MSC certification of plaice fisheries in area IIIa

Basic investigations and development of a management plan

DTU Aqua report no. 302-2015

By Jakob Hemmer-Hansen, Clara Ulrich, Jesper Boje, Asbjørn Christensen, Henrik Degel, Karin Hüssy and Lotte Worsøe Clausen

DTU Aqua
National Institute of Aquatic Resources

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Contents

1 Executive summary

This report describes the main findings from a multi-disciplinary project on population identification and connectivity patterns in European plaice (*Pleuronectes platessa*) carried out at DTU Aqua 2013-2014. We also discuss how the results from this work have contributed to the ICES advisory process and have resulted in changed management practices for the species. The focus area for the project was ICES Division IIIa (Skagerrak-Kattegat), but valuable insights were also attained from neighbouring areas. The main findings for the Skagerrak and Kattegat can be summarised as follows:

Drift modelling: Results showed connectivity patterns between the North Sea and Skagerrak, but with large interannual variability, and that there is a potential for both local recruitment and inflow from the North Sea (German Bight in particular) in the Skagerrak. Eggs and larvae spawned in Kattegat will primarily settle along the Danish and Swedish coast of Kattegat, supporting a hypothesis of local recruitment in this region.

Otolith growth back-calculation: Results showed significant differences in growth between Skagerrak and Kattegat, but not within these areas. Differences in growth between Eastern North Sea and Western Skagerrak do exist, but are weak and could be explained by i) two different stocks with different growth rates but considerable migration across area boundaries, ii) two separate stocks with marginally different growth rates, or iii) a single stock with limited mixing after the first year of life.

Tagging data: There is globally a high residency of fish, with most fish being recaptured in the area where they were released. However, a significant proportion of migrations were observed between the North Sea and the Skagerrak, with fish migrating into Skagerrak during feeding (summer-autumn) and returning into the North Sea during spawning (winter-spring).

Genetic data: New genetic markers were identified, allowing the establishment of new genetic baselines for plaice in the region. These evidenced genetic differentiation between the North Sea and the Baltic Sea. The results showed that populations in the Skagerrak and Kattegat were not very different from each other and that they grouped genetically between the North Sea and Baltic Sea. Results from analyses on individual fish showed that a relatively large proportion of fish collected in the Skagerrak in spawning season had a North Sea genetic profile, indicating population mixing in the area.

Analyses of survey and catch data: The analyses of standard assessment data have implied that the approach agreed by ICES in 2012 was not robust and should not be continued further. IBTS Q1 in Skagerrak cannot be considered a reliable index of abundance of the local population during spawning. It cannot, however, be ascertained whether it is because the survey design is inappropriate for this species at this time of year, or because the population density fluctuates from year to year. Secondly, the analyses have provided a much better understanding of the seasonality in the populations' density, explaining more clearly the likely relationships between North Sea and Skagerrak and providing a key for interpreting the biological studies above, supporting the observations of the distinct population in Skagerrak together with patterns of migration.

Collectively, results from the individual research disciplines confirmed the heterogeneity of plaice stocks from the North Sea to the Baltic Sea. In Division IIIa, our results have confirmed the presence of a unique Skagerrak population, but also that a high level of connectivity exists between the North Sea and the Skagerrak.

These results fed directly into the ICES advisory work, and exploratory stock assessments were used to evaluate alternative options for assessing and managing plaice in the Skagerrak. The final decision was to split area IIIa in two (Subdivisions 20 and 21) and to include the Skagerrak component into the North Sea assessment and the Kattegat component into the assessment for areas 22 and 23 (i.e. defining one plaice stock in SD21-23). For Skagerrak, this decision means that there will be a risk of local depletion of Skagerrak components since the stock assessment will be driven by the far larger North Sea component. It is therefore important that measures are taken to protect local Skagerrak components from over-exploitation. Optimally, the proportions of local Skagerrak plaice in the catches could be monitored by use of genetics, but until methods are fully developed for this purpose, alternative approaches, such as survey monitoring and fisheries information in combination with management measures, could be applied to limit risks of local depletion in the Skagerrak.

We recommend that future work concentrates on i) new genetic assignment of individual fish to the different populations across a broader diversity of locations in time and space, ii) establishment of a combined baseline where individual fish are both genetically assigned and their growth is back-calculated from otolith data in order to quantify the correlation between these two population indicators and iii) a reconsideration of the appropriateness of IBTS sampling design in Skagerrak, together with the needs for other stocks including cod and herring. This information would be valuable for future assessment and monitoring of plaice in the Skagerrak and Kattegat.

In summary, the current project has contributed successfully to improve our understanding of population structuring and connectivity in European plaice, and has consequently been a valuable contribution to improved management procedures for the species in a highly dynamic area between the North Sea and the Baltic Sea. The study has also shown that a multi-disciplinary approach is very efficient for addressing fisheries management issues, and we recommend that similar approaches are applied in future work in this and other species.

2 Background to the project

A reliable stock assessment and a sound management plan, outlining management procedures, are fundamental requirements for MSC certification of marine fisheries[1]. European plaice (*Pleuronectes platessa*) has traditionally been managed as separate units in the North Sea and Baltic Sea (Figure 1). However, issues and uncertainties around the plaice stock structure in the transition area between the North Sea and the Baltic Sea have been long standing. The area IIIa, i.e. Skagerrak (ICES area IIIaN) and Kattegat (ICES area IIIaS) is not large compared to the neighbouring seas, but it offers such a great variability in hydrographical conditions (temperature, salinity, depth, sediment, stream etc.) that the population structure of many marine species inhabiting this area is particularly complex.

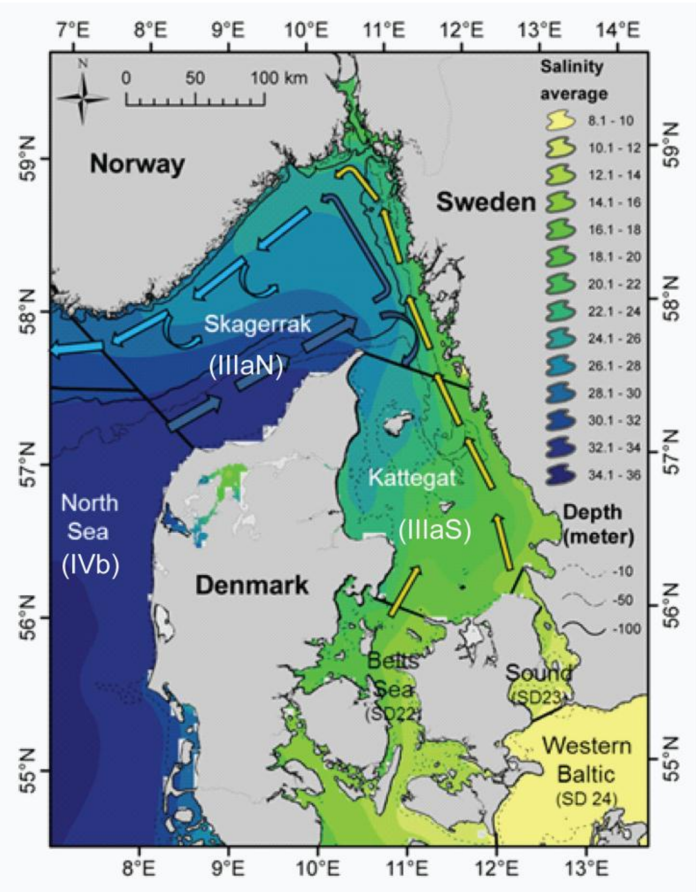

Figure 1. Hydrographical map of the area with average surface salinity, depth and currents (yellow: Baltic current, dark blue: north Jutland current, azure: Skagerrak costal current). Salinity data from DHI. Currents redrawn from Danielssen et al. (1997). The black straight lines delimitate the management areas (from Ulrich *et al.* 2013). ICES areas are shown in brackets.

Until 2002, a unique plaice stock was defined over the entire area IIIa in a standard analytical way. In 2003, the assessment was considered to be too unreliable to form the basis of advice,

[1] MSC Fishery Standard: Principles & Criteria and Criteria for Sustainable Fishing, 1 May 2010

and no catch forecast was presented[2]. The various data entering the assessment have been scrutinized over the years afterwards, but no major flaws in the raw data were observed. Much effort was then dedicated to investigate the appropriateness of the established stock identity and understand the possible origins and dynamics of the various plaice populations, based on comprehensive literature review and analysis of available data (ICES 2012; Ulrich *et al.* 2013). This work concluded that plaice in Skagerrak and Kattegat were likely not belonging to the same stock units, and should therefore be assessed separately. Focusing more particularly on the linkages between the North Sea and ICES Division IIIa, new hypotheses on plaice stock structure were formulated as follows (from Ulrich *et al.* 2013): "*In summary, catches in the Western Skagerrak are therefore expected to be a mix of: i) adult North Sea plaice whose distribution extends beyond the North Sea boundary; ii) juvenile North Sea plaice that hatched in area IIIa and return to the North Sea to spawn; iii) local populations spawning along the Danish coast. In the area further East towards the Swedish coast and Northern Kattegat, fish densities have dropped to historically low levels and catches are low. This area doesn't seem to benefit from North Sea adults migrating into the Kattegat. Therefore, catches in this area may be mostly constituted of categories ii) and iii) above. Finally, catches in the Kattegat (South from Læsø) and in the Belt Sea may mostly be constituted of local populations, although some North Sea juveniles (category ii) may still have settled in these more southerly areas*."

ICES (ICES 2012) also formulated hypotheses on the stock structure in the Baltic, suggesting that the plaice populations in the Sound (SD 23) and the Belts (SD 22) were likely linked to the Kattegat, but that the stock structure in the Western and Eastern Baltic (mainly SDs 24 and 25) and the linkages with SD21-23 were more uncertain. On the basis of this work, separate assessment and advice have been conducted for plaice in Kattegat, the Belts and the Sound (SD 21-23) and plaice in the Baltic (SD 24-32). Assessment of plaice in Kattegat, the Belts and the Sound (SD 21-23) has been performed by the ICES WGBFAS group since 2013 using the estimates of spawning stock biomass (SSB) and F from an analytical assessment in a Data Limited Stock approach (DLS, category 2 – trends-only analytical assessment). For plaice in SD 24-32 a DLS category 3 approach (survey trend only) was performed based on survey information only as no analytical assessment was possible.

In the Skagerrak, plaice has been evaluated by ICES WGNSSK on the basis of DLS category 3 using IBTS survey data (ICES 2014a). An effort was done in 2012 to clarify the appellation of the various sub-areas in this transition zone, as it was realised that what was commonly referred to as "Skagerrak East" and "Skagerrak West" had different meanings in Denmark and Sweden. The area SD IIIa was thus divided into different sub-areas (Figure 2), representing the putative areas where the various sub-populations were assumed to be distributed as summarised above. These areas are used in the present report.

[2] http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2003/oct/ple-kask.pdf

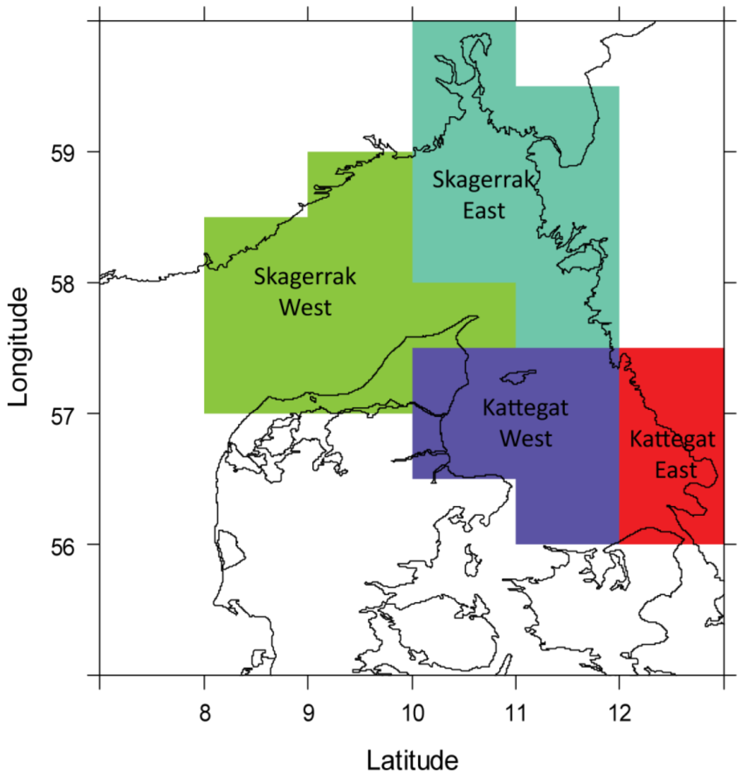

Figure 2. Areas defined within ICES division IIIa. From ICES (2012).

At the same time, the North Sea Regional Advisory Council (NSAC) worked towards the development of a tentative management plan for plaice in Skagerrak indexed on the management plan for the North Sea, in order to support MSC accreditation for plaice fisheries[3] (Table 1). This was used by EU and Norway as the basis for setting the 2014 TAC in Skagerrak (ICES 2014a).

[3] http://www.nsrac.org/reports/meetings-c/skag-plaice/skagerrak-and-kattegat-working-group-16th-april-2013-copenhagen/

Table 1. The Plaice Skagerrak Harvest Control Rule, as suggested by the NSAC in 2013

SKA TAC		WEST SKA SURVEY INDEX TREND		
		RISING	NO TREND	FALLING
NS SSB TREND	RISING	FIXED %	FIXED %	REVIEW HCR and ask ICES to advice interim TAC
	NO TREND	FIXED %	FIXED %	FIXED %
	FALLING	REVIEW HCR and ask ICES to advice interim TAC	FIXED %	FIXED %

The work summarized above evidenced however that the information available was fairly scarce and often not up to date, and that many uncertainties remained. The alternative hypotheses on stock structure could only be formulated qualitatively, and could not be verified. This absence of clear conclusions prevented further steps to be taken towards improved assessment and management, and it was evident that new data was necessary to progress on the biological understanding of the population structure. Funding was sought from the Danish EFF (European Fisheries Fund), and a new project was launched in January 2013, aiming at collecting and collating new information from different sources (otoliths, genetics, hydrodynamic modelling and tagging). The project had three objectives: 1) characterize population structuring in area IIIa and neighbouring areas, 2) Describe population dynamics (early life stage drift, adult migration and growth characteristics) of plaice from different areas and 3) Provide the basis for and suggest possible management plans for plaice fisheries in area IIIa.

The project ran until 31th December 2014, and the results were presented and used in the ICES Plaice Data Compilation Workshop in December 2014 and Benchmark Workshop on plaice (WKPLE) in February 2015. This report summarises the scientific outcomes of the project, and the management actions that have followed the project.

3 Project structure

In this project, we have applied a multi-disciplinary approach to identify stock structure and – dynamics of plaice in area IIIa. However, although ICES area IIIa was the main focus area for the project, valuable insights were also obtained from neighbouring areas (see below).

We have applied oceanographic modelling of early life stages to investigate connectivity between spawning and nursery areas, used growth characteristics determined from otolith growth patterns to identify differences between geographic areas, collated and analysed tagging data from the 1900s to the 1960s to investigate migratory patterns, used genetic markers to identify genetically independent populations as well as individual fish and analysed survey and fisheries data to assess their relevance as an abundance index for plaice. By synthesising information across results obtained from these different approaches, it was possible to get a more complete picture of population connectivity and – dynamics for all life stages of plaice.

The work in the project was divided into four work packages (Figure 3). In WP1, samples of otoliths (for growth estimation) and tissue (for genetic analyses) were collected from research programmes at DTU Aqua. In WP2, we used genetic markers and otolith growth characteristics to identify independent biological populations in area IIIa and neighbouring areas. In WP3, we focused on patterns of connectivity between these areas by using information from otoliths, genetics, drift modelling and tagging. Furthermore, analyses of survey and fisheries data provided other insights on our ability to monitor the various populations and assess the origin of catches. Finally, results were synthesized to provide the basis for the development of management recommendations and a management model in WP4. In the following section (section 4), we summarize results from each of the research areas in the project before synthesizing across all findings.

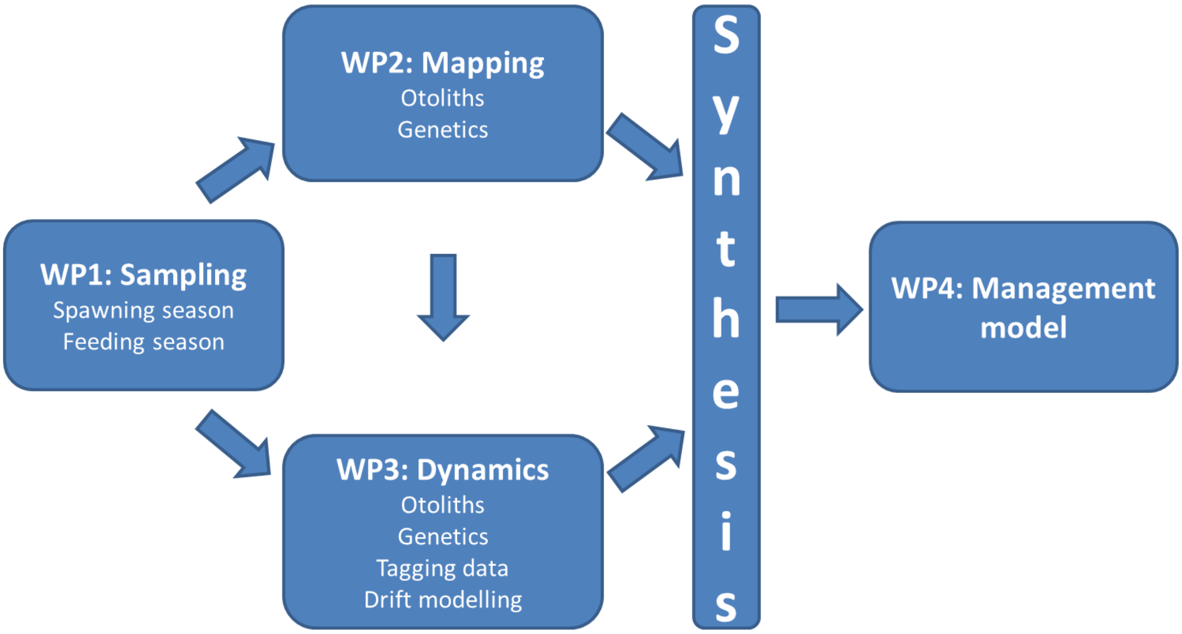

Figure 3. Project structure. The work in the project was structured into four work packages, and also included a synthesis of findings from the different research areas as a basis for providing management recommendations towards the end of the project.

Danish fishermen, represented by Danish Fishermen's Association, have participated at both external and internal meetings where project progress and results have been presented. These meetings included a NSAC plaice focus group meeting in April 2013, where project outline and aims were presented, and an internal synthesis meeting at DTU Aqua towards the end of the project in 2014, where project results were presented and management implications discussed. Results have also contributed directly to the ICES advisory work at the plaice data collection and benchmark meetings in 2014 and 2015. Finally, a scientific symposium entitled "Accounting for sub-stocks in stock assessment and management: challenges and opportunities" was held at DTU Aqua in April 2015. The theme of the symposium was based directly on the experiences gained through the present and similar EFF projects on other stocks, carried out over the last few years.

4 Results of biological studies (WP2 and WP3)

The original division of the identification of unique populations and the study of interactions and connectivity between these populations into two separate work packages (WP2 and WP3, see above) proved somewhat arbitrary as results accumulated during the project, because most research disciplines contributed information to improve our understanding of both topics. Consequently, we will provide integrated insights on both topics from the various research disciplines in the following section.

4.1. Hydrodynamic transport of eggs and larvae

4.1.1 Background and Methods

As part of the multi-disciplinary investigation of the spatial ecology of plaice in Kattegat/Skagerrak we conducted hydrodynamic “in silico” (simulated) drift experiments of pelagic early life-stages of plaice. To extend the study of Hufnagl *et al.* (2013), who focused on the North Sea, to Kattegat/Skagerrak, we applied a rather similar setting, with minor refinements reflecting available biological knowledge. The drift experiments were setup in the modular IBMlib framework, and the underlying coupled physical-biologeochemical 3D model was the operational HBM-ERGOM model operated by The Danish Meteorological Institute (DMI) at 10 km horizontal resolution and up to 77 vertical z-layers.

The biological model is summarized below:

Dynamic particle equations: Integrated forward using standard algorithms, including stochastic dispersal effects reflecting subscale turbulence. The results below are based on medium resolution runs with 1 representative egg/larvae per km^2, or 100000 representative eggs/larvae in total. This means that rare recruitment events are not resolved, but the overall transport patterns should emerge from this resolution level.

Ontogeny: Parameterised following Bolle *et al.* (2000) and Hufnagl *et al.* (2013), with dynamic stage durations, depending on ambient temperature.

Behaviour and mortality: Larvae were assumed to die if they did not encounter a suitable settlement habitat in the demersal period. Other parameters are summarized in Table 2.

Table 2. Behaviour and mortality parameters included in the IBM.

	Horizontal	Vertical	Mortality (1/year) (Wennhage, 1999)
Pelagic egg	Passive	Positively buoyant corresponding to Stokes drift at ρ = 1020 kg/m3	33.4
Pelagic larvae	Passive	Passive	16.5
Demersal larvae	Passive, settles if habitat is OK	Seeks toward bottom with an average velocity of 4 mm/s.	5.86

Subscale dispersal: Horizontal diffusivity: following Hufnagl *et al.* (2013) we apply daily mean values of 100 m2·s−1 (Gurney *et al.* 2001). As data does not contain dynamic vertical diffusivity we apply a typical value 0.01 m2/s (Stewart 2009).

Spawning period: Literature indicates "late February and early March" (Nielsen *et al.* 2004) even though other timings are encountered. We apply March 1 as spawning peak and explore variations to this as part of the uncertainty test suite.

Spawning habitats: Potential spawning areas in Kattegat/Skagerrak are as indicated in Cardinale *et al.* (2011), subject to the requirement that depth is 10-40 m in at least 50 % of the habitat cell. Additionally, Jammer Bay (the shallow area in Western Skagerrak where most fisheries occur) was included, following Cardinale *et al.* (2011) again subject to the requirement that depth is 10-40 m. To extend the conclusions of Hufnagl *et al.* (2013) we also considered larvae advected into Kattegat/Skagerrak from spawning areas at Dogger Bank and the German Bight. Spawning areas coloured by major region are shown in Figure 4a.

Settlement habitats: These are generated as fractional cells of the underlying hydrodynamic grid. We apply the biological condition that substratum should be soft and at 0-10m depth; we scanned each coastal hydrodynamic grid cell using high resolution substratum (GEUS 1999) and topography (IOWtopo2, rev.03) data sets to determine the fraction appropriate for settlement; this cell fraction was associated with a rectangle along the hydrodynamic grid coast line. In this way, settlement habitat volumes are locally consistent with subscale high resolution (<10 km) substratum and topography data. Resulting settlement habitats are shown in Figure 4b.

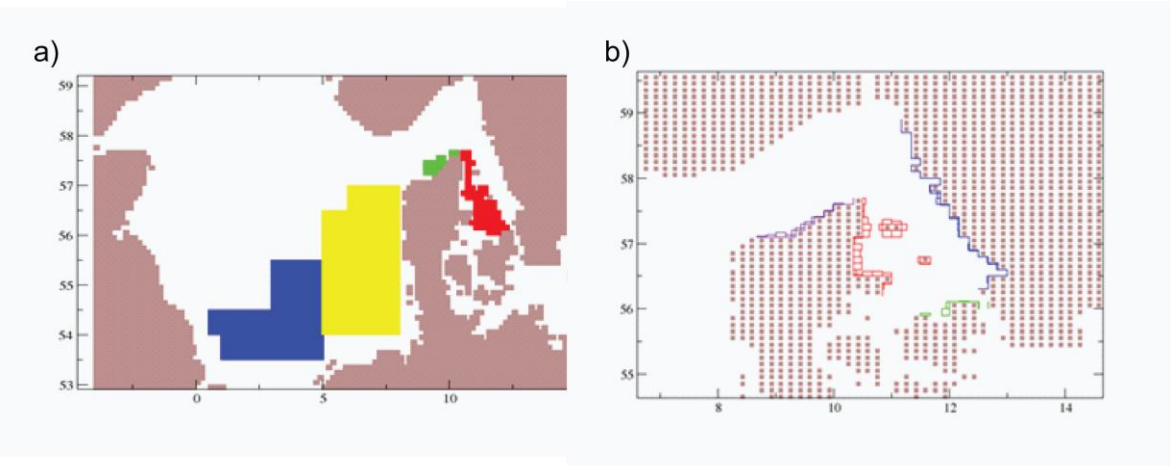

Figure 4. Spawning areas in the model setup, projected onto 10x10 km grid cells coloured according to regional association (a; blue: Dogger Bank, yellow: German Bight, green: Skagerrak, red: Kattegat), and coastal settlement habitats coloured according to regional association (b; purple=Jammer Bay, red=Jutland, blue=Swedish coast, green=Zealand). Coastal settlement habitats are rectangles thinner than the underlying coastal grid cells, reflecting local habitat suitability.

4.1.2 Results and Discussion

The core result computed from in silico drift experiments is the transport probability from spawning to settlement areas. When gridding spawning to settlement areas, as in Figure 4, the transport probability becomes a matrix Tij, where i is the settlement site index and j is the spawning site index. To illustrate this, we chose the year 2013. When Tij is summed over i, we get the probability of settling Tj, given that one is spawned in area j. This is plotted in Figure 5a. Notice that the figure only includes settling habitats included in Figure 4b. Larvae from Dogger/German Bight will typically recruit to other areas than those shown in Figure 4b. Therefore, these larvae will have a larger overall survival chance if *all* potential settling habitats (also outside Kattegat/Skagerrak) are included. Conversely, if Tij is summed over j, we get the influx to sites i, given that spawning is homogeneous over spawning areas; this is a kind of sink index, from a population dynamics perspective, and is shown in Figure 5b for 2013.

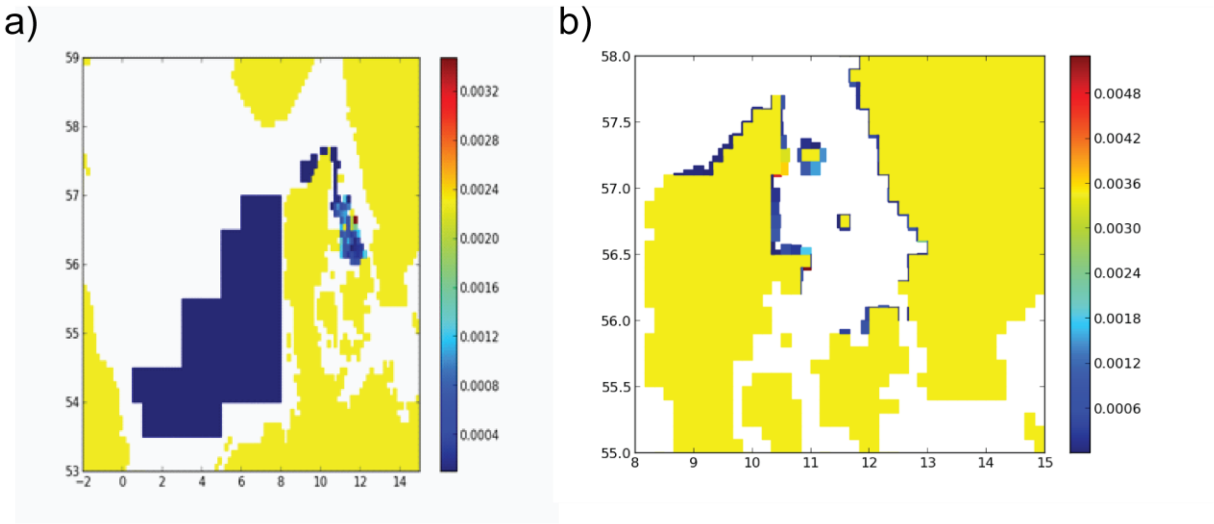

Figure 5. Relative survival probability colour plotted by spawning area for 2013 (a) and sink index colour plotted by settlement area for 2013 (b).

Figure 6a shows the final position of larvae spawned from Dogger and German Bight. This includes both successful larvae that settle (in coastal areas) and unsuccessful larvae that expire the demersal larval period (and die by assumption), and Figure 6b shows the source contributions to different nurseries in 2013. We see that Kattegat spawning grounds almost exclusively supply local nursing areas; a small part of the recruitment in the Jammer Bay originates from German Bight spawning, as also observed by Hufnagl *et al.*, (2013). Interestingly, locally spawned larvae in the Jammer Bay are retained in the Skagerrak/Kattegat system in this year. The underlying assumption in this plot is that spawning intensity per unit area is the same for all spawning locations. However, if the spawning intensity is higher in some areas (which is likely the case in the North Sea), this may still impact population dynamics in Kattegat/Skagerrak, because the recruitment contribution is the product of transport probability and spawning intensity.

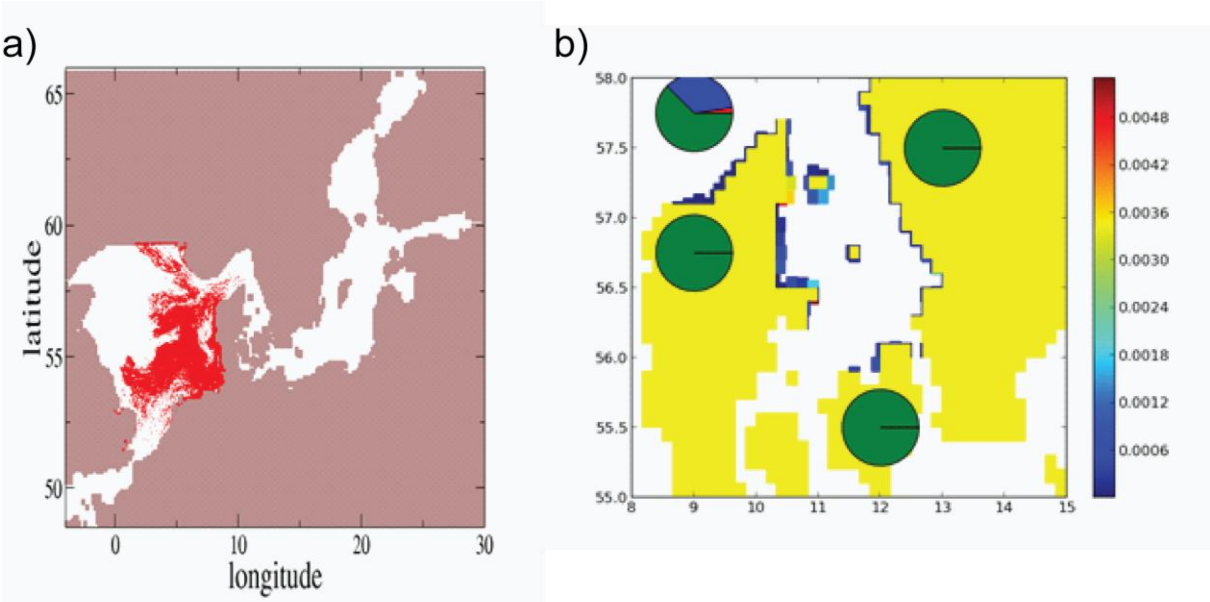

Figure 6. Final position of successful and unsuccessful settlers spawned from Dogger and German Bight with a relatively low influx to Kattegat/Skagerrak in 2013 (a), and source contributions to settlement in different areas in 2013 (b). In Each pie in (b), green indicates propagules originating from Kattegat, red from the German Bight and blue from the Skagerrak area in Figure 4a.

Table 3 shows the transport probabilities from different spawning areas in three different years, including all spawning and nursery areas in Figure 4. These results show that there is a large variability in drift patterns between years. In these three simulated years, eggs and larvae from North Sea Dogger Bank do likely not drift into Skagerrak and beyond. The inflow from North Sea German Bight is very variable from year to year, but it is likely that some North Sea juveniles can settle along the Skagerrak and Kattegat coast line. The drifting patterns of eggs and larvae spawned in Skagerrak are similar to those of German Bight. Finally, those spawned in Kattegat will primarily stay within Kattegat and settled along the Danish and Swedish coasts.

Table 3. Probability (P*10^6) for an egg spawned in source region (in column) to settle in destination region, for 3 different years.

Destination\source	German Bight	Skagerrak	Kattegat	Dogger Bank
1994				
Jammerbugt	0.755	2.652	7.578	0
Jutland	34.203	154.183	263.022	0
Sweden	178.484	671.547	343.167	
Zealand	7.780	41.154	11.968	
2012				
Jammerbugt	8.184	141.698	32.602	0
Jutland	0.172	17.038	1052.508	0
Sweden	0.018	1.564	141.705	0
Zealand	0	0	22.068	0
2013				
Jammerbugt	0.164	2.484	4.404	0
Jutland	0	0	450.545	0
Sweden	0	0	147.399	0
Zealand	0	0	29.280	0

Focusing on the Skagerrak area, Figure 7 illustrates the strong interannual variability in connectivity patterns between spawning areas and nurseries for the period 1994-2013. It is evident that there is a potential for both local recruitment and inflow of eggs and larvae from the North Sea. However, connectivity is far from static, but may vary by orders of magnitude. This is a strong example of the match-mismatch dynamics (Cushing 1969) in the current systems. Even though these types of calculations are associated with uncertainty in the biological parameterization, they herald the variability envelope that can be expected in nature.

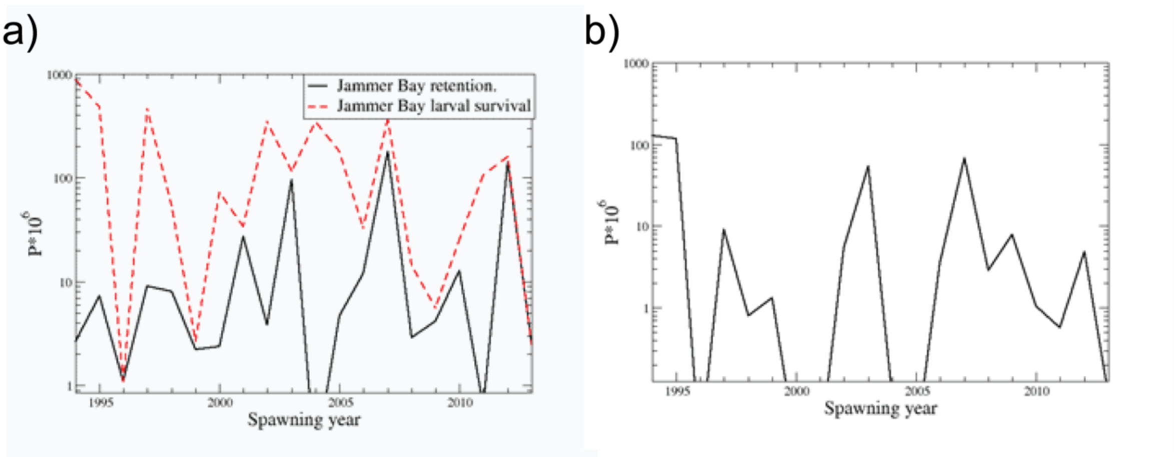

Figure 7. Time series of recruitment variability. Jammer Bay retention probability and Jammer Bay spawning success probability in a) and North Sea (Dogger, German Bight) influx probability to Kattegat/Skagerrak nurseries in b).

Figure 8 illustrates travel length statistics for different nurseries. Recruits to the Swedish coast (Figure 8b) have clearly on average travelled longer than recruits along the east Jutland coasts (Figure 8a). The biological implication is probably that Swedish recruits are more exposed to mortality variability than recruits on the Danish side.

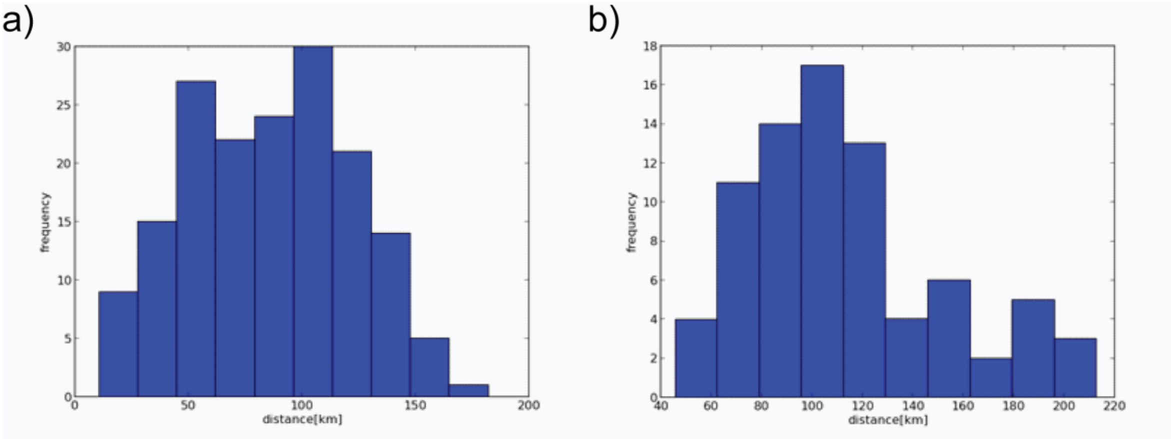

Figure 8. Travel length statistics for settlers at Jutland (a) and Sweden (b) in 2013.

4.1.3 Conclusions

In summary, results showed connectivity patterns between the North Sea and Skagerrak, but with large interannual variability, and that there is a potential for both local recruitment and inflow from the North Sea (German Bight in particular) in the Skagerrak. Eggs and larvae spawned in Kattegat will primarily settle along the Danish and Swedish coasts of Kattegat, supporting a hypothesis of local recruitment in this region.

4.2 Growth characteristics

4.2.1 Background and Methods

Growth of fish depends on endogenous (i.e. size, physiology, reproductive state, genotype etc.) and exogenous factors (i.e. physical and chemical environment and food availability). Growth is known to differ between areas, and is therefore a robust measure for identifying areas with limited mixing between neighbouring populations or stocks. Traditional size-at-age data fall short of providing unbiased growth estimates owing to size selectivity of the gear used and fishing pressure, amongst other factors. Instead, we used the growth chronologies recorded in the otoliths of each individual fish. While two genetically distinct populations may experience similar growth rates leading to inconclusive results with respect to the degree of separation, differences in growth rates between genetically distinct populations suggest that only a limited degree of mixing between the two areas occurs.

Growth rates for each individual fish, from hatch to capture, can be estimated from the fish's otoliths. Otoliths are found in the inner ear of the fish and consist of calcium carbonate, protein and trace elements which are deposited on the otoliths surface forming visually identifiable patterns as a response to seasonal variations in environmental temperature, food availability and metabolic processes responding to these, much like the annual rings in trees. The width of an annual growth zone in the otolith reflects the fish's somatic growth. The otoliths are thus naturally occurring bio-loggers and provide a tool to estimate the fish's age and somatic growth throughout its life.

Otoliths from three sampling years (2002, 2005 and 2008, predominantly Q1 and Q2) representative of different periods in plaice stock size, were selected (n = 841, 896 and 991 for the three years respectively, covering 15 year classes). An overview of the samples used by year and area is given in Table 4. The age range was tabulated to individuals >2 and <8 years in order to analyse mature individuals only, cover the age classes caught in the fishery and avoid results heavily influenced by a few old individuals. Samples were spread evenly between statistical rectangles within the ICES subdivisions 25, 24, 22, 21, 20 and 4B. While the Baltic Sea focus area was exclusively examined based on these areas, the North Sea/Skagerrak/Kattegat focus area was analysed by areas defined in Figure 2 (Skagerrak E, Skagerrak W, Kattegat E and Kattegat W).

Table 4. Overview over otolith samples used in this study

		Years		
Area	2002	2005	2008	Total
4B		84	273	357
Skagerrak W	104	50	346	500
Skagerrak E		50		50
Kattegat W	50	199	52	251
Kattegat E	277			277
22	71	194	123	388
24	151	203	100	454
25	903	899	993	2795

Otolith images were digitised under standardised light and image capture settings. Otolith growth within each year of an individual's life was measured (Figure 9), where the transition from transparent (dark) zone to opaque (white) zone corresponds to the end of winter. Fish size at previous age was back-calculated based on these measurements using the scale-proportional approach (Campana 1990), resulting in a growth curve for each individual fish from hatch to capture.

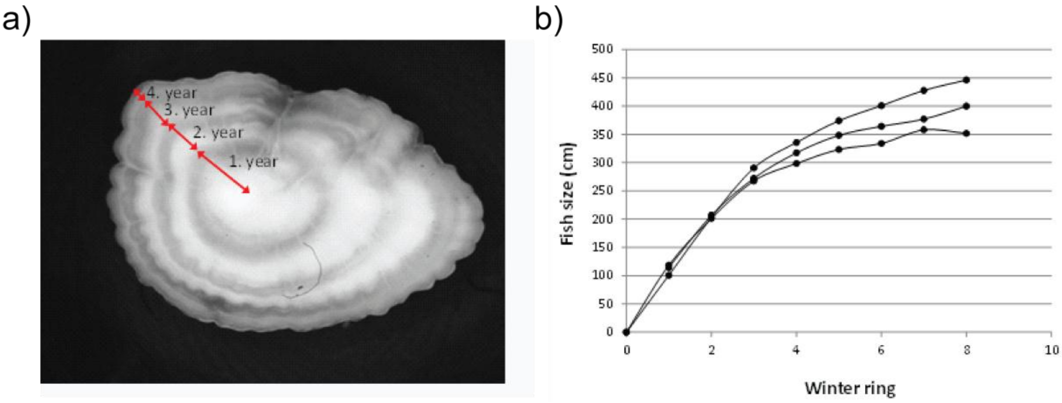

Figure 9. Image of plaice otolith showing how growth was measured (a) and examples of resulting growth curves for three fish (b).

The growth curves were analysed using Linear Mixed Effects Models (LMEM) with log(winter ring) and sampling area as fixed effects and individual fish nested within cohort as random effects. The following sub models representing different scenarios of area effects on intercept and slope were compared using ANOVA:

(1) SL = log(winter ring) + (log(winter ring) | year class /fish)
(2) SL = area + log(winter ring) + (log(winter ring) | year class /fish)
(3) SL = area*log(winter ring) + (log(winter ring) | year class /fish)
(4) SL = area + area*log(winter ring) + (log(winter ring) | year class /fish)

The interpretation of these models is:

- Model (1) A setup where there is no area effect at all
- Model (2) There is an area effect on the intercept but not on the slope, indicating that individuals have a different origin but similar growth rates throughout the rest of their lives.
- Model (3) There is an area effect on the slope but not the intercept, indicating that the individuals have had a similar size during their first year of life, but have experienced different growth rates throughout the rest of their lives.
- Model (4) There is an area effect on both intercept and slope, indicative of spatio-temporal separation of the analysed groups of fish.

The least complex model with the lowest Akaike Information Criterion (AIC) was selected as the model describing the growth patterns most adequately. Post-hoc comparisons of significant area effects were analysed using Tukey Contrasts for multiple comparisons using α=0.05 as significance level. It should be noted that Model (1) and (2) do not allow conclusions on whether individuals from different areas mix or not, as they may be separate in space and time but experience the same growth rates. Differences in intercepts of the LMEM between areas suggest different recruitment mechanisms and size at settling, while differences in slope indicate a general difference in growth rate between areas.

In the following results it is important to note that the graphical representation of the growth curves is somewhat misleading as the low sample sizes in the older age classes are visually represented on equal terms as the younger age classes with high sample sizes. The statistical analyses on the other hand are exclusively driven by the younger age classes. Conclusions are based on the statistical tests, not the graphs.

4.2.2 Results and Discussion

4.2.2.1 Focus on Eastern/Western Baltic Sea (ICES SDs 22, 24 and 25)

The model that explained most of the variability in growth patterns was model (4), indicating significant area effects on both intercept and slope between the analysed areas. The average growth curves are shown in Figure 10a (Note: No sex available for SDs 22-25 samples). Post-hoc pairwise comparison between neighbouring areas showed that no significant differences were found between SDs 24 and 25. However, growth patterns differ significantly between SDs 22 and 24. Growth in SD 22 is over the entire age range much lower than in the other areas. In all cases, area effects had significant impact on both intercept and slope of the LMEM. Model fits and pairwise comparison between areas are shown in Tables 5 and 7. While it is not possible to conclude whether SDs 24 and 25 consist of genetically distinct populations or just have similar growth rates owing to the prevailing environmental conditions, the observed differences in growth between SD 24/25 and 22 suggest that substantial mixing of plaice does not occur between these areas.

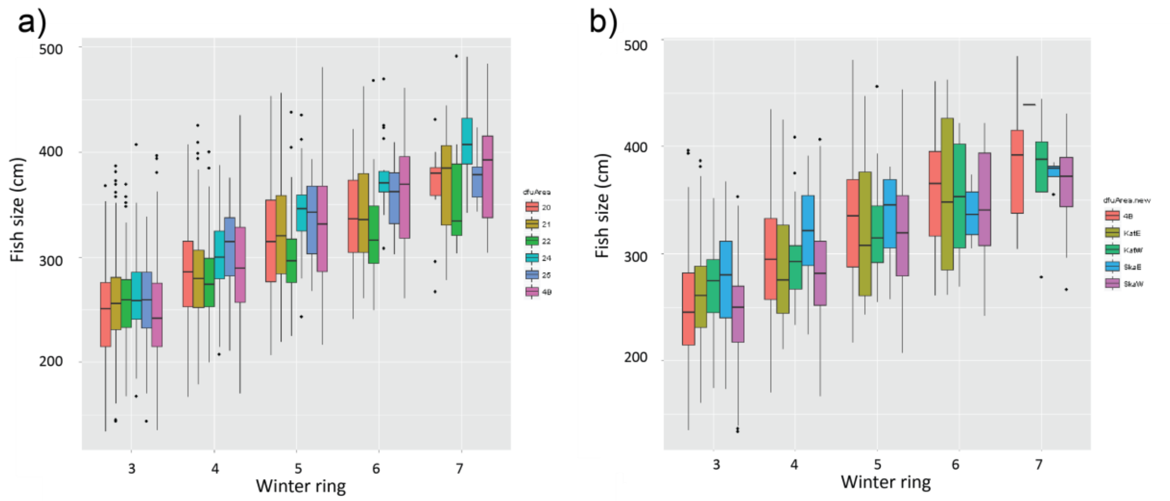

Figure 10. Boxplot of fish size (cm) in relation to age. Horizontal bars = mean distance, upper and lower boundaries of each box = interquartile range, whiskers = 95% range of values and individual dots = 5% outliers. Colours represent different areas, Based on ICES SD's (a) and on Figure 2 areas (b), see also Figure 2.

Table 5. Results of the pairwise comparison between ICES areas. Bold numbers represent geographically adjacent areas (see also Figure 1). Statistically different areas are marked with an asterisk.

	20	21	22	24	25
4B	**0.005** *	< 0.001	< 0.001	< 0.001	< 0.001
20		**< 0.001** *	< 0.001	0.617	0.900
21			**1.000**	< 0.001	< 0.001
22				**< 0.001** *	< 0.001
24					**0.998**

Table 6. Results of the pairwise comparison between areas in Figure 2. Bold numbers represent geographically adjacent areas. Statistically different areas are marked with an asterisk.

	Skagerrak W	Skagerrak E	Kattegat W	Kattegat E
4B	**0.041** *	0.274	< 0.001	< 0.001
Skagerrak W		**0.978**	< 0.001	< 0.001
Skagerrak E			**0.001** *	0.129
Kattegat W				**0.565**

4.2.2.2 Focus on North Sea/Skagerrak and Kattegat (areas defined in Figure 2)

These analyses were based on females only, but the general trends are also observed in males. The model that explained most of the variability in growth patterns was model (4), indicating significant area effects on both intercept and slope of the LMEM between the analysed areas. The average growth curves are shown in Figure 10b. Post-hoc pairwise comparison between neighbouring areas found significant differences in growth between areas 4B and Skagerrak W as well as Skagerrak E and Kattegat W. But no significant differences were found between the eastern and western areas within Kattegat and Skagerrak respectively. Model fits and pairwise comparison between areas are shown in Tables 6 and 7. Growth in 4B was consistently higher than in Skagerrak and Kattegat. These results suggest that there is limited mixing between the North Sea, Skagerrak and Kattegat. However, there is only a marginal statistical difference in growth between 4B and Skagerrak W ($p = 0.041$), a difference that is exclusively attributable to differences in the slope of the LMEM. This raises the question of whether these results are indicative of i) two different stocks with different growth rates but considerable migration across area boundaries, ii) two separate stocks with marginally different growth rates, or iii) a single stock with limited mixing after the first year of life.

Table 7. Details of the LMEM results of area effects on the intercept and slope of the fish size on log(winter ring) relationship.

Area units	Area	Intercept	Slope	df	t values
ICES areas	4B	-6.813 ***	145.978 ***	2707	-3.547 / 61.579
	20	101.345 ***	140.091 ***	2707	25.813 / 62.970
	21	18.622 ***	134.028 ***	2707	25.813 / 60.301
	22	18.376 ***	127.423 ***	2707	9.526 / 51.521
	24	2.915 ns	144.977 ***	2707	1.569 / 58.396
	25	2.145 ns	148.978 ***	2707	1.053 / 57.481
Figure 2 areas	Skagerrak W	17.721 **	183.375 ***	941	2.757 / 44.097
	Skagerrak E	24.934 ns	208.014 ***	941	1.945 / 24.087
	Kattegat W	79.122 ***	143.036 ***	941	8.200 / 0.906
	Kattegat E	60.133 ***	173.248 ***	941	5.532 / 23.496
	4B	17.034 ns	196.325 ***	941	1.624 / 45.953

*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ns = $p \geq 0.05$. t values shown as for: intercept / slope

4.2.3 Conclusions

These results suggest that plaice throughout the study area are relatively sedentary, in that significant differences in growth patterns were detected between adjacent areas. In both focus areas, the present results suggest the occurrence of distinct groups. But whether these groups are genetically distinct populations or geographically separated stock components as a result of limited migration cannot be resolved with these analyses. Within the Baltic Sea, there are at least two different populations/stocks: one in SD 24-25, the other in SD 22. In the North Sea/Skagerrak/Kattegat the present results suggest the occurrence of two main plaice stocks with a distinct Kattegat stock and mixing occurring between 4B and the Skagerrak.

4.3 Adult migration

4.3.1 Background and Methods

In order to improve knowledge on migrations and population affiliations, we have compiled and analysed historical data from plaice tagging experiments conducted since the beginning of 1900. The analyses were focussing on migration and stock structure of plaice in the North Sea, Danish waters and the Baltic Sea, especially in relation to the existing management areas in order to evaluate their justification.

Data on Danish tag releases from the North Sea, Skagerrak, Kattegat, the Belt Sea and the western Baltic in the period 1903-1964 were analysed. The total number of releases amounted to approx. 40000 tags, with the majority tagged in the North Sea and the Belt Sea. The tagging started in 1903-4 in Kattegat, Skagerrak and the North Sea, while the Belt Sea taggings was initiated in 1922. Releases were performed in all seasons but mainly concentrated in March-May and September-November. Plaice were caught in several ways for the purpose of tagging, mostly by semi-scientific or exploratory fishery using a variety of gears. Likewise, several tag types were used, mainly Petersen discs (fixed tag) and Carlin tags (dangling tag).

A precise recapture site or a geographic position was not provided with all recaptures, but often a location name was recorded. These locations were used to calculate approximate positions. Some locations are unknown and recaptures were therefore not included in the detailed analyses. For the analyses of migration between areas, recaptures were calibrated with nominal landings as a proxy for fishing effort, as measures of fishing effort were not available for the time series. The resolution of landing data for calibration is by year and ICES divisions for the years 1903–1971.

4.3.2 Results and Discussion

A total of approximately 12000 recaptures were recorded from the 40000 tagged specimens (Table 8 and Figure 11). Although a comprehensive material, the data is highly unbalanced with respect to tagging year, area, season, tag type and numbers released.

Table 8. Taggings by main area.

Release area	Period	Number tagged
Belt Seas and Baltic	1922-1963	13604
Kattegat	1904-1964	3494
Skagerrak	1903-1941	1899
North Sea	1903-1961	20895

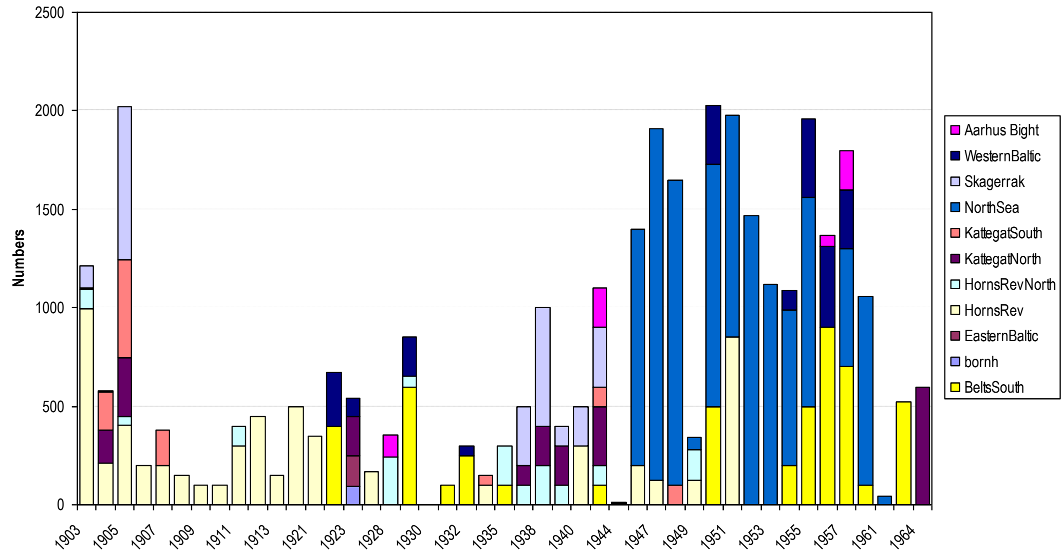

Figure 11. Number of tagged plaice by location 1903-1964.

Using the management areas as suggested by the ICES benchmark group (ICES 2012 and Figure 2), the far majority of all recaptures are taken within the tagging area (Table 9). All main areas except the Eastern Skagerrak have a high residency of recaptures of about 87-99%. Among the releases in the North Sea, 96% of recaptures were resident within the North Sea while the remaining 4% were recaptured in the westernmost Skagerrak. Within Skagerrak, releases in the western part revealed 87% residence and a substantial part (11%) migrated to the North Sea, while only 2% migrated in opposite direction into the Kattegat and the Belts (21-23). Few fish were recaptured from taggings in East Skagerrak, and results from this area should be interpreted with caution. Here, no residency was observed and all recaptures found in adjacent areas. The remaining areas, Kattegat and the Belts (21-23) and the Baltic (24-25) both exhibits high residency with only a few percent of recaptures outside the areas.

Table 9. Distribution of recaptures in relation to release areas.

	Release management area				
Recapture management area	Ivabc	Skagerrak W	Skagerrak E	21-23	24-25
Ivabc	**96**	**11**	0	0	0
Skagerrak W	**4**	**87**	39	1	0
Skagerrak E	0	0	**0**	0	0
21-23	0	2	61	**98**	1
24-25	0	0	0	1	**99**

The predominant migrations are illustrated in Figures 12 and 13. Figure 12 illustrates the overall distribution of recaptures considering the release area and Figure 13 illustrates the direction of the migrations. All migrations are categorized as either being in the direction towards North Sea, the Baltic or as being resident. Skagerrak appears associated with the North Sea and vice versa while the remaining areas, the Belts and the Baltic seem resident.

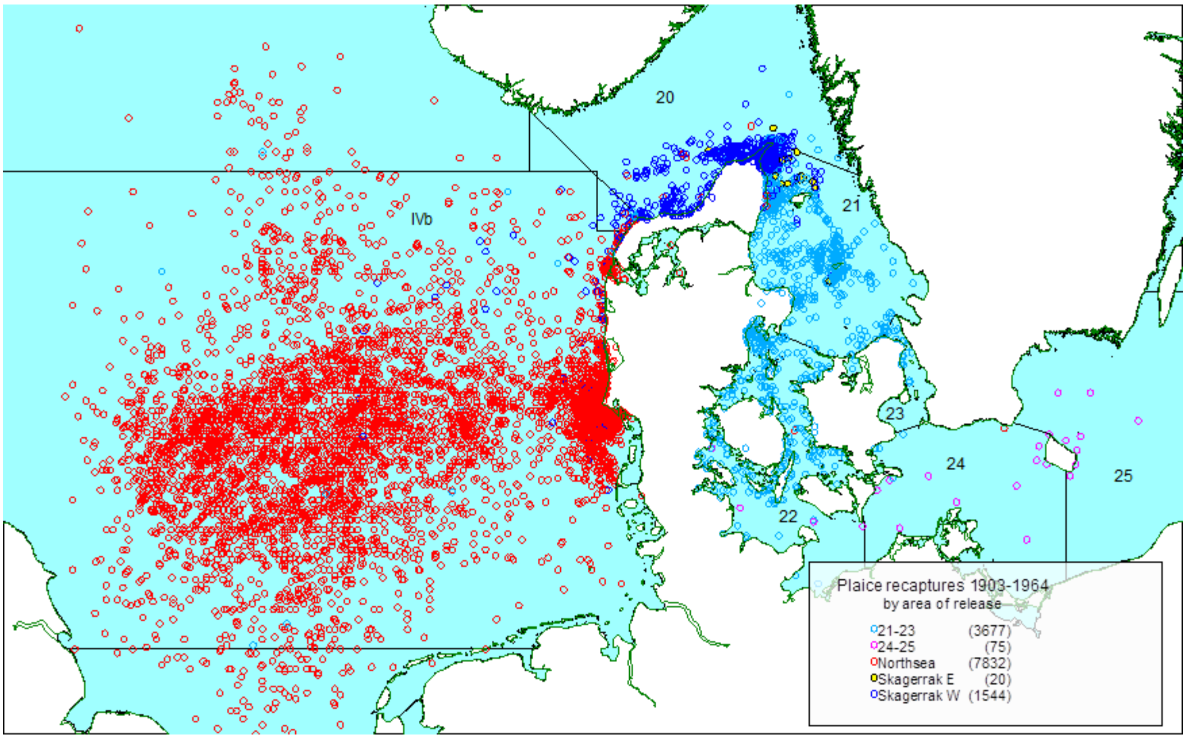

Figure 12. Overview of all recaptures from taggings in 1903-1964. Each recapture is shown by tagging area as indicated in legends in addition to total numbers of recaptures by area in brackets.

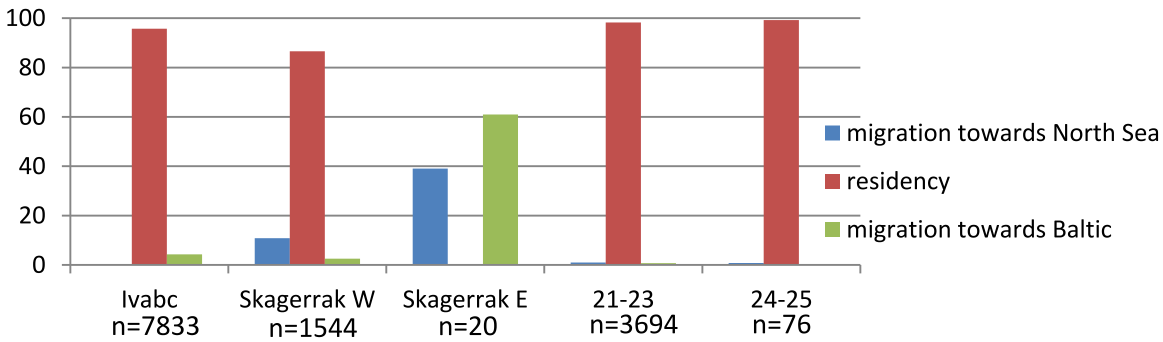

Figure 13. Proportion of movement of plaice towards the North Sea or the Baltic or residency. Numbers of recaptures (before calibration) are indicated.

In order to reveal information on possible spawning units and their movements, both mature fish and spawning season were defined. Maturity is not amongst the recorded parameters at release and therefore it was assumed that fish above 28 cm were mature. Spawning time is not precisely known for the Danish waters but there are historical records from winter and spring. Therefore, January to April was selected for this purpose. By selecting releases assumed mature in the spawning season and recaptures outside this period in the likely feeding season, a measure of 'real population' connectivity could be obtained. Figure 14 provides the movement pattern given this selection in data. There is a strong connectivity between the North Sea and the Skagerrak, with mutual movements. More than 20% of the fish from the North Sea migrated to Skagerrak during summer-autumn, and about 15% of the fish tagged in the spawning season in Skagerrak moved to the North Sea. In contrast to this were mature fish in the Belts and the Baltic almost entirely resident. This might suggest that plaice in the North Sea and Skagerrak mixes substantially during the feeding season.

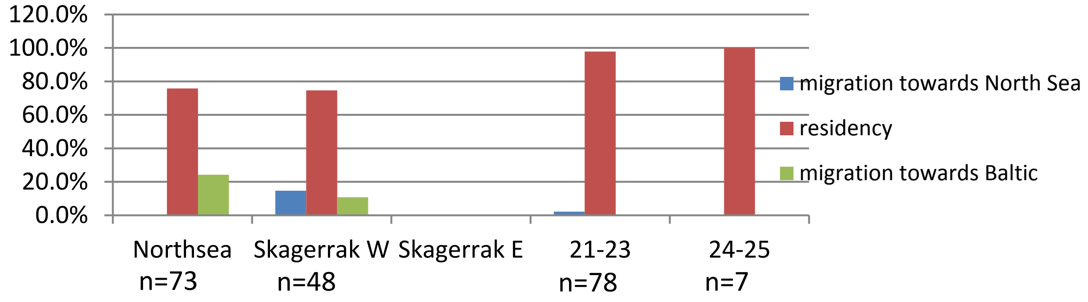

Figure 14. Proportion of seasonal movement towards the North Sea, the Baltic or residency. The graph is based on fish >28 cm released in January-April (spawning season) and recaptured in July-November (feeding season).

Applying the similar selection of data to juvenile fish recaptures (less than 29 cm) showed that almost all fish were resident within the management area and did not perform longer migrations at any time of the year, except for the North Sea where a migration into Skagerrak was observed (14%) in the same order of magnitude as for mature fish. Thus, both immature and mature fish from the North Sea seem to perform feeding migrations into Skagerrak in summer/autumn. The expected return migrations to assumed spawning grounds are exemplified by Figure 15, where a substantial movement (54%) is observed from Skagerrak to the North Sea in the spawning season. However, this proportion is based on very few observations in Skagerrak, and should therefore be interpreted with caution. The actual recapture locations of the mature fish that were recaptured in spawning season are provided in Figure 16 and although few observations from Skagerrak, the recaptures from both the Kattegat and the Skagerrak have moved farther into the North Sea (red and yellow points in the North Sea).

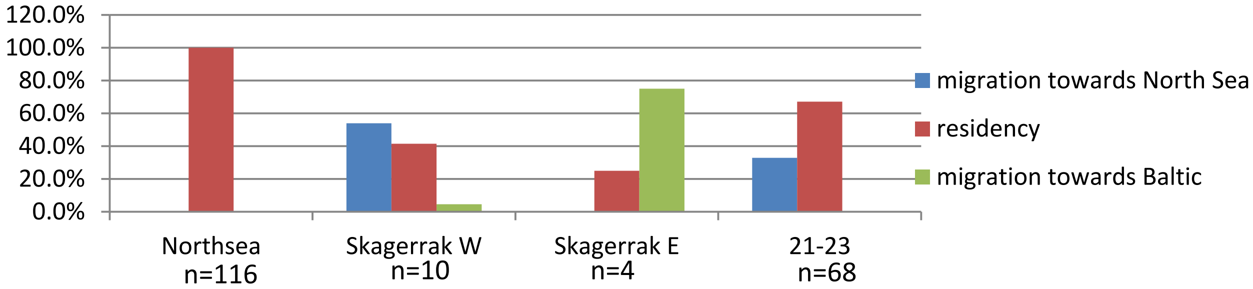

Figure 15. Proportion of seasonal movement towards the North Sea, the Baltic or residency. The graph is based on fish >28 cm released in July-November (feeding season) and recaptured in January-April (spawning season).

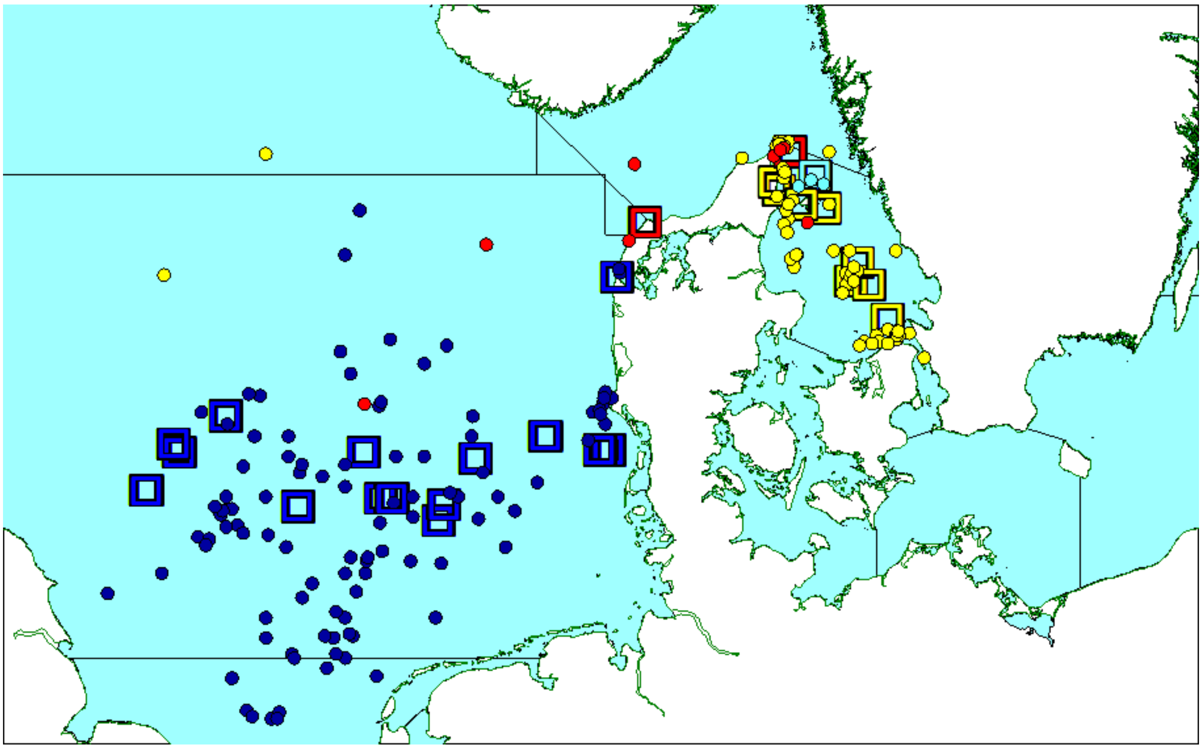

Figure 16. The selected recaptures from Figure 15. In this outline each observation (recapture) is shown with legend marking area of release. The larger squares indicate release sites with corresponding colour by area.

As a measure of natal homing, behaviour of mature fish released in spawning season and recaptured at least one year later in spawning season were analysed. This selection is not illustrated but revealed 100% residency for all areas except for Skagerrak East where no fish fulfilled these selection criteria. This suggest that fish caught in spawning season in every area most likely will return to the same area in the years after within spawning season and is perceived as a spawning 'robustness'.

A plot of distance migrated against recapture month in same area as released for mature fish (Figure 17) showed that the months with lowest migratory activity was April-July. This suggests a validation of spawning in April-May and a post spawning occurrence in the area.

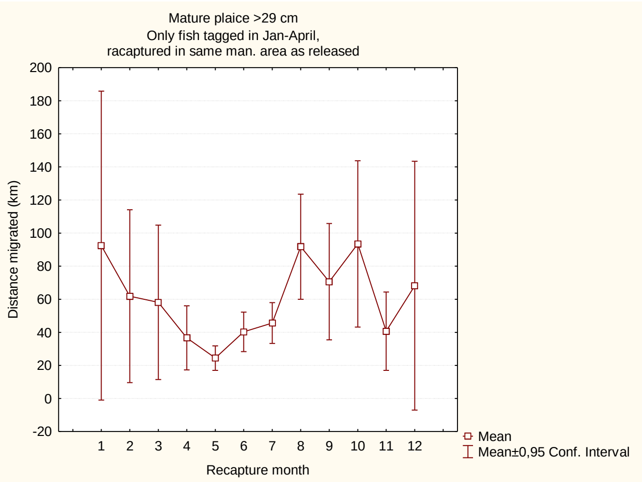

Figure 17. Plot of distance migrated versus month of recapture. Only mature plaice that were tagged in spawning season and recaptured in same area (Figure 2 areas) were included.

4.3.3 Conclusion

The tagging data represents a past period where the biological regime might have been different from the present regime. Also, the data are very unbalanced, with few observations in the Baltic and with periods and numbers of releases differing from area to area. Nevertheless, these data constitute a very large material and gather the major tagging data programs conducted on plaice in this region. Analyses of recapture patterns clearly illustrate that the North Sea plaice population has a high connectivity with plaice in the Skagerrak. Overall, plaice populations in the Kattegat, the Belts and the Baltic seem resident although minor migrations between areas are observed. When analysing behaviour of assumed mature fish, a high proportion of those tagged in the North Sea seem to migrate into western Skagerrak in the feeding season (summer-autumn). This behaviour is also seen for mature fish in Skagerrak, so outside spawning season a mix between the two assumed components is likely substantial (15-54% of recaptures). However, within the spawning season the mature fish seem highly resident in all areas and may even return to same spawning grounds (see also Hunter *et al.* 2003). The immature fish in the North Sea are also observed to partly follow the feeding behaviour of the mature fish as a fraction of the immature also migrated into Skagerrak in summer and autumn.

4.4 Genetic population structure

4.4.1 Background and Methods

As for many marine fish species levels of genetic structuring have been found to be low in European plaice (Hoarau *et al.* 2002; Was *et al.* 2010). In particular, earlier work has identified a lack of clear genetic structuring between samples collected in the Baltic Sea and North Sea (Was *et al.*, 2010). However, prior to this project, it was not known if these results reflected the existence of one panmictic population distributed widely across both areas, or if it was a result of limited statistical power available with the applied methods.

The aim of the genetic work in this project was to apply state-of-the-art genomics approaches to the study of population differentiation of plaice samples collected from the Baltic to the North Sea. To this end, a first step in the project was to develop new genetic markers in plaice through high throughput next generation sequencing of restriction enzyme digested genomic DNA (RADseq, Hohenlohe *et al.* 2010). This method allows for the characterization of thousands of genetic markers, even in species where limited genomic resources are available, and is a promising method for a range of applications in marine fishes (Hemmer-Hansen *et al.* 2014). Following the characterization of new genetic variants (Single Nucleotide Polymorphisms, SNPs), tissue samples from 118 individuals were selected for genotyping through sequence capture technology. These samples were collected at spawning time to represent spawning population from different management areas (Figure 18).

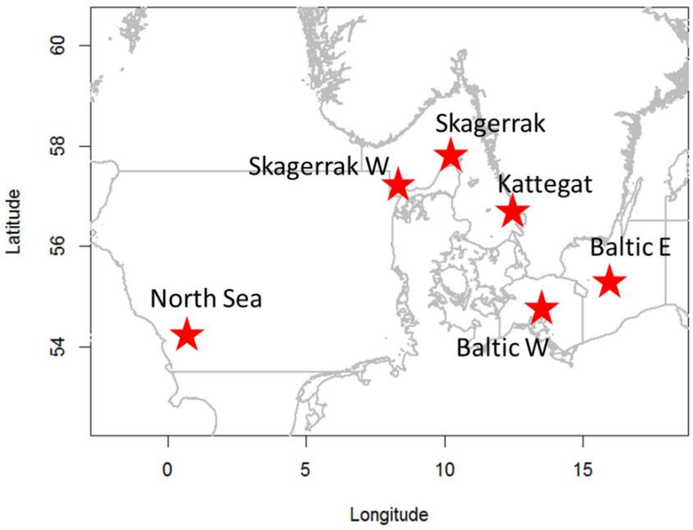

Figure 18. Sampling sites of adult plaice for genetic analyses

Genetic differentiation between samples was estimated as pairwise F_{ST}[4] (Weir and Cockerham 1984) in the R package GENETICS and exact tests for population differentiation in GenePop (Rousset 2008), and further visualized by a multidimensional scaling plot based on pairwise F_{ST} estimates. A principle component analysis conducted in the R package ADEGENET was used to examine genetic variation at the individual level.

4.4.2 Results and Discussion

RAD sequencing of genomic DNA identified more than 800.000 new SNPs in European plaice, of which approximately 20.000 were selected for genotyping in 118 individuals. Of these, 5.605 were used in analyses of population structure. Pairwise tests for sample differentiation showed that all samples were significantly different, although levels of divergence between some samples were relatively low (Table 10). However, pairwise estimates of around 2% between North Sea and Baltic Sea samples correspond to what has been observed in other marine fishes in the region (Limborg *et al.* 2009), and the multidimensional scaling plot showed that samples grouped genetically according to geography, corresponding to a genetic gradient from the Baltic Sea through the transition zone (Kattegat/Skagerrak) to the North Sea (Figure 19). Most of the variation between samples was explained by this gradient.

Table 10. Pairwise F_{ST} (Weir and Cockerham 1984) between samples of plaice

	Baltic E	Baltic W	Kattegat	Skagerrak	Skagerrak W	North Sea
Baltic E						
Baltic W	0.001					
Kattegat	0.004	0.001				
Skagerrak	0.008	0.006	0.002			
Skagerrak W	0.010	0.008	0.002	0.001		
North Sea	0.020	0.018	0.008	0.005	0.003	

[4] F_{ST} is a measure of the degree to which genetic variation is distributed between samples. It theoretically ranges from 0 (no difference between samples) to 1 (complete genetic isolation). A F_{ST} of 1% means that 1% of the total genetic variance can be explained by variation between samples.

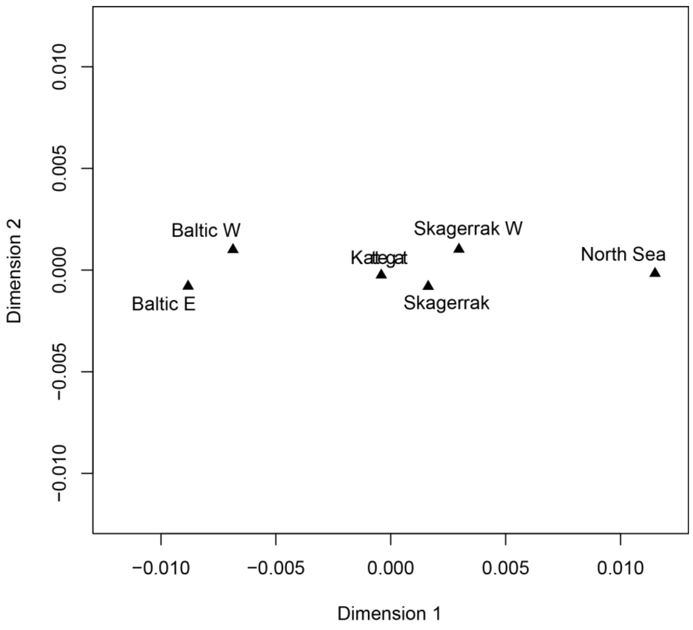

Figure 19. Multidimensional scaling plot of pairwise estimates of population differentiation (F_{ST}; Weir and Cockerham 1984).

The results clearly suggest the existence of different genetic populations in the North Sea, the transition zone and the Baltic Sea. When analysing variation at the level of individual fish, it is evident that a significant level of genetic variation is also found within samples (Figure 20). Individuals are grouped according to sampling location, and follow the same gradient from the Baltic Sea to the North Sea as observed for the entire samples. However, it is also evident that samples collected in the Kattegat and Skagerrak may be composed of mixtures of fish with local genetic signatures (i.e. intermediate signatures between Baltic and North Sea populations) and fish with genetic signatures matching one of the Baltic or North Sea populations. These results also support the presence of local populations in the transition zone, and further indicate mixing of different populations in the Skagerrak and Kattegat. In addition, signals of mixture with the North Sea are most pronounced in the western parts of the Skagerrak, as these fish are more likely to display a North Sea-like genotype. Conversely, mixing between Baltic Sea and transition zone populations is most pronounced for the Kattegat sample.

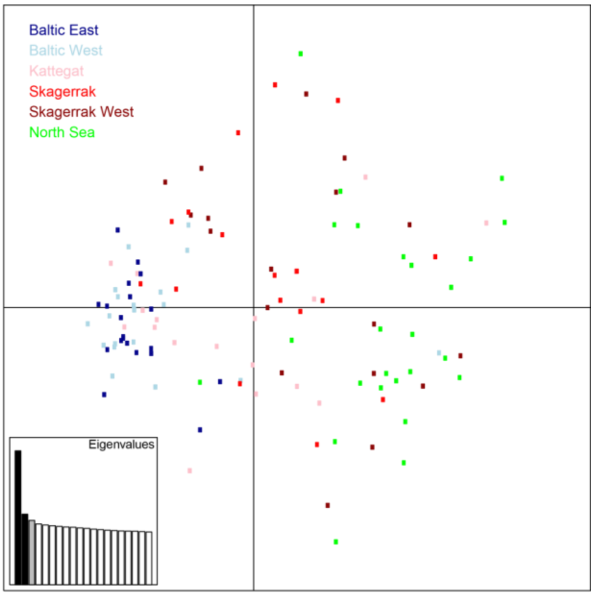

Figure 20. Principle component analysis of 118 plaice individuals based on analysis of 5.605 SNP markers. Samples are coloured according to geographical origin of samples.

4.4.3 Conclusion

In conclusion, the genetic data provide unprecedented resolution for determining the genetic population structure of plaice in the North Sea and Baltic Sea area. Results suggest both unique population signatures and signals of mixing which is particularly evident in the transition zone samples collected from the western Skagerrak and the Kattegat. Thus, data also indicate that mixing of populations may be substantial, even near spawning time when the current samples were collected. It must be assumed, however, that migrants will return to their natal population to spawn, otherwise it would appear unlikely that signals of population differentiation could be sustained over time. A quantification of mixing proportions in the Skagerrak is associated with some uncertainty due to relatively low sample sizes. However, the finding that around half of the fish collected in the Skagerrak display a North Sea genotype (Figure 20) could indicate that a relatively large proportion of plaice in the Skagerrak originates from the North Sea population. Still, it will be important to quantify mixture proportions with higher certainty in future work. In addition, it should be noted that these samples were collected in 2012 and 2013, representing a period with a high SSB in the North Sea, and thus potentially higher levels of inflow to the Skagerrak than in periods with lower North Sea SSB.

4.5 Analyses of survey and fisheries data in the North Sea and Skagerrak

4.5.1 Background and Methods

In addition to the main project components reviewed above, further studies were performed to investigate the advice approach agreed in 2012, which uses IBTS Q1 as an index of local abundance (ICES 2012). Shortly after though, concerns were raised on the very large confidence intervals of the Skagerrak West and Skagerrak East indices. ICES WKPLE (ICES 2015a) investigated these further, and it became clear that the indices were based on very few hauls, with high variability in average CPUE per haul. Furthermore, an additional haul was performed in 2014 in the more shallow waters (less than 30m deep) and yielded the highest CPUE of the time series starting in 1991. Until more hauls are taken in shallow waters it is impossible to disentangle the effect of depth from the random effect of a single outlier haul; nevertheless, this observation raised concerns that the IBTS was not covering well the distribution area of plaice in Skagerrak during spawning season. A number of plots and maps were produced to investigate the relevance of IBTS as an abundance index for plaice. Data were explored for both Q1 and Q3, and for Skagerrak, for the North Sea and for Skagerrak+North Sea. Alternative area definitions in Skagerrak were also explored, to assess if calculating indices on fewer hauls restricted on the main plaice fishing areas would improve them. But no obvious improvements were observed and Skagerrak was considered as a whole area afterwards.

4.5.2 Results and Discussion

Plaice densities in Q1 in Skagerrak are patchy and relatively low, as shown by IBTS and fishery data. There are many hauls with zero catch of plaice, especially below 50 m deep. The average density in IBTS Q1 has fluctuated over the years without trends. There are some (although weak) correlations between recruitment in the North Sea and summer abundance in Skagerrak at adult ages, and also between abundance in Skagerrak during summer and abundance in the North Sea (both summer and spring, Figure 21a and 21b).

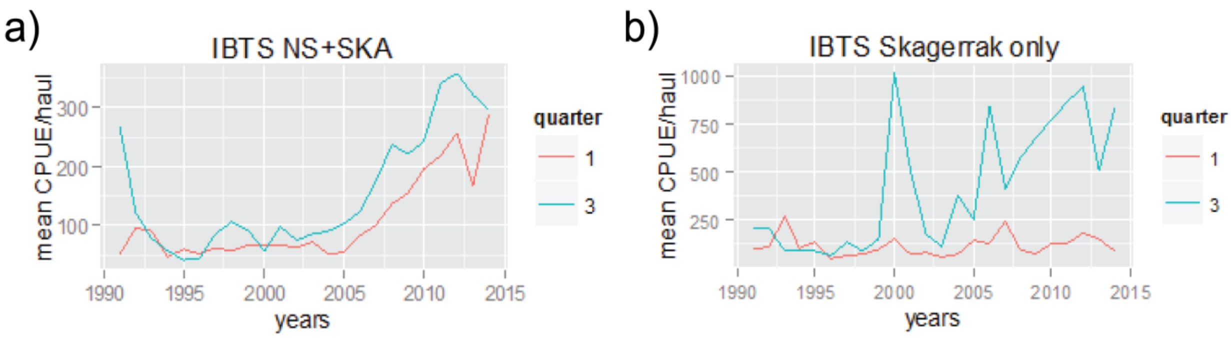

Figure 21. IBTS abundance index for the North Sea and Skagerrak combined (a) and for the Skagerrak only (b).

The fishery is highly seasonal, with most catches being taken in the late summer period (Figure 22).

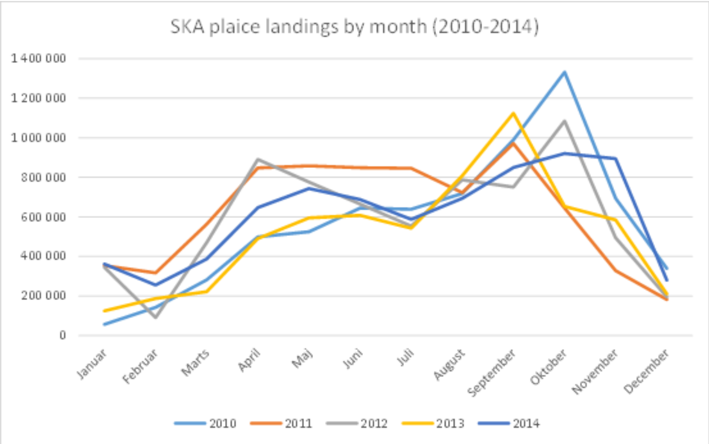

Figure 22. Monthly distribution of Danish plaice landings (kilograms) in Skagerrak.

The interannual consistency of IBTS Q1 in Skagerrak is poor, with poor tracking of cohorts potentially spawning in Skagerrak (Figure 23). This can result from IBTS hauls being outside of Q1 plaice distribution, but this can also indicate that the evidence of a permanent population is blurred. Ultimately, IBTS Q1 in Skagerrak alone cannot be considered a very reliable index for assessment and advice. IBTS Q3 in Skagerrak is more internally consistent, and the high densities are well matched with the commercial data. It indicates higher densities of plaice during summer feeding season.

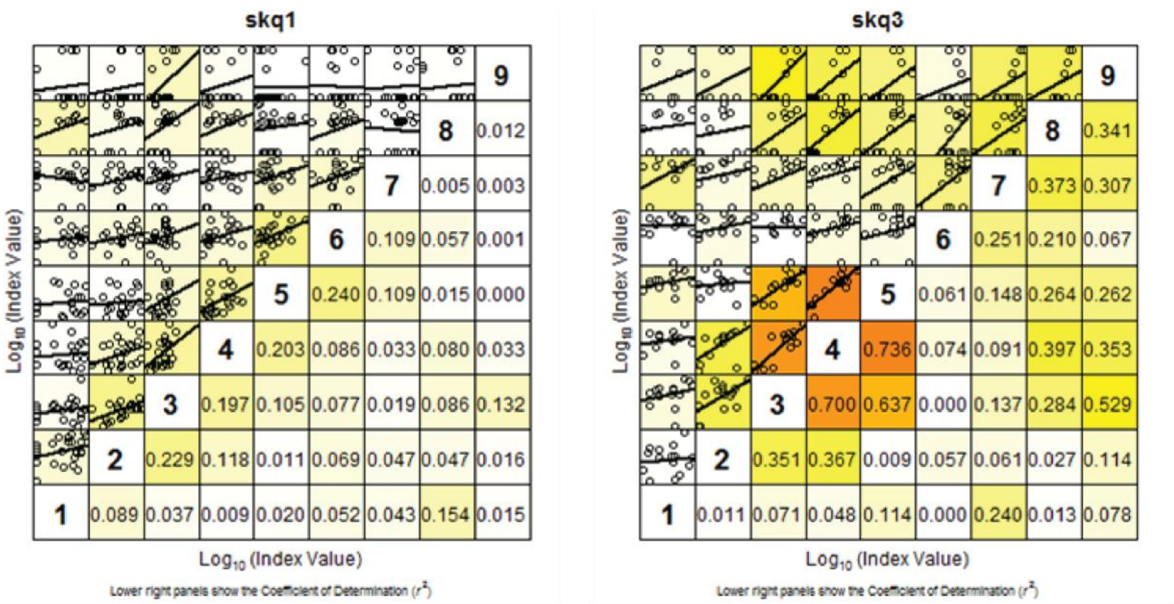

Figure 23. Internal consistency of IBTS Q1 and Q3 in Skagerrak

The internal consistency of IBTS in the North Sea is globally good (Figure 24). During summer season (Q3), this consistency is further improved when including Skagerrak.

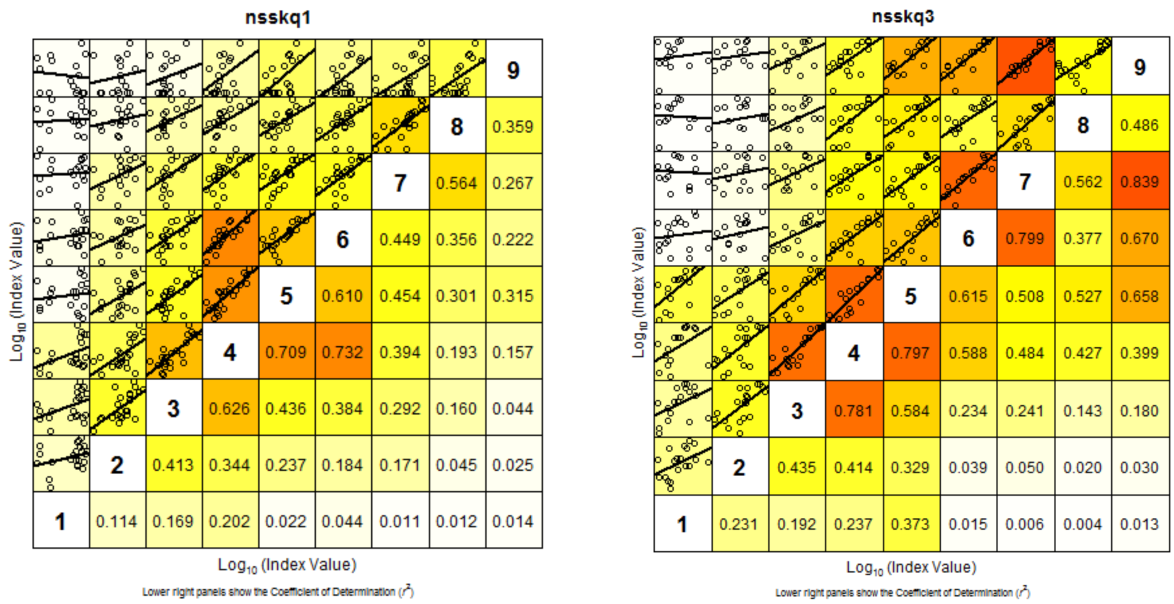

Figure 24. Internal consistency of IBTS Q1 and Q3 in the combined area North Sea + Skager-rak

4.5.3 Conclusion

The analyses above have implied that the approach agreed by ICES in 2012 was not robust, and should not be continued further. ICES WKPLE concluded that IBTS Q1 in Skagerrak cannot be considered a reliable index of abundance of the local population during spawning. It cannot, however, be ascertained whether it is because the survey design is inappropriate for this species in this time of year, or because the population density fluctuates from year to year. Secondly, the analyses have provided a much better understanding of the seasonality in the populations' density, explaining more clearly the likely relationships between North Sea and Skagerrak. They provide a new key for interpreting the biological studies above, supporting the observations of the distinct population in Skagerrak together with the patterns of migrations. These observations, based on standard assessment data routinely collected every year, have been the decisive factor for choosing to lump or split the stock for assessment and management, as explained in section 6 below.

5 Synthesis of findings from the current project

5.1 Evidence of local populations

Evidence from the work in this project confirms that population structure and – dynamics of plaice in area IIIa and neighbouring areas is indeed complex (see also ICES (2012) and Ulrich *et al.* (2013)). Previous work has resulted in a changed perception of ICES Division IIIa as a biological unit: WKPESTO (ICES 2012) gave documentation that qualified for at split between IIIaN (SD 20, Skagerrak) and IIIaS (SD 21, Kattegat). The existence of local populations in the Skagerrak and Kattegat is supported by data on growth characteristics, which showed differences between these areas, limited adult migration between these two areas, the presence of significantly differentiated genetic samples and the finding of a substantial potential for local retention of early life stages. These data strongly suggest the existence of local and unique populations in the two areas, and that these populations are biologically different from those in neighbouring areas in the North Sea and transition area.

5.2 Evidence of population mixing between Skagerrak and North Sea

In addition to the evidence for local population components presented above, there is also evidence to support the hypothesis of substantial interaction and mixing between populations in different areas. Drift modelling shows large levels of inter-annual variation, and that there is a potential drift of eggs and larvae from spawning grounds in the North Sea into Skagerrak in some years. Both Skagerrak and Kattegat have suitable nursery grounds, and these habitats may therefore be inhabited by juveniles originating from both North Sea and local spawning grounds. Tagging data and genetic data further suggest that both adults, as part of their feeding behaviour, and juveniles may actively migrate between areas; from the North Sea to the western parts of the Skagerrak, in particular. The existence of genetic differentiation between the North Sea and the Skagerrak and results from tagging indicate that such migration is followed by homing to natal spawning grounds in the North Sea and/or poor survival and reproduction of North Sea individuals in the Skagerrak. Yet, these fish may still contribute significantly to the local fisheries in Skagerrak and Kattegat. As for North Sea fish, spawning fish in Skagerrak and Kattegat are also displaying strong homing to natal spawning grounds, as indicated by tagging data. Collectively, these data show that mixing of biological populations may occur on most life stages in the Skagerrak and Kattegat.

These conclusions from biological data are well supported by the survey and fisheries data used in stock assessment. While assessment data usually apply a time step of a full year, a stronger focus on seasonal patterns has provided a much better understanding of the dynamics of the mixing between North Sea and Skagerrak and the likely origin of catches. Globally, the population density during spawning in Skagerrak is not very well tracked by existing surveys, but the information currently available does not point towards major trends in plaice density over the time period. Fishing on spawning aggregations in the area is limited.

During summer, there is likely an important inflow from the North Sea population, entering the Skagerrak to feed. This inflow has increased over the recent years, consistent with the increase of abundance of the North Sea stock. By far the largest part of the fishery occurs in this period, and in the most westerly part of the Skagerrak close to the North Sea border.

As data material is still relatively limited, it is difficult to quantify proportions of North Sea fish in the Skagerrak area at present. However, tagging data suggest that around 50% of fish tagged in Skagerrak migrate to the North Sea at spawning time, and genetic data suggest that around half of the fish collected in the Skagerrak during spawning time have a North Sea origin. Considering the increasing abundance during summer in recent years, it is possible that this proportion might be even higher during summer, although no genetic data were analysed from this season. Also, the internal consistency in IBTS Q3 improves when including Skagerrak in the survey area, indicating a better coverage of the stock summer distribution area. Altogether, this suggests that North Sea plaice may constitute a substantial proportion of plaice in the Skagerrak, both during winter and summer. Therefore, a large proportion of the commercial catches recorded for Skagerrak may belong to the North Sea population component.

5.3 Population mixing in Kattegat and Baltic Sea

Although this study was not specifically designed to investigate population structure and –connectivity in the transition zone and the Baltic Sea, some important insights did emerge from the data synthesis. Here, both growth trajectories and genetic data suggest limited differentiation between plaice in SD24 and SD25, while both types of data and tagging data suggest that these populations are different from populations in the transition zone (SD21-23). Genetic data also indicate that substantial migration may occur between the Baltic and transition zone populations, as fish collected in the Kattegat may also show Baltic Sea genetic signatures, indicating that they may in fact be migrants.

6 Implication to management (WP4)

The timing of the project was well correlated with the advisory work scheduled by ICES, as the ICES benchmark for plaice (WKPLE; ICES 2015a) took place in February 2015. Therefore, many of the project outcomes were framed by the need to improve the basis for stock advice in the Skagerrak, in particular. This section summarises therefore the reasoning and the conclusions that have taken place in the ICES benchmark WKPLE in 2015, as well as their implications.

6.1 Focus area North Sea-Skagerrak

As explained in section 2, the advice for plaice in Skagerrak did not have an adequate quality prior to this project. It was based on considerations of an exploratory combined assessment for the North Sea + Skagerrak and trends in IBTS Q1 index. The advice itself was formulated as a Data Limited Stock category 3 (survey-based only), but concerns were raised since 2013 on the validity of this approach, owing to the large variability and instability of the survey index.

The analyses on stock ID summarised above have confirmed what had been hypothesised in 2012, i.e. that catches in Skagerrak are a mix of local and North Sea populations. However, the new tools developed in this project do not (yet) provide an operational tool for routine separation of catches, where individual fish caught could be allocated to either the North Sea or the local populations (as is e.g. currently done for herring stocks in area IIIa, ICES 2014b, and cod in the western Baltic Sea, ICES 2015b). This means that the situation is a kind of a "half-empty/half full glas" dilemma, where several options can be chosen. Because the relative proportion between the two components is not well known, and because the current survey indices on spawning populations are performing poorly and are not very reliable, one can chose either of two approaches:

- In terms of biological units, it might be preferable to consider Skagerrak as a stock unit distinct from the North Sea ("splitting option"). However, it is currently difficult to define and evaluate quantitative management objectives for the local population, and to monitor trends towards achieving these.

- In terms of quantitative stock assessment and fisheries management, it might be preferable to consider Skagerrak as a part of the global North Sea stock ("lumping option"). However, because of the differences in size between the two populations, there is a risk of depletion of the local Skagerrak population if the fisheries on it increase as a consequence of the increase in the North Sea stock

As part of the current project and together with the EFF project "Optimal sustainable use of cod stocks accessible for Danish fisheries" (J.no.33010-13-k-0269), an exploratory workshop was held in EU Joint Research Centre (JRC) in Ispra, Italy, in December 2014. The aim of the workshop was to explore the possibilities of assessing local populations of plaice and cod within the larger North Sea-Skagerrak area[5]. Using catch and survey data compiled by sub-areas, exploratory assessments (method: a4a) were performed across different aggregation areas. For plaice, assessments were performed for the North Sea alone, for the Skagerrak alone, and for the combined North Sea + Skagerrak area. The results showed that an assessment of Skagerrak plaice as a stand-alone stock was performing poorly. As shown above, the Q1 and Q3 surveys display very different trends, and the assessment was extremely sensitive to the assumptions used. In particular, a trial run was performed to account for the increasing summer abundance in Q3 linked to the inflow of the North Sea stock in Skagerrak by introducing a time trend in the survey catchability estimate. This run returned completely opposite stock trends compared to the assessment with a constant catchability hypothesis, for an equally good model fit (Figure 25). It was concluded that no quantitative assessment of the local population in Skagerrak was possible with the current data, unless making strong assumptions on stock mixing in the catches; assumptions which cannot be quantified with the currently available biological data. In consequence, the “splitting option” above would imply that no quantitative advice could be provided by ICES for this stock.

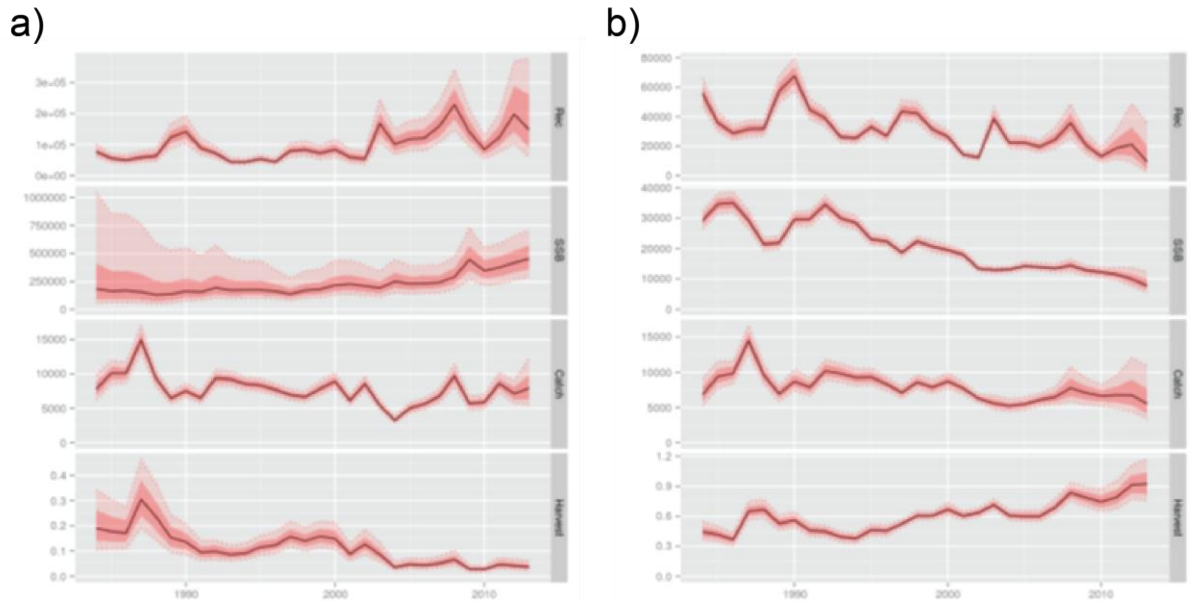

Figure 25. Exploratory assessments for plaice in Skagerrak. Standard assessment using IBTS Q1+Q3 (a) and assessment accounting for a time effect in IBTS Q3 (b).

[5] https://fishreg.jrc.ec.europa.eu/documents/75108/188503/2014-a4asrp-ns.pdf

Conversely, the “lumping option” is much easier to handle, as Skagerrak catch data can easily be added to the North Sea assessment. Preliminary revision of the current Fmsy reference point have indicated a difference of around 0.01 for the combined stock compared to the North Sea stock alone. Consequently, assessment and management for the combined area can be provided with the current data. Additionally, ICES WKPLE (ICES 2015a) performed analyses supporting the use of ICES IBTS survey (Bottom Otter Trawl survey) as an additional tuning fleet for the combined stock, since the assessment of the North Sea stock is currently only performed using Beam Trawl Surveys that do not cover the Skagerrak. Therefore, the lumping option allows some quantitative advice to be provided for the Skagerrak, but does not currently allow for routine monitoring of the local population in the Skagerrak.

Clearly, neither the lumping nor the splitting options are satisfactory solutions at present, since none of them allow for an adequate monitoring and conservation of the local population in Skagerrak. The management plan proposed by the North Sea Advisory Council (NSAC) since 2012 aimed at formulating a pragmatic trade-off between the two options that would provide a quantitative management objective based on the qualitative knowledge on stock mixing. The current EFF project was also initially formulated along those lines, and suggested to perform simulation-based management strategies evaluation (MSE) of this management plan. However, the most recent developments before and during ICES WKPLE (ICES 2015a) have altered this point of view. The most recent considerations on the poor performance of IBTS Q1 as an abundance index for the local stocks, on the pronounced seasonal pattern of the fishery and on the current challenges with formulating a quantitative monitoring of catches from the local stocks have balanced towards the view that the lumping option was preferable, in the sense that it allows applying the usual mechanism of quantitative analytical assessment and advice for the area.

Additionally, since plaice in the North Sea and in the Skagerrak are managed by different TACs, it has been considered that the management system already contains some mechanisms for reducing the fishing pressure in the Skagerrak if deemed necessary (for example with a unilateral reduction of TAC in Skagerrak). It was therefore suggested that in terms of management, the ICES advice for Skagerrak could include a number of additional considerations:

- In the short-term, a qualitative warning to managers could be included in the advice, for example like this: “Skagerrak is assessed together with the North Sea on the basis of important stock mixing and the predominance of catches occurring on summer feeding aggregations in the Western Skagerrak. Nevertheless, it is well established that there are also important local populations resident in the Skagerrak, and therefore, ICES advises that the ratio of catches between the Skagerrak and the North Sea should not increase, and that major transfers of fishing effort from the North Sea to the Skagerrak are prevented".

- In the medium-term, ICES WGNSSK would conduct routine observations of the survey and fisheries patterns in Skagerrak using standard data, to detect any departures from the current situation, including for example the following indicators:
  - IBTS Q1 biomass.
  - Spatio-temporal patterns of the fishery.
  - Trends in effort, catches and CPUE by fleet, area and season.
  - Correlation of North Sea recruitment with IBTS Q3 in Skagerrak.

- In the longer-term, the current progresses on the biological knowledge of the stock in Skagerrak should be sustained. Additional genetic allocation of individual fish to the different populations should be performed to obtain a better quantification of the mixing in different areas and seasons, and the survey coverage should be improved in the Skagerrak.

On this basis, and given the current challenges with quantifying the local stock proportions further, it was concluded that proceeding with MSE simulations would not provide much additional knowledge, since strong quantitative assumptions would still have to be made on the productivity of the local stock and on the amount of stock mixing during summer.

These conclusions and suggestions were reviewed during ICES WGNSSK in May 2015 (ICES 2015c). The catch and survey datasets used in the report were updated with the most recent data, which did not show any deviation from the trends and hypotheses described here. Therefore, the changes suggested in WKPLE (ICES 2015a) were accepted and implemented in the assessment. The advice was published for the combined stock North Sea – Skagerrak[6].

6.2 Focus area Kattegat–Baltic Sea

The whole area from Skagerrak, through Kattegat, the Belt Sea area, the Western Baltic Sea to the Eastern border of the distribution of the plaice in the area east of Bornholm constitutes a transition area, which can make it difficult clearly to define the number of unique plaice populations as well as their distribution boundaries. Plaice in Kattegat and the Western Baltic Sea was until 2002 included in the Skagerrak-Kattegat (IIIa) plaice stock but consistent problems with establishing an assessment which could be accepted as base for biological advice led to a suggestion for revision of this and the surrounding stocks by the WKPESTO workshop in 2012 (ICES 2012). Here, it was suggested to recognize Kattegat together with the Belt

[6] http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2015/2015/ple-nsea.pdf

Sea area and Western Baltic (Sub-divisions 21, 22 and 23) as an independent stock. The suggestion was built on available literature and information from historical tagging. The split between Skagerrak and Kattegat was rather well documented but the border to Sub-division 24 was less conclusive. The eastern Baltic Sea area was defined as an additional stock including Sub-division 24-32. Both stocks were initially defined as "Data limited stocks" until it was investigated if 1) the stock structure was correct and 2) sufficient historical data was available to perform an analytical assessment. Until then, the biological advises for both stocks were based on information from scientific surveys only, but supported by a preliminary analytical assessment for the Kattegat-Western Baltic stock. Although the current project focused specifically on stock and management issues in area IIIa and has confirmed the split of the IIIa stock into a Kattegat component different from the rest of IIIa, the results generated in the project have also added significant knowledge to the question if plaice in area 24-26 can be considered as a separate stock. Growth investigations suggest significant difference between SD 24 and SD 22 and this is supported by only minor migration between the two areas. At the same time insignificant difference in growth is observed between SD 24 and SD 25. The genetic investigations show only little difference between SD 24 and SD 25 but are less conclusive concerning the difference between SD 24 and Belt Area as no genetic samples were investigated from SD 22. Based on these results the ICES benchmark group (WKPLE) in 2015 concluded that plaice in SD 21 to SD 23 should be recognized as one stock (PLE21-23) and plaice in SD 24 to SD 32 as another separate stock (PLE24-32).

The WKPLE investigated the possible options for carrying out assessments for PLE21-23 and PLE24-32 and an analytical assessment was approved for PLE21-23. However, this was not possible for PLE24-32 due to the limited amount of historical data available. An exploratory assessment run was made by merging the two stocks in order to investigate if this would change the perception of the combined stock compared to the perception of the PLE21-23 stock. As expected, the two runs gave very similar perceptions as both stocks show similar abundance trends in scientific surveys and historical catches, which are both input data for the assessments.

The management area definitions did not change with the new stock definitions, and consequently assessment and management areas are not coherent. Kattegat is still a separate management area and as consequence, the PLE21-23 stock involves both the Kattegat management area and SD 22 and SD 23 of the Baltic Sea management area. As long as the developments in both stocks are parallel, this might not give rise to problems which cannot be handled, but in a situation where the two stocks show opposite trends, it might be difficult to manage the area in a way, which supports the biological advice for both stocks and takes the best long term management of both areas into account.

7 Conclusions and outlook

In conclusion, this EFF project has made major progresses. The biological data collected and analysed have brought new knowledge and new evidences on the co-existence of distinct populations on fishing grounds, and the spatio-temporal patterns of stocks mixing have been highlighted. Altogether, there is now a much more robust understanding of the processes underlying the population dynamics of plaice in the transition area between the North Sea and the Baltic Sea.

The results from the project contributed directly to making informed decisions and suggestions during ICES WKPLE 2015 for assessment, advice and management (see above). A direct outcome of this EFF project is that a quantitative ICES advice based on an analytical assessment (ICES DLS category 1) will be available for each area (NS-Skagerrak and plaice in SD21-23) in 2015. This is a major improvement compared to the situation until 2014.

For Skagerrak, the most important issue is now the need to avoid the depletion of the local Skagerrak population, since the risk of it is increased if the large North Sea population is more productive than the local Skagerrak population and if the local population cannot be routinely monitored adequately. Recommendations are being made to prevent such depletion to occur, and it is important that the situation is monitored closely. Consequently, this project has also highlighted the need to develop further and implement tools for reliable quantification of proportions of population components in the Skagerrak catches. Another issue to resolve in the near future is that a new ICES benchmark will be needed for the combined North Sea-Skagerrak stock, in order to officially integrate the final development into the common assessment and advice.

For the Kattegat and Baltic, the most important issue is that this EEF project has confirmed the decision already made in 2011 to consider plaice from sub-division 21, 22 and 23 as one stock separated from the plaice in Skagerrak as well as from the plaice in sub-division 24 and 25. There is now a solid base for the future development of an assessment providing sufficiently reliable input to the management of plaice in the area.

Finally, it should be noted that not all biological issues could be answered during this project, and new knowledge has also triggered new questions. A number of new investigations would be needed to clarify the remaining shadowed areas. These new investigations may not be as expensive and time-consuming as those presented here, since they are primarily extensions and fine-tuning of the results obtained in this project. They include:

- New genetic assignment of individual fish to the different populations across a broader diversity of locations in time and space, and in particular:
    - In Western Skagerrak during summer and autumn.

    - In Eastern North Sea during spring and summer.
    - In the Belt Sea (area 22).
    - In eastern and western parts of area 24.

- A combined baseline where individual fish are both genetically assigned and their growth is back-calculated from otoliths in order to quantify the correlation between these two indicators of distinct populations.

- Reconsidering the global adequacy of IBTS sampling design in Skagerrak, together with the needs for other stocks including cod and herring.

- Estimating the magnitude and distribution of spawning in Skagerrak, Kattegat, the Belt and the Baltic by means of direct sampling in spawning season.

We would recommend that these topics are addressed in future research to strengthen and support future management of plaice in the Skagerrak and surrounding areas.

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