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Calculation of Stock Weight- and Fecundity-at-Age during the Spawning Season Used to Assess the Northern Contingent of Atlantic Mackerel (*Scomber scombrus*)

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The spawning stock of the northern contingent of Atlantic mackerel is currently evaluated with a custom state-space, age-structured stock assessment model. We revised the methods for estimating two key input matrices: stock weight- and fecundity-at-age during the spawning season. The newly calculated weight-at-age did not differ meaningfully from previously used matrices, whereas fecundity-at-age estimates were notably higher and constrained to be less variable than those used in the preceding 2021 assessment. The updated methodology enhances replicability and the revised matrices are considered more biologically realistic. The presented improvements were incorporated into the 2023 assessment, contributing to its accuracy.

1. INTRODUCTION

Since 2017, the stock status of the northern contingent of Atlantic mackerel (*Scomber scombrus*) has been evaluated with a state-space censored catch-at-age stock assessment model (Doniol-Valcroze et al. 2019). This model provides estimates of spawning stock biomass (SSB), recruitment (age 1 fish) and instantaneous fishing mortality (F). The information used to feed the model consists of fisheries-independent data such as an egg production index based on the annual mackerel egg survey and fisheries-dependent data such as catch statistics and biological samples from the commercial fishery. The methods for estimating the stock's weight-at-age (WAA) and fecundity-at-age (FAA) during the spawning season were revised in this research document. The main objective of this revision was to obtain more biologically realistic estimates when assessing temporal trends in age-specific morphological traits by reducing potential sources of bias such as size-selectivity of gear (Myers and Hoenig 1997, Thorson and Simpfendorfer 2009) along with heterogeneous spatio-temporal sampling (Gonzalez et al. 2021). The revised values were used in the 2023 stock assessment.

1.1. WEIGHT-AT-AGE

The mean WAA of the mackerel stock ($W_{a,y}^{stock}$) is an essential model input to estimate the Spawning Stock Biomass (SSB) on June 1st with the following equation:

$$(eq. 1) SSB_y = \sum_{a=1}^A N_{a,y} W_{a,y}^{stock} P_{a,y},$$

where SSB is the product of stock abundance N in June, mean stock weight W^{stock} and proportion mature P by age class a (with a ranging from 1 to 10+, and 10+ being the plus-group) during the year y . The SSB of the stock in June is essential in determining the stock-recruitment curve and has traditionally also been presented in plots and tables describing stock status. The stock weight-at-age in the above equation ($W_{a,y}^{stock}$) differs from the mean catch WAA ($W_{a,y}^{catch}$), which is used to estimate the total biomass caught by the fishery, based on the Baranov catch equation:

$$(eq. 2) CT_y = \sum_{a=1}^A N_{a,y} \frac{F_{a,y}}{Z_{a,y}} [1 - \exp(-Z_{a,y})] W_{a,y}^{catch},$$

where the total biomass caught by the fishery CT is calculated by multiplying the stock abundance N by the proportion of fish that died because of fishing mortality (F = the instantaneous fishing mortality rate and Z = the instantaneous total mortality rate) and the mean weight W of fish in the catch (W^{catch}), by age class a during the year y .

In previous assessments (e.g., Smith et al. 2022), the annual mean WAA of the fish caught in the commercial catch ($W_{a,y}^{catch}$) was used to impute the WAA of the stock ($W_{a,y}^{stock}$) in January and June. The mean WAA of landed fish was (Smith et al. 2022) and still is (Van Beveren et al. 2024) estimated based on the size composition of the catch, with lengths being transformed into weights using quarterly log-log mass-length linear regressions. Patterns in $W_{a,y}^{catch}$ could therefore reflect true biological fluctuations in fish weight, or more likely, reflects a shift in the landings in terms of seasonality, spatial distribution or gear type, which limits its value for assessing true biological change. However, $W_{a,y}^{stock}$ is essential to the assessment model (see eq. 2). For the first time, we directly estimate $W_{a,y}^{stock}$ in June to improve model accuracy (see eq. 1) and provide a more reliable representation of the biological condition of the stock compared to $W_{a,y}^{catch}$.

The annual catch-based WAA used as input in the previous stock assessments was estimated from the weights of all fish caught in the commercial fishery regardless of time of the year, then

smoothed by way of cubic splines, with a smoothing factor of 0.5, to avoid biologically unrealistic changes (Figure 1A). Although the impact of smoothing was demonstrated to have little impact on the model result (Smith et al. 2022), a less subjective smoothing method would be preferable such as mixed-effects models that filter out noise, fill in missing values and consider years and cohort effect (Cadigan 2023). In this research document, we develop a new matrix of stock WAA in June ($W_{a,y}^{stock}$), which is more appropriate for converting stock numbers into stock biomass and which has more biological meaning because the weight of the fish caught only during this period instead of those throughout the year are considered. The SSB, which results from the product of several variables including the WAA, should also be more realistic since we use the weight of mature fish exactly at the time of the spawning season (Brosset et al. 2020; Van Beveren et al. 2022).

1.2. FECUNDITY-AT-AGE

The annual FAA of mature fish ($fec_{a,y}$) is another important input variable into the stock assessment model. It is used to link estimates of fish abundance to observations of Total Egg Production (TEP) :

$$(eq. 3) TEP_y = q \sum_{a=1}^A N_{a,y} \exp(-Z_{a,y} t_s) fec_{a,y} Fem_{a,y} P_{a,y},$$

where TEP in year y corresponds to the product of June fish abundance ($N_{a,y} \exp(-Z_{a,y} t_s)$, where t_s is either the timing of the survey or June), fecundity (fec), the proportion of females (Fem) and the proportion mature fish (P), summed over all age-classes a (1 to 10+) and multiplied by a catchability coefficient (q), as the index is assumed to be relative.

In the previous stock assessment, the annual fecundity of female mackerel during the spawning season was for the first time disaggregated by age (Figure 1B; Smith et al. 2022), to reflect the recent changes in the assessment model proposed following the management strategy evaluation (MSE) carried out by Van Beveren et al. (2020a,b). The results of a study on West-Atlantic mackerel fecundity (Pelletier 1986) were used to model fecundity of stage 5 (i.e., ripe) females (fec_i) as a function of their respective gonad masses (GM_i) and age (a_i), using the following equation :

$$(eq. 4) \log(fec_i) = \alpha + \beta_1(GM_i) + \beta_1(a_i) + \varepsilon_i$$

Smith et al. (2022) estimated this relationship using a generalized linear model with a Gaussian distribution and identity link function. Model coefficients were then used to predict individual fecundities of the stage 5 females in the commercial fishery samples, collected during the months of June and July in the Northwest Atlantic Fisheries Organization (NAFO) Division 4T. The annual mean FAA was previously obtained by averaging the model-predicted fecundities by age. Missing combinations of year and age were filled via linear interpolation for ages 2 to 10+ and fecundity of age 1 females was extrapolated using the model coefficients (eq. 4).

In this research document, the model used to predict FAA was revised. We verified whether assumptions and conditions for the linear regression (i.e. independence of errors, homoscedasticity, normality of error distribution) were met, as those elements were not discussed at the last stock assessment. Other combinations of explanatory variables were also evaluated in order to improve the reliability and accuracy of the FAA matrix.

2. METHODS

2.1. DATA

2.1.1. Biological data

Samples of Atlantic mackerel are acquired annually through the Department of Fisheries and Oceans Canada's (DFO) commercial port sampling program. The number of samples requested by each region, month and gear type is proportional to the anticipated landings in that category. Port samplers first collect a random sample of at least 150 mackerel from a landing and record the length-frequency of these fish, with 5 mm precision. They then send a length-stratified subsample of two fish per length-class to the Maurice-Lamontagne Institute (MLI) for further analyses. Technicians at MLI determine the biological characteristics of each fish; fork-length (nearest 1 mm), mass (nearest 0.1 g), sex, gonad mass (nearest 0.01 g), maturity stage and age standardized to January 1st through examination of the otoliths. The biological database contains information from 1973 to the year of the assessment.

2.1.2. Fecundity data

Pelletier et al. (1986) estimated the fecundity of 214 female West-Atlantic mackerel ready to spawn (stage 5 gonads) caught between May and August of 1982 to 1985. Fish were collected from the commercial fleet in the Gulf of St. Lawrence and on the southeastern coast of Nova Scotia. Defrosted gonads were placed in modified Gilson's fluid to release the eggs, before being filtered to retain eggs equal to or greater than 140 μm . Eggs were kept in different volumes of water (1000 to 4000 ml) and 2 to 6 sub-samples of 1 ml were taken then placed in a petri dish to count the number of eggs. Fecundity of each fish was estimated by multiplying the mean egg count across subsamples (number of eggs/ml) by the dilution factor (ml) based on the method described by Walsh (1983).

2.2. ESTIMATION OF WEIGHT-AT-AGE

The mean WAA of mackerel on June 1st was estimated with biological samples from the commercial fishery. After age-weight outliers were removed, the weights of all fish from selected NAFO Divisions, gear type and period were averaged by year and age class (with ages 10+ grouped together). The assessment model is not sex-specific, and mackerel does not have sex-specific growth (Neja 1990, Villamor et al. 2004), so this factor was omitted. Based on a resampling protocol, highly uncertain values resulting from an insufficient number of weighed fish were removed, before a noise-reduction and gap-filling model was applied. Details of each step are described below.

2.2.1. Outlier removal

Outliers can have a non-negligible effect on the estimation of the mean weight of each age class. To check if outliers were present in the complete biological database, all the individual fish weighed since 1973 were aggregated by age. Extreme weights outside the 0.01 - 99.9 percentiles by age were removed from subsequent analyses (Figure 2).

2.2.2. Sample selection

From 1973 to 2022, most of the biological samples of Atlantic mackerel were collected from June to October. We are however only interested in the weight of fish during the spawning season, which mostly occurs from June to July (Brosset et al. 2020, Van Beveren et al. 2022). Samples from both months were selected and combined, as they reflect the entire period of

interest. There was no significant difference in fish weight-at-age between June and July in all years (Figure 3). Samples outside the period of interest cannot be used to inform fish weight during the spawning period, because in this fishery changes in the timing of fishing and thus sample collection correlate with changes in space and gear type, and their effect on growth is confounded (Thorson and Simpfendorfer 2009).

Fish sampled in June and July were caught in various NAFO divisions and with different gear types. Most samples originated from NAFO Divisions 4V, 4W, 4X, and in particular 4T (Figure 4), which is the main spawning area of the northern contingent of Atlantic mackerel (Grégoire 2012, 2013, Van Beveren et al. 2022). Across all indicated divisions, fish were predominantly sampled from landings of stationary uncovered pound nets, gillnets (unspecified type), driftnets, set gillnets along with hooks and lines (Figure 5). There is a trade-off between bias and uncertainty in sample selection of NAFO divisions and gear type; combining multiple gear types or regions might create a slight bias if there is a difference in selectivity and change in sample availability, but combining data from multiple divisions and gear types might reduce uncertainty as the number of available samples increases. There is insufficient information to appropriately determine the effect of differences in selectivity. We therefore explored the impact of subsetting by NAFO division and gear type by considering four different combinations (Figure 6):

1. 4T + gillnets;
2. 4T + gillnets & hooks and lines;
3. 4TVWX + gillnets;
4. 4TVWX + gillnets & hooks and lines.

For each selection of samples, the weight of all fish of a given age and year class was averaged and the standard deviation was determined.

2.2.3. Determining the minimum number of fish needed

There were some combinations of age and year where the number of fish sampled was insufficient to precisely estimate the weight parameters (mean and standard deviation). To obtain a better idea of the relationship between sample size and precision, we performed a resampling process:

1. Calculate the mean WAA (μ) for all the fish of age a sampled during the whole time series (considered to be the “true” weight of that age class);
2. Randomly sample the weight (x) of i fish of age a (i = sample size) ;
3. Calculate the average weight (\bar{x}) of the sampled fish (considered to be the “estimated” weight of that age class) and calculate the relative error ($\frac{\mu - \bar{x}}{\bar{x}}$);
4. Repeat steps 2 to 3 for all sample sizes $i = 1, \dots, 100$;
5. Repeat steps 2 to 4 until 1000 iterations are reached;
6. For each samples size (i), calculate the mean relative error and the 95% confidence interval across the 1000 iterations.

The result of the resampling process was plotted (Figure 7) and used to determine a minimum number of fish needed to estimate fish WAA. Note that the algorithm should slightly overestimate potential error, as all years were pooled together to obtain a “true” reference weight, thereby overestimating population variance and thus potential error. A minimum threshold of 10 fish was used to determine WAA, as this is when potential relative error started

to level off (Figure 7). Based on the simulation results, relative error in WAA is highly unlikely to exceed 10% for ages 3+ (Table 1).

2.2.4. Filling in the gaps and smoothing the matrix

The WAA matrix is noisy and small amplitude variations might not be representative of true population changes. In order to filter out noise and fill in gaps for missing age and year combinations, a mixed-effect model developed by Cadigan (2023) and written in TMB (Template Model Builder; Kristensen et al. 2016) was used. The mean annual WAA (W_{ay}) is predicted as follows:

$$(\text{eq. 5}) \log(W_{ay}) = \text{Age}_a + \text{Year}_y + \text{Cohort}_c + \text{Age}_a * \text{Year}_y + \varepsilon_{ay},$$

where Age_a is a fixed effect parameter of length A (number of age classes), Year_y is a random effect parameter of length Y (number of years) that follows a Gaussian first-order autoregressive (AR1) process (with parameters ρ_{Year} and σ_{Year}), Cohort_c is a random effect parameter of length C (number of cohorts) that also follows a Gaussian AR1 process (with parameters ρ_{Cohort} and σ_{Cohort}), $\text{Age}_a * \text{Year}_y$ is a random effect parameter matrix (dimension $A * Y$) that follows a separable Gaussian AR1 process for age and year (with parameters ρ_{devAge} , ρ_{devYear} and σ_{dev}) and ε_{ay} are the residuals. The latter are based on the standard deviation associated with each quantity ($\varepsilon_{ay} \sim N(0, \sigma_{\text{pred}})$), but can be multiplied by a regularization term (l ; $\sigma_{\text{pred}} = \sigma_{\text{pred}} * l$) to drive the result towards a more realistic solution (see shrinkage or regularization). For predictions of the weight-at-age, no shrinkage on the error was applied to avoid over-smoothing.

2.3. ESTIMATION OF FECUNDITY-AT-AGE

Pelletier (1986) provided linear models that described the relationships in log space between fecundity and gonad mass, length, age, fish weight or day of the year. This study is currently the most valid and recent information about the effect of different factor on fecundity of the northern contingent Atlantic mackerel. Variations in mackerel fecundity were best explained by gonad weight (GW ; Table 2), and this relationship was therefore applied to estimate annual fecundity during many stock assessments ($\log_{10}(\text{fec}_i) \sim 4.32 + 0.75 * \log_{10}(GW_i)$; including Smith et al. 2020). To estimate fecundity per age class during the 2021 stock assessment, a new linear model explaining fecundity as a function of both gonad weight and age was used ($\log(\text{fec}_i) \sim 1.24 + 0.0139 * a_i + 0.008.23 * GW_i$; Smith et al. 2022). Both explanatory variables are correlated (Person's coefficient of 0.57, Figure 8) and should not have been included in the same model. We hence present a new model and approach to predict FAA.

2.3.1. Model to predict fish fecundity

Mackerel fecundity is related to factors such as fish age, length, weight, gonad mass, its gonadosomatic index (GSI), which is the ratio between gonad and body weights, and the day of the year (DOY) the fish was captured. Variables associated with fish life history (age, length, weight, gonad mass) are unsurprisingly all positively correlated (Figure 8). We therefore focussed on age in combination with the GSI as predictors, as the GSI has more explanatory power than the correlated DOY (Table 2, Figure 8). There was no correlation between the GSI and age (Variance Inflation Factor = 1.02).

Linear models with and without an interaction term were considered (R package *stats*, *lm* function):

1. $\log(\text{fec}_i) \sim \beta_0 + \beta_1 * \log(a_i) + \beta_2 * \log(\text{GSI}_i) + \varepsilon_i$
2. $\log(\text{fec}_i) \sim \beta_0 + \beta_1 * \log(a_i) + \beta_2 * \log(\text{GSI}_i) + \beta_3 * \log(a_i) * \log(\text{GSI}_i) + \varepsilon_i$

The most parsimonious model was selected based on the Akaike Information Criterion (AIC).

When examining the relationship between fecundity and age and GSI (Figure 8), unidirectional outliers were present, indicating that for certain fish fecundity might have been underestimated, yet never overestimated. Macroscopic determination of pre-spawning fish is subject to error; these low fecundity fish might have been individuals that have already started spawning (stage 6+ fish). In order to give less weight to those values, a robust linear regression was fitted using the *lmRob* function in the *robust* package. The assumptions underlying the linear regressions were investigated graphically (independence of errors, homoscedasticity of residuals, normality of errors).

2.3.2. Prediction of fish fecundity

The linear regression model was employed to predict fecundity of fish in the biological database. First, individual stage 5 females sampled from May to July and aged 2 to 10+ were selected. Individuals with a potentially erroneous age reading or GSI were removed (Figure 9, 10 and 11). The average GSI by age was then calculated and used as the response variable in the linear model to predict fecundity on a log scale, before being back-transformed to provide an FAA matrix. Note that this approach is slightly more precise than the approach used during the 2021 assessment, which involved fecundity prediction on an individual level and subsequent averaging and back-transformation (Smith et al. 2022). Fecundity predictions were not performed outside the scope of age and GSI values on which the linear model was trained (Figure 12). There was no temporal shift over time and lower variability since the mid-1980s in the timing of sample collection (Figure 13) which might have resulted in an overall underestimation of GSI or age and thus fecundity, and we validated that predictions were on the same scale as the original values reported by Pelletier (1986) (Figures 14 and 15).

To determine the minimum number of fish required to obtain an acceptable precision level, a resampling process was performed identical to that applied for the WAA (see section 2.1.2). Results showed that a relatively high number of fish (>20) would need to be analyzed annually per age class to avoid errors in fecundity of >10% (Table 1, Figure 16). However, for most age-year combinations, relatively few data were available (Figure 17), so only FAA estimates based on at least 3 fish were kept based on the first quartile of the number of fish available for all age-year combinations.

Stage 5 females of age 1 were absent from the biological database, which prevents the estimation of their annual fecundity. Age 1 fecundity was therefore estimated by multiplying age 2 fecundity by the ratio of age 1 to age 2 fecundity (0.727) predicted using Pelletier's (1986) model (Table 2, variable "age"). Note that as age 1 fish are mostly immature based on the identification of maturity stages in relation to age of fish sampled annually in the commercial fishery. They contribute relatively little to total egg production, and the impact of any error in the determination thereof on our perception of stock state is tempered.

2.3.3. Filling in the gaps and smoothing the matrix

Like WAA, raw FAA estimates are variable over time, in part as a result of observation and statistical error rather than true biological change. In order to smooth annual values and fill gaps for missing age and year combinations, the mixed-effect model proposed by Cadigan (2023) was again used. In contrast to its application for WAA, an arbitrary shrinkage factor of 0.5 was applied to the coefficients of variation (CV), to reduce the effect of large variations in estimated fecundity of fish of a given age and year class. A slightly poorer output was obtained when fecundity estimates based on few data points were kept but attributed CV higher than 0.5.

3. RESULTS

3.1. WEIGHT-AT-AGE

Trends in and absolute values of WAA were similar for each subset of data combinations (i.e. NAFO Divisions, gear and month), except that more data were available for age 1 fish when including samples from the hook and line fishery (Figure 6). The overall similarity between subsets is a consequence of the dominance of samples from the 4T gillnet fleet; data availability did not increase significantly by including the neighbouring area (4VWX) or a second gear type (hook and line; Figures 18 and 19). Hereafter, WAA is based strictly on fish caught with gillnets in NAFO 4TVWX during June and July, in order to exclude any potential effect of gear selectivity. A region-specific effect is expected to be minor, given most mackerel migrate from 4VWX to 4T during this period.

The mixed-effect model used to smooth the matrix and fill in gaps performed well (Figures 20, 21, 22 and 23). Standardized residuals in relation to year, cohort, age and model predictions were normally distributed and showed no important patterns (Figure 20). An unsurprising small undulating pattern in residuals over time or cohorts was visible, which was however not age-class specific (Figure 20). Standardized residuals were larger for age 2 (Figure 20 and 21). Results of the mixed-effect model showed that, as expected, the age-effect accounts for most of the variation in WAA (Figure 23). The effects of “year” and “cohort” were of similar magnitude.

In previous assessments, June stock WAA was imputed with catch WAA. Despite the clear distinctions in meaning and estimation processes between $W_{a,y}^{stock}$ (presented here) (Table 3, Figure 24) and the previously used $W_{a,y}^{catch}$, there were no major changes in the dominant patterns for ages 2 to 10+ (Figure 25). In both sets of WAA, the largest and sharpest increase occurred from the late 70s to the early- to mid-80s. A smaller bump remained visible around roughly the 1995 cohort. Differences between the two time series were in part related to the level of smoothing; the type and strength of smoothing applied drives the degree of interannual variability. Independent of the smoothing approach applied, $W_{a,y}^{stock}$ was for all ages typically higher during the early years (early to late 70s), indicating that the change in fish weight at the end of the 70s might not have been as pronounced as previously thought. Stock weight of age 1 fish was also lower throughout nearly the entire $W_{a,y}^{stock}$ time series. Age 1 fish contribute relatively little to SSB, and changes in their estimated weight therefore have a relatively small impact on the stock assessment.

3.2. FECUNDITY-AT-AGE

Fecundity was best explained by the age and GSI of the fish ($R^2 = 0.56$; Table 4). Both variables had a significant effect ($p < 0.01$), with the GSI having the largest effect size (Table 5). The model adequately described the data (Figure 26 and 27); the predicted versus observed values followed a 1:1 relationship (Figure 28), residuals were normally distributed (Figures 29 and 30), and residual variance was homogenous (Figure 31).

Results of the mixed-effect model, which properly fitted the data (Figure 32, 33, 34 and 35), showed that the age-effect accounted for most of the variation in FAA. There was also a notable increasing effect of year (Figure 35). The model, after applying a CV shrinkage factor of 0.5, smoothed out all short-term variability, so that only the long-term increase in fecundity across all age classes remained (Figure 34). The 6% increase in fecundity between 1968 and 2022 across all age classes (Table 6, Figure 36) was driven by an overall increase in the GSI (Figure 37).

The new estimates of FAA differed substantially from those presented during the 2021 stock assessment in terms of their order of magnitude, trend, and interannual variability (Figure 38).

For all age classes, the new estimates were 1.5 to 3 times greater than the original estimates and varied substantially less between years, even before we smoothed the series. The new estimates were deemed more realistic, as their order of magnitude corresponded with the observations made by Pelletier (1986) and the approach applied to obtain these estimates of FAA was considered superior in terms of the modelling and validation according to the peer-review process.

4. DISCUSSION

We presented a simple approach to determine the West-Atlantic mackerel WAA in June and a revised approach to calculate FAA. The new WAA is highly similar to the matrix used before, whereas FAA is meaningfully different. Both matrices were smoothed with a state-space model that includes a year, age, and cohort effect, which reflects the underlying biological processes better than the previously applied “loess” function. In addition, potential sources of bias resulting from size-selectivity of fishing gear and heterogenous spatio-temporal sampling have been minimized for both the WAA and the FAA to reflect temporal trends that are more biologically realistic or plausible. Both matrices improve our perception of stock state and were therefore used in the 2023 assessment.

The newly estimated increase in FAA might affect our perception of stock state, as it links observed egg production with fish abundance estimates and, consequently, SSB (see Bernal et al. 2012). When fecundity increases, fewer fish are required to produce the observed number of eggs, which should lead to a proportional decrease in estimated SSB. This minor shift in FAA throughout the time series is biologically plausible. It is attributed to a demonstrated rise in the GSI, for which no source of bias (e.g., due to sampling) could be identified. Long term trends in fecundity are common in small pelagic fish (e.g., Lambert 2008, Brosset et al. 2016, Burbank et al. 2024). Many factors can drive such change, including parental quality (e.g., body condition), food availability, environmental conditions (e.g., temperature) and evolutionary factors (Lambert 2008). Often, shifts in fecundity occur alongside changes in other life-history traits, such as body condition, weight or size (Brosset et al. 2016, Barrett et al. 2022, Burbank et al. 2024). However, for mackerel, there is currently no evidence of a correlation between fecundity or GSI and these other traits, which do not show similar long-term trends as FAA (see Brosset et al. 2016 for body condition estimates and this document for changes in weight).

Further research might be needed to better understand changes in fecundity. Currently, we operate under the assumption that the relationship between fecundity and both GSI and age is time-invariant, due to the lack of data to suggest otherwise. It is however conceivable that this relationship could vary over time, for example due to factors such as average egg size and weight. Egg development processes, which are currently not considered, might also have changed (e.g., atresia or the failure of a follicle to develop, and recruitment of oocytes during the reproductive phase). Moving forward, it will be important, for both FAA and WAA, to ensure that sufficient samples are collected during May to July, ideally including younger fish.

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TABLES

Table 1. Minimum number of fish required to obtain a relative error in weight (WAA) or fecundity (FAA) of 10% or lower, by age class.

Age	Number of fish	
	WAA	FAA
1	35	-
2	25	46
3	10	22
4	10	26
5	10	25
6	10	26
7	11	27
8	9	24
9	8	18
10+	8	22

Table 2. Results of linear regressions relating fecundity of stage 5 female mackerel to various variables. (GSI = Gonadosomatic index, sigma = residual standard deviation, n = number of fish)

Variable	Intercept	Coefficient	R ²	R2 adjusted	sigma	n
Gonad weight	4.34	0.75	0.61	0.61	0.13	221
GSI	4.77	0.93	0.44	0.44	0.16	221
Fish weight	2.75	1.06	0.36	0.36	0.17	222
Day of the year	13.45	-3.48	0.36	0.36	0.17	222
Length	-1.84	2.93	0.26	0.26	0.18	222
Age	5.38	0.46	0.23	0.23	0.19	193

Table 3. Weight-at-age (kg) estimated with the mixed-effect model, based on fish caught with gillnets in June and July in NAFO divisions 4TVWX.

Year	1	2	3	4	5	6	7	8	9	10+
1968	0.128	0.273	0.368	0.434	0.502	0.554	0.593	0.632	0.665	0.718
1969	0.128	0.27	0.361	0.429	0.498	0.55	0.588	0.628	0.661	0.714
1970	0.127	0.268	0.356	0.42	0.491	0.545	0.583	0.623	0.656	0.709
1971	0.128	0.267	0.353	0.415	0.481	0.537	0.578	0.617	0.65	0.703
1972	0.128	0.268	0.352	0.411	0.474	0.526	0.569	0.61	0.643	0.696
1973	0.127	0.267	0.352	0.409	0.469	0.517	0.556	0.6	0.635	0.687
1974	0.132	0.277	0.365	0.426	0.486	0.533	0.569	0.611	0.651	0.707
1975	0.139	0.289	0.381	0.444	0.509	0.554	0.589	0.628	0.665	0.727
1976	0.146	0.299	0.39	0.454	0.52	0.569	0.601	0.638	0.671	0.729
1977	0.151	0.31	0.4	0.46	0.527	0.576	0.612	0.644	0.675	0.728
1978	0.156	0.321	0.413	0.47	0.533	0.582	0.617	0.654	0.679	0.73
1979	0.161	0.332	0.429	0.488	0.547	0.591	0.626	0.663	0.693	0.739
1980	0.167	0.35	0.454	0.518	0.579	0.619	0.649	0.686	0.717	0.769
1981	0.168	0.365	0.48	0.549	0.617	0.658	0.682	0.714	0.744	0.798
1982	0.163	0.359	0.488	0.568	0.639	0.685	0.709	0.733	0.757	0.81
1983	0.154	0.335	0.462	0.556	0.636	0.682	0.709	0.733	0.748	0.793
1984	0.15	0.317	0.435	0.53	0.627	0.684	0.713	0.739	0.753	0.789
1985	0.148	0.313	0.416	0.504	0.604	0.682	0.722	0.75	0.768	0.803
1986	0.147	0.308	0.408	0.479	0.57	0.652	0.715	0.755	0.774	0.813
1987	0.144	0.303	0.398	0.466	0.539	0.612	0.679	0.742	0.774	0.814
1988	0.141	0.301	0.398	0.461	0.531	0.586	0.646	0.715	0.772	0.825
1989	0.139	0.296	0.397	0.464	0.529	0.582	0.622	0.685	0.748	0.828
1990	0.139	0.29	0.387	0.459	0.527	0.575	0.613	0.654	0.71	0.796
1991	0.137	0.29	0.381	0.449	0.523	0.574	0.607	0.646	0.68	0.757
1992	0.137	0.286	0.379	0.439	0.51	0.567	0.603	0.636	0.667	0.722
1993	0.137	0.286	0.375	0.439	0.501	0.555	0.598	0.635	0.661	0.712
1994	0.139	0.291	0.38	0.44	0.507	0.552	0.592	0.638	0.668	0.713
1995	0.14	0.297	0.391	0.451	0.514	0.566	0.597	0.64	0.679	0.73
1996	0.14	0.299	0.399	0.464	0.527	0.572	0.611	0.643	0.68	0.741
1997	0.14	0.3	0.402	0.474	0.542	0.587	0.619	0.659	0.685	0.743
1998	0.141	0.301	0.404	0.478	0.554	0.604	0.636	0.668	0.703	0.749
1999	0.14	0.299	0.4	0.475	0.553	0.611	0.647	0.679	0.704	0.76
2000	0.137	0.295	0.396	0.468	0.545	0.606	0.651	0.687	0.711	0.757
2001	0.136	0.29	0.391	0.464	0.54	0.6	0.647	0.693	0.722	0.767
2002	0.135	0.284	0.379	0.452	0.528	0.586	0.632	0.68	0.719	0.769
2003	0.134	0.281	0.371	0.439	0.514	0.573	0.617	0.664	0.705	0.764
2004	0.132	0.278	0.367	0.428	0.498	0.558	0.602	0.647	0.688	0.749
2005	0.132	0.277	0.366	0.426	0.489	0.543	0.59	0.635	0.674	0.735
2006	0.131	0.278	0.367	0.428	0.491	0.538	0.579	0.627	0.667	0.726
2007	0.132	0.277	0.367	0.428	0.492	0.538	0.572	0.614	0.657	0.717
2008	0.134	0.282	0.37	0.435	0.498	0.546	0.579	0.614	0.651	0.714
2009	0.136	0.288	0.379	0.441	0.509	0.556	0.592	0.626	0.655	0.713
2010	0.137	0.29	0.384	0.448	0.512	0.564	0.598	0.635	0.663	0.712
2011	0.138	0.292	0.387	0.454	0.52	0.567	0.606	0.641	0.671	0.72
2012	0.137	0.29	0.386	0.453	0.521	0.571	0.604	0.643	0.672	0.722

Year	1	2	3	4	5	6	7	8	9	10+
2013	0.138	0.291	0.387	0.454	0.524	0.576	0.611	0.645	0.678	0.727
2014	0.14	0.297	0.391	0.46	0.531	0.585	0.624	0.661	0.688	0.742
2015	0.14	0.297	0.395	0.46	0.532	0.587	0.627	0.667	0.697	0.745
2016	0.138	0.294	0.393	0.461	0.529	0.584	0.624	0.665	0.698	0.749
2017	0.137	0.289	0.387	0.458	0.528	0.578	0.619	0.66	0.694	0.747
2018	0.137	0.289	0.384	0.455	0.529	0.583	0.618	0.66	0.695	0.75
2019	0.138	0.289	0.383	0.449	0.524	0.581	0.621	0.658	0.693	0.748
2020	0.14	0.293	0.385	0.451	0.52	0.578	0.622	0.663	0.693	0.749
2021	0.141	0.298	0.391	0.455	0.523	0.576	0.622	0.668	0.702	0.753

Table 4. Comparison of linear models relating fecundity to fish age and/or the gonadosomatic index (GSI), with or without an interaction effect, based on data from Pelletier (1986). (AIC = Akaike Information Criterion, R^2 = variance explained)

Equation	AIC	R^2	Δ AIC
$\log(\text{fecundity}) \sim \log(\text{GSI}) + \log(\text{age})$	-415	0.56	0
$\log(\text{fecundity}) \sim \log(\text{GSI}) + \log(\text{age}) + \log(\text{GSI}) * \log(\text{age})$	-413	0.56	2
$\log(\text{fecundity}) \sim \log(\text{GSI})$	-359	0.41	56
$\log(\text{fecundity}) \sim \log(\text{age})$	-309	0.23	106

Table 5. Result of the robust linear regression relating mackerel pre-spawning (stage 5) fecundity (log-scale) with fish age and the gonadosomatic index (GSI), based on data from Pelletier (1986).

Coefficient	Estimate	Standard error	t-value	p-value
Intercept	10.80	0.22	49.97	< 2e-16
$\log(\text{GSI})$	0.71	0.08	8.38	1.36-14
$\log(\text{age})$	0.41	0.06	7.31	8.00e-12

Table 6. Fecundity-at-age estimated with the mixed-effect model, based on samples collected from May to July.

Year	1	2	3	4	5	6	7	8	9	10+
1968	265110	364670	463776	534883	599311	646487	664760	727743	750829	818377
1969	264716	364127	463085	534087	598419	645525	663770	726659	749711	817159
1970	264304	363561	462365	533256	597488	644521	662738	725529	748545	815889
1971	263875	362971	461614	532390	596518	643474	661662	724351	747330	814564
1972	263427	362355	460831	531487	595506	642383	660540	723123	746062	813182
1973	262961	361713	460015	530546	594451	641245	659370	721842	744741	811742
1974	262474	361044	459164	529564	593351	640059	658150	720506	743363	810240
1975	262286	360786	458836	529185	592927	639601	657679	719991	742831	809660
1976	262325	360839	458903	529264	593014	639695	657776	720097	742941	809780
1977	262461	361026	459140	529537	593321	640026	658116	720469	743325	810198
1978	262549	361148	459296	529716	593521	640242	658338	720713	743576	810472
1979	262639	361271	459453	529897	593724	640461	658563	720959	743830	810749
1980	262619	361243	459417	529856	593679	640412	658513	720904	743773	810687
1981	262499	361079	459208	529615	593408	640120	658212	720575	743434	810317
1982	262429	360982	459085	529474	593250	639949	658037	720383	743236	810101
1983	262630	361259	459437	529879	593704	640439	658541	720934	743805	810721
1984	263061	361851	460191	530748	594678	641490	659621	722117	745025	812051
1985	263777	362836	461442	532192	596296	643235	661415	724081	747051	814260
1986	264601	363969	462884	533854	598158	645244	663481	726343	749385	816804
1987	265071	364616	463706	534803	599221	646390	664660	727634	750716	818255
1988	265567	365299	464575	535804	600343	647601	665905	728996	752122	819787
1989	266013	365912	465354	536704	601351	648688	667023	730220	753385	821164
1990	266358	366387	465958	537400	602131	649530	667889	731168	754363	822229
1991	266802	366997	466734	538295	603134	650611	669001	732385	755619	823599
1992	267411	367835	467800	539525	604512	652097	670529	734058	757345	825480
1993	268245	368982	469259	541207	606397	654131	672620	736347	759707	828054
1994	268886	369864	470380	542500	607846	655694	674227	738107	761522	830032
1995	269760	371066	471910	544264	609822	657825	676419	740506	763997	832731
1996	270609	372233	473394	545976	611740	659895	678546	742836	766401	835350
1997	271563	373546	475063	547901	613897	662222	680939	745455	769103	838296
1998	272620	375000	476913	550034	616287	664800	683590	748357	772097	841559
1999	274054	376972	479421	552927	619528	668296	687185	752293	776158	845985
2000	275444	378885	481853	555732	622671	671686	690671	756109	780095	850276
2001	276742	380670	484123	558350	625604	674850	693925	759671	783770	854282
2002	277813	382143	485997	560511	628025	677462	696610	762611	786803	857588
2003	278911	383654	487919	562728	630509	680142	699365	765627	789915	860980
2004	279817	384900	489503	564555	632557	682350	701636	768113	792480	863776
2005	281064	386615	491685	567071	635376	685391	704764	771537	796012	867626
2006	282119	388067	493530	569200	637761	687964	707409	774433	799000	870882
2007	282788	388987	494701	570550	639274	689596	709087	776269	800895	872948
2008	283262	389639	495530	571506	640345	690752	710275	777571	802238	874411

Year	1	2	3	4	5	6	7	8	9	10+
2009	283590	390090	496103	572167	641086	691551	711097	778470	803166	875423
2010	284040	390710	496891	573076	642104	692649	712227	779707	804441	876813
2011	284513	391359	497717	574029	643172	693801	713411	781003	805779	878271
2012	284721	391645	498081	574448	643642	694308	713932	781574	806368	878913
2013	285662	392939	499727	576347	645769	696602	716292	784157	809033	881818
2014	286441	394011	501091	577919	647531	698503	718246	786296	811240	884223
2015	287042	394839	502143	579132	648890	699969	719754	787947	812943	886080
2016	287453	395404	502862	579962	649820	700972	720785	789076	814108	887349
2017	287738	395796	503360	580537	650464	701667	721499	789858	814915	888229
2018	287948	396084	503726	580959	650937	702177	722024	790432	815507	888875
2019	288193	396421	504155	581453	651491	702775	722638	791105	816201	889631
2020	287884	395996	503614	580830	650792	702021	721863	790256	815326	888677
2021	287118	394943	502275	579285	649061	700154	719943	788154	813157	886313
2022	286553	394165	501286	578145	647783	698775	718526	786603	811556	884568

FIGURE

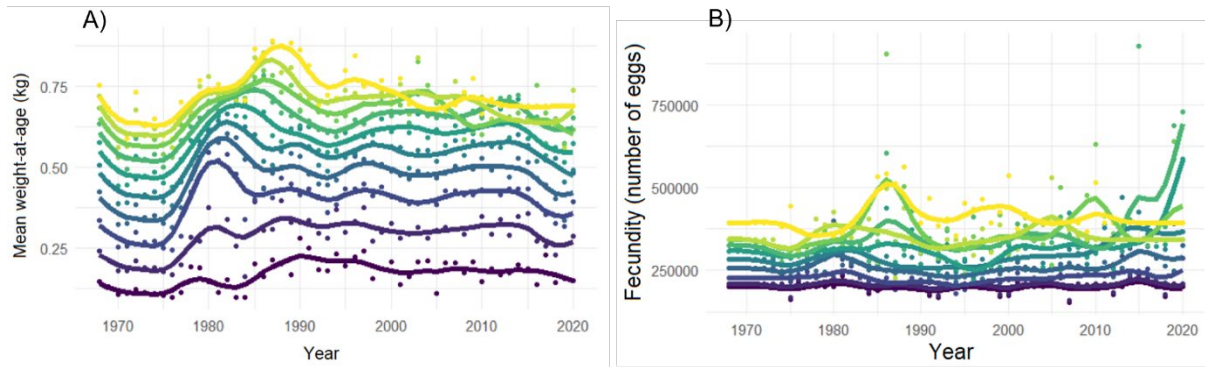


Figure 1. (A) Weight- and (B) fecundity-at-age of Atlantic mackerel used during the 2021 stock assessment. Points indicate raw values and lines are the smoothed values used as model input. Ages range from 1 (purple) to 10+ (yellow). (Adapted from Smith et al. 2022).

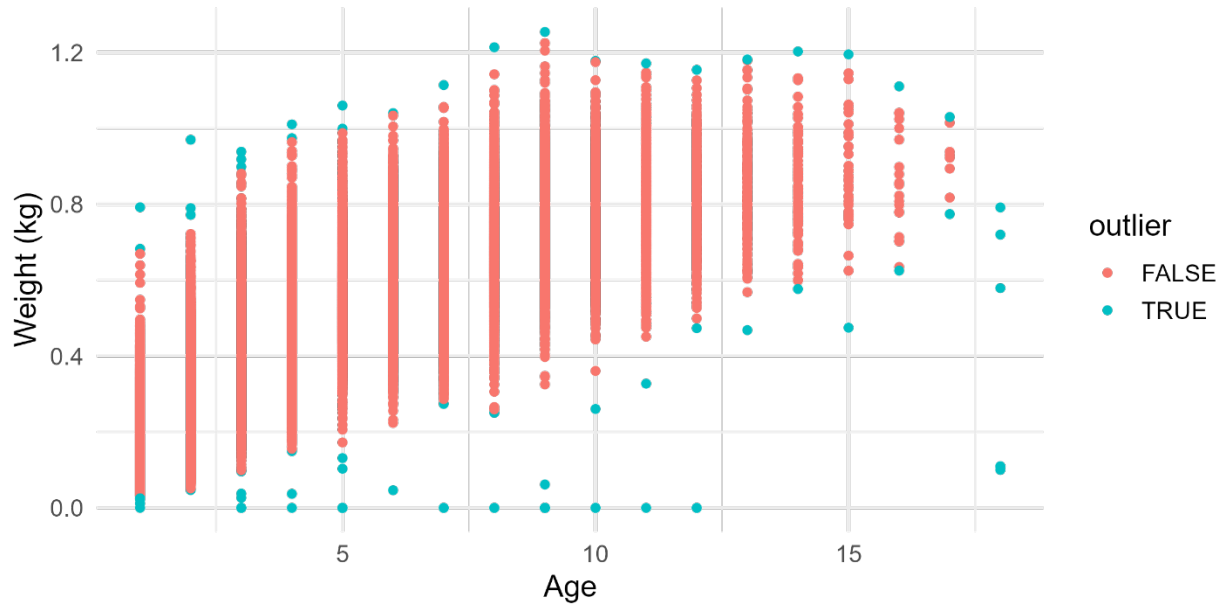


Figure 2. Weight-at-age of Atlantic mackerel sampled in June and July. Outliers are indicated in blue and were removed from the calculation of annual weight-at-age.



Figure 3. Boxplots of annual mackerel weight-at-age in June and July. The age is indicated above each graph. Age class 10 is a plus-group.

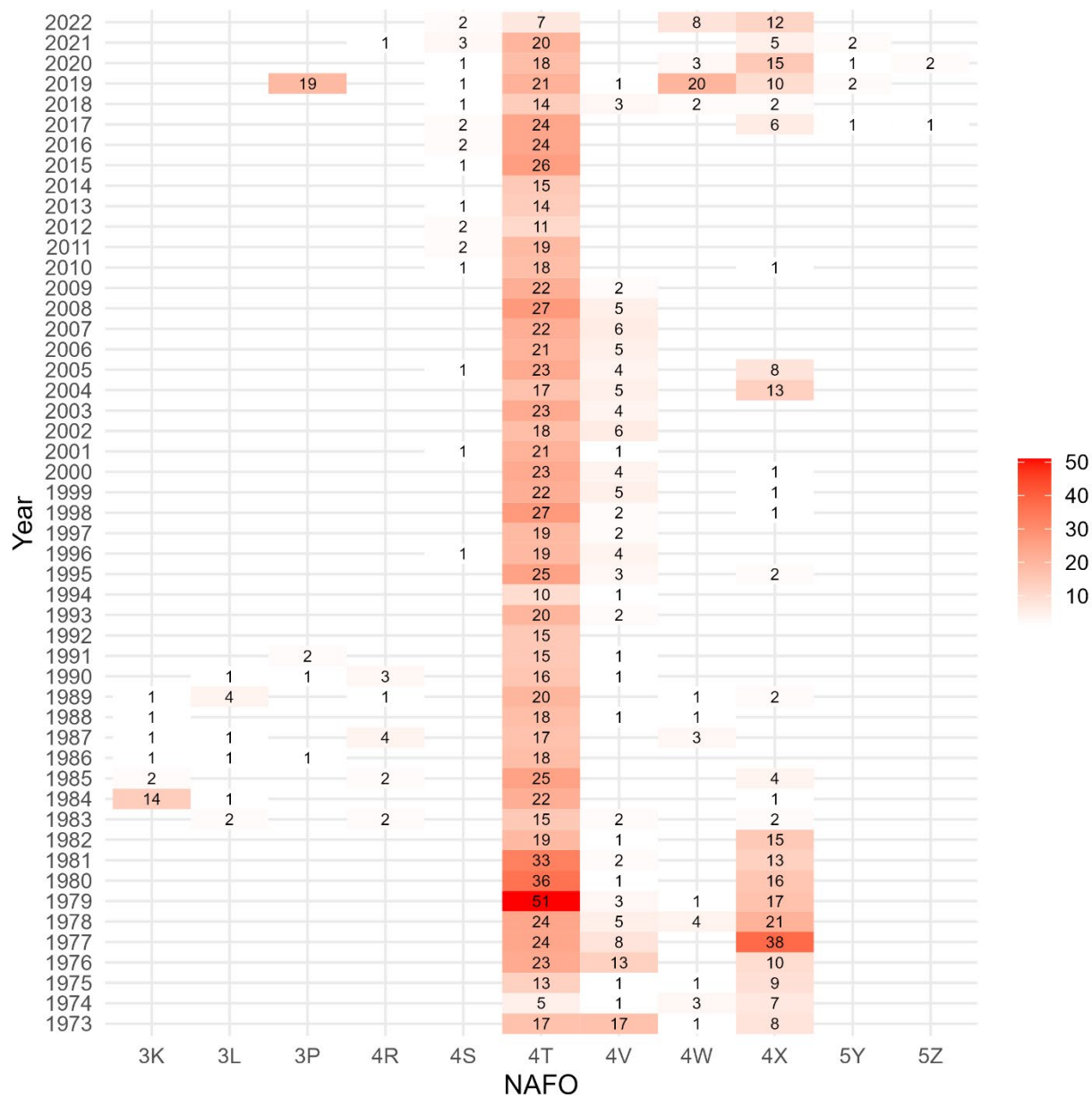


Figure 4. Number of biological samples in the commercial fishery collected during June and July, per NAFO division.

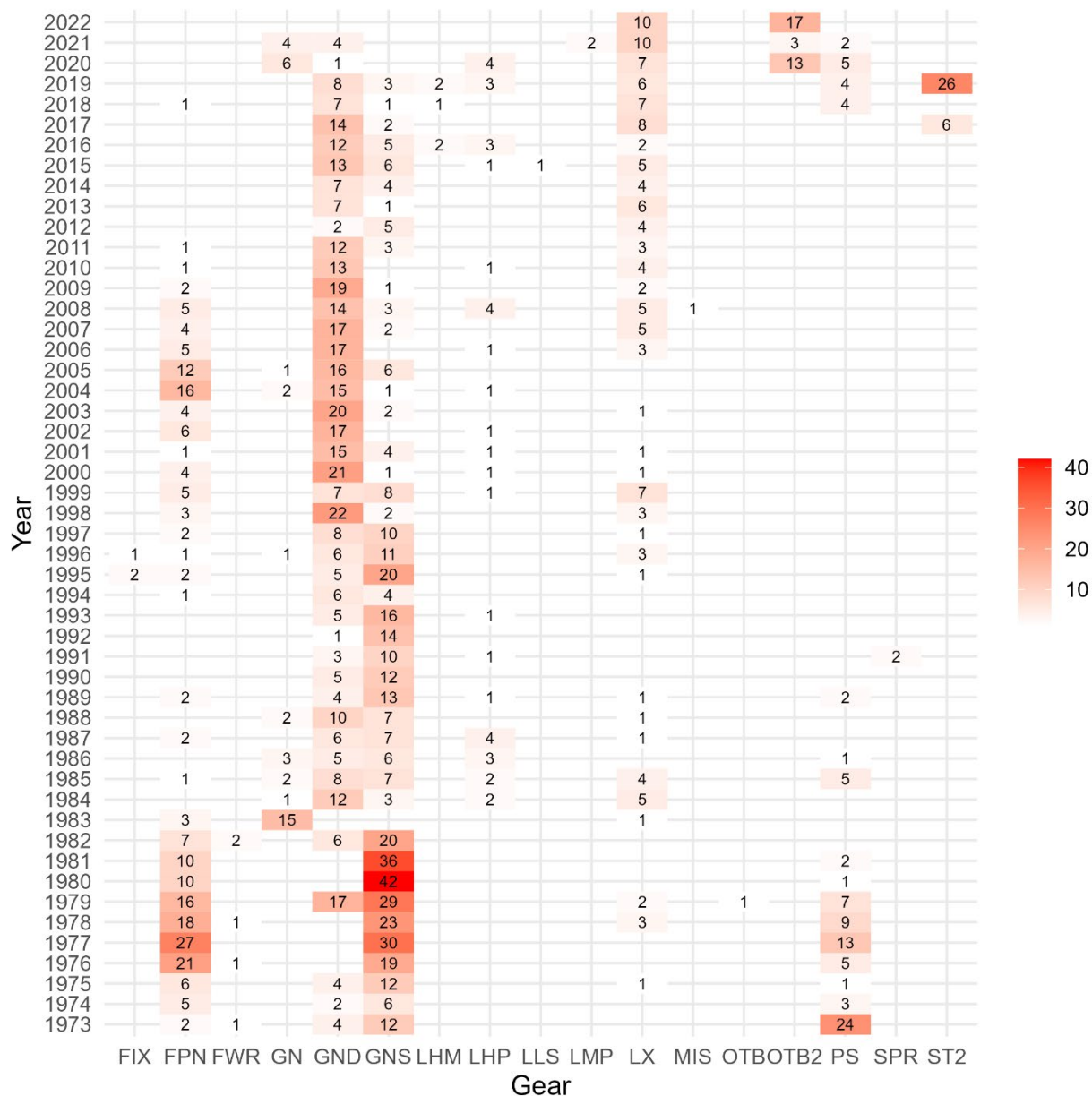


Figure 5. Number of biological samples in the commercial fishery collected during June and July in NAFO divisions 4TVWX, per gear type. (FIX: Traps (not specified), FPN = Stationary uncovered pound nets, FWR = Barriers, fences and weirs, GN = Gillnets (not specified), GND = Driftnets, GNS = Set gillnets (anchored), LHM = Handlines and pole-lines (mechanized), LHP = Handlines and pole-lines (hand-operated), LLS = Set longlines, LMP = Handline (unspecified), LX = Hooks and lines (not specified), MIS = Unspecified fixed gear, OTB = Bottom otter trawl, OTB2 = Stern otter trawl, PS = Purse seine, SPR = Pair seine, ST2 = Shrimp trawl (stern) without grid).

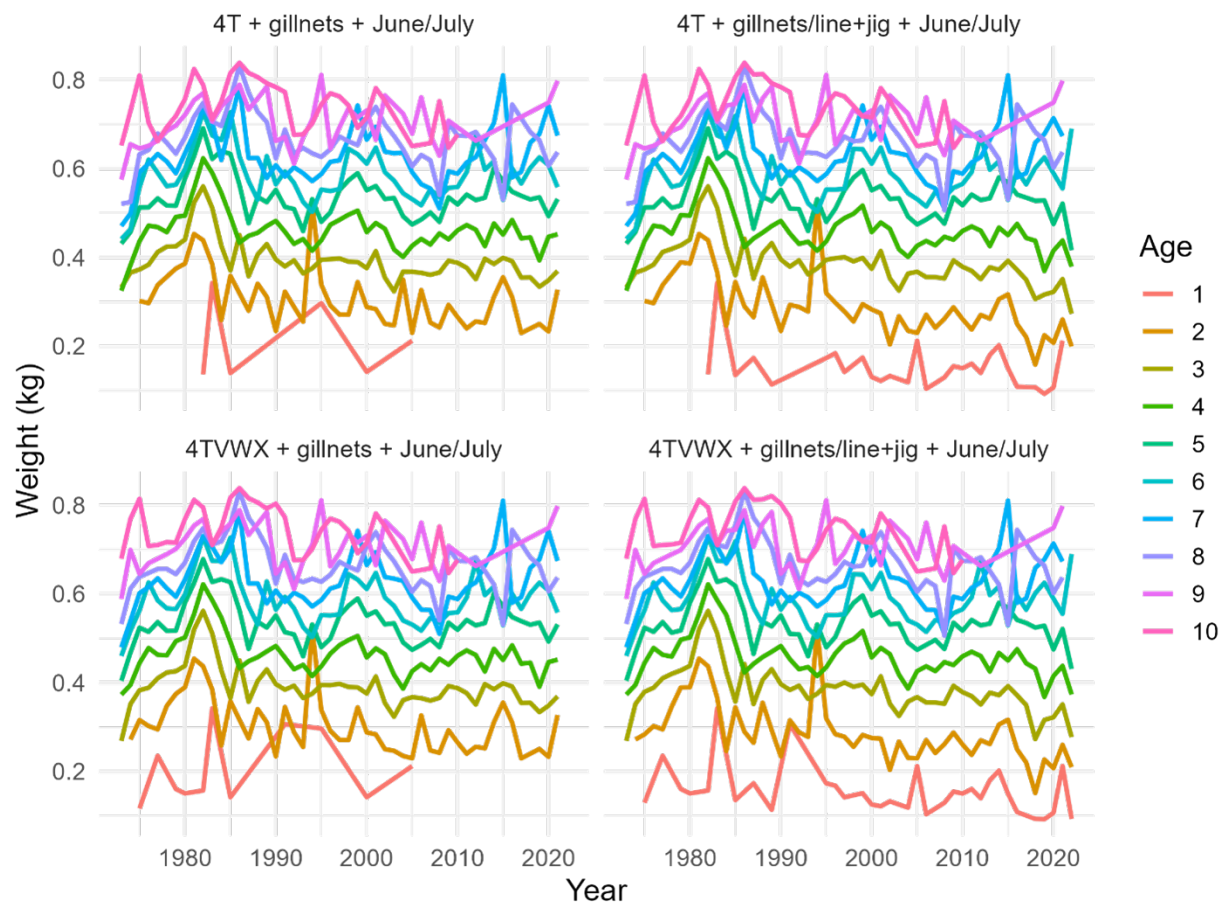


Figure 6. Weight-at-age of Atlantic mackerel sampled in the commercial fishery during June and July for different combinations of NAFO divisions and gear types. Age class 10 is a plus-group.

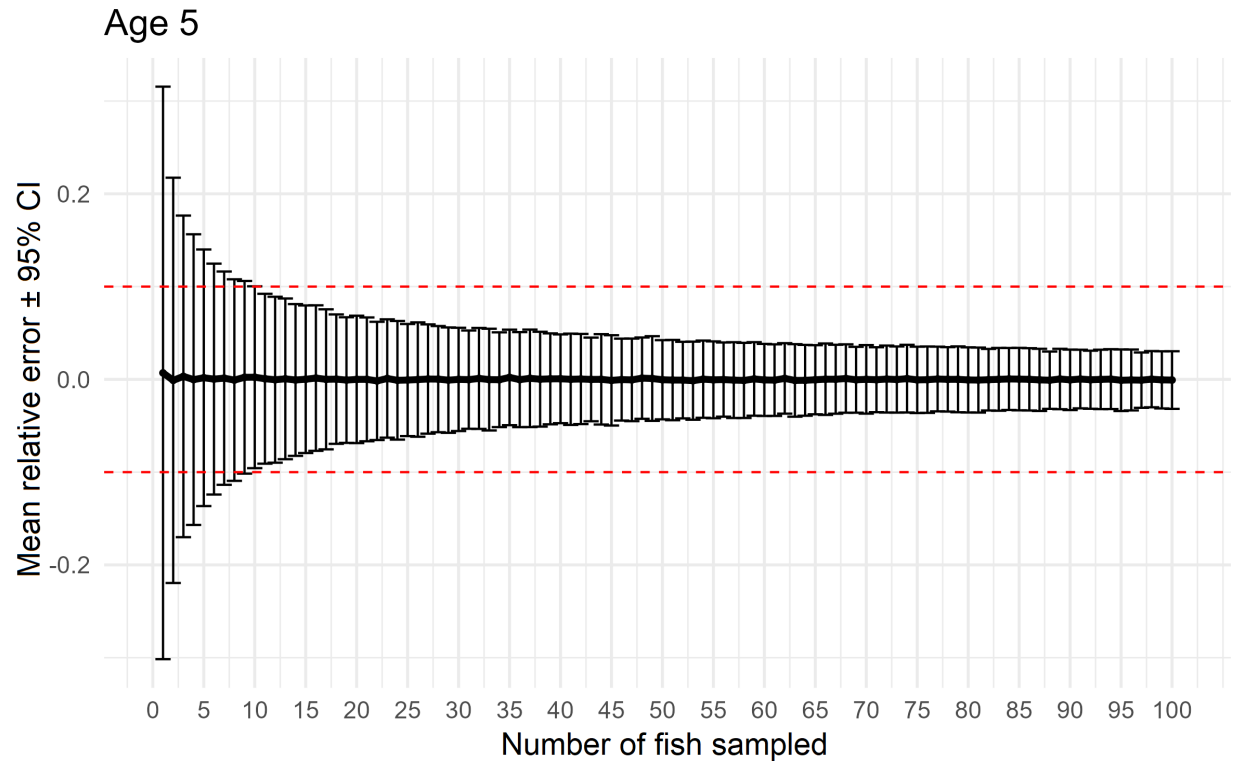


Figure 7. Mean relative error (with 95% confidence interval) in the estimation of age 5 average fish weight as a function of the number of fish available. The arbitrary level of relative error accepted in this study (red dashed lines) was between 0.1 and -0.1.

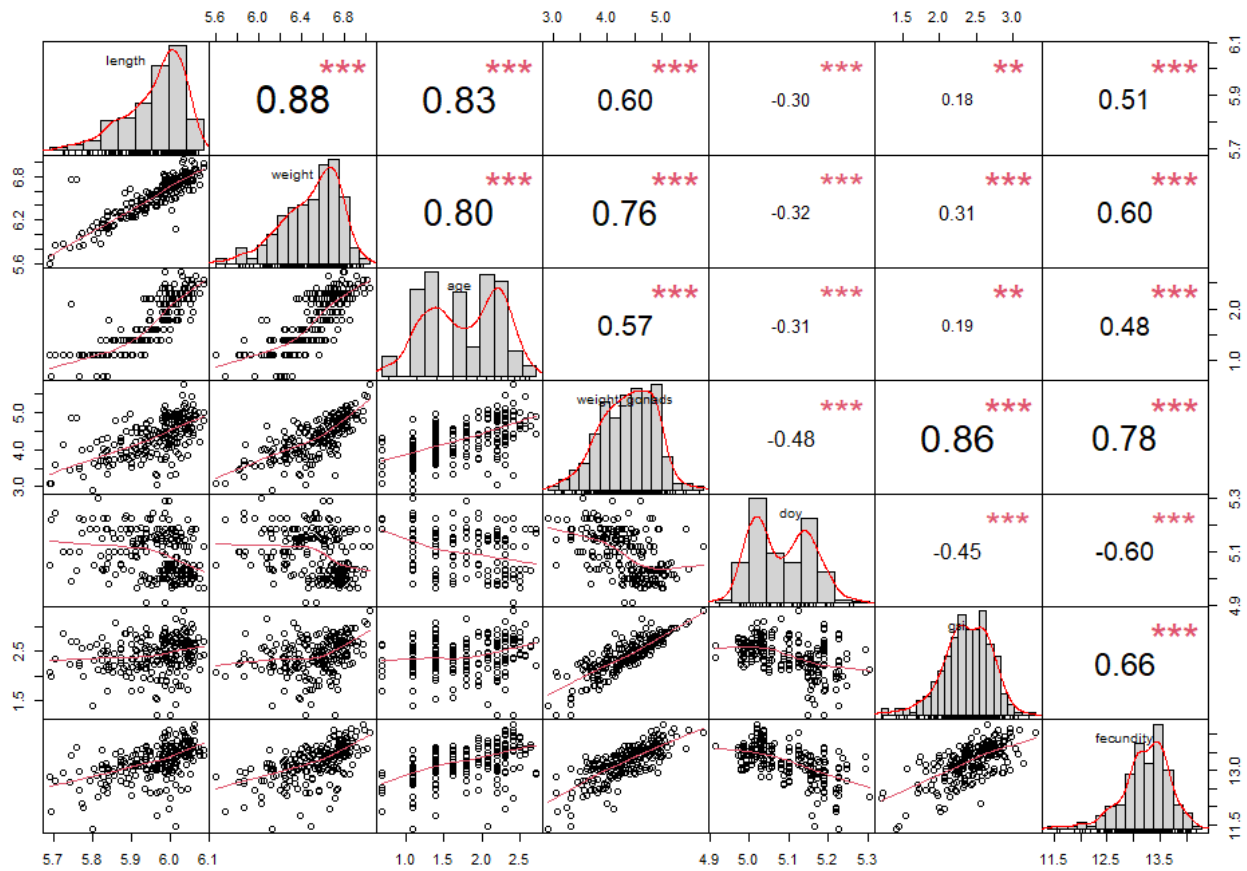


Figure 8. Correlation matrix of stage 5 females Atlantic mackerel fecundity (egg numbers), length (cm), weight (g), age, gonad weight, day of the year (day), and gonadosomatic index (gsi) in log space (data from Pelletier 1986). Histograms represents the relative frequency of the values of each variable, the right part of the matrix indicates the Pearson correlation coefficient and the left part of the matrix shows bivariate scatterplots with a fitted line. Red stars represent the significance level (p-values) of the correlation estimates ("****" = 0.001, "***" = 0.01, "**" = 0.05, "." = 0.1, " " = 1).

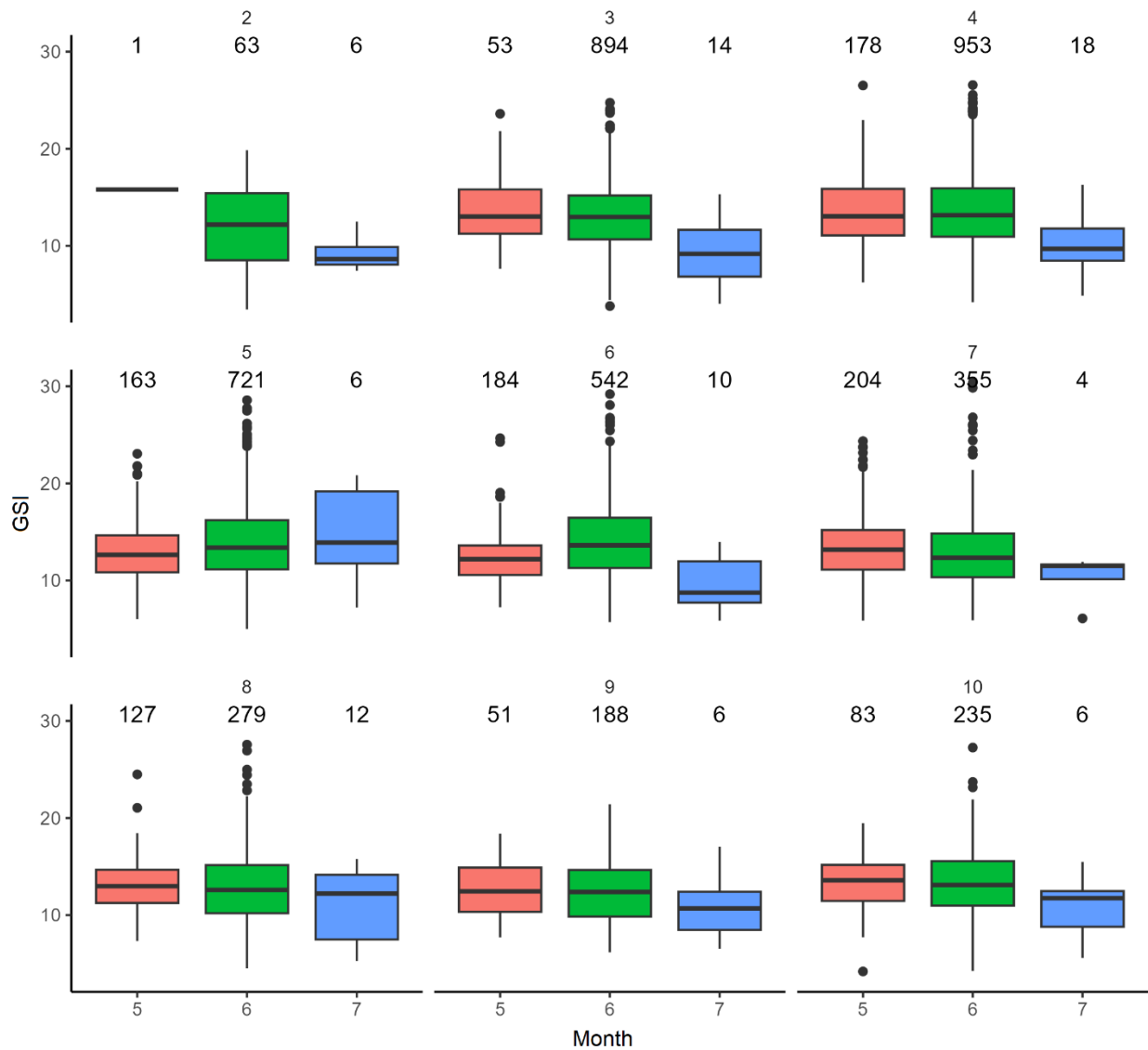


Figure 9. Boxplots of gonadosomatic index (GSI) at age (2 to 10+) values of stage 5 females sampled during May (red), June (green) and July (blue). The age is indicated above each graph and the number of fish sampled is indicated above each boxplot. Age class 10 is a plus-group.

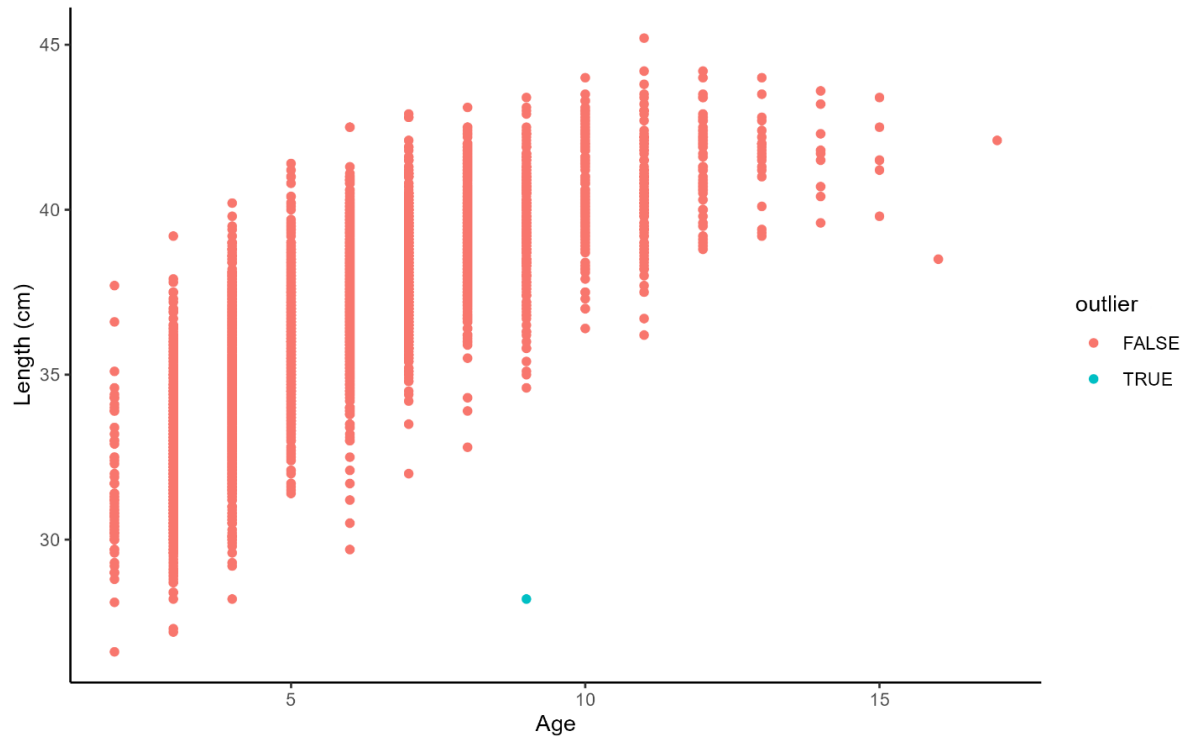


Figure 10. Length-at-age of stage 5 female Atlantic mackerel sampled from May to July. Outliers are indicated in blue and were removed from the calculation of the annual mean fecundity-at-age.

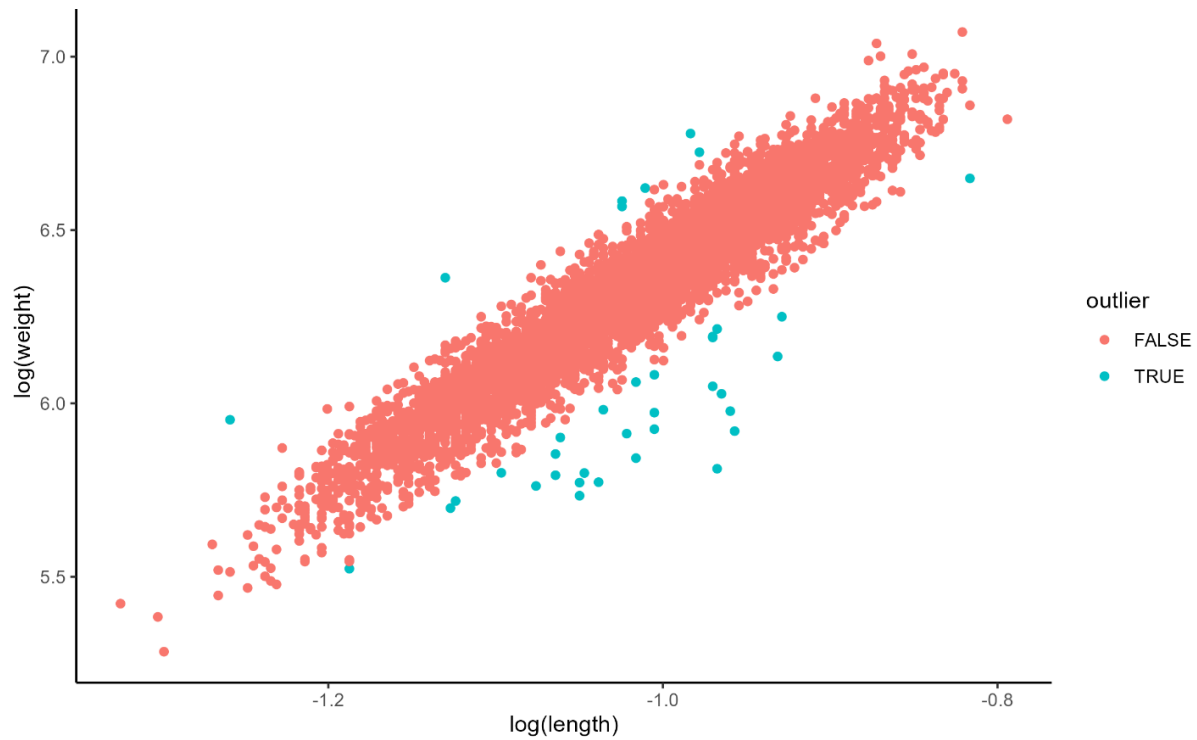


Figure 11. Length-weight relationship of stage 5 females sampled from May to July. Outliers are indicated in blue and were removed from the calculation of the annual mean fecundity-at-age.

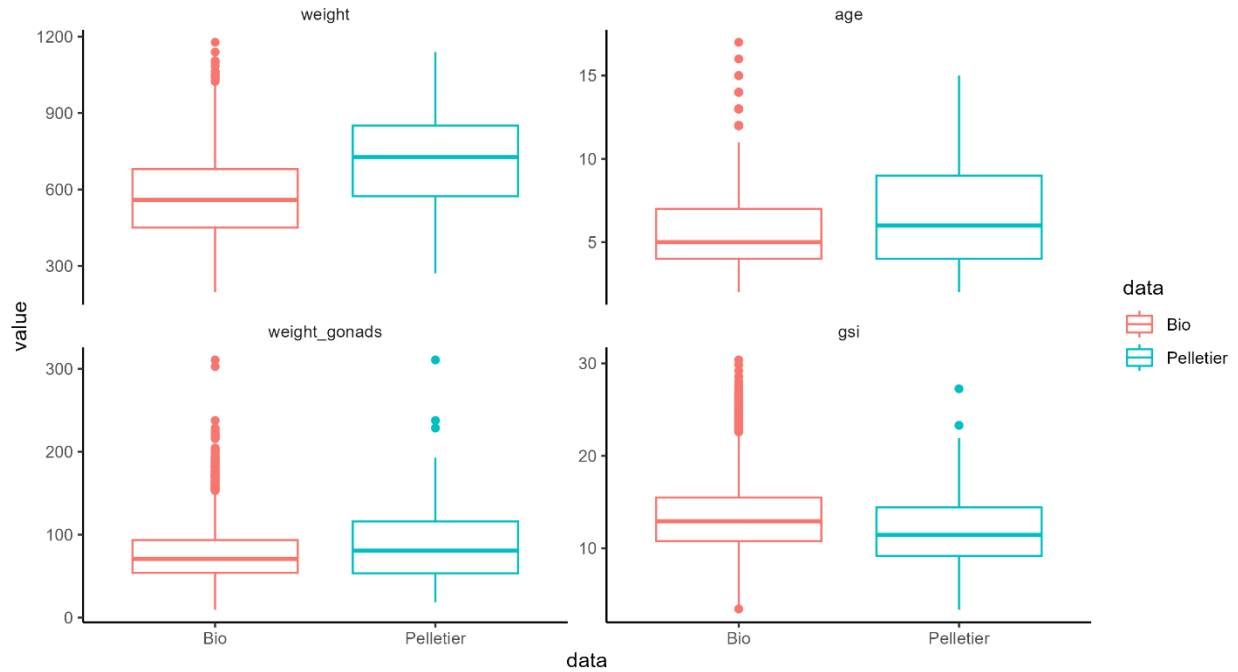


Figure 12. Boxplots of weight, age, gonad weight and gonadosomatic index (gsi) of stage 5 females in Pelletier's study (blue) and sampled in the commercial fishery (Bio) from May to July (red) between 1982 and 1985.

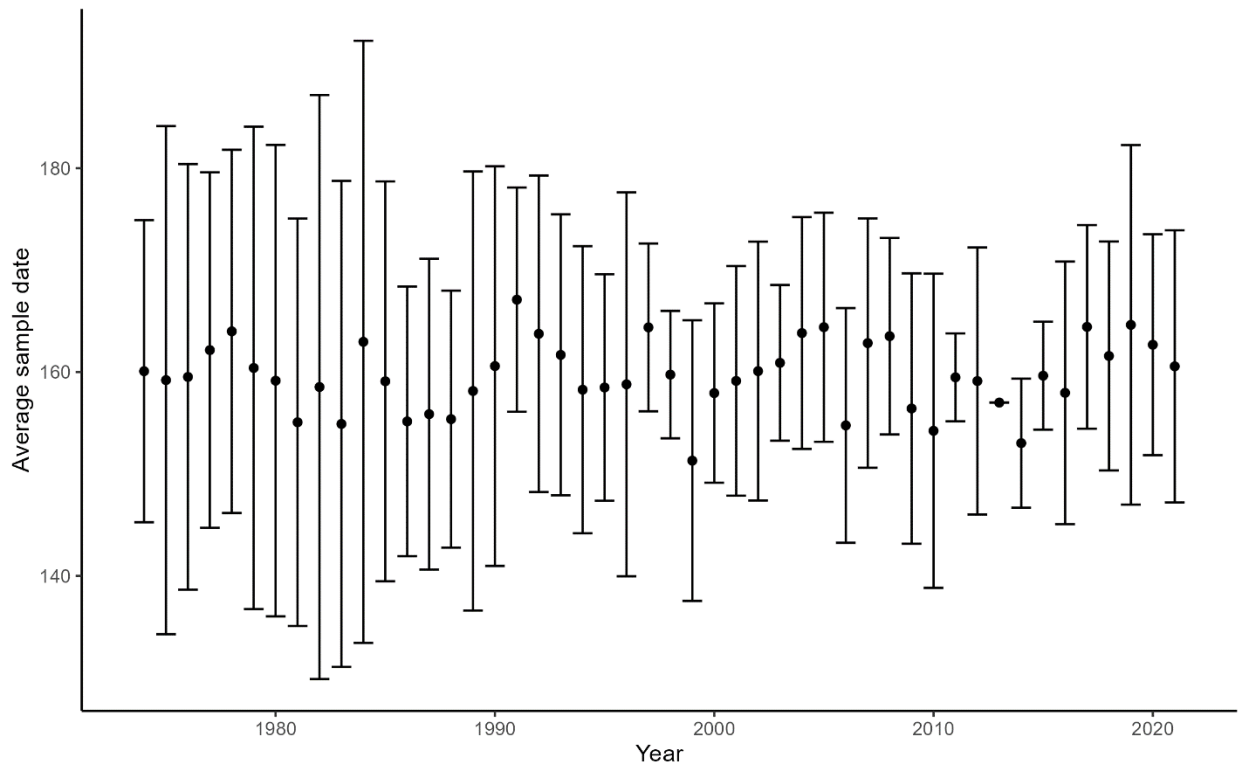


Figure 13. Average date (\pm 95% Confidence intervals) of stage 5 female samples collected in the commercial fishery from May to July.

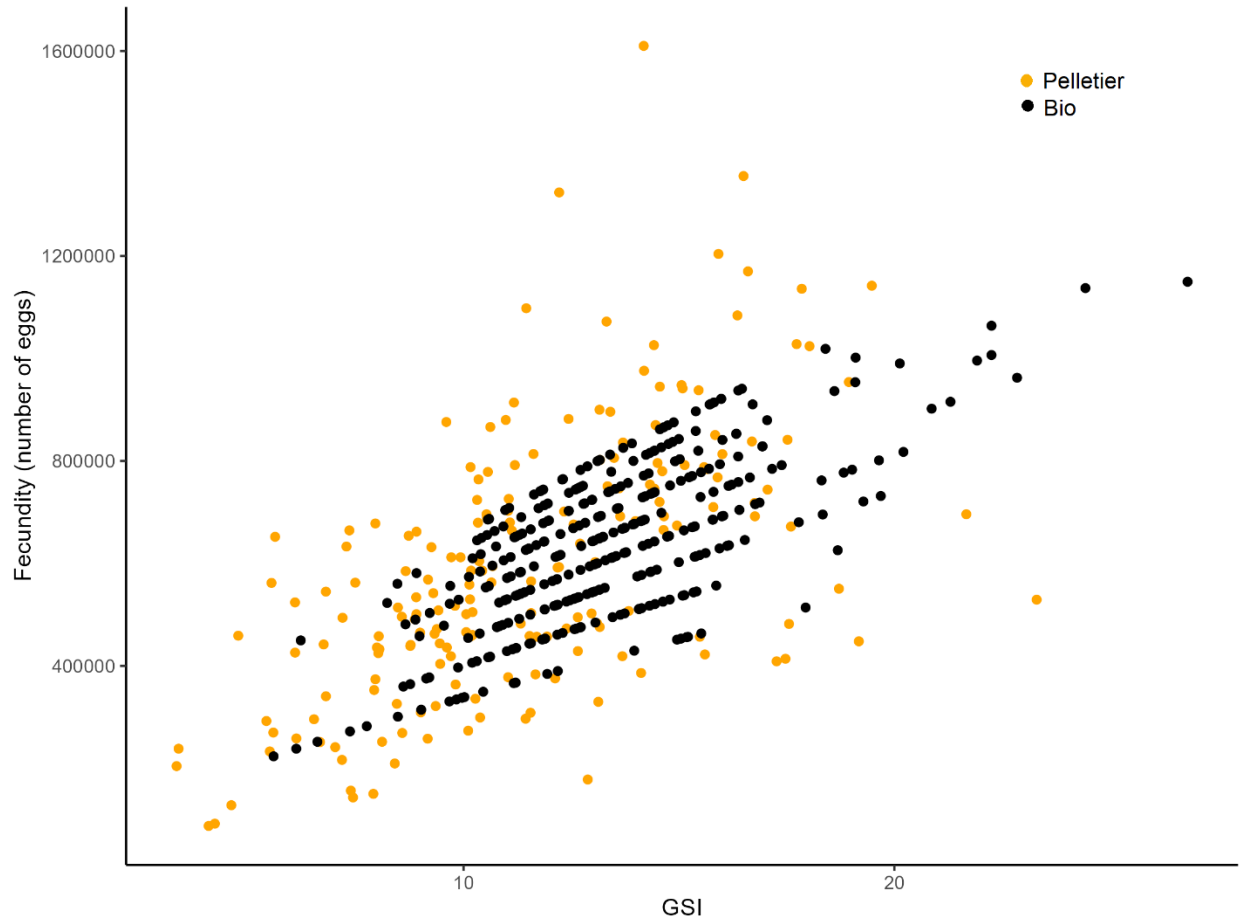


Figure 14. Fecundity in relation to the gonadosomatic index (GSI) of stage 5 females observed in Pelletier's study (1986; orange dots) and estimated using the robust linear regression coefficients with fish sampled in the commercial fishery (Bio) from May to July (black dots).

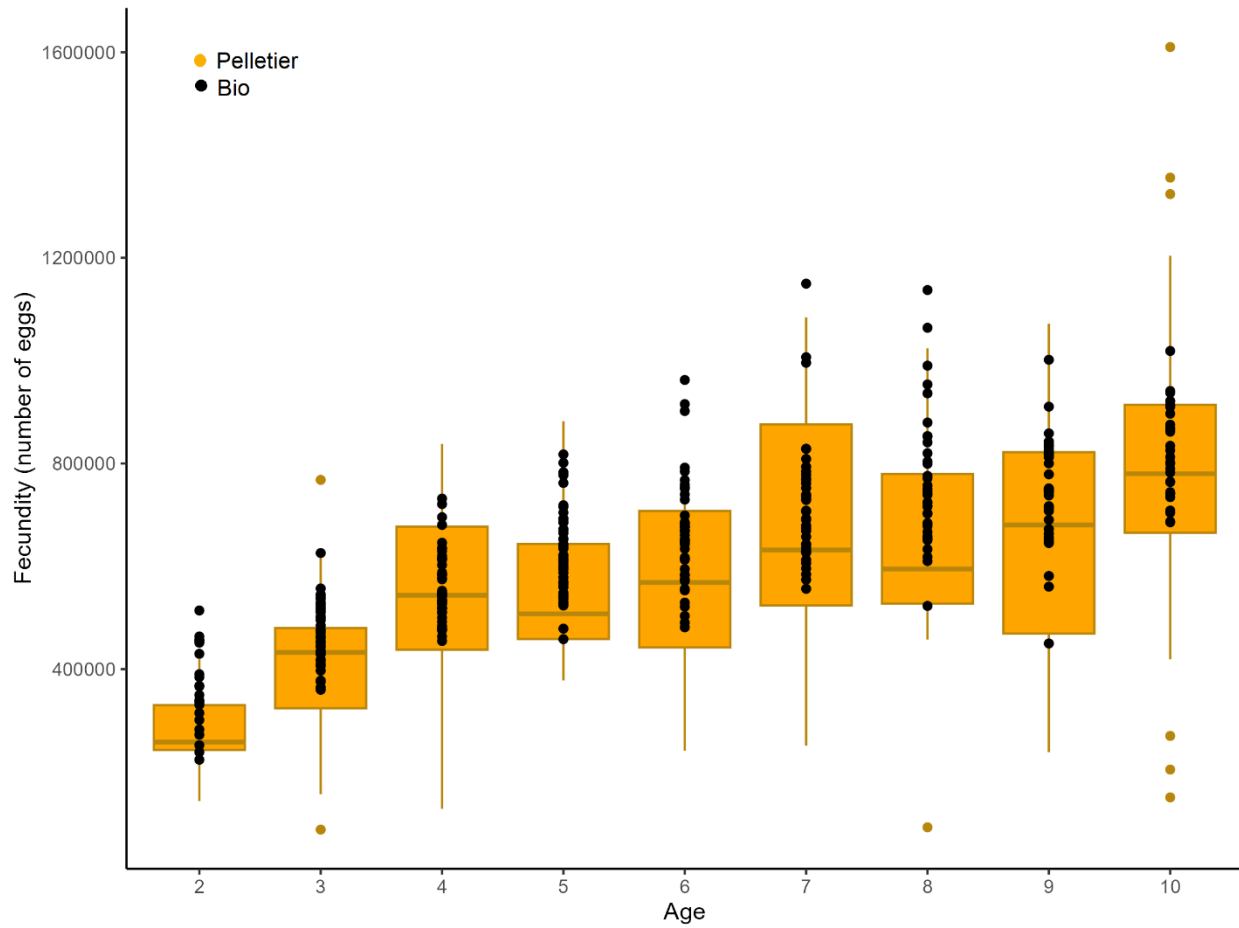


Figure 15. Fecundity in relation to age of stage 5 females in Pelletier's study (orange boxplots) and estimated for the fish sampled in the commercial fishery (Bio) from May to July using the robust linear regression coefficients (black dots). Age class 10 is a plus-group.

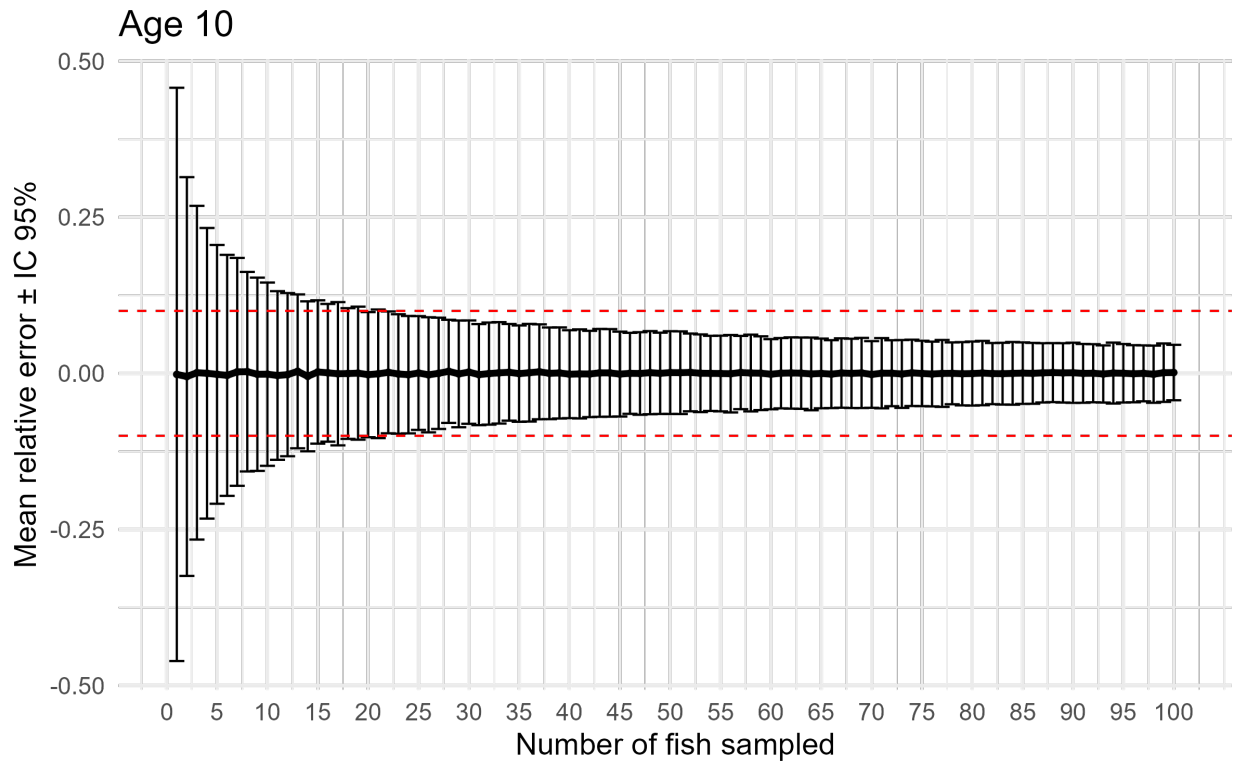


Figure 16. Mean relative error (with 95% confidence interval) in the estimation of age 10 stage 5 females sampled from May to July as a function of the number of fish available. The arbitrary level of relative error accepted in this study (red dashed lines) was between 0.1 and -0.1.

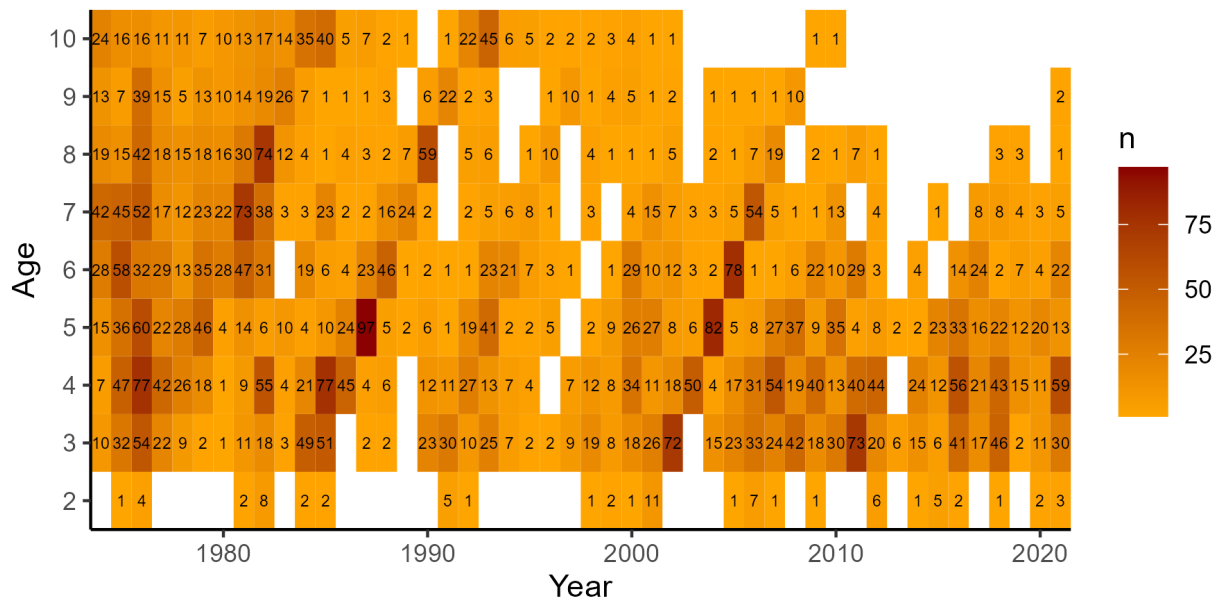


Figure 17. Number of stage 5 females from each age class sampled from May to July. Age class 10 is a plus-group.

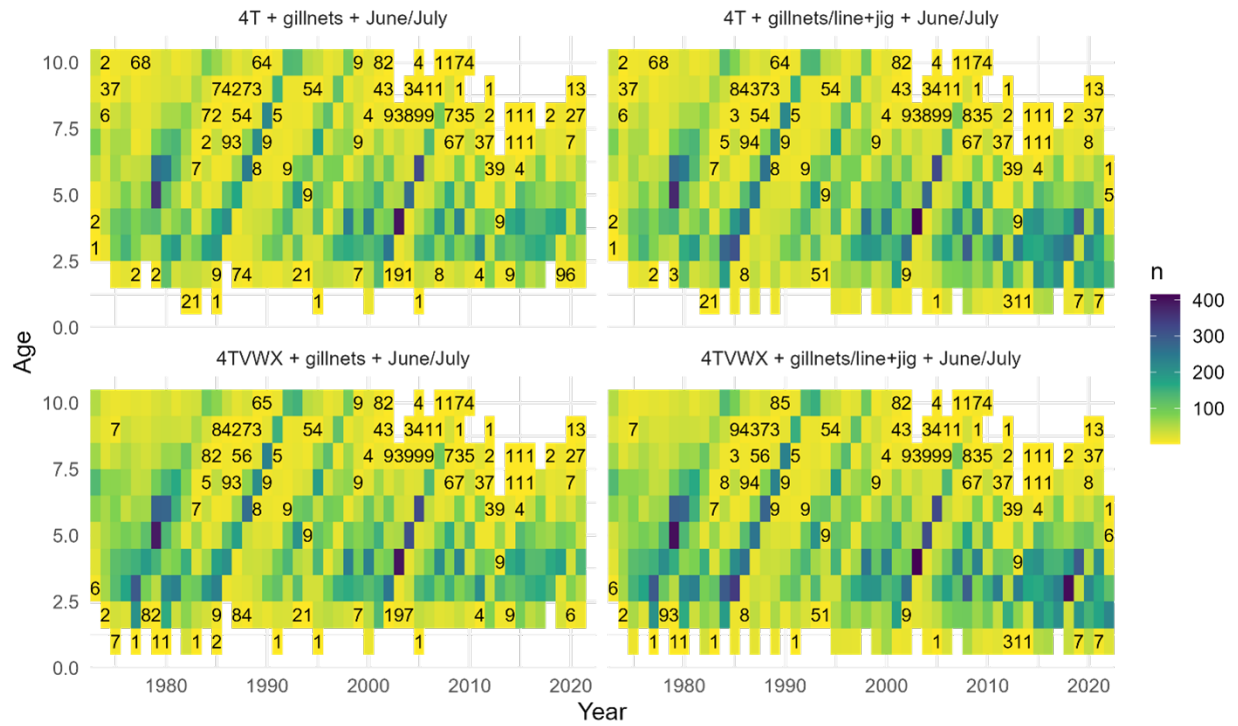


Figure 18. Number of fish sampled during June and July for different combinations of NAFO divisions and gear types. Age class 10 is a plus-group.

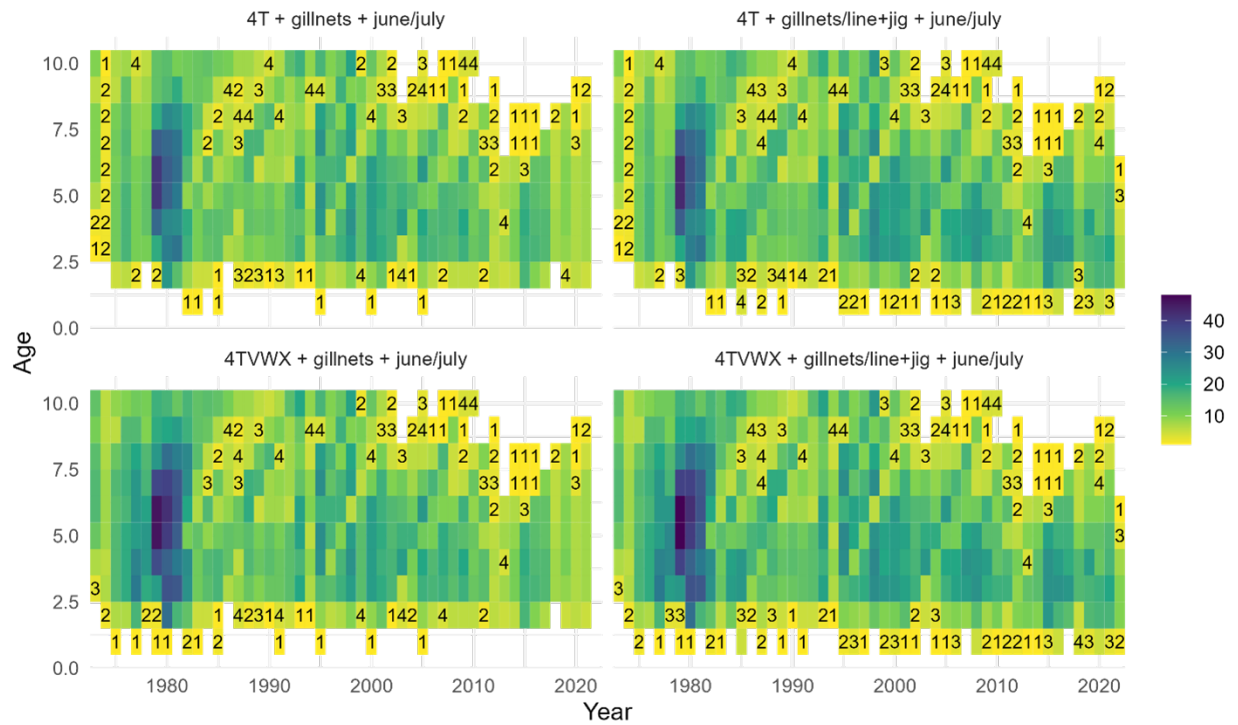


Figure 19. Number of samples during June and July for different combinations of NAFO divisions and gear types. Age class 10 is a plus-group.

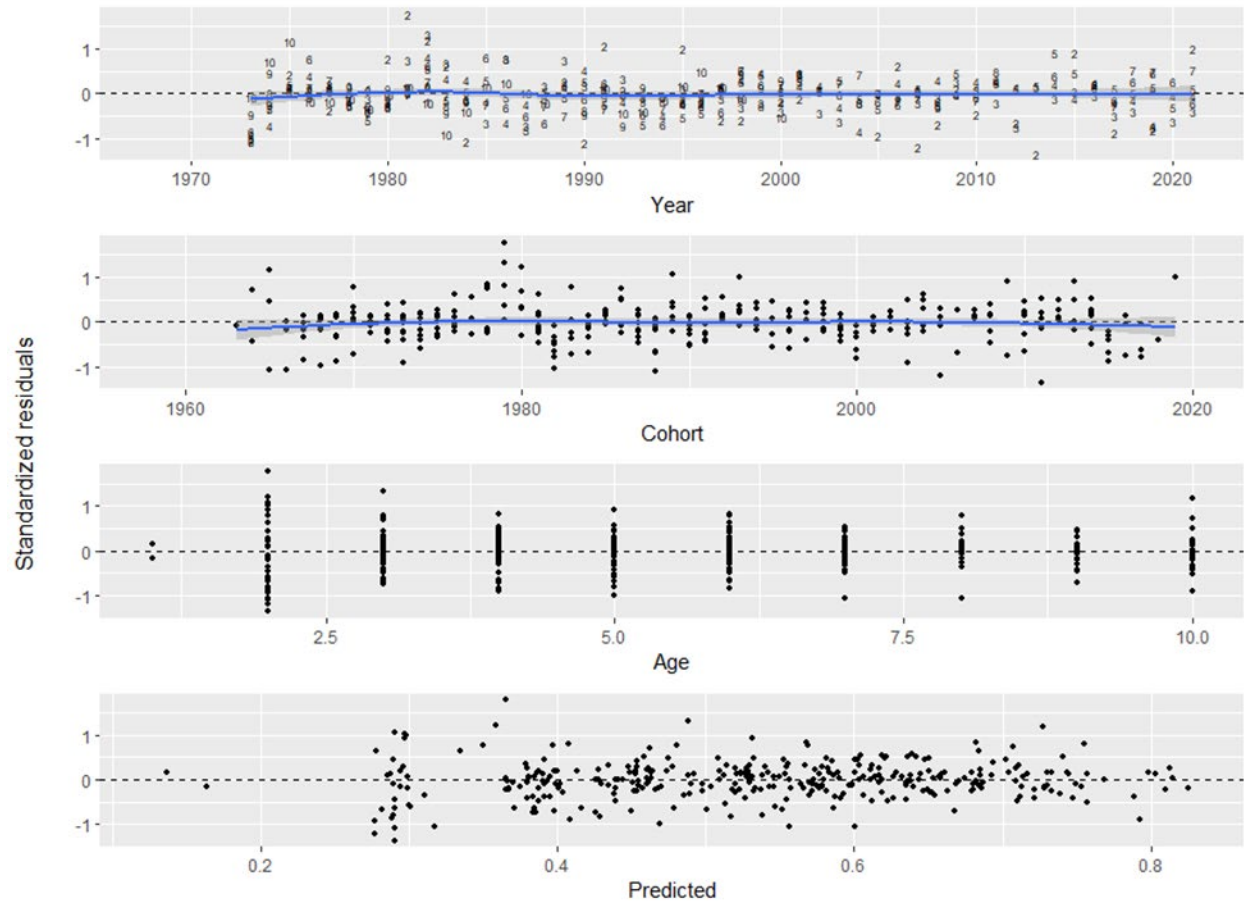


Figure 20. Standardized residuals of the weight-at-age mixed-effect model in relation to year, cohort, age and predictions. Blue lines are smoothers that help show trends. Age class 10 is a plus-group.

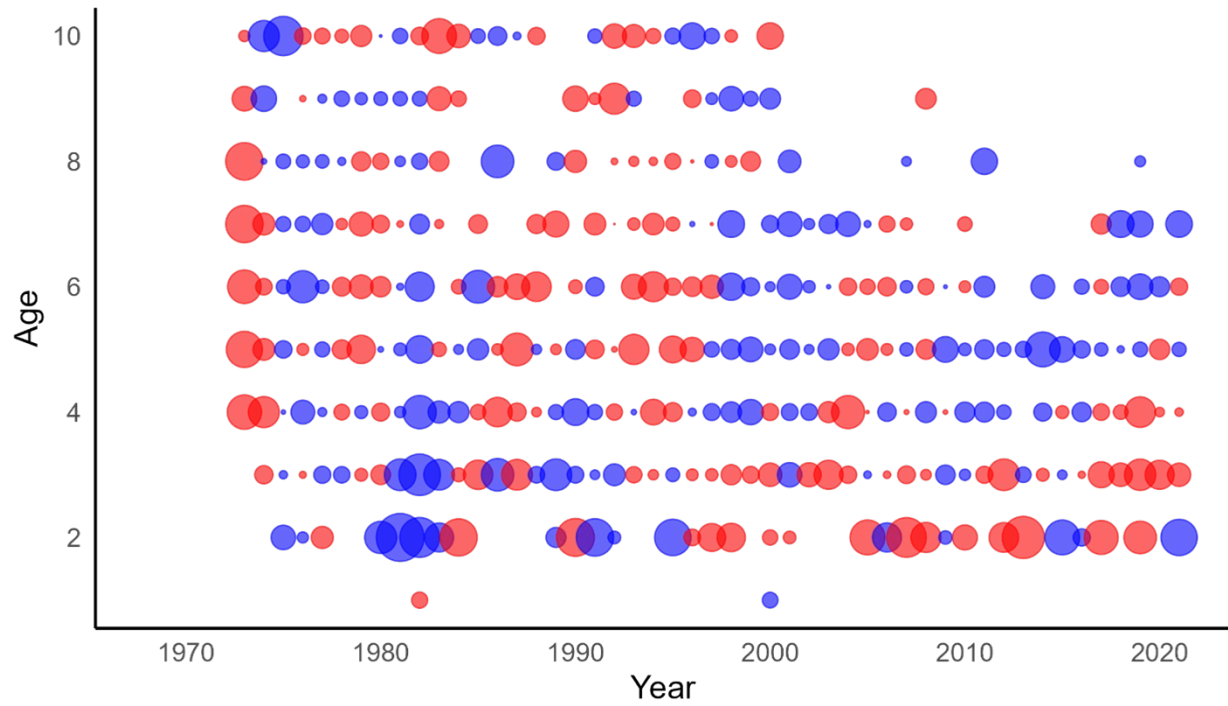


Figure 21. Standardized residuals of the weight-at-age mixed-effect model, by year and age. The size of the bubbles indicates the absolute value of the residual and the color indicates whether they are positive or negative (red +; blue -). Age class 10 is a plus-group.

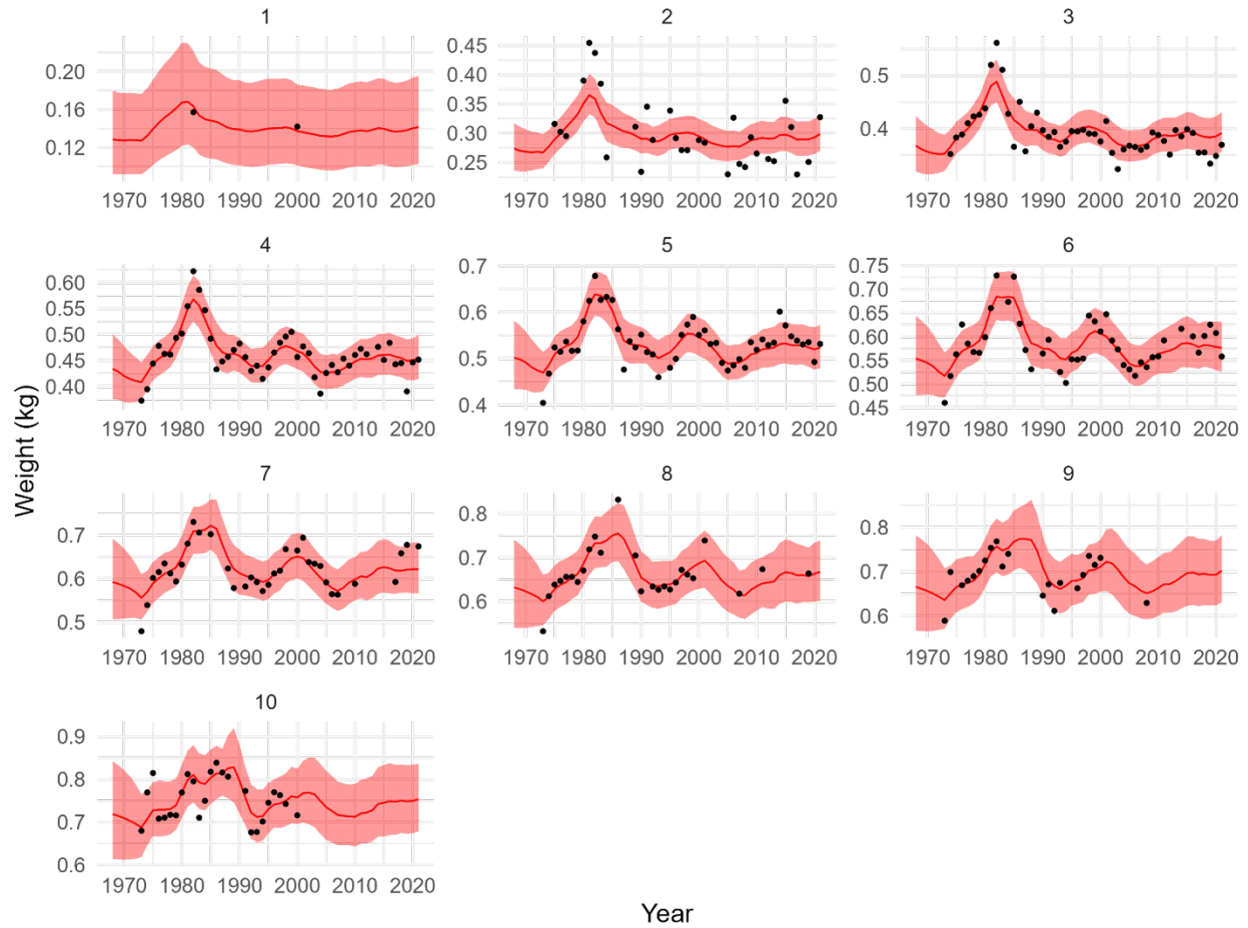


Figure 22. Observed (points; black) and predicted (lines; red) weight-at-age in June and July. Ribbons (red) indicate the 95% confidence interval. Age class 10 is a plus-group.

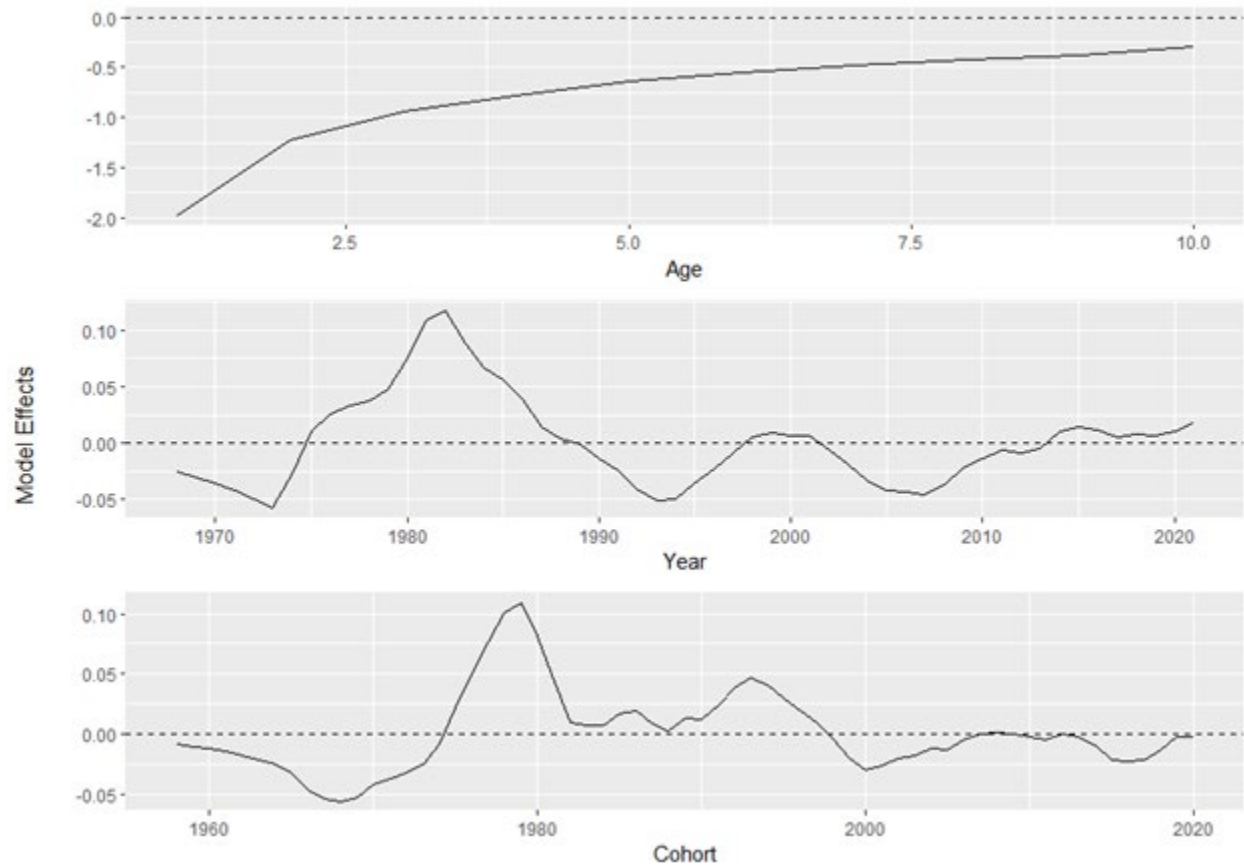


Figure 23. Estimated effect sizes of age, year and cohort in the mixed-effect model used to predict weight-at-age. Age class 10 is a plus-group.

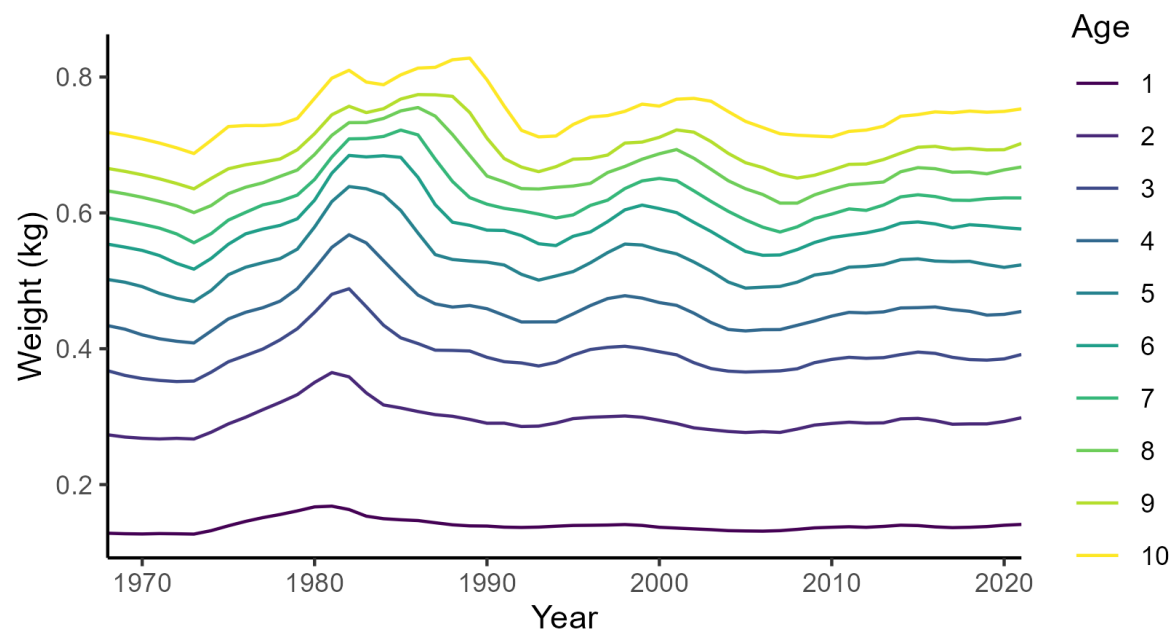


Figure 24. Weight-at-age of fish sampled during June and July predicted by the mixed-effect model and used in the assessment. Age class 10 is a plus-group.

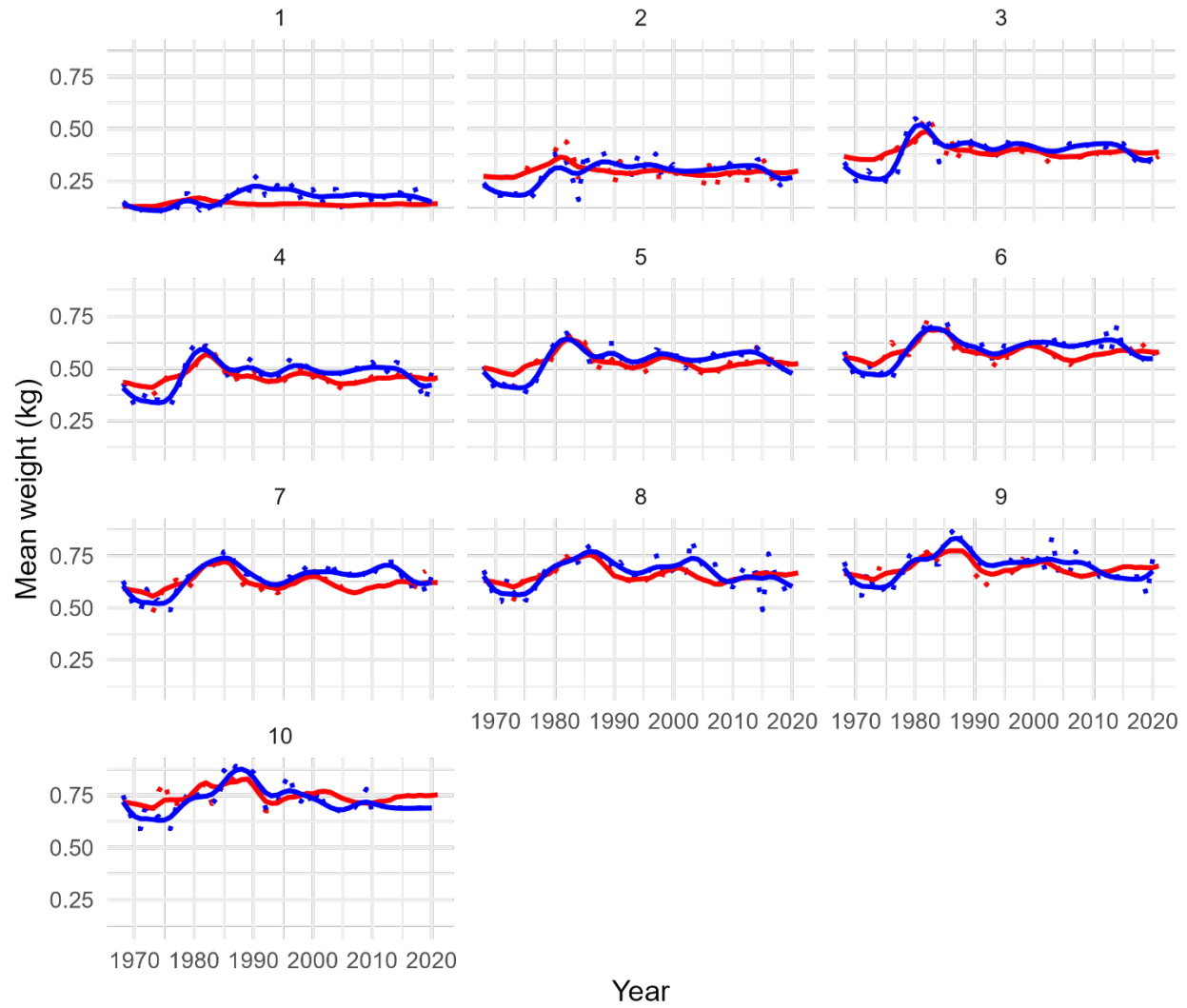


Figure 25. Raw (dots) and smoothed (lines) weight (kg) per age (panels) used in the 2021 (blue; Smith et al. 2022) and 2023 assessment (red). Age class 10 is a plus-group.

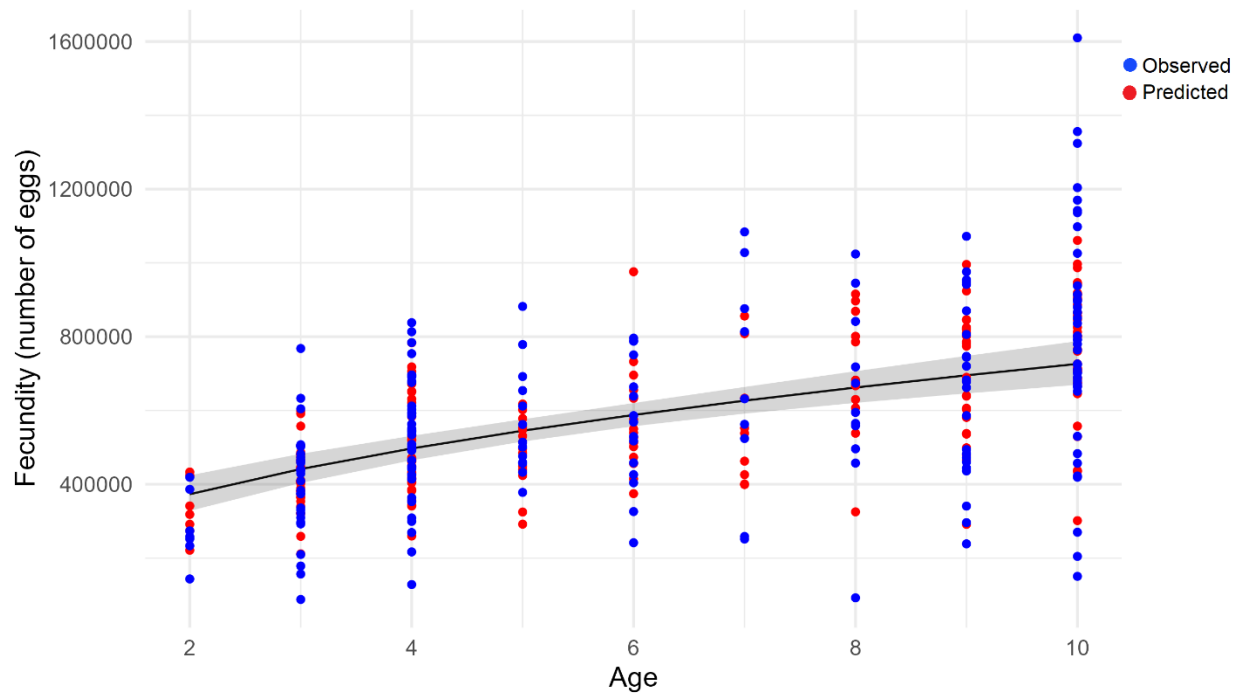


Figure 26. Fecundity in relation to age (red = model predictions, blue = observed values). The black line and shaded ribbon represent the marginal mean and the 95% confidence intervals, respectively, of this relationship as predicted by the robust regression. Age class 10 is a plus-group.

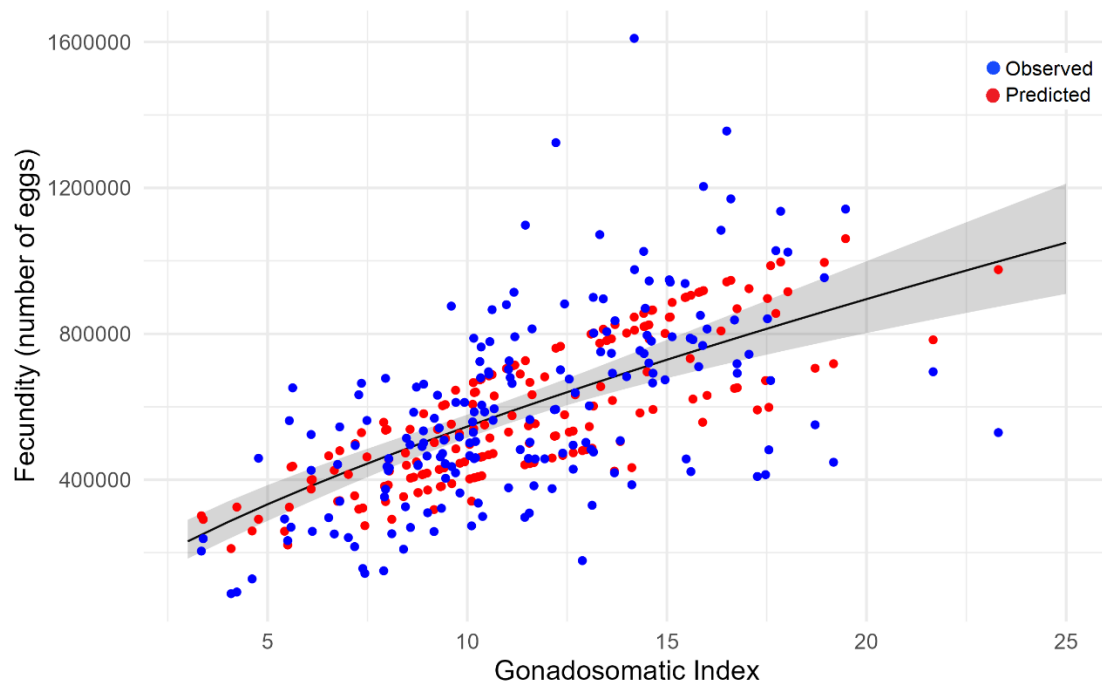


Figure 27. Fecundity in relation to the gonadosomatic index (red = model predictions, blue = observed values). The black line and shaded ribbon represent the marginal mean and the 95% confidence intervals, respectively, of this relationship as predicted by the robust regression.

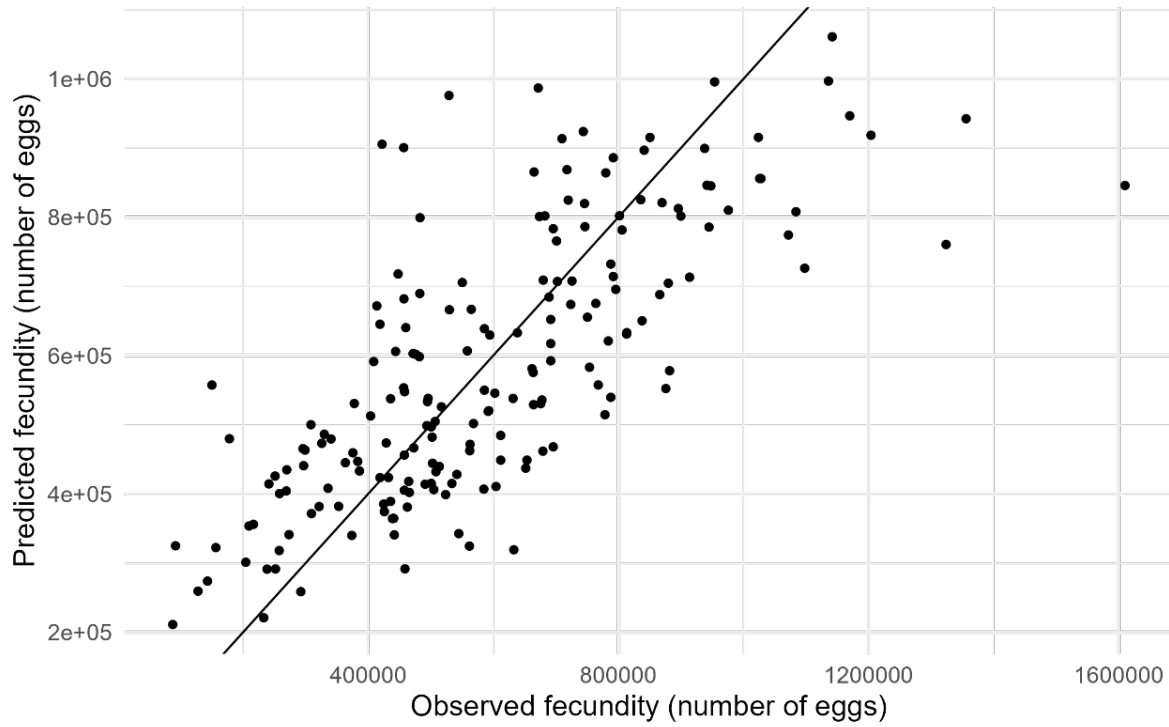


Figure 28. Predicted versus observed fecundity of stage 5 females (data from Pelletier 1986). The line represents a 1:1 ratio.

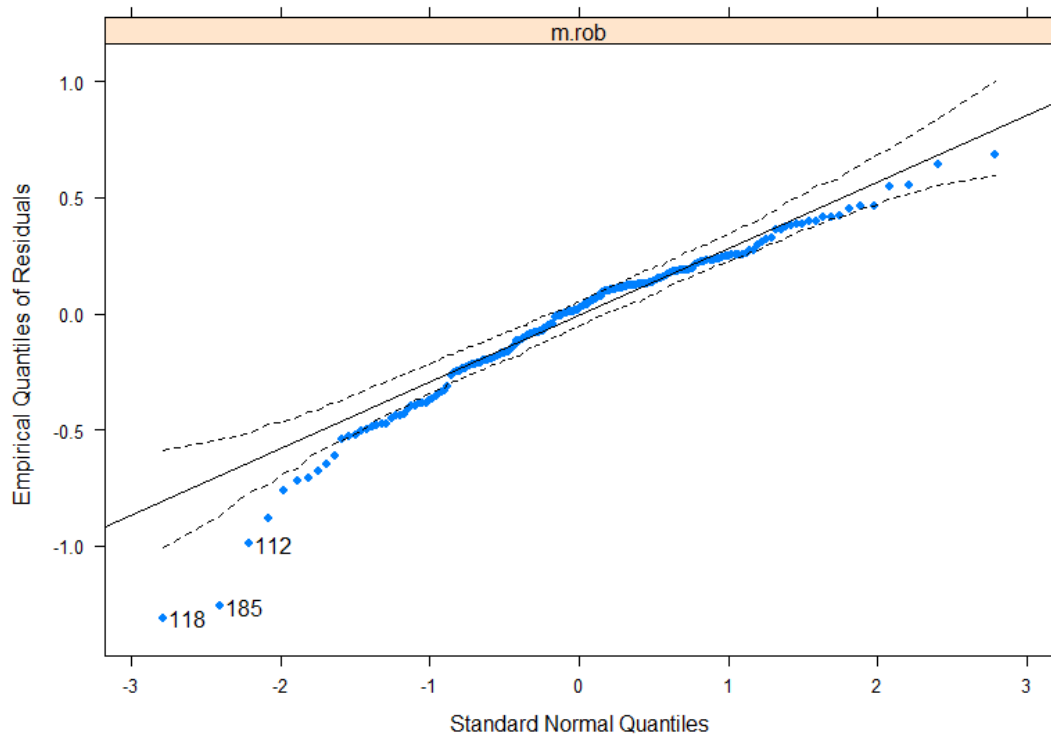


Figure 29. Quantile-Quantile (QQ) plot resulting from the robust linear regression relating stage 5 female fecundity to age and the gonadosomatic index. Points identified with numbers represent low fecundity values that were given less weight in the estimation of regression coefficients.

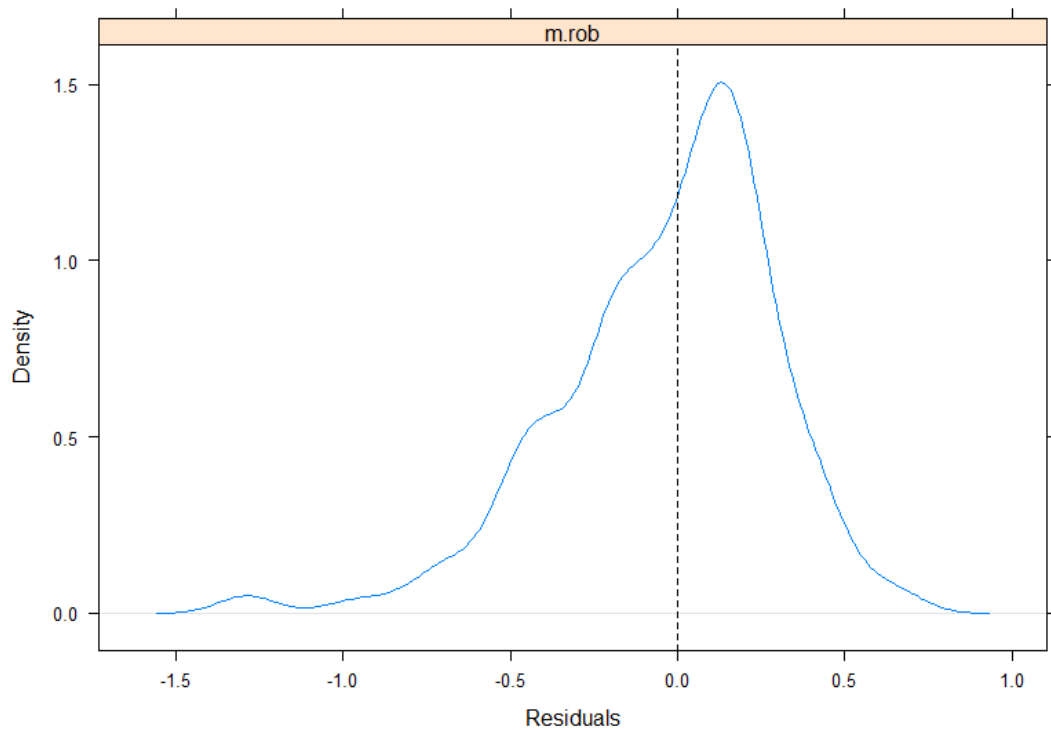


Figure 30. Kernel density plot displaying the distribution of standardized residuals from the robust linear regression predicting stage 5 females fecundity.

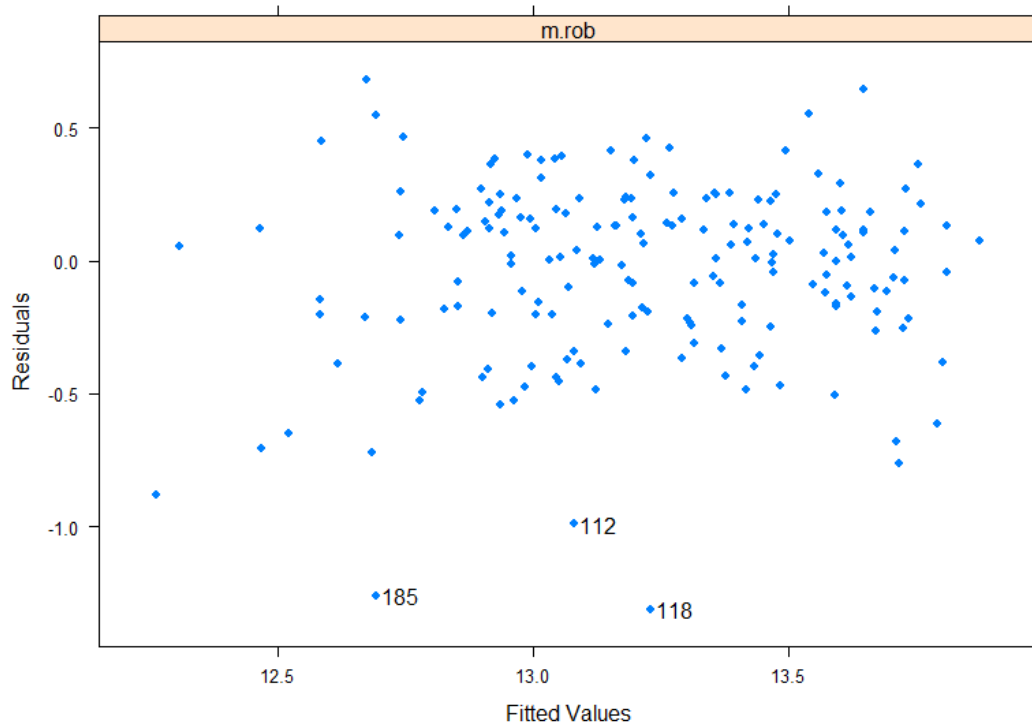


Figure 31. Standardized residuals in relation to fitted values from the robust linear regression predicting stage 5 females fecundity. Points identified with numbers represent low fecundity values that were given less weight in the estimation of regression coefficients.

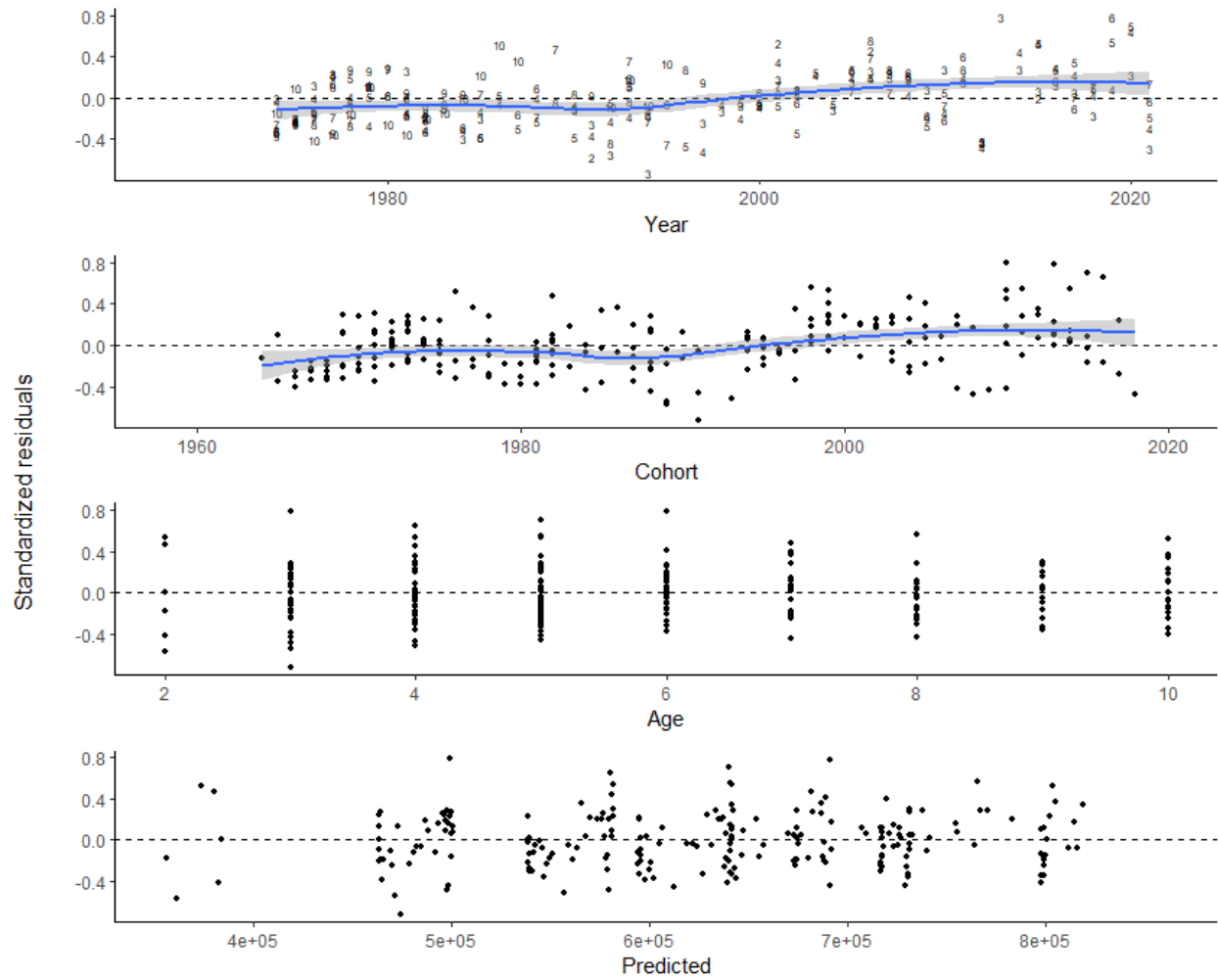


Figure 32. Standardized residuals of the fecundity-at-age mixed-effect model in relation to year, cohort, age and predicted estimates. Blue lines are smoothers that help show trends. Age class 10 is a plus-group.

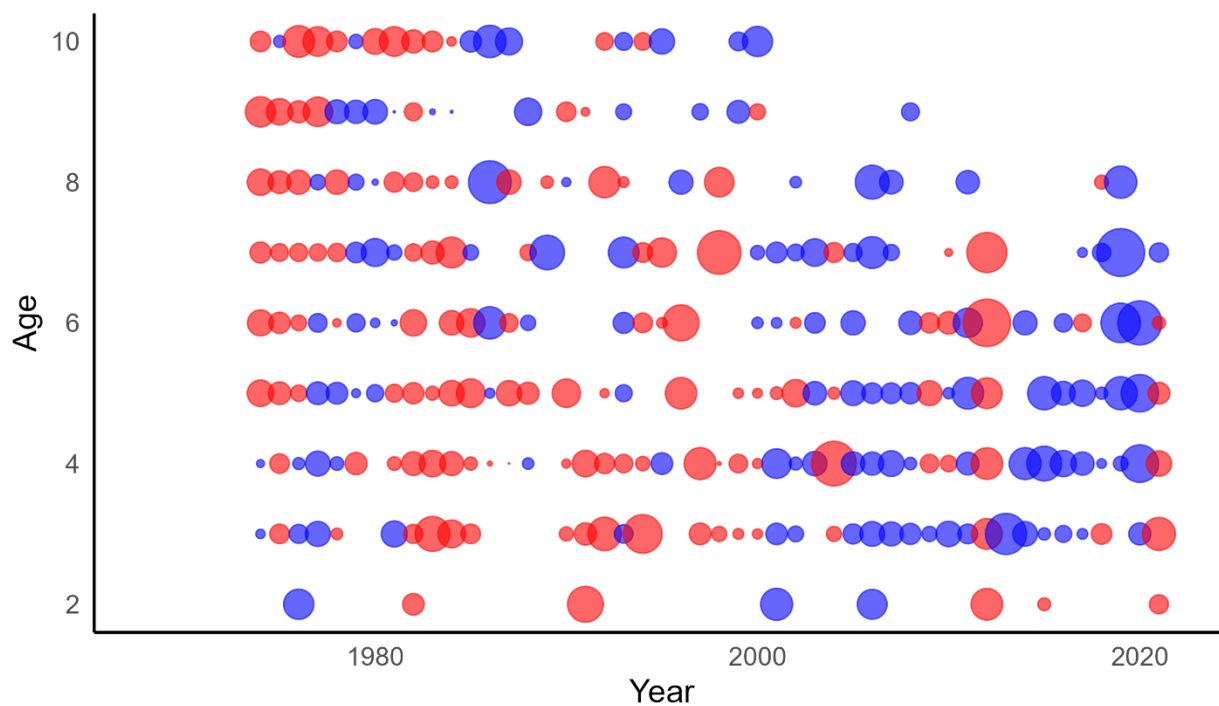


Figure 33. Standardized residuals of the fecundity-at-age mixed-effect model, by year and age. The size of the bubbles indicates the absolute value of the residual and the color indicates whether they are positive or negative (red +; blue -). Age class 10 is a plus-group.

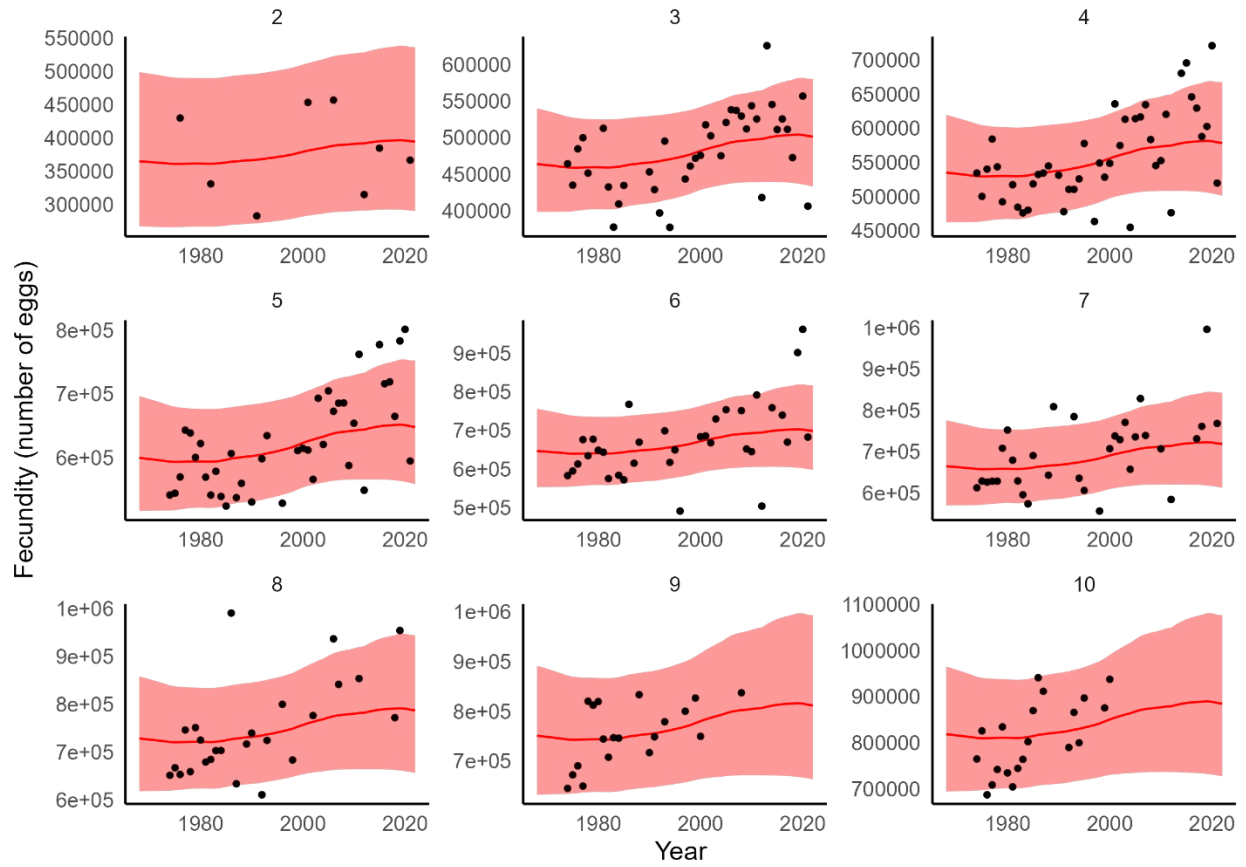


Figure 34. Observed (points; black) and predicted (lines; red) fecundity-at-age from May to July. Ribbons (red) indicate the 95% confidence interval. Age class 10 is a plus-group.

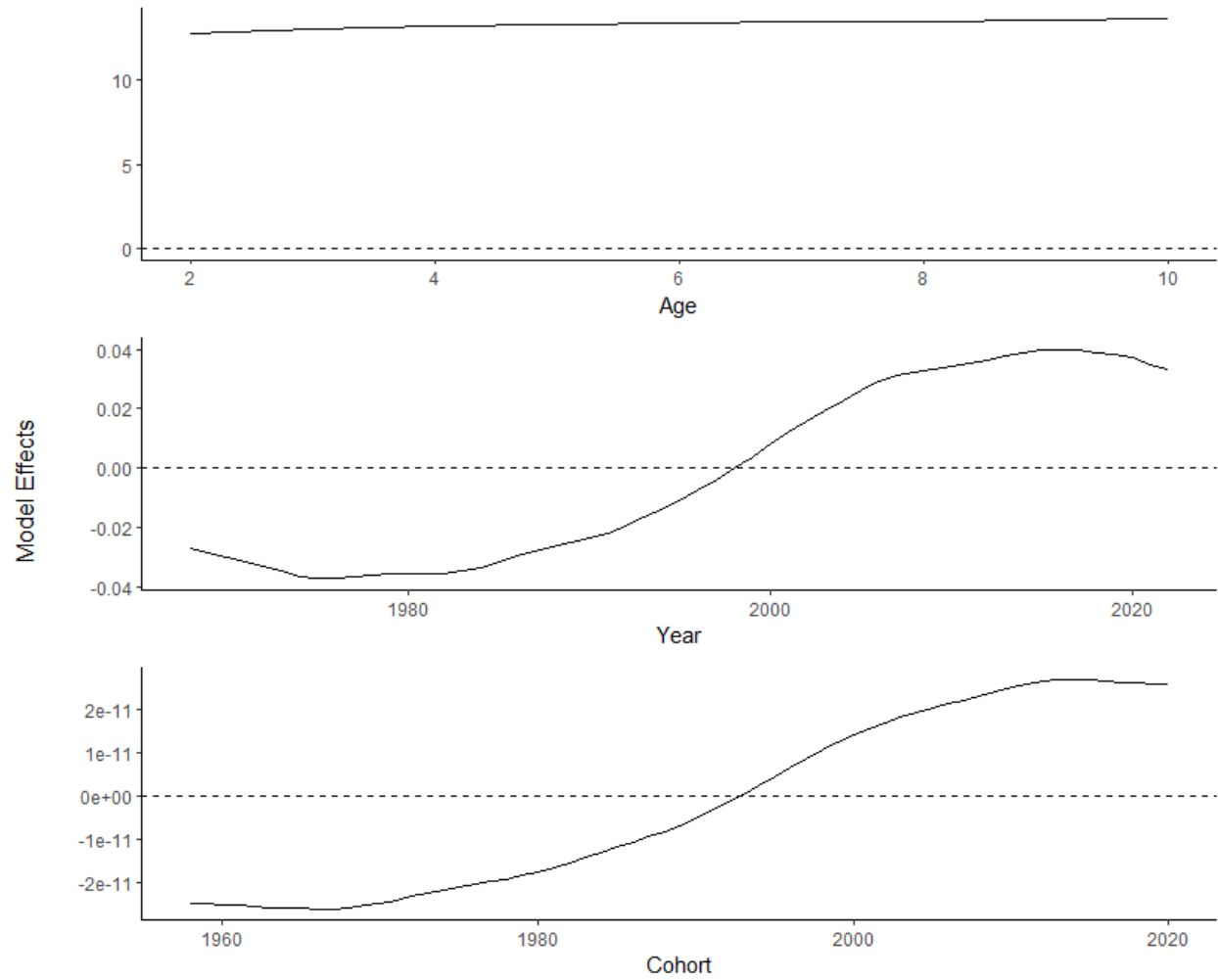


Figure 35. Estimated effect sizes of age, year and cohort in the mixed-effect model used to predict fecundity-at-age. Age class 10 is a plus-group.

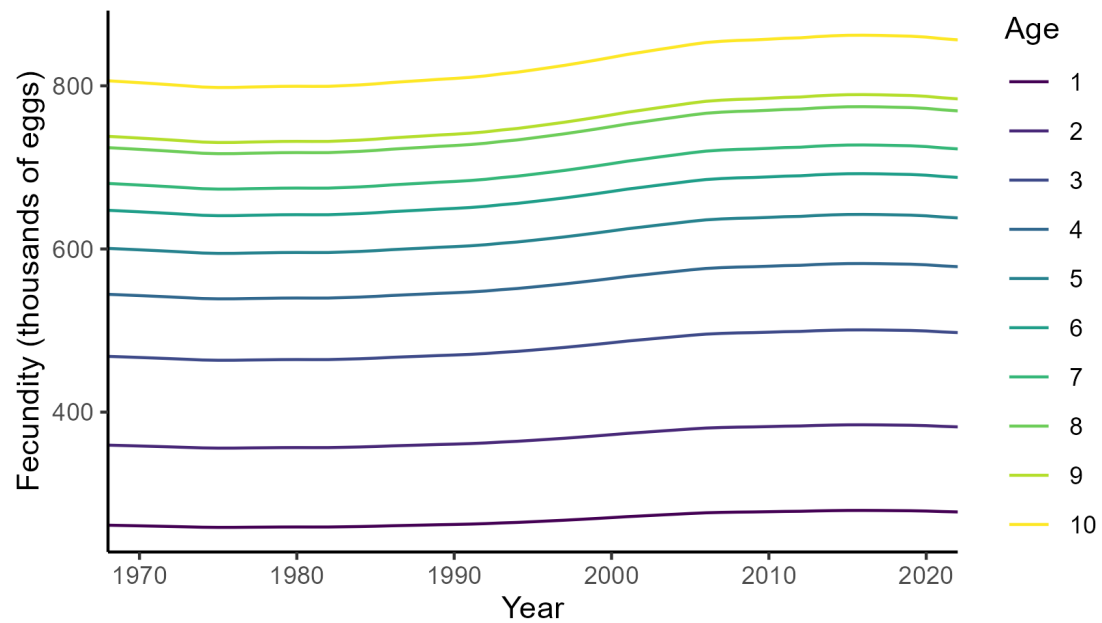


Figure 36. Fecundity-at-age of fish sampled during from May to July predicted by the mixed-effect model and used during the assessment. Age class 10 is a plus-group.

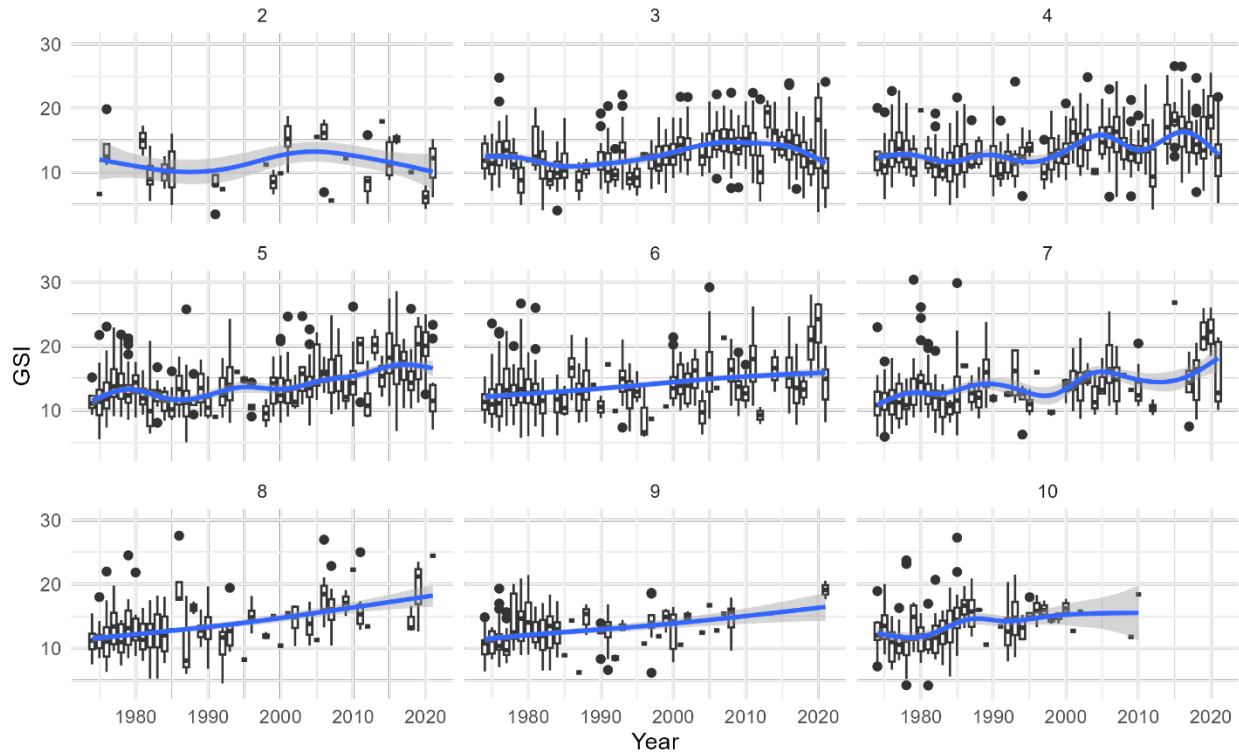


Figure 37. Evolution (1973-2021) of the gonadosomatic index (GSI) of stage 5 females in the commercial fishery from May to July, by age (facets; 2 to 10). A smoothed conditional mean based on a generalized additive model (GAM) was plotted (blue) to help visualize trends. Age class 10 is a plus-group.

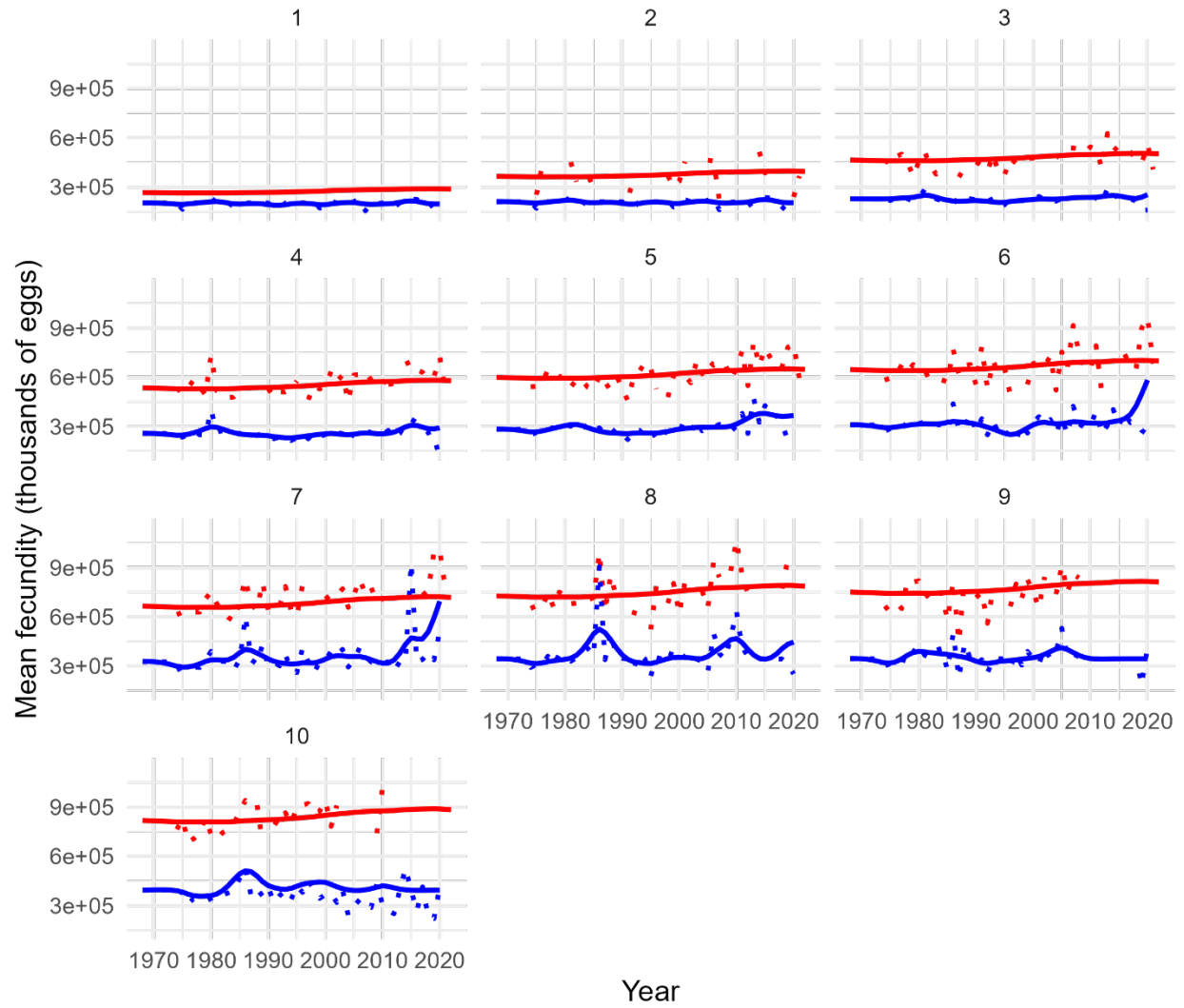


Figure 38. Raw (dots) and smoothed (lines) fecundity (kg) per age (panels) used in the 2021 (blue; Smith et al. 2022) and 2023 assessment (red). Age class 10 is a plus-group.