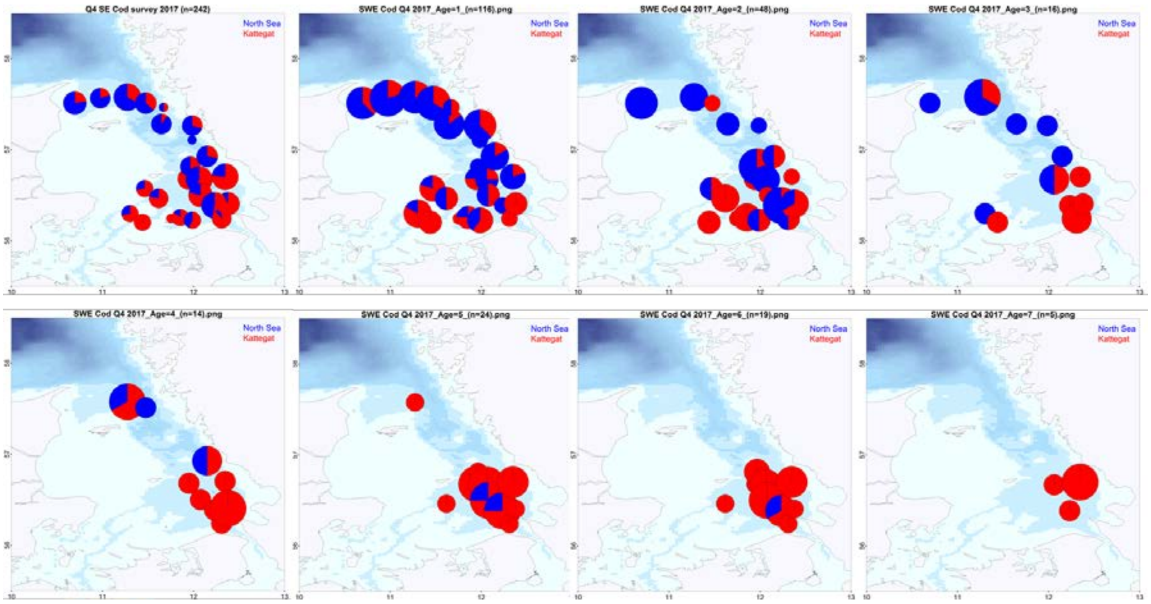

Figure 8. Proportion of North Sea (blue) and Kattegat/transition zone (red) cod in quarter 1, 2017. Data are represented by different ages. Size of pie is proportional to sample size and fish age and total number of fish (n) is shown above each map. All fish shown in top left plot.

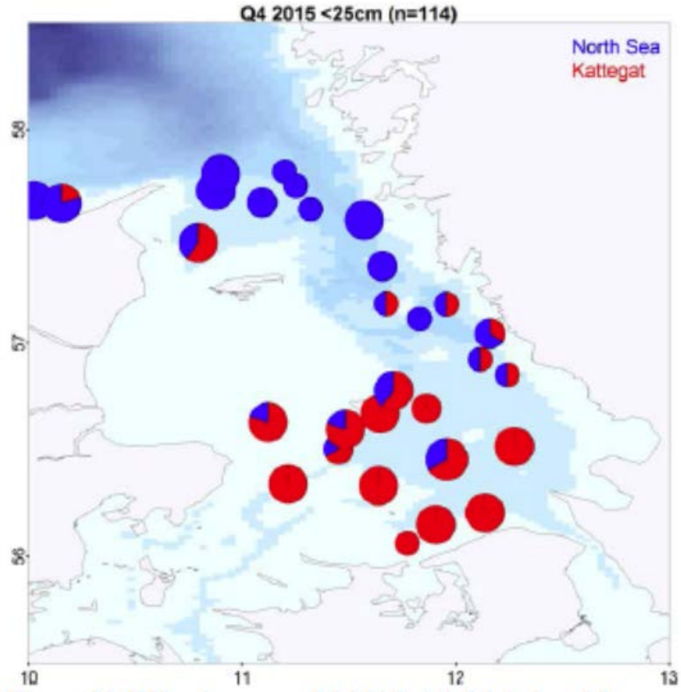

Figure 9. Proportion of North Sea (blue) and Kattegat/transition zone (red) among cod < 25 cm quarter 4, 2015. Size of pie is proportional to sample size and total number of fish (n) is shown above map.

Analyses of fish in spawning condition confirmed that spawning in the Kattegat, and in particular in the southernmost parts, is dominated by fish of local Kattegat/transition zone origin (Figure 10)

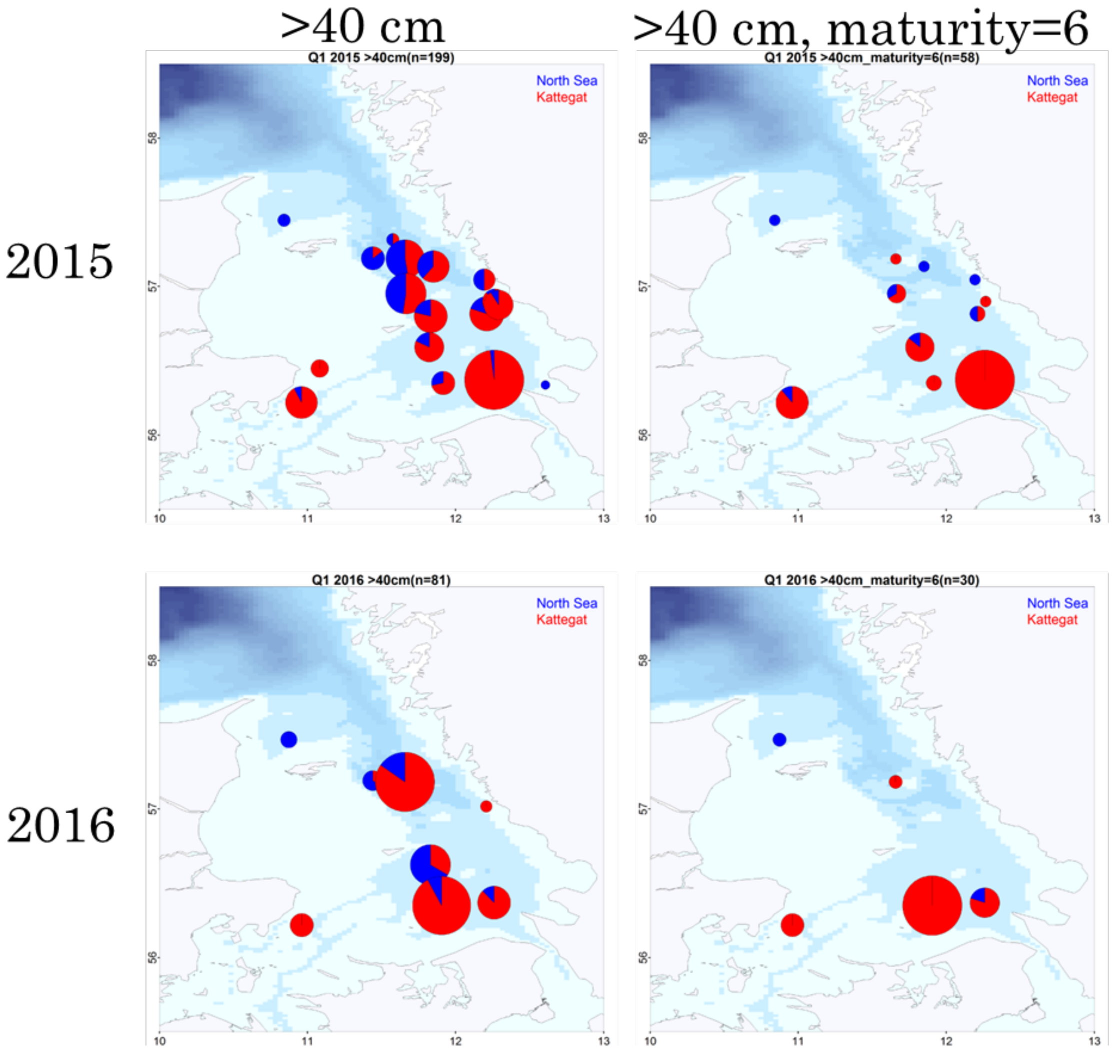

Figure 10. Proportion of North Sea (blue) and Kattegat/transition zone (red) cod in quarter 1, 2015 (top) and 2016 (bottom). Fish > 40 cm are shown on the left and fish > 40 and determined to be in spawning condition are shown on the right. Size of pie is proportional to sample size and total number of fish (n) is shown above each map.

A substantial inter-annual variation in the proportion of fish of North Sea origin was observed. A dramatic example of this effect was evident when fish of age 2 in 2013 and 2015 were compared (Figure 11). In 2013, the majority of the 2 year old fish were of North Sea origin, while the 2015 data showed a higher proportion of local Kattegat/transition zone origin, in particular in the southernmost parts of the Kattegat. It is likely that these patterns are affected by conditions outside the Kattegat, for example by a combination of oceanographic conditions and the size of spawning population the North sea/Skagerrak which could influence the transport of early life stages from the North Sea into the Kattegat.

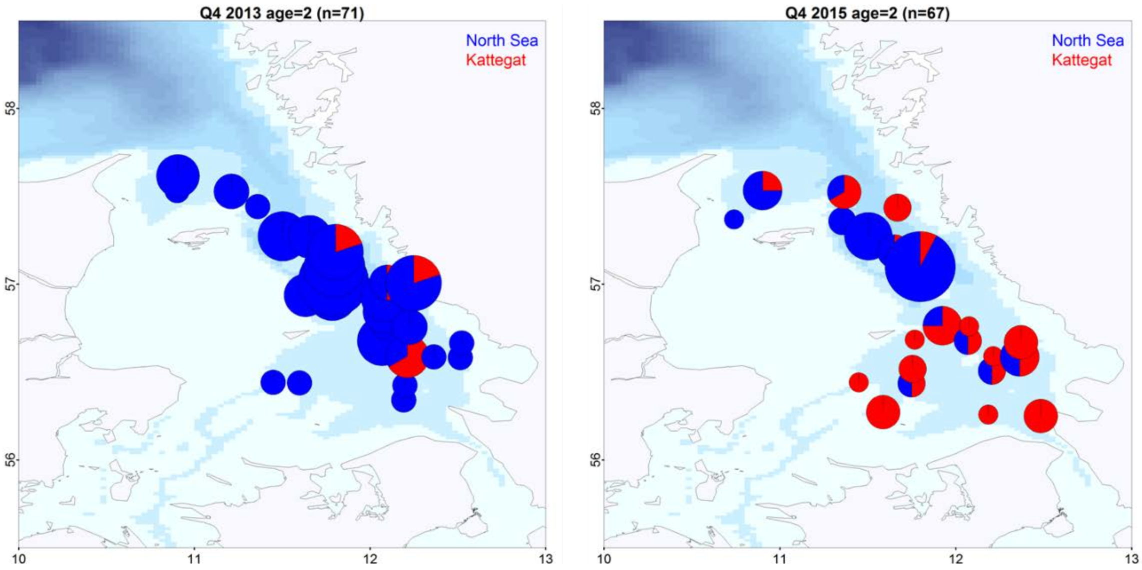

Figure 11. Proportion of North Sea (blue) and Kattegat/transition zone (red) 2-year old cod in quarter 4, 2013 (left) and 2015 (right). Size of pie is proportional to sample size and total number of fish (n) is shown above each map.

Finally, data from 1996 and 1998 indicated that mixing of the two populations in the Kattegat is not a new phenomenon. Although spatial resolution was lower than for the more recent data, there was also a tendency towards higher proportions of North Sea origin in the northern areas (Figures 12 and 13).

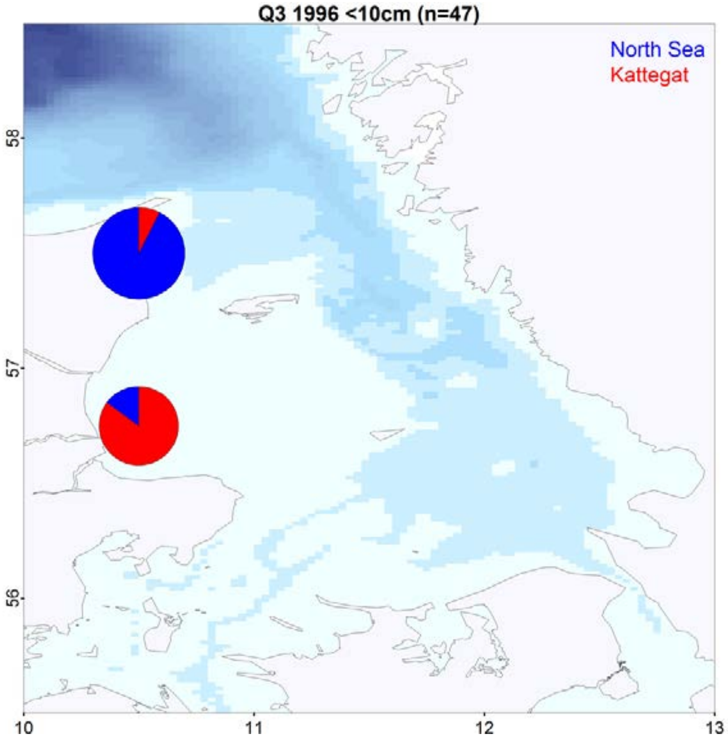

Figure 12. Proportion of North Sea (blue) and Kattegat/transition zone (red) cod in quarter 3, 1996. Size of pie is proportional to sample size and total number of fish (n) is shown above map.

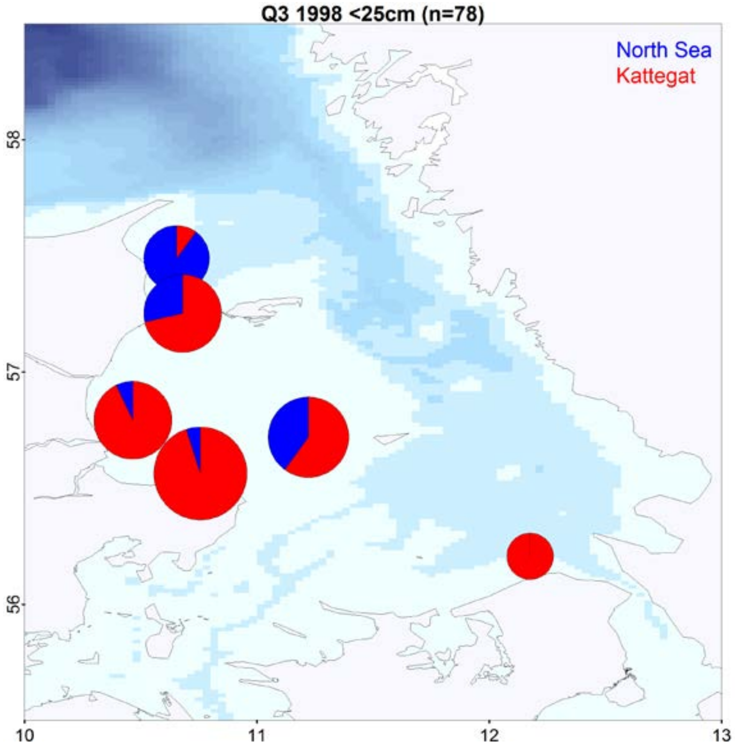

Figure 13. Proportion of North Sea (blue) and Kattegat/transition zone (red) cod in quarter 3, 1998. Size of pie is proportional to sample size and total number of fish (n) is shown above map.

Collectively, the genetic data support the hypothesis of inflow of North Sea early life stages followed by return migration for spawning when the North Sea fish reach sexual maturity. The large inter-annual variability in mixing proportions may at least partly be driven by variable inflow of juveniles from the North Sea population, hence stressing the need for monitoring the proportion of North Sea origin among juveniles and for tracing the proportions as the cohort grows to estimate more specifically when return migration takes place.

2.4 Samples from the Kattegat, microchemistry

2.4.1 Materials and methods

From the genotyped individuals (Table 3), subsamples were selected to ensure adequate sample sizes from the northern and southern Kattegat within the size ranges < 25cm, 45 – 55 cm, > 60cm, as well as of the two genotypes found in the area (overview in Table 4). Otoliths were embedded, sectioned through the core and analyzed for chemical composition as the baseline samples. Additionally, otolith growth chronologies were obtained for each individual from otolith images by measuring the widths of successive opaque and translucent growth bands along the laser track and LA ICP-MS data were thereafter assigned to the corresponding zones of the otolith and element concentration values averaged by zone (Figure 14).

Table 4. Overview over samples used in this study by genotype and sampling area

	Kattegat		North Sea		TOTAL
Age	north	south	north	south	
0	11	12	55	24	102
1		7	21	6	34
2	14	19	23	19	75
3	3	10	5	3	21
4	15	37	3	4	59
5	1	4		1	6
6	2	5			7
8		1			1
TOTAL	46	95	107	57	305

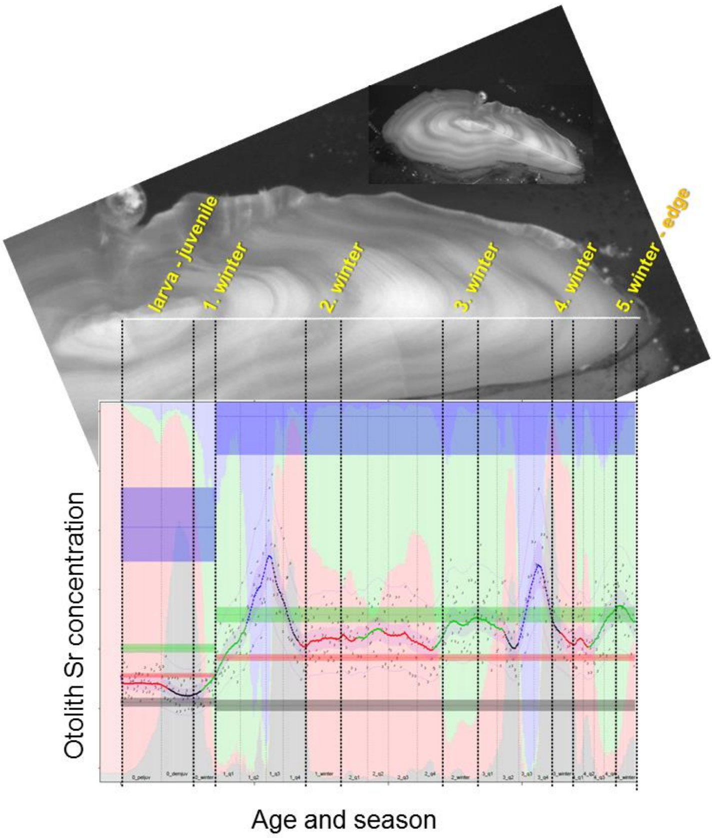

Figure 14. Image of otolith cross-section with laser track indicated with a white line, and the corresponding otolith Sr profile with habitat use indicated by colors corresponding to the attraction areas in Figure 6 (North Sea = blue, Kattegat = green, western Baltic = red, eastern Baltic = black). Boundaries of growth zones are outlined by vertical black lines linking the visual image with the corresponding sections of the Sr profile. This particular individual is 4 years old, was born in the western Baltic/Øresund, spent most of its life in western Baltic/Øresund/Kattegat and performed two migrations into the North Sea in summer/fall of its second and fourth year of life.

2.4.2 Results and Discussion

The elemental fingerprints in the pelagic juvenile stage differed significantly between the two genotypes (MANOVA, df = 7 on 292, $p < 0.05$). Significant differences occurred in all elements except for P (ANOVA, df = 1, $p < 0.05$ for all except P). Of particular interest are Sr, Ba and Mn, where Sr was higher in the North Sea genotype, while Ba and Mn were higher in the Kattegat genotype (Table 5). Differences between year-classes within the two genotypes were not significant (MANOVA, df = 7 on 292, $p > 0.05$).

Table 5. Concentration of elements in the pelagic juvenile stage by genotype with ANOVA statistics (ns = not significant, * < 0.001)**

Element	Kattegat genotype	North Sea genotype	df	F	p
Sr	1555.0	1639.3	1	12.34	***
Ba	18.1	15.7	1	7.56	***
Mn	13.8	7.5	1	101.18	***
Mg	117.8	79.9	1	13.38	***
P	301.3	301.4	1	0.001	ns
Cu	0.7	0.4	1	11.9	***
Zn	5.5	3.2	1	22.82	***

The otolith Sr levels in the early life stages are considerably lower than during the adult stages for two reasons (compare Table 5 and Figure 5). Firstly, many of the environmentally regulated elements in the otoliths are incorporated at a lower concentration in juveniles than in adult fish, suggesting an ontogenetic development in transport mechanisms from environment to otolith (Hughes *et al.*, 2016; Jessop *et al.*, 2008; Kalish, 1989). Secondly, larval and pelagic juvenile cod occur at shallower depths above/near the halocline than adults and therefore experience lower salinities. Surface salinities also show a geographic decline from the North Sea to the eastern Baltic and are therefore a reliable tracer for natal origin. Unfortunately, no larval otolith samples were available to be used as baseline, therefore an accurate assignment of the early life stages is not possible. The conclusions here are therefore based on the approach that if elemental fingerprints are identical between genotypes, they have been spawned in the same area – the Kattegat. If the fingerprints are significantly different between genotypes, they originated from different area, where a non-Kattegat origin may be either the Skagerrak or the North Sea.

The LDA showed that 83% of the North Sea genotype and 68% of Kattegat genotype were correctly classified to their respective genotype with an overall classification success of 75%. LDA makes use of all dimensions for classification of individuals. For visualisation of the classifications, however, only two dimensions are practical, where the first two explain the majority of the variation. In the present analyses, the first four discriminant functions explained most of the variation between genotypes. The biplot of the first two discriminant functions against each other with loadings (representing individual elements) shows that in particular Sr, Ba and Mn drive genotype-specific fingerprints in the pelagic juvenile stage (Figure 15, left panel). In this plot, LD1 explains 41.4% of the variation in elemental fingerprint between genotypes and LD2 21.1%. A considerable part of the variation (12.5%) is thus explained by dimensions that are orthogonal to the first two dimension, and thereby impossible to represent visually. Together, the MANOVA and LDA results document that cod of different genotypes captured at the same locations in the Kattegat have different spawning origin. Implicit in this is that North Sea cod therefore must have been spawned in the North Sea or Skagerrak but not the Kattegat.

In order to address during variation between life stages (pelagic juvenile, demersal juvenile, first winter, first, second etc. year of life), the ANOVA, MANOVA and LDA analyses were repeated for each of the progressively older life stages. The results for the demersal juvenile stage and the first winter mirrored those for the demersal stage, with significant differences between genotypes (MANOVA, df = 7 on 292, $p < 0.05$), where differences were primarily driven by Sr, Ba and Mn (Figure 15, middle and right panels). The classification success decreased correspondingly from 83% to 72% and 50% in the North Sea genotype and from 68% to 62% and 51% in the Kattegat genotype, which is illustrated by the increasing overlap between groups in the LDA biplot (Figure 15). From age 2 onward, differences between genotypes were not significant (MANOVA, df = 7 on 292, $p > 0.05$). This suggests that North Sea cod drift into the Kattegat during their early life stages, and that this process may continue to the end of the first winter.

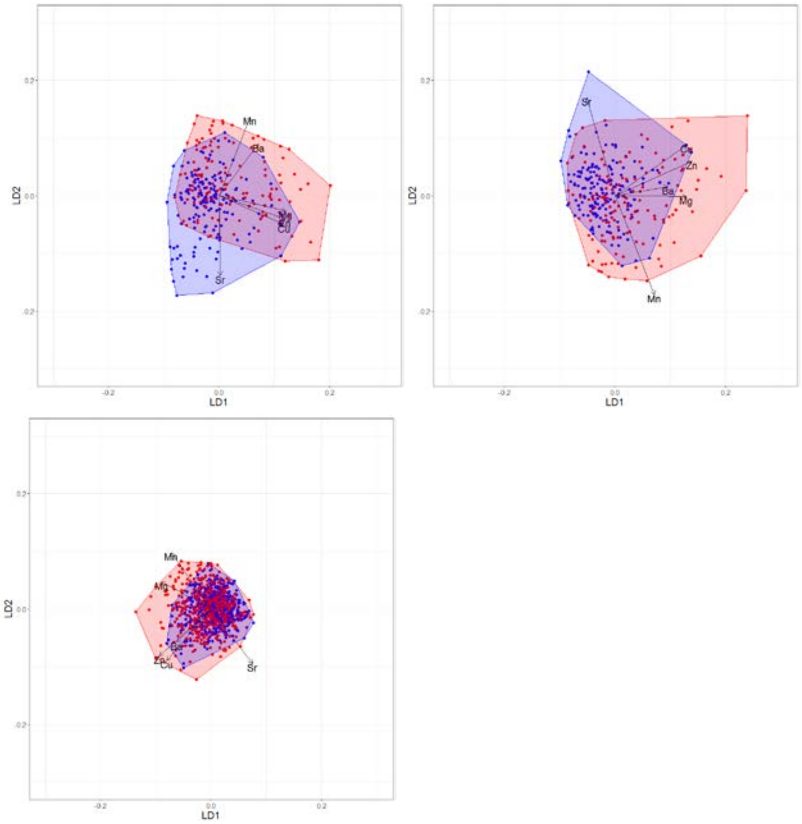

Figure 15. Biplot of the first two discriminant functions of the LDA analyzing elemental fingerprints in the pelagic juvenile stage (left panel), the demersal juvenile stage (middle panel) and the first winter (right panel). Colours represent genotypes Kattegat (red) and North Sea (blue), and arrows the direction and strength of the loadings (= elements).

The elements driving this differentiation (Sr, Ba and Mn) are under strong environmental control. Strontium (Sr) is known to reflect ambient salinity, owing to the fact that the Sr content in marine habitats is fairly constant worldwide, and mixing with freshwater not only dilutes salinity but also the Sr concentration (Kraus and Secor, 2004; Walther and Limburg, 2012). Because otolith Sr concentration is strongly correlated with ambient concentrations, otolith Sr is a useful proxy for environmental salinity and is globally used to track movements of fish between marine and freshwater and within estuaries, (Bath *et al.*, 2000; Elsdon and Gillanders, 2003; Miller, 2011; Sturrock *et al.*, 2012). The higher Sr concentrations in the North Sea genotype is thus consistent with a spawning area in more saline water than the Kattegat. Barium shows a nutrient-like distribution in the aquatic environment that is strongly related to environmental salinity with depletion in surface waters, with higher concentrations in freshwater and nearshore areas (Elsdon and Gillanders, 2005; Walther and Limburg, 2012). Highest Ba concentrations generally occur at salinities between 5 and 20 psu (Walther and Limburg, 2012). The barium (Ba) concentration in otoliths almost exclusively reflects ambient concentrations (Bath *et al.*, 2000; Elsdon and Gillanders, 2003; Hicks *et al.*, 2010; Miller, 2011; Reis-Santos *et al.*, 2013). Consistent with the hypothesis that the North Sea genotype is spawned in a more offshore environment, Ba concentrations were higher in the Kattegat genotype. Manganese (Mn) concentrations on the other hand are known to increase in hypoxic areas owing to the reduction of manganese oxides from the sediment with decreasing ambient oxygen content. Otolith Mn concentrations have proven useful for tracking hypoxia exposure in e.g. Baltic cod (Limburg *et al.*, 2011, 2015). Prolonged seasonal hypoxia is known to occur in the Kattegat (Rosenberg *et al.*, 1992, 1996), which is reflected in the much higher Mn concentration during the early life stages of the Kattegat genotype.

The rapidly decreasing classification success from the pelagic juvenile stage to the end of the first winter and the lack of significant differences in environmentally related elements (Sr, Ba, Mn) in subsequent years, suggests that the North Sea genotype arrived in the Kattegat during the early life stages. Inter-annual and inter-individual variability in drift duration may also explain the lack of a stronger separation of individuals in the pelagic juvenile stage and the gradually decreasing classification success between the two genotypes with age.

Habitat assignments, based on Sr concentrations alone, were obtained from the state-space migration model for all time periods of each individual’s life. Examination of individual cod migration patterns showed that 45% of individuals from both genotypes remained resident within the Kattegat all their adult life without undertaking any migrations out of the area. Two percent of the Kattegat genotype individuals spent the majority of their life in the Øresund or western Baltic and had only entered the Kattegat relatively recently. No individuals had spent the majority of their life in the North Sea or the eastern Baltic.

From the individual habitat assignments, genotype-specific percentages of habitat use were calculated for each time interval. For both genotypes, less than 10% of the fish showed a “North Sea signal”, indicative of migrations into the Skagerrak/North Sea, for ages 1 - 3 (Figure 16, upper panel). Somewhat higher percentages (15 - 20%) occurred occasionally. In the North Sea genotype, a considerably higher percentage (>30%) of migrations to the Skagerrak/North Sea and back to the Kattegat occurred during age 4 with proportions increasing toward winter (Figure 16, lower panel). The percentage of individuals of the Kattegat genotype assigned to having a Skagerrak/North Sea habitat use did not seem to vary over fish age. However, a clear geographic pattern was evident, in that throughout the ages examined, more cod from northern catch locations had a Skagerrak/North Sea signal than those from the southern locations.

When examining the distribution of all habitat assignments, the most notable observation is that in both genotypes, approximately 20 - 30% of the individuals' habitat use was assigned to the western Baltic (Figure 17). In the Kattegat genotype, up to 4% of individuals had a Sr level that was assigned to the eastern Baltic Sea for restricted periods of time around fall and winter (Figure 17).

Migration patterns of fish older than four years could not be analyzed for the North Sea genotype, as no samples of this genotype were available.

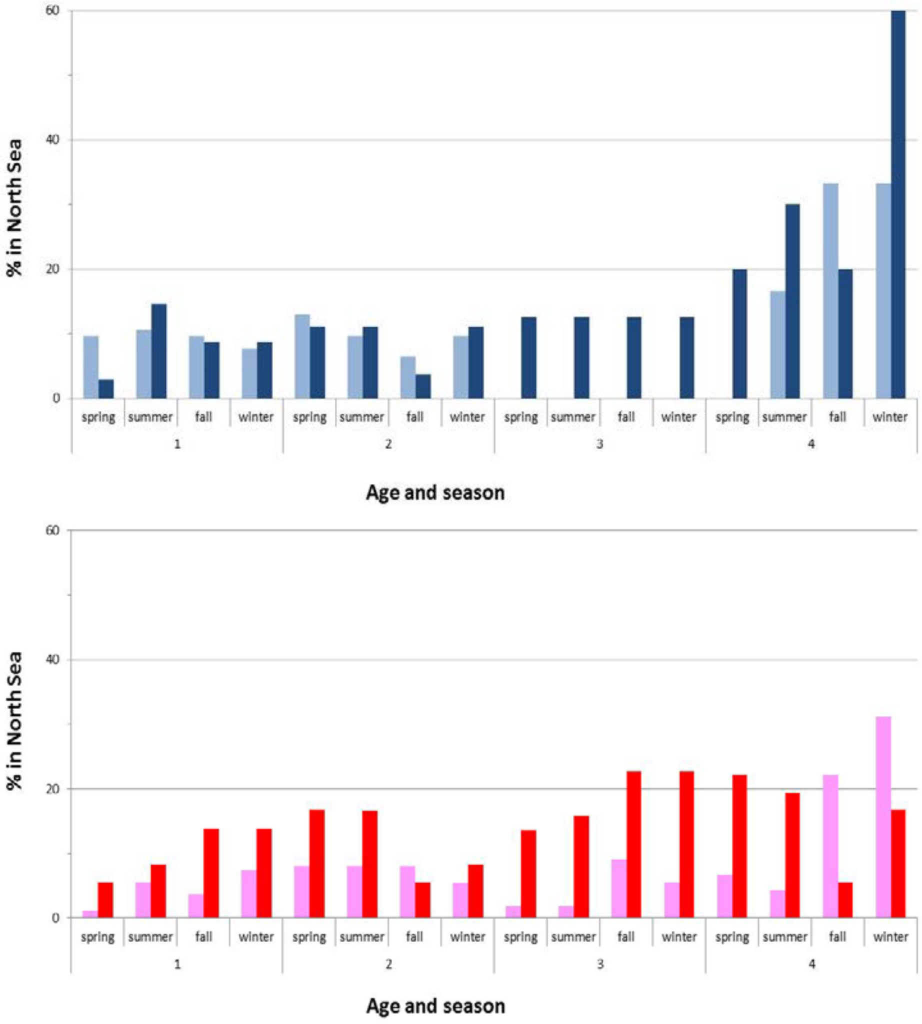

Figure 16. Percentage of individuals with a strontium signal assigned to the North Sea for the two genotypes by age and season. Colours represent genotypes Kattegat (red) and North Sea (blue), where colour shade corresponds to sampling area, where dark = north and light = south. Apparently missing values in the North Sea genotype are true zero values.

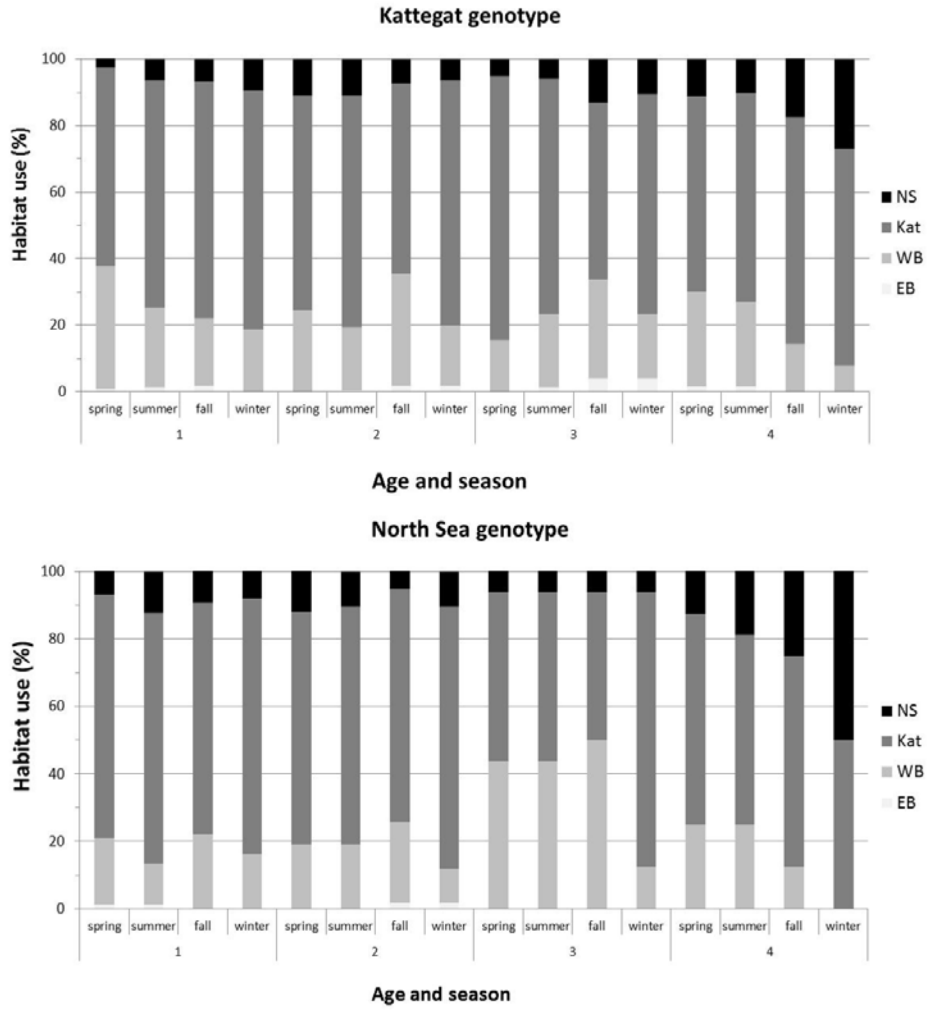

Figure 17. Percentage distributions of signals corresponding to the North Sea (black), the Kattegat (dark grey), the western Baltic Sea (light grey), and the eastern Baltic Sea (white) for the two genotypes separately.

A surprising result of this study was the large proportion of individuals from both genotypes assigned to have a western Baltic Sea elemental signature. The salinity regimes in the western Baltic and Kattegat differ considerably from each other with mean bottom salinities of 10 – 15 psu and 30 - 33 psu respectively. This salinity gradient lies within the ideal range for discriminating habitat use (Kraus and Secor, 2004; Walther and Limburg, 2012), and the results should therefore be reliable. However, the migration patterns of tagged cod discussed above do not suggest a pronounced migration further south than the Øresund. Over the last decades, dynamics in stock size have changed considerably, with unknown impact on migratory behaviour. Considerable numbers of eggs and larvae spawned in the western Baltic Sea, more specifically the Great Belt and the Kiel Bay, may drift into the Kattegat and Skagerrak depending on wind conditions prevailing during the spawning season (Huwer et al., 2016). Provided that these individuals also show philopatric migration behaviour, one would expect to find seasons with high assignments to the western Baltic Sea. A clear seasonal pattern with higher proportions of western Baltic Sea signals in spring (the main spawning season of western Baltic cod) was, however, not evident. The occurrence of 2% cod with a clear western Baltic/Øresund signal over most of their lives but captured in Kattegat further suggests considerable connectivity between these areas. The genetic methods used in this project were not designed to separate between stocks from Kattegat/Øresund/western Baltic and it is therefore not possible to assess which stocks or stock components contribute to the observed signal. Additionally, baseline samples representing the western Baltic cod stock were from Kiel Bay in SD 22 but did not cover the Belt Sea or Øresund. We therefore recommend to extend the baseline to include samples with a higher spatial resolution with a stronger focus on these areas and simultaneously focus genetic analyses to address stock identification in this part of the transition area.

3. Synthesis and implications to stock assessment

3.1 Synthesis of results

The results from our study have improved our understanding of the complex patterns of connectivity between the North Sea and Kattegat. Our main finding can be synthesized as follows:

- Cod in the Kattegat consist of a mixture of at least two genetically distinct cod populations: “North Sea cod” and “Kattegat/transition zone cod”.
- There is a north-south gradient in mixing proportions, with higher proportions of North Sea fish in the Northern parts of the Kattegat.
- There is a clear tendency towards decreasing proportions of North Sea origin with age/size.
- Spawning in the southern parts of the Kattegat is dominated by fish of local origin.
- The North Sea genotype is advected by ocean currents from their natal origins in the North Sea during their early life stages. This transport mechanism seems to be finished by the end of their first winter.
- Decreasing proportions of North Sea fish with age/size and among spawning fish suggest that North Sea fish leave the Kattegat when they reach sexual maturity.
- There is considerable inter-annual variation in mixing patterns, most likely linked to a combination of year class strength in the North Sea/Skagerrak and oceanographic conditions.
- Adult cod in Kattegat exhibit a heterogeneous migration activity.
- Migrations to the North Sea and western Baltic Sea do not seem to be associated with specific times of the year and are therefore presumably not recurrent spawning/feeding migrations but rather follow a random pattern.
- Kattegat genotype: Approximately 70% of the cod remain residents in the Kattegat throughout their first four years of life. Independent of season, ca 10 % of the cod undertake return migrations to the North Sea, and 20-30% migrate to the western Baltic and even as far as the eastern Baltic and subsequently return to the Kattegat.
- North Sea genotype: Similarly to the Kattegat genotype, the majority (70%) of the North Sea genotype remains resident in the Kattegat during their first four years of life. Towards the fall/winter of their fourth year of life, an increase in return migrations to the North Sea occurs. Approximately 20% of the North Sea genotype migrates to the western Baltic Sea to return to the Kattegat.

3.2 Implications to stock assessment and management

Stock assessment for cod in the Kattegat has for several years estimated that substantial unallocated removals from the stock occur, which has caused uncertainties in especially fishing mortality estimates. The causes for these unallocated removals have not been well understood.

An important outcome of this project is an improved understanding of these unallocated removals estimated in the assessment model. The results from this project confirmed that substantial migration of North Sea cod from the Kattegat back to North Sea likely takes place. This could explain a large part of the mismatch between survey and fisheries catch, which has shown that more fish disappear from the Kattegat than is caught in fisheries.

3.2.1 Stock assessment analyses

Several exploratory analyses were made which included the new information on stock mixing and migration in stock assessment for cod in the Kattegat, to account for the North Sea stock component.

At the ICES benchmark (WKBALT 2017), the new genetic information on proportions of North Sea and Kattegat cod within the Kattegat were used to derive stock-specific biomass trends adjusting survey indices so these would represent the Kattegat population only. The trends in survey indices were generally similar for the entire Kattegat area and for the Kattegat stock. This suggests that the dynamics in cod biomass in the Kattegat in the analysed years represented also the dynamics of the Kattegat cod population. Although the exact values and inter-annual changes in survey indices depended on the assumptions on stock mixing over the years applied in the analyses, as the genetic information is restricted to selected years.

Another type of analyses estimated a relative change in fishing impact in recent years. The calculation methods are described in Vinther and Eero (2013). In the analyses conducted in relation to ICES benchmark (WKBALT 2017), an attempt was made to estimate fishing impact for the Kattegat cod population instead of the entire area of Kattegat. The analyses used the predicted spatial distribution of cod based on survey data, combined with fishing effort and an assumption on the selectivity of fishing gears. The results suggested a reduction in fishing impact on cod in the Kattegat approximately by factor 5 since 2007. A similar trend was obtained for the Kattegat cod component in preliminary analyses, when taking into account the spatial distribution of the true Kattegat cod, based on the available genetic data. These analyses should be followed up in future, to elucidate how changes in fishing effort affect the different stocks of cod found in the Kattegat. The analysis of fishing impact on cod in the Kattegat has been updated with the most recent survey and fishery data (Figure 18) and used in March 2019 as data input by the Danish and Swedish authorities for the evaluation of the closed (cod) areas in Kattegat.

An exploratory stock assessment model run with SAM model was made for the Kattegat cod population, where both survey and catch data for the Kattegat area were divided to stocks using the genetic information available. This exercise involved crude assumptions that the proportion of North Sea cod in the Kattegat is the same for all years. The results showed similar trends in spawning stock biomass (SSB) and fishing mortality (F) compared to the previous stock assessment for the area, but with lower estimates of recruitment and SSB.

Development of a modified version of stock assessment model (SAM) was also initiated that would allow to take migration more explicitly into account in the stock assessment model, to be able to separate fishing mortality from migration. The analyses conducted assumed that migration of North Sea cod into the Kattegat takes place during a short period, e.g. as juveniles, and that fishing mortality (F) and natural mortality (M) are the same for the two components within the Kattegat, such that the emigration mortality (I) of North Sea cod back to the North Sea can be estimated. From cod density distributions and maps providing information on stock origin (Figure 19) it is, for each location and time, possible to estimate density of cod and their origin. From this, the number (index) of Kattegat and North Sea cod can be calculated, by integrating over the full Kattegat area. This index can be used to obtain a ratio between the two components, provided that “catchability” is the same for the two components and in subsequent ages.

The analyses demonstrated that it may be possible to account for migration in stock assessment model incorporating proportions of juvenile North Sea and Kattegat cod, and assuming return migration to take place when the fish become mature. An important part of this work was to identify what is needed in terms of data and modelling efforts to move forward with this approach that would enable the uptake of stock mixing information in stock assessment.

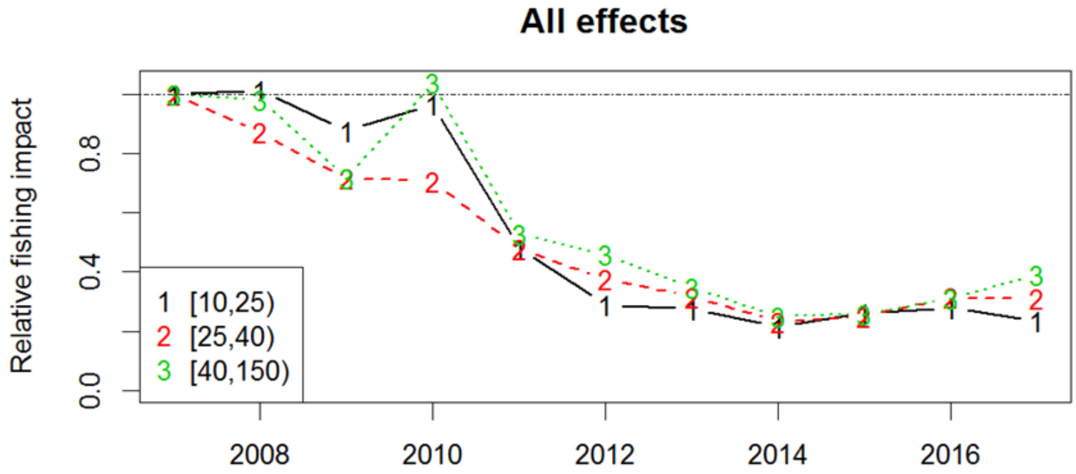

Figure 18. Relative fishing impact by cod size groups.

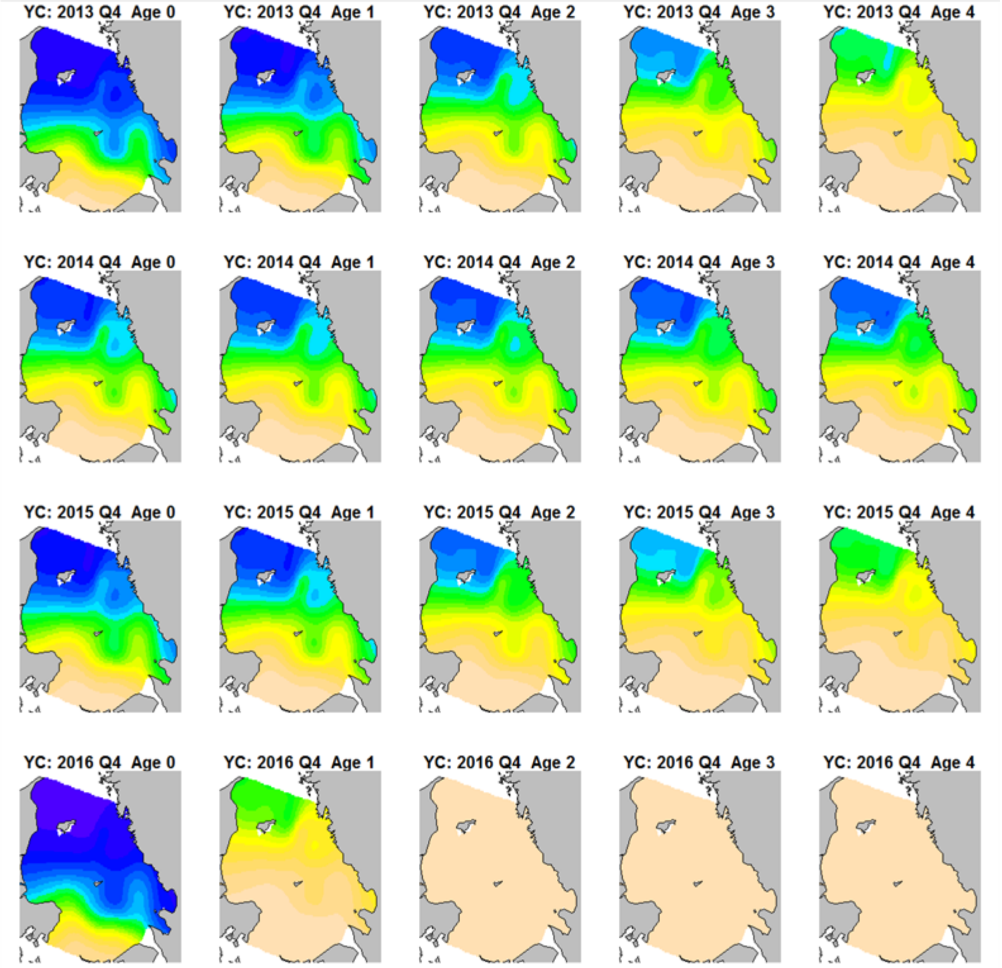

Figure 19. Predicted probability of Kattegat origin by year class (yc) and age. Blue colours indicate low probability of Kattegat cod. YC year class.

3.2.2 Management implications

The results of this project revealed that inflow of cod from the North Sea into the Kattegat and return migration takes place to a significant extent. Thus, the cod caught in fisheries in the Kattegat originates from different populations, which complicates fisheries management in this area. The new information on stock origin allowed a confirmation of the hypothesis that a large part of the estimated unallocated removals is likely caused by migration, i.e. not due to un-allocated fisheries catch, which is important information for fisheries management.

The analyses conducted also indicated similar trends in cod abundance and fishing impact for the entire Kattegat area and when roughly trying to separate out the Kattegat cod population. This suggests that the assessment and management for the Kattegat area is presently adequately reflecting the situation of the Kattegat population as well. However, the present data and knowledge is still insufficient to quantify fishing mortality, which is necessary for full quantitative stock assessment and estimating management reference points. Still, the results of the project enabled us to identify a road map for future work to conclude on the most appropriate approach for dealing with the stock mixing issue in stock assessment and management of cod in this area in the future.

4. Conclusions and outlook

In this project, we have contributed to a better understanding of the dynamics and underlying causes of population mixing of Atlantic cod in the Kattegat. As such, the project has contributed to future sustainable management of cod through the identification of new procedures for data collection and stock assessment, which is able to take migration between neighbouring areas into account.

In order to improve our understanding of the dynamics of inflow of North Sea cod into the Kattegat and outflow of cod from Kattegat into the Skagerrak, it is necessary to extend the time series of the stock separation information. First, this is necessary for a time series of stock specific data, which is needed to be able to conduct a stock specific assessment, including estimates of fishing mortality. Secondly, time series of stock proportions covering different stock sizes of cod in the Skagerrak and Kattegat and potentially different environmental conditions would help to understand how the proportion of North Sea cod within the Kattegat may vary over time. This is important for identifying the most cost-efficient way of dealing with the mixing issue in this area. Further, continued monitoring of the North Sea component in the Kattegat is needed to be able to account for any potential changes in stock proportions in fisheries management in the future. The analyses of stock proportions of juvenile cod are currently ongoing within the EMFF project FORTORSK (J. nr. 33113-B-17-092).

The current project has also raised new questions regarding the connectivity within the transition zone, in particular regarding the separation of the southern parts of Kattegat, Øresund and the western Baltic Sea, where the Kattegat is currently considered as a separate unit for stock assessment and management. In this project, we have developed a very useful approach (microchemistry and genetics) for improving our understanding of population connectivity on local geographical scales. We recommend that future work should focus on a better coverage of spawning groups in the transition zone as well as further development of high powered genomic methodology and refinement of the microchemistry approach to local geographical scales within an environmental gradient with particular focus on separating between endemic Kattegat, Øresund and western Baltic cod stocks. This will allow an integrated understanding of the full system and connectivity from the North Sea to the Baltic Sea.

5. Dissemination of project results

Project results have been disseminated throughout the project period to relevant stakeholders within the scientific community, advisory groups and industry. In addition to contributing to the advisory work in ICES working groups, the project was presented to stakeholders from industry and management at several occasions.

5.1.1 Examples of specific dissemination activities

NSAC meeting on Kattegat cod, January 2016, Charlottenlund (Appendix 1)

Presentation of project results to the Danish Ministry of Environment and Food, January 2017, Copenhagen (Appendix 2)

ICES WKBALT benchmark workshop, February 2017, Copenhagen. (Appendix 3, Appendix 4)

NSAC Skagerrak and Kattegat Working Group meeting, October 2017, Copenhagen (Appendix 5)

DanFish trade exhibition, October 2017, Aalborg (Appendix 6)

“Authenticate” workshop, November 2017, Tórshavn (Appendix 7)

The analytical methodology for analyzing migrations based on otolith microchemistry was presented at the 6th International Otolith Symposium in Keelung, Taiwan on the 16-20 April 2018 (Appendix 8)

Final project meeting, June 2018, Lyngby (Appendix 9, Appendix 10, Appendix 11). Meeting also covered in “Fiskeritidende”, 9. June 2018 (vol. 25).

“Day of the cod” seminar, September 2018, Lyngby (Appendix 12)

Stakeholder meeting, project “MarGen”, December 2018, Tjärnö, Sweden (Appendix 13)

Support acknowledged at building entrance, DTU Aqua, Silkeborg (Appendix 14)

The results of the spawning origin and adult cod migrations will be presented at the 5th International Sclerochronology Conference in Split, Croatia in June 2019.

6. Acknowledgements

We thank colleagues at SLU Aqua for collaboration on sampling, analyses and the interpretation of genetic data.

Danish and Swedish fishermen and representatives from the Danish Fishermen PO are acknowledged for assistance with sample collection and for discussions of project results, for example through participation at some of the outreach activities listed under 5.1.1.

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