

A THIRTY-FIVE YEAR TIME SERIES ANALYSIS OF ATLANTIC SALMON IN
ICELAND

by

TRYGGVI PAUL MCDONALD

(Under the Direction of JAMES W. PORTER)

ABSTRACT

The findings in this dissertation support the Grilsefication Hypothesis (McDonald 2001) and demonstrate a profound shift in Atlantic Salmon Life History phenomena due to commercial fishing pressure on Atlantic salmon in Iceland. A time series analysis, 1974-2008, was performed from the rod-catch data of the Icelandic rivers Haffjardara, Haukadalsa, Hofsa, Laxa in Adaldal, Midfjardara, and Vatnsdalsa. The proportions of migratory, multi-sea winter salmon and non-migratory one-sea winter grilse were plotted over time and show a shift that favors grilse. Additionally, the mean weights for both salmon and grilse are declining. These data suggest that we are seeing a profound life history shift in Atlantic salmon from iteroparity to semelparity, and a non-migratory life history change favored over a migratory one. The data indicate that Atlantic salmon in Iceland have adapted key life history parameters in response to the increased cost of migration. This response to the commercial exploitation in the Western Greenland fishery has led to grilsefication of the stock.

INDEX WORDS: Atlantic salmon, *Salmo salar*, time series analysis, grilsefication, commercial fishery, West Greenland, rod-catch.

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DEDICATION

For my family, without whose many sacrifices these words would not be before you. Special places of honor belong to Utgerdamadur Tryggvi Ofeigsson, Anna Tryggvadottir McDonald, Dr. Harold Paul McDonald and Dr. Lawrence Patton McDonald for instilling a sense of wonder and love for the natural world.

For *Salmo salar*, “The Leaper”, “The King of Fish”.

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“For many years past I have scarecely done anything else either officially or privately, except to attend to and carefully watch the interests of the King of Fish, the Salmon, the great *Salmo salar*.”

Frank Buckland (1880), Physician, Natural Historian, and Zoophagist.

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CHAPTER 1

INTRODUCTION

For thousands of years, the winter destination of migratory Atlantic salmon was a mystery. It was known that the fish left the natal rivers of their birth, for the ocean, but was not known where they went. It was only late in the 1950's with the advent of sonar detectors on nuclear submarines traveling thru the Davis Strait, off the West coast of Greenland, that they discovered massive shoals of this fish. The destination of mixed-stock (different country of origin) migratory Atlantic salmon had been uncovered. The race to exploit them on the high seas began, despite the fact that according to United Nations Convention on the Law of the Sea (UNCLOS) they are the property of the country in whose natal rivers and streams they were born. The Convention for the Conservation of Salmon in the North Atlantic Ocean entered into force on 1 October 1983 and created an inter-governmental organization, the North Atlantic Salmon Conservation Organization (NASCO, 2010).

In 2001, I hypothesized in my M.S. thesis (The Grilsefication of Atlantic Salmon in Iceland) that, according to evolutionary theory and life history theory, the removal of migratory, multi-sea winter (MSW) salmon from the annual breeding cohort by the commercial fleets on the west coast of Greenland might favor one-sea winter (1SW), non-migratory grilse (McDonald 2001). This analysis utilized a twenty-two year time

series from 1974-1996, on one river, Haffjardara, and seemed to support the grilsefication hypothesis.

The importance of the hypothesis to the understanding of the dynamic changes that migratory MSW stocks are undergoing merited an expanded investigation on a larger spatial scale and over a longer temporal scale to insure that the original investigation was not an outlier. Even if other rivers did not support the hypothesis, further investigation might still be warranted, due to the high degree of heritability for sea-age of return (Jonasson *et al.* 1997). In his sea ranching and selective breeding program, Jonasson found that the heritability for sea-age at return to be 0.98 ± 0.01 .

The fact that commercial exploitation in West Greenland removed a massive portion of the MSW salmon's annual reproductive effort from the breeding cohort over an extended period of time. It was hypothesized that if the fishery pressure was large enough in selecting against migratory salmon on the high seas, then an analysis of the entire river fishery (all rivers over a longer time series) would reveal significant reductions in multi-sea winter specimens, and their replacement by non-migratory single-sea winter individuals (grilse). I call this the grilsefication hypothesis because selection favors grilse over salmon. If correct, the analysis would be expected to show similar trends in other rivers in Iceland.

The grilsefication hypothesis predicts that we will see 1) a reduction in average size as measured by weight, 2) earlier age of reproduction, and 3) a change from iteroparity (multiple reproductive events) to semelparity (single reproductive events). This predicted life history change from migratory multi-sea winter (MSW) salmon to

(1SW) salmon has been lacking. This study seeks to answer these questions by an examination of relevant data from six Icelandic rivers over a thirty-five year period.

Applied Life History Theory

In 1997, Helfman (Helfman *et al.* 1997) wrote that “Life history theory predicts that individuals in populations exposed to high levels of adult mortality should respond by reproducing at smaller average sizes and ages, shifting from multiple to single reproductive seasons (from iteroparity to semelparity), and having shorter life spans...It is unknown whether these shifts reflect 1) selection for genotypically determined differences in life history traits or 2) adjustments in the phenotype of remaining individuals.”

Both Atlantic and Pacific salmon are anadromous, born in freshwater streams and rivers, undergo physiological changes that allow them to adapt to the saltwater environment, where they quickly grow before migrating back to their natal streams to continue the cycle. Atlantic salmon are capable of multiple spawnings (iteroparity), whereas the five species of North American Pacific salmon (*Onchorhynchus* spp.) are semelparous and are only capable of a single, annual reproductive events. It is estimated that fewer than ten percent of returning Atlantic salmon are able to survive the rigors of reproduction, recondition themselves and make it back to sea, becoming a multi-return salmon upon spawning again (Mills 1989).

It has been shown that Pacific salmon displayed a decrease in size and number in response to the commercial fishery (Ricker 1981). It is expected that a similar directional shift in the decrease in weight would be the response of Atlantic salmon in Iceland, due to the commercial fishery in West Greenland that lasted until the mid-1990's. Ricker's

study is similar to this one with the exception that Pacific salmon cannot change from semelparity to iteroparity, because they are iteroparous reproducing once before dying.

Mr. Orri Vigfusson, a businessman and appointee to North Atlantic Salmon Conservation Organization (NASCO), organized and led a private effort (North Atlantic Salmon Fund) to buy out the West Greenland fishery. This was later followed up in 1998 with NASCO making the closures permanent, with the exception of an internal-fishery limited to a twelve mile limit and twenty tons. The time series for the six rivers is from 1974 to 2008, which includes a decade after the West Greenland fishery closure. If the closure of the Greenland fishery cannot be shown to have had a concomitant increase in the returning MSW component to their natal rivers, then an alternate hypothesis must be advanced to explain this counter intuitive finding.

Alternate Hypotheses

Life History Theory predicts that it would be expected to observe an earlier age of reproduction, correlated with lower mean-weights for both salmon and grilse. The null hypothesis is that no change in the mean-weight or the proportion of salmon to grilse in the returning salmon stocks would be observed. If the null hypothesis is rejected, for instance if a decrease in the mean-weight is observed, or the grilse composition of the stocks has changed over the time series, then alternate hypotheses must be advanced. It may be that over an extended time an introgression to the genome has occurred and migratory salmon were selected against by commercial exploitation, favoring 1SW grilse. It may also hold true that changing biotic and abiotic factors in the North Atlantic continue to act as an additive effect to natural mortality selecting against MSW salmon

migration, despite the cessation of the large scale harvest in West Greenland in the mid-1990's.

One of the significant of effects of commercial exploitation, besides a decrease in average size, is the shrinking of age-structure leaving stocks with low population numbers open to further decline due to stochastic events. In reviewing fifty years of larval surveys off the California coast, Chih-hao Hsieh et al (2006) noted that besides the increased variability in abundance, that even after “accounting for life-history effects, abundance, ecological traits and phylogeny. The increased variability of exploited populations is probably caused by fishery-induced truncation of the age structure, which reduces the capacity of populations to buffer environmental events.” So not only would salmon move from multiple reproductive events to single reproductive events, but because there are fewer year classes available to return to any given river or stream, environmental variability may thus have a greater effect on return rates and the population as a whole (Hsieh 2005; Hsieh *et al.* 2006).

Darimont *et al* (2009) looked at forty exploited prey species in an effort to quantify how quickly high-exploitation rates can change the phenotype and found that “harvested organisms show some of the most abrupt trait changes ever observed in wild populations, providing a new appreciation for how fast phenotypes are capable of changing. These changes, which include average declines of almost 20% in size-related traits and shifts in life history traits of nearly 25%, are most rapid in commercially exploited systems and, thus, have profound conservation and economic implications. Specifically, the widespread potential for transitively rapid and large effects on size- or

life history-mediated ecological dynamics might imperil populations, industries, and ecosystems” (Darimont *et al.* 2009)

CHAPTER 2

DATA ORIGIN AND FORMAT

“The fishing season in Icelandic rivers is 3 1/2 months during the period from 20th of May to 30th of September. The daily fishing period is 12 hours, between sunset to dawn, and fishing is always closed between 3 AM to 7 AM. In most Icelandic rivers rod and line is the only fishing gear allowed. Only a fixed number of rods are used in each river as decided by the Directorate of Freshwater Fisheries. In the early 1970s when the number of rods allowed in each river was decided a rule of thumb of 1 fish/day/rod, on the average was applied. The fishing effort has remained almost unchanged for the past 30 years (Guðbergsson 2007).”

Guðbergsson (2007) further notes that “The catch is recorded in special logbooks in the fishing lodges. The logbook recordings were established in 1946. At the end of each fishing season the logbooks from every river are gathered and statistical information are processed by the Institute of Freshwater Fisheries. The results are sent back to the fisheries associations as well as new logbooks before the next fishing season.” Record keeping in this manner has been standardized since 1974.

As described in the McDonald (2001) thesis. The data are from the recreational rod-catch fishery in Iceland and are categorized in the following format.

Column number and description.

“1-2 Year 3-4 Month 5-6 Day 9-11 Pool where caught 14 Species (1= salmon, 2= Aortic char, 3= sea-run Brown trout, 4=unknown) 18 Number of fish caught, if more than one on the same line 21 Sex (1=male, 2=female, 3=unknown) 23-26 Weight in pounds where 1 lb. = 500g 28-30 Length in centimeters 32 Bait used (1=fly, 2= other, 3= worm)”

Here is an example from the dataset from McDonald 2001: “740623 0 1 1 1 14.0 0 1 and this means: 1974, June 23, pool 0, species is Atlantic salmon, one salmon was caught, it was a male fish, that weighed 14.0 pounds, no length was recorded, the salmon was rod caught, while fly fishing.”

A bimodal distribution can be used to differentiate salmon from grilse. The concern that this statistical method of segregating salmon from grilse may be misclassifying underweight salmon as grilse and overweight grilse as salmon was not found to be statistically significant. The bimodal segregation method is a valid method to segregate MSW salmon from 1SW grilse, after confirmation by individual scale analysis by the Icelandic Institute of Freshwater Fisheries.

“Males up to 4 kg and females up to 3.5 kg are grilse and larger fish are salmon. This deviation in to sea age has been confirmed with aging by scales. (Guðbergsson 2007).” For this analysis, the cutoffs provided by the Icelandic Institute of Freshwater Fisheries were used.

CHAPTER 3

RIVER SELECTION

Genetic research (Danielsdottir *et al.* 1997) has shown that there are genetically distinct populations of Atlantic salmon that populate the rivers in Iceland . As one might expect, the closer geographically the rivers are, the lower the value of genetic distance for the forty-nine loci that were chosen, the more closely related the salmon are. They were also able to show that in large river systems, there may be more than one genetically distinct population. Similar geographic trends were seen when the least significant differences between rivers were examined for the proportion of salmon to grilse (Table 1).

After the grilsefication hypothesis was proposed and supported (McDonald 2001), it was decided to expand the scope of the research to include more rivers with as great a geographical distribution as possible and include as many genetically distinct populations as possible. The present Director of the Icelandic Institute of Freshwater Fisheries, Dr. Guðjónsson and their statistician Mr. Guðbergsson and I were able to set the parameters to help narrow down the possible candidate rivers.

There are nearly one hundred salmon rivers in Iceland, but the difficulty was in finding the most suitable data sets possible. Essentially, it was necessary to eliminate any rivers that had major changes over the time period in question, such as anthropogenic modifications like impoundments, changes in catch per unit effort, changes in the length

of season, supplemental stocking and the addition of fish passage devices (construction of fish ladders) that increased the salmon's range in the river by increasing the effective length of a river and thus its carrying capacity. Data are from 1974 to 2008, giving a thirty-five year time series. Upon closer examination, it was decided that six rivers met the established rubrics outlined above, meriting further analysis.

From the west coast, two rivers separated by the Snaefellsness peninsula were selected, Haffjardara and Haukadalsa. From the Northwest coast the rivers Midfjardara and Vatnsdalsa were selected, on the Northeast coast, Laxa in Adaldal and the Hofsa River on the East coast. It must be noted that a component of the northern rivers, have migrated not to the West coast of Greenland, but instead found in the fishery north of the Faeroe Islands. This is especially true of the river Hofsa on the East coast. The Faeroese fishery is not exclusively a MSW fishery like that found in West Greenland, grilse also comprised a portion of the commercial catch (Scarnecchia *et al.* 1991). The commercial salmon fishery near the Faeroe Islands was closed in the early 1990's and quotas ended in 2001 (North Atlantic Salmon Conservation Organization 2010).

CHAPTER 4

STATISTICAL ANALYSIS

All statistic analysis procedures were performed with SAS version 9.2 (SAS Institute; Cary, N.C.). Below are descriptions of the procedures used.

PROC FREQ

This procedure is used to obtain the summary statistics of the data sets and performs a chi-square test of the variables.

PROC UNIVARIATE

This procedure is used to produce the data summary of the distribution of variables. This procedure calculates the median, mode, and range of weights for the different sexes, salmon, grilse, rivers and years.

PROC SORT

This procedure sorts the data according to the selected variables.

PROC CORR

This procedure is used to compute correlation coefficients associated with the data.

PROC AUTOREG

This procedure obtains a regression analysis and forecasts linear models with auto-correlated errors.

PROC GLM

This procedure fits general linear models, explaining the effects of the class explanatory variables.

PROC MIXED

This procedure fits mixed linear models to data. The mixed linear model generalizes the standard linear model used in the GLM procedure; the data may exhibit correlations and variability.

PROC NLP

This procedure allows for the minimizing or maximizing of continuous non-linear functions where there is equality and inequality or constraints to upper and lower limits.

CHAPTER 5

RESULTS

We know that the commercial exploitation of migratory Atlantic salmon in the West Greenland fishery removed a large portion of MSW salmon from returning to the breeding population in their natal stream since the early 1960's (North Atlantic Salmon Conservation Organization 2010). Both parametric and non-parametric fits were applied, logarithmic transformation was unnecessary to smooth the data and a linear fit was utilized to highlight trends. By analyzing the data sets and plotting the proportion of true migratory salmon vs. non-migratory grilse we get:

- 1) An accurate depiction of whether or not we can determine any increases or decreases in the composition of salmon and grilse in the individual rivers.
- 2) An idea of how quickly the increased the reduction of MSW salmon, favoring non-migratory grilse, accelerated or induced "grilsefication".
- 3) Lastly, by combining the grilse/salmon proportions of all rivers, we are able to make an inference of make up for Icelandic salmon as a whole as a function of time.

Overview of the Weight Distributions

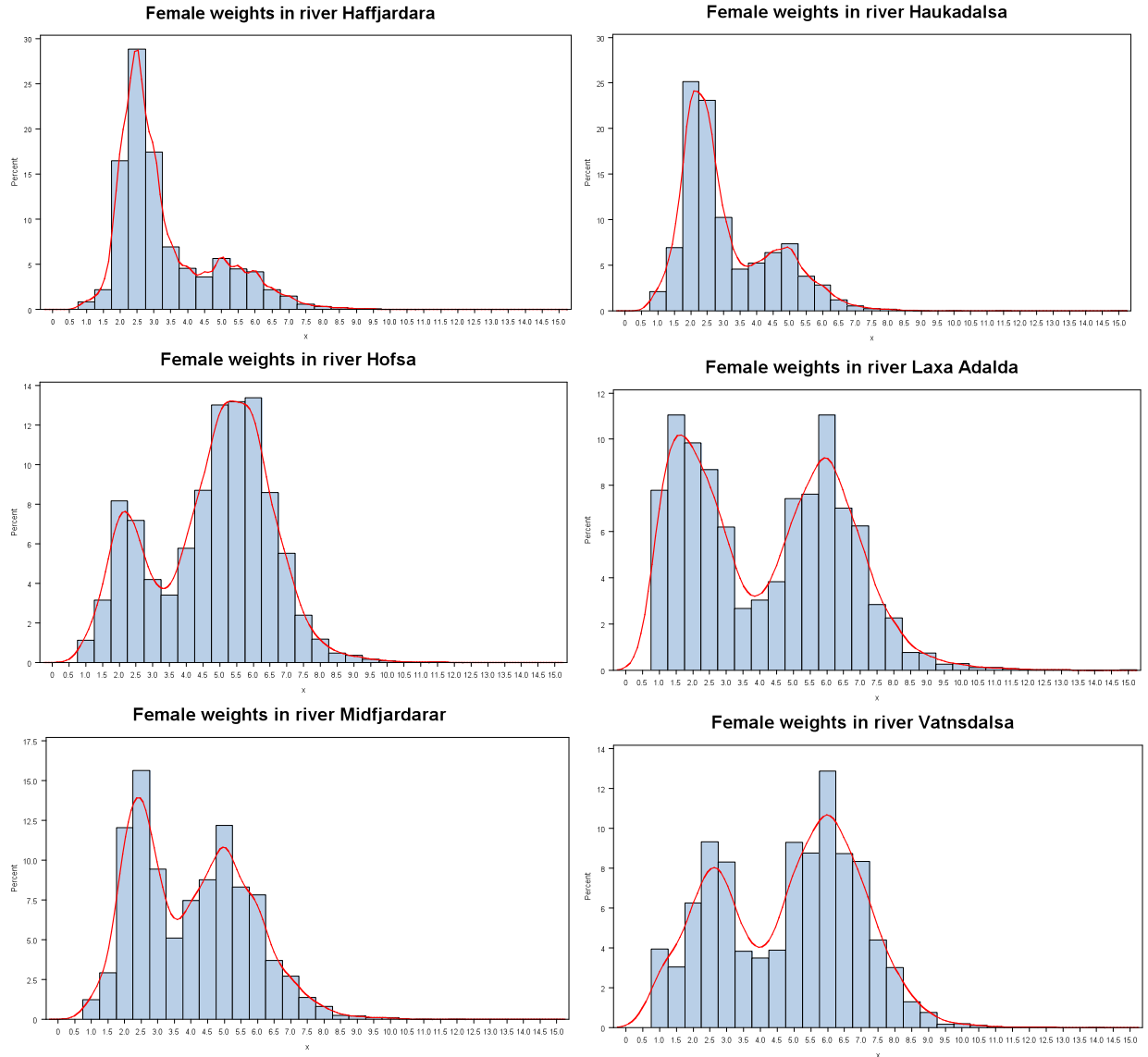


Figure 1. Weight Distribution, in kilograms, of Females by River

The histograms are the distribution by weight in kilograms of female and male Atlantic salmon before segregating grilse from salmon. Female Atlantic salmon (Figure 1) have a much more defined bimodal distribution compared to the males (Figure 2).

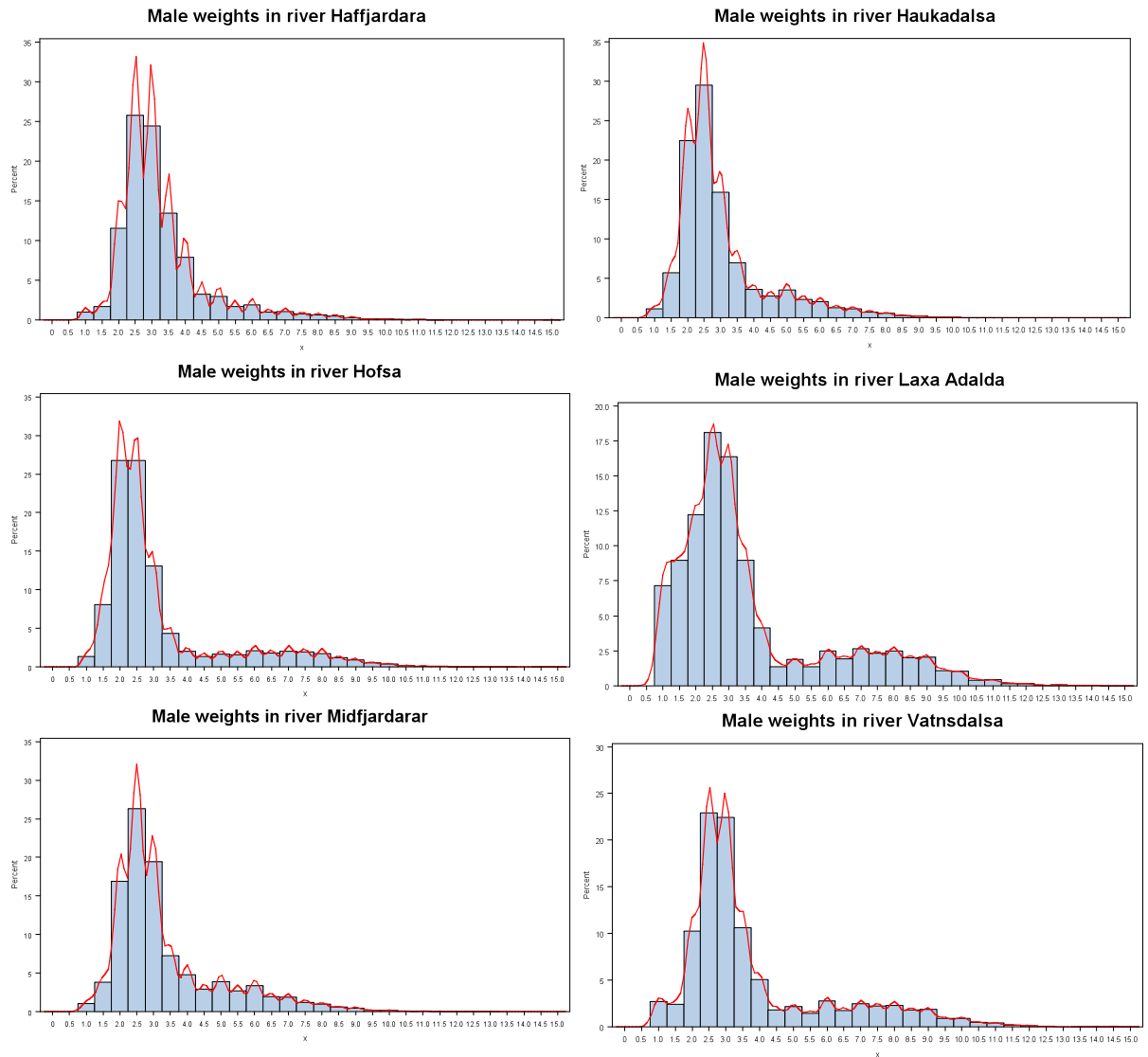


Figure 2. Weight Distribution, in kilograms, of Males by River

Males on all rivers statistically displayed a much longer “tail” in the bimodal distribution.

Changes in Average Weight from 1974-2008

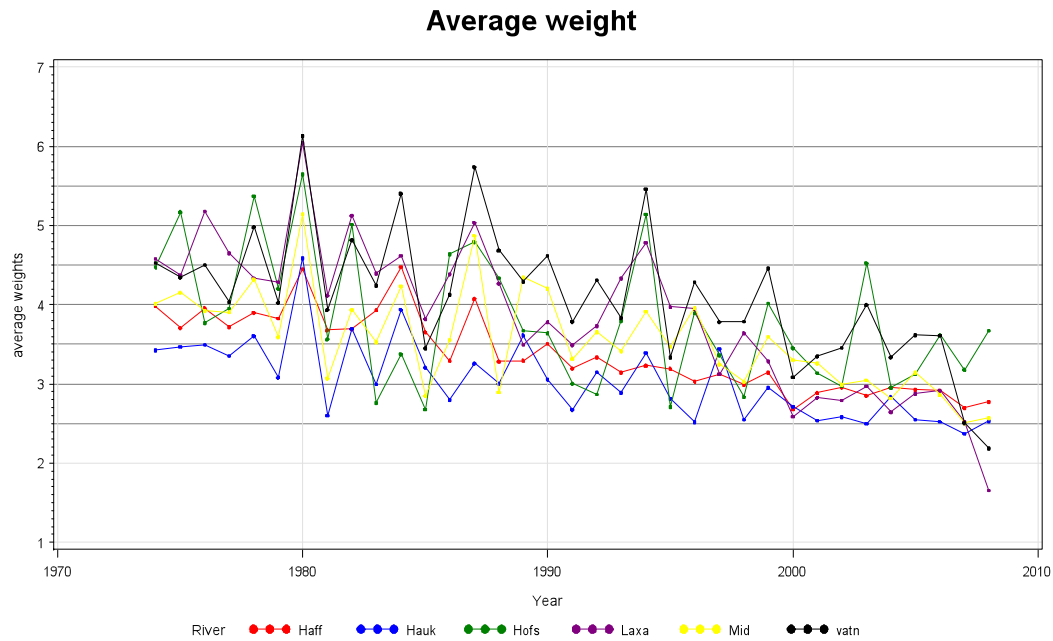


Figure 3. Changes in Average Weight, in kilograms, by River over Time

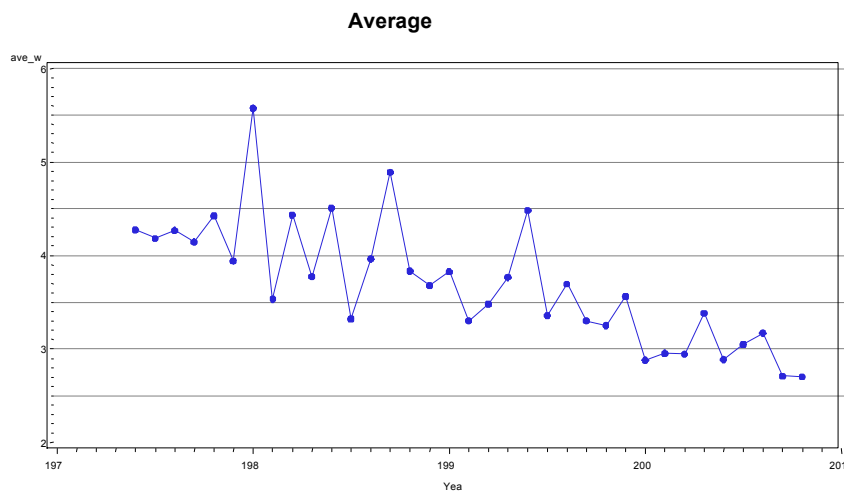


Figure 4. Overall Population Changes in Average Weight, in kilograms, over Time.

Table 1. Analysis of Variance for all fish on all rivers

R-Square	Coeff Var	Root MSE	Avg. wt. Mean
0.579138	11.667	0.431574	3.699207

Table 2. Parameter Estimates for the Variable Weight on all Rivers.

Parameter	Estimate	Standard Error	t Value	Pr > t	95% Confidence Limits	
Intercept	4.575	0.149	30.69	<.0001	4.272	4.879
t	-0.049	0.007	-6.74	<.0001	-0.063	-0.034

Upon examination of figures 3 and 4, the changes in average weight over time by river (Figure 3) and the entire population over time (Figure 4), it seems significant that grilsefication has been underway for some time. Closer examination of the male and female components of salmon and grilse populations reveal that it is a bit more nuanced than that, with female salmon on the northern rivers doing better than expected.

In figure 4, we are looking at the entire data set of all rivers over the extended geographic range in Iceland, supporting the grilsefication hypothesis. Tables 1 and 2 are from the linear regression run on the salmon population as a whole. Fish are indeterminate in growth and variability in ocean temperatures in near Arctic oceans explains the variation from year to year (Scarnecchia *et al.* 1989; Friedland *et al.* 2003). The R-Squared is 0.579138 and is a fair estimation of goodness of fit, given the annual variability in weight in the subpolar Arctic, but the main point of the graph is that the slope is negative (-0.049), strongly supporting the grilsefication hypothesis.

Average Weights by River for both Female and Male Salmon and Grilse

The following are compilations of the individual linear regressions run for male and female salmon and grilse by river. The average weights, in kilograms, were plotted for all rivers for both males and females for both salmon and grilse. A linear regression was used to highlight trends over time. Note that for all rivers, the average weight trends downward for both salmon and grilse and for both sexes. The exception is that for female salmon found in the northern rivers Laxa in Adaldal, Midfjordara, and Vatnsdalsa, the trend is increasing.

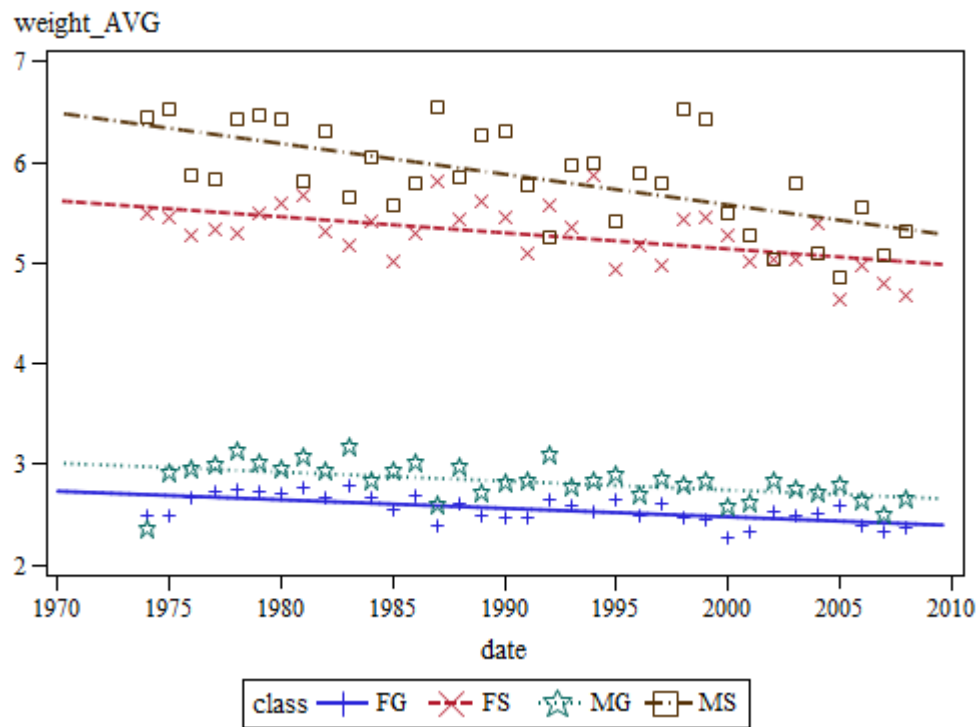


Figure 5. Haffjardara River. Average weight for Female Grilse (FG), Female Salmon (FS), Male Grilse (MG), and Male Salmon (MS).

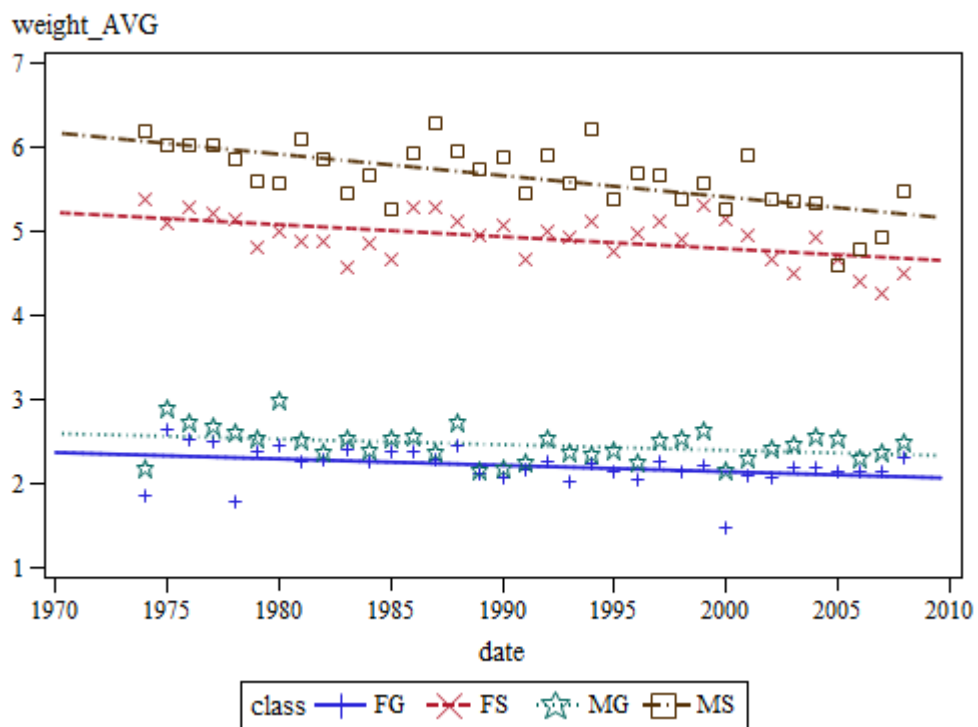


Figure 6. Haukadalsa River. Average weight for Female Grilse (FG), Female Salmon (FS), Male Grilse (MG), and Male Salmon (MS).

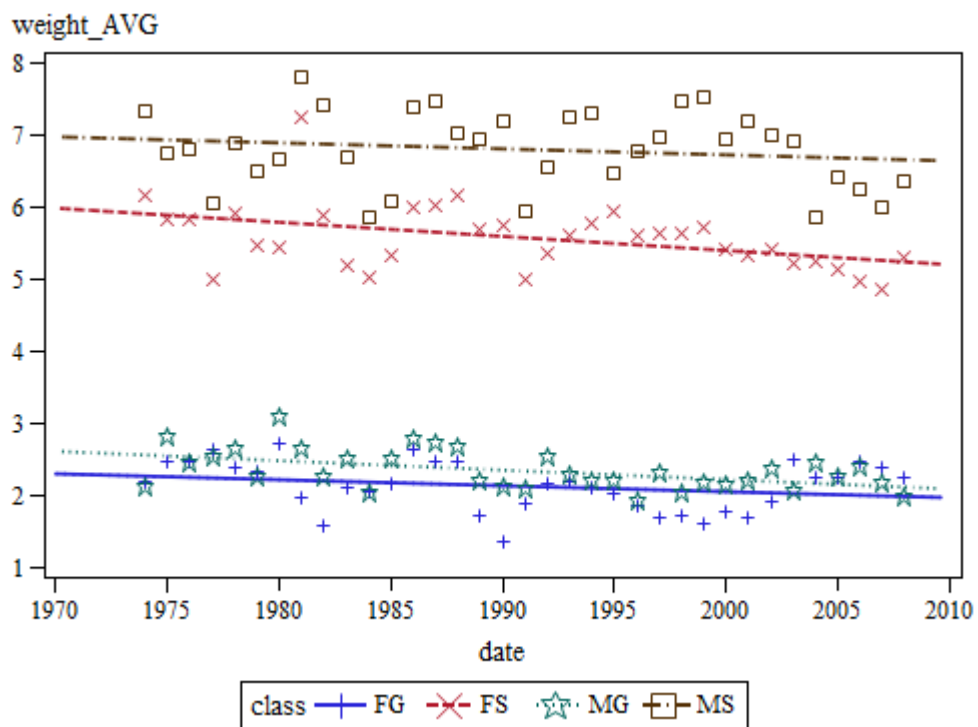


Figure 7. Hofsa River. Average weight for Female Grilse (FG), Female Salmon (FS), Male Grilse (MG), and Male Salmon (MS).

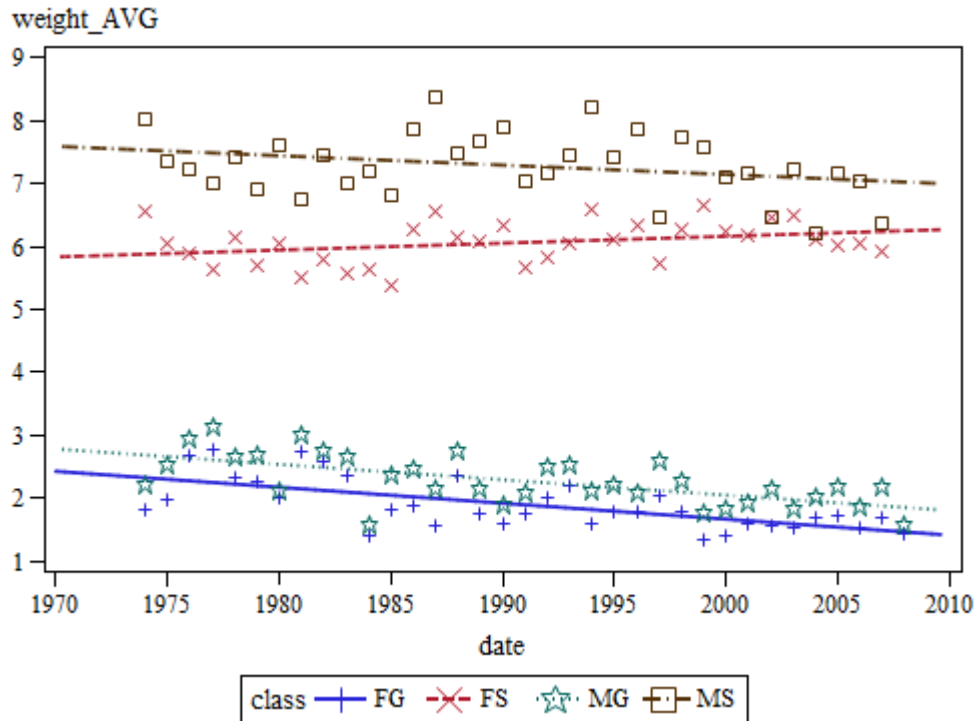


Figure 8. Laxa in Adaldal River. Average weight for Female Grilse (FG), Female Salmon (FS), Male Grilse (MG), and Male Salmon (MS).

Table 3. Intercept and Slope for Laxa in Adaldal.

Parameter Estimates for Laxa in Adaldal					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	6.04292	0.05607	107.77	<.0001
Year	1	0.01099	0.00565	1.95	0.061

The slope of the linear regressions for average weight are negative for all salmon and grilse on all rivers with the exception of female salmon on the Northern Icelandic rivers (Figures 8, 9, and 10), which all had positive slopes. Tables 3, 4, and 5 contain the information needed to attach values to the trendlines for Figures 8, 9, and 10. The trendline or slope from the regressions for Laxa in Adaldal is a positive 0.01099,

Midfjordara 0.00216, and Vatnsdalsa 0.0099. Additional detailed information regarding the linear regressions can be found in appendices A (Female Salmon), B (Male Salmon), C (Female Grilse), D (Male Grilse), and E (All Salmon and Rivers), and F (Sex Ratios for Salmon).

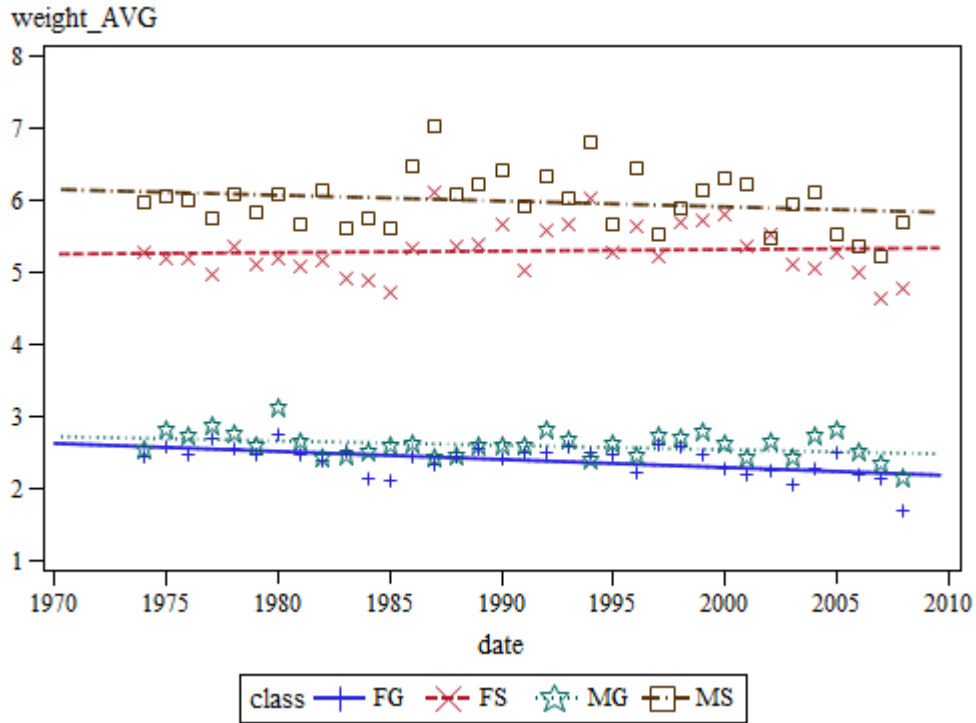


Figure 9. Midfjordara River. Average weight for Female Grilse (FG), Female Salmon (FS), Male Grilse (MG), and Male Salmon (MS).

Table 4. Intercept and Slope for Midfjordara.

Parameter Estimates for Midfjordara					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	5.29539	0.06122	86.5	<.0001
Year	1	0.00216	0.00595	0.36	0.719

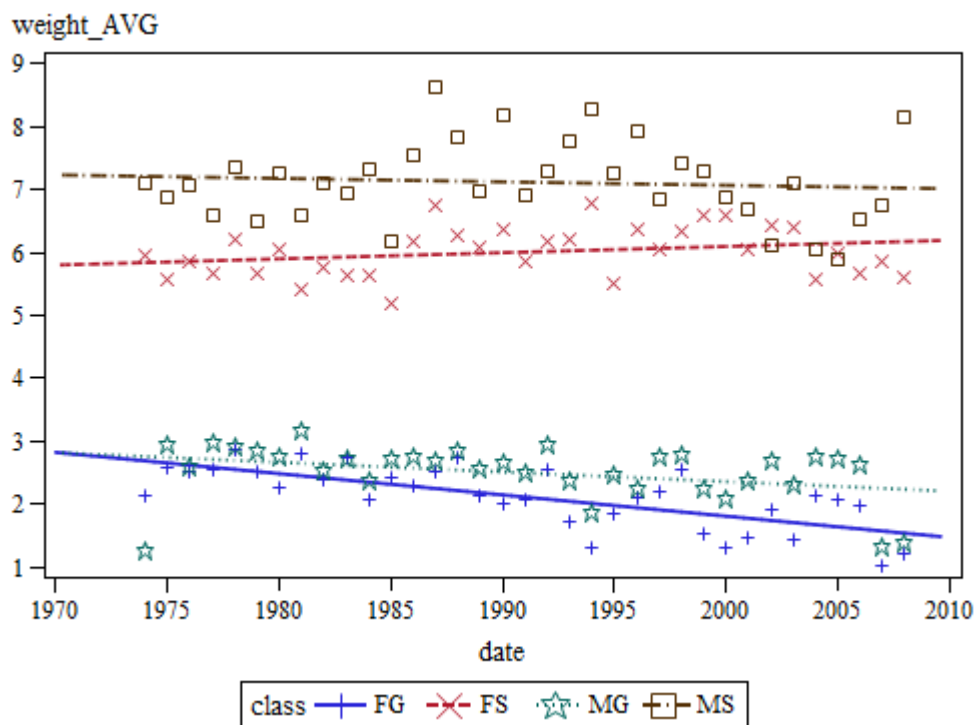


Figure 10. Vatnsdalsa River. Average weight for Female Grilse (FG), Female Salmon (FS), Male Grilse (MG), and Male Salmon (MS).

Table 5. Intercept and Slope for Vatnsdalsa.

Parameter Estimates for Vatnsdalsa					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	5.98764	0.06696	89.42	<.0001
Year	1	0.0099	0.0065	1.52	0.138

Proportion of Salmon to Grilse

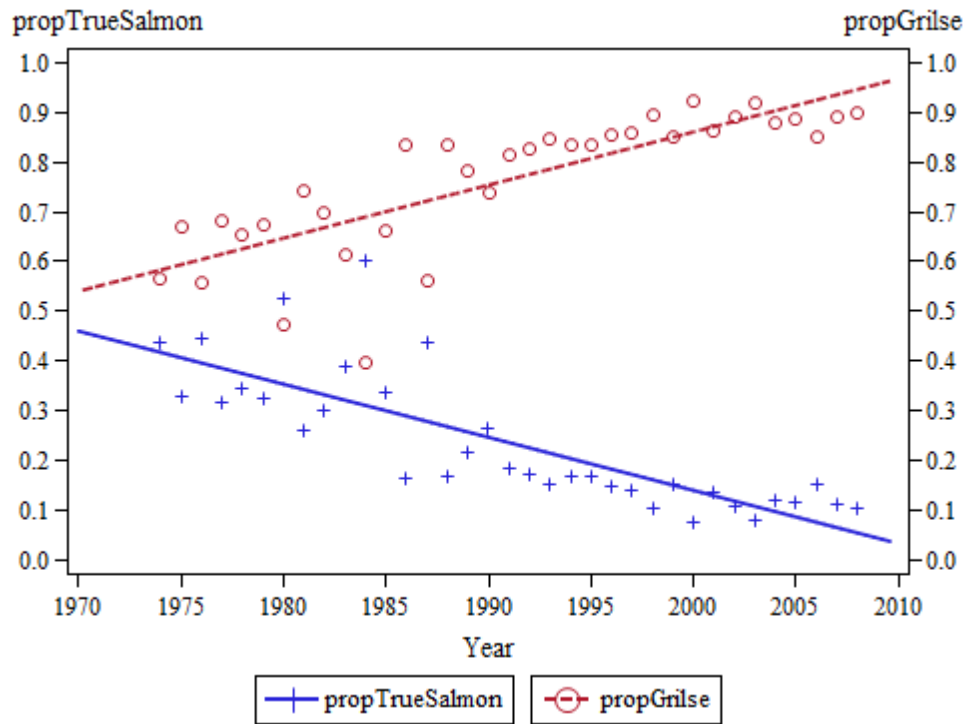


Figure 11. Haffjardara River. Proportion of true migratory salmon to non-migratory grilse.

Haffjardara is located on the west coast and has traditionally been predominantly a grilse river as can be seen in figure 11. While both salmon and grilse are *Salmo salar*, to help differentiate between MSW salmon v. 1SW grilse, “True” was added to salmon to make the case clear. These data demonstrate strong divergence since 1974 in the proportions of “true” multi-sea winter salmon and grilse in the river catch on Haffjardara.

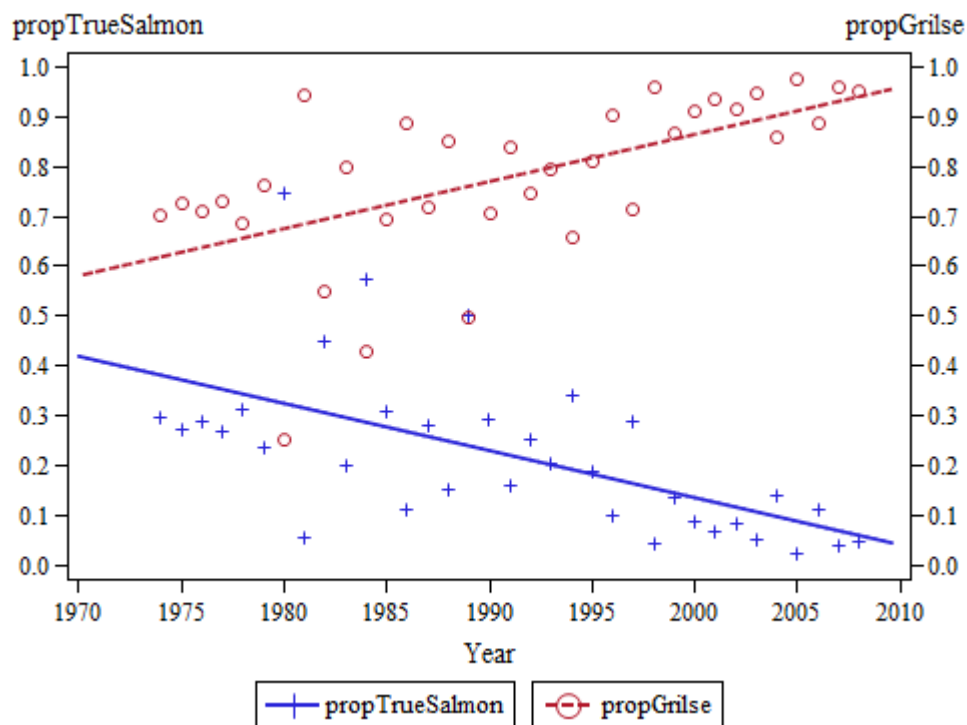


Figure 12. Haukadalsa River. Proportion of true multi-sea winter salmon to 1 sea winter grilse.

Haukadalsa is also located on the west coast and has traditionally been predominantly a grilse river as can be seen in figure 12. Given the trend line it the population may have been more balanced prior to 1974, but the divergence is unmistakable.

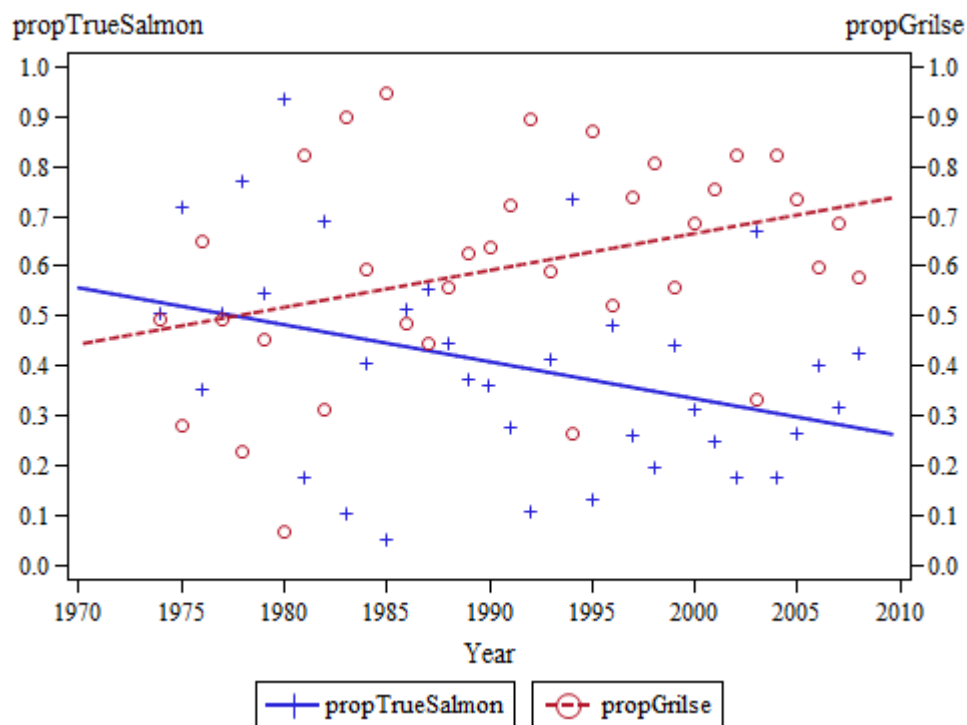


Figure 13. Hofsa River. Proportion of true multi-sea winter salmon to 1 sea winter grilse

Hofsa is the only river in the study on the East coast. It shows a delay in the onset of grilsefication when compared with the rivers on the West coast that may be attributed to reduced harvest pressure of the Faroese fishery compared with that of the West Greenland fishery.

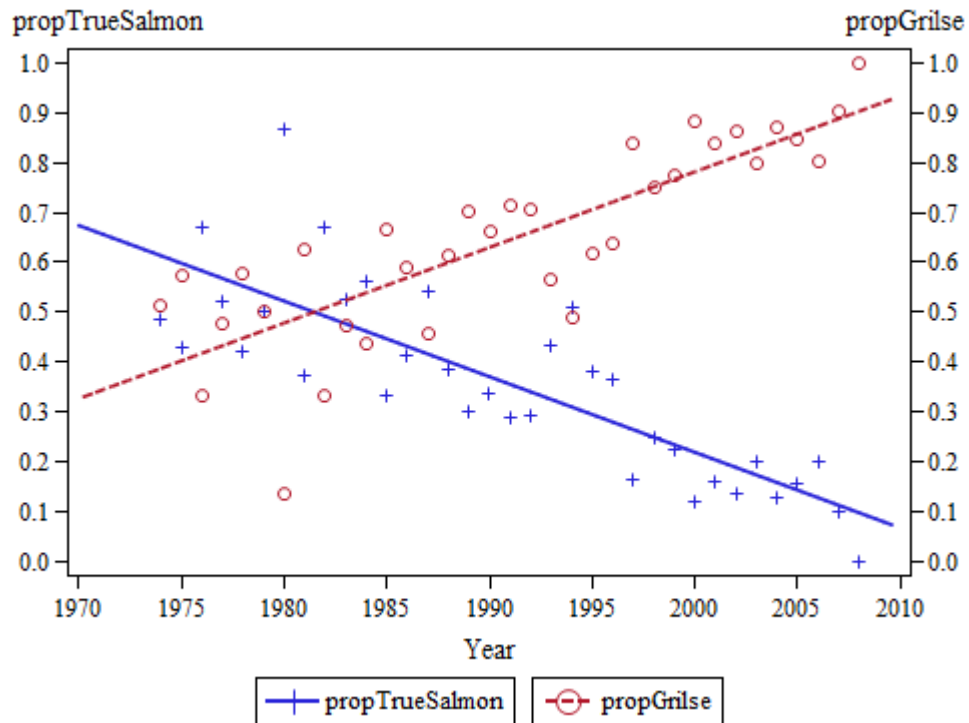


Figure 14. Laxa in Adaldal River. Proportion of true multi-sea winter salmon to 1 sea winter grilse

The Laxa in Adaldal is one of three rivers on the north coast and the furthest to the Northeast. The divergence is seen clearly, but again the change occurs in the time series later than the rivers on the West coast.

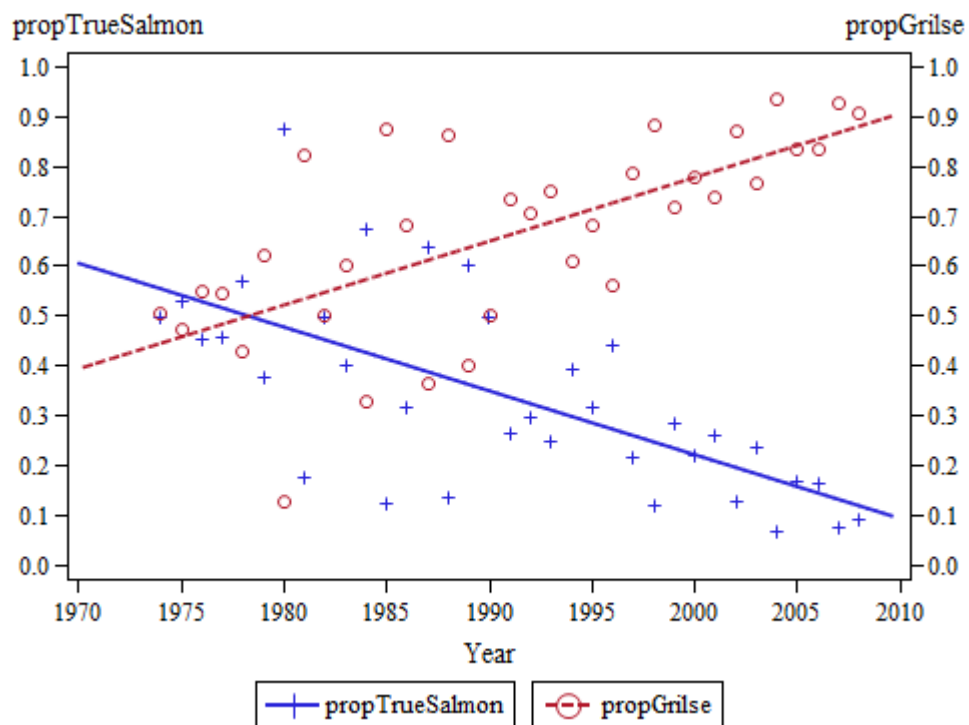


Figure 15. Midfjordara River. Proportion of true multi-sea winter salmon to 1 sea winter grilse

Also located on the north coast, Midfjordara shows a clear divergence of the proportion of salmon and grilse.

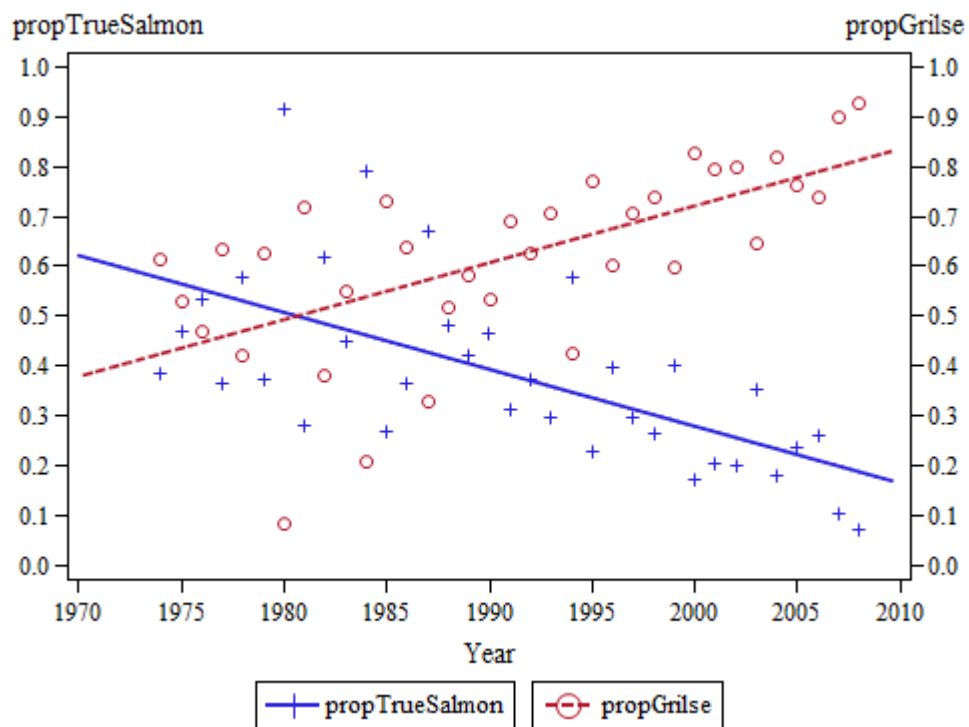


Figure 16. Vatnsdalsa River. Proportion of true multi-sea winter salmon to 1 sea winter grilse

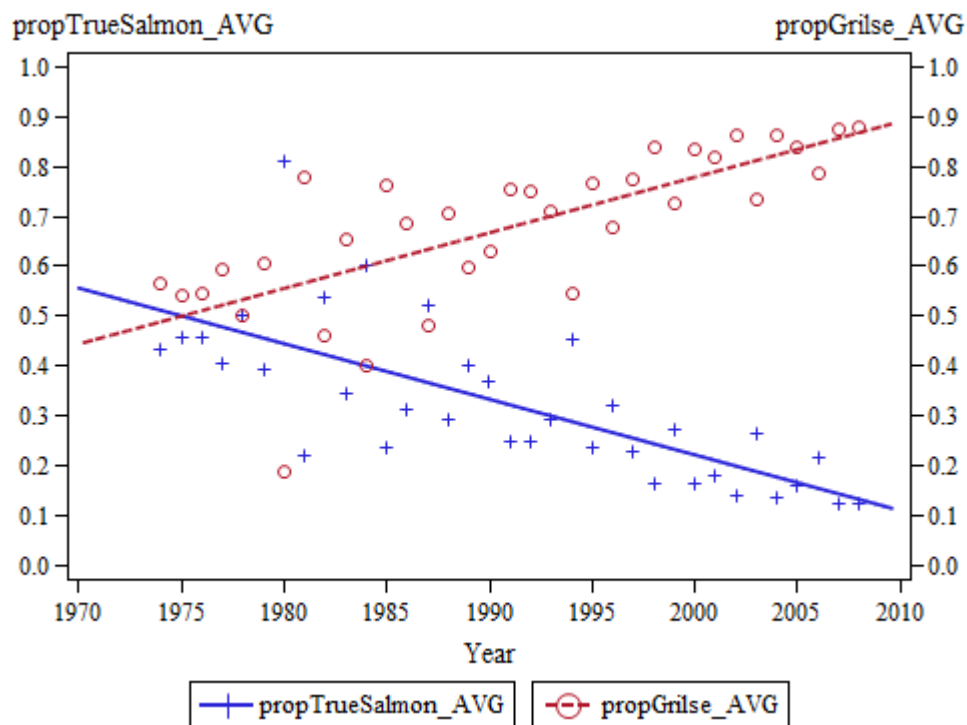


Figure 17. All rivers. Proportion of true multi-sea winter salmon to 1 sea winter grilse

Figure 17. includes the entire data set of all rivers for all years. The trend favoring grilsefication seems to be very dramatic and profound for the time series.

Tests of Significant Differences Between Rivers

To see if the proportion of salmon to grilse in the individual rivers were statistically related, the Least Significant Difference (LSD) procedure was used to compare the rivers. In Table 6. the rivers with means of the same letter(s) are not significantly different in their ratios of salmon to grilse.

Table 6. t-Grouping of rivers by the ratio of salmon to grilse.

Means with the same letter are not significantly different.				
t Grouping		Mean	N	river
	A	2.2370	35	Hofsa
	A			
B	A	2.0219	35	Vatnsdalsa
B	A			
B	A	1.7992	35	Laxa Adalda
B	A			
B	A	1.7734	35	Midfjardara
B				
B		1.3803	35	Haukadalsa
B				
B		1.3622	35	Haffjardara

Haffjardara and Haukadalsa, on the west coast showed the earliest divergence and the highest proportion of grilse at the beginning of the dataset. They share a statistically significant mean salmon to grilse ratio (B). The northern rivers, Midfjardara, Laxa in Adaldal, and Vatnsdalsa were similarly grouped together and were the only ones to show an increase in the mean weight of female salmon (Figures 8, 9, and 10), independent of the ratio of salmon to grilse (B A). Hofsa is the only river on the east coast in the study and a significant linkage with the other rivers was not shown (A). Some of the salmon from Hofsa migrate to the Faeroe islands and not to West Greenland like the other rivers (Scarnecchia *et al.* 1991). The observation is that the individual populations, in the different geographic regions (West, North, and East), behave similarly to each other and are grouped together statistically. The geographic similarities of salmon/grilse proportions in Table 1 mirror the similarities in genetic variation in wild salmon populations Danielsdottir found in 1997.

Differences in the Observed Sex Ratio

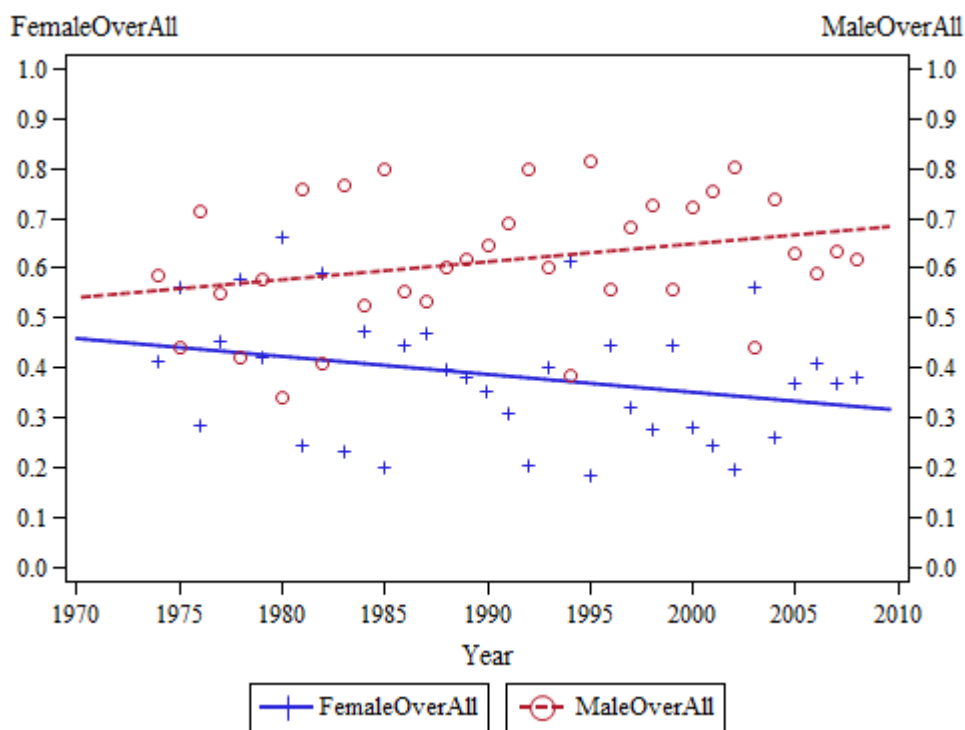


Figure 18. The Hofsa River, Sex Ratio for Female and Male Salmon.

In the the river Hofsa, the ratio of male to female salmon was higher than the expected 50:50 proportion typically observed in nature. There exists differential mortality between the sexes and “management precautions should still be taken as the fishery strongly selects large females, which could have evolutionary impacts on populations over the long term” (Gauthier-Ouellet *et al.* 2009) .

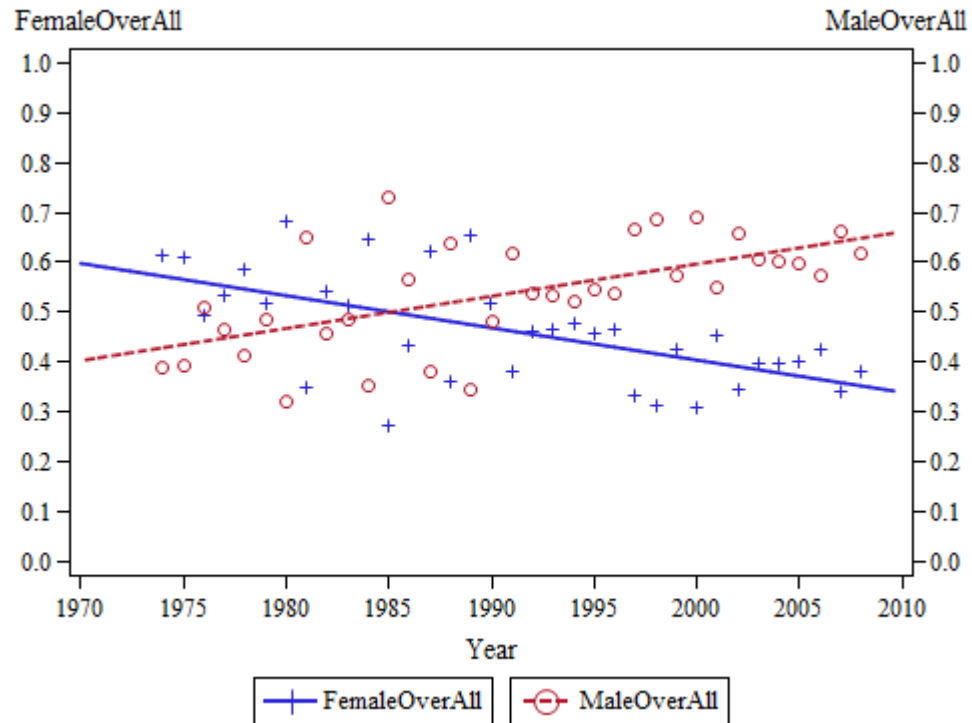


Figure 19. The Midfjordara River, Sex Ratio for Female and Male Salmon.

The same differential mortality or lack of recruitment of female salmon, to the rod fishery, is also observed to be occurring in Midfjordara (Figure 19) and to a lesser extent in Vatnsdalsa (Figure 20). Midfjordara seems to be fairly proportionate until the late 1990's when the disparity between the sexes becomes apparent.

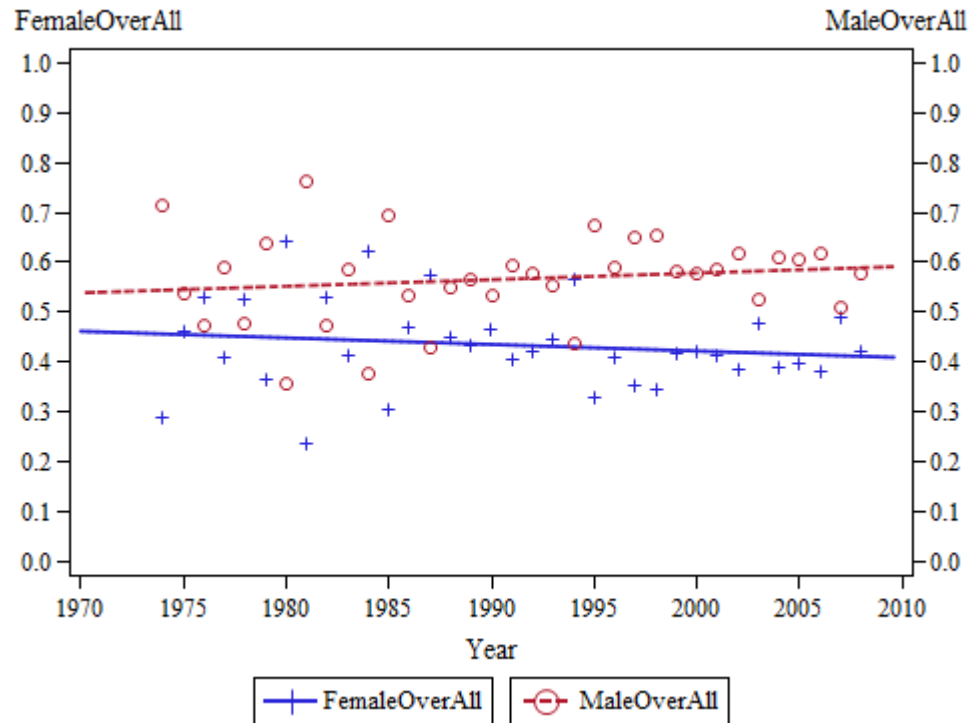


Figure 20. The Vatnsdalsa River, Sex Ratio for Female and Male Salmon.

The disparity of recruitment between the sexes noted in Hofsa and Midfjardara are not as extreme in Vatnsdalsa. The ratio of male and female salmon begin to diverge in 1990, but approach parity for the years 2003 and 2007. The trend showing divergence is there, but not quite as extreme as that seen in Hofsa and Vatnsdalsa.

Table 7. t-Grouping of rivers by the ratio of male salmon to female salmon.

Means with the same letter are not significantly different.				
t Grouping		Mean	N	river
	A	5.4069	35	Hofsa
	B	2.7398	35	Vatnsdalsa
	C	1.9608	35	Midfjardara
	C			
D	C	1.7672	35	Laxa Adaldal
D				
D	E	1.3352	35	Haffjardara
	E			
	E	1.1363	35	Haukadalsa

The Least Significant Difference (LSD) procedure was used to compare the ratios of male salmon to female salmon. As the analysis confirms what we observed in figures 18, 19, and 20, Hofsa, Vatnsdalsa, and Midfjardara are statistically similar in their sex ratios and decline in the proportion of returning female salmon. Laxa a in Adaldal is intermediate, with Haffjardara and Haukadalsa approaching the more normal or expected 50:50 ratio of males to females.

CHAPTER 6

DISCUSSION

Recruitment of the MSW portion of the annual spawning cohort is at the heart of the grilsefication hypothesis. It is known that the West Greenland fishery exclusively removed the MSW salmon component. These had greater fecundity than their 1SW grilse counterparts, displaying differential reproductive success (Garant *et al.* 2003; Garant *et al.* 2005). The effect of the fishery may have had a greater genetic component and impact on smaller populations and is dealt with extensively (Bruyn 2008), it has also been observed in isolated small populations of cutthroat trout (Whiteley *et al.* 2010).

There is a high degree heritability for sea age of return. Essentially, multi-sea winter salmon tend to have offspring that are multi-sea winter salmon and one-sea winter grilse tend to produce offspring that are one-sea winter grilse (Jonasson 1993; Jonasson 1996; Jonasson *et al.* 1997; Koljonen and Pella 1997). Beginning in the mid-1960's, the high-seas commercial fishery may have caused genetic drift favoring 1SW grilse, especially on smaller rivers with more isolated populations. In Population Genetics and Fishery Management, Allendorf noted that "Differential survival and reproduction of fish with different genotypes will change the genetic composition of the harvested population" (Ryman and Utter 1987). While Atlantic salmon display a high degree of phenotypic plasticity, it remains to be seen if changes to the genotype will be expressed phenotypically other than a reduction in size. The earlier age of reproduction proposed

by the grilsefication hypothesis may be the only way to note a shift in the genetic composition and a life history change due to the lack of recruitment of MSW salmon over an extended period. “Determining whether phenotypic changes in harvested populations are due to evolution, rather than phenotypic plasticity or environmental variation, has been problematic. Nevertheless, it is likely that some undesirable changes observed over time in exploited populations (e.g., reduced body size, earlier sexual maturity, reduced antler size, etc.) are due to selection against desirable phenotypes—a process we call “unnatural” selection. Evolution brought about by human harvest might greatly increase the time required for over-harvested populations to recover once harvest is curtailed because harvesting often creates strong selection differentials, whereas curtailing harvest will often result in less intense selection in the opposing direction” (Allendorf and Hard 2009).

In the early 1990’s, Orri Vigfusson of the North Atlantic Salmon Fund, began raising money for net buyouts on the west coast of Greenland. That has been followed up by the North Atlantic Salmon Conservation Organization, with a NASCO convention in 2003 finalizing the commercial closures (Chase 2003). In the future, we might expect to see an increase in the recruitment of MSW salmon in the breeding cohorts in their natal rivers. An examination of the data was unable to detect an increase in the MSW component of the cohort; we must then consider other possible alternatives that may help explain the apparent continued grilsefication of Atlantic salmon stocks.

Upon leaving the density-dependent factors of their natal streams, marine survival is dependent on a number of biotic and abiotic factors, principally predation, foraging success, and sea surface temperature. It has been thought that the majority of Icelandic

stocks move directly from their respective rivers to the west coast of Greenland, but a recent “Merry-Go Round Hypothesis” has been suggested for stocks of both N. American and European salmon (Dadswell *et al.* 2010). Dadswell et al, reviewed data covering the last 50 years and found marked N. American salmon in Norwegian waters, salmon tagged in the Faeroes found in Canadian waters, and marked European salmon in Newfoundland, Labrador, and to the east and west of Greenland. The study proposes the post-smolts enter the North Atlantic subpolar gyre on their respective sides of the Atlantic following a gyre model. “Marked North American smolts were captured off Norway, the Faroe Islands, east and west Greenland, and adults tagged at the Faeroes were recovered in Canadian rivers. Marked European smolts were recovered off Newfoundland and Labrador, west and east Greenland, and adults tagged in the Labrador Sea were captured in European rivers. High Caesium-137 (¹³⁷Cs) levels in *S. salar* returning to a Quebec river suggested 62.3% had fed at or east of Iceland, whereas levels in 1 sea-winter (SW) Atlantic Canada returnees indicated 24.7% had fed east of the Faeroes. Lower levels of ¹³⁷Cs in returning 1SW Irish fish suggest much of their growth occurred in the western Atlantic. These data suggest marine migration of *S. salar* follows a gyre model and is similar to other open-ocean migrations of epipelagic fishes”. This may have added increased pressure on salmon stocks from the open-ocean pelagic fisheries, in addition to the now closed west Greenland commercial fishery.

Investigating the recruitment of Atlantic salmon in Europe, Friedland (2009) found that there was a negative correlation in post-smolt survival associated with elevated summer sea surface temperatures. Regarding the North Atlantic Oscillation (NAO) and post-smolt survival, they found that the Multi-decadal Oscillation was a better indicator

of the “climate forcing index” for determining sea surface temperatures and European Atlantic salmon post-smolt survival and recruitment (Friedland *et al.* 2009).

Beaugrand *et al.* (2003) noted a “match/mismatch” in the planktonic prey available to larval Atlantic cod, *Gadus morhua*, regarding climate change and the modification of the planktonic community that negatively affects cod biomass and recruitment. Furthermore in 2002 they describe a northward change in warm-water copepod abundance in the North Atlantic Oscillation. If the gyre model is correct then Atlantic salmon may be subject to some of the same zooplankton abundance and seasonal timing issues regarding the survival of cod (Beaugrand *et al.* 2003).

In his seminal paper detailing the decline of Pacific salmon because of the commercial exploitation, Ricker (1981) noted a decrease in the meristic measure of body size induced by gear selectivity (net size), not unlike the directional shift observed with grilsefication (Figure 4.)

Because farmed salmon are selected based upon fast growth characteristics, slower maturing MSW are deselected in the breeding scheme in favor the faster maturing grilse (Jonasson 1993; Jonasson 1996). Escapement, straying, and hybridization of farmed fish have become a concern to many fisheries managers. The consequences and problems of the loss of genome heterozygosity resulting from the escapement of farmed salmon, hybridization, and the reduction in fitness of wild salmon have been reasonably documented. (McGinnity *et al.* 1997; Philip *et al.* 2003; McGinnity *et al.* 2004; McGinnity *et al.* 2007; Philip 2009)

Using a “spatial and temporal genetic approach” Gudmundsson (2007) examined the allelic variation of salmon of the Elldaar River in Reykjavik, Iceland after an earlier

incursion of farmed fish in the late 1980's and early 1990's, from sea ranching experiments into the river. The Gudmundsson study is important in that they examined several microsatellite markers to examine the intrusion into the genome after the escapement of farmed fish and the consequent introgression into the genome. They concluded that there was not a loss of genetic diversity and the "observed biological changes that have occurred in the salmon population are neither due to outbreeding depression, resulting from hybridization with farmed fish, nor due to inbreeding depression of isolated breeding units"(Guðmundsson 2007). It should be noted that the farmed fish that escaped and interbred with the Ellidaar River salmon were of Icelandic origin of several mixed populations, so the loci selected may or may not confirm an intrusion into the genome or that the farmed fish were less fit in the wild and were selected against over time. Increasing the number of loci sampled may yield additional information regarding the stability of populations (Tallmon *et al.* 2010). A mitochondrial DNA comparison of the samples used in the study may aid in confirming the maternal breeding lines, beyond the variation in the selected alleles of salmon in the Ellidaar River.

In the introduction it was stated that the grilsefication hypothesis predicts that we will see 1) a reduction in average weight, 2) earlier age of reproduction, and 3) a change from iteroparity (multiple reproductive events) to semelparity (single reproductive events)." The data show a profound shift in the three conditions set forward that life history theory predicts over the thirty-five year period. The West Greenland commercial fishery selected against multi-sea winter salmon, changing the phenotype and proportions of returning salmon and grilse.

With the cessation of the commercial MSW fishery, it was hoped that the population could be shown to recover. On the northern rivers, females are doing better and deserve further investigation, but the rest of the salmon are declining. Because Atlantic salmon display a large amount of phenotypic plasticity, the question is whether the phenotypic change has resulted in a change in the genotype and only time will tell as successive generations are studied.

What began as a directional shift, induced by the effects of selection by the commercial fishery for MSW salmon, changing biotic and abiotic factors in the North Atlantic may have had an additive or synergistic effect over time on mortality during their ocean phase.

CHAPTER 7

CONCLUSION

Chih-hao Hsieh et al (2009) when looking at 29 coastal species of fish in California and dividing them into exploited and unexploited categories over a fifty-year time frame concluded that “after accounting for life-history effects, abundance, ecological traits and phylogeny. The increased variability of exploited populations is probably caused by fishery-induced truncation of the age structure, which reduces the capacity of populations to buffer environmental events. Therefore, to avoid collapse, fisheries must be managed not only to sustain the total viable biomass but also to prevent the significant truncation of age structure.” Once the truncation is observed, all measures possible must be taken to prevent pushing salmon through a “bottleneck” and the resultant loss of genome heterozygosity. There is also the possibility that because of the small population sizes we may need to examine the genetics more closely to determine if there is an effective population size and include that consideration in any management prescriptions (Hsieh *et al.* 2009; Chih-hao *et al.* 2010; Luikart *et al.* 2010).

The data from 1974 to 2008 are not supportive of an increased return of the MSW component. Because MSW salmon have been selected against for so long, it is incumbent upon fishermen to return any MSW salmon when they are caught. In order to reduce density dependent competition between the progeny of MSW salmon and 1SW grilse, it may also be wise to keep all grilse that are caught, an anti-grilsefication

campaign if you will. Unless we are able to bring Atlantic salmon back from the abyss and return them to a more “normal” age structure and maximize heterogeneity, they may not be able to survive any number of stochastic events such as the elevation in sea surface temperatures, diseases and parasites from farmed fish, or the ability to adapt to changes required to survive modifications in the timing and composition of forage species necessary for survival on the high seas prior to returning to their natal streams.

Genetic variation or heterozygosity and population size should be taken into consideration in management decisions or legislation (Laikre *et al.* 2009; Laikre *et al.* 2010; Luikart *et al.* 2010; Whiteley *et al.* 2010). Ecological and life history characteristics that affect gene flow need to be taken into account as a precautionary predictive measure to track gene flow as it affects viability (Whiteley *et al.* 2004). “Relatively little is known about specific agents of selection affecting salmonids, or how wild populations respond to multiple and often contrasting selective pressures. What is the strength of artificial selective pressures, such as fish culture, fisheries exploitation or human-induced environmental change compared to natural and sexual selection (Garcia de Leaniz *et al.* 2007)?”

How long will it take for an anti-grilsefication campaign to turn the tide? If the changes noted are a function of phenotypic plasticity then we would expect to see a gradual return to a cohort composition similar to that prior to the West Greenland commercial harvest, if the changes are genetically based then it may take longer for Atlantic salmon to realize an increase in genome heterozygosity and to return to their former composition (Allendorf *et al.* 2008; Stenseth and Dunlop 2009). Stenseth and Dunlop (2009) go on to note that “a population is expected to recover more slowly from

genetic than from plastic changes, and genetic change might even be irreversible. Given the high harvesting pressure on larger and older individuals, the result might be ‘juvenescence’ of populations, possibly leading to increased variability in abundance and reduced genetic variability”.

Gudmundsson (2007) was able to show a return to a “normal” genetic composition after an incursion of farmed fish and a disease outbreak in the river Ellidaar, while noting “faster growth of juveniles, earlier smolting and skewed sex ratio of returning adults in recent years”. Recent microsatellites markers were compared with older samples (1948-2005) and found the salmon to be “panmictic” in the river system. If the recovery seen in Ellidaar is possible, where we have a known introgression into the genome, then it may be possible to make similar inferences regarding the recovery of MSW salmon in the six rivers in this study.

The interactions between farmed and wild populations must be minimized not only to prevent them from interbreeding in rivers and streams, but also to reduce the transmission of diseases and parasites. Outbreaks of disease similar to that seen in the aquaculture community in Chile may have catastrophic effects on wild populations. Chilean salmon production went from 400,000 tons in 2005 to only 100,00 tons in 2010, due to an outbreak of Infectious Salmon Anemia (Asche *et al.* 2009).

From an economic point of view, the average catch is one fish/rod/day for the recreational fishery, a minimum cost greater than \$1000.00 per day (lodging, meals, fishing permit, and guide) per rod, and a mean weight (over the 35 year time series) of 3.7 kilograms, a single fish is worth more than \$100.00/lb. That’s excluding the cost of airfare, hotels, shopping, restaurants, auto rental, and other miscellaneous items that

would be typically purchased in Iceland both prior to and after salmon fishing that are a direct benefit to the wider economy. Setting aside the fact that according to International law all salmon are the property of the country in whose natal streams they were born and any high seas harvest is considered illegal, that same salmon harvested on the high seas fetches just a few dollars/lb on the wholesale market (in 2006 the market value of whole farmed 8-10 lb Atlantic salmon was \$2.06/lb (Analyst 2006)). The business model of net buyouts in Greenland, begun by NASF and followed up by NASCO, begins to make sense from the point of view of economic, natural resource management, and the national interest of Iceland. According to an Interim Report of the Socio-Economics Working Group on the value of the rod-catch in Iceland, “The average salmon price for the landowner is close to 30,000 ISK (330 €) per fish” (NASCO 2008). That is just to the farmer or landowner who leases out his property for salmon fishing, not to the broader economy. When a price can be affixed to a natural resource, then a cost-benefit analysis can be performed. It is Atlantic salmon in this example; similar methodology may be applied to the management and conservation of other species.

As a practical matter, increasing the carrying capacity of the natal streams is recommended. “An evolutionary approach to salmon conservation is required, aimed at maintaining the conditions necessary for natural selection to operate most efficiently and unhindered. This may require minimizing alterations to native genotypes and habitats to which populations have likely become adapted, but also allowing for population size to reach or extend beyond carrying capacity to encourage competition and other sources of natural mortality. (Garcia de Leaniz *et al.* 2007).” Where possible, fish passage devices (fish ladders) should be installed on impassable portions of rivers, extending the range of

the river systems and increasing the carrying capacity. Amending oligotrophic streams with additional nutrient input to boost primary production and increasing carrying capacity may also be considered.

Every effort should be made to land all rod caught MSW salmon as quickly as possible, so they expend the least amount of energy prior to being released. The nets used to land salmon on the river bank should be constructed of natural fibers rather than synthetic ones, to help preserve the external mucus coating. Ghillies, who act as guides and water bailiffs, and fishermen may also want to consider wearing gloves that minimize the removal of the mucus coating, while handling them prior to release. Taking time for a picture while the salmon is out of water should be minimized to decrease mortality and avoid the moniker “camera killer”. These recommendations may seem excessive, but from Stenseth and Dunlap’s (2009) comments on the Darimont’s demonstration of rapid shifts due to harvest induced changes, state that “a precautionary approach requires that management strategies be designed under the assumption that harvesting-induced evolution might occur. The potential costs of ignoring that possibility are severe — most notably, the resulting changes may be difficult or impossible to reverse.”

Recommendations for future research should include additional study of post-smolt survival and changing sea surface temperatures in the North Atlantic, changes in primary production and macro zooplankton assemblages, genetic study of individual populations from an Evolutionary Biology perspective, and the correlations between the commercial harvest for fishmeal of the preferred forage species such as capelin, sand eels, krill, etc, or what Daniel Pauly (Pauly *et al.* 1998) calls “fishing down marine food webs,” and salmon recruitment.

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APPENDICES

APPENDIX A

REGRESSION OF AVERAGE WEIGHT FOR FEMALE SALMON BY RIVER

Changes in Average Weight Over Time

Average Weight Female Salmon

River: Haffjardara

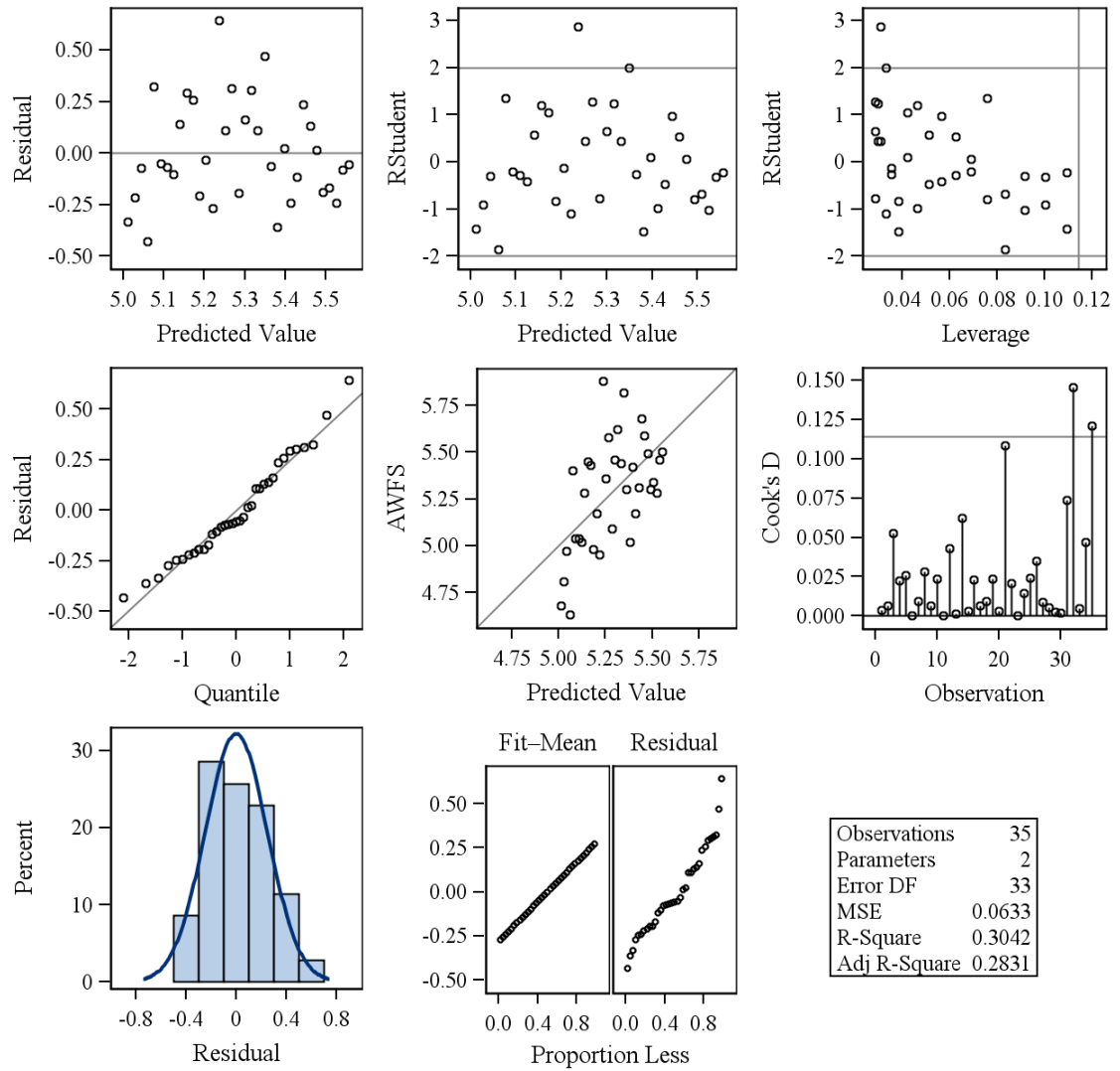
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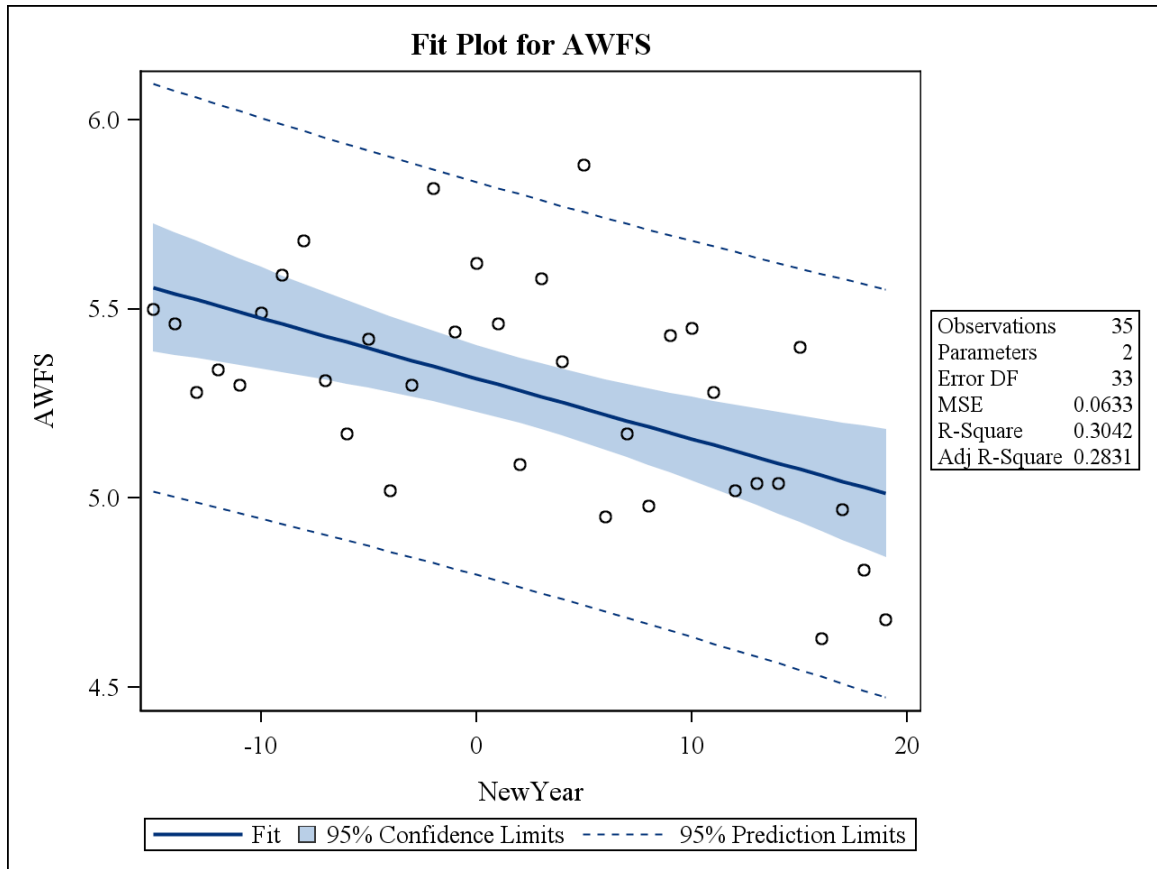
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.91296	0.91296	14.42	0.0006
Error	33	2.08871	0.06329		
Corrected Total	34	3.00167			

Root MSE	0.25158	R-Square	0.3042
Dependent Mean	5.28457	Adj R-Sq	0.2831
Coeff Var	4.76071		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	5.31655	0.04335	122.64	<.0001
NewYear	1	-0.01599	0.00421	-3.80	0.0006

Fit Diagnostics for AWFS





River: Haukadalsa

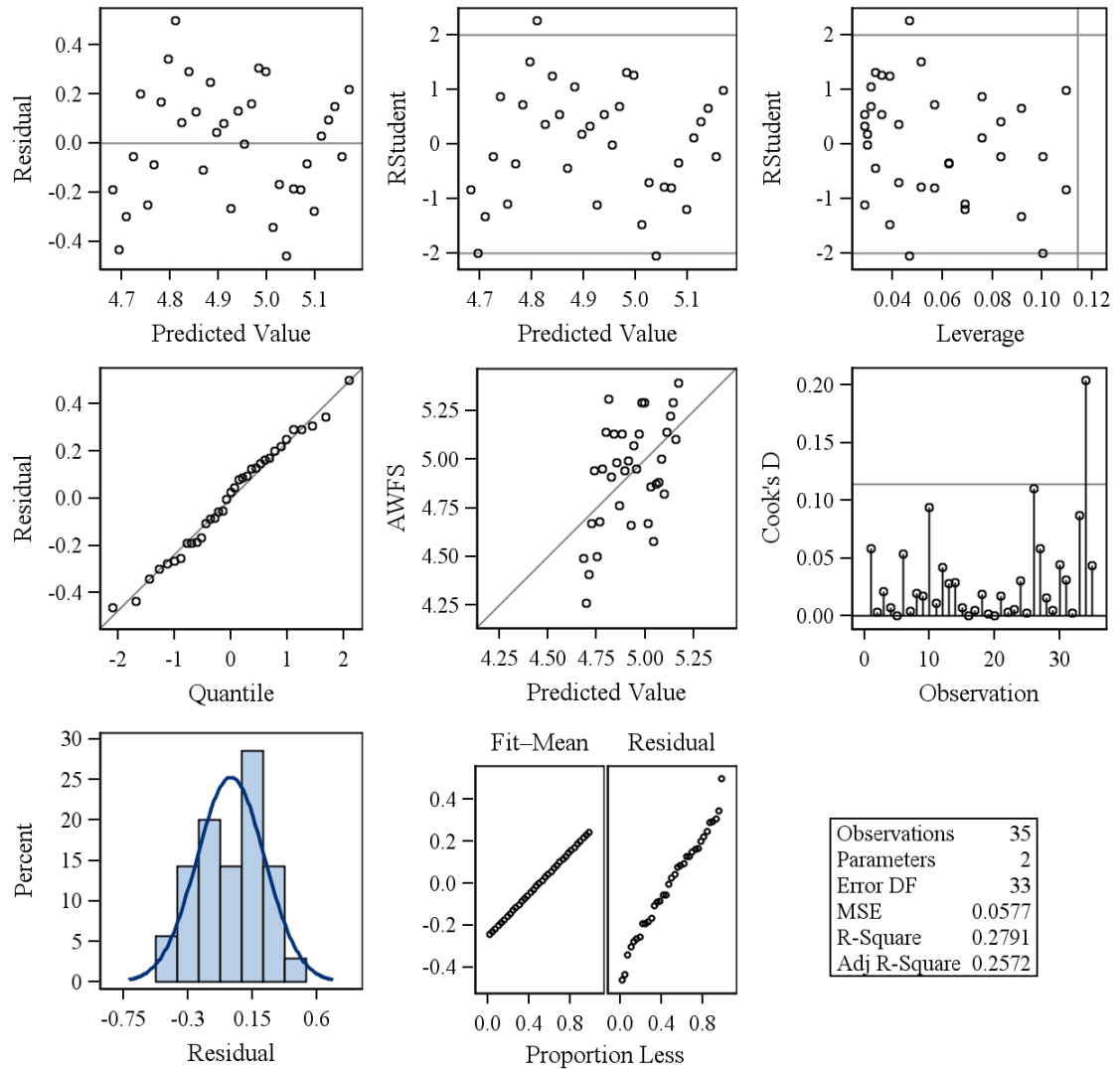
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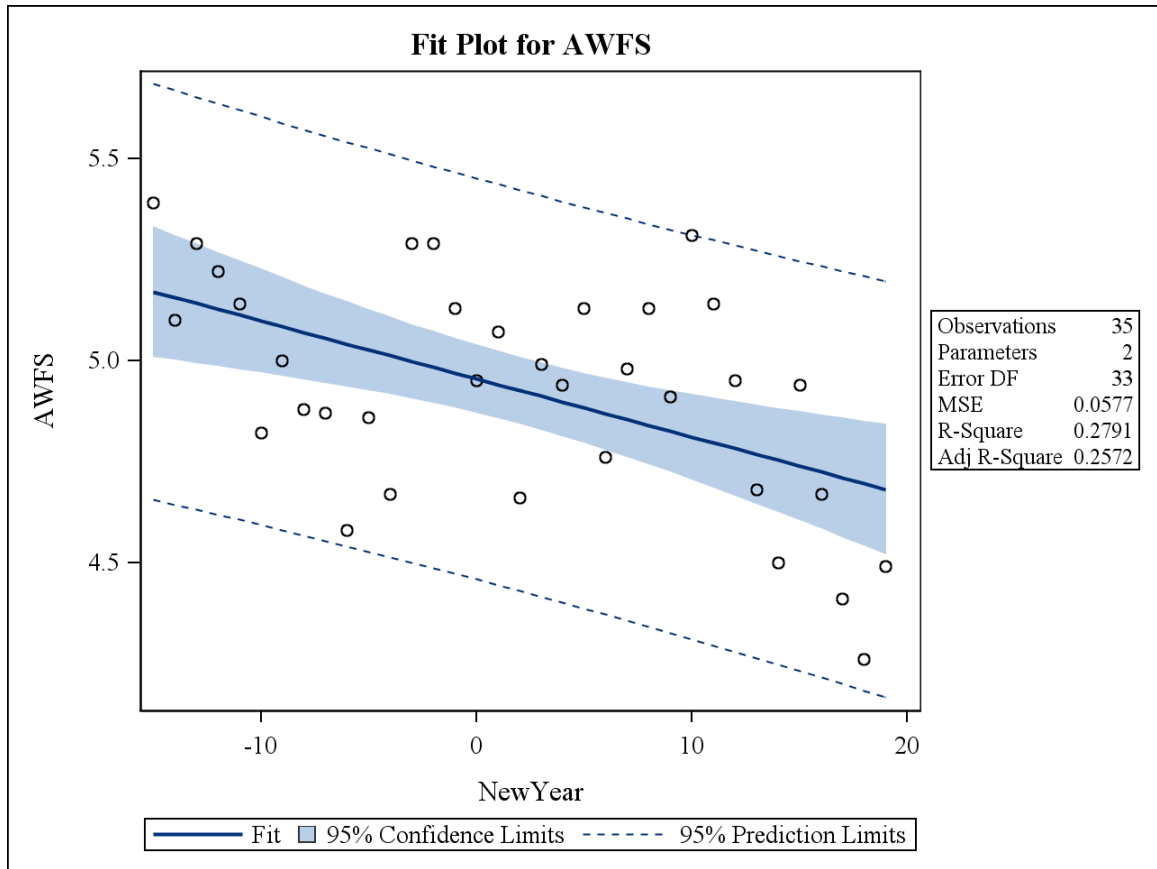
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.73688	0.73688	12.78	0.0011
Error	33	1.90338	0.05768		
Corrected Total	34	2.64026			

Root MSE	0.24016	R-Square	0.2791
Dependent Mean	4.92571	Adj R-Sq	0.2572
Coeff Var	4.87569		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	4.95445	0.04138	119.72	<.0001
NewYear	1	-0.01437	0.00402	-3.57	0.0011

Fit Diagnostics for AWFS





River: Hofsa

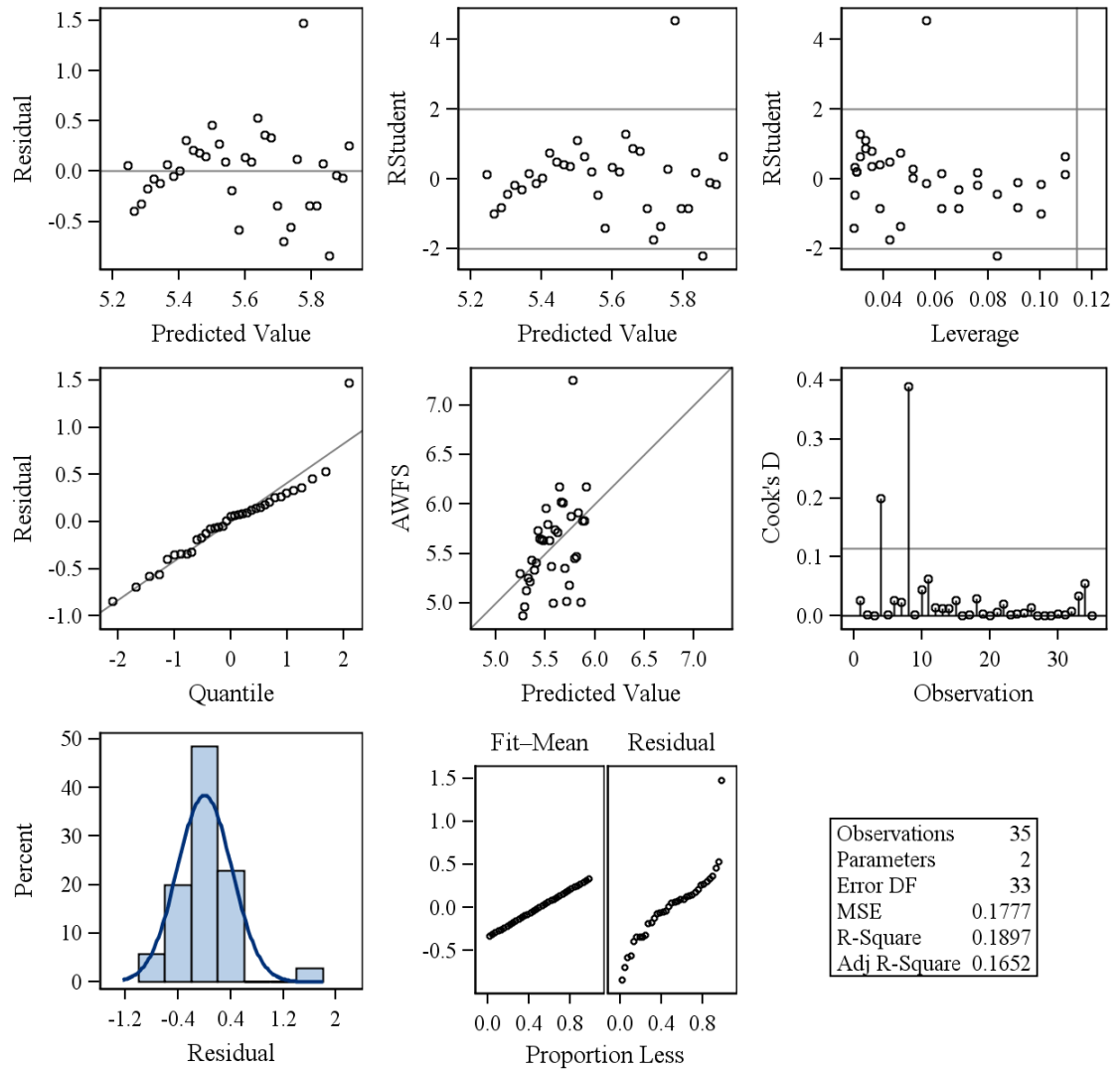
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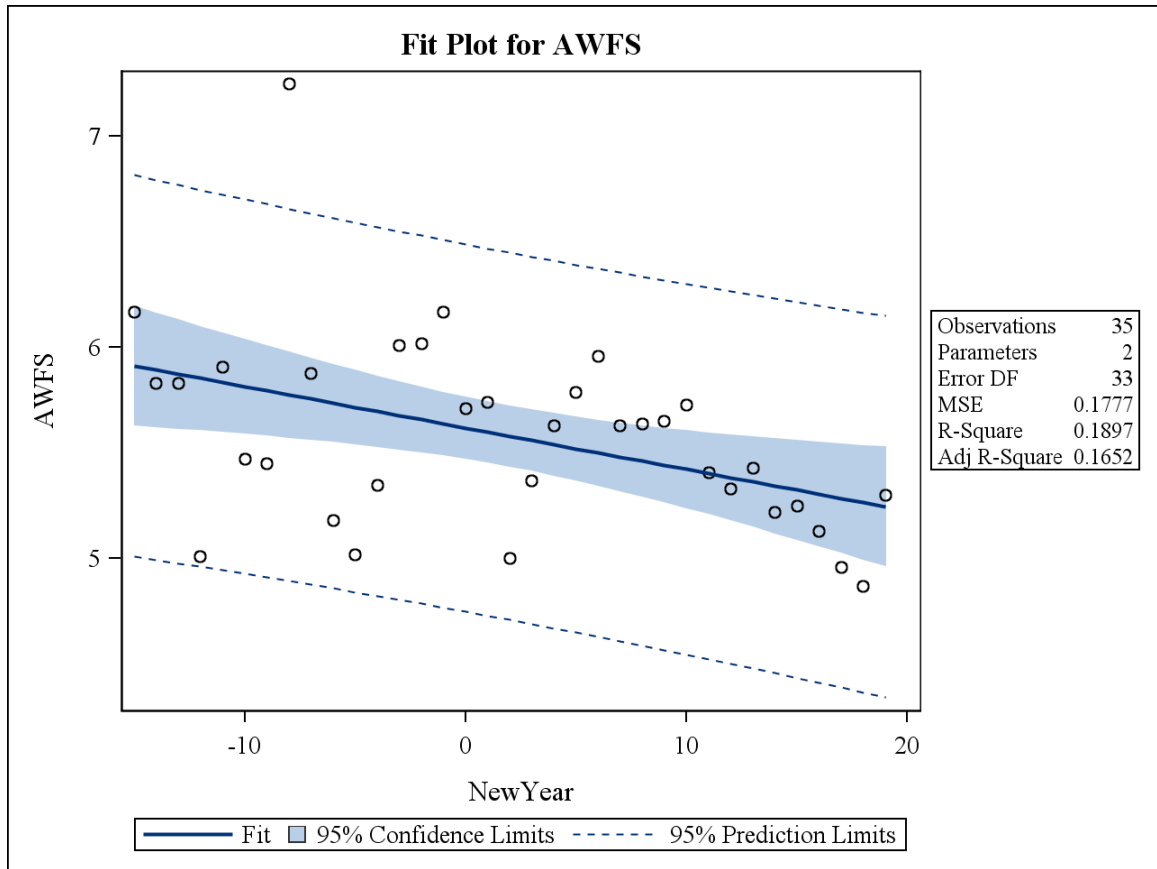
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	1.37294	1.37294	7.73	0.0089
Error	33	5.86426	0.17770		
Corrected Total	34	7.23720			

Root MSE	0.42155	R-Square	0.1897
Dependent Mean	5.58000	Adj R-Sq	0.1652
Coeff Var	7.55467		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	5.61922	0.07264	77.36	<.0001
NewYear	1	-0.01961	0.00706	-2.78	0.0089

Fit Diagnostics for AWFS





River: Laxa in Adaldal

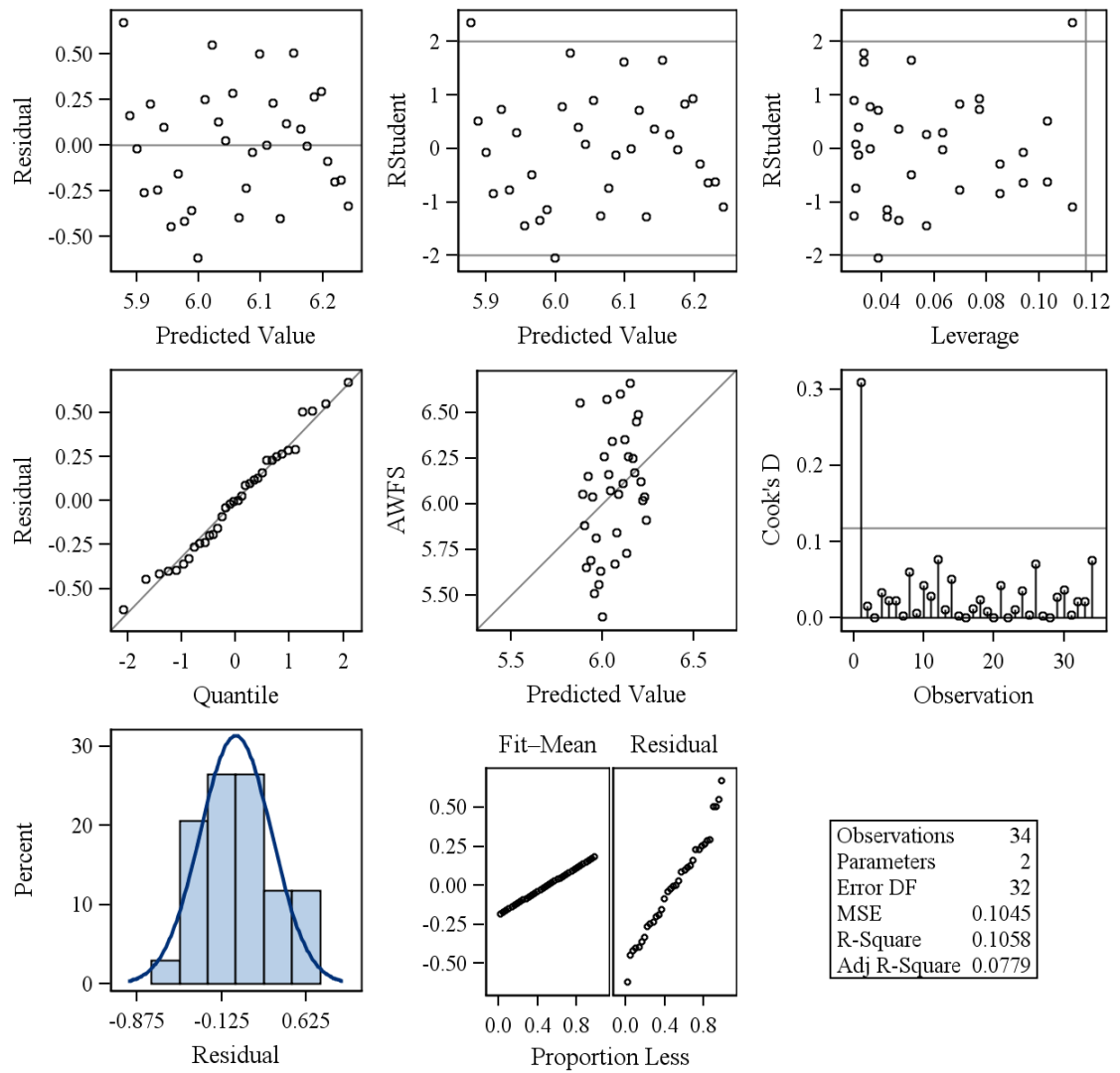
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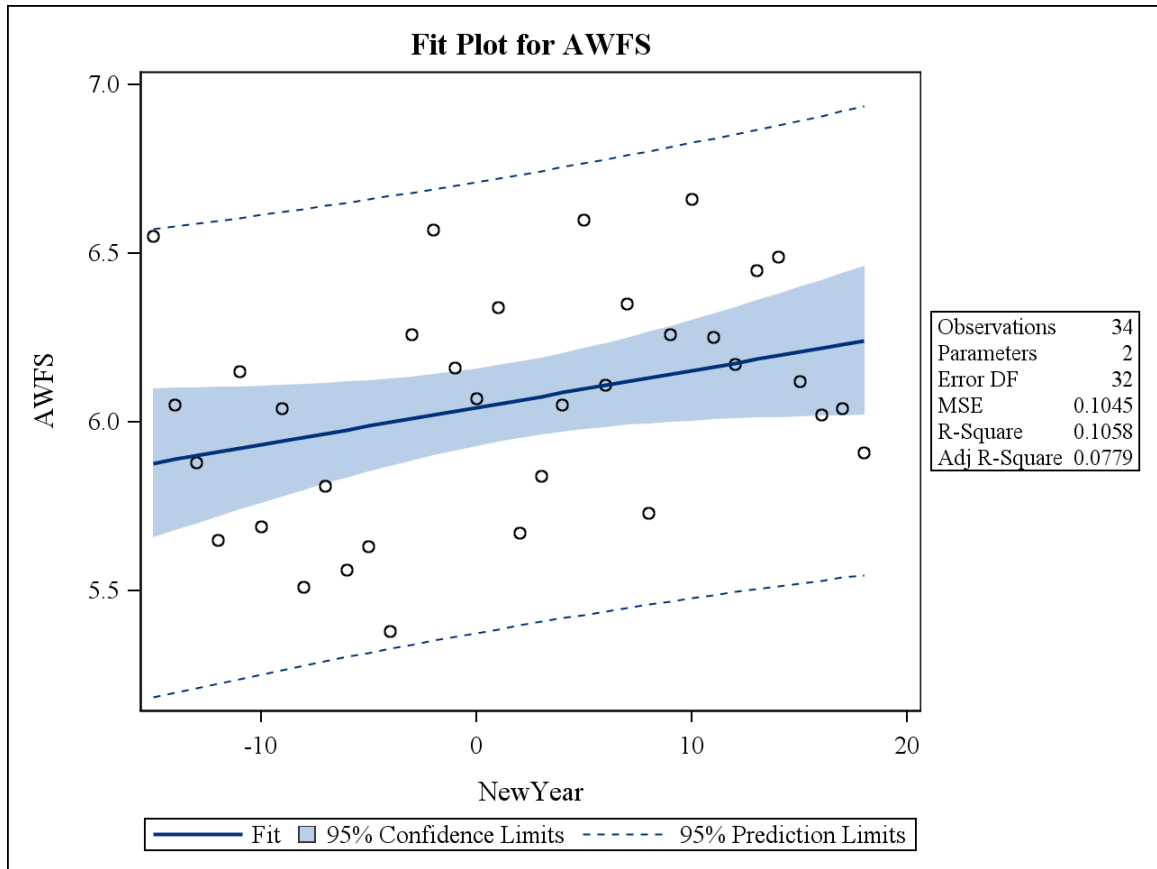
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.39559	0.39559	3.79	0.0605
Error	32	3.34240	0.10445		
Corrected Total	33	3.73799			

Root MSE	0.32319	R-Square	0.1058
Dependent Mean	6.05941	Adj R-Sq	0.0779
Coeff Var	5.33364		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	6.04292	0.05607	107.77	<.0001
NewYear	1	0.01099	0.00565	1.95	0.0605

Fit Diagnostics for AWFS





River: Midfjardara

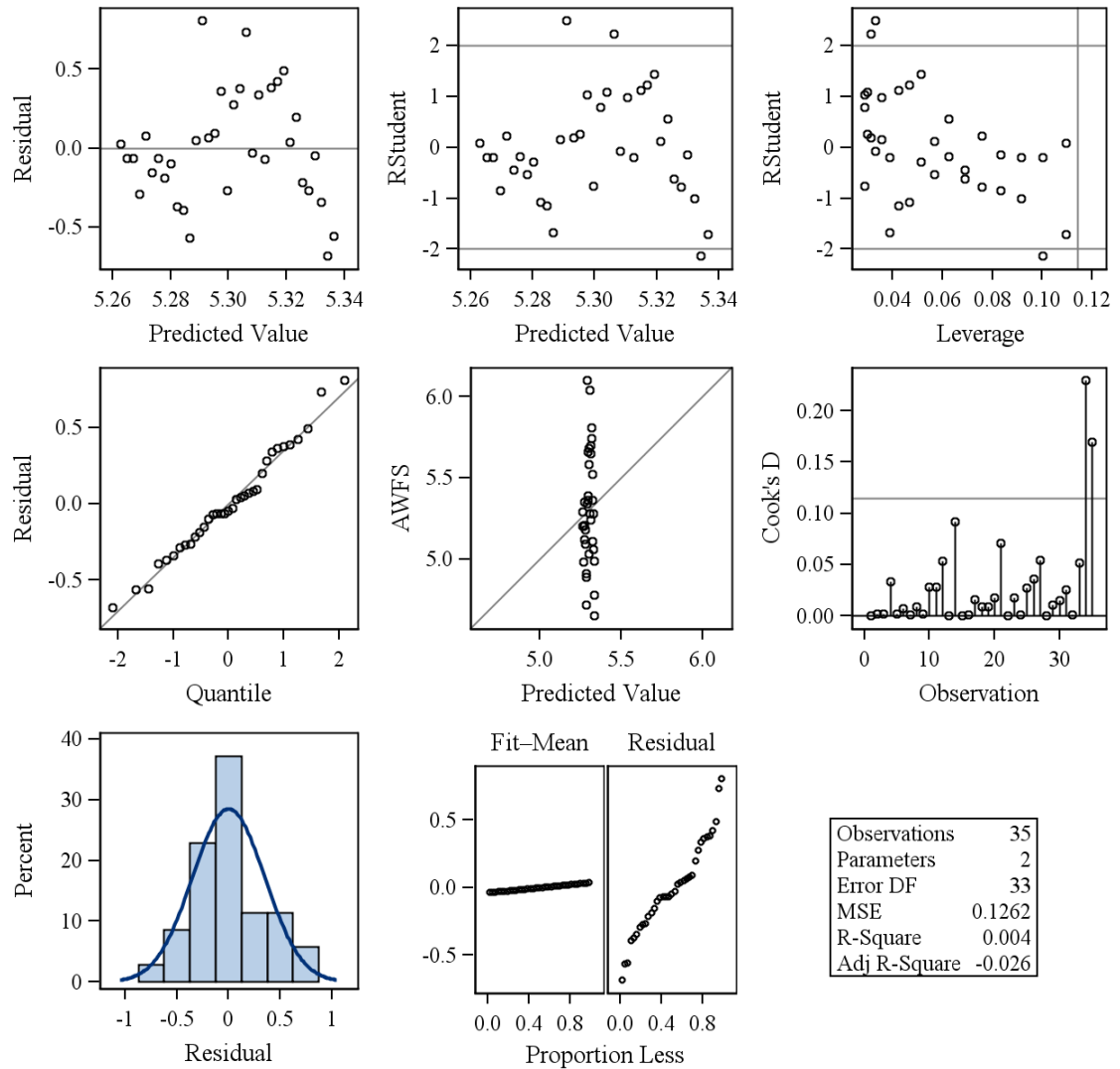
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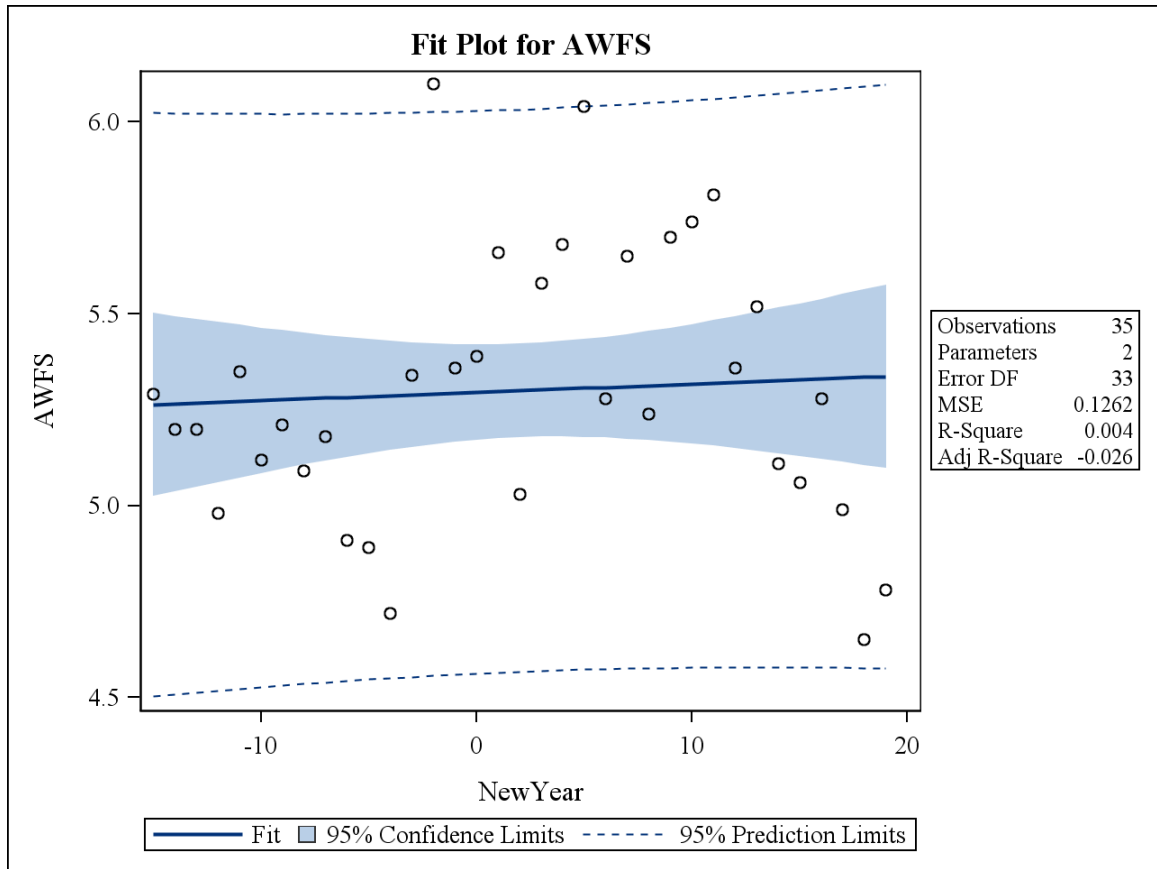
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.01665	0.01665	0.13	0.7188
Error	33	4.16545	0.12623		
Corrected Total	34	4.18210			

Root MSE	0.35528	R-Square	0.0040
Dependent Mean	5.29971	Adj R-Sq	-0.0262
Coeff Var	6.70380		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	5.29539	0.06122	86.50	<.0001
NewYear	1	0.00216	0.00595	0.36	0.7188

Fit Diagnostics for AWFS





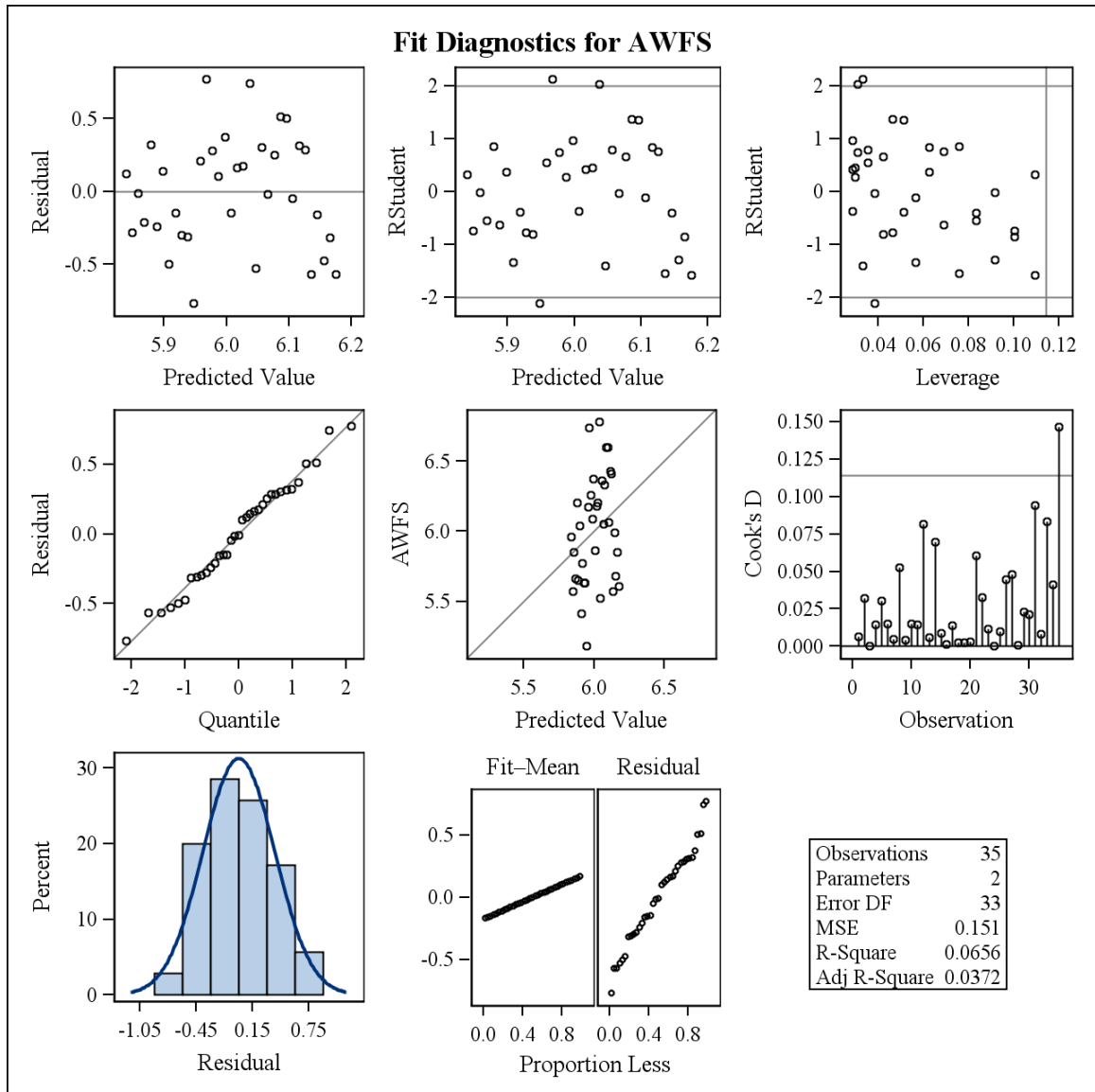
River: Vatnsdalsa

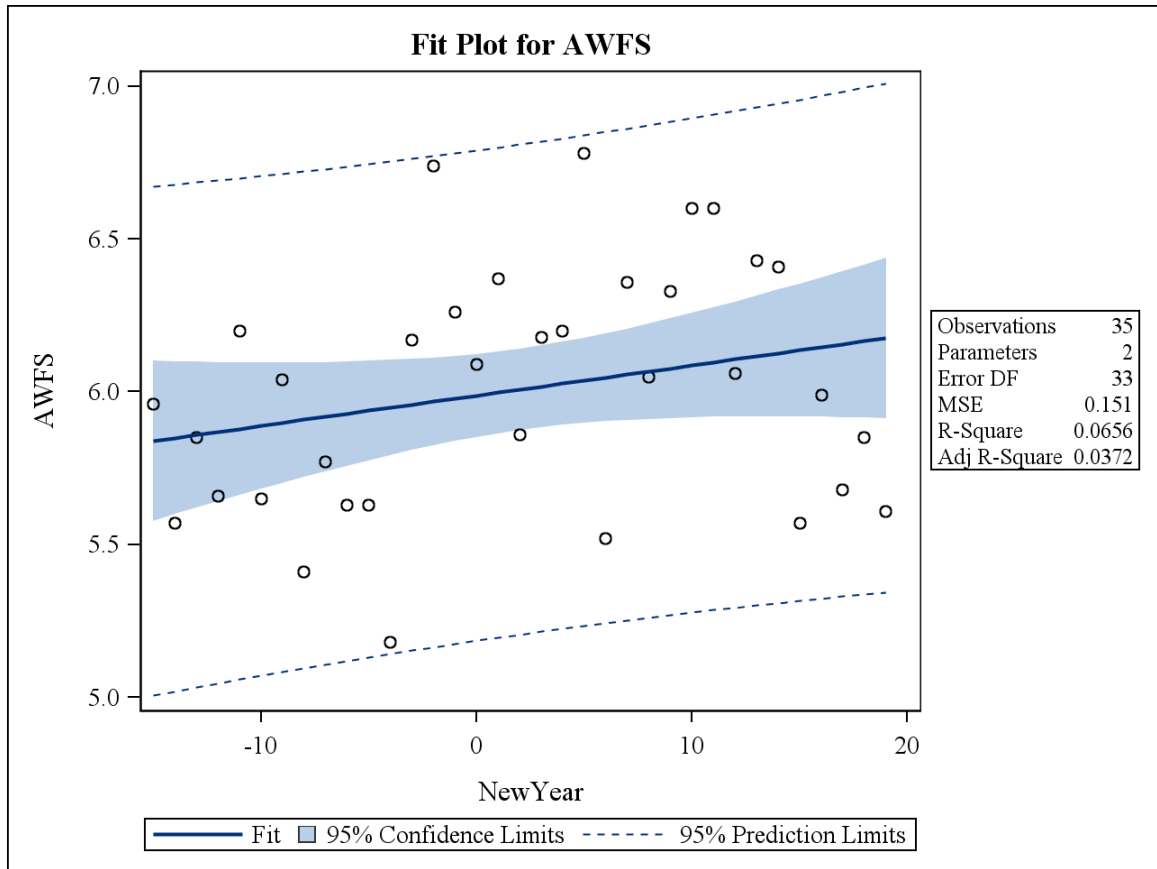
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Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.34964	0.34964	2.32	0.1376
Error	33	4.98383	0.15103		
Corrected Total	34	5.33347			

Root MSE	0.38862	R-Square	0.0656
Dependent Mean	6.00743	Adj R-Sq	0.0372
Coeff Var	6.46898		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	5.98764	0.06696	89.42	<.0001
NewYear	1	0.00990	0.00650	1.52	0.1376





APPENDIX B

REGRESSION OF AVERAGE WEIGHT FOR MALE SALMON BY RIVER

Changes in Averages Weight Over Time

Average Weight Male Salmon

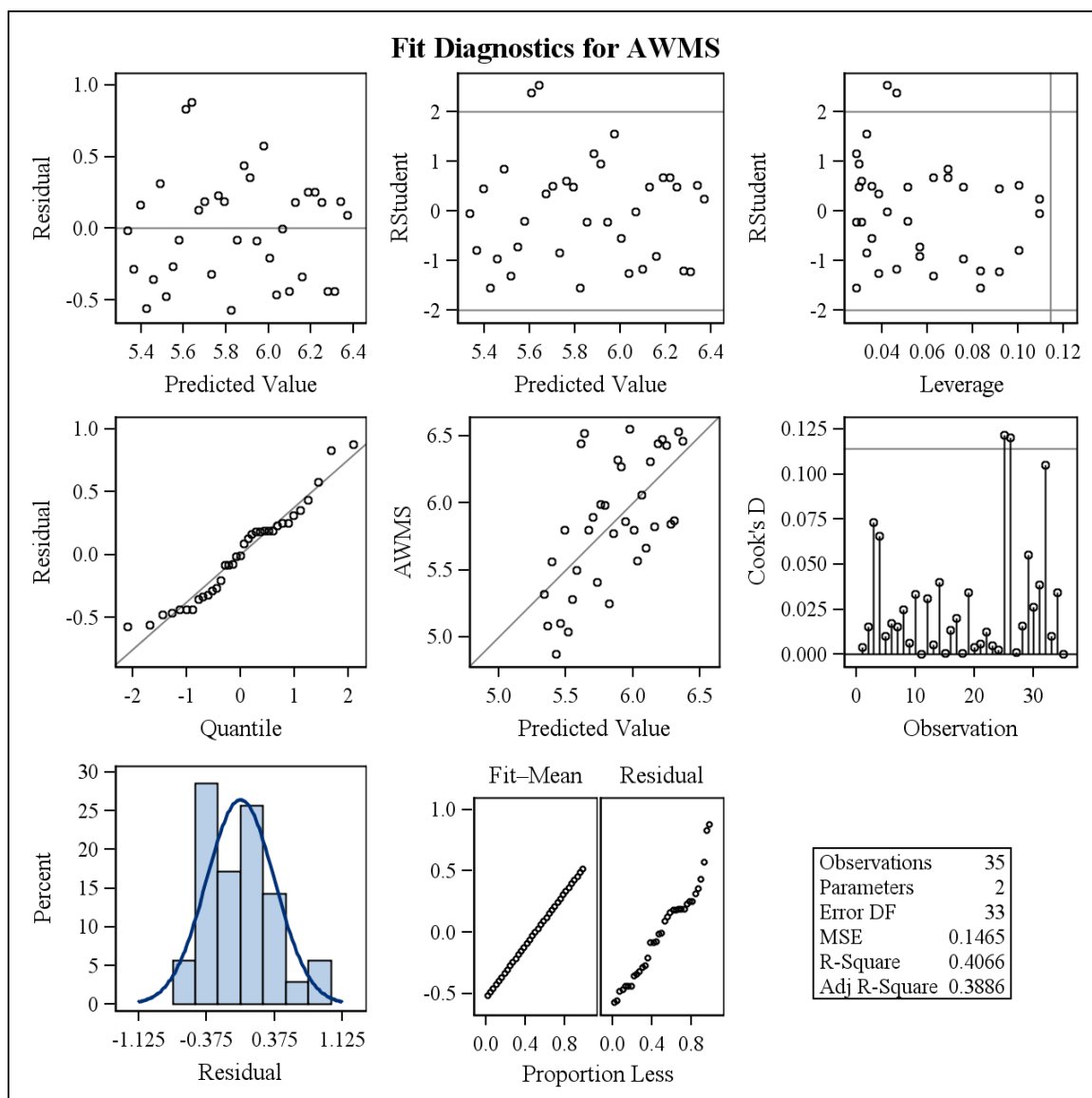
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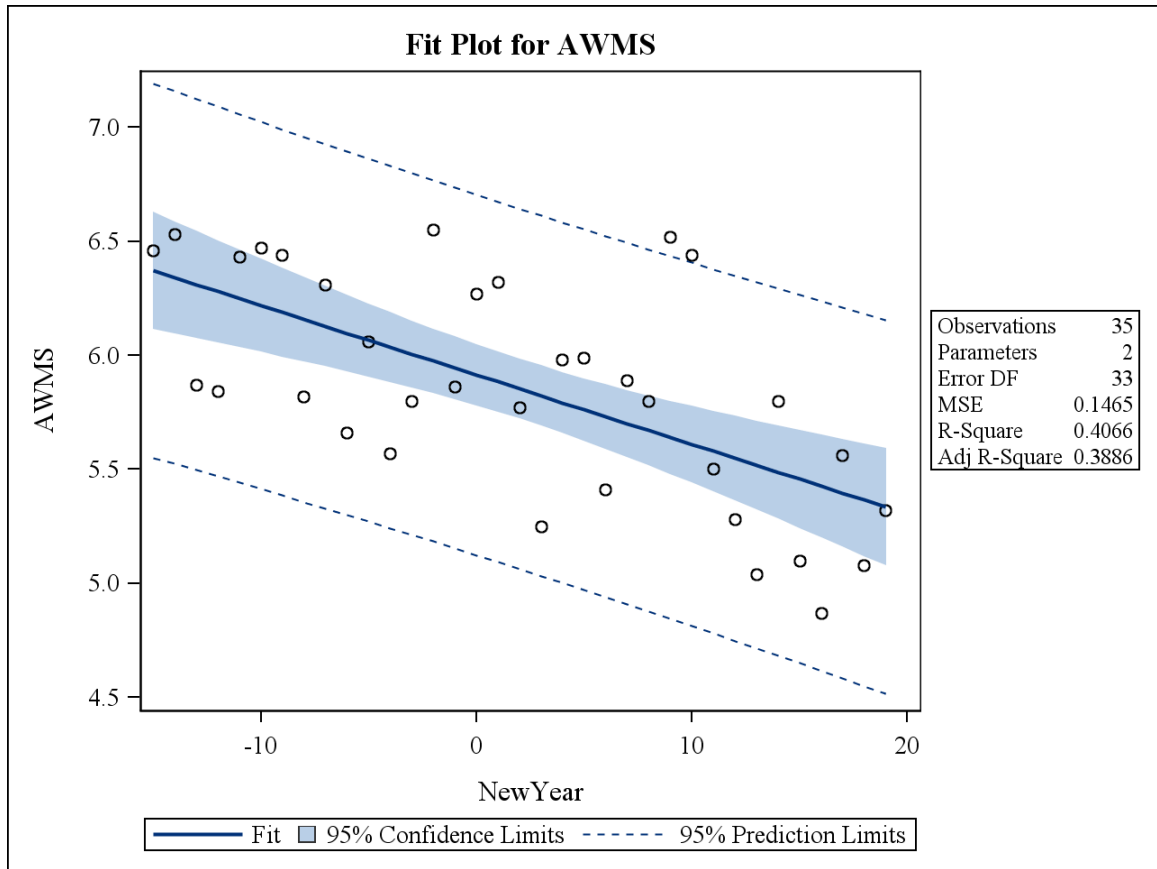
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Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	3.31337	3.31337	22.61	<.0001
Error	33	4.83558	0.14653		
Corrected Total	34	8.14895			

Root MSE	0.38280	R-Square	0.4066
Dependent Mean	5.85314	Adj R-Sq	0.3886
Coeff Var	6.54001		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	5.91407	0.06596	89.66	<.0001
NewYear	1	-0.03046	0.00641	-4.76	<.0001





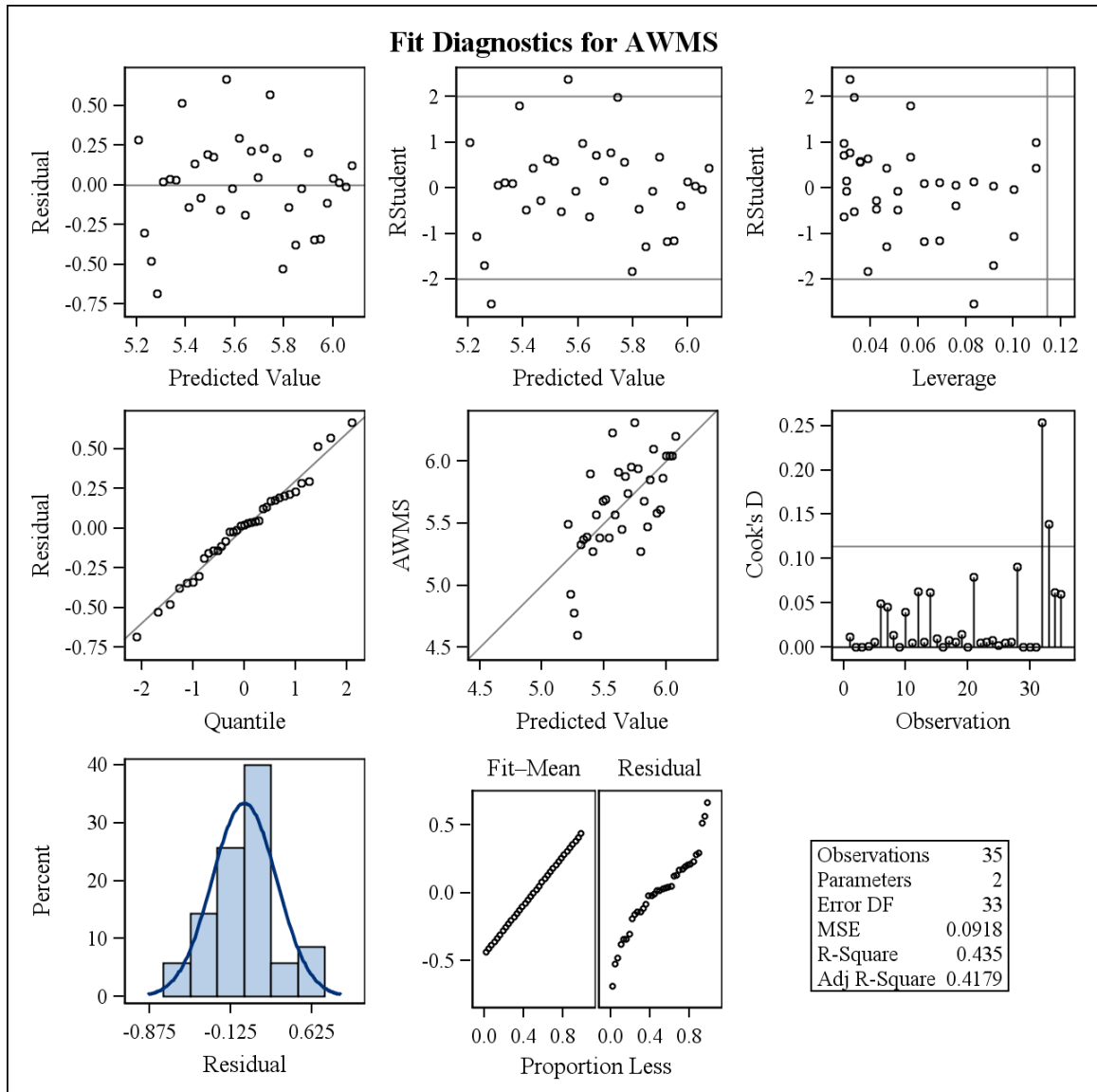
River: Haukadalsa

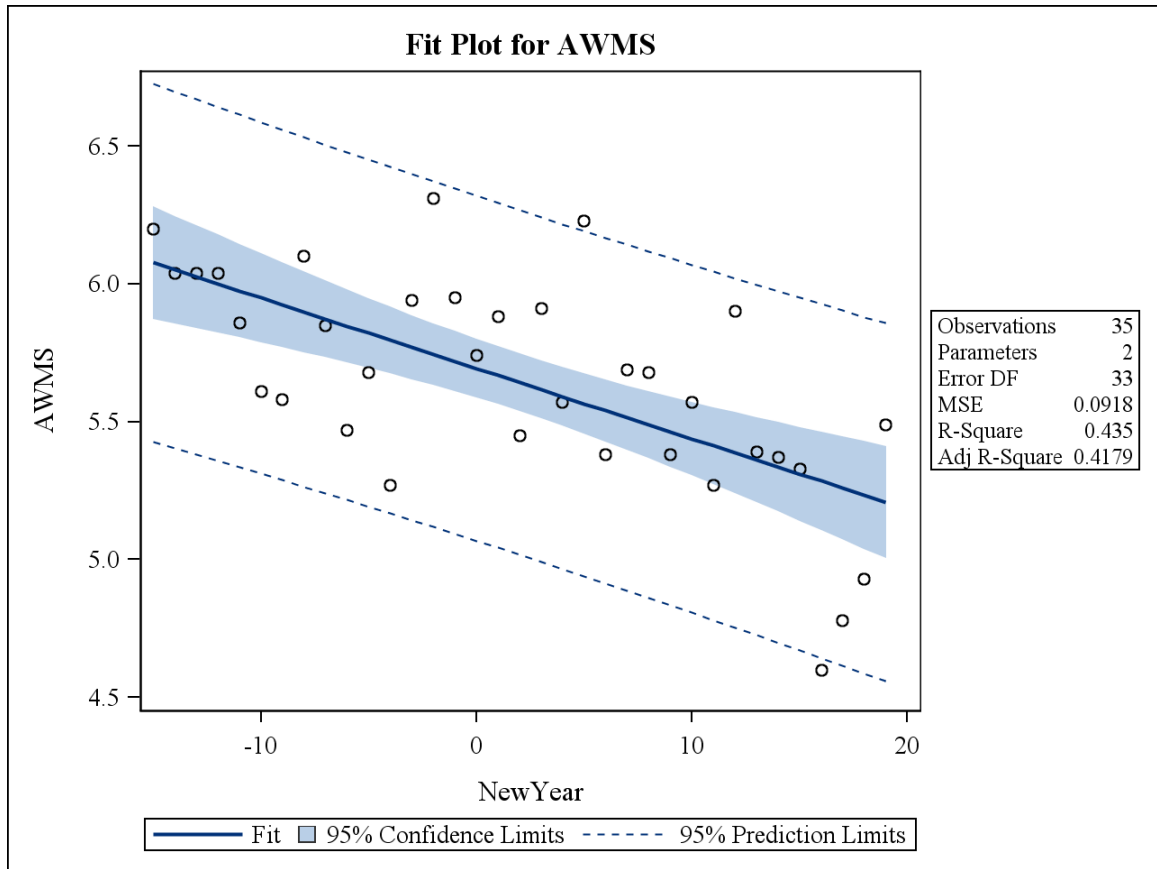
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Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	2.33237	2.33237	25.41	<.0001
Error	33	3.02965	0.09181		
Corrected Total	34	5.36202			

Root MSE	0.30300	R-Square	0.4350
Dependent Mean	5.64229	Adj R-Sq	0.4179
Coeff Var	5.37012		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	5.69341	0.05221	109.05	<.0001
NewYear	1	-0.02556	0.00507	-5.04	<.0001





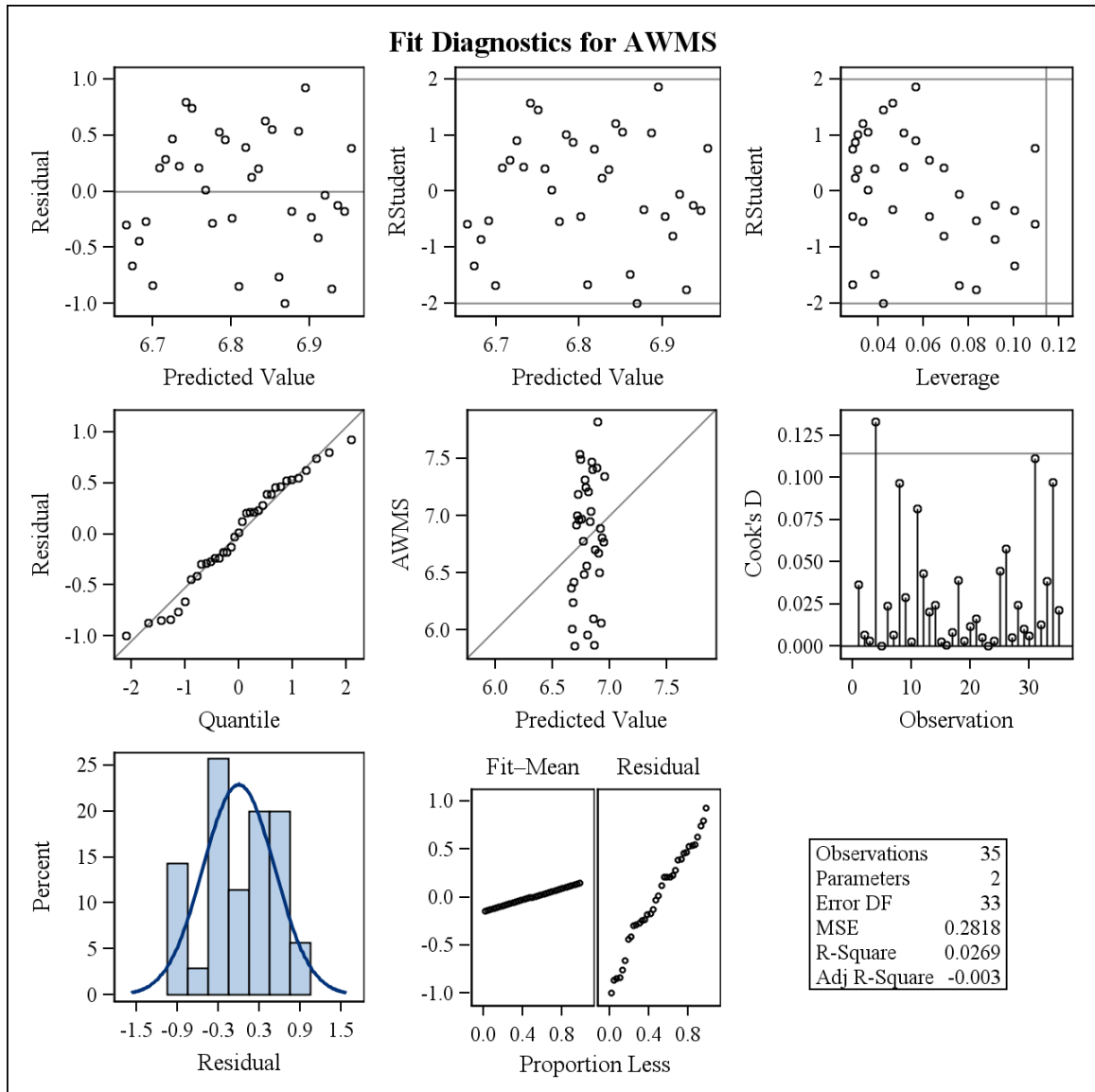
River: Hofsa

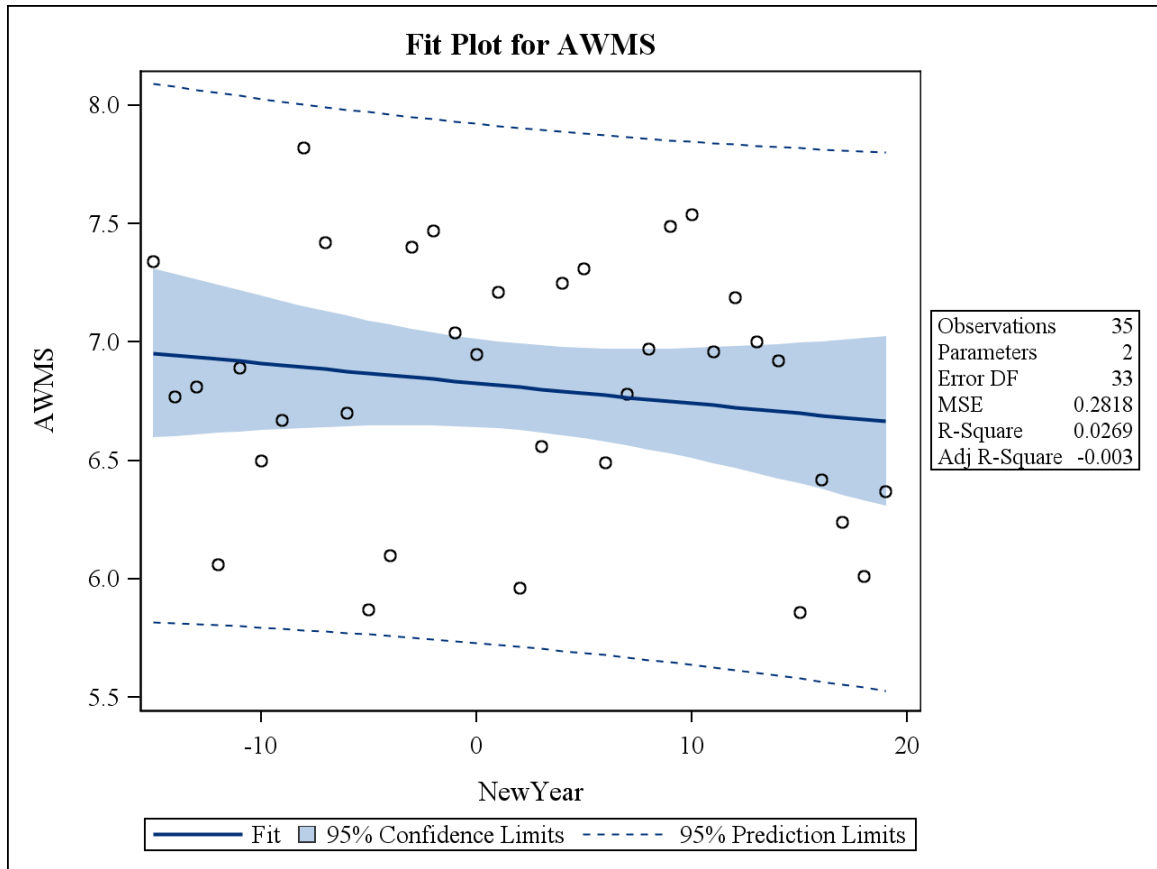
Number of Observations Read	35
Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.25717	0.25717	0.91	0.3464
Error	33	9.29913	0.28179		
Corrected Total	34	9.55630			

Root MSE	0.53084	R-Square	0.0269
Dependent Mean	6.80971	Adj R-Sq	-0.0026
Coeff Var	7.79534		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	6.82669	0.09147	74.63	<.0001
NewYear	1	-0.00849	0.00888	-0.96	0.3464





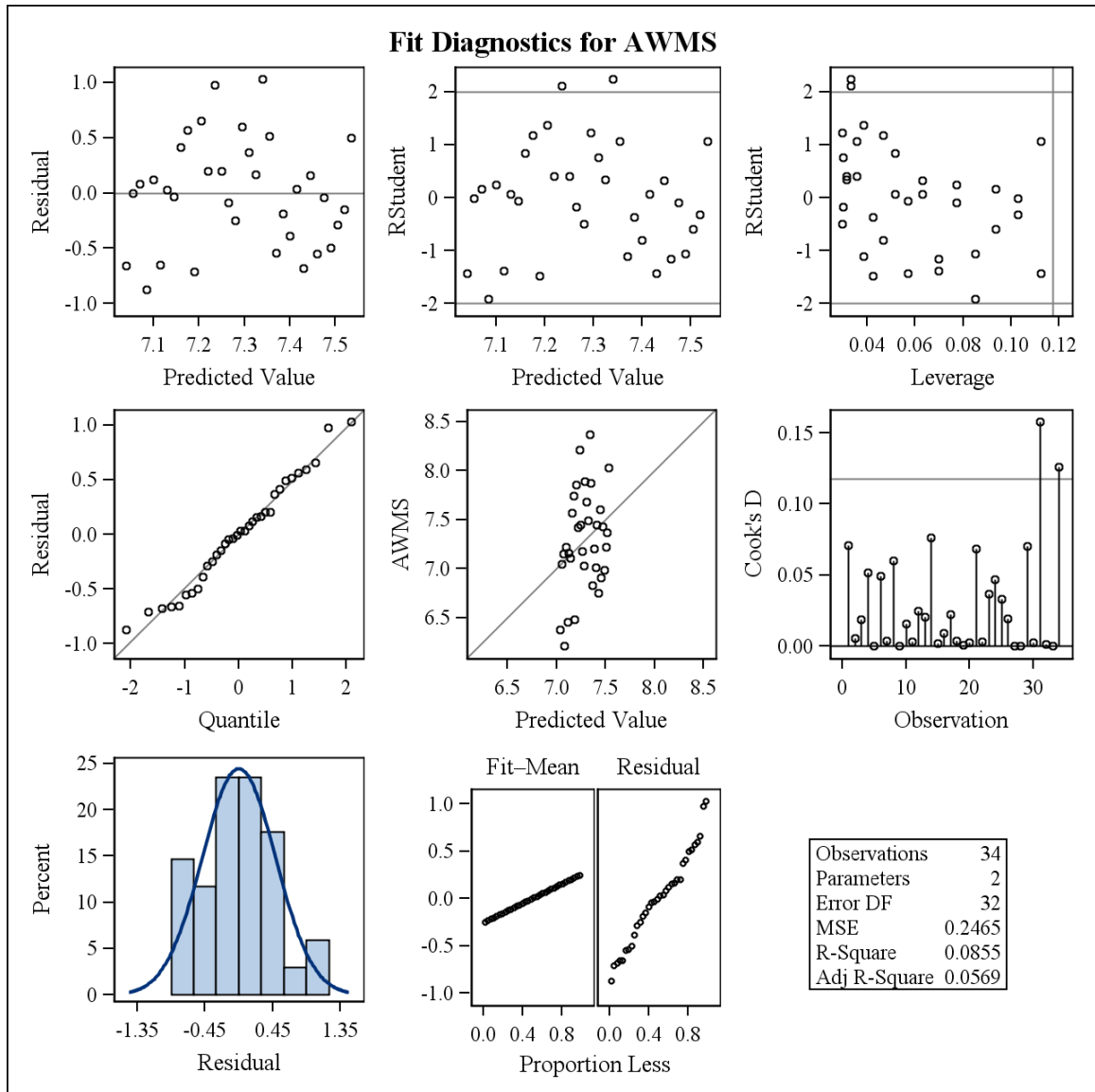
River: Laxa in Adaldal

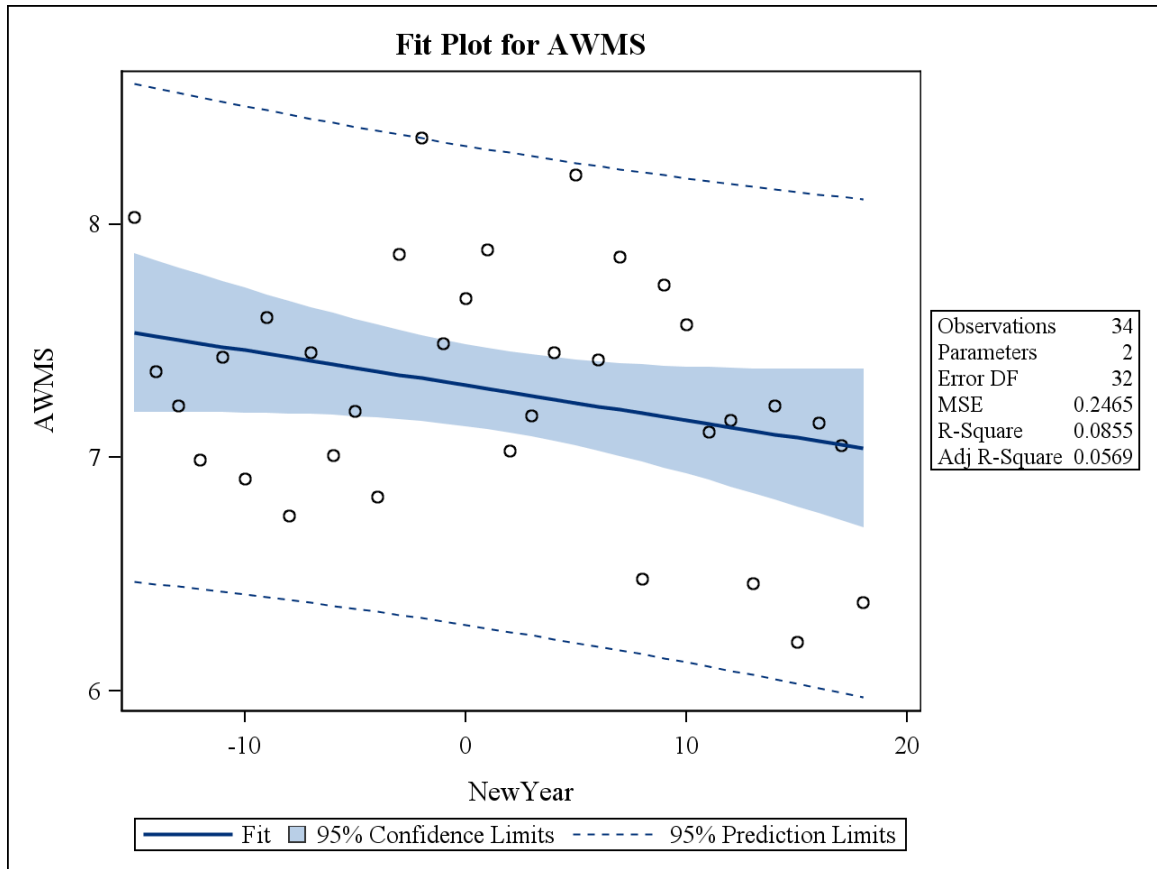
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Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.73714	0.73714	2.99	0.0934
Error	32	7.88712	0.24647		
Corrected Total	33	8.62426			

Root MSE	0.49646	R-Square	0.0855
Dependent Mean	7.28735	Adj R-Sq	0.0569
Coeff Var	6.81263		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	7.30987	0.08613	84.87	<.0001
NewYear	1	-0.01501	0.00868	-1.73	0.0934





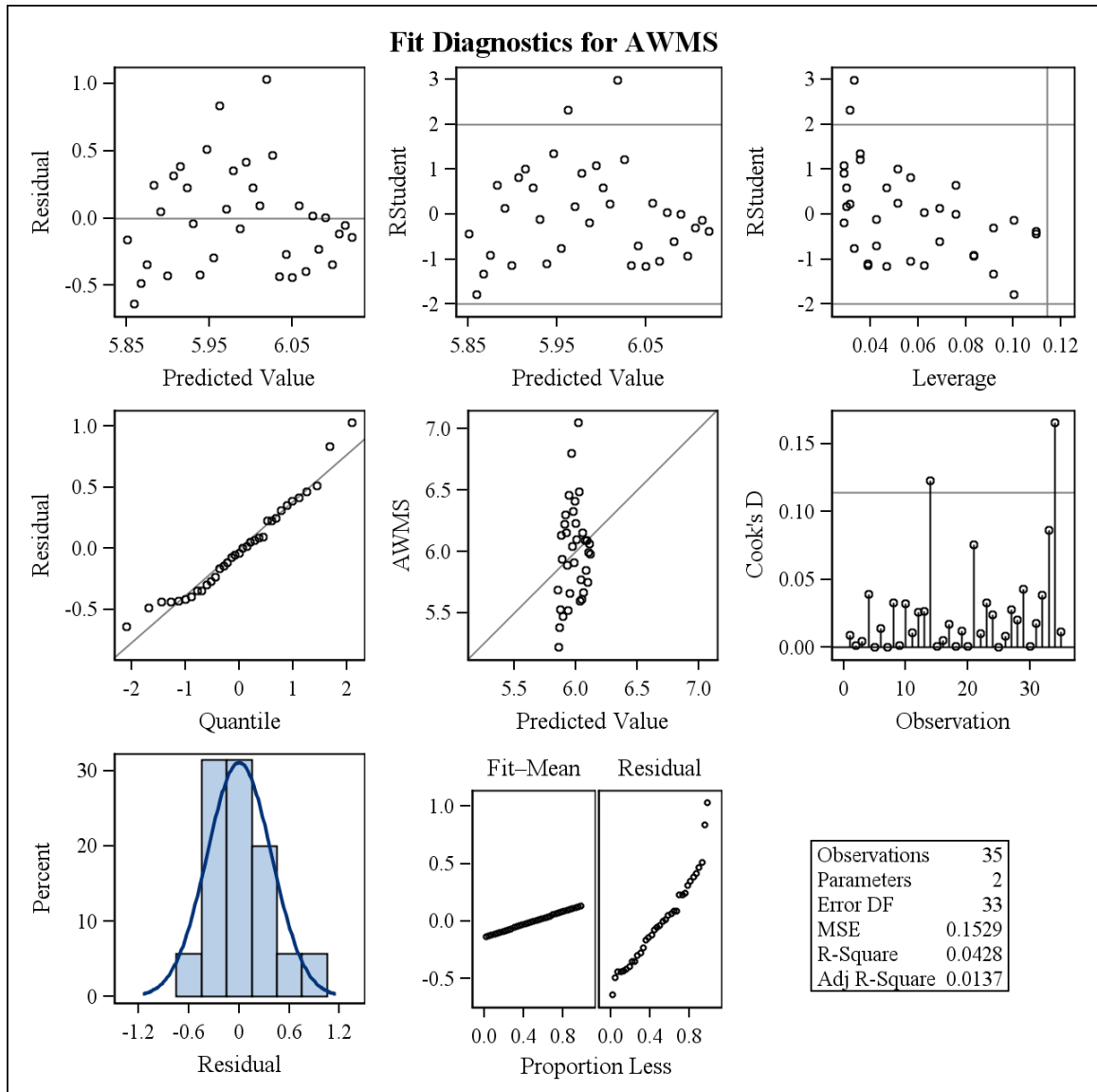
River: Midfjardara

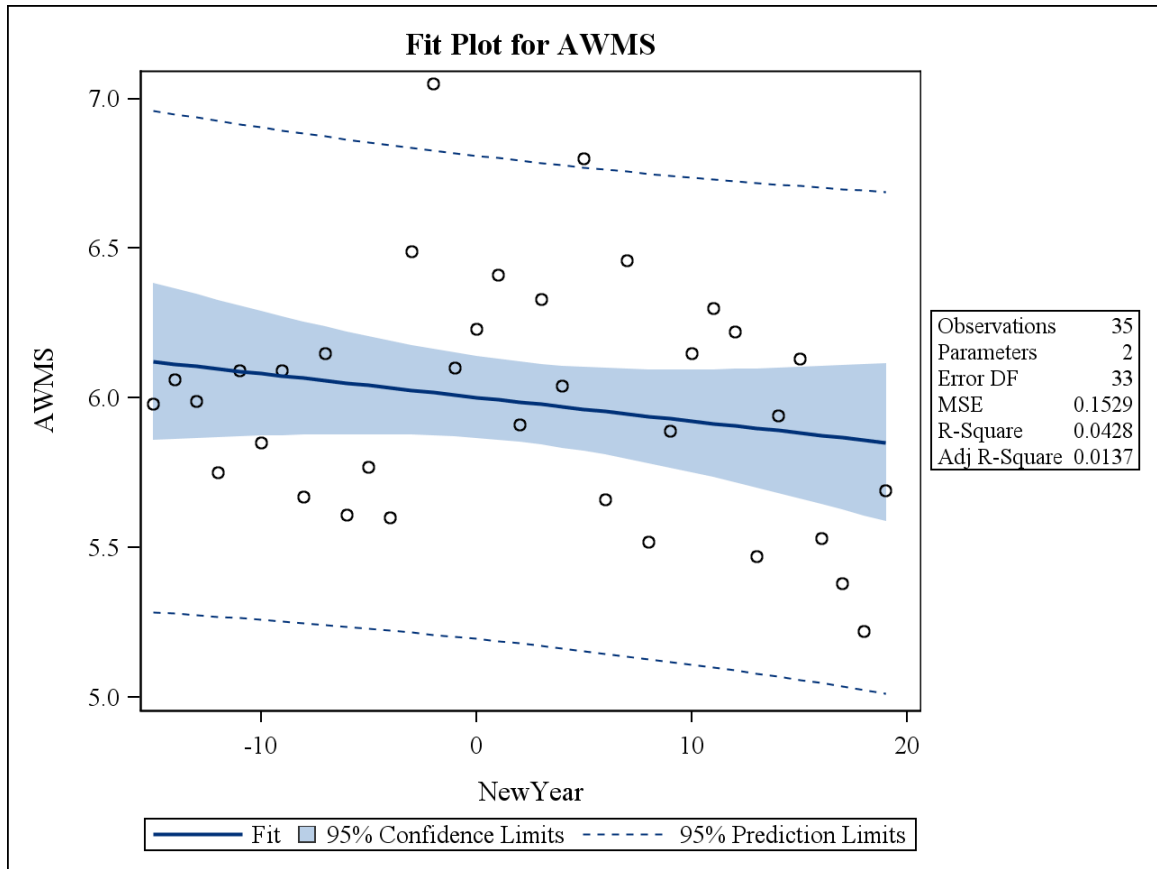
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Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.22529	0.22529	1.47	0.2333
Error	33	5.04410	0.15285		
Corrected Total	34	5.26939			

Root MSE	0.39096	R-Square	0.0428
Dependent Mean	5.98657	Adj R-Sq	0.0137
Coeff Var	6.53065		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	6.00246	0.06737	89.10	<.0001
NewYear	1	-0.00794	0.00654	-1.21	0.2333





River: Vatnsdalsa

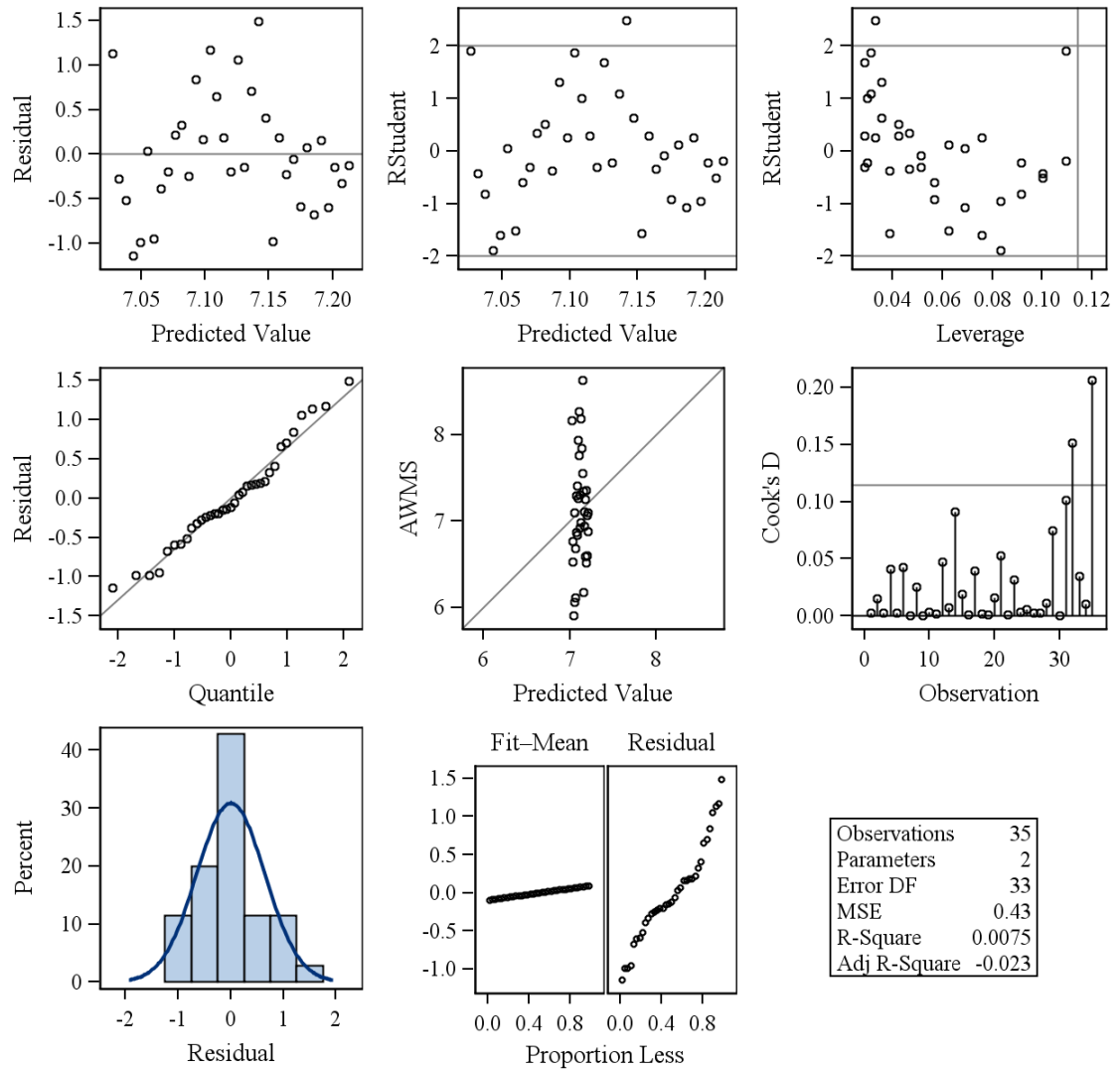
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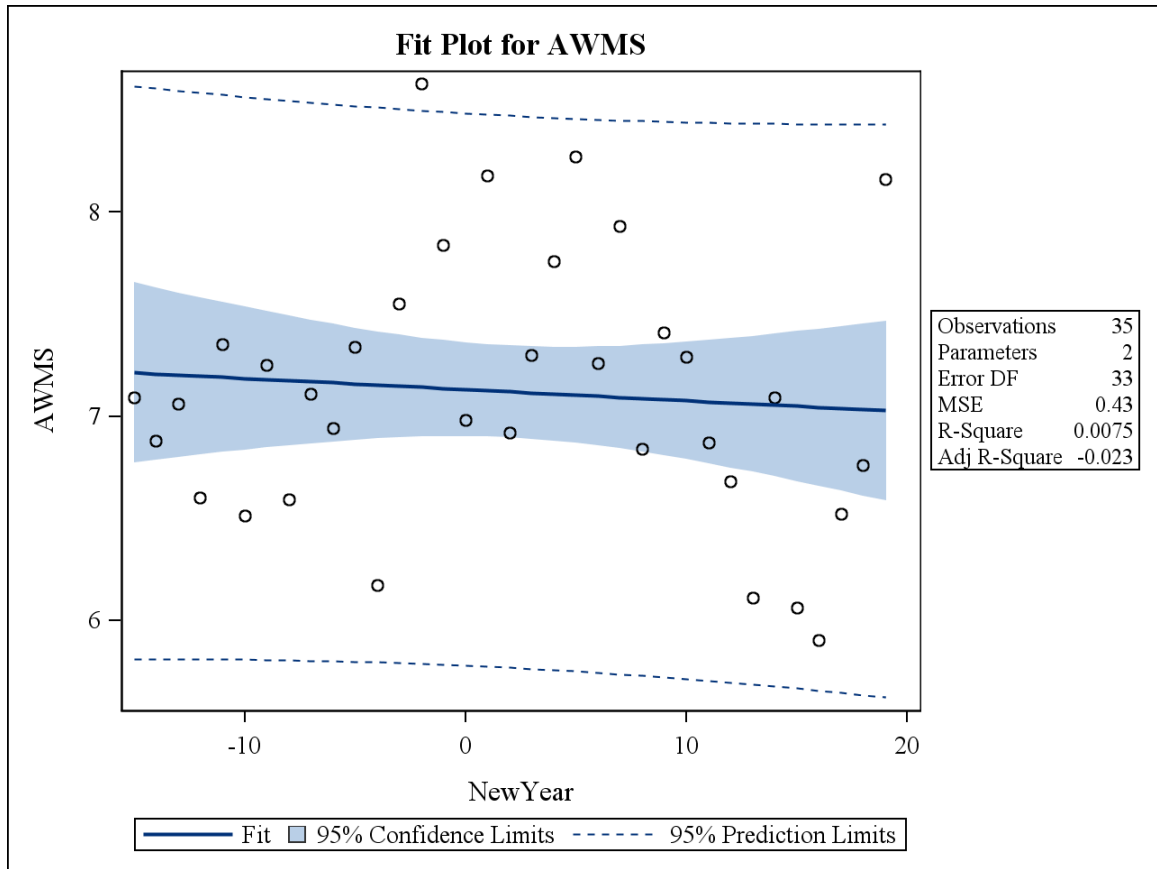
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.10695	0.10695	0.25	0.6213
Error	33	14.19025	0.43001		
Corrected Total	34	14.29720			

Root MSE	0.65575	R-Square	0.0075
Dependent Mean	7.12000	Adj R-Sq	-0.0226
Coeff Var	9.20997		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	7.13095	0.11299	63.11	<.0001
NewYear	1	-0.00547	0.01097	-0.50	0.6213

Fit Diagnostics for AWMS





APPENDIX C

REGRESSION OF AVERAGE WEIGHT FOR FEMALE GRILSE

Changes in Average Weight Over Time

Average Weight Female Grilse

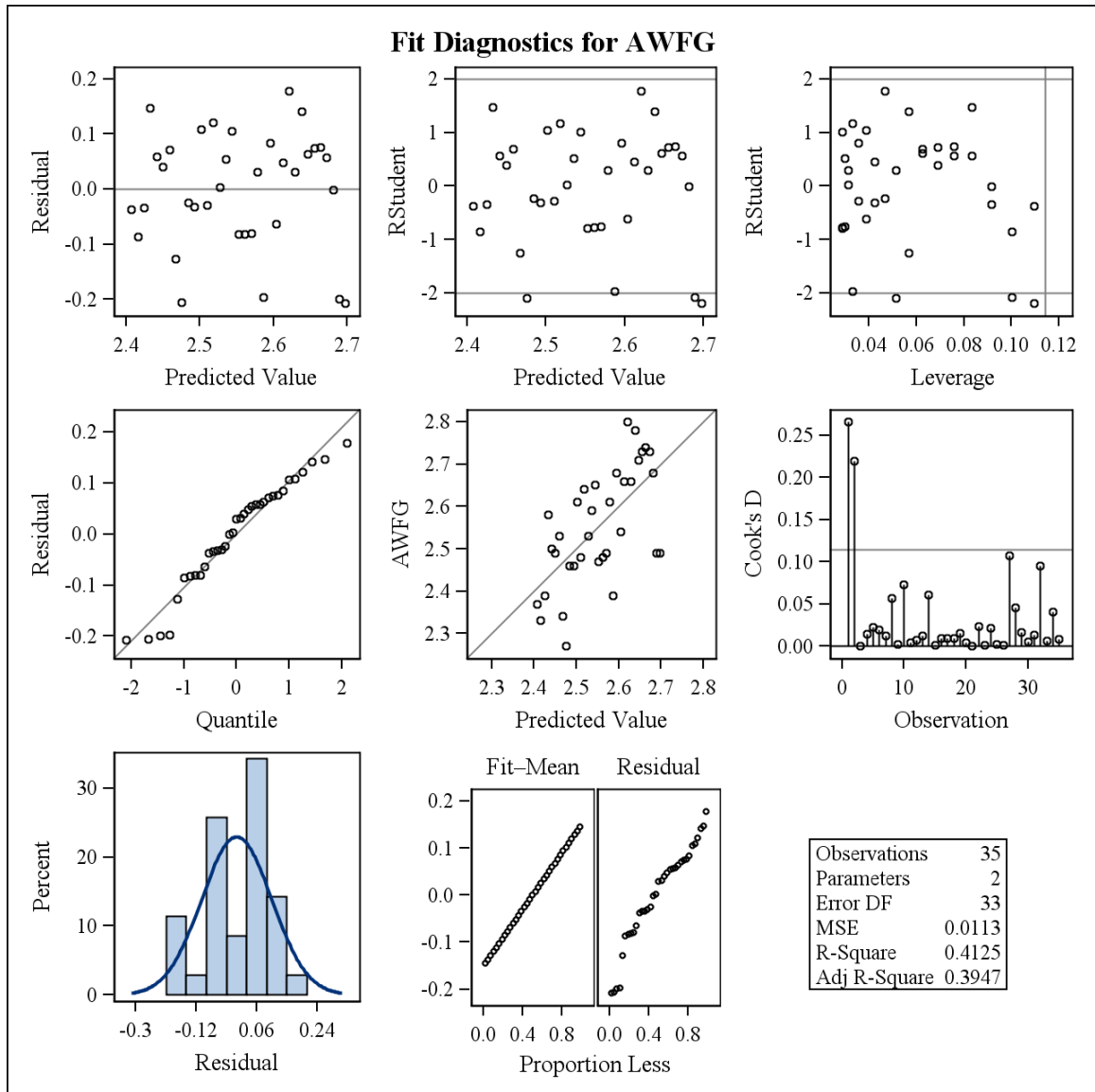
River: Haffjardara

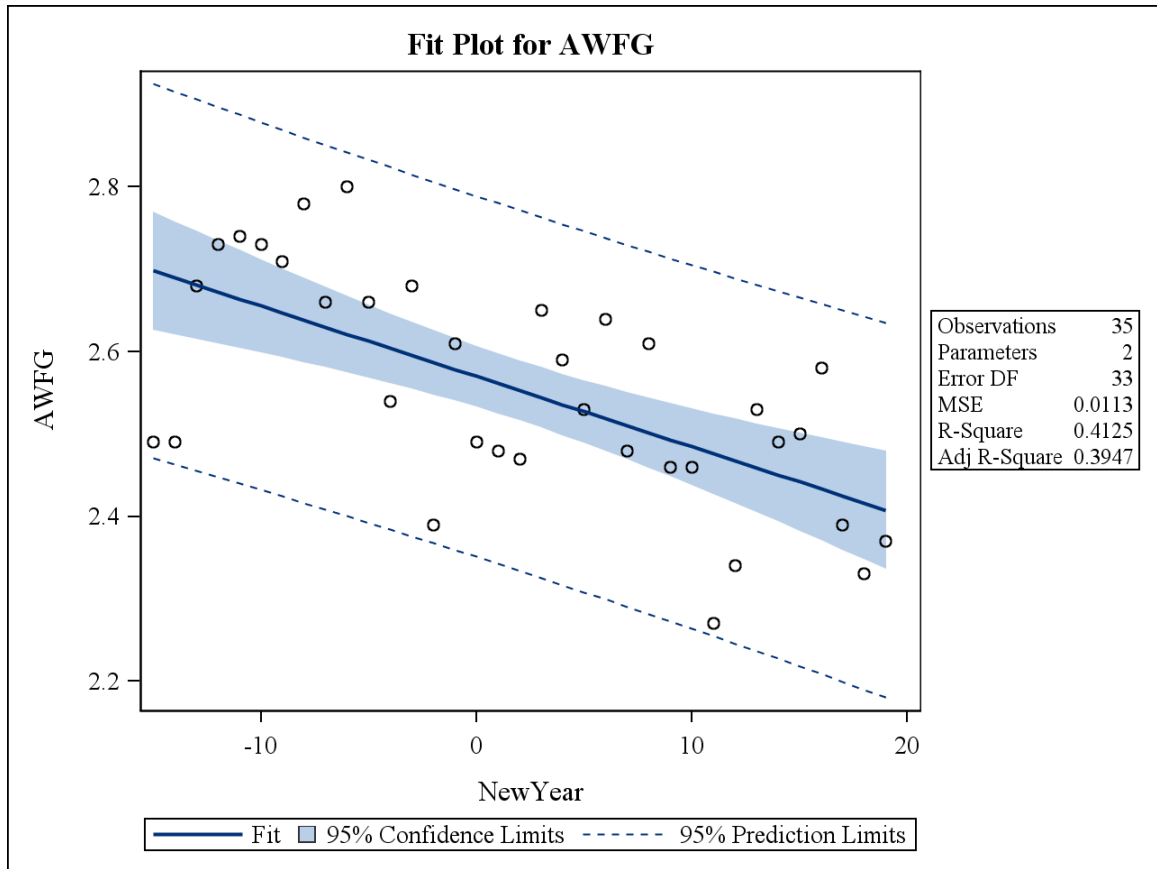
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Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.26075	0.26075	23.17	<.0001
Error	33	0.37137	0.01125		
Corrected Total	34	0.63211			

Root MSE	0.10608	R-Square	0.4125
Dependent Mean	2.55286	Adj R-Sq	0.3947
Coeff Var	4.15546		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.56995	0.01828	140.59	<.0001
NewYear	1	-0.00855	0.00178	-4.81	<.0001





River: Haukadalsa

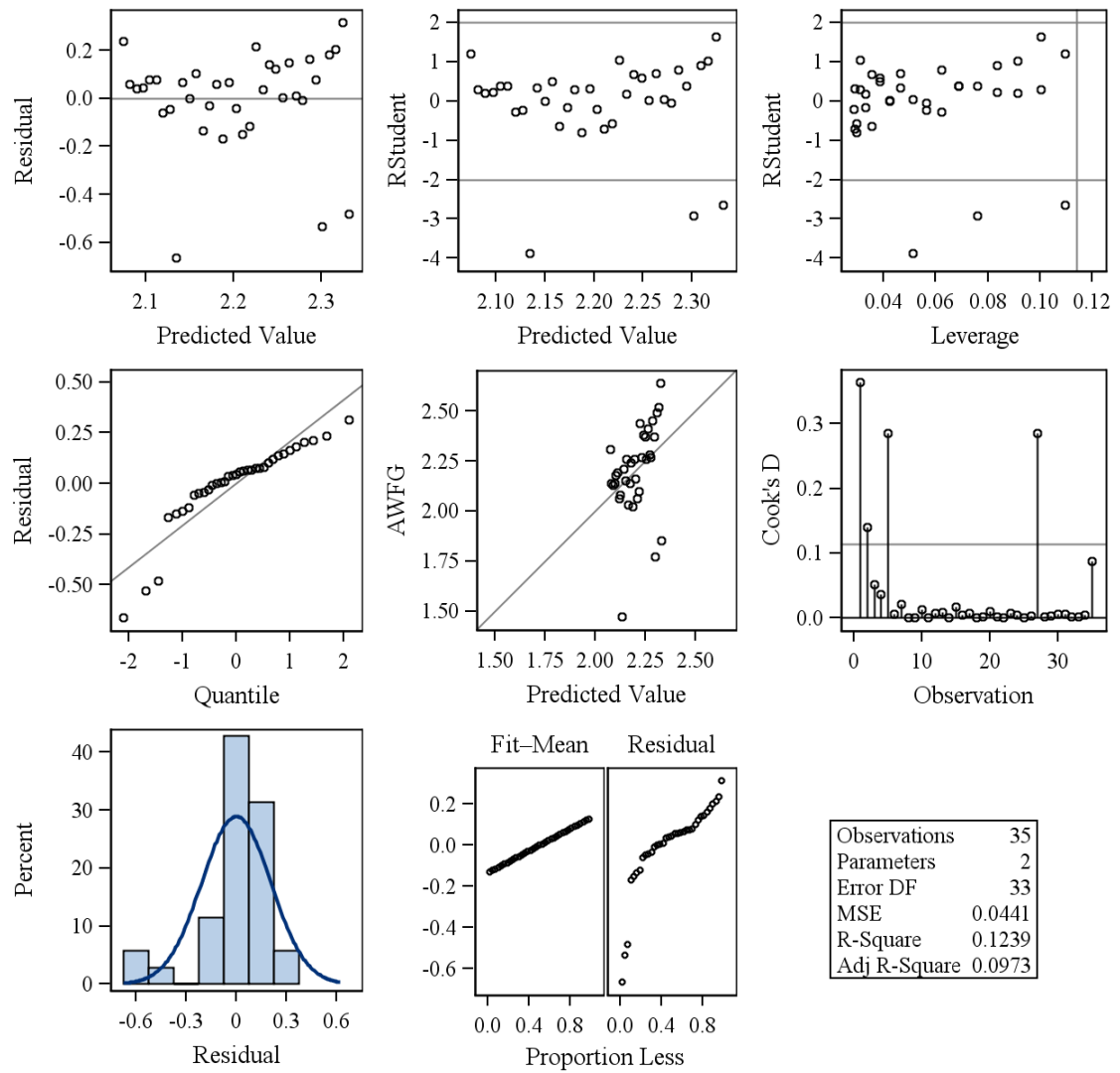
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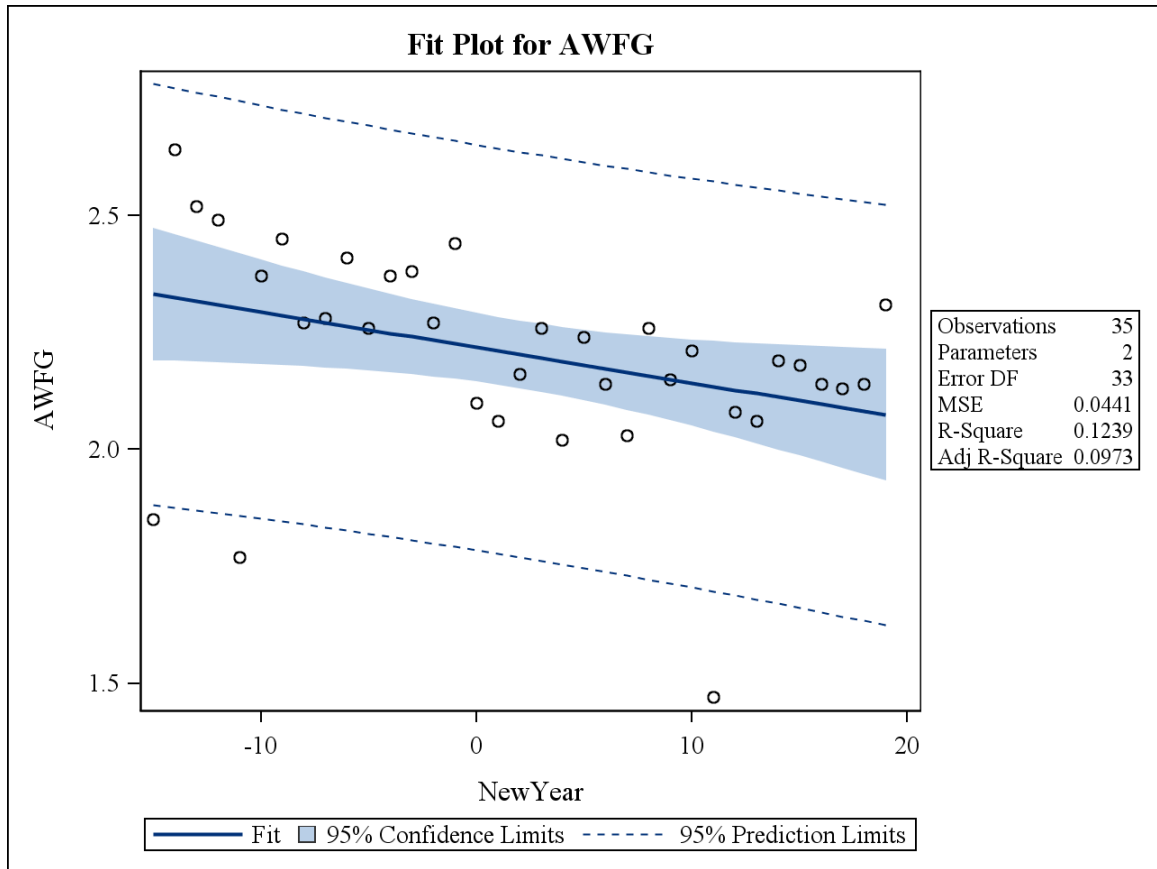
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.20572	0.20572	4.67	0.0381
Error	33	1.45480	0.04408		
Corrected Total	34	1.66051			

Root MSE	0.20996	R-Square	0.1239
Dependent Mean	2.20286	Adj R-Sq	0.0973
Coeff Var	9.53143		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.21804	0.03618	61.31	<.0001
NewYear	1	-0.00759	0.00351	-2.16	0.0381

Fit Diagnostics for AWFG





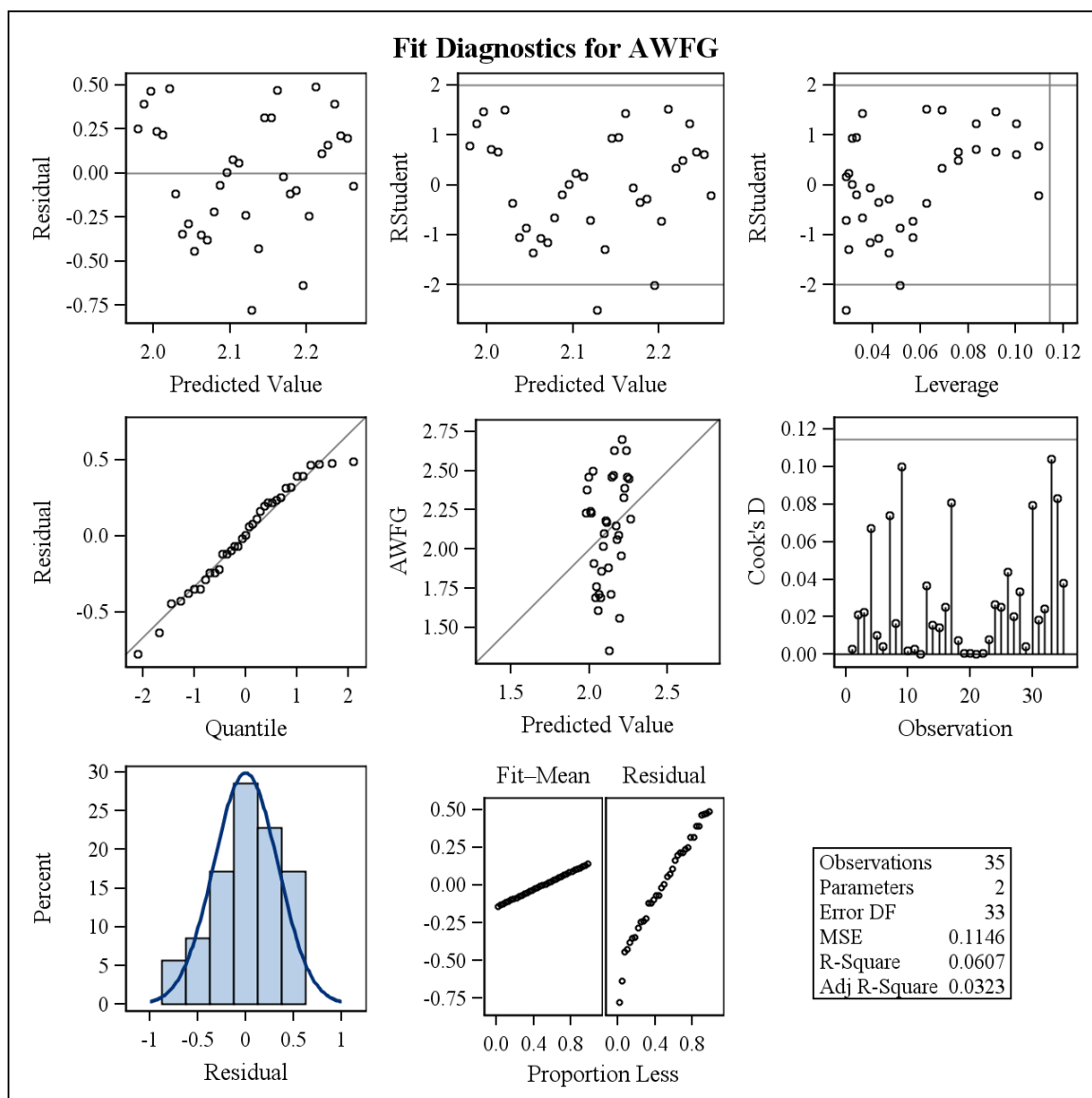
River: Hofsa

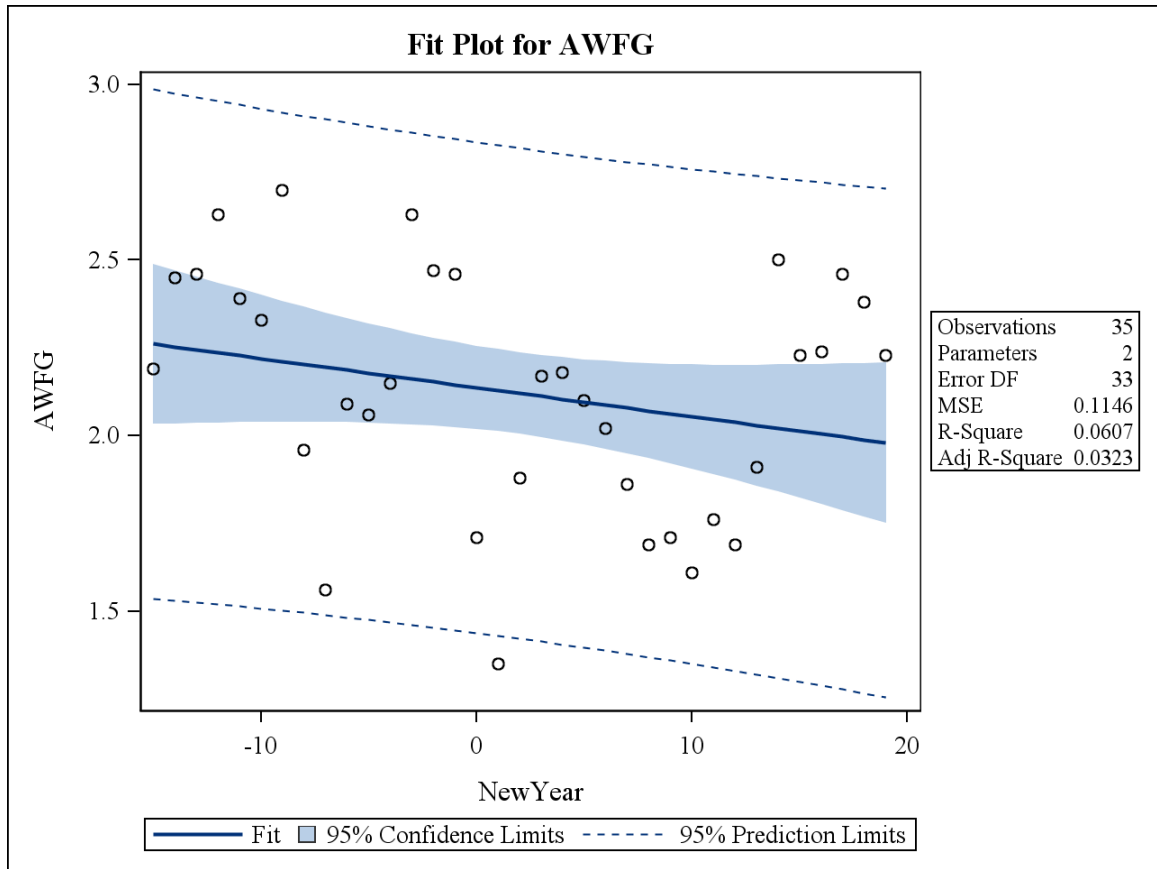
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Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.24459	0.24459	2.13	0.1535
Error	33	3.78170	0.11460		
Corrected Total	34	4.02630			

Root MSE	0.33852	R-Square	0.0607
Dependent Mean	2.12029	Adj R-Sq	0.0323
Coeff Var	15.96586		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.13684	0.05833	36.63	<.0001
NewYear	1	-0.00828	0.00567	-1.46	0.1535





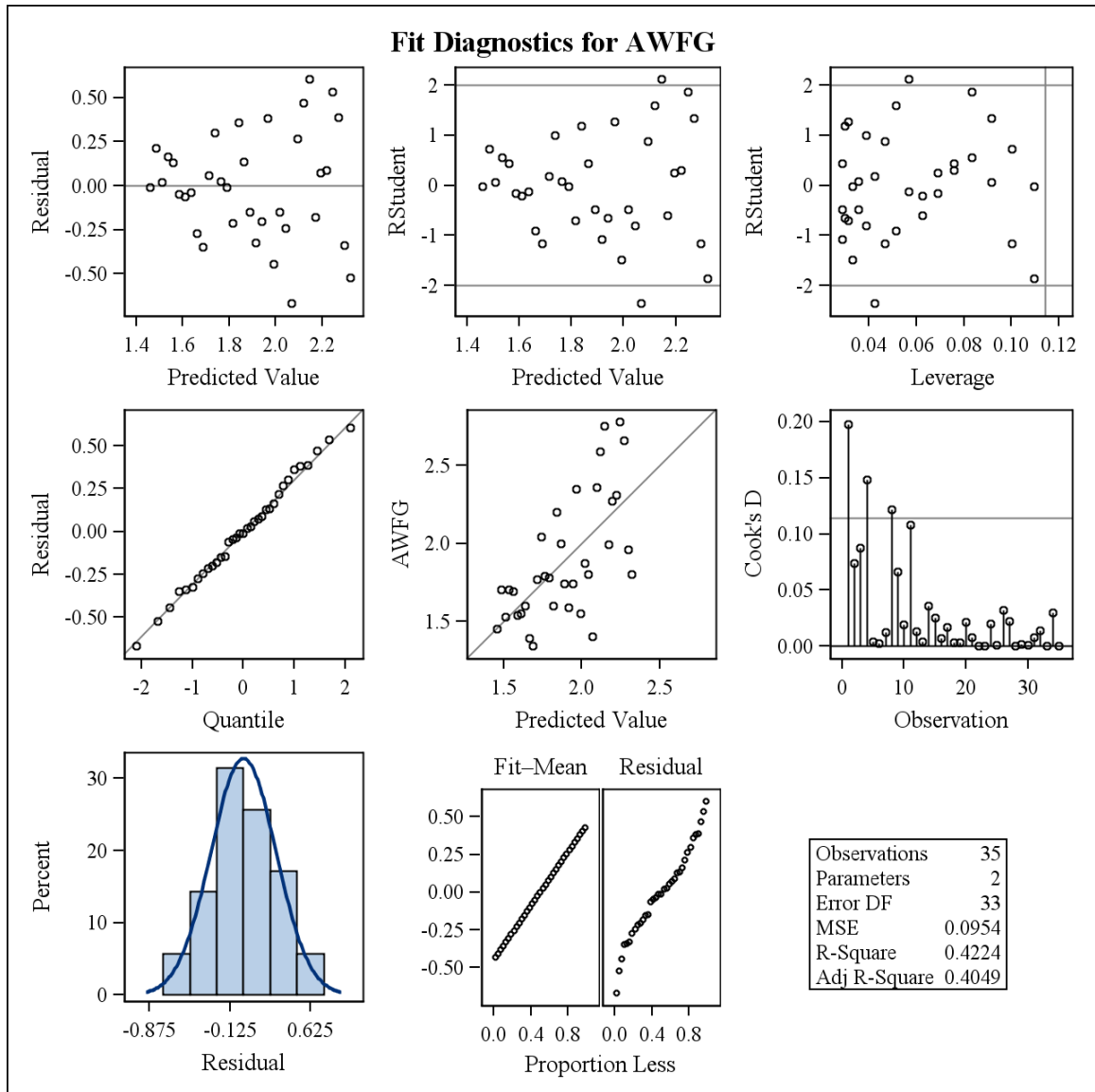
River: Laxa in Adaldal

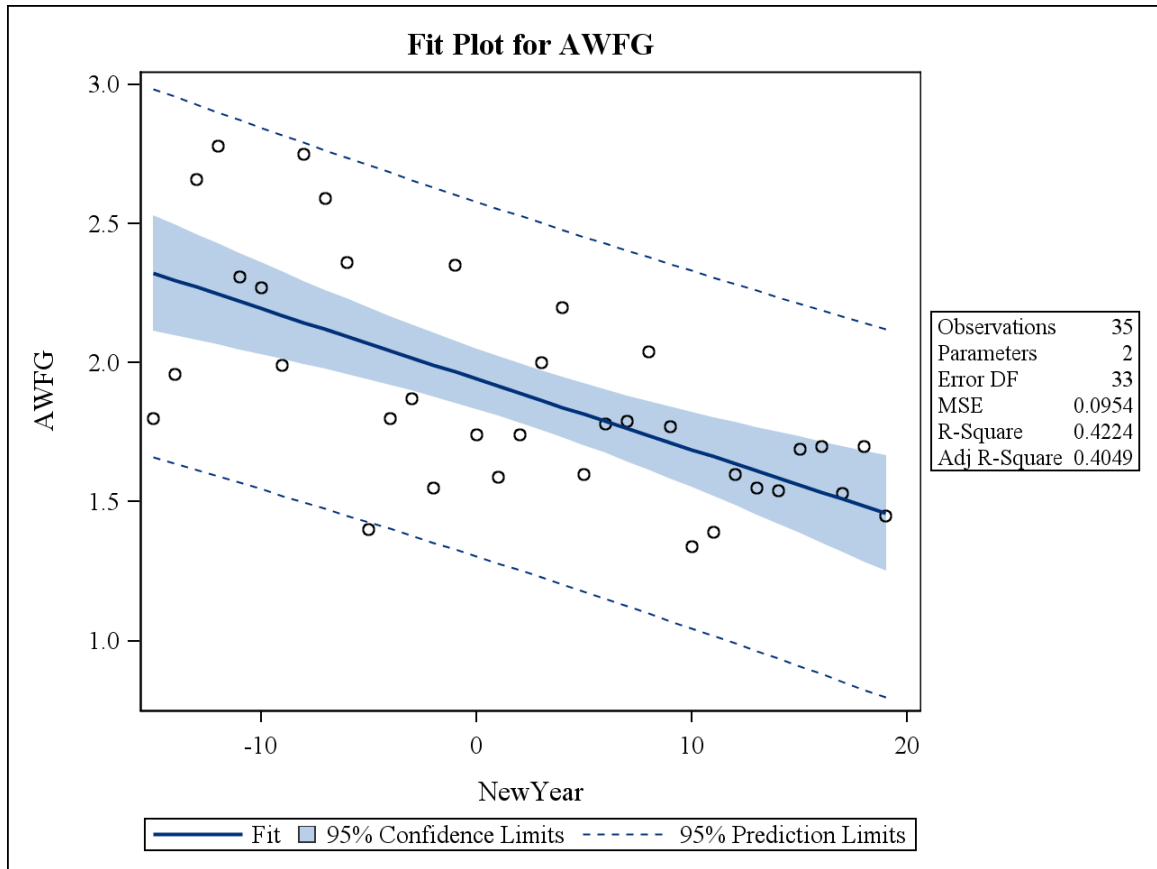
Number of Observations Read	35
Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	2.30281	2.30281	24.13	<.0001
Error	33	3.14866	0.09541		
Corrected Total	34	5.45147			

Root MSE	0.30889	R-Square	0.4224
Dependent Mean	1.89086	Adj R-Sq	0.4049
Coeff Var	16.33605		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	1.94165	0.05323	36.48	<.0001
NewYear	1	-0.02540	0.00517	-4.91	<.0001





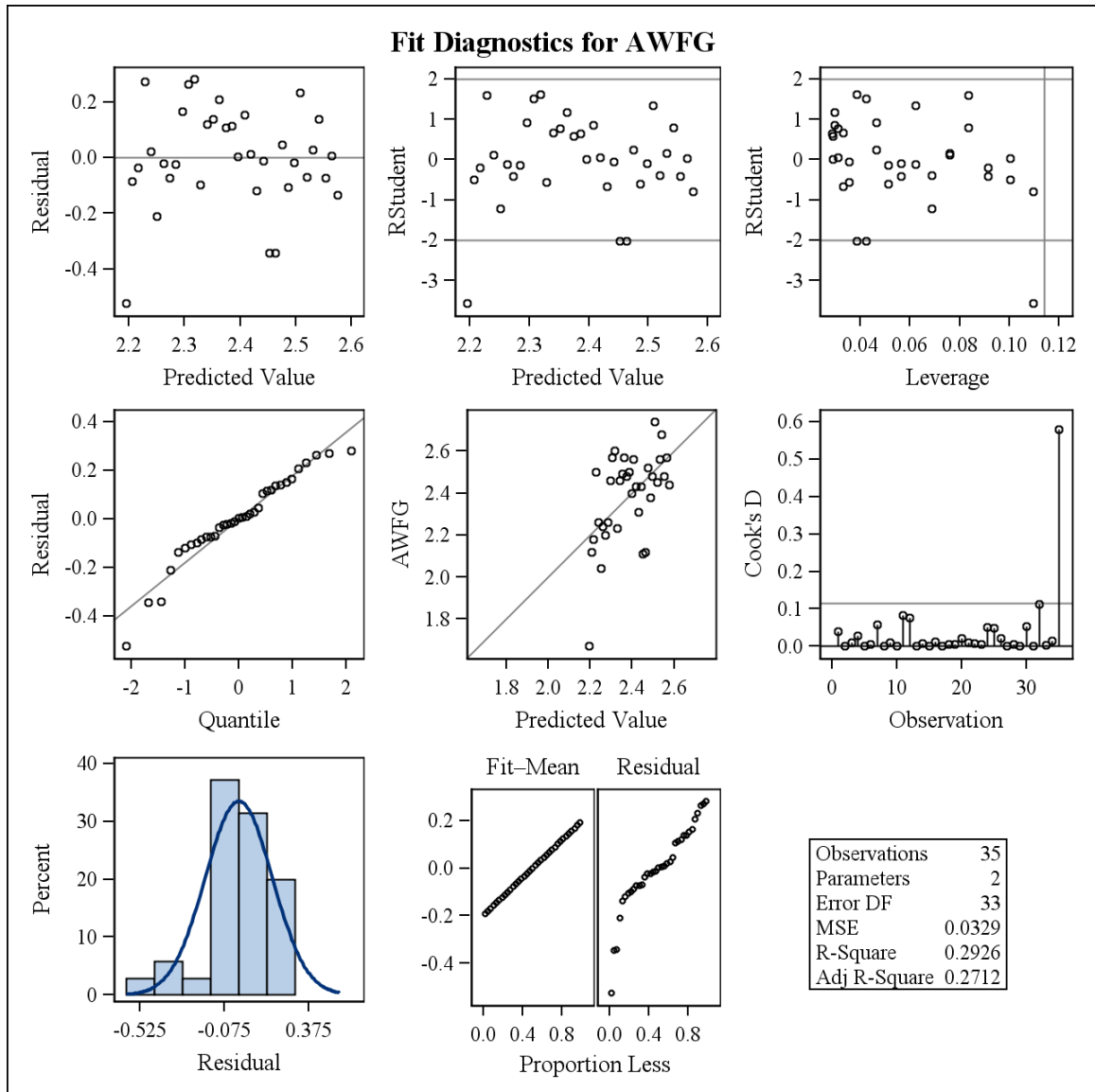
River: Midfjardara

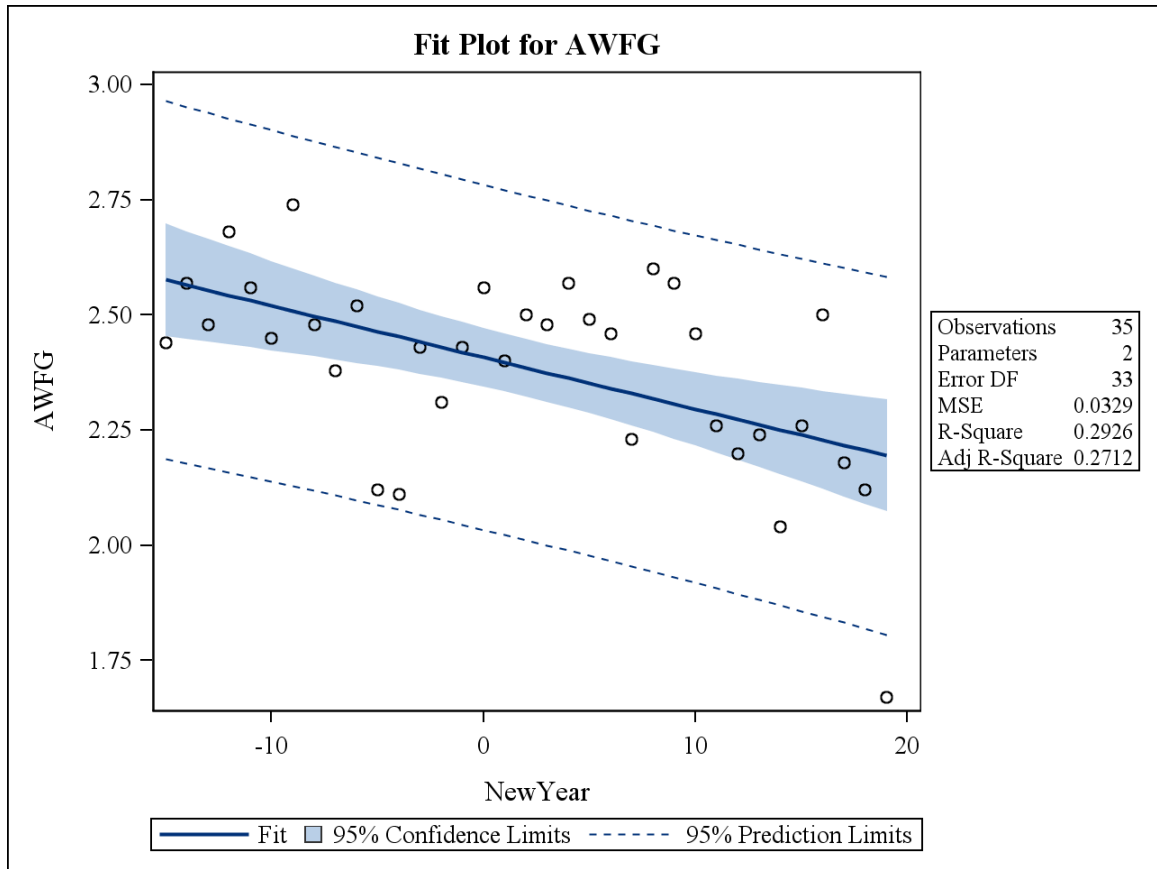
Number of Observations Read	35
Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.44863	0.44863	13.65	0.0008
Error	33	1.08464	0.03287		
Corrected Total	34	1.53327			

Root MSE	0.18130	R-Square	0.2926
Dependent Mean	2.38543	Adj R-Sq	0.2712
Coeff Var	7.60011		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.40785	0.03124	77.08	<.0001
NewYear	1	-0.01121	0.00303	-3.69	0.0008





River: Vatndalsa

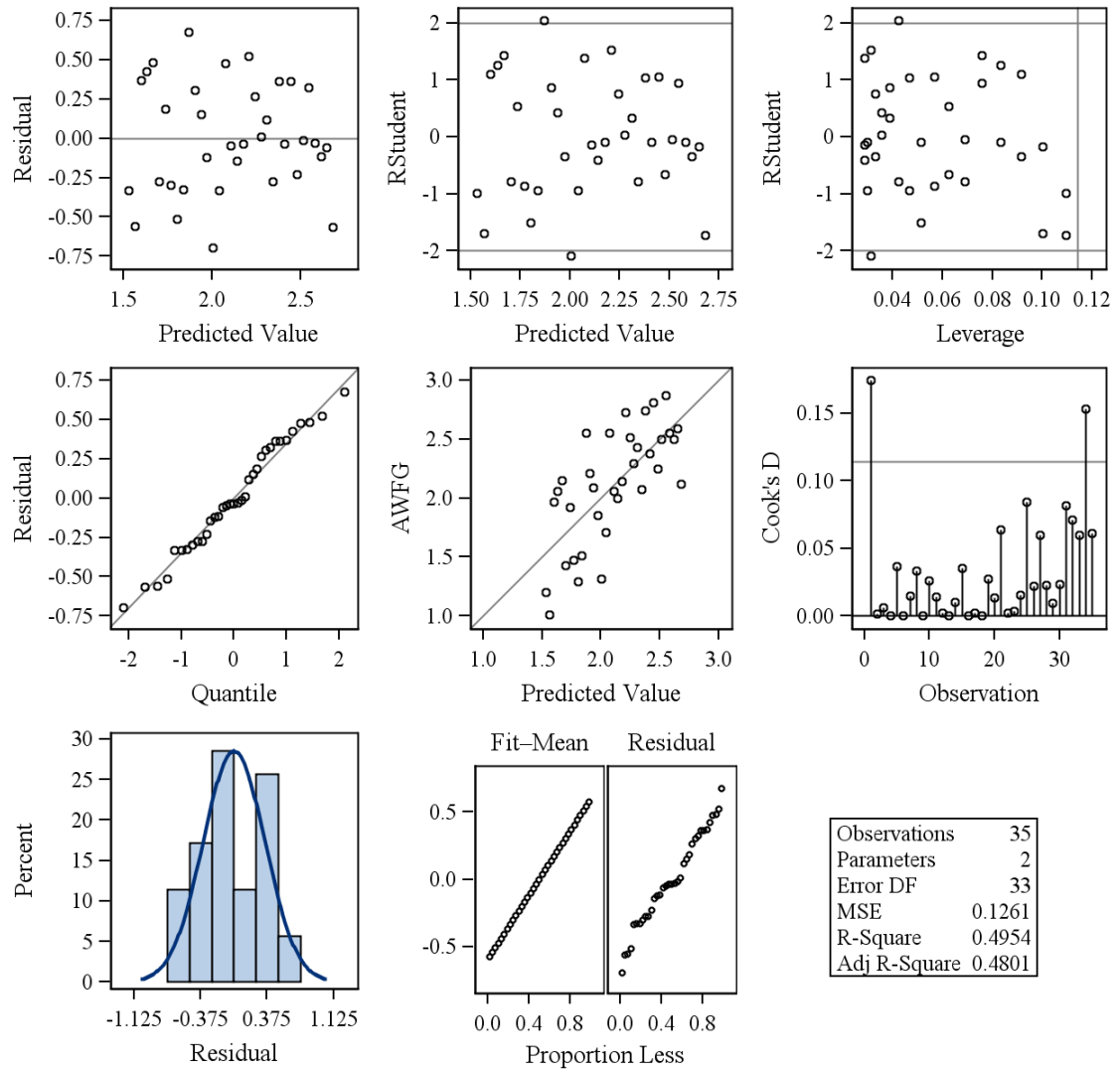
Number of Observations Read	35
Number of Observations Used	35

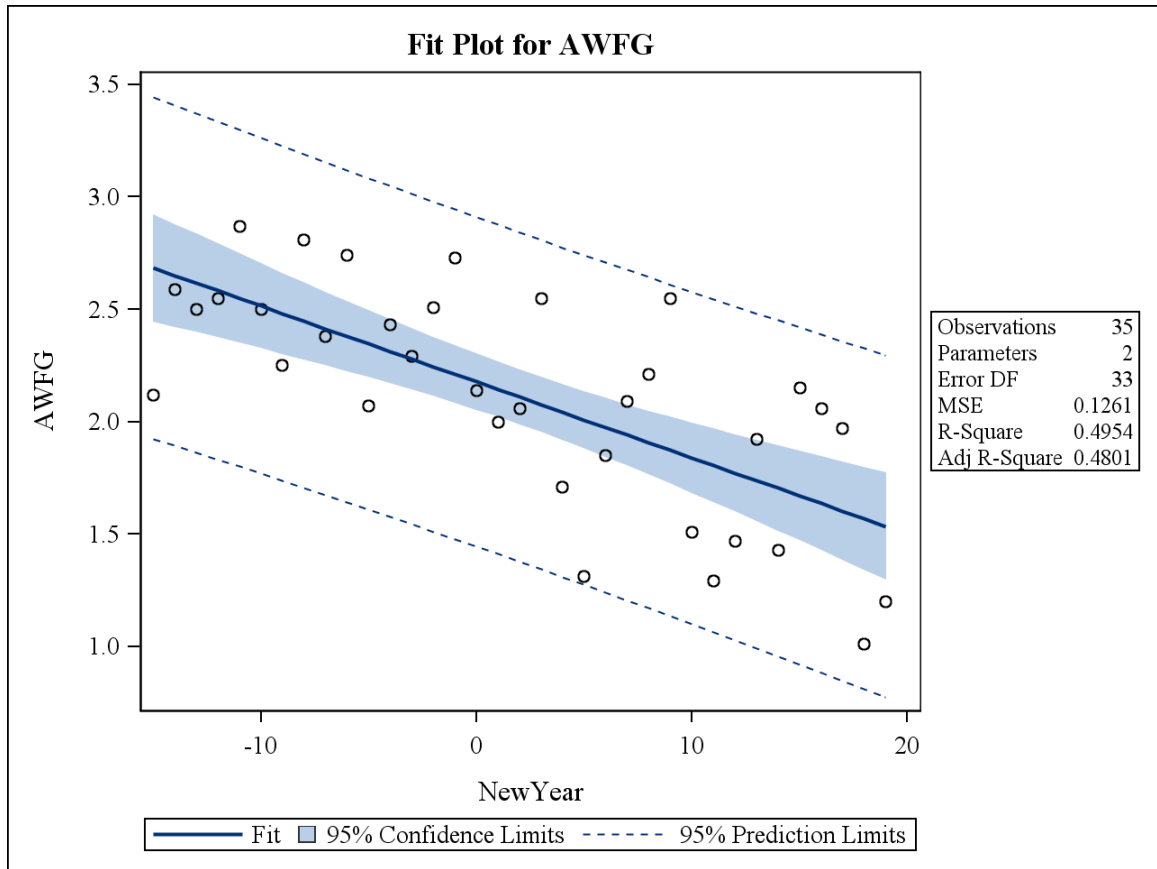
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	4.08622	4.08622	32.39	<.0001
Error	33	4.16285	0.12615		
Corrected Total	34	8.24907			

Root MSE	0.35517	R-Square	0.4954
Dependent Mean	2.10914	Adj R-Sq	0.4801
Coeff Var	16.83963		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.17681	0.06120	35.57	<.0001
NewYear	1	-0.03383	0.00594	-5.69	<.0001

Fit Diagnostics for AWFG





APPENDIX D

REGRESSION OF AVERAGE WEIGHT FOR MALE GRILSE

Changes in Average Weight Over Time

Average Weight Male Grilse

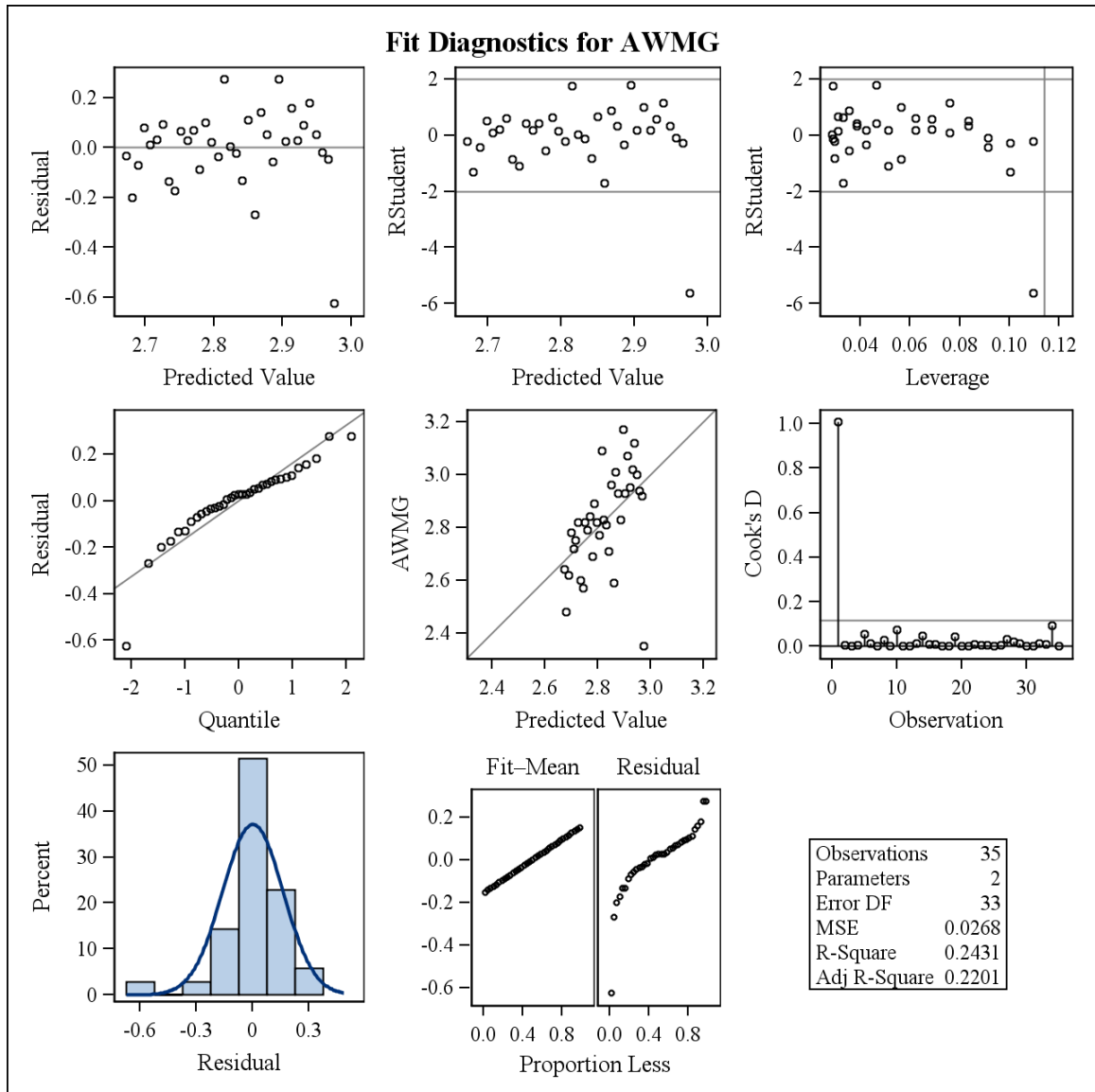
River: Haffjardara

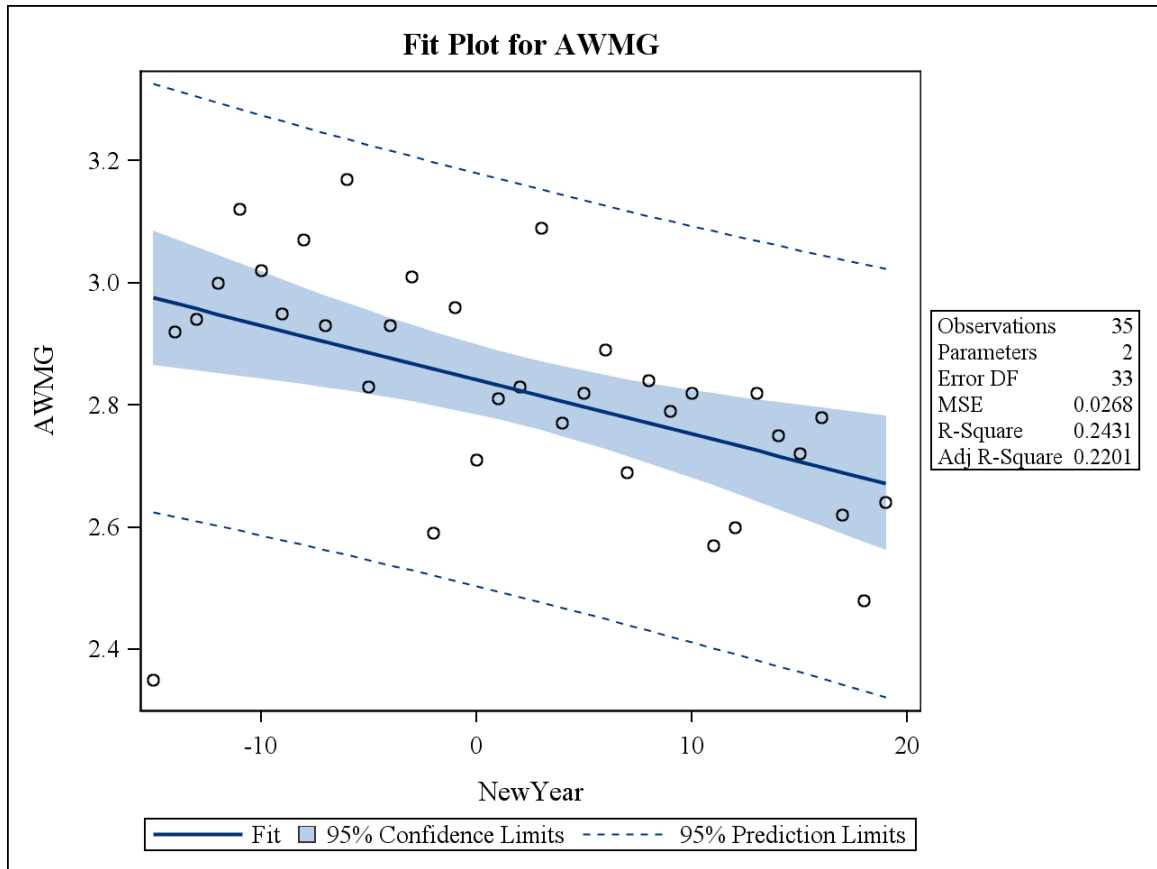
Number of Observations Read	35
Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.28397	0.28397	10.60	0.0026
Error	33	0.88424	0.02680		
Corrected Total	34	1.16822			

Root MSE	0.16369	R-Square	0.2431
Dependent Mean	2.82371	Adj R-Sq	0.2201
Coeff Var	5.79707		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.84155	0.02821	100.74	<.0001
NewYear	1	-0.00892	0.00274	-3.26	0.0026





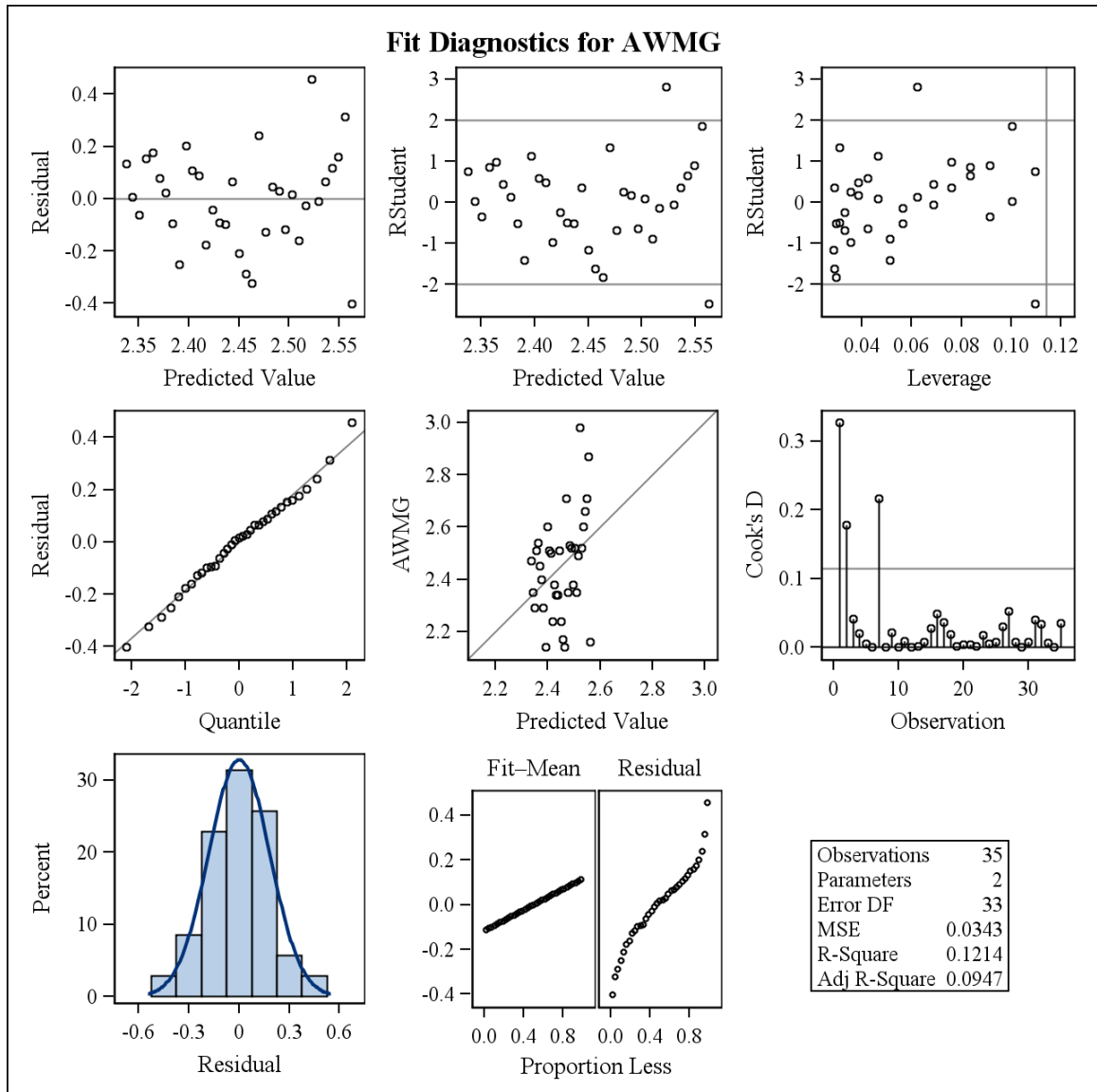
River: Haukadalsa

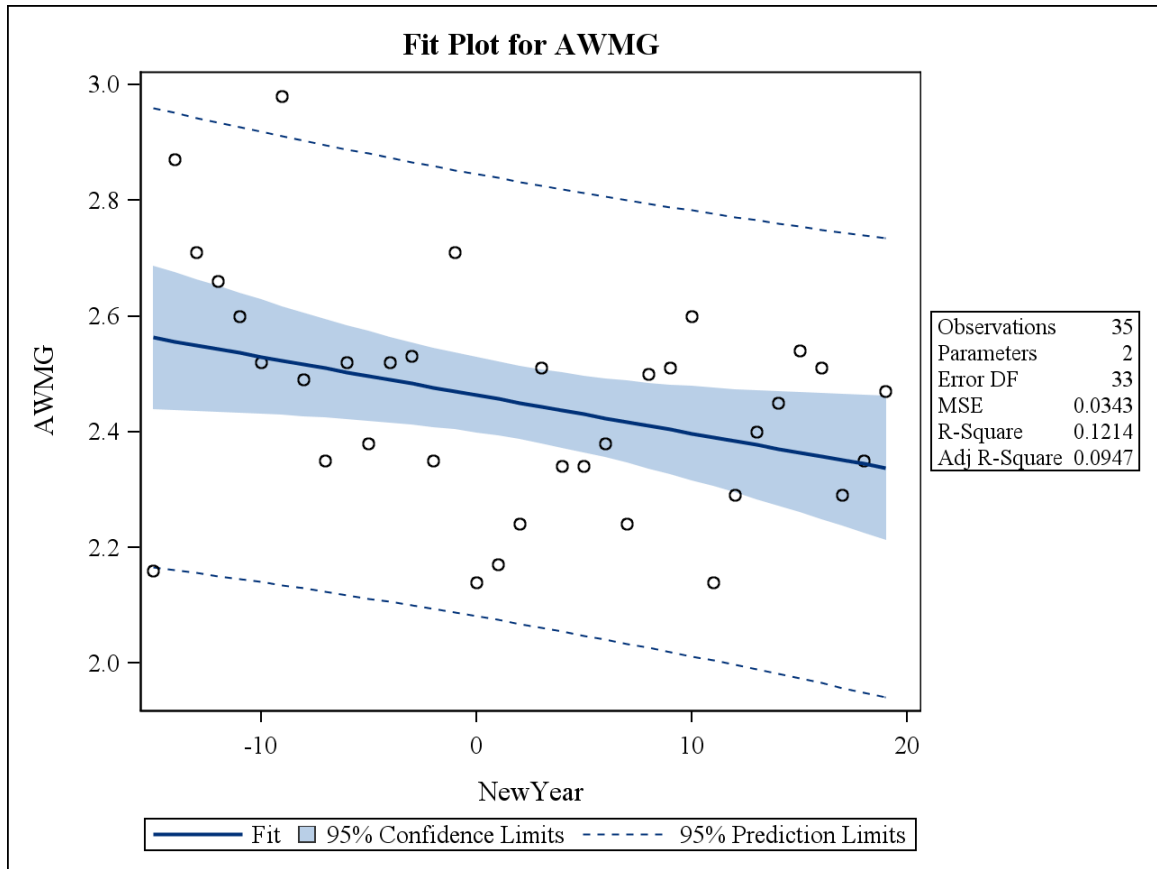
Number of Observations Read	35
Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.15614	0.15614	4.56	0.0403
Error	33	1.13055	0.03426		
Corrected Total	34	1.28670			

Root MSE	0.18509	R-Square	0.1214
Dependent Mean	2.45029	Adj R-Sq	0.0947
Coeff Var	7.55391		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.46351	0.03189	77.24	<.0001
NewYear	1	-0.00661	0.00310	-2.13	0.0403





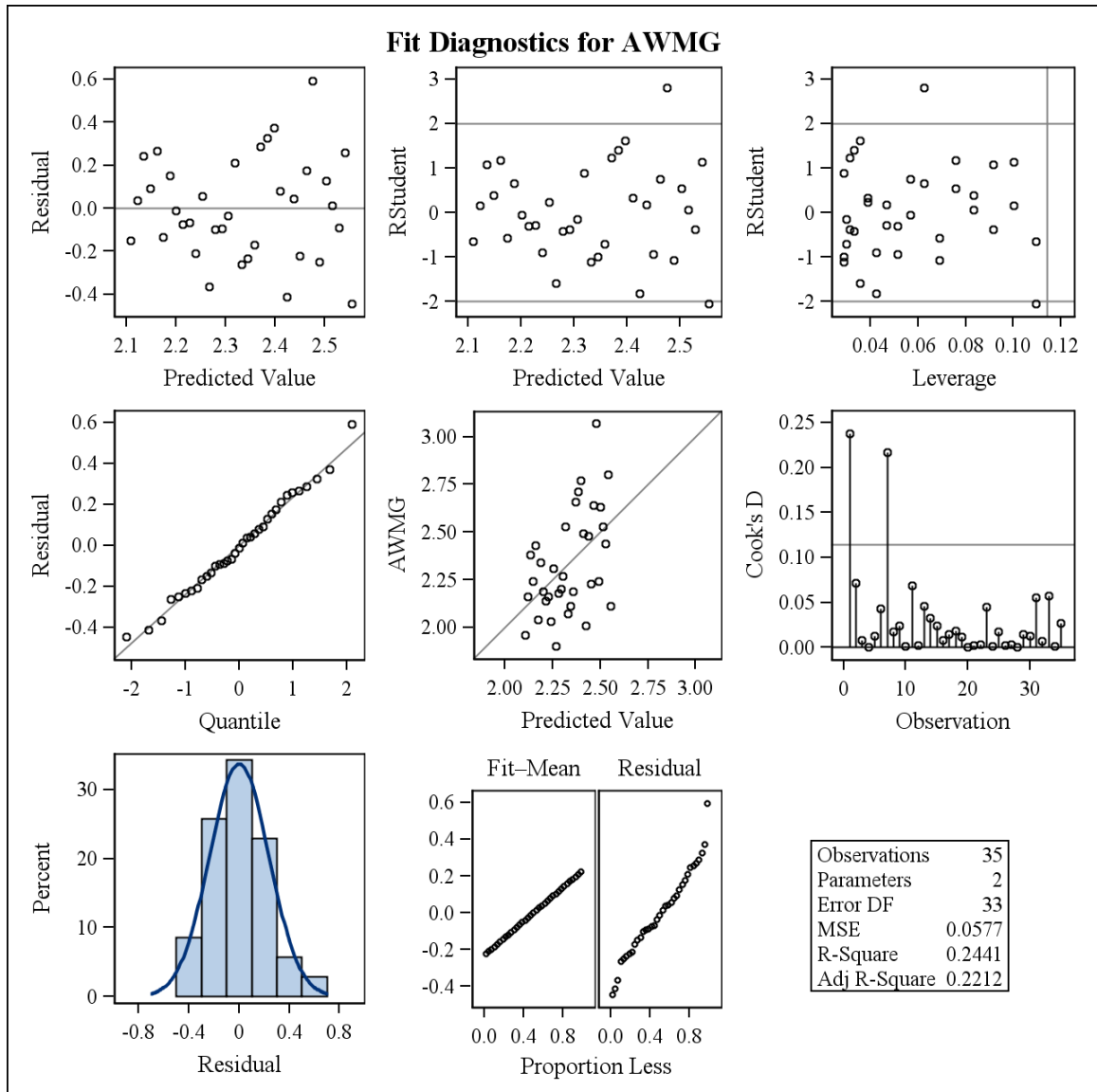
River: Hofsa

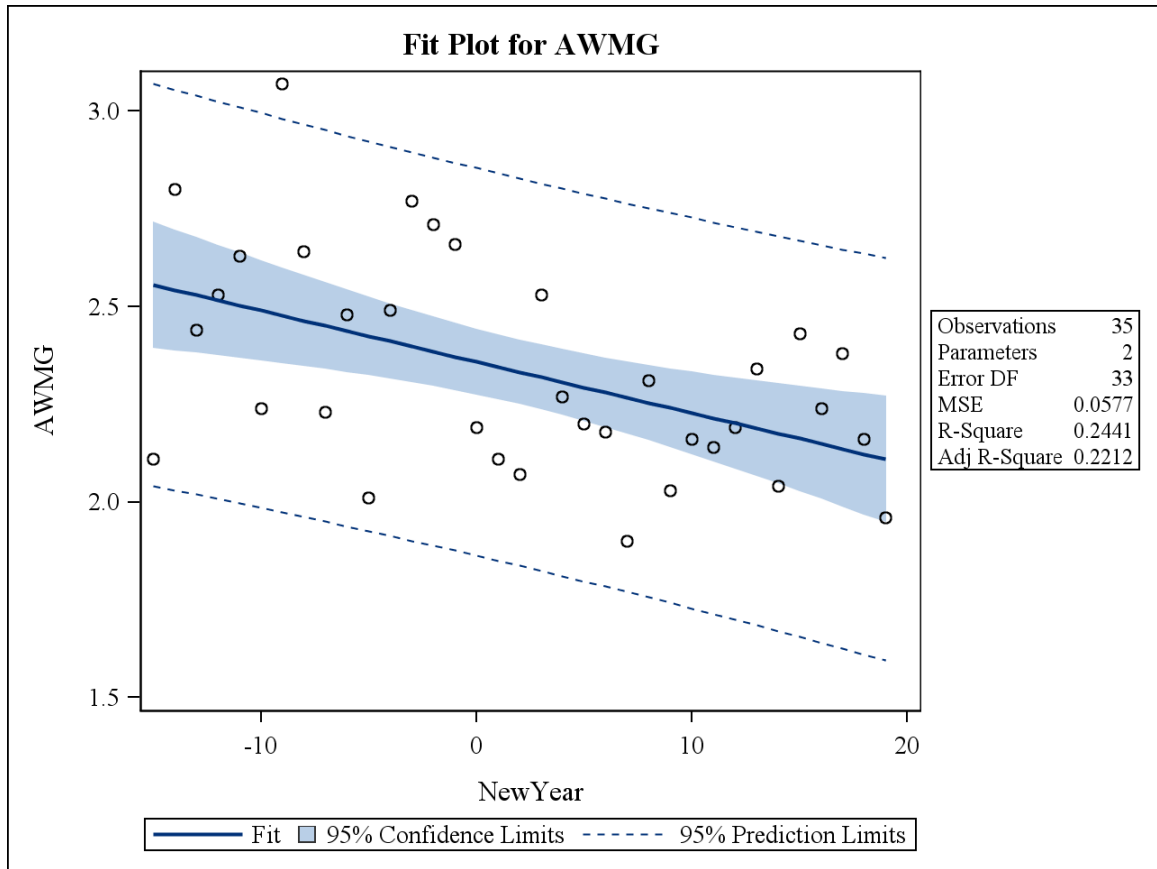
Number of Observations Read	35
Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.61509	0.61509	10.66	0.0026
Error	33	1.90438	0.05771		
Corrected Total	34	2.51947			

Root MSE	0.24023	R-Square	0.2441
Dependent Mean	2.33257	Adj R-Sq	0.2212
Coeff Var	10.29876		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.35882	0.04139	56.98	<.0001
NewYear	1	-0.01313	0.00402	-3.26	0.0026





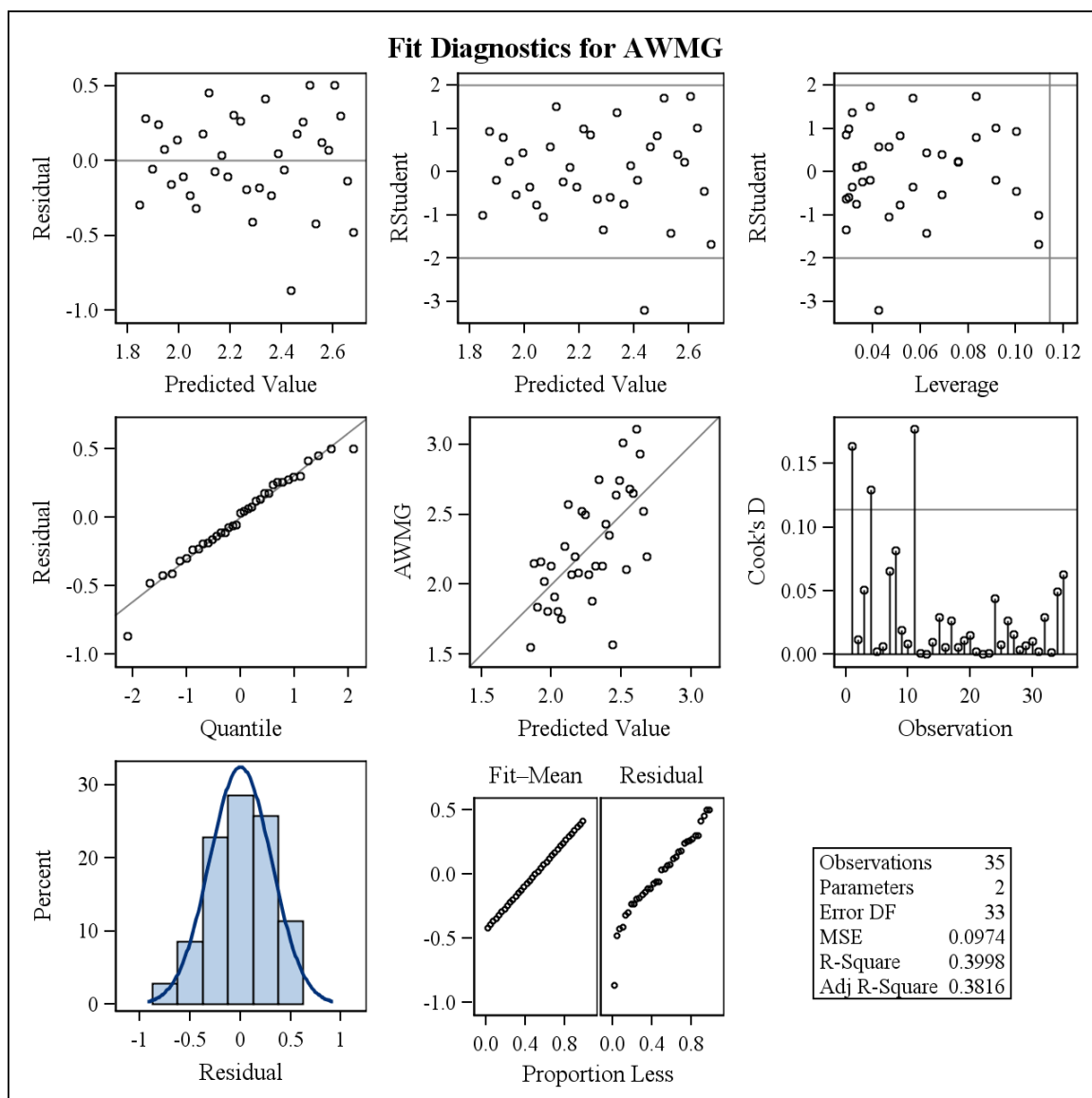
River: Laxa in Adaldal

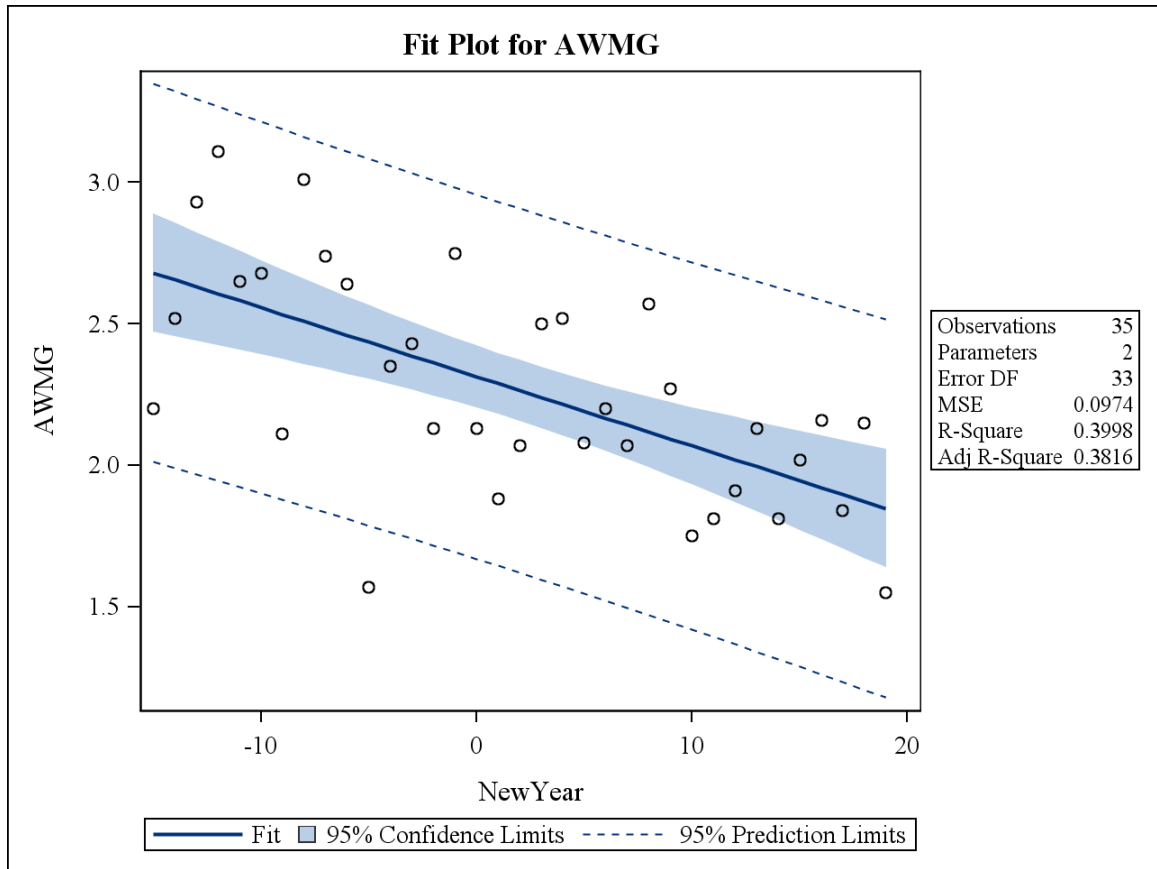
Number of Observations Read	35
Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	2.14118	2.14118	21.98	<.0001
Error	33	3.21486	0.09742		
Corrected Total	34	5.35604			

Root MSE	0.31212	R-Square	0.3998
Dependent Mean	2.26400	Adj R-Sq	0.3816
Coeff Var	13.78630		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.31298	0.05378	43.01	<.0001
NewYear	1	-0.02449	0.00522	-4.69	<.0001





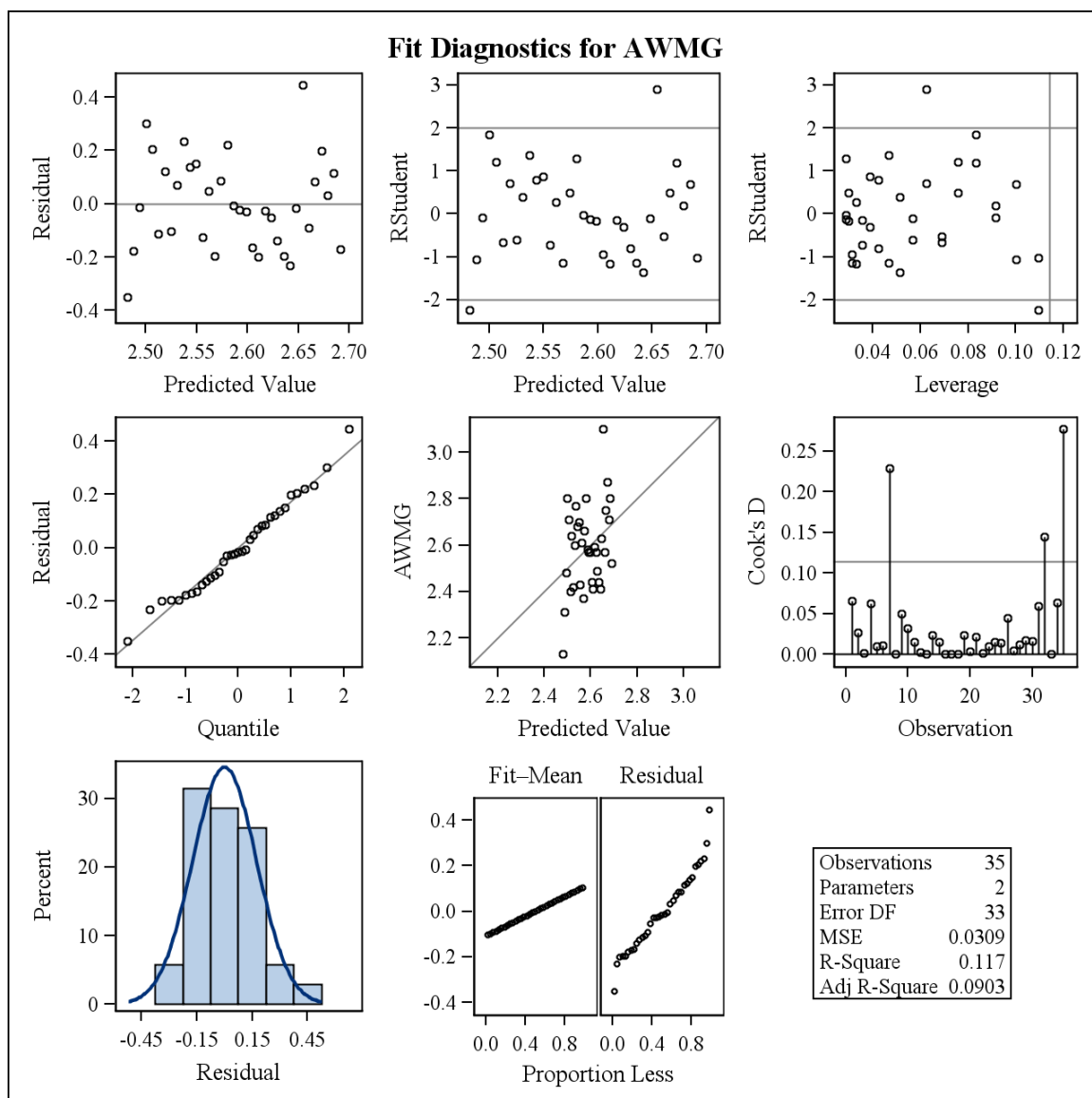
River: Midfjardara

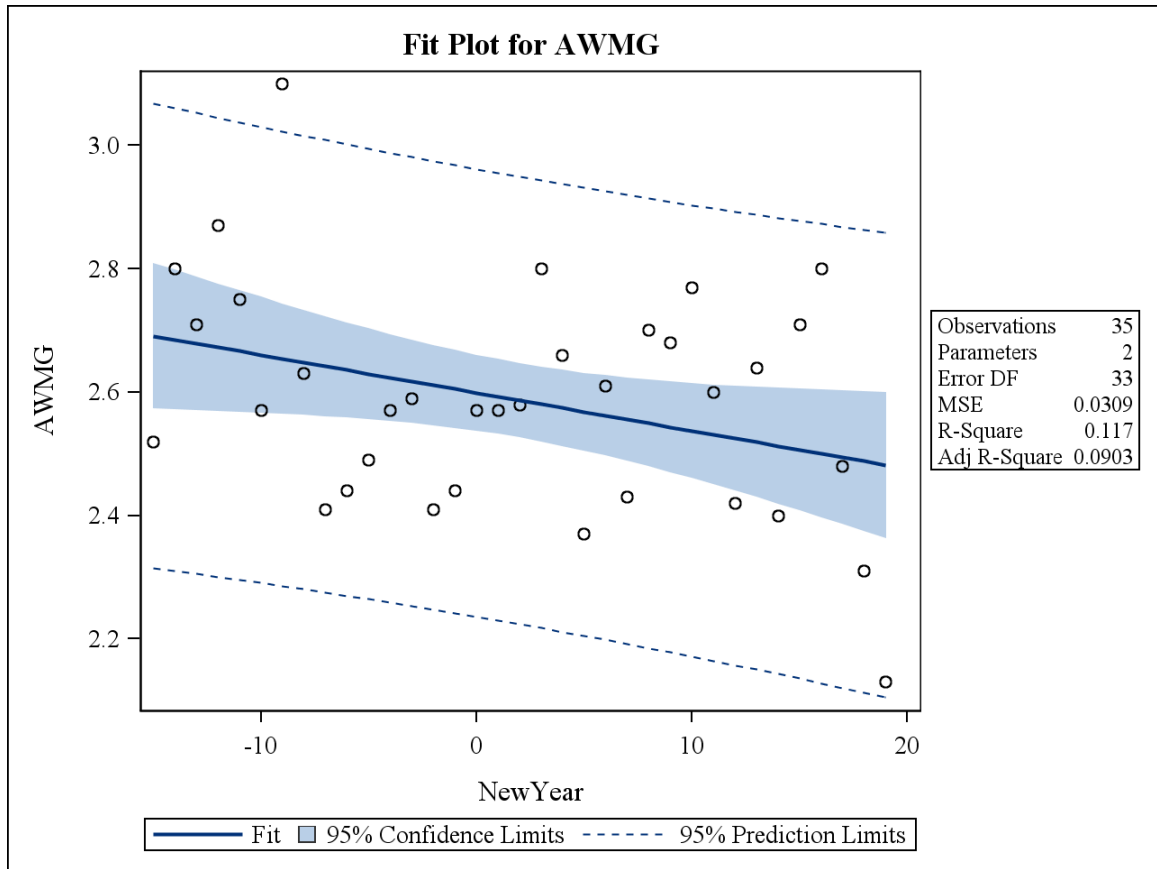
Number of Observations Read	35
Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.13508	0.13508	4.37	0.0443
Error	33	1.01931	0.03089		
Corrected Total	34	1.15439			

Root MSE	0.17575	R-Square	0.1170
Dependent Mean	2.58657	Adj R-Sq	0.0903
Coeff Var	6.79471		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.59887	0.03028	85.82	<.0001
NewYear	1	-0.00615	0.00294	-2.09	0.0443





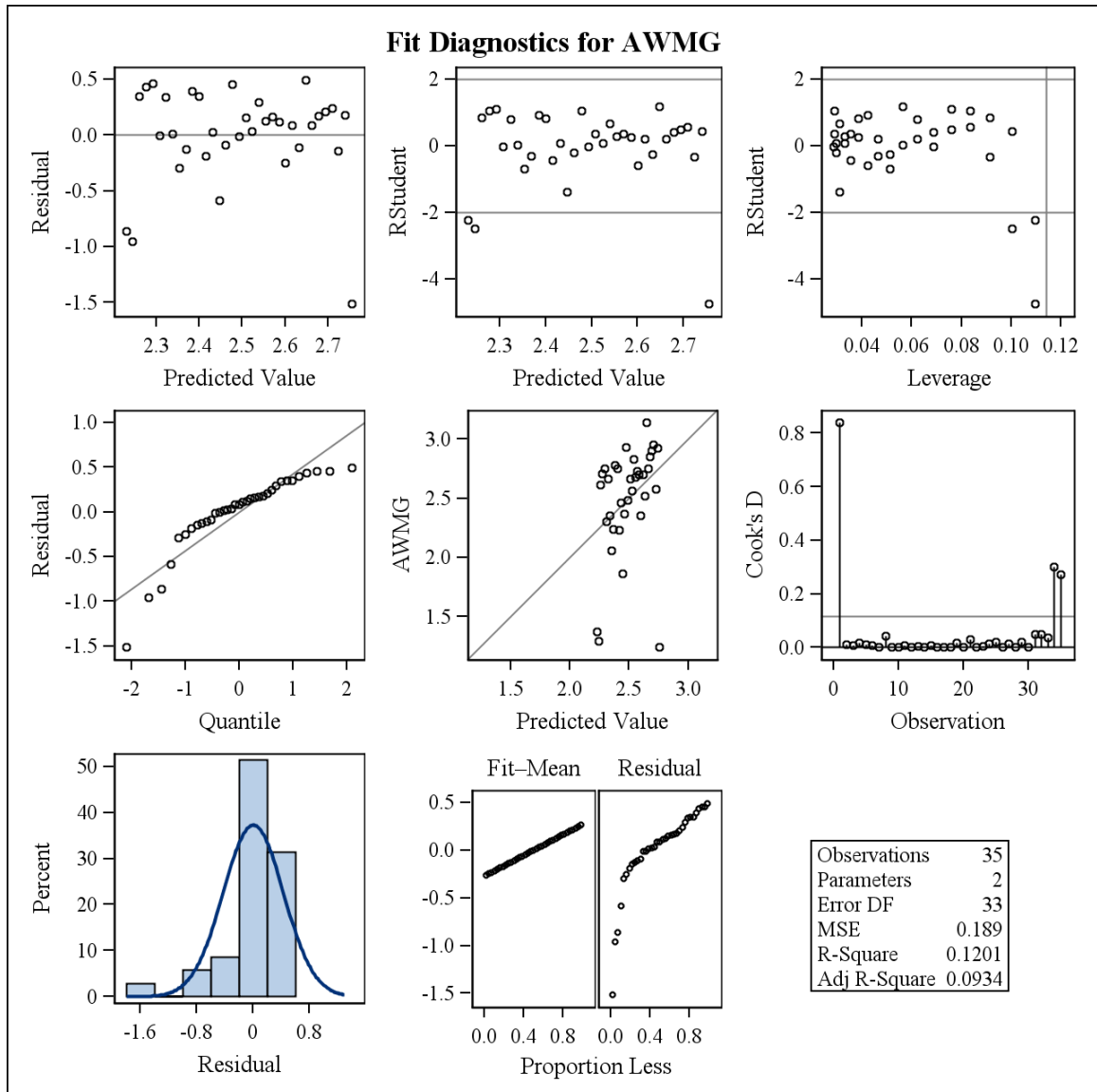
River: Vatndalsa

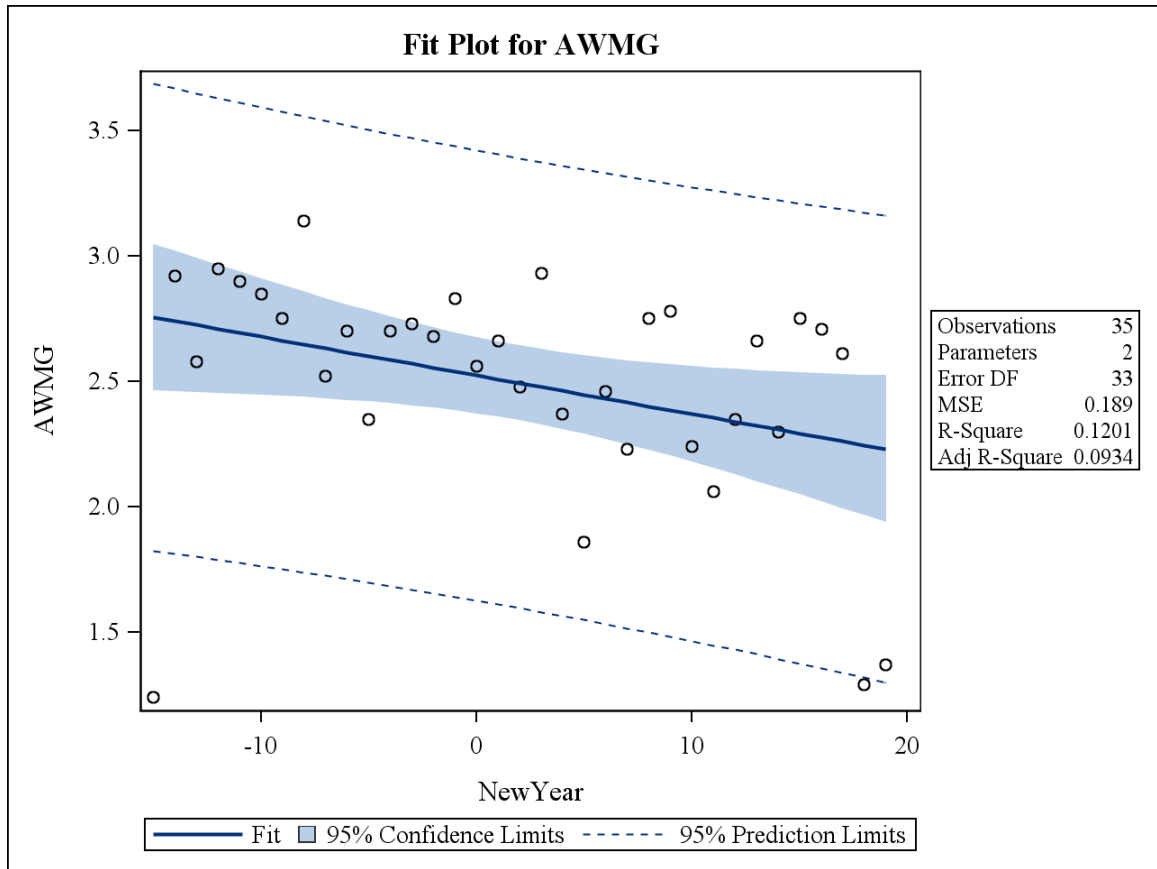
Number of Observations Read	35
Number of Observations Used	35

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.85135	0.85135	4.50	0.0414
Error	33	6.23701	0.18900		
Corrected Total	34	7.08835			

Root MSE	0.43474	R-Square	0.1201
Dependent Mean	2.49314	Adj R-Sq	0.0934
Coeff Var	17.43749		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > t
Intercept	1	2.52403	0.07491	33.69	<.0001
NewYear	1	-0.01544	0.00728	-2.12	0.0414





APPENDIX E

CHANGES IN AVERAGE WEIGHT OVER TIME FOR ALL RIVERS

The General Linear Model Procedure

Number of Observations Read	35
Number of Observations Used	35

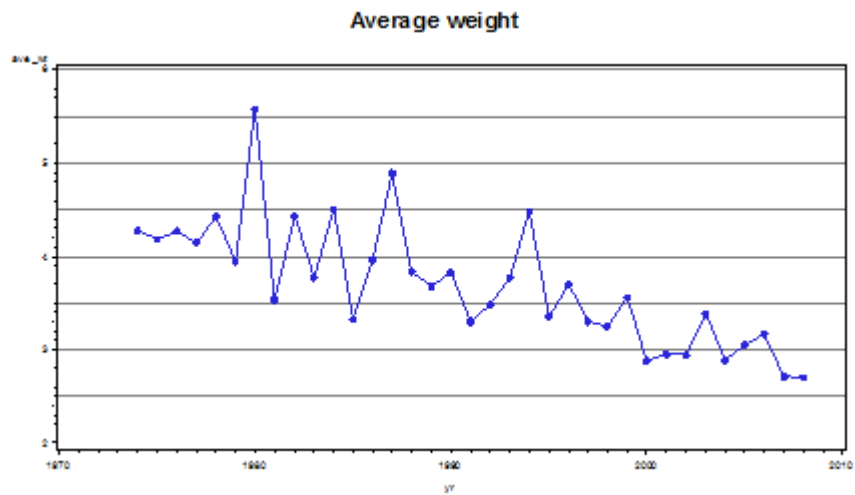
Dependent Variable: Average Weight

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	8.458	8.458	45.41	<.0001
Error	33	6.146	0.186		
Corrected Total	34	14.604			

R-Square	Coeff Var	Root MSE	ave_wt Mean
0.579138	11.66666	0.431574	3.699207

Source	DF	Type III SS	Mean Square	F Value	Pr > F
t	1	8.458	8.458	45.41	<.0001

Parameter	Estimate	Standard Error	t Value	Pr > t	95% Confidence Limits	
Intercept	4.575	0.149	30.69	<.0001	4.272	4.879
t	-0.049	0.007	-6.74	<.0001	-0.063	-0.034

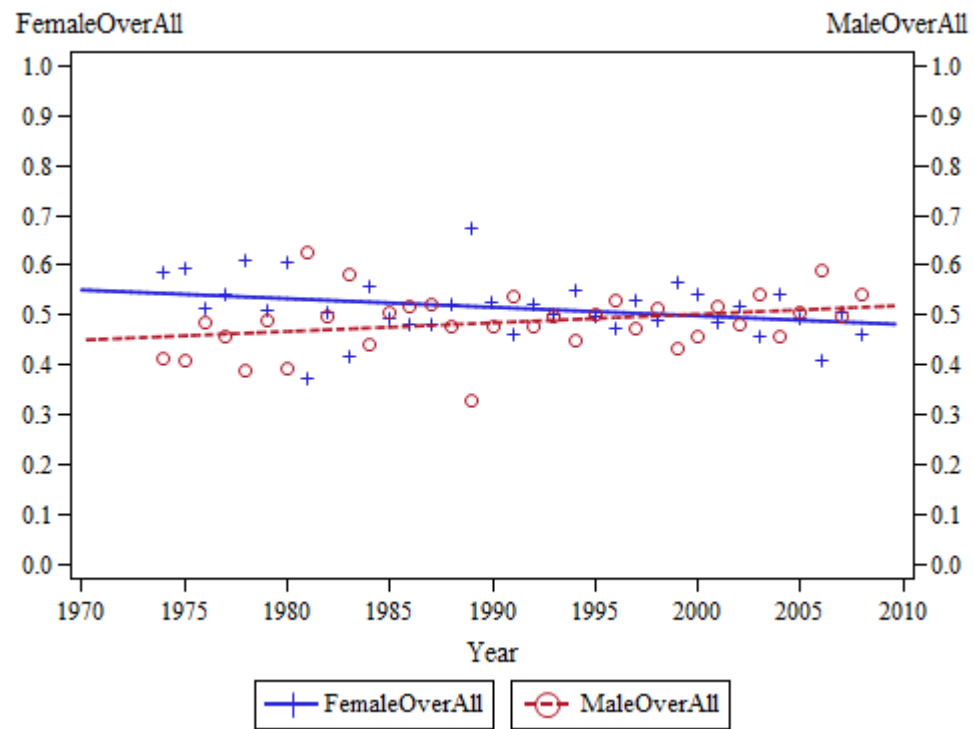


Changes in Overall Average Weight Over Time

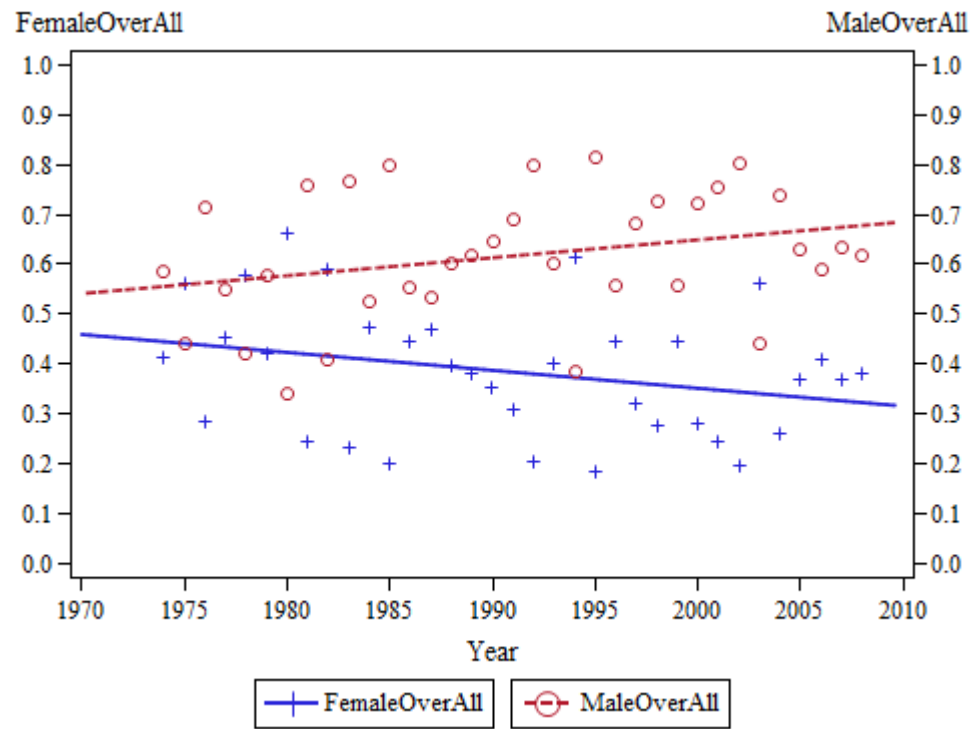
APPENDIX F

SEX RATIOS OF SALMON BY RIVER

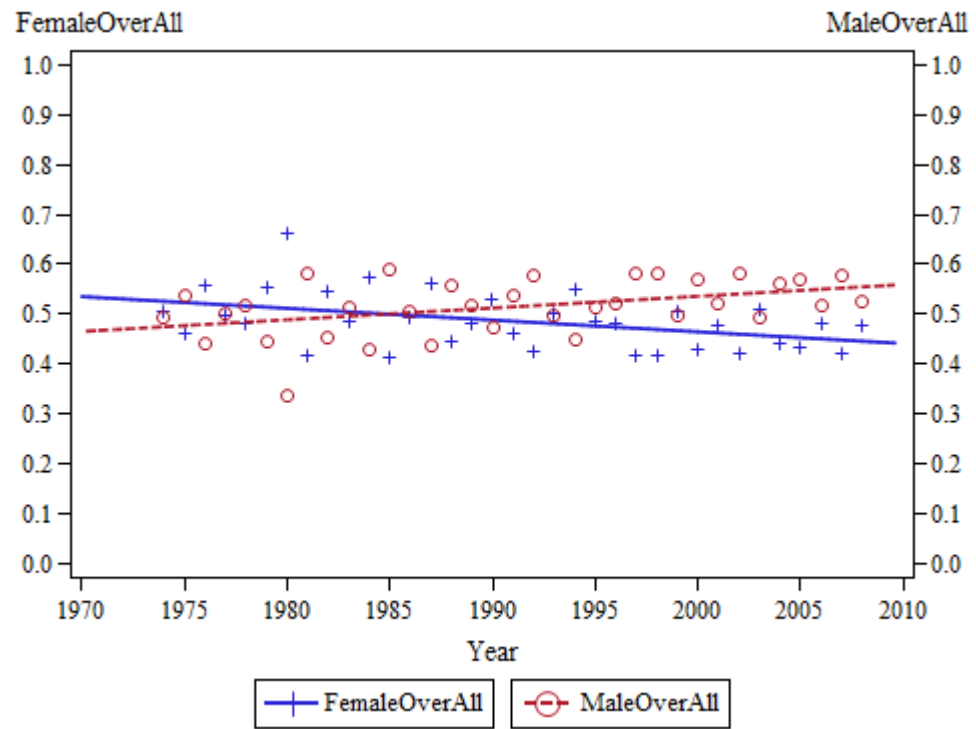
River: Haukadalsa



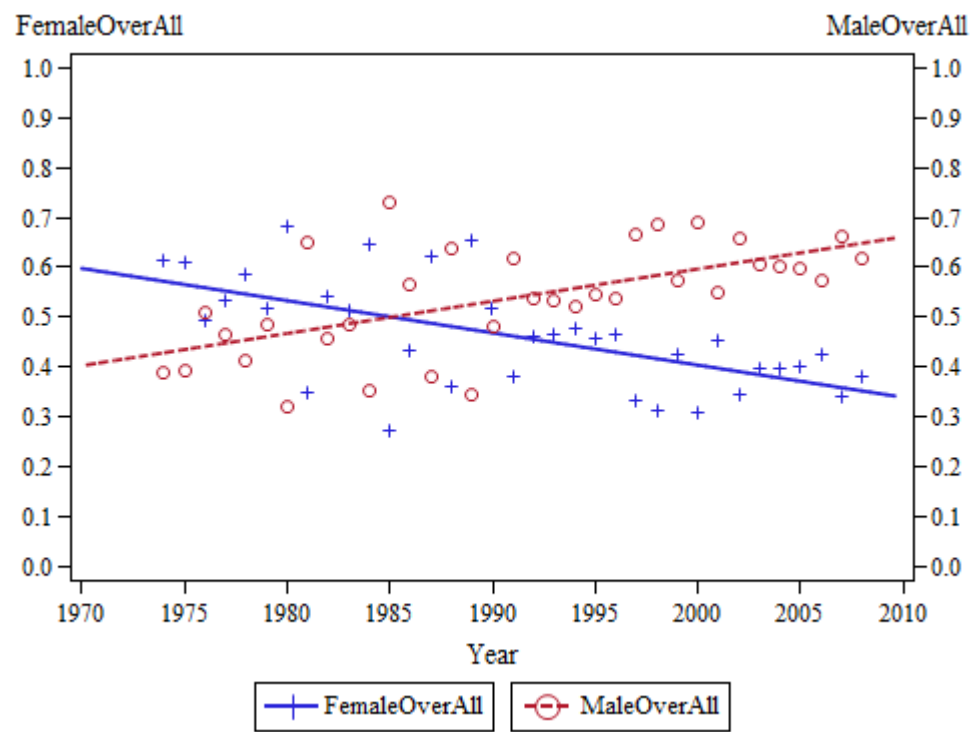
River: Hofsa



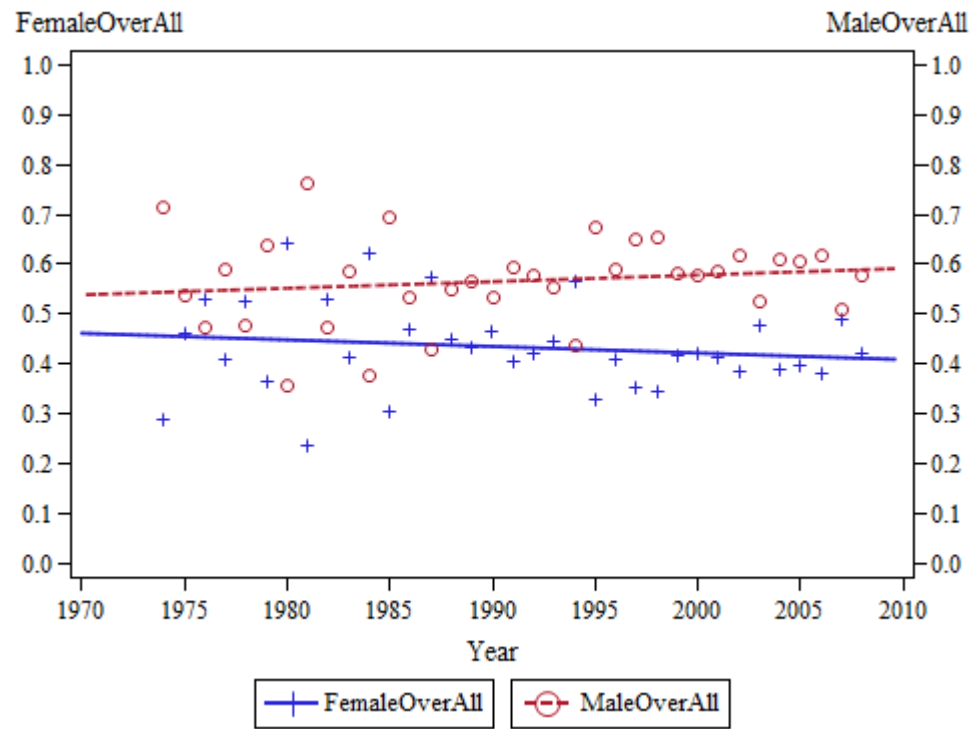
River: Laxa in Adaldal



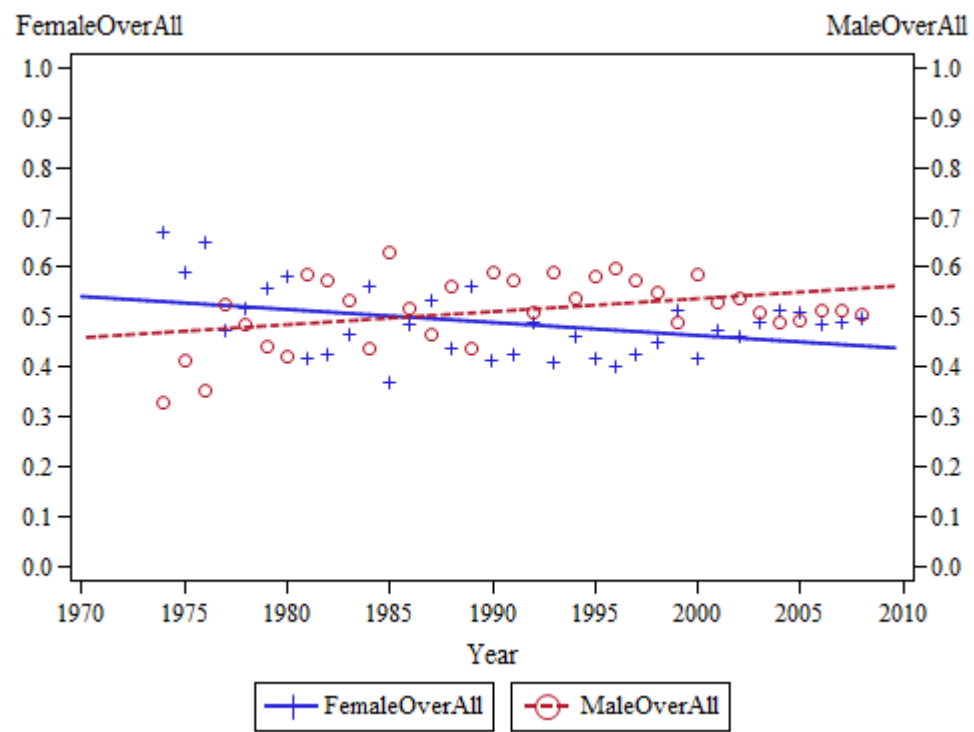
River: Midfjardara



River: Vatndalsa



River: Haffjardara



Means with the same letter are not significantly different.				
t Grouping		Mean	N	river
	A	5.4069	35	Hofsa
	B	2.7398	35	Vatnsdalsa
	C	1.9608	35	Midfjardararf
	C			
D	C	1.7672	35	Laxa Adalda
D				
D	E	1.3352	35	Haffjardara
	E			
	E	1.1363	35	Haukadalsa

