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EXTENDED ABSTRACT (article in progress) – NOT TO BE CITED WITHOUT PRIOR REFERENCE TO THE AUTHOR

Modelling the mixing of herring stocks between the Baltic Sea and the North Sea from otolith data.

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Abstract

Herring catches in the Western Baltic, Kattegat and Skagerrak consist of a mixture of stocks, mainly North Sea Autumn Spawners (NSAS) and Western Baltic Spring Spawners (WBSS), which is managed through a single TAC. Catches of these two stocks are split using otolith microstructures from Danish and Swedish commercial landings and surveys samples for the purpose of stock assessment. But the split estimates from sampling data are highly variable and noisy. Better understanding of the migration and exploitation patterns involved could therefore potentially improve the stock assessment as well as provide solutions to the complex management of this mix. The stock specific seasonal trends in distribution of the two main stocks from otolith data were analysed using, a Generalized Linear Mixed Model (GLMM) of stock composition. The results show a clear seasonal and age related pattern and are consistent with existing ideas about the migration patterns of WBSS and NSAS within IIIa and adjacent waters. This work therefore provides the foundation for the development of a more rational management of the herring stocks in this area.

Keywords: Herring, Kattegat, Skagerrak, Western Baltic, Eastern North Sea, Autumn spawners, Spring spawners, mixing, GLMM

INTRODUCTION

Atlantic herring (*Clupea harengus* L. 1757) display large variations in migration and homing behaviour, and genetic studies have identified population structure across both small and large geographic scales (e.g., Bekkevold et al., 2005, 2007; Mariani et al. 2005). In ICES subdivisions 20 (Skagerrak, area IIIaN), 21 (Kattegat, ICES area IIIaS) and 22-24 (Western Baltic) a number of herring sub-populations spawning in either winter, spring or autumn occur sympatrically and are exploited in a mixture by the fishery (ICES 2006). These sub-populations are gathered into stock units for assessment and management purposes (ICES 1998). Although the relatively high spatio-temporal overlap of stocks may bear a high potential for gene flow (Iles and Sinclair 1982; Ruzzante et al., 2006), it has been shown that herring spawning components uphold significant reproductive isolation, possibly affected by selective differences among spawning and/or larval habitats (Bekkevold et al., 2005). To ensure conservation of herring population diversity in an area, all stock components and their natural migration patterns must be considered in the compilation of scientific advice on the fishery (Stephenson 2001), since variable compositions in mixed areas together with asynchronous population dynamics may lead to over-fishing of individual stock components if not all components are managed to ensure (or achieve) sustainable exploitation (McPherson et al 2001; Secor et al 2009).

The general patterns of the dynamics of the larger herring populations in the area are qualitatively known (Payne et al. 2009, ICES, 2010b; Figure 1). The main spawning area of the WBSS herring is considered to be Greifswalder Bodden at Rügen Island (ICES, 1998), where it spawns during March-May. The majority of 2+ ringers migrate out of the western Baltic during the 2nd quarter of the year to feed in Division IIIa and in Eastern North Sea and return to the Western Baltic in the 1st quarter for spawning (Aro 1989, Biester, 1979; Rosenberg and Palmèn 1982; Johannesen and Moksness 1991). The extent of the migration is age and season dependent and highly variable (Clausen et al., 2006). While feeding in the Skagerrak, Kattegat and North Sea, the WBSS herring mix with juveniles of the North Sea Autumn Spawner (NSAS) herring stock, which use the area as one of their main nursery grounds (Iles and Sinclair 1982). It is unclear whether the two stocks form mixed schools in this region or whether schools retain their identity: regardless, WBSS and NSAS herring are caught together in the same haul (ICES 2009) and thus are exploited as a mixed fishery.

However, these patterns are qualitatively known in nature, but have never been fully quantified and modelled. The ICES Herring Assessment Working Group (HAWG) annually makes use of routinely collected biological samples of the catch to estimate the composition of the catches in terms of stock components. The proportion of autumn, winter and spring spawning fish in the sample can be estimated with a relatively high degree of confidence using either genetic methods (Ruzzante et al., 2006) or otolith-based methods (Moksness and Fossum, 1991; Mosegaard and Madsen, 1996; Clausen et al., 2007). The estimated proportions are then applied to the catch data to estimate the total catch of each spawning type. For providing TAC (total allowable catch) advice, a simple 1-year average of the most recent catch composition is used in the short-term forecast procedures (ICES, 2010a).

However, given the small size of the WBSS stock compared to NSAS stock (100 kt vs 1300 kt in 2009; ICES 2010a), it has become increasingly important to get a better quantification of the mixing between the two stocks in order to provide robust advice on both short-term and long-term management strategies (ICES, 2010b, Ulrich et al., 2010). This study examines the historic mixing of the two stocks in order to quantify both the potential fixed seasonal patterns and the inter-annual variability around them and propose robust standard procedures for forecast and projections.

The results included in this extended abstract here are those used by (ICES, 2010b), based on the data available at that time. However, a more comprehensive analysis is currently being undertaken, based on a larger data set including more years of data, and merged with scientific surveys data. As results of this ongoing work were only preliminary, they are not included yet into the present manuscript.

MATERIAL AND METHODS

Determination of hatching month

The method for separation of the herring stock components has developed in the past decade. Prior to 1996, the splitting key used by ICES was calculated from a sample-based mean vertebral count (VS). In the period from 1996 to 2001 splitting keys were constructed using information from a combination of vertebral count and otolith microstructure methods (ICES, 2001). From 2001 and onwards, the splitting keys have been constructed solely using the otolith microstructure (OM) method which uses visual inspection of season-specific daily increment pattern in the larval otolith, with the exception of the splitting key made for the mixture area in Sub Division IVaE, where vertebral counts currently are the only method used to split the mixed stock (ICES, 2004; Clausen *et al.*, 2007).

The transition from the sample based VS method to the individual based OM method increased precision considerably (Mosegaard and Madsen 1996). The OM method was validated by Clausen *et al.* (2007) and the study showed that the method can discriminate herring with different hatching times, even when a sympatric existence of herring with different spawning times is the case (Brophy and Danilowicz 2002, 2003, Bekkevold *et al.*, 2007). However, different populations with similar spawning periods may not be resolved with the present level of analysis (Mosegaard *et al.*, 2001, Clausen *et al.*, 2007).

Data

Danish and Swedish harbour samples collected between 2002 and 2009 were used as basic information on the relative proportions of the spawning type composition: given changes in sampling programs and stock identification methods, data prior to 2002 were not considered reliable enough and were thus not included in the dataset. In total, 932 samples, including 29752 fish measured, aged and with identified hatch month, were included. Fish with hatch month between March and June were considered as WBSS, other were pooled and assumed to be NSAS.

Statistical model

The historic mixing of the two stocks was examined in a statistical framework, in order to quantify both the potential fixed seasonal patterns and the inter-annual variability around them and propose robust standard procedures for forecast and projections. Analyses followed to a large extent the approach developed by Bierman *et al.*, (2010) on mixing sub-stocks within the North Sea Herring stock.

Generalized linear mixed models (GLMM) on logit proportion of WBSS in the samples (*split*) were fitted with restricted maximum likelihood (REML) approach, using the `glmer` function in the `lme4` package (Bates & Maechler, 2010) in R (R Core Team, 2010).

Various models were tested, with several combinations of parameters including age, season and area as fixed additive effects and year, yearclass and sample as random effects; Particular attention was dedicated to establishing the most appropriate levels for the plusgroup (from 11+ down to 3+), for the time scale (month, quarter or semester), and for the geographical resolution. This parameter was either considered as categorical variables through grouping the statistical rectangles into various area and subareas definitions, or as continuous data using latitude and longitude. A One-dimensional projection line running through the whole area was also considered.

These various combinations of parameters were compared using an ANOVA. In most cases, the best models could be selected by both the AIC and the BIC criteria. However, in the few cases where the BIC and the AIC were in non-agreement in selecting the best model, the BIC criteria was chosen in order to prioritize the reduction in parameters number.

RESULTS

The final model retained included additive, crossed and random effects as follows:

$$\log\left(\frac{p}{1-p}\right) = A_i + Q_j + \beta_1 x + \beta_2 y + \beta_3 x \cdot y + \gamma_{A_i} x + \delta_{A_i} y + U_{key} + U_{year} + U_{cohort} + \varepsilon$$

With p the proportion of WBSS, A_i the age effect from 0 to 4+, Q_j the quarter effect, x the centralised longitude, y the centralised latitude, key the sample effect with $U_{key} \sim N(0, \sigma_{key})$, $U_{year} \sim N(0, \sigma_{year})$ and $U_{cohort} \sim N(0, \sigma_{cohort})$.

Most fixed effects were highly significant (Table 1), and the residuals were independent of the fitted value (Figure 2).

The actual effect of each coefficient from the GLMM output on the split is inspected using their inverse

$\frac{e^{coef}}{1 + e^{coef}}$, that returns a proportion number between 0 and 1 (Figure 2). The main outcome of the analysis is the evidence of a clear pattern suggesting increasing proportions of WBSS with age (there is hardly any NSAS in the samples beyond age 3), space (with decreasing proportions with decreasing longitude and increasing latitude, i.e. from SouthEast to NorthWest) and season (with more WBSS in the

samples during the second semester compared to the first). Age distribution was also significantly correlated with latitude and longitude.

The analysis of the random effects suggests that a large proportion of the variability is due to the large dispersion of the samples, with a very high σ_{key} (1.69, corresponding to a CV close to 0.5 on the inverse logit). This indicates that the samples are likely not binomially distributed, and may often contain significantly more of either spawning type than the average pattern suggests.

On the contrary, the variability from year to year is not particularly high, with $\sigma_{year} = 0.64$ on the logit scale ($\sim CV=0.28$). There has been a decreasing year effect from 2002 to 2007, but this has then reverted and 2009 is the highest positive effect observed.

The cohort effect has also fluctuated over time, with a positive effect of the cohorts born after 2002. Residuals were plotted versus fitted proportions to reveal any trend in estimation errors of the components (Figure 3) and no real trend is seen.

The global spatial pattern by age and quarter can be summarised on the maps Figure 4.

The same model as above was also fitted for each year individually (though without the U_{year} term and the U_{cohort} term which then is redundant with the age information), in order to evaluate the potential mismatch between forcing the sample data in a long-term pattern as above, or letting the coefficients reflect more freely the year-to-year variability in the data (Figures 5 and 6). Not all yearly models converged properly, and some coefficients were sometimes poorly estimated due to insufficient sampling coverage, in particular for age 0. However, they generally did not exhibit a widely different picture of the main patterns compared to the model fitted on all years.

The observed average split value from the samples across the main regions was compared to the fitted models, both with all years included and with each year fitted individually (Figures 7 and 8.). The consistency was in many cases highly satisfying, and particularly for the well sampled strata around the NorthEast Jutland (NorthEastSkagerrak and North Kattegat). However, some particular deviations were also observed, without that these could be linked to a repeated pattern in time and space, or without that this could be easily explained by any other factors than a potential insufficient sampling in the strata. However, This could potentially bear important consequences, in particular at the edge of the distribution area. Notably, the model captures a very high presence of WBSS during Quarter 4. While this is a sensible outcome for IIIa as the fish are assumed to migrate back across the area towards spawning grounds, this may be erroneous for area IV (Transfer area) as WBSS would have already left this area of summer feeding and should then be less numerous during Quarter 4. But the very low sampling level in this area doesn't allow the model to infer this properly.

When both approaches (Long term model and yearly models) were applied to the international landings by ICES Rectangle from area IIIa (fleets C andD), using the relative age distribution by area from yearly HAWG reports to evaluate the differences of Catch-At-Age that could enter in the assessment, there were on average only very small deviations between using the split models or taking the raw average of the samples (Figure 9). This indicates that using the split may not dramatically affect the perception of

the catch ratios and subsequent F at age in the assessment for the ages 3 to 6 used for computing the F_{bar} . However, more differences were observed for ages 0 to 2, where most of the mixing occurs. Furthermore, this apparent consistency hides some larger variations at the Quarter level (Figure 10). It is to be noted that due to some discrepancies between the total landings estimated over years by HAWG and the sum of total international landings used here, these figures are not directly comparable to the HAWG figures.

Discussion

The analysis of spawning type composition in catches from Division IIIa, the transfer area and ICES Subdivisions 22-24 in the period from 2002 to 2009 show clear differences in spatial and temporal distribution pattern and mixing of the two main stocks NSAS and WBSS. The results of a crossed latitude x age effect indicate a northward trend in emigration of NSAS as fish gets older and increased proportions of WBSS in third and fourth quarter point to the recurring asynchronous feeding and spawning migrations of the two stocks. These results are largely consistent with the existing empirical knowledge (e.g. Payne 2009, ICES 2010b and references here in). They are also consistent with the findings of previous studies using marking experiments (Biester 1979), parasites as biological tags (Grabda, 1974, van Deurs and Ramkaer 2007), genetic studies (Bekkevold et al., 2005, 2007) and acoustic surveys (Nielsen et al, 2001), which suggest a northward feeding migration towards Division IIIa and the North Sea every summer performed by adult WBSS herring from the spawning areas of the Rügen Island on the German coast in Western Baltic, returning to the southern Kattegat and the Sound for overwintering. The dynamics of WBSS herring in the spawning area in the Western Baltic could not be fully characterised from our analyses as spawning determinations from Subdivisions 22-24 are largely underrepresented in the samples, leading to a non-significant coefficient estimate for this area. Nevertheless, the model suggests a proportion of WBSS in Q3 and Q4 in this area that is close to 100% at all ages, confirming the absence of NSAS herring around the WBSS spawning areas.

Our results provide evidence for the occurrence of large proportions of juvenile and young NSAS in IIIa. It has long been accepted that an unknown and possibly variable proportion of NSAS drift as larvae across the North Sea from spawning areas along the UK east coast and the Channel and into the Skagerrak and Kattegat nursery grounds (Burd, 1978; Heath et al, 1997). The proportion of NSAS decreases with increasing age due to both emigrations of NSAS fish out of this area and increasing immigration from WBSS into the area. The metamorphosed NSAS juvenile 0 group fish begin to appear in the eastern North Sea (German Bight and Skagerrak) in the third quarter of the year (International Bottom Trawl Survey (IBTS) results shown in Heath et al, 1997) and appear to stay there (and to a much lesser degree in other coastal areas) until they are 2 years old when they actively migrate to join the NSAS adult population feeding in the central and northern North Sea (Wallace, 1924). Furthermore the positive cohort effect observed corresponds to the cohorts of low North Sea herring recruitment, which could logically suggest that when the recruitment in the North Sea is poor there is proportionally a lower proportion of NSAS in the area IIIa.

The restriction of juvenile WBSS to nursery grounds in the Western Baltic is supported by Brielmann (1989). The discovery of multiple genetically distinct spring spawning populations from inner Danish waters and Swedish fjords (Bekkevold et al., 2005, 2007; Ruzzante et al., 2007) could also be the source of the juvenile WBSS observed in Division IIIa. The otolith-based method applied here has the potential for distinguishing between spring, winter and autumn hatched individuals. The method is not capable of distinguishing between the same-season but locally founded and genetically different spawning populations (Bekkevold et al, 2007; Clausen et al, 2007). Additionally, a minor degree of uncertainty was observed applying this method for stock identification, where the most frequent error was misclassification across winter-and autumn-hatched individuals (Clausen et al., 2007). For stock assessment of North Sea herring the winter and autumn spawning components are pooled by HAWG (ICES, 2009) and therefore also in the present study regarded as a component of NSAS. Bierman et al, (2010) included this additional source of uncertainty using a Bayesian framework for estimating landings of winter- and autumn spawners in North Sea herring, and showed this issue did not affect dramatically the general outcome of the analyses.

Major outcomes of our study were that i) the inter-annual variability was generally less important than initially expected, however, ii) the variability between samples within the same stratum could be extremely large.

The outcome of i) is important, as it shows that over the studied period, the predictable age- and season-based migration model explained the largest part of the observed patterns, and the effect of the unpredictable inter-annual variation, although statistically significant, was minor (less than 0.5% decrease in residual variance with the GLMM with and without year included). There have not been very strong differences observed over time, and no trends in the estimate of the year effect can yet be found out of the relatively short time-series. The outcome of ii) is also important, as it underlines the extreme variability in samples. It has always been acknowledged that these stocks are so dynamic that a large number of samples is necessary to capture the actual mixing proportion; indeed the scientific resources dedicated to this sampling program are large compared to its relatively small economic value. However, our results raise major questions as to whether this already large sampling program is sufficient for a consistent stock assessment. The observed average proportions vary from strata to strata, and this has direct consequences for the estimated catch-at-age data used in the assessment. The assessment is usually considered as accurate (without bias) but with low precision (ICES, 2009, Payne et al, 2009, Ulrich et al, 2010), and noise in the catch-at-age matrix could be a potential source of uncertainty. The sometimes large deviations between the model fit and the observations could be the effect of sample variability itself more than of an inappropriate model.

The consequences of these two points are that our results are potentially directly applicable for further investigation in a stock assessment and biological advice perspective. In terms of assessment, it would be important to compare the performances of the current assessment with those of an assessment based on a catch-at-age matrix smoothed by the mixing model. Alternatively, the stability of the seasonal pattern could sustain the implementation of a combined assessment model incorporating the

mixing process, as is currently being developed by Berg and Nielsen (unpublished). In terms of management advice, the current procedure is to use a one-year average in the short-term projections (ICES, 2009), but this could also be potentially replaced by a potentially more robust procedure based on our results. However, it is clear that in spite of the sample variability, the strong explanatory power of the model is largely due to the large number of samples available for the analysis. Therefore, we do not believe that the current model fit should replace the sampling program in the future, but rather that a routine update of the model estimate with the annual sampling data could potentially be more robust for assessment purposes than the current averaging procedure. Our results also advocates for a revision of the sampling programme to get a better coverage of the seasonal pattern of the main stocks in the area.

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Table 1. Summary of the GLMM model fitted on split samples

```

> summary(SplitModel)
Generalized linear mixed model fit by the Laplace approximation
Formula: y ~ 0 + age + lat + long + Q + age:lat + age:long + lat:long + (1 | key) + (1 | year) + (1 | yearclass)
Data: dd.1.m
AIC BIC logLik deviance
4881 5012 -2418 4837
Random effects:
Groups Name Variance Std.Dev.
key (Intercept) 2.86940 1.69393
yearclass (Intercept) 0.65531 0.80951
year (Intercept) 0.41947 0.64767
Number of obs: 2868, groups: key, 925; yearclass, 12; year, 8

Fixed effects:
Estimate Std. Error z value Pr(>|z|)
age1 -2.464997 0.364139 -6.769 1.29e-11 ***
age0 -5.774506 0.398053 -14.507 < 2e-16 ***
age2 0.004183 0.357736 0.012 0.9907
age3 2.409474 0.365285 6.596 4.22e-11 ***
age4 3.531342 0.381420 9.258 < 2e-16 ***
lat -2.226399 0.147279 -15.117 < 2e-16 ***
long -0.106574 0.070411 -1.514 0.1301
Q2 0.255798 0.197639 1.294 0.1956
Q3 2.668511 0.176932 15.082 < 2e-16 ***
Q4 2.667168 0.178886 14.910 < 2e-16 ***
age0:lat 0.198957 0.239806 0.830 0.4067
age2:lat 0.846567 0.127472 6.641 3.11e-11 ***
age3:lat 1.342066 0.182656 7.348 2.02e-13 ***
age4:lat 1.816838 0.216397 8.396 < 2e-16 ***
age0:long 0.326062 0.138132 2.361 0.0182 *
age2:long 0.346978 0.063410 5.472 4.45e-08 ***
age3:long 0.727386 0.079457 9.154 < 2e-16 ***
age4:long 0.900302 0.085278 10.557 < 2e-16 ***
lat:long 0.459213 0.100131 4.586 4.52e-06 ***
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

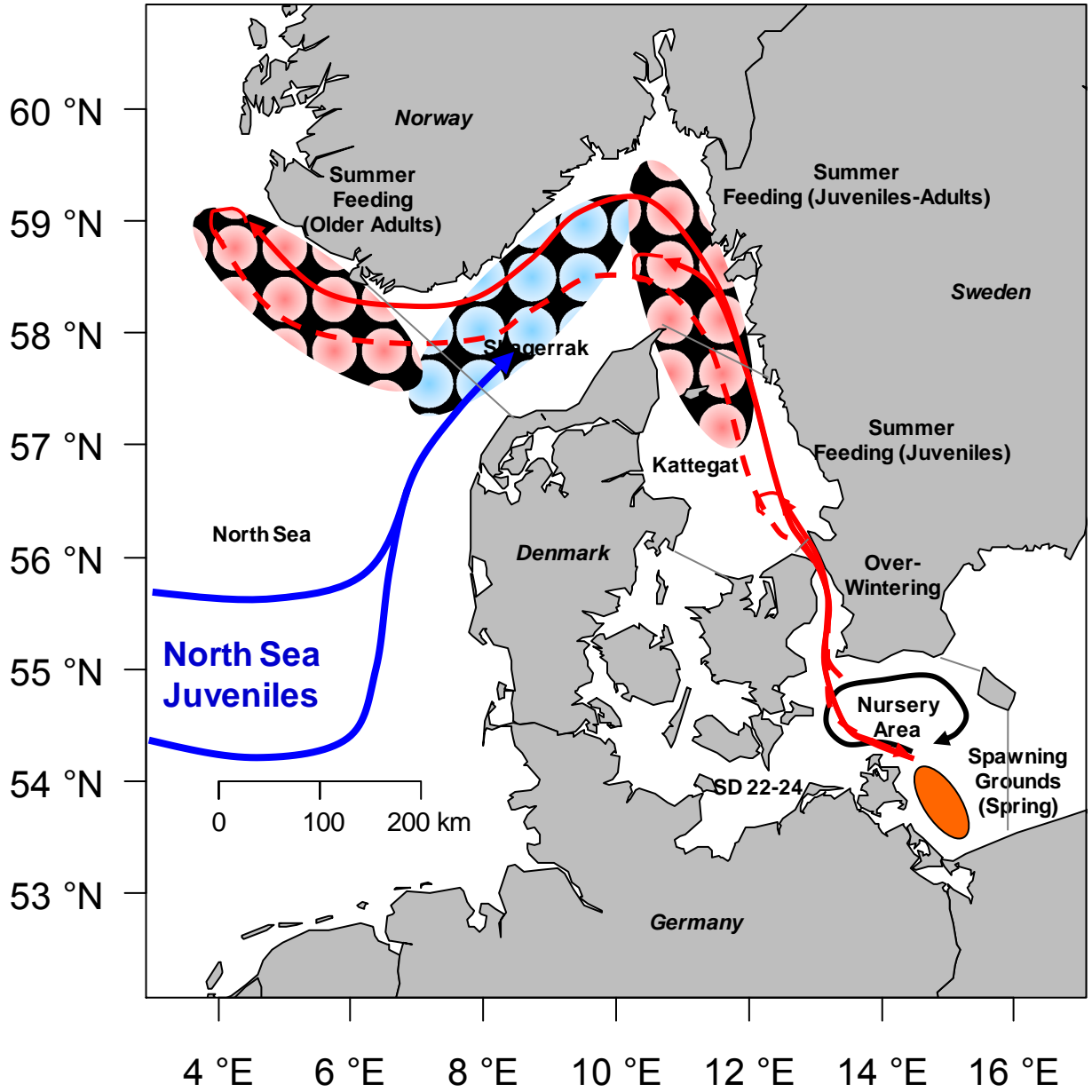


Figure 1. Qualitative summary of herring migrations

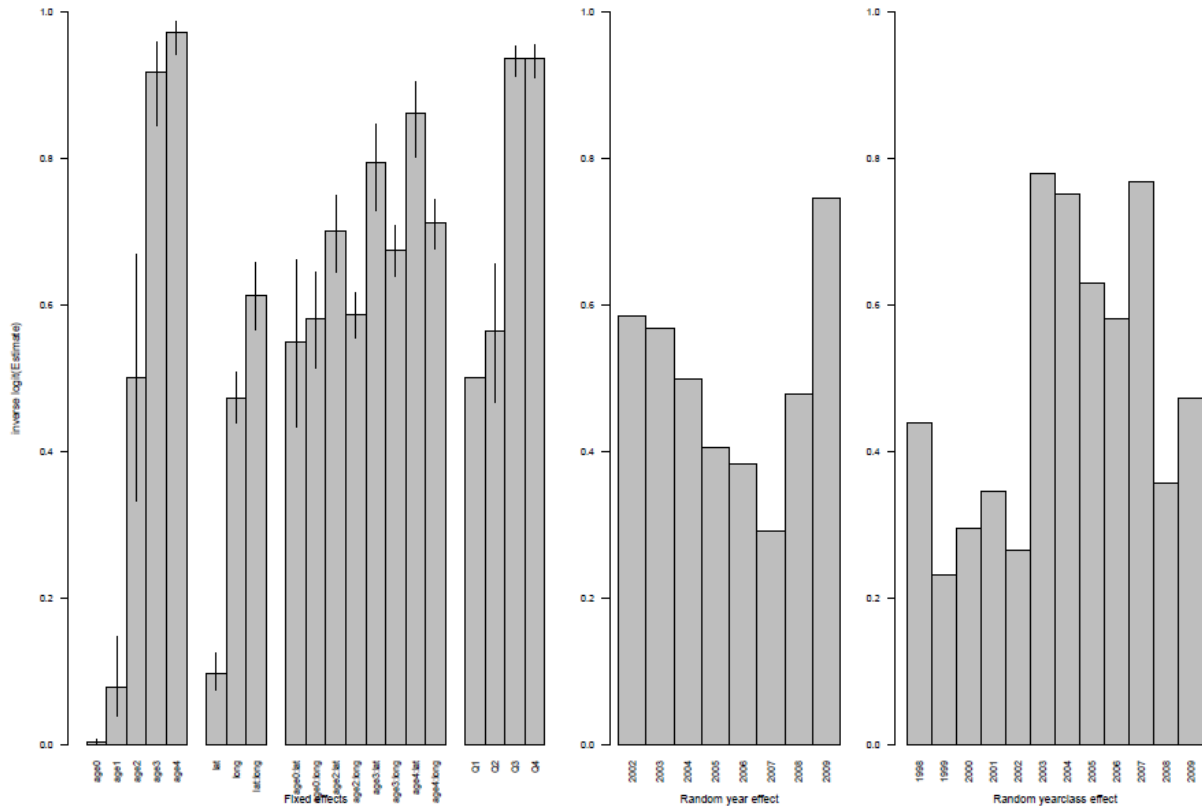


Figure 2. GLMM analysis of the split samples. InverseLogit values and confidence intervals for the model fitted with all years included.

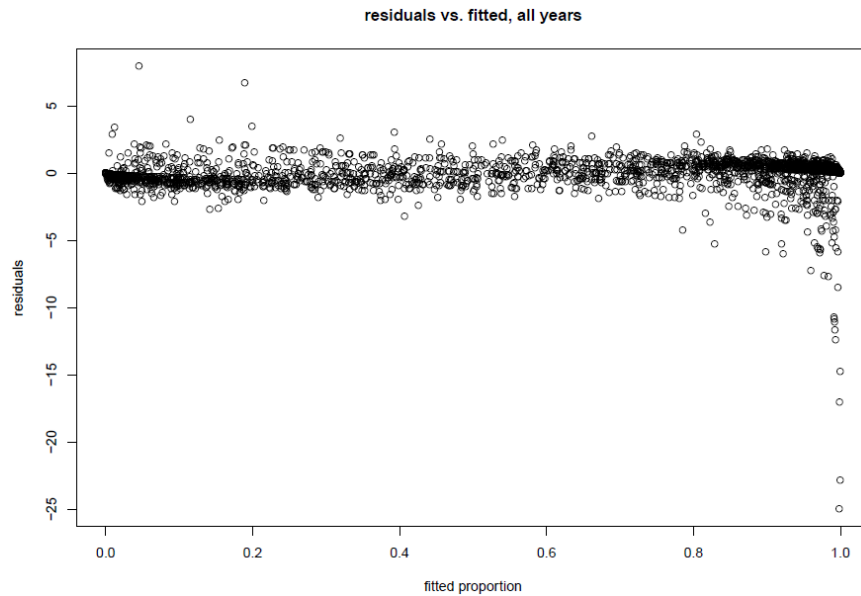


Figure 3. GLMM analysis of the split samples. Residuals (in logit scale) versus fitted proportion.

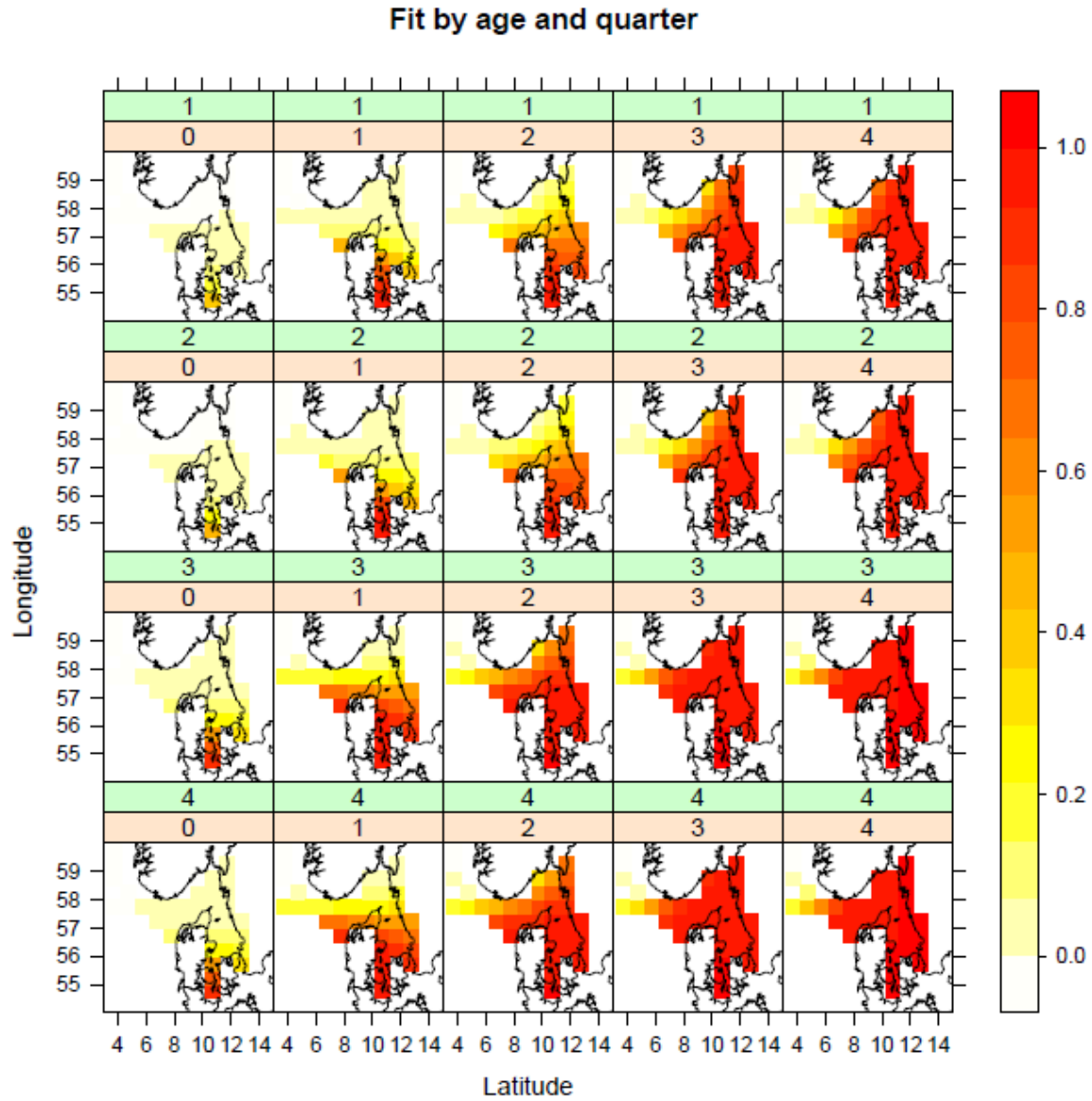


Figure 4. GLMM analysis of the split samples. Average spatial split pattern by age (in rows) and Quarter (in columns)..

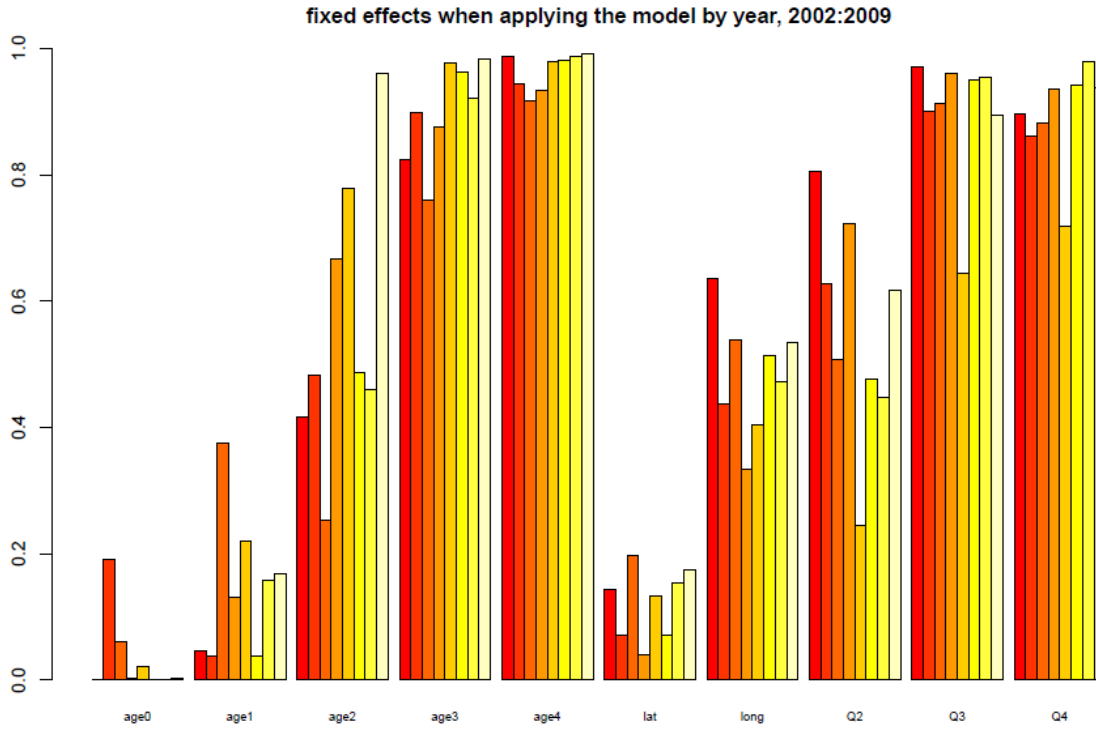


Figure 5. GLMM analysis of the split samples. InverseLogit values of the single fixed effects for the model fitted with each year individually.

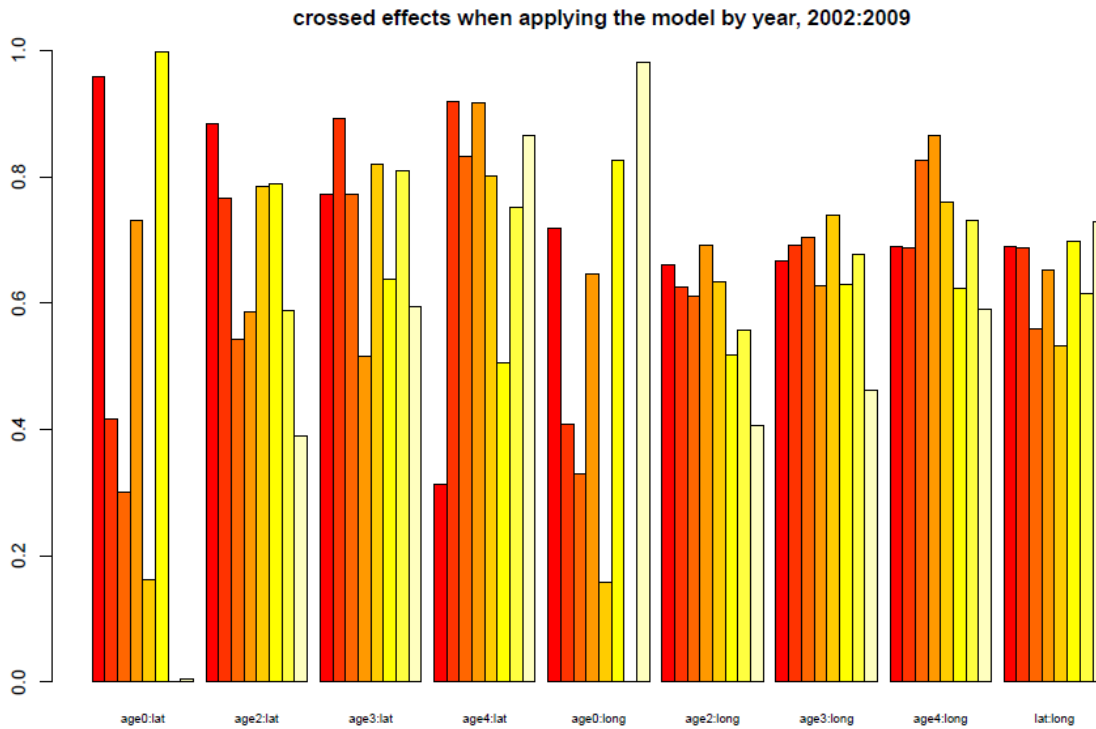


Figure 6. GLMM analysis of the split samples. InverseLogit value of the fixed crossed effects for the model fitted with each year individually.

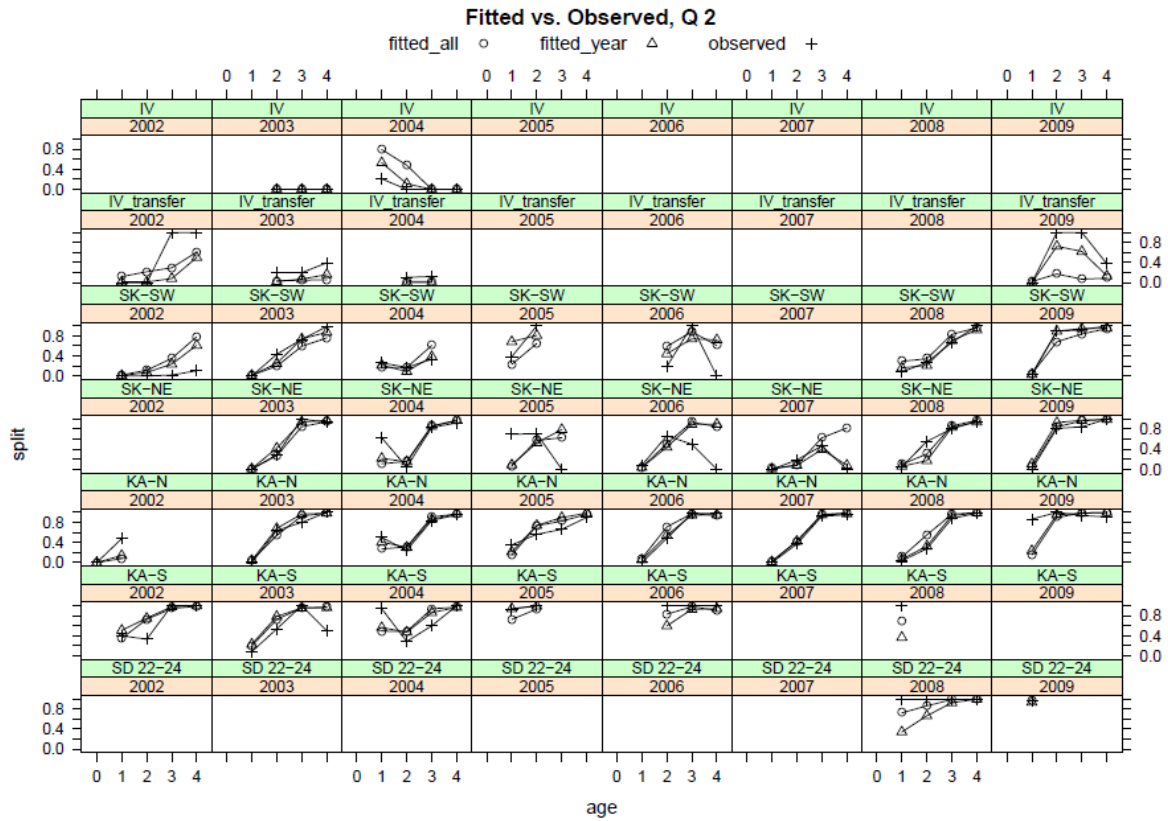
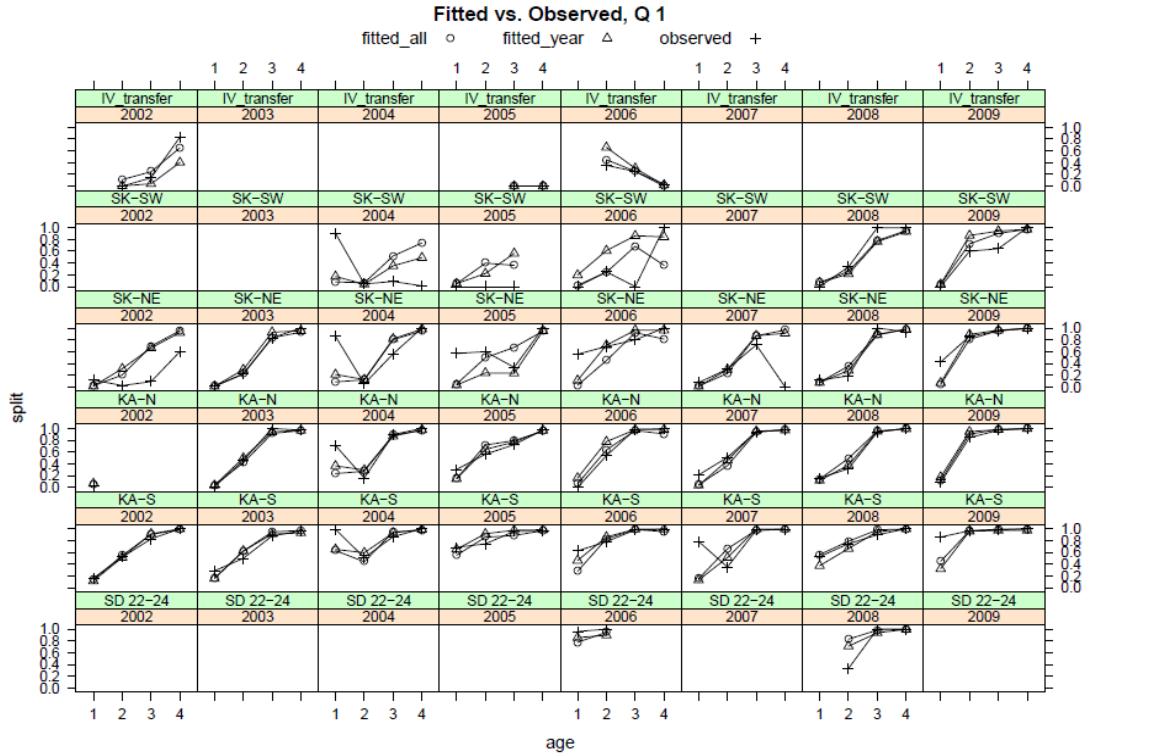


Figure 7. GLMM analysis of the split samples. Fitted vs. Observed, Quarter 1 and 2.

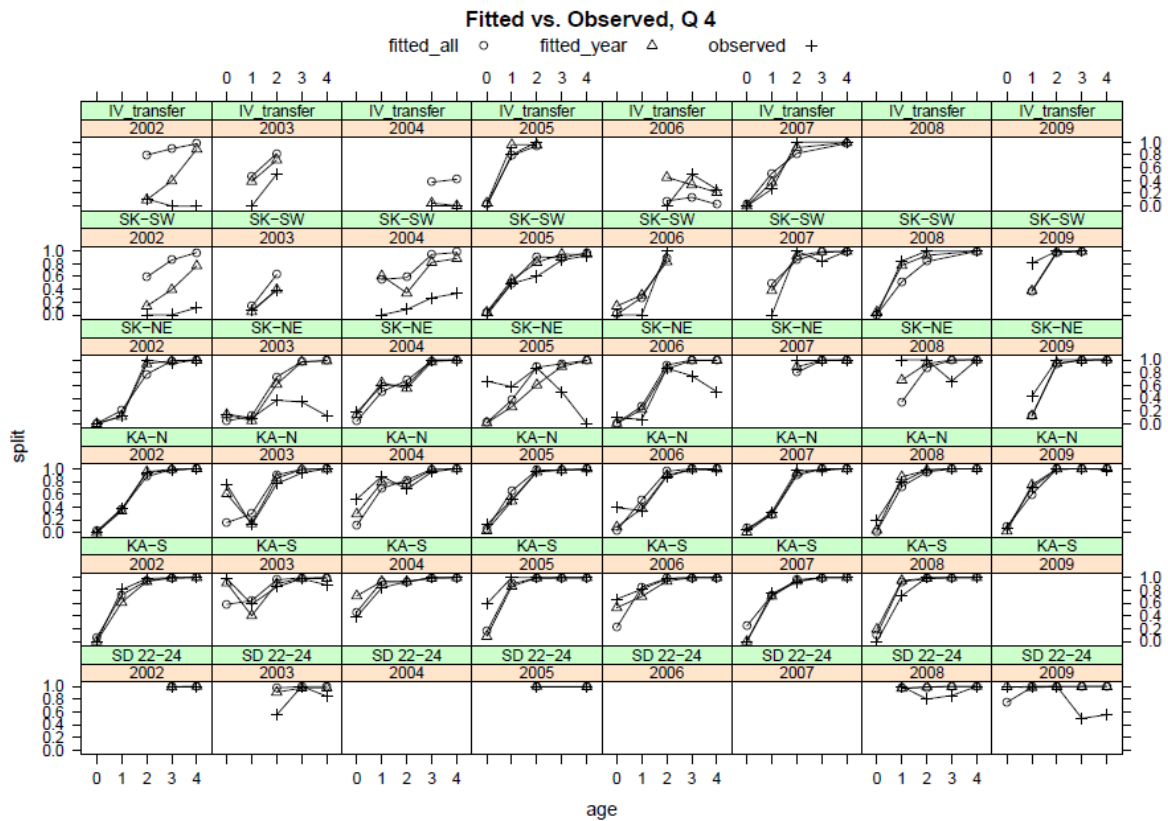
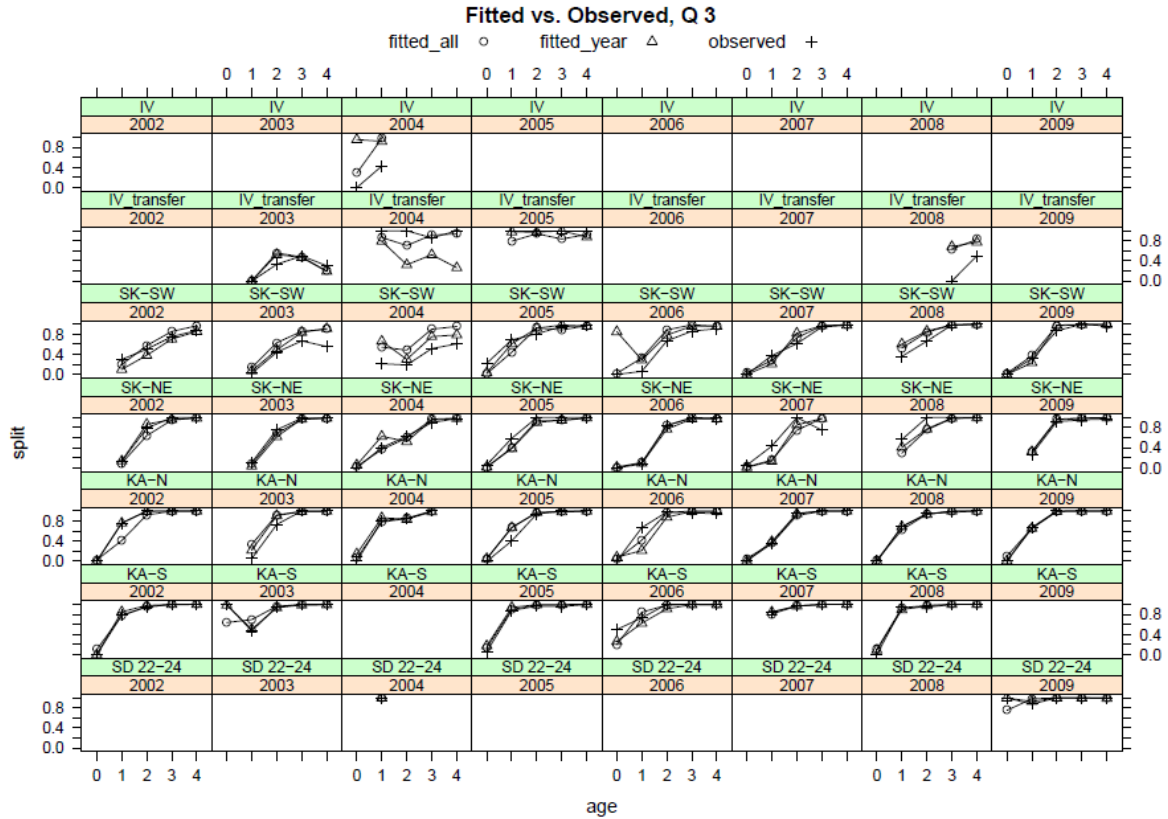


Figure 8. GLMM analysis of the split samples. Fitted vs. Observed, Quarter 3 and 4.

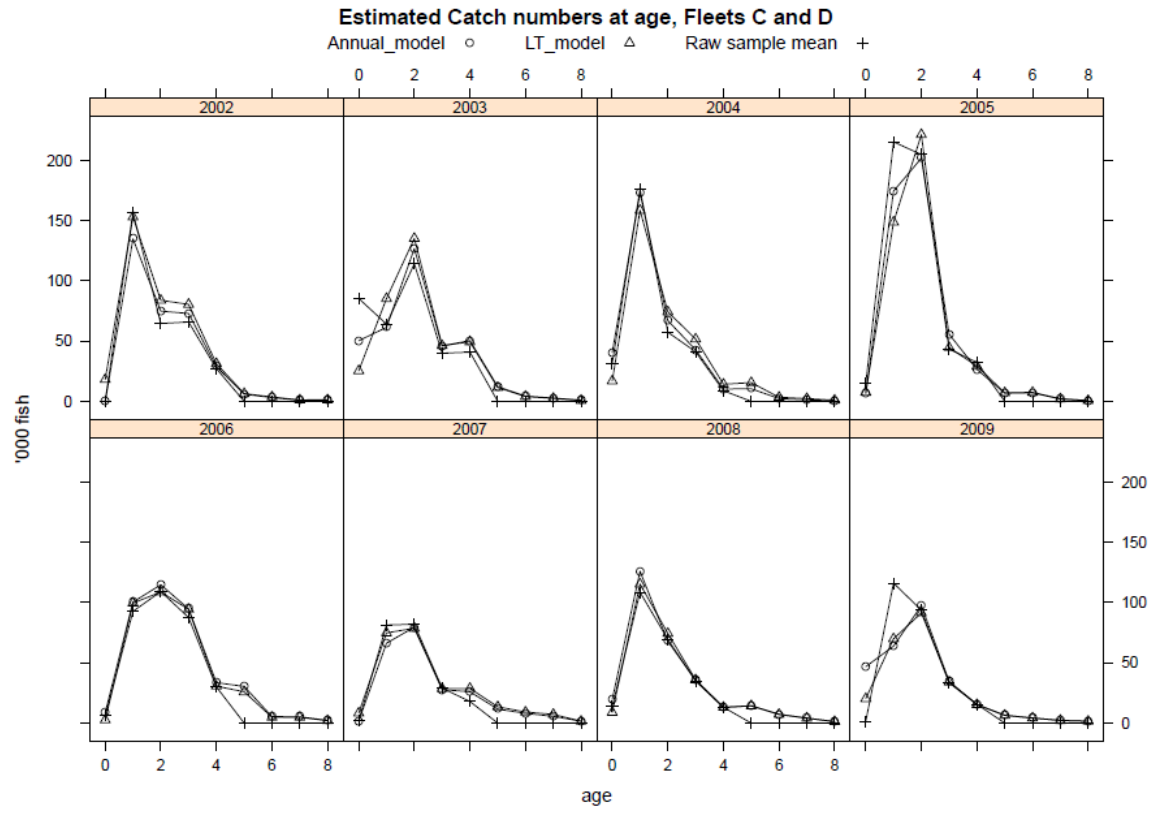


Figure 9. GLMM analysis of the split samples. WBSS age distribution in area IIIa using the three split approaches, all year.

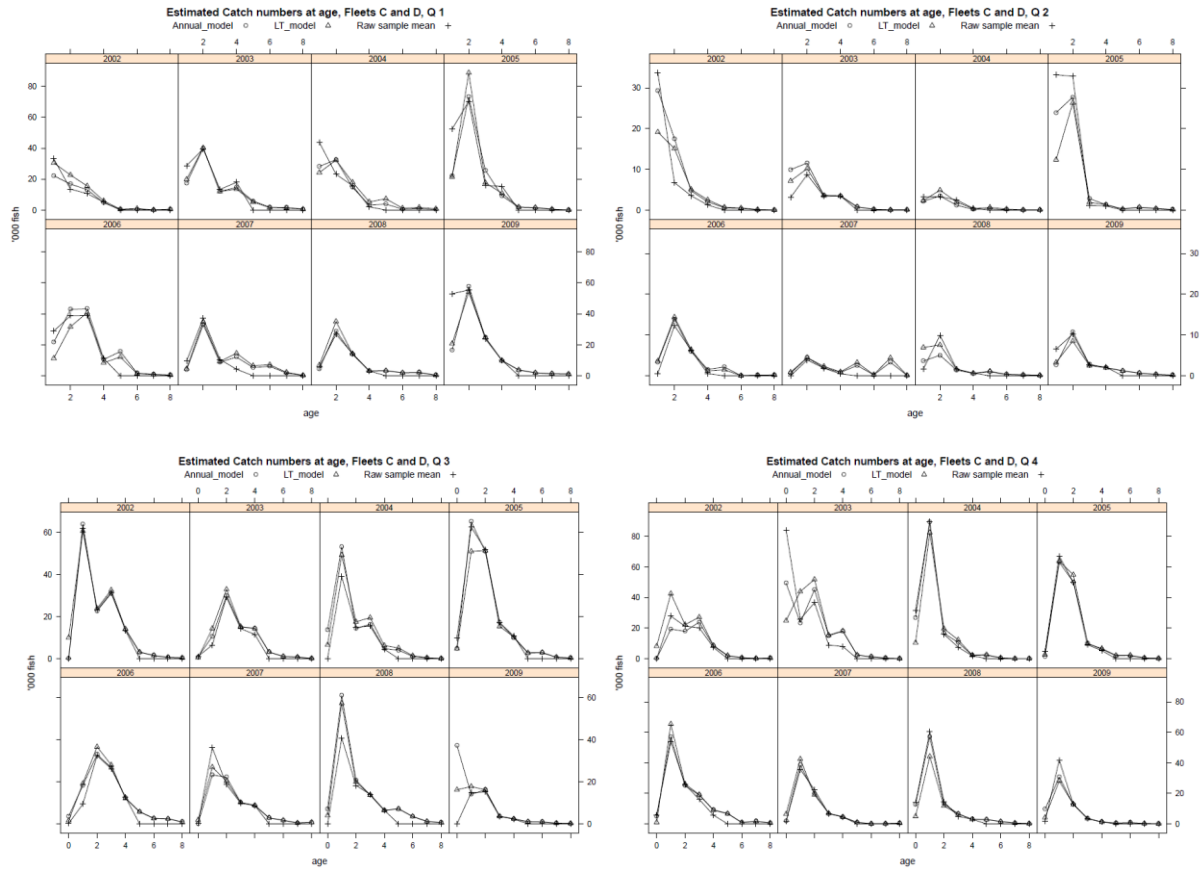


Figure 10. GLMM analysis of the split samples. WBSS age distribution in area IIIa using the three split approaches, by Quarter.