Life history analyses

14 November, 2022

1 Introduction

The stock assessment incorporates life history information in two ways: through the weight-at-age matrix that links the abundance-based population dynamics to observed landings (and thus scales the model) and through the weight-at-age and maturity-at-age schedules which define spawning stock biomass and thus impact spawning stock biomass and biomass-based biological reference points. The following analyses give context to the life history data, highlighting changes over space and time as well as any sex-based differences.

1.1 Data

The data used in the models below are derived from (1) state biological data submissions; (2) NEFSC spring and fall bottom trawl surveys; (3) NEFSC port sampling; and (4) NEAMAP and ChesMMAP surveys. States and agencies were solicited for any bluefish life history data they had on characteristics such as age, fork length, sex, maturity status, etc. Notably, not all the yield from this data call aligned exactly with previous data calls (e.g., from the 2015 benchmark assessment); however, after a suite of comparative analyses the Working Group deemed that the data calls were similar enough (Figs. 2 and 3) and opted to work with the new data set with the addition of ages and lengths from the historical data set that were not present in the new data set.

1.2 Life history processes and observations

It is important to note that the sampling programs discretely observe bluefish as they undergo their annual dynamic processes of migration, growth and reproduction. Important contextual information that informs the observations we used includes:

- Some bluefish undergo seasonal migration, appearing in the northern Mid-Atlantic Bight during the summer and fall months, while other populations remain resident during that period (Shepherd et al. (2006)).
- Annulus formation is estimated to occur from April to September in the Mid-Atlantic (VanderKooy et al. (2020)).
- Birthdays may range from June to September (VanderKooy et al. (2020)) as bluefish are known to have a protracted spawning period and an individual bluefish may spawn multiple times per year (Robillard et al. (2008)).

The timing of annulus formation, birthdays and spawning periods is important to consider as these physiological processes interact with the spatiotemporal pattern of data observations up and down the Atlantic coast. The sampling programs that collected data

for this study used various sampling gears and came from commercial, recreational and fishery independent sources; the impacts of these differences in sampling are not considered in this working paper.

2 Methods

The equations that are used to define the metrics examined in this working paper are given below. When models are compared based on various factors the data sets were split on that factor (i.e., as opposed to fitting a model with categorical variables as effects). This approach simplifies the analyses by reducing the number of decisions that need to be made regarding interaction terms, model evaluations, etc. However it also makes it difficult to determine whether any differences are notable from a statistical perspective. Each sample in the various data sources was weighted equally; in other words there was no treatment given to repeated measures in this analysis and the sampling programs were treated as equally representative of bluefish life history characteristics.

2.1 Mean length-at-age

The mean length-at-age is calculated as

$$\bar{L}_a = \frac{1}{n_a} \sum_{i=1}^{n_a} L_{i,a} \qquad (1)$$

where $\bar{L}_a$ is the average length at age a, n_a is the number of individuals at age a and $L_{i,a}$ is the fork length of the ith individual.

2.2 Mean weight-at-age

The mean weight-at-age is calculated as

$$\bar{W}_a = \frac{1}{n_a} \sum_{i=1}^{n_a} W_{i,a} \qquad (2)$$

where $\bar{W}_a$ is the average weight in kg at age a, n_a is the number of individuals at age a and $W_{i,a}$ is the weight of the ith individual.

2.3 Length-at-age

Length-at-age is modeled using the von Bertalanffy growth equation

$$\hat{L}_a = L_\infty(1 - e^{-k(a-t0)}) + \epsilon \qquad (3)$$

where $\hat{L}_a$ is the expected length at age a and L_∞, k and t_0 are estimated parameters and $\epsilon \sim \mathcal{N}(0, \sigma^2)$. When the data points were all weighted equally, it was clear by eye that the curve did not fit older ages due to the scarcity of sampling of older individuals. The solution was to use weighted nonlinear regression to account for uneven sample sizes across ages. The

same von Bertalanffy model above was fit, with weights applied to each data point. The weight w assigned to a data point at age a was $w_a = \frac{1}{n_a}$ where n_a is the number of records available at age a. The weighted sum of squares SS is then

$$SS = \sum_{a=1}^{A} \sum_{i=1}^{n_a} w_a (L_{i,a} - \hat{L}_{i,a})^2 \qquad (4)$$

where A is the number of ages, $L_{i,a}$ is the observed fork length of individual i of age a and $\hat{L}_{i,a}$ is the predicted length of individual i of age a.

A potential issue with the weighted least squares fit was that there were some older ages with very few observations. To avoid over-weighting those data, any ages that had fewer than 30 samples were assigned the same weighting as the age category that had smallest number of samples that was still larger than 30.

2.4   Weight-at-length

Prior to weight-at-length analyses the data set was checked for outliers. Any weights that were greater than three standard deviations outside the mean for the 1 cm size bin they were a member of were removed.

Weight-at-length analyses followed the allometric growth equation

$$W = aL^b e^\epsilon \qquad (5)$$

where W is weight in kg, L is fork length in cm, a and b are estimated parameters and $\epsilon \sim \mathcal{N}(0, \sigma^2)$. The model was fit using linear regression as

$$\log W = \beta_0 + \beta_1 \log L + \epsilon \qquad (6)$$

where $\beta_0 = \log a$ and $\beta_1 = b$. After the model was fit, the parameters were back transformed as $a = e^{\beta_0}$ and $b = \beta_1$.

2.5   Maturity-at-age

Maturity-at-age is modeled using a logistic function:

$$\log\left(\frac{p_A}{1 - p_A}\right) = \alpha_0 + \alpha_1 A + \epsilon \qquad (7)$$

where p_A is the probability that an individual of age A is mature, α_0 and α_1 are estimated parameters and $\epsilon \sim \mathcal{N}(0, \sigma^2)$. The estimated probability of maturity-at-age is then calculated as

$$\hat{p}_A = \frac{e^{\alpha_0 + \alpha_1 A}}{1 + e^{\alpha_0 + \alpha_1 A}} \qquad (8).$$

The above approach was used for the 2015 benchmark assessment and for the analyses here that used exclusively NMFS trawl and port sampling data. For the analyses that also

included the various state data sets timing of sampling was also included. Two-month wave (e.g., Wave 1 is Jan/Feb) was used to represent the timing of sampling, and this effect was included in the logistic GLM. The estimated probabilities including the wave effect were

$$\hat{p}_{A,W} = \frac{e^{\alpha_0 + \alpha_1 A + \alpha_2 W}}{1 + e^{\alpha_0 + \alpha_1 A + \alpha_2 W}} \qquad (9).$$

where W was a categorical variable representing two month wave and α_2 was the wave effect. As the mid-year maturity was of interest, the final schedule was the average of the Wave 3 and Wave 4 predictions-at-age.

2.6   Age structures

Historically, scales were used for bluefish ageing, though more recent research has shown otolith ageing to be more accurate (Sipe and Chittenden Jr (2002); Robillard et al. (2009); VanderKooy et al. (2020)). During the early part of the time series scales were the only age structure that was collected, but otoliths began to dominate during the late 1990s (Fig. 4). Differences in mean length-at-age between otoliths and scales were modest in most cases (Fig. 1); the analyses that follow use both scale and otolith ages together.

Most ages were used as they were recorded; North Carolina scale ages during 1985-2000 were adapted however. Following the 2015 benchmark, these data were adapted due to concerns over their consistency with other records; in particular these fish did not appear to be aged assuming a January 1 birthdate (National Marine Fisheries Service (2015)). The working group adapted North Carolina ages by (1) assuming all spring age-0 samples were age-1 fish, and (2) bumping other ages up one year if they fell outside the 95% confidence interval for what the working group considered to be reliable first semester fish of that age based on other data sources. For more information see National Marine Fisheries Service (2015).

3   Results and discussion

3.1   Length- and weight-at-age

3.1.1   Models

von Bertalanffy and allometric growth models generally fit the data well (i.e., there was little residual patterning; Fig. 5). Notably, the von Bertalanffy model fit improved when each data point was weighted by the inverse of the number of individuals that were sampled at that age; due to oversampling of younger ages the naïve model fit was skewed towards fitting the younger ages and led to overestimates of fork length at older ages.

Weight-at-length was generally well explained by the allometric growth model (Fig. 6), although there was some residual patterning: at middle sizes from approximately 25-35 cm the residuals appeared to be positively biased (Fig. 7). When split by season and region, it was evident that the most extreme patterns arose in the south during semester 1 and in the north during semester 2 (Fig. 8). Possible explanations include a deficiency in the

allometric growth model as applied to the bluefish population for estimating weight at these sizes or bias derived from sample collection in space and time. The residuals tended to increase in size for larger individuals but this is because variance tends to increase with the mean.

The von Bertalanffy parameters from the model fit using all data (Table 1) were similar to those found by Salerno et al. (2001) (note that the source of the Salerno et al. data was the NEFSC fall bottom trawl, one of the components of this data set). The Salerno et al. estimates were based on data collected offshore while the estimates compiled in this study included additional inshore sources (e.g., state surveys); this suggests that there are limited inshore-offshore differences in growth (or, and perhaps more likely, that the same population of fish caught offshore is also caught inshore); however, note the differences in North Carolina in Section 3.1.2.

The data used by Salerno et al. were collected during 1985-1996; that their parameters are similar to those estimated here suggests that growth has not changed substantially over time. This is confirmed for the most part when the length-at-age data are viewed on a decadal scale; however, when the data are organized into cohort decades (i.e., all the fish born during the same decade were grouped together), bluefish born during the 2000s appear to have experienced a different growth pattern which was slower over the ages most commonly encountered in the commercial and recreational fisheries (Fig. 9). Note that the Salerno study used scales exclusively for ageing whereas the current study used both scales and otoliths for ageing (Fig. 4). Differences in age estimates from one age structure to another could contribute to observed differences in size at age over time.

Some differences in von Bertalanffy parameters were found between the 2015 benchmark assessment and the models produced using the data from the Research Track call (Table 1). This discrepancy could be the result of the weighted least squares version of the von Bertalanffy model that was used in the Research Track implementation. However, the effective difference is small because a reduction in L_∞F is offset by an increase in K (i.e., these parameters tend to be negatively correlated). Considering ages 0-6, the Benchmark version predicted a higher length-at-age from ages 0-2 while the Research Track version estimated a higher length-at-age for ages 3-6; over the range of ages considered in this assessment the length-at-age estimates were similar.

Length-at-age varied modestly by semester especially at younger ages (Table 2 and Fig. 11), whereas weight-at-age varied more at older ages (Table 4 and Fig. 13). This is in line with expectations as second semester fish are older than first semester fish and expected to weigh more due to feeding patterns. The length-at-age difference disappears at older ages (Fig. 11) but persists for weight-at-age (Fig. 13), probably due to intra-annual changes in feeding patterns.

Length-at-age appeared to vary by geographic region (Table 3 and Fig. 12) but weight-at-age did not (Table 5 and Fig. 14). Sampling timing varied by region so the length-at-age differences should be further examined before application.

Decadal differences in growth appeared primarily in length-at-age. Weight-at-length models were also developed on a decadal scale (Fig. 10) but for the most part, there was no

variability in weight-at-age. The apparent exception was fish that were born during the 2020s; however, because the maximum age of these individuals was 1 and the maximum size was 47.8 cm, these samples did not cover a comparable range of sizes so the 2020s model may not be representative. The intra-decadal geographic and temporal distribution of sampling over time should be examined before making conclusions on decadal differences.

Neither length-at-age nor weight-at-age varied by sex (Figs. 15 and 16). This finding supports that of Salerno et al. (2001) and references therein.

3.1.2 Empirical distributions

The empirical mean length-at-age was also calculated. The overall pattern was similar to the von-Bertalanffy growth model described earlier (Fig. 17). When the data were split into semesters it was evident that second semester length-at-age was larger at younger ages during the period of fastest growth (Fig. 18). Splitting the data by geographic region (Fig. 19) revealed some differences in length-at-age: size tended to be smaller in the south, but it should be noted that the timing of sampling was not accounted for here which could make a difference especially at younger ages when individuals grow faster.

Ages three and four exhibited bimodal size distributions in the south. This pattern was caused by the North Carolina data. Larger age-3 and age-4 North Carolina samples were primarily sampled from offshore fisheries as opposed to inshore sampling programs which tended to capture smaller fish of the same age. These differences appear to be true effects (i.e., as opposed to ageing error) because these samples were aged by otoliths; thus it is important to consider the contribution of the North Carolina inshore and offshore samples to the development of the age-length key in terms of how well those data represent the southern region.

The annual length-at-age data described here – though organized as age distribution by length group – supported the age-length keys (directly in the case of the traditional keys and as the basis of the models in the case of the multinomial keys) (see working paper Celestino et al. Development of Bluefish Age-Length Keys).

3.2 Maturity-at-age

Bluefish mature quickly; over 40% were mature at age-1 and over 90% by Age-2 (Table 6). The 2015 benchmark assessment estimates, which relied only on NMFS data to estimate maturity-at-age, were similar to the results that included NMFS data through 2022; however, subtle differences were observed in the maturity schedule when data from other sources were also included. The "Midyear model" (that used all available data and where sample timing by wave was included and the average maturity for ages 3 and 4 was used) predicted slightly higher maturity at age-1 and slightly lower maturity at age-2 than the NMFS-only data set. The NMFS-only analyses did not incorporate time of year in its logistic model which could partly explain the difference. However, given the differences in inshore and offshore growth in the North Carolina data set noted above spatial or sampling processes could also contribute to these observed differences.

Bluefish maturity did vary by semester of sampling; individuals sampled later in the year were more likely to be mature (Table 7, Fig. 20). There was no observed difference in maturity by sex (Table 8, Fig. 21). These figures and tables only used the NMFS trawl survey and port sampling data sets.

The macroscopic observations that were used here to develop the maturity schedule differed from the findings of Robillard et al. (2008), where histological data were used. The differences were especially evident in age-1 maturity. The schedule developed using macroscopic observations estimated approximately 40% of individuals were mature where as Robillard et al. (2008) estimated approximately 20% maturity. We did not note macroscopic observations in this data set to differ dramatically by data source. One major difference is that Robillard et al. (2008) used females only; however this difference is not likely to account for the disparity as the macroscopic observations did not indicate a difference between male and female maturity schedules (Fig. 21). The observations here were similar to those of Salerno et al. (2001) (Table 6) which used some of the same data (the NMFS data available at the time) and were also based on macroscopic observations. The cause of the disparity in age-1 maturity between histological and macroscopic observations was not evident and the overestimation of age-1 maturity by macroscopic observation is a possibility. However, more research and additional data would be necessary before ignoring macroscopic data in favor of a histological approach.

4   Research recommendations

- This simple approach to modeling split the data according to various variables (e.g., sex, semester). A more robust approach that would allow for the quantification of differences across various factors would be to include categorical variables such as sex and semester in the same model; this way it could be stated explicitly whether observed differences were statistically significant.

- Dynamic random effect models. The different variations of the growth and maturity models that were fit here used discrete sets of data (e.g., models fit by decade). In addition, the source of the data was not accounted for. A possible approach would be to fit dynamic life history models where parameters such as L_∞ or K vary over time. In addition, the data sources could be incorporated as random effects; this would account for the varying characteristics of observations that occur across the different sampling programs.

5   Tables

Table 1: von Bertalanffy parameters as estimated in this study, Salerno et al. 2001 and the 2015 Benchmark.

Model	Linf	K	t0
This study	86.0	0.254	-0.593
Salerno et al., 2001	87.2	0.260	-0.930
2015 benchmark	113.0	0.126	-1.604

Table 2: von Bertalanffy parameters by semester.

Semester	Linf	K	t0
1	87.9	0.22	-0.61
2	84.6	0.27	-0.62

Table 3: von Bertalanffy parameters by region.

Geo	Linf	K	t0
North	83.6	0.28	-0.84
South	105.0	0.13	-1.44

Table 4: Allometric growth parameters by semester and including the entire data set.

Semester	a	b
1	0.0000140	2.957
2	0.0000120	3.027
-	0.0000137	2.972

Table 5: Allometric growth parameters by region.

Geo	a	b
North	0.0000135	2.983
South	0.0000138	2.968

Table 6: Maturity-at-age through age-6 as calculated in various studies. The Working Group retained the maturity-at-age schedule used during the 2015 benchmark for the primary model runs.

Age	Bench 2015	NMFS 2022	Midyear model	Salerno 2001	Robillard 2009
0	0.00	0.000	0.000	0.00	0.00

Age	Bench 2015	NMFS 2022	Midyear model	Salerno 2001	Robillard 2009
1	0.40	0.417	0.456	0.41	0.21
2	0.97	0.965	0.926	0.98	0.86
3	1.00	0.999	0.995	1.00	0.92
4	1.00	1.000	1.000	1.00	1.00
5	1.00	1.000	1.000	1.00	1.00
6	1.00	1.000	1.000	1.00	1.00

Table 7: Maturity at age by semester.

Semester	0	1	2	3	4	5	6
1	0.003	0.108	0.822	0.994	1	1	1
2	0.010	0.466	0.987	1.000	1	1	1

Table 8: Maturity at age by sex.

Sex	0	1	2	3	4	5	6
Female	0.026	0.440	0.959	0.999	1	1	1
Male	0.020	0.413	0.960	0.999	1	1	1

Table 9: Maturity at age by decade when the fish were spawned.

CohortDecade	0	1	2	3	4	5	6
1980	0.015	0.353	0.951	0.999	1	1	1
1990	0.006	0.429	0.990	1.000	1	1	1
2010	0.064	0.524	0.947	0.997	1	1	1

Table 10: Maturity at age by Region.

Geo	0	1	2	3	4	5	6
North	0.015	0.461	0.979	1.000	1.000	1	1
South	0.020	0.238	0.824	0.986	0.999	1	1

6   Figures
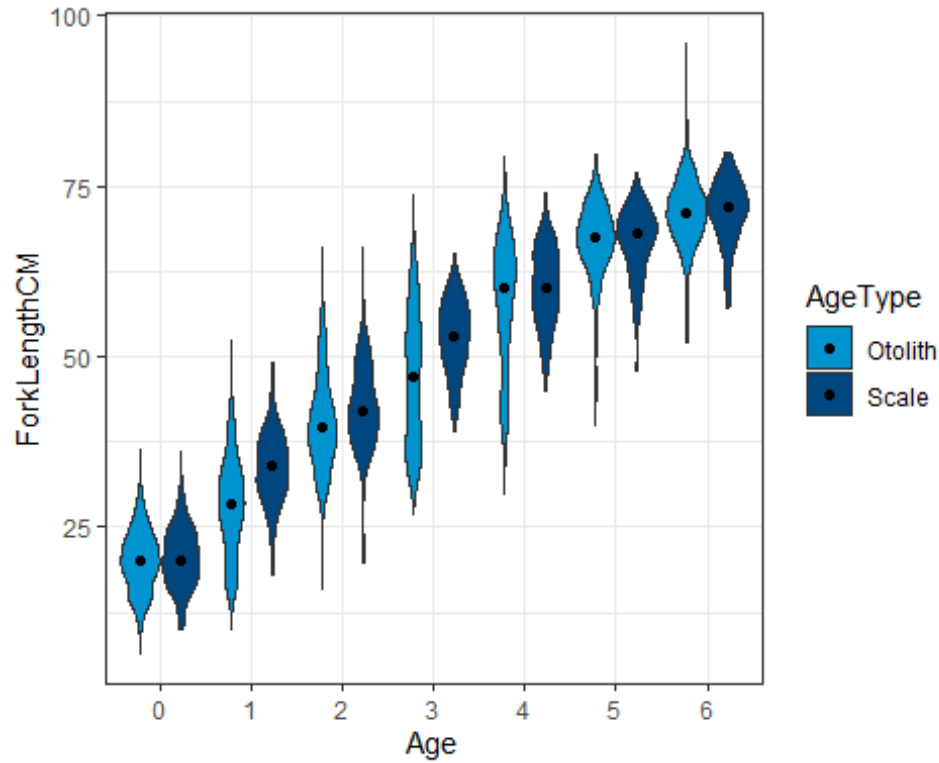
Figure 1: Violin plots comparing overall measurements of size-at-age between scales and otoliths. Points represent median values. Length-at-age is generally similar between the two structures, though scale ages are larger at ages 1-3. Sampling programs typically collect either scales or otoliths and collection may differ in time and space which could contribute to these differences.
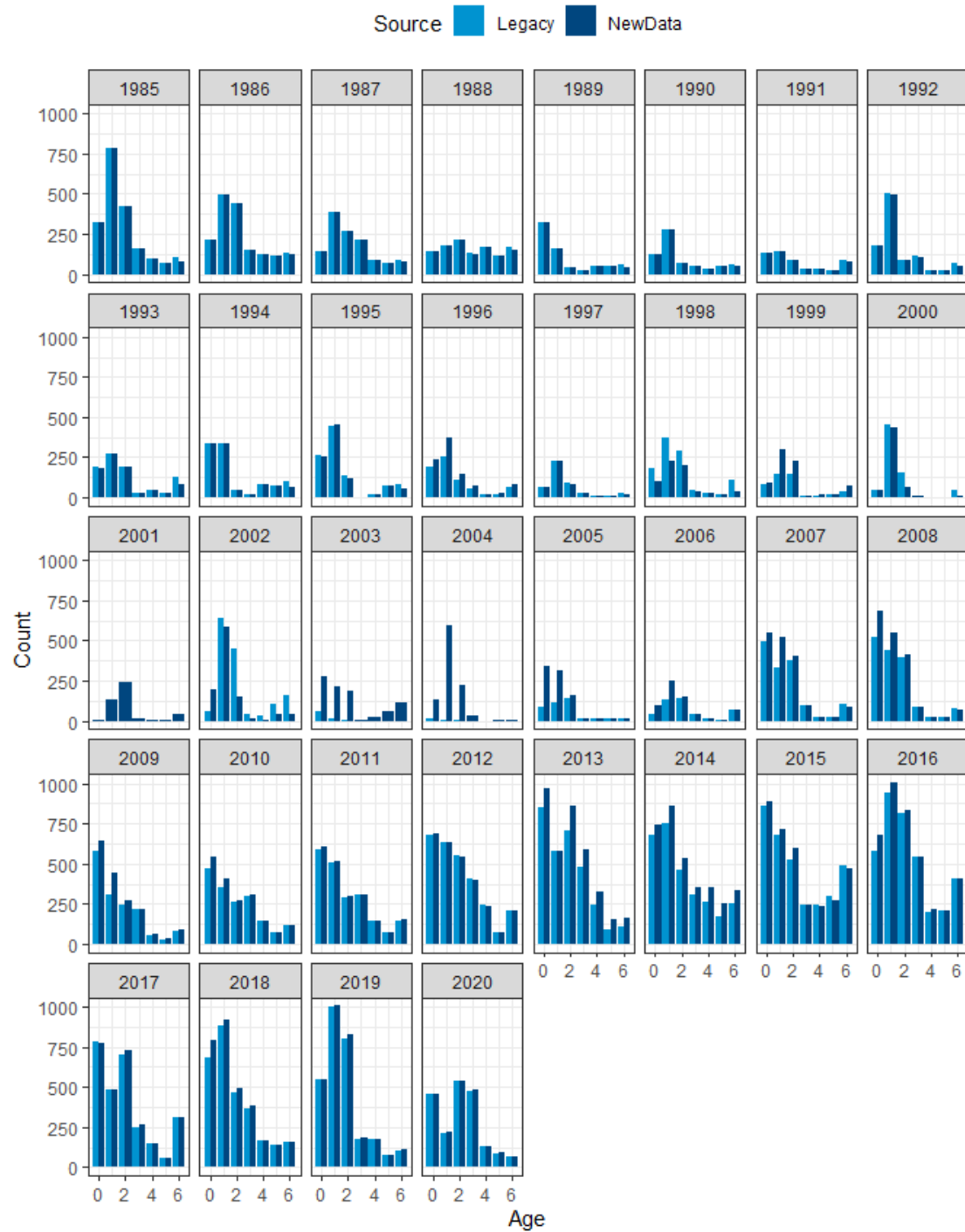
Figure 2: Counts of sampled individuals by age from the new and legacy data sets. Considerable amounts of new data came from North Carolina, South Carolina and Virginia during 2001, 2003 and 2004.
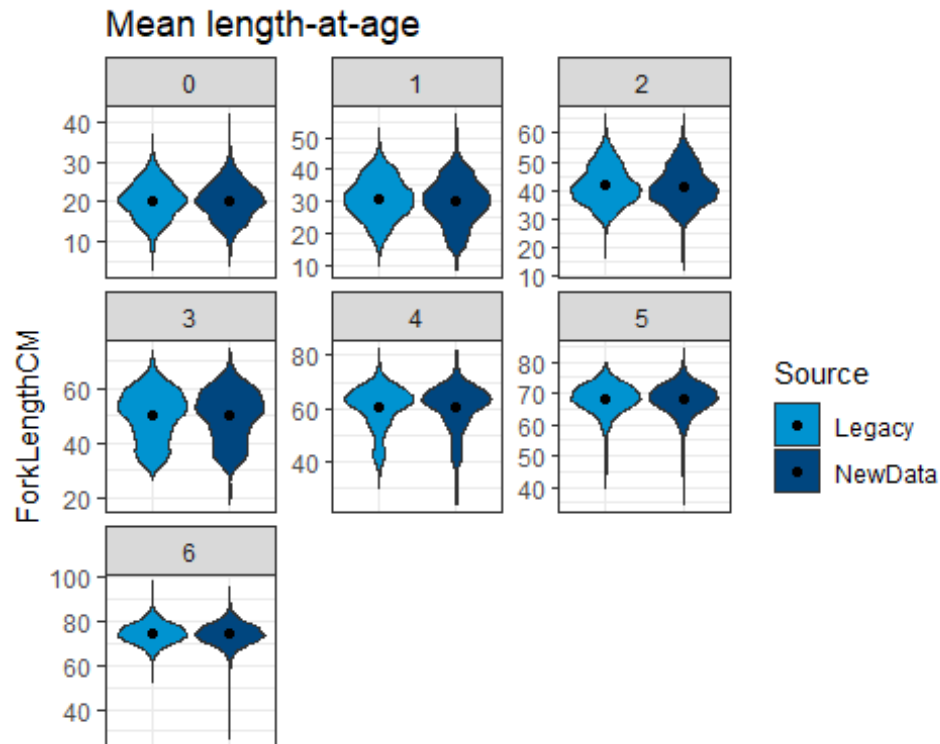
Figure 3: Mean length-at-age comparison from the new and legacy data sets. Tests at various spatial and temporal scales did not suggest appreciable differences in the data sets. Age 6 represents the plus group.
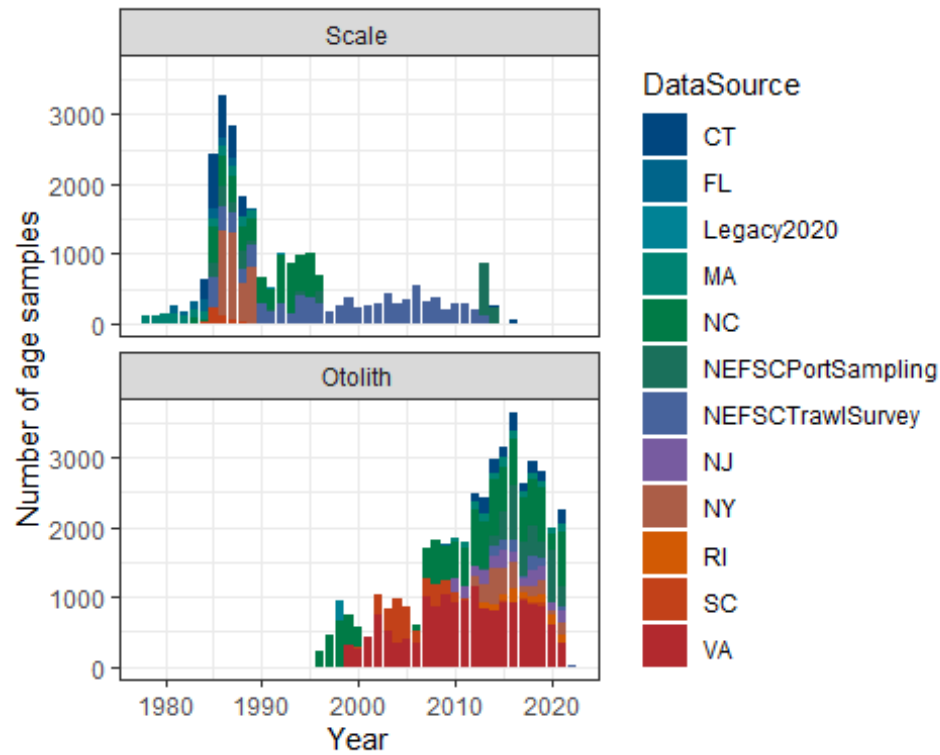
Figure 4: Age samples collected by program. Legacy data are age samples that appeared in previous assessments but corresponding samples could not be found during the latest data submission.
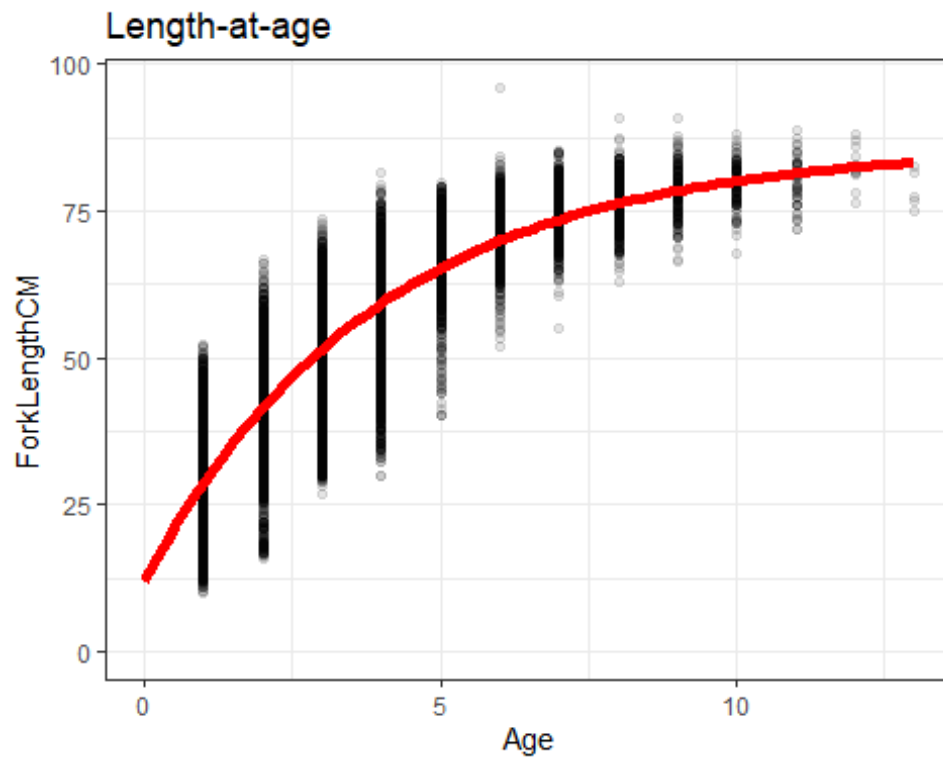
Figure 5: Fitted von Bertalanffy growth model using all data.
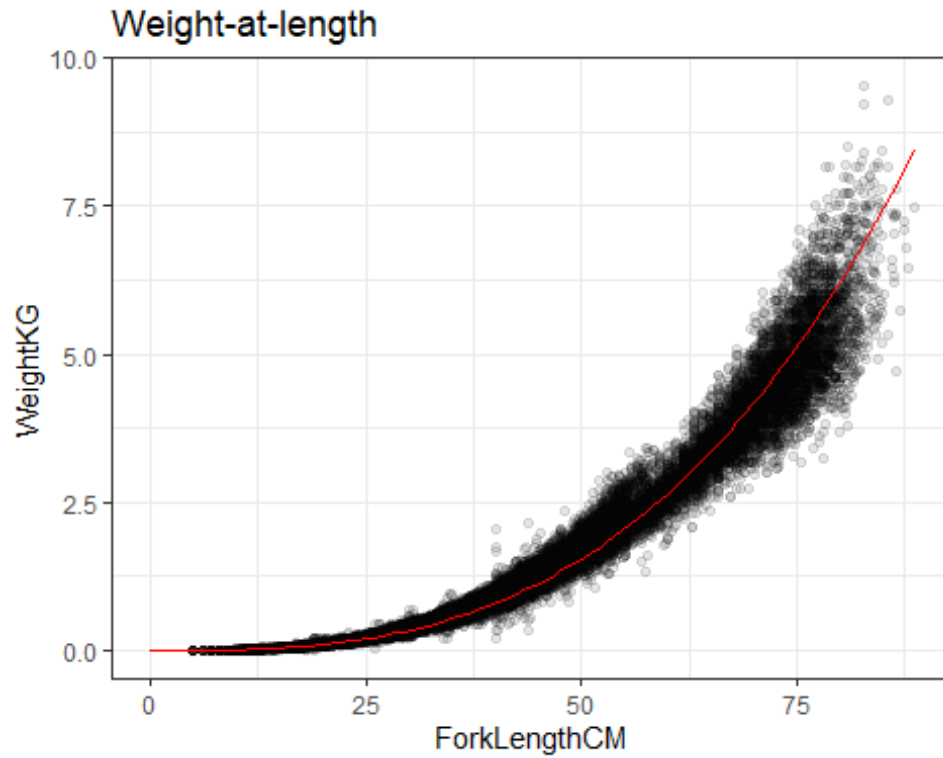
Figure 6: Fitted allometric growth model using all data.
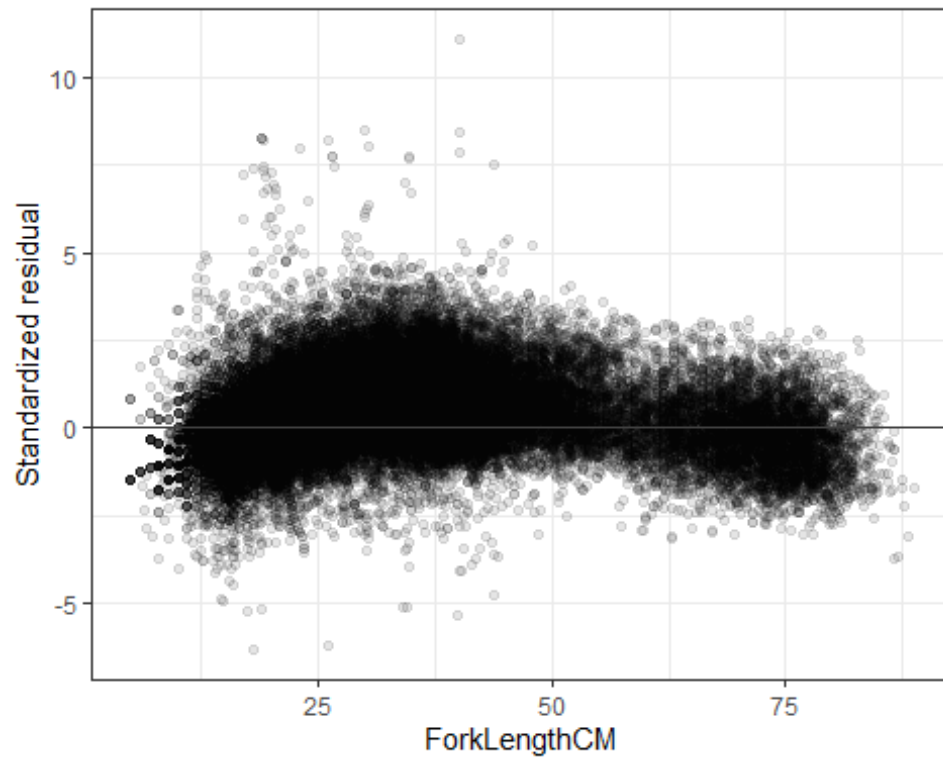
Figure 7: Allometric growth residuals. Residuals were standardized by grouping records by fork length, calculating the grouped standard deviation, and dividing each record by that value.
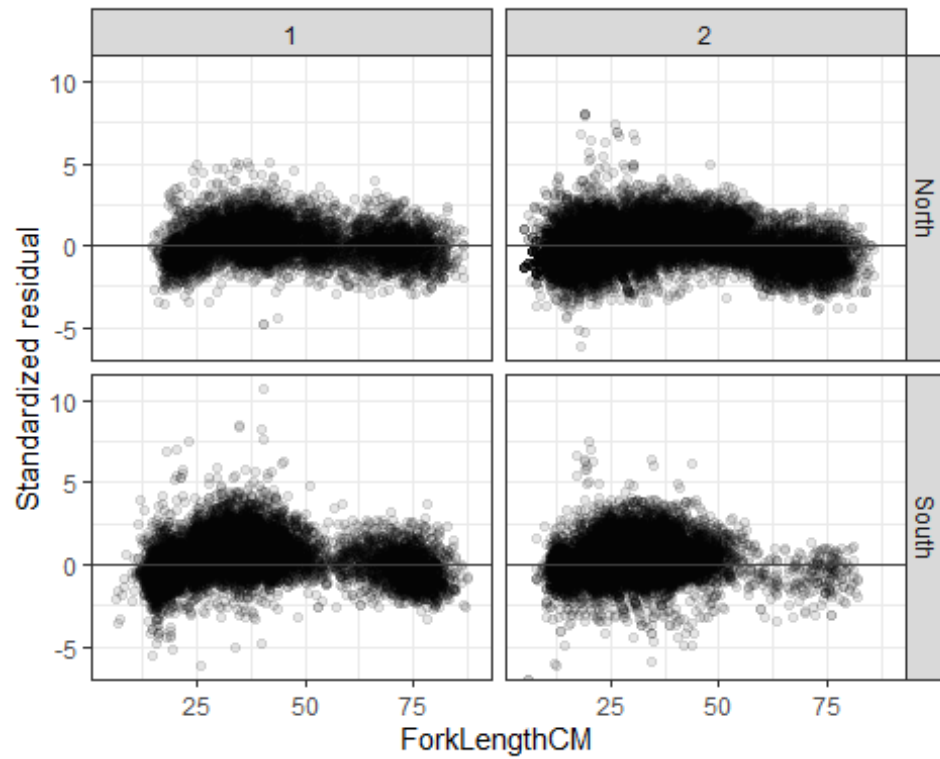
Figure 8: Allometric growth residuals by region and semester. Residuals were standardized by grouping records by fork length, calculating the grouped standard deviation, and dividing each record by that value.
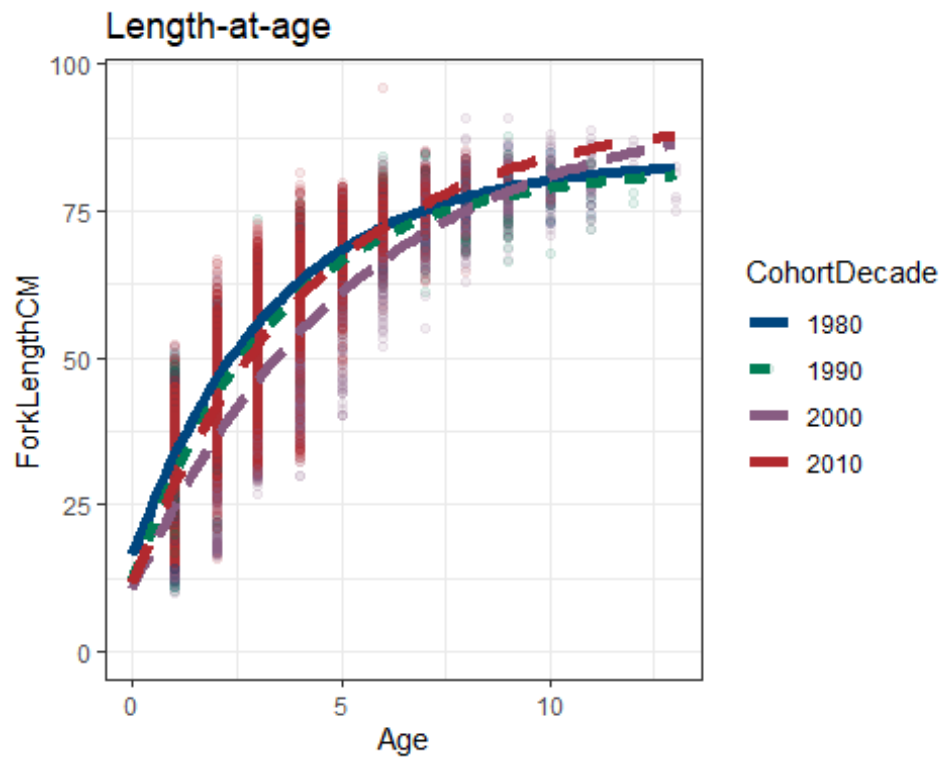
Figure 9: Fitted von Bertalanffy growth model by decade when the fish were spawned.
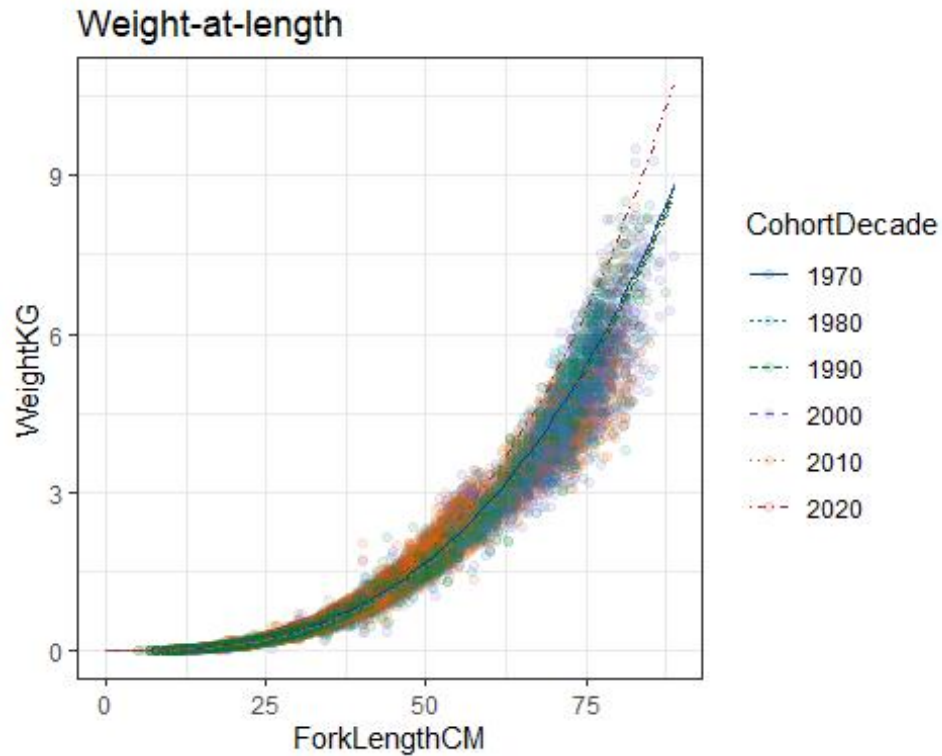
Figure 10: Allometric growth model fitted by decade when the fish were spawned.
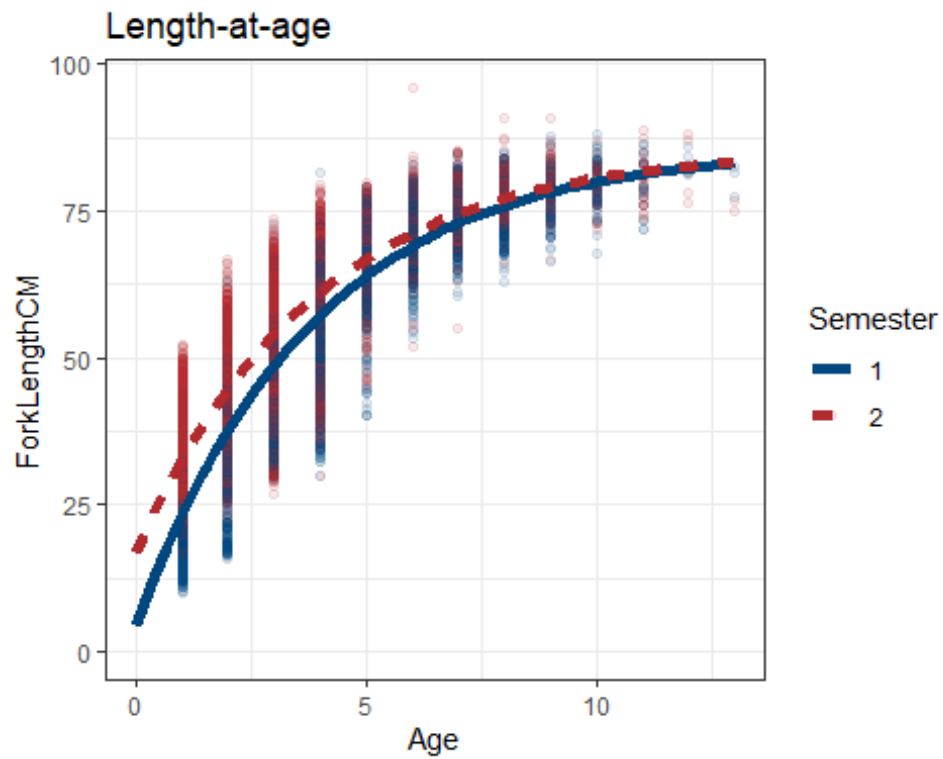
Figure 11: von Bertalanffy growth model fitted by semester.
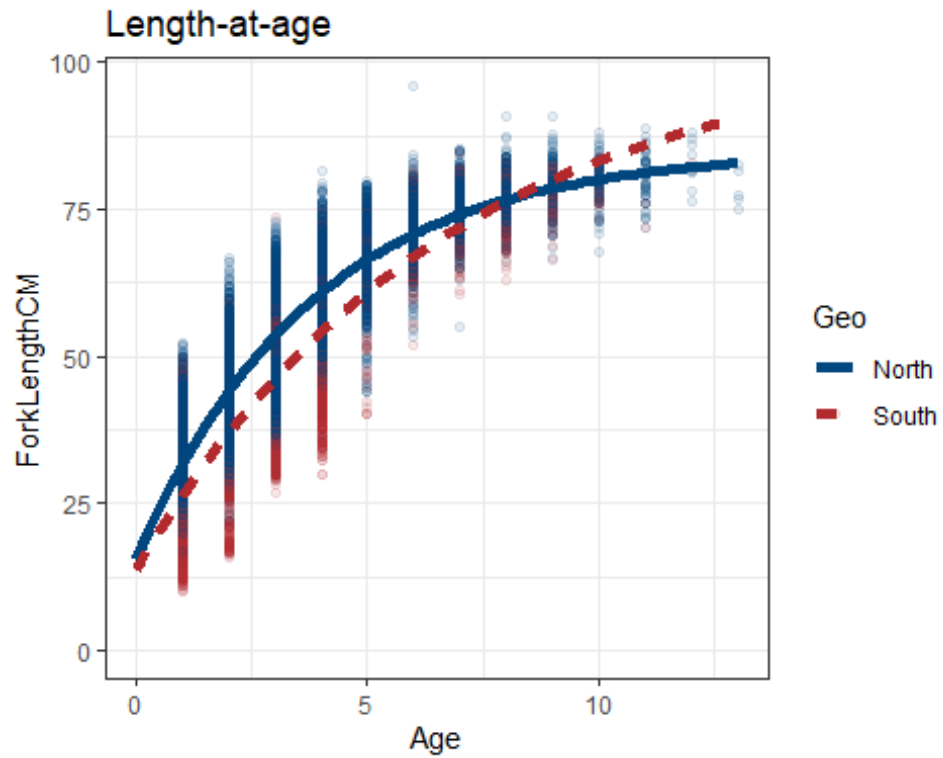
Figure 12: von Bertalanffy growth model fitted by region.
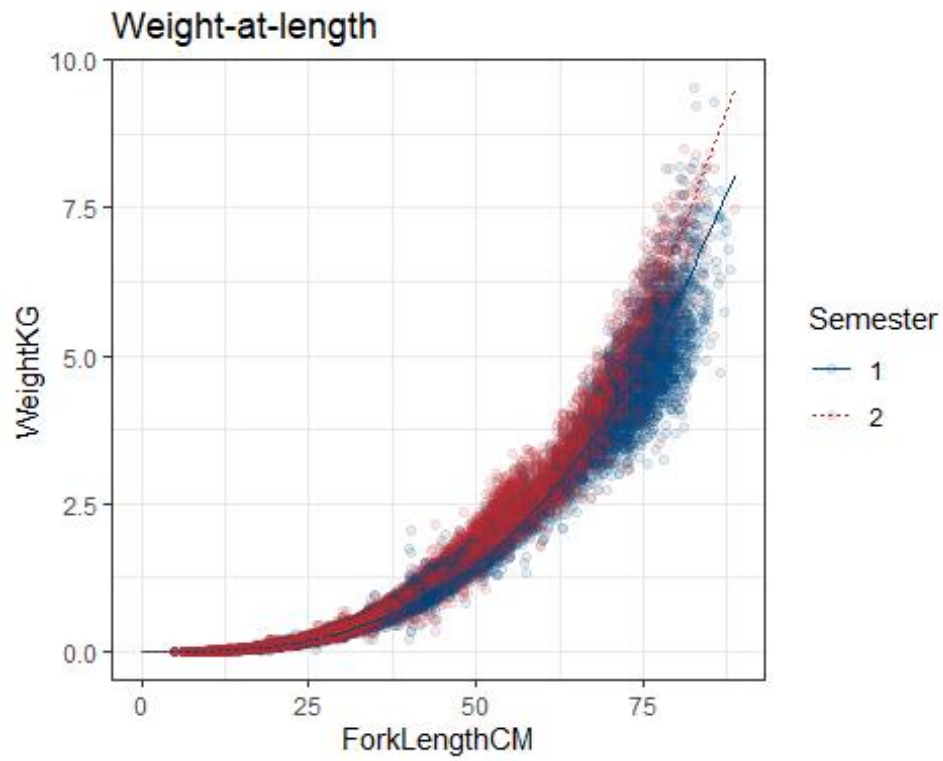
Figure 13: Allometric growth model fitted by semester.
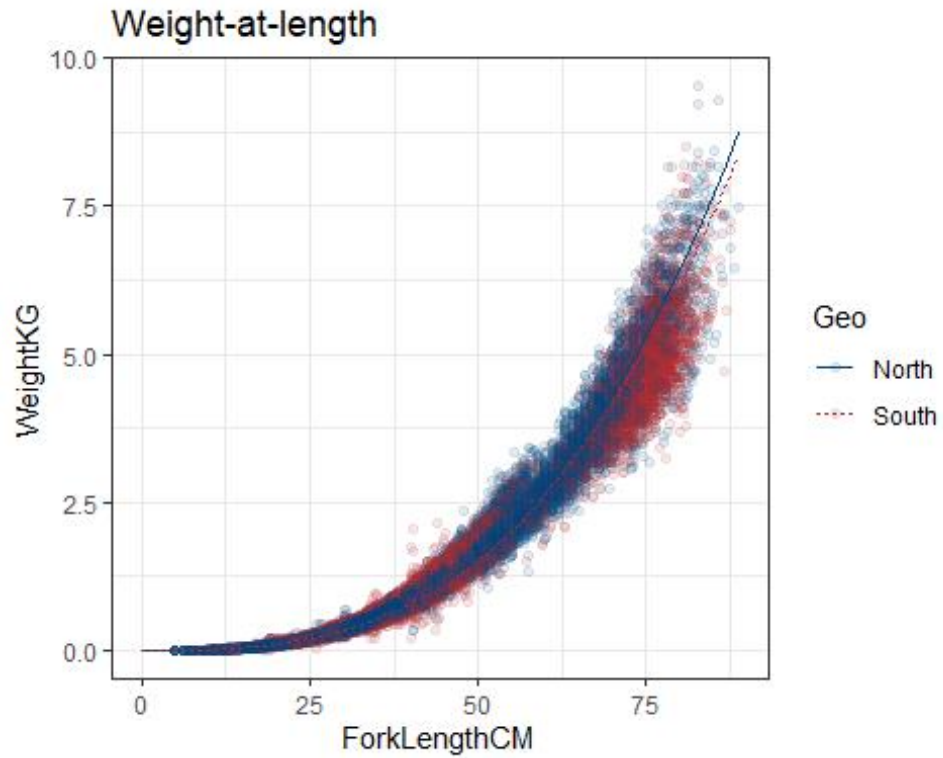
Figure 14: Allometric growth model fitted by geographic region.
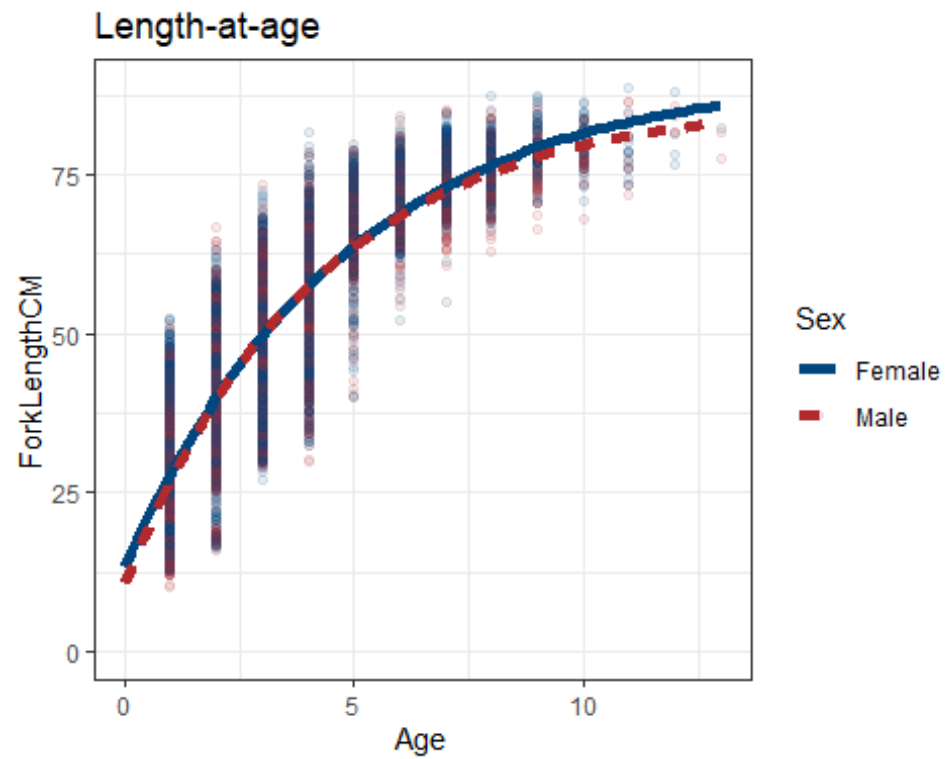
Figure 15: von Bertalanffy fits by sex.
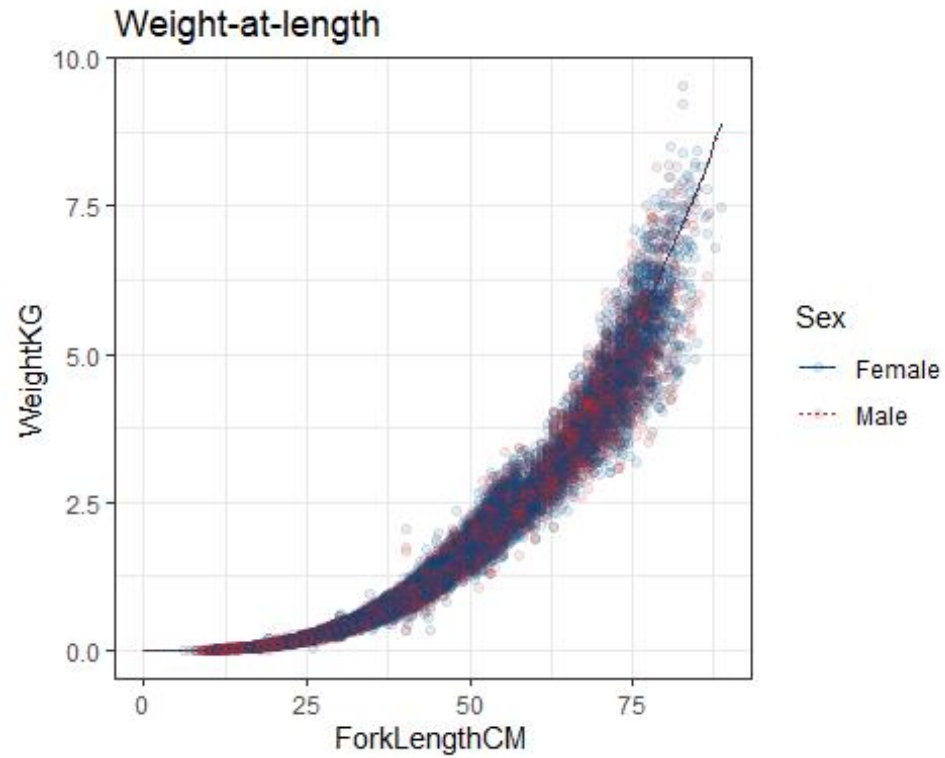
Figure 16: Allometric growth model fits by sex.
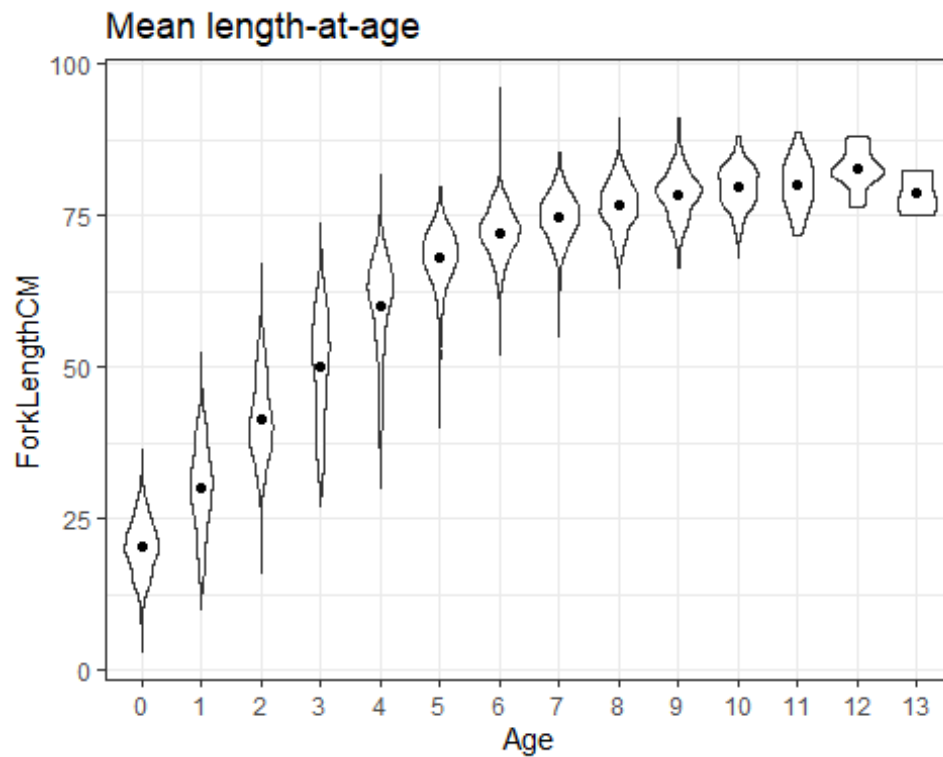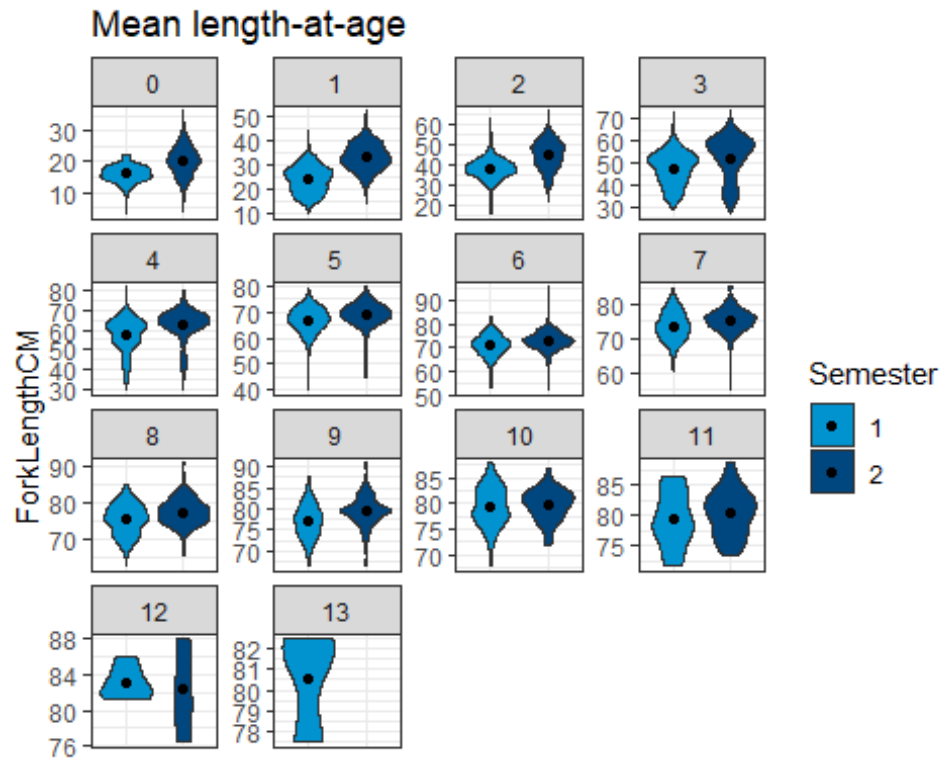
Figure 17: Violin plot of overall mean length-at-age.

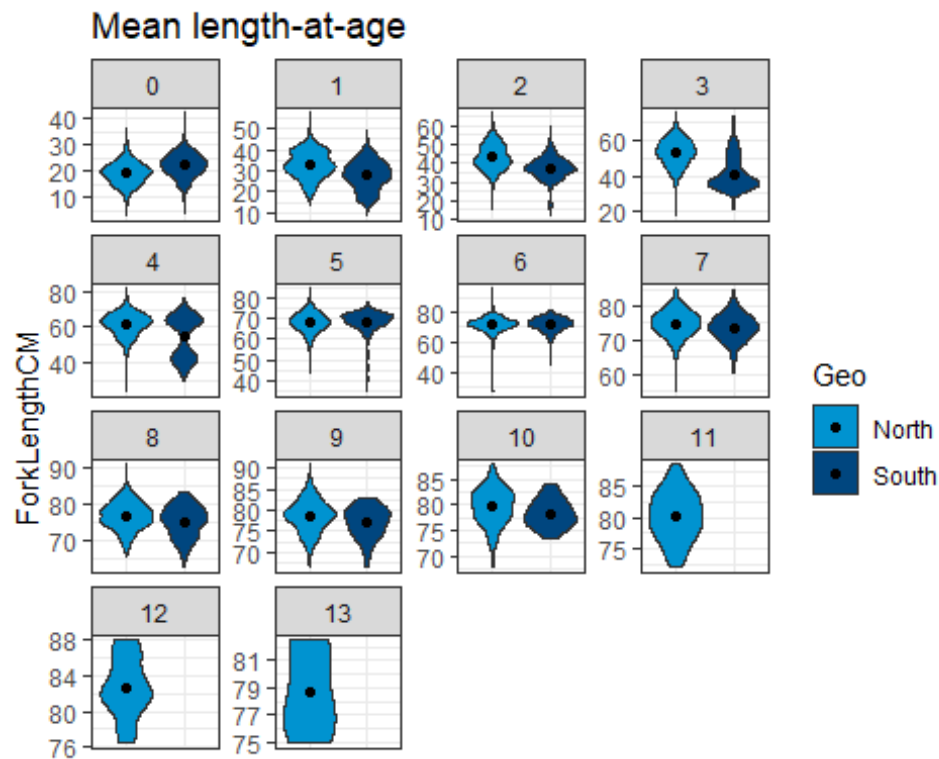*Figure 18: Violin plot of mean length-at-age by semester.*

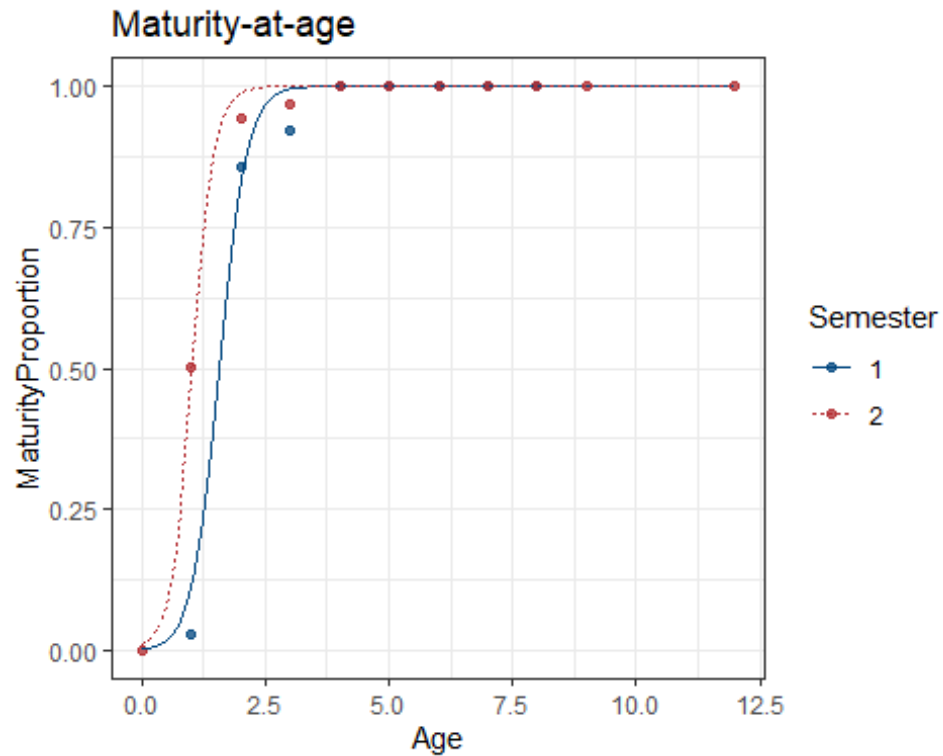*Figure 19: Violin plot of mean length-at-age by geographic region.*

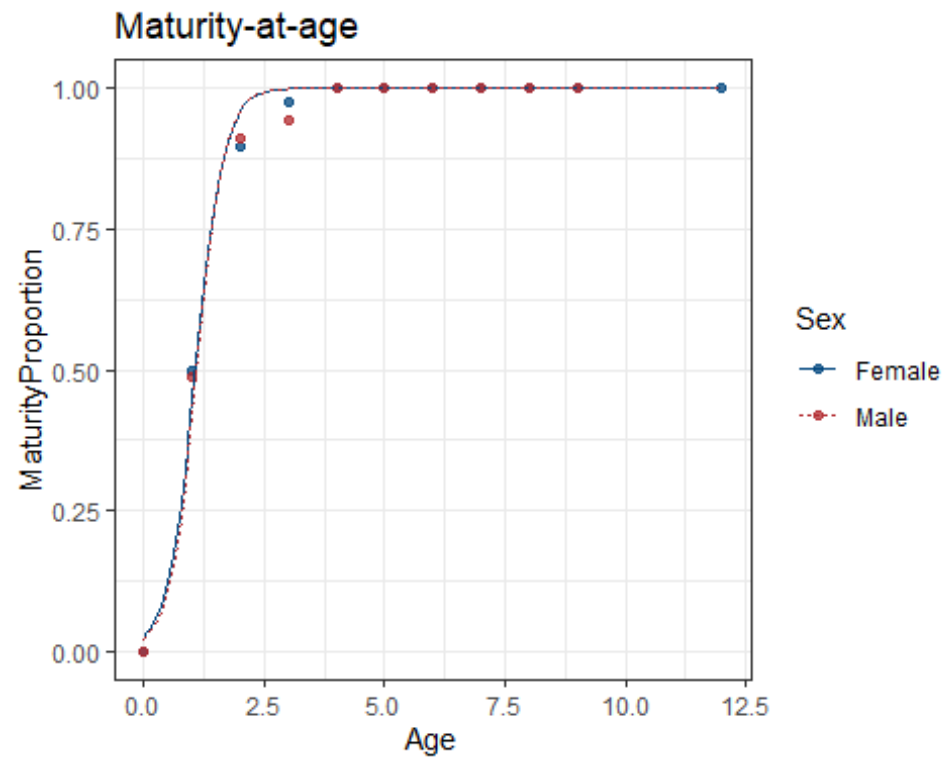*Figure 20: Maturity-at-age fits by semester. Points represent observed proportions.*

Figure 21: Maturity-at-age fits by sex. Points represent observed proportions.
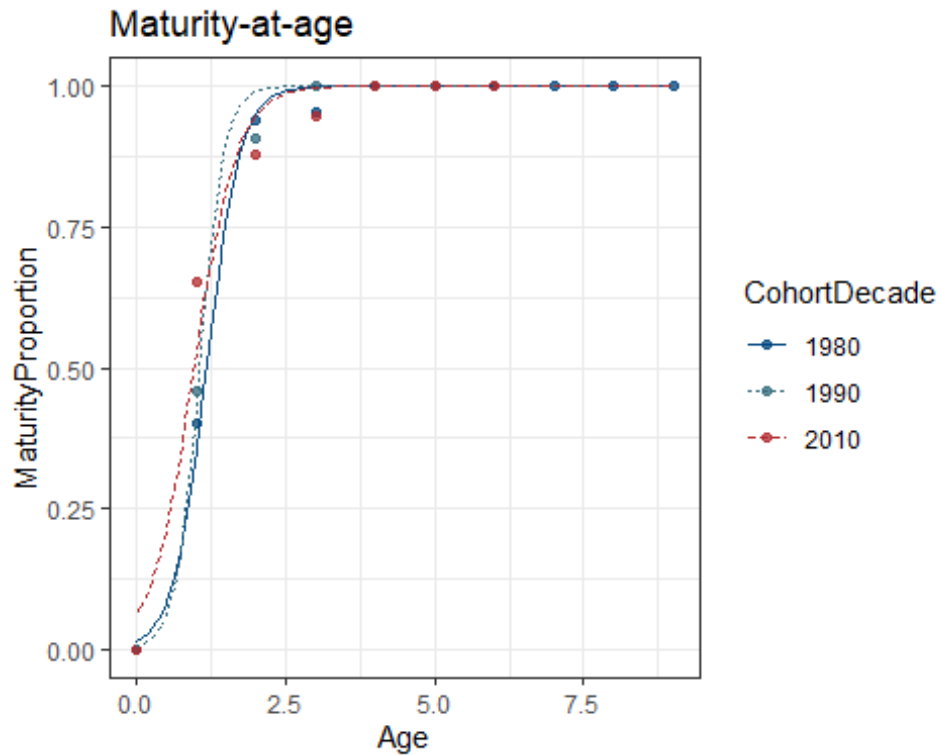
Figure 22: Maturity-at-age by decade when the fish were spawned. Points represent observed proportions.

Sources cited

National Marine Fisheries Service. 2015. Age data decisions made at 2015 assessment workshop.

Robillard, E., C. S. Reiss, and C. M. Jones. 2008. Reproductive biology of bluefish (Pomatomus saltatrix) along the East Coast of the United States. Fisheries Research 90(1-3):198–208.

Robillard, E., C. S. Reiss, and C. M. Jones. 2009. Age-validation and growth of bluefish (Pomatomus saltatrix) along the East Coast of the United States. Fisheries Research 95(1):65–75.

Salerno, D. J., J. Burnett, and R. M. Ibara. 2001. Age, growth, maturity, and spatial distribution of bluefish, Pomatomus saltatrix (Linnaeus), off the northeast coast of the United States, 1985-96. Journal of Northwest Atlantic Fishery Science 29.

Shepherd, G. R., J. Moser, D. Deuel, and P. Carlsen. 2006. The migration patterns of bluefish (Pomatomus saltatrix) along the Atlantic coast determined from tag recoveries. Fishery Bulletin 104(4):559–571.

Sipe, A. M., and M. E. Chittenden Jr. 2002. A comparison of calcified structures for aging bluefish in the Chesapeake Bay region. Transactions of the American Fisheries Society 131(4):783–790.

VanderKooy, S., J. Carroll, S. Elzey, J. Gilmore, and J. Kipp. 2020. A practical handbook for determining the ages of Gulf of Mexico and Atlantic coast fishes, 3rd edition. Gulf States Marine Fisheries Commission; Atlantic States Marine Fisheries Commission, Ocean Springs, MS.