TRYGGVI PAUL MCDONALD
The Grilsefication of Atlantic Salmon in Iceland
(Under Direction of JAMES W. PORTER)

In this thesis I present evidence that the high-seas fishery, in the past, has selected for a non-migratory lifestyle. A time series analysis was performed from the catch statistics of the Icelandic river Haffjardara. The mean weights for multi-seawinter salmon and one-seawinter grilse were plotted over time and were shown to trend downwards for the years 1974-1996. These data suggest that salmon are spending less time at sea and are returning at an earlier age to their natal rivers. The multi-seawinter salmon were harvested at sea before they could reproduce. The data indicate that the salmon have adapted their lifestyle in response to the increased risk of migration. This response has led to grilsefication of the stock.

INDEX WORDS: Atlantic salmon; Salmo salar; Grilsefication; Over-fishing

THE GRILSEIFICATION OF ATLANTIC SALMON IN ICELAND

by

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DEDICATION

I would like to dedicate this to my family, who instilled an sense of wonder and love for the natural world and without whose many sacrifices these words would not be before you. Most especially, Tryggvi Ofeigsson, Anna Tryggvadottir McDonald, Dr. Harold Paul McDonald, Dr. Lawrence Patton McDonald.

Additionally, I would like to include my advisor, mentor, and friend Dr. James W. Porter. His vision, wisdom, and sense of humor are only eclipsed by the genuine care and interest he has in his students.

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I'm sure that I have left a lot of people out, especially at the Institute of Ecology. Thank you Patsy, John (especially for the formatting of this thesis), Thelma *et all.*

TABLE OF CONTENTS

CHAPTER 1

INTRODUCTION

ATLANTIC SALMON AS A TOTEM SPECIES

Atlantic salmon, *Salmo salar,* has been important to humans for several thousand years. One of the earliest examples is a prehistoric (~25,000 years before present) relief painting in the caves of Gorge d'Enfer in Les Eyzies, France (Falkus 1984). The Romans called them *Salmo* from the Latin word salise meaning, "to leap". *Salar* is most probably from the Latin *salarius* meaning "of the sea" (Mills 1989).

The European literature on fly fishing for Atlantic salmon originates in Britain with Dame Juliana Berners' A Treatyse of Fysshynge Wyth an Angle (c.1496). Izaak Walton had this to say in The Compleat Angler (1653): "The salmon is the moost stately fyssh that only man maye angle to in fresshe water." It "is accounted the king of fresshe water fish, and is ever bred in rivers relating to the sea, yet so high, or far from it, as admits of no tincture of salt, or brackishness." Numerous authors that have written about "the king of salmonids", time has only increased the number of tomes written about them and their importance as a totem species throughout their range.

AN OVERVIEW OF THE PHYLOGENY AND BIOLOGY OF ATLANTIC SALMON

Both the Pacific and Atlantic salmon belong to the family Salmonidae. Pacific salmon belong to the clade Oncorhynchus and Atlantic salmon to the clade Salmo. Members of the genus *Salmo* are *Salmo salar* (Atlantic salmon) and *Salmo trutta* (Brown trout). It is not certain whether the original ancestral line originated in salt or freshwaters. Biological evidence seems to favor freshwater, because members of Salmonidae are unable to breed in saltwater. There are five species of Pacific salmon, which die upon spawning (semelparous). Conversely, Atlantic salmon are capable of reconditioning themselves after spawning to complete the cycle again (iteroparous). They may spend the winter in their natal river and return to the ocean in the spring. Salmon that over-winter in freshwater are called kelts. On average, less than ten percent survive to return to the sea and return another year to spawn again (Mills 1989).

Most salmon are anadromous. They are born in fresh water; migrate to the ocean to feed, and then return to fresh water to spawn. This is a common reproductive strategy also seen in shad, sturgeon, and other fishes. The young forage in their natal stream, and upon reaching a particular point in their maturation they migrate downstream to the ocean. At sea, they feed on marine fishes and macrozooplankton.

The life history of *Salmo salar* is fairly complicated when compared with most fish. The mature salmon, upon returning from the sea, excavate a gravel bed known as a redd. In the fall, the eggs are deposited and fertilized in concert. Salmon have relatively low fecundity, producing anywhere from 2000 to 15,000 eggs (as compared to bluefin tuna, which broadcast several million eggs which become part of the planktonic soup). The eggs hatch out of their redds the following spring. The newly hatched salmon are called “alevins”, and their yolk sack provides nutrition for growth. When the yolk sac is absorbed, the alevins emerge from the redd and are then called “fry”. At this point, the fry forage for food and are subject to density-dependent competition. As they mature further they develop vertical barring that helps to hide them from aquatic, aerial, and terrestrial predators. The vertical barring is known as parr marks or markings. They are thus known as parr at this point in their maturation. Some parr are sexually mature at this stage and are referred to precocious parr.

After one to eight years in the stream, most parr undergo smoltification, which involves major physiological, morphological, and endocrinological changes. They develop chloride cells in their gills and take on the silvery appearance common to mature salmon (Mills 1989). The smolts then make the seaward migration in the spring, imprinting on the odor of the stream, usually migrating seaward on the high spring tides. Smolts (average 14.8 cm according to Hutchings and Jones, 1998) must go out to sea to reach full maturity. Upon entry into the estuary or coastal waters, smolts are considered post-smolts (Mills 1989).

No river system could support a population of fully mature salmon because they would be limited in the nutritional resource base required to sustain them (McLean 1982, Mills 1989). In the sea, their primary food sources are: capelin, herring, sand eels, and macrozooplankton (Mills 1989, 2000).

Upon leaving their natal rivers, Atlantic salmon pursue one of two lifestyles, migratory and nonmigratory (Mills, 1989). Multi-seawinter salmon (2+SW) migrate principally to the coastal waters of Greenland and the Faeroe Islands, where, until recently, they have faced the high-seas fishery. Nonmigratory one sea winter grilse

(1SW), on the other hand, remain in coastal waters.

Of particular interest is the homing instinct in salmon. It has been shown that they are able to detect weak magnetic fields and in fact contain a ferromagnetic compound called magnetite that acts as a compass and aids in migration (McLean 1982, Walker 1985). Once they come near to their natal stream, olfactory recognition takes over. The odor of dissolved organic matter, inorganic minerals, and the specific water chemistry lead salmon not only to the river system, but also to the very stream where it began life as fertilized egg years before (Hasler, Scholz, and Horrall, 1978, Dittman and Quinn 1996).

PURPOSE OF THIS STUDY

Ricker (1981) illustrated that because of the selectivity of commercial fisheries in British Columbia, over a twenty-five year period, the five species of Pacific salmon declined in numbers and body size. This was negatively correlated with changes in sea-surface temperatures or thermohaline structure, it was concluded that the meristic and numeric trends were the result of the attendant drift of the genome because of the long-term removal of stocks by the commercial fishery.

Similar declines have been noted in Atlantic salmon populations (Schaffer 1979, Ritter and Marshall 1980, Porter et al 1986). The question is whether or not Atlantic salmon, which display a high degree of phenotypic plasticity, have had a change in their genotype based upon observed changes in their phenotype. Wolfarths' (1986) genetic analysis in conjunction with life history theory implies that older Atlantic salmon age classes will be selected against in favor of an earlier age of reproduction. Lewontin

(1984) argues that there isn't any evidence to show that phenotypic changes attributed to life history theory are correlated with allelic variation.

The selective pressure of the commercial high-seas fishery may have created genetic drift favoring a nonmigratory lifestyle. This is shown by the phenotypic change of sea-age at maturity. According to Upton (1992), "the loss of a wild population's genetic variability reduces a given species' ability to adapt to changes in its environment, unwittingly, we may be selecting for fish populations of less desirable characteristics and less viability". It is worth noting that with the advent of genotyping we can now discriminate between the countries of origin and even differentiate the genetic makeup between neighboring rivers and streams (Bermingham 1991, Friedland *et al* 1994, Reddin 1982, Taggart 1995). This should make it easier in the future to quantify the possible incursion into the genotype that is expressed in the phenotype

For the past six years, the Atlantic Salmon Fund has purchased the commercial salmon fishing quotas in Greenland and the Faeroes. When the dataset is updated, we may see a correlation between the reduction in the migratory (2+SW) catch, and a commensurate increase of 2+SW salmon in the rivers. If no increase can be shown, then it is postulated that environmental conditions (sea surface temperature, salinity structure…etc) may be to blame for the lack of migratory salmon recruitment. Even taking mate selection into account, it may be that the salmon are being swamped in the fight for the best breeding areas and suitable 2+SW mates, especially in areas that have to deal with the escapement of salmon from aquaculture (Gausen and Moen 1991). It may also be that the genome has or is becoming fixed and genetic modeling of the data is necessary.

The grilsefication hypothesis proposes that according to life history theory, we should see a reduction in the average size in addition to a reduction of multi-seawinter salmon (2+SW) and an increase grilse (1SW). This study asks the question is grilsefication taking place? This study is original in that it offers a time series analysis of relatively high quality data that presents possible evidence of grilseification. We have seen the reduction in size in other fishery populations, but until now, we have not seen demonstrable evidence to show a life history change from multi-seawinter to single seawinter.

CHAPTER 2

DATA ANALYSIS

DATA ORIGIN AND FORMAT

The data are from the recreational rod fishery on the Haffjardara River on the West coast of Iceland. Scandinavians are known for their record keeping. The Icelandic government, in the 1930's, decreed that records of all fish caught in and around Iceland be kept. A new book is started at the beginning of every season, to record the date, place, meristic measures, sex, and species for every fish that is caught. Scales are collected from each fish for later analysis.

Ghillies serve as guides for the sportsmen and water bailiffs for the farmers cooperative that leases the fishing rights. The ghillies are taught how to weigh, measure, and collect scales (below the dorsal fin and along the lateral line) from the salmon. The Icelandic Freshwater Fisheries Institute is the repository for the catch data from all the rivers in Iceland. The data go as far back as the 1930's but were not standardized until 1974. The older data are useful for anecdotal evidence of population structure, but may not stand up to statistical analysis.

Since 1974 the Haffjardara River has had the same number of rods, the same number of hours per day that are fished (i.e. the catch per unit effort has remained constant over the time period in question 1974-1996), and the number of days in the fishing season has remained constant (June-August). The scales that are used to weigh the fish are certified each year before the season begins. The data are in the following format:

Column	
1-2	Year
3-4	Month
5-6	Day
9-11	Pool where caught
14	Species (1= salmon, 2= Artic 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: 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, it weighed 14.0 pounds, no length was recorded, the salmon was caught on a fly.

The data were narrowed to the essential portions for this time-series analysis, year, species, and sex. Any missing data points or unknowns were removed from the dataset. We are not concerned with other species of fish in this river for two reasons: 1) it is not within the scope of this thesis and 2) the river in question is not known for its' production of other sea-run species.

CHAPTER 3

RESULTS

Catch data was analyzed for the Haffjardara river (1974-1996 and approximately 15,300 fish), in Iceland. Bimodal weight distributions were made for each year class to segregate the grilse from the salmon. For this stock, it was observed that the male grilse were less than 7 lbs. and female grilse less than 8 lbs. This observation was supported by determining the age of the fish by counting the annuli. The ageing was performed by the staff at the Institute of Freshwater Fisheries in Iceland. The annuli are yearly marks laid down during periods of slower growth in winter. It is possible, by visual inspection, to distinguish between the slower freshwater growth and more rapid saltwater growth (Iversen 1996). The weight frequency distributions and cohort size of both salmon and grilse for each sex and year class were then plotted. The percentage of the annual cohorts that were composed of grilse and salmon were examined and plotted against each other, as were the ratios of grilse to salmon. Statistical analyses were performed using SAS for personal computers (SAS Institute). The figures presented were created using Microsoft Excel and Sigma Plot. A logarithmic regression line was also added to fit the trends in figures 1-6, because the data are not normally distributed. A linear regression was used to fit the trends in figures 7-10.

The results are presented in graphic form in figures 1-10 and tabular form in tables 1 and 2. Wild salmon display sexual dimorphism, female salmon are larger than the males. The total numbers of grilse and salmon were plotted for each year class. The proportion of annual cohorts that were composed of grilse and salmon were examined and plotted against each other, as were the ratios of grilse to salmon.

Figures 1-4 show steep declines in average mean weights for grilse and salmon of each sex. Figures 5 and 6 show an increase in the total numbers of grilse and a commensurate decrease in the numbers of salmon.

Figures 7 and 8 show the proportion of the total catch that is made up of grilse and salmon respectively ($r^2 = 0.47$, $P > 0.0003$). The linear fit for the proportion of grilse returning is: grilse%= 0.42089 + 0.01224 x (year class). The slope of the regression trend line for the proportion of grilse returning is positive, indicating an increase in the numbers of grilse returning as compared with the total cohort for each year class. The linear fit for the percentage salmon returning is: salmon%= 0.57911 – 0.01224 x (year class). The slope of the regression trend line for the proportion salmon returning is negative, indicating a decrease in the numbers of salmon returning as compared with the total cohort for each year class.

Figure 9 combines figures 7 and 8 to show the divergence of salmon and grilse populations. The linear regression indicates that the grilse and salmon populations began diverging from each other beginning in the early to mid 1980's.

The linear regression in Figure 10 shows a statistically significant increase in the ratio of grilse: salmon ($r^2 = 0.56$, $P > 0.0001$). The linear fit of grilse: salmon ratio is: grilse: salmon = 0.60987 + 0.07325 x (year class). When the dataset begins in 1974 the ratio is 0.55 grilse to salmon, the dataset ends in 1996 that ratio has increased to nearly 3:1 (2.84).

CHAPTER 4

DISCUSSION

Like all common pool resources, Atlantic salmon are not immune to overexploitation. Grilse (1SW) are non-migratory and remain in protected coastal waters. Multi-seawinter salmon (2+SW) migrate principally to the coastal waters of Greenland and the Faeroe Islands, where, until recently, they have faced the high seas Fishery. This selective fishery may have created directional genetic drift favoring grilse (1SW). Sea ranching studies by Jonasson *et al*, (1997) found a genetic correlation for grilse return rate to the total return rate to be 0.98 ± 0.01. Multi-seawinter salmon largely produce multi-seawinter offspring. Kaillio-Nyberg, I., M. Koljonen (1997) found that the male portion of genetic inheritance for age at maturity was more important (P=0.67) than the female portion (P=0.178). Gjerde *et al* (1994), in Norwegian aquaculture strains, noted a significant heritable correlation between the age at maturity between parents and offspring of 2+SW salmon.

The North Atlantic climate and sea surface temperatures are mostly determined by the North Atlantic Oscillation (NAO). The NAO index is the difference in atmospheric pressure between the Icelandic Low and the Azores High. Changes in the index can cause changes in the Atlantics' deep convection, circulation, precipitation, sea surface temperatures, storms, the production of zooplankters, and recruitment of fishes (Mills 2000).

Correlations have been shown between sea surface temperatures and post-smolt growth and survival (Friedland *et al*, 1993, Friedland and Reddin 1993,). Friedland (1998) suggests that both environmental factors and genetic makeup control the return of two seawinter salmon in North America. Short-term environmental conditions can change the ratio of grilse to salmon (Scarnecchia et al 1989, Gudjonsson et al, 1995). Isaksson (1994) was able to show that variations in the ocean temperatures west of Iceland and climate changes were correlated with changes in return rate in Icelandic salmon. Additionally, the age of sexual maturity is shown to be influenced by sea temperatures (Scarnecchia 1983, Martin and Mitchell 1985). Climactic variation explains the variation between year classes. It does not account for the long-term decline in abundance or the continued decline in salmon and increase in grilse recruitment. It may explain the goodness of fit in the linear regressions in figure 9 ($r^2 = 0.47$) and figure 10 ($r^2 = 0.56$)

Abiotic, environmental conditions (sea surface temperature, salinity structure…etc), attendant biotic linkages, and the directional drift of the genome may favor grilse and reduce salmon recruitment. Changing sea temperature can affect the ratio of grilse to salmon positively or negatively. A salmons survival on the high seas is more tenuous than that of grilse. While salmon must manage the changing climatic conditions in the open ocean and migrate thousands of miles, nonmigratory grilse remain in coastal waters. The cost of staying out for additional seawinters increases the risk of falling prey to predators, disease, changing environmental conditions, and stochastic events.

CHAPTER 5

CONCLUSION

The data presented here indicate that the age classes of the spawning population in the Haffjardara River are trending steadily downward and grilseification may be taking place. This is consistent with *a priori* assumptions that life history theory predicts.

Scarnecchia (1983) explained much of the variation in percentages of returning grilse in Icelandic stocks. While numbers of returning grilse vary from year class to year class, the percent returns for grilse and salmon (Figure 9) show that it was in the early to mid-1980's that the divergence of 1SW and 2+SW stocks occurred. Scarnecchia did not have a long enough time series to see the trend when he made his observations in 1983.

We know that the commercial exploitation of migratory stocks has exerted strong predatory pressure. "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" (Helfman *et al*, 1997).

Perhaps the greatest threat to Atlantic salmon from over-harvest is " the loss of genetic diversity within and among populations of marine species" (Upton, 1992). The selective fishery for migratory stocks may have created a genetic bottleneck favoring a non-migratory life history. "Differential survival and reproduction of fish with different genotypes will change the genetic composition of the harvested population" (Allendorf et al, 1987). Several year classes (1-4 years at sea) return each season to breed. It is vital that cross-cohort reproduction take place in order to maintain genome heterozygosity (Saunders and Schlom, 1985). Consequently, not only has the fishery been removing the migratory age classes from recruitment, but because of the high degree of heritability for the sea-age of return for spawners, increased the proportion of non-migratory grilse across *Salmo salars's* range (Reddin, 1992).

The North Atlantic Salmon Fund, The Atlantic Salmon Trust, and other organizations have been purchasing the salmon quotas from the fisheries in the Faeroe Islands and Greenland for the last five years. Potter (1996) has predicted an increase in the multi-seawinter component of the yearly cohort. Until the data set can be updated, we are unable to show a reversal in the trend toward grilsefication If a reversal cannot be seen, genetic modeling may be required to explain whether or not the trait for multi-sea winter salmon has been selected against in favor one sea winter grilse.

It may be that long term changes in climatic conditions and the removal of migratory (2+ SW) stocks by the high-seas fishery have the increased exclusion of the heritable trait for age of maturity and other local adaptations that were originally part of the genome. The trend favoring the grilseification hypothesis may be supported by the time-series analysis, for the period 1974-1996, of the river Haffjardara River in Iceland. Additional rivers need to be examined before any statements about the general population-level dynamics can be made about the S. salar in Iceland.

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APPENDIX A

LIST OF FIGURES

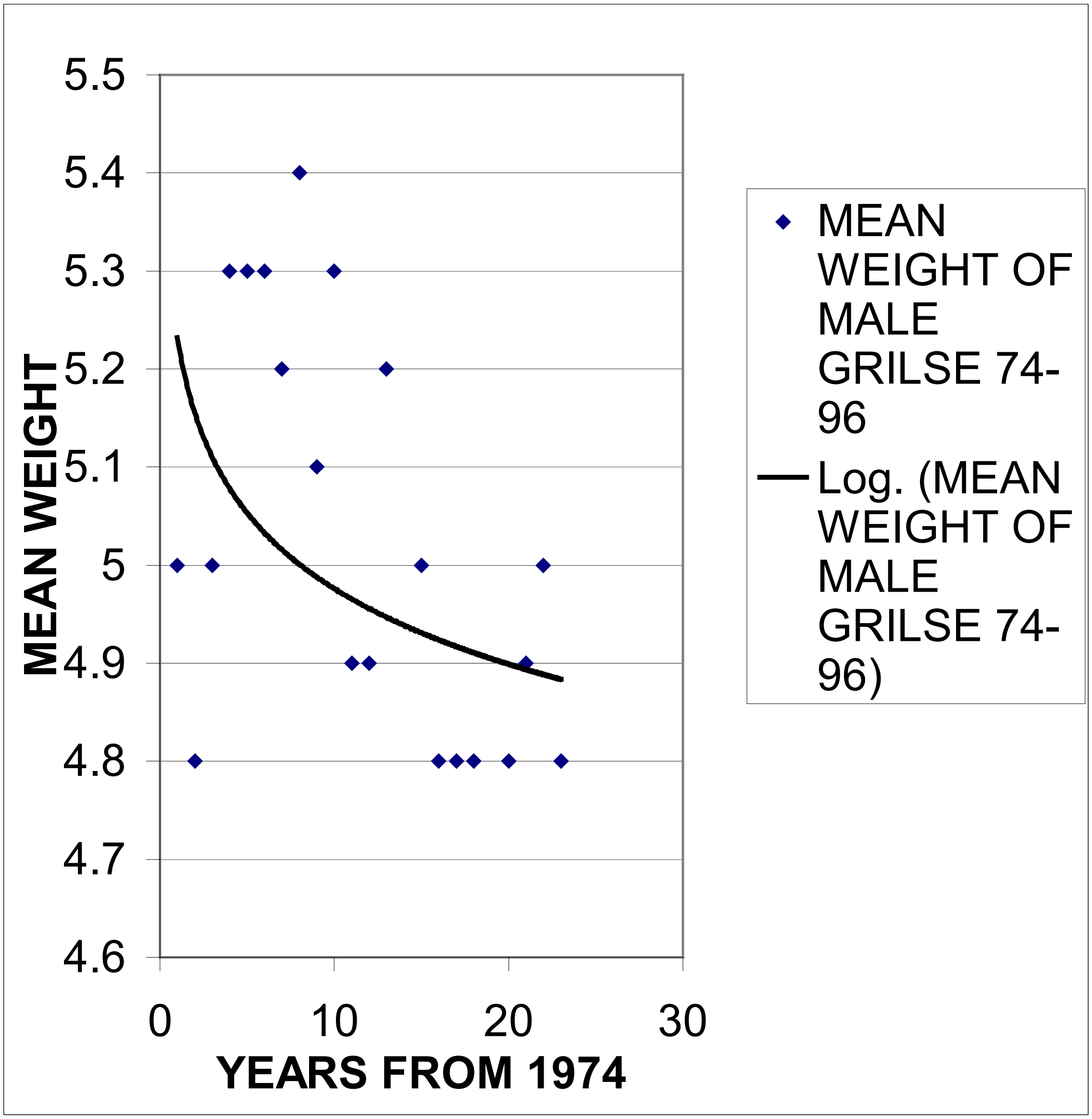

Figure 1. The mean weight of male grilse caught in each year class from1974-1996.

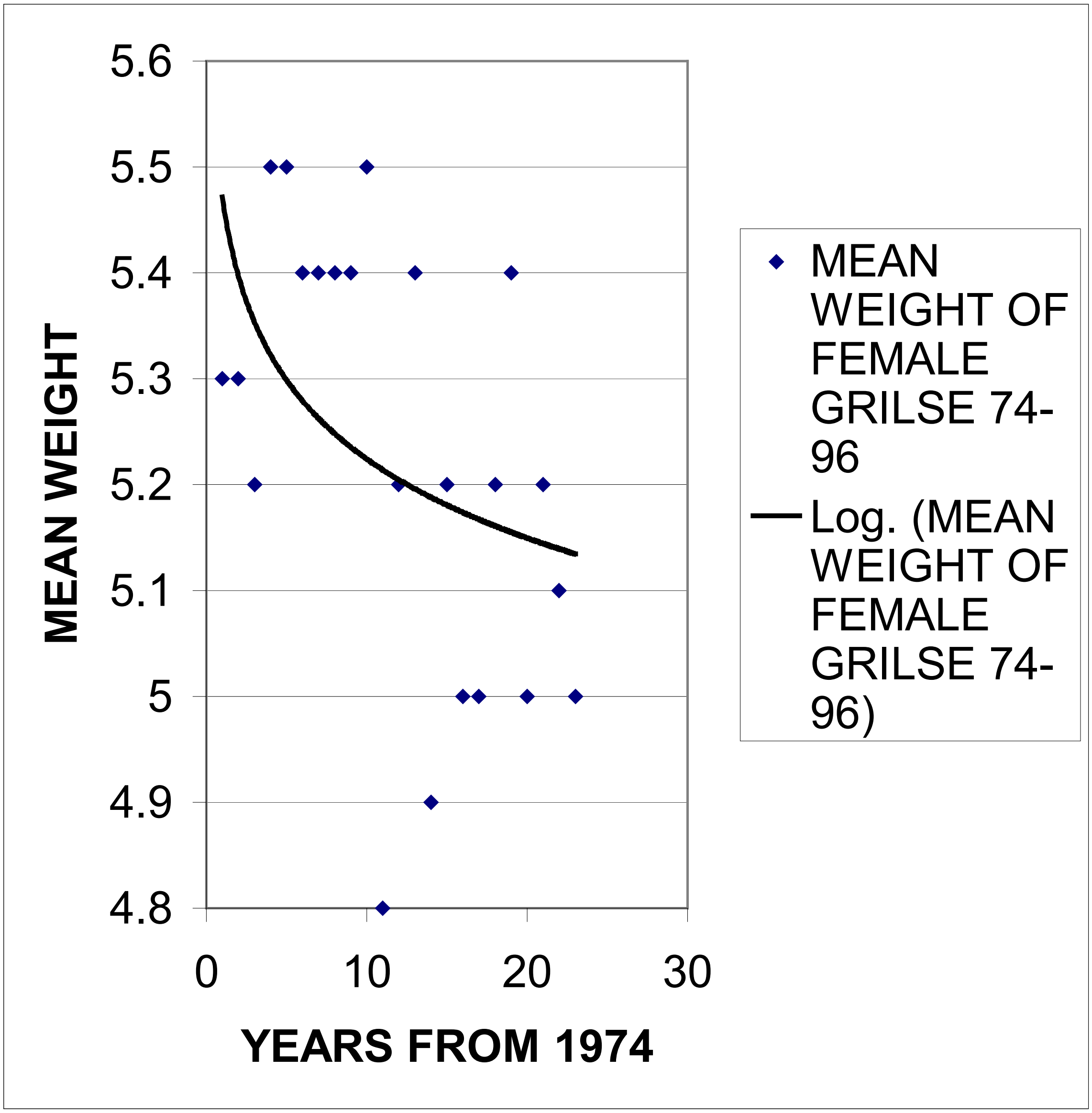

Figure 2. The mean weight of female grilse caught in each year class from1974-1996.

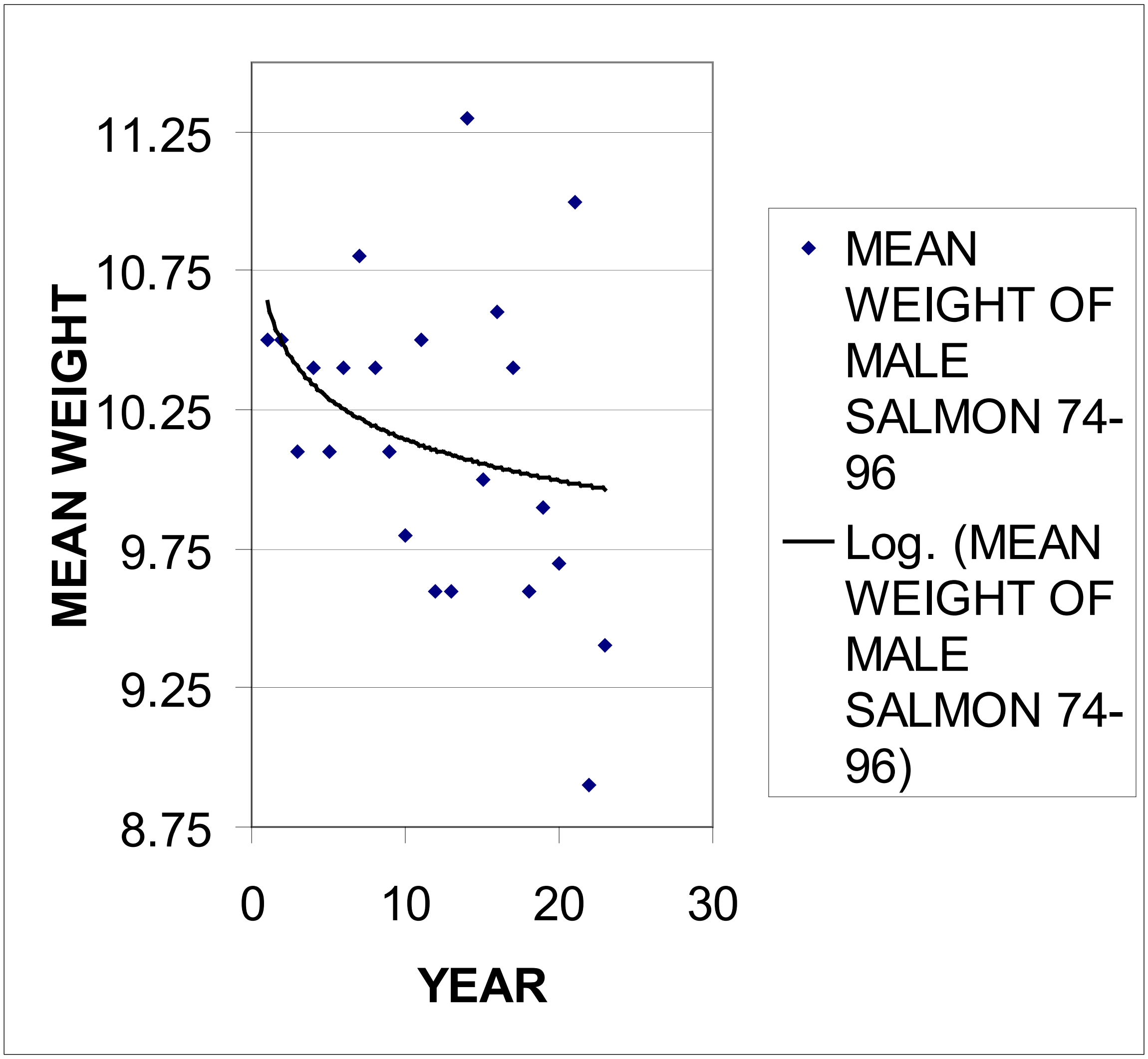

Figure 3. The mean weight of male salmon caught in each year class from1974-1996.

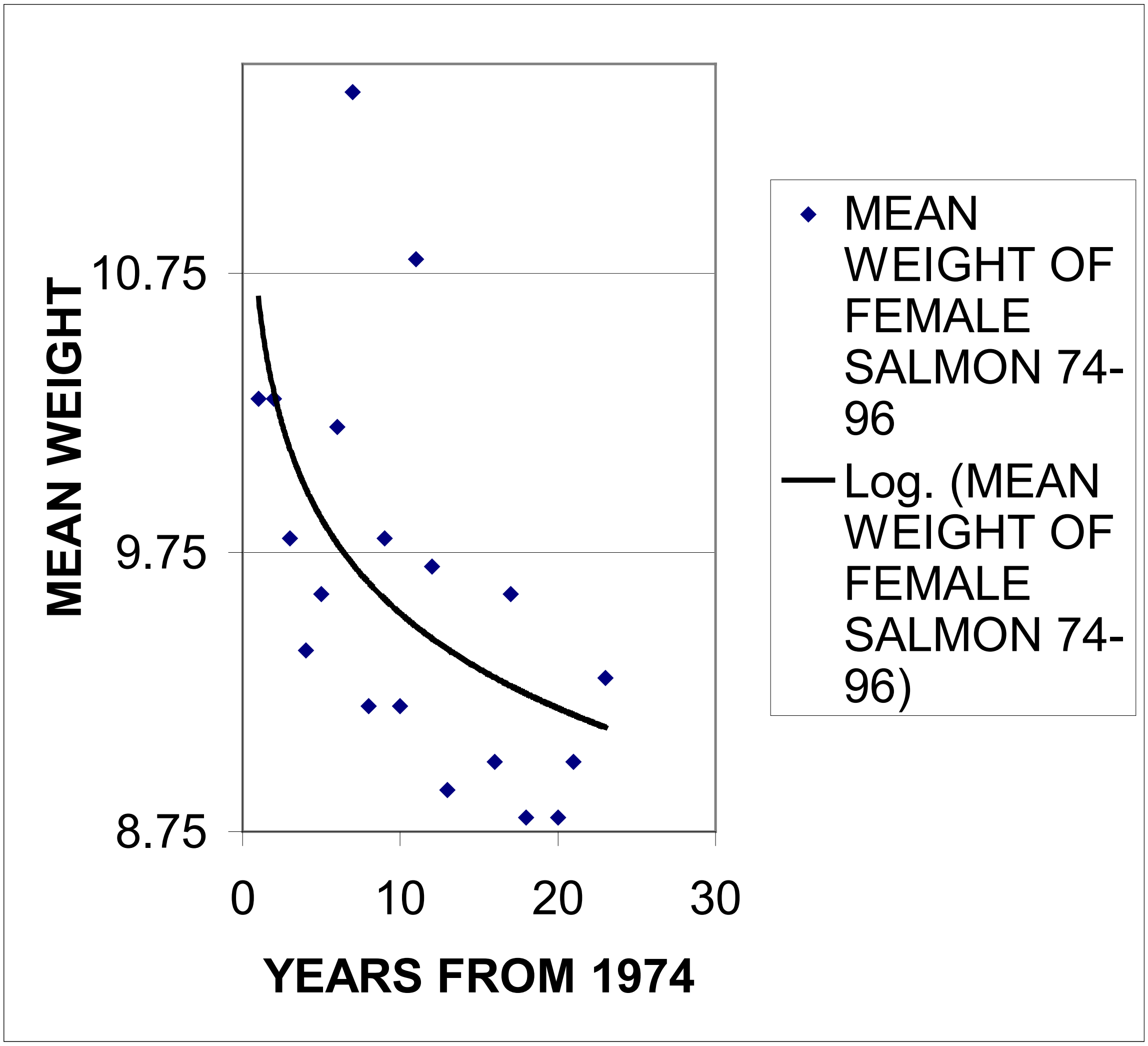

Figure 4. The mean weight of female salmon caught in each year class from1974-1996.

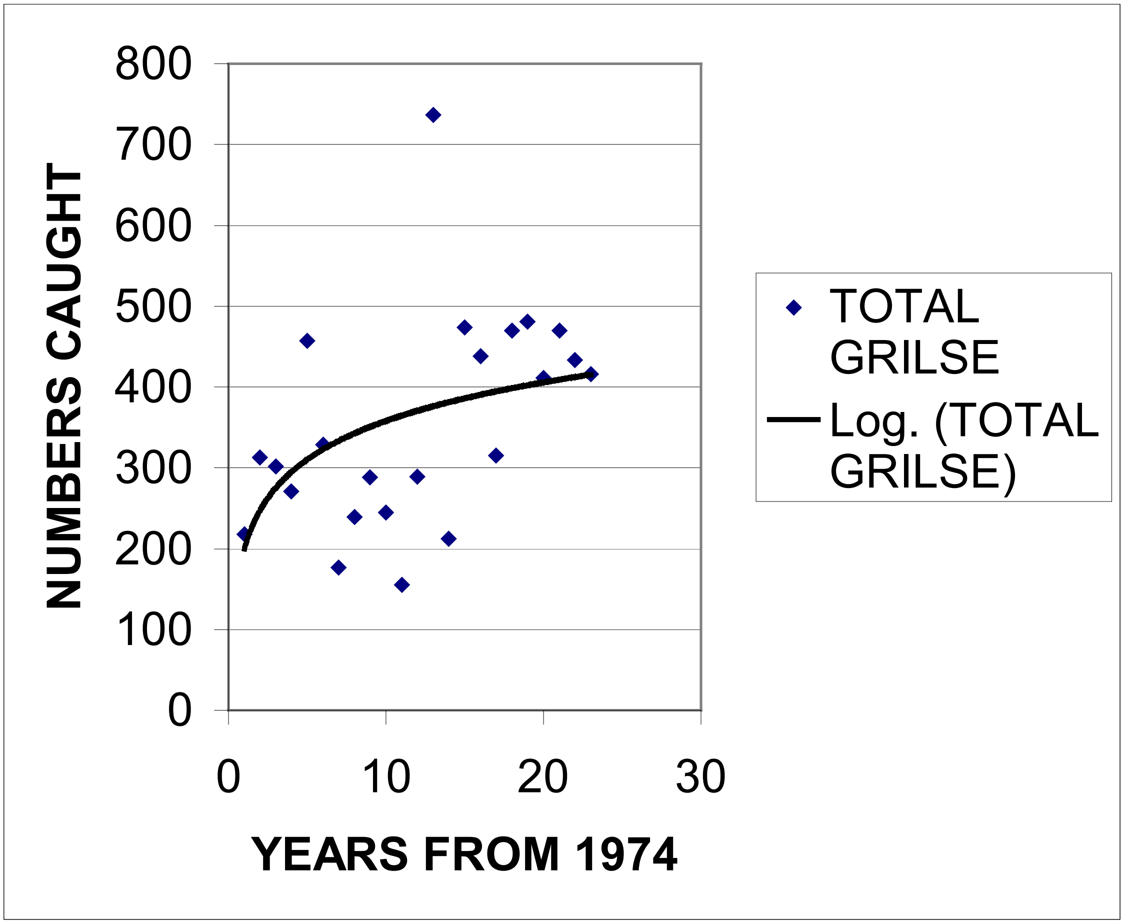

Figure 5. The total catch of grilse for the year classes 1974-1996.

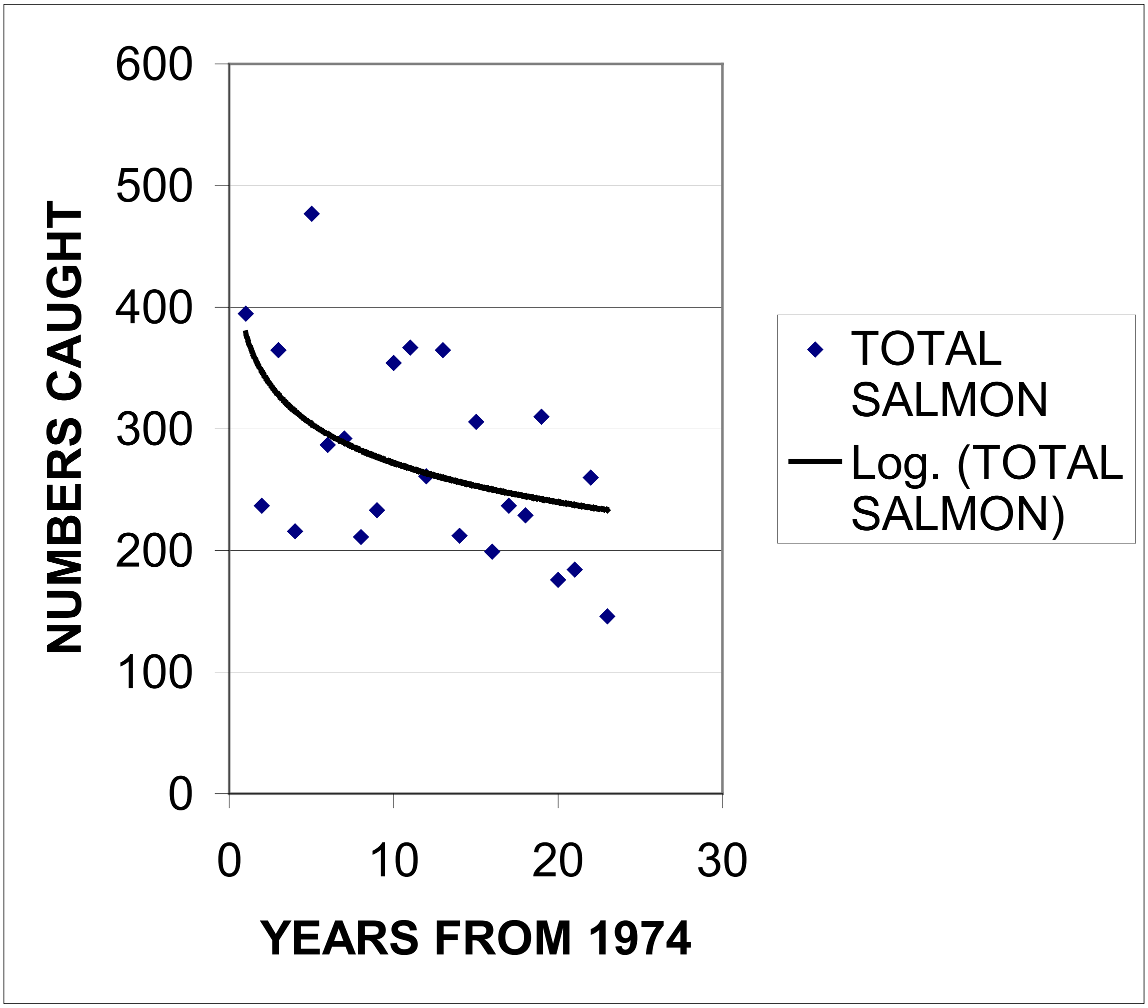

Figure 6. The total catch of salmon for the year classes 1974-1996.

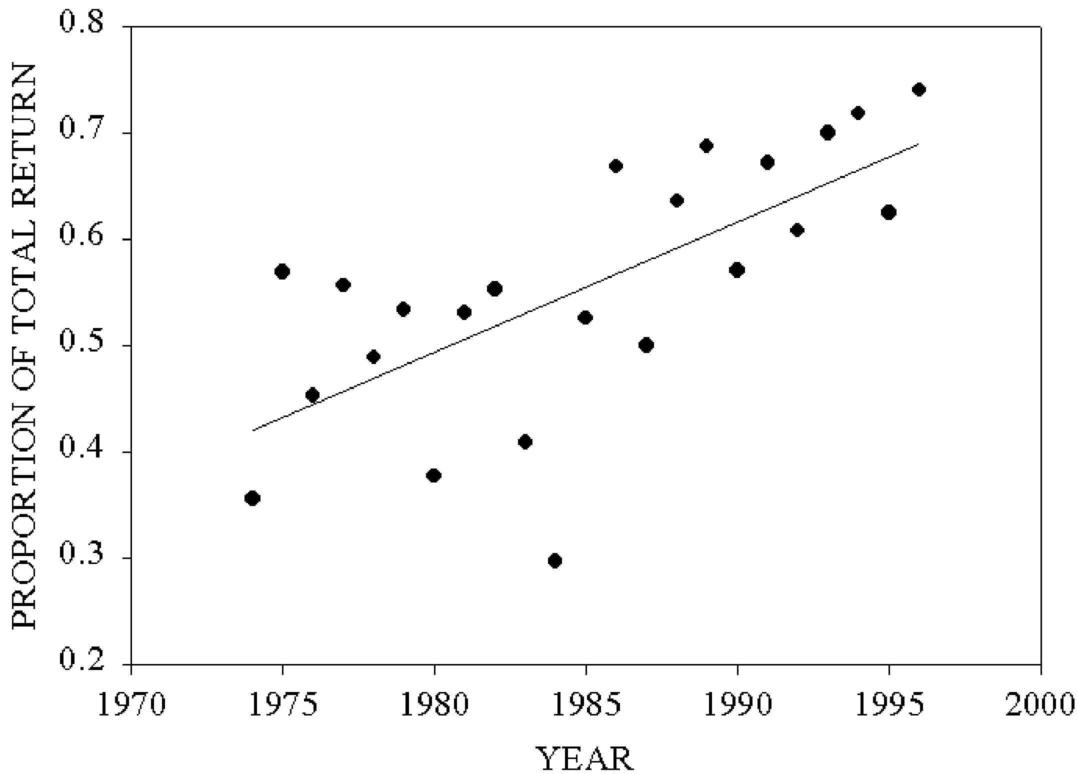

Figure 7. Percentage of the annual cohort that is composed of grilse for the years 1974-1996.

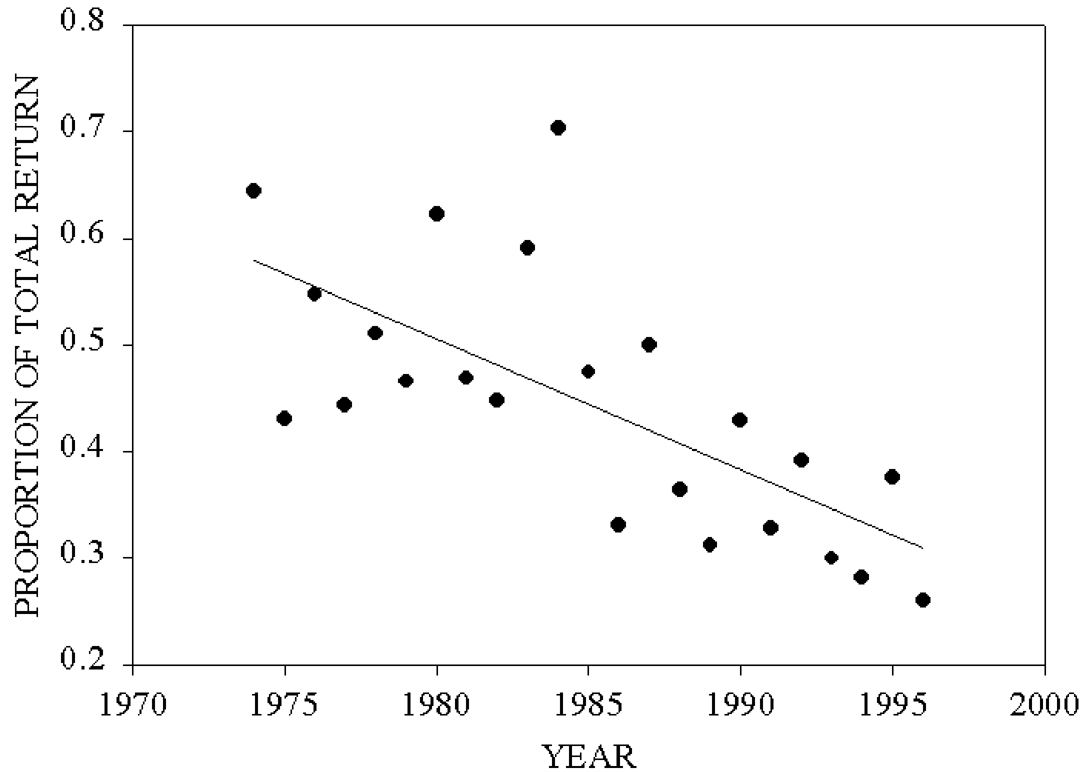

Figure 8. Percentage of the annual cohort that is composed of salmon for the years 1974-1996.

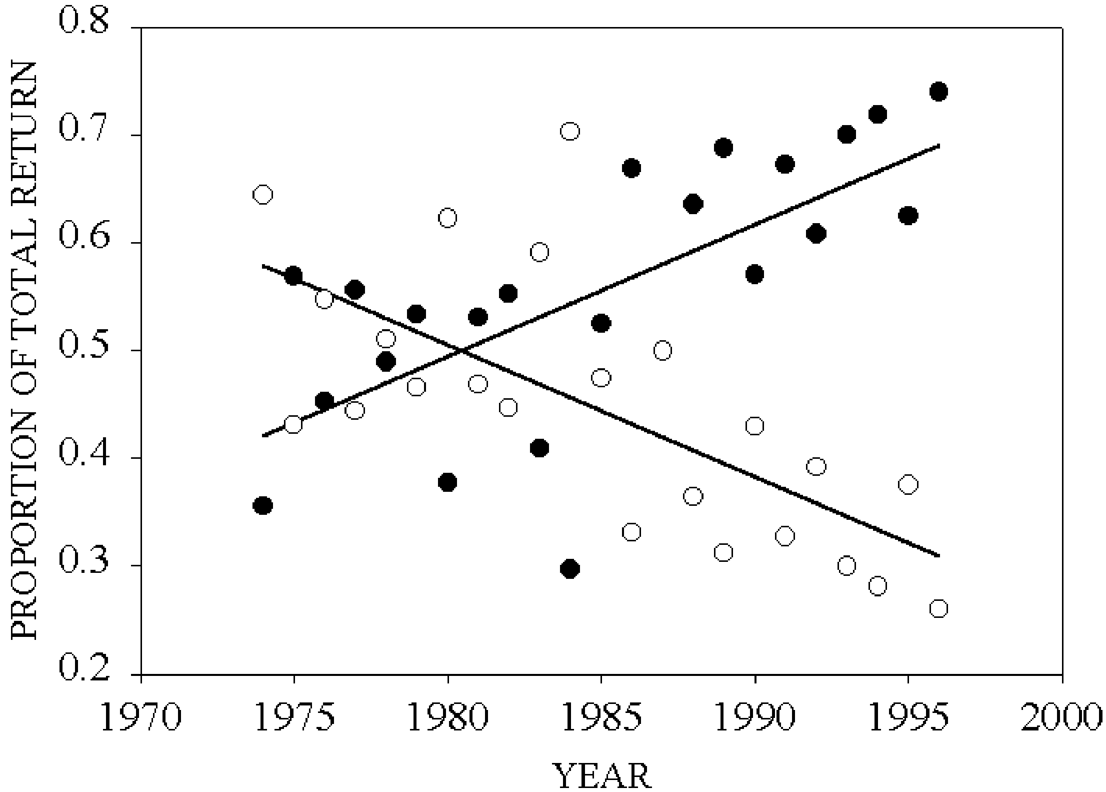

Figure 9. The combined rate of return for both grilse and salmon ($r^2 = 0.47$).

● = grilse

○ = salmon

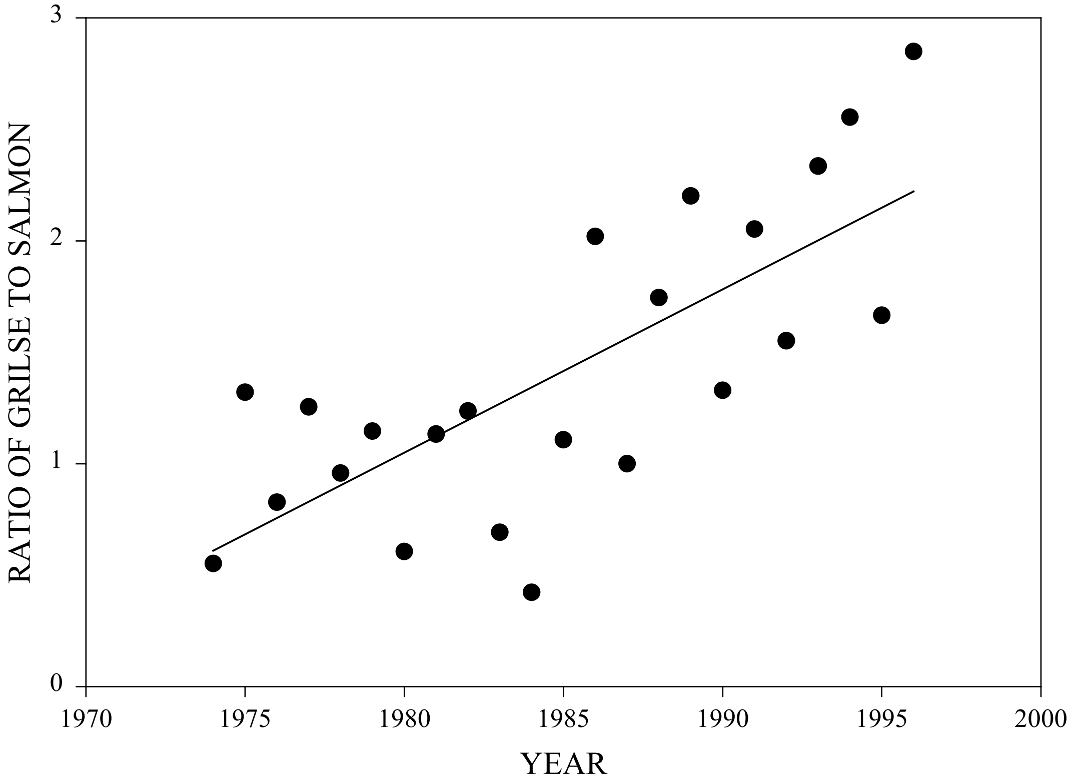

Figure 10. The ratio of grilse to salmon for the years 1974-1996 (r^2 = 0.56).

APPENDIX B

LIST OF TABLES

YEAR	MALE GRILSE TOTAL RETURN	FEMALE GRILSE TOTAL RETURN	MALE SALMON TOTAL RETURN	FEMALE SALMON TOTAL RETURN	GRILSE/ SALMON RATIO
1974	49	169	115	280	0.55
1975	131	182	95	142	1.32
1976	117	185	126	239	0.82
1977	154	117	103	113	1.25
1978	213	244	231	246	0.95
1979	140	189	132	155	1.14
1980	82	95	116	176	0.6
1981	124	115	140	71	1.13
1982	183	105	116	117	1.23
1983	141	104	180	174	0.69
1984	95	60	134	233	0.42
1985	177	112	171	90	1.1
1986	338	399	231	134	2.01
1987	114	98	83	129	1
1988	288	246	185	121	1.74
1989	215	223	63	136	2.2
1990	197	118	131	106	1.32
1991	269	201	132	97	2.05
1992	220	261	185	125	1.55
1993	254	157	92	84	2.33
1994	254	216	99	85	2.55
1995	232	201	169	91	1.66
1996	262	154	78	68	2.84

TABLE 1. The catch statistics for year classes 1974-1996 for grilse and salmon segregated by sex and year class and the ratios of grilse/salmon by year class.

YEAR	MEAN WEIGHT MALE GRILSE	MEAN WEIGHT FEMALE GRILSE	MEAN WEIGHT MALE SALMON	MEAN WEIGHT FEMALE SALMON
1974	5	5.3	10.5	10.3
1975	4.8	5.3	10.5	10.3
1976	5	5.2	10.1	9.8
1977	5.3	5.5	10.4	9.4
1978	5.3	5.5	10.1	9.6
1979	5.3	5.4	10.4	10.2
1980	5.2	5.4	10.8	11.4
1981	5.4	5.4	10.4	9.2
1982	5.1	5.4	10.1	9.8
1983	5.3	5.5	9.8	9.2
1984	4.9	4.8	10.5	10.8
1985	4.9	5.2	9.6	9.7
1986	5.2	5.4	9.6	8.9
1987	4.5	4.9	11.3	11.9
1988	5	5.2	10	8.3
1989	4.8	5	10.6	9
1990	4.8	5	10.4	9.6
1991	4.8	5.2	9.6	8.8
1992	4.5	5.4	9.9	8.1
1993	4.8	5	9.7	8.8
1994	4.9	5.2	11	9
1995	5	5.1	8.9	8.5
1996	4.8	5	9.4	9.3

Table 2. The mean weights for grilse and salmon segregated by sex and year class.