

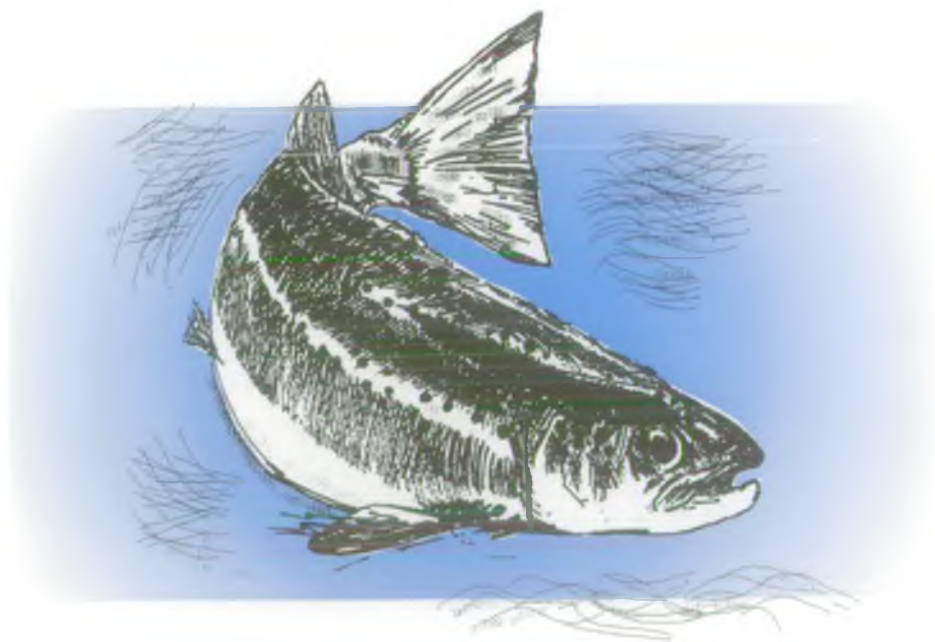


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SEA TROUT

CATCH STATISTICS



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NATIONAL RIVERS AUTHORITY

FISHERIES TECHNICAL REPORT NO.2

ANALYSIS OF SEA TROUT CATCH STATISTICS FOR ENGLAND AND WALES

This report has been compiled by the Institute of Freshwater Ecology, Windermere Laboratory under contract to the NRA. The Institute of Freshwater Ecology is part of the Terrestrial and Freshwater Sciences Directorate of the Natural Environment Research Council.

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SUMMARY

The chief objectives were to assess the spatial and temporal variability of rod and commercial catches of sea-trout, Salmo trutta L., in the North West, Welsh, South West, Wessex and Northumbria (+ Yorkshire Esk) regions of the National Rivers Authority, to classify the major sea-trout rivers according to mean catch and variability in catch, and to identify rivers that do not fit into this scheme. The data base comprised annual rod catches from 67 rivers and annual commercial catches from 36 rivers in England and Wales.

The analyses of spatial variability (variation in catches between rivers for each year) demonstrate that catches from different rivers in a region varied synchronously in time. The mean catch for all rivers in a region and the corresponding CV (Coefficient of Variation) therefore provide succinct summaries of temporal changes in catch size and the relative variability between catches from different rivers. The latter was fairly stable between years for catches from the North West, Welsh and South West regions, but varied considerably for catches from the Wessex and North East regions, usually reflecting the larger fluctuations in mean catch. Mean catch varied considerably between years in all regions and although 1989 catches were low in all except the North East, similarly low values have occurred in previous years. Although not used in the analyses, 1990 catches were included for comparison and were low compared with previous catches.

When all rod catches from 67 rivers and all commercial catches from 36 rivers were treated as single data sets, the temporal variability (variation in catches between years for each river) was strongly density-dependent on mean catch. The proportion of the between-years-variation in catches that could be explained simply by variations in the overall mean catch for each river was 93% for rod catches and 98% for commercial catches.

A classification of rivers according to mean annual catch and relative temporal variability showed that rivers with high temporal variability usually provided low catches whilst those with low variability usually provided high catches. These differences support the conclusion that populations of sea-trout in rivers with low catches will be regulated chiefly by density-independent factors (chiefly fluctuations in climate) whilst those in rivers with medium to high catches will be regulated chiefly by density-dependent factors. Such differences have implications for the management of the different sea-trout populations.

KEY WORDS

Salmo trutta, sea-trout, rod catches, commercial catches, river classification.

1. INTRODUCTION

1.1 Background

Although it is obvious that the size of animal populations varies considerably in both time and space, it is a difficult task to obtain reliable measures of this variability in the field. Such information is important for many aspects of ecology from pest outbreaks to conservation of endangered species and from the theory of population dynamics to the stability of communities and ecosystems (see recent review by McArdle, Gaston and Lawton 1990). It has become clear in recent years that variation in population density often depends upon the mean density, i.e. both spatial and temporal variability in numbers are density dependent. For many species, the relationship between the variance and mean density is well described by a power function (see reviews by Taylor 1984, 1986, McArdle et al 1990).

There are few large data sets suitable for the analysis of both temporal variability and large-scale spatial variability. Notable exceptions from sites distributed throughout Great Britain are light-trap catches of moths, suction-trap catches of aphids and annual census data for singing male birds. Extensive analyses of these data sets have shown that for most species, both spatial and temporal variance was proportional to a fractional power of mean density (Taylor and Woiwod 1980, 1982, Taylor, Woiwod and Perry 1980, Taylor et al 1985). Use of a power function to describe the variance-mean relationship would therefore seem to be appropriate for similar data sets.

Rod and commercial catches of sea-trout in England and Wales provide one of the few additional data sets suitable for the study of spatial and temporal variability. Records of annual catches are available for all the major rivers supporting large populations of sea-trout and, for most rivers, these records have been kept for many years. As with all catch data, the size of the catch can depend upon not only population density but also many other factors that include the effort used to catch the animals, the correct recording of all animals caught, and environmental factors affecting the efficiency of the catching methods. Similar problems are probably applicable to the moth and aphid catches mentioned above. An additional problem with the sea-trout data is that the catches include fish from different year-classes. The catches may be indicative of the total population of sea-trout returning to spawn in the river, but they provide no information on survivor density from each year-class. A similar problem must be applicable to the data for singing birds mentioned above. In spite of all these problems, the pragmatic approach adopted here is to analyze the data first and then discuss if any discrepancies could be due to the inadequacies of the data sets.

1.2 Objectives

These are summarised in the following terms of reference.

1. To assess the spatial variability of sea-trout rod catch data for the principal sea-trout

rivers within and between the South West, Wessex, North West, Northumbria and Welsh NRA Regions.

2. To assess the temporal variability of sea-trout rod catch data for the principal sea-trout rivers within and between the South West, Wessex, North West, Northumbria and Welsh NRA Regions.
3. To assess the spatial and temporal variability of all significant commercial sea-trout fisheries under the NRA's control.
4. To use the analyses for temporal variability to classify the major sea-trout rivers in England and Wales according to mean catch and variability in catch.
5. To identify rivers that do not fit into this classification scheme.

2. METHODS

2.1 Data base

Information was obtained from six regions of England and Wales but data for the North Yorkshire Esk were combined with those from Northumbria so that five data sets were available for analysis. Catch data from earlier years were excluded when they were available for only a few rivers in a region. A few rivers were also excluded because catches were not always recorded. The final choice of years and rivers therefore provided a symmetrical data base for each region so that catch records were available for all rivers in all years.

A summary of the data base (Table 2.1) shows that large data sets were obtained for rod catches from the North West, Welsh and South West regions, but long data runs were also obtained for four rivers in the Wessex region and five rivers in the North East (four in Northumbria and Yorkshire Esk). Data sets for commercial catches were available for fewer rivers but were adequate for analyses of spatial and temporal variability in the North West, Welsh and South West regions. The smaller data sets for Wessex and North East regions restricted the analyses to temporal variability.

2.2. Statistical analyses

A summary of the data matrix (Table 2.2) shows that each catch can be used to calculate either the spatial mean catch (\bar{x}_i) and variance (s_i^2), or the temporal mean catch (\bar{x}_j) and variance (s_j^2). The standard formulae used to calculate the mean and variance are given in Table 2.2.

The working model for the relationship between mean catch and variance, both spatial and temporal, is a fractional power function:

$$s^2 = a \bar{x}^b \quad (1a)$$

This model can be fitted in the form of a linear regression:

$$\log_{10} s^2 = \log_{10} a + b \log_{10} \bar{x} \quad (1b)$$

The transformation and the fitting techniques have been critically evaluated by Taylor, Woiwod and Perry (1978). It should be noted that the log transformation not only provides a linear relationship but also stabilizes variance.

An alternative method of fitting the model is to use the geometric mean regression which is more appropriate when large errors occur in both the dependent and independent variable (Ricker 1973, Perry 1981, Taylor and Woiwod 1982, McArdle 1988). Both methods can produce biased estimates of a and b , but it has been found using simulated samples that the results from the two regression methods are usually similar, especially when there is a high

correlation between $\log s^2$ and $\log \bar{x}$ (McArdle et al 1990). As this was usually the case in the present investigation, the standard least - squares regression (equation 1b) was used in the analyses.

The value of b in equation 1 provides useful information on the relationship between variability and mean catch. Variability increases or decreases with increasing mean catch for $b > 2$ and $b < 2$ respectively. For $b = 2$, the absolute variability increases with mean catch but the relative variability remains constant. These relationships are also shown by the coefficient of variation (CV) which is related to equation 1 thus:

$$CV = \frac{s}{\bar{x}} = \frac{\sqrt{s^2}}{\bar{x}} = a^{0.5} \bar{x}^{(0.5b-1)} \quad (2)$$

where values of constants a and b are the same as those in equation 1. It is obvious that CV also increases or decreases with increasing mean catch for $b > 2$ and $b < 2$ respectively, and that CV is constant for $b = 2$. These relationships are illustrated in Figure 2.1. As the CV provides a useful method of illustrating the relationship between variability and mean catch, it was also used in the present investigation.

Table 2.1 - Summary of data base

Rod catches

North West (1976-1989); 13 rivers: Ribble + Hodder, Wyre, Lune, Kent, Leven + Crake, Duddon, Esk, Irt, Ehen, Derwent + Cocker, Ellen, Eden, Esk (Border).

Welsh (1974-1989); 28 rivers: Wye, Usk, Ogmore, Neath, Tawe, Loughor, Tywi + Cothi + Gwili, Taf, E + W Cleddau, Nevern, Teifi, Aeron, Ystwyth, Rheidol, Dyfi, Dysynni, Mawddach, Artro, Dwyrhyd, Glaslyn, Dwyfawr, Llyfni, Gwyrfai, Seiont, Ogwen, Conwy, Clwyd + Elwy, Dee.

South West (1953-1989); 17 rivers: Axe, Otter, Exe, Teign, Dart, Avon + Erme, Yealm, Plym, Tavy, Tamar, Lynher, Looe, Fowey, Camel, Taw, Torridge, Lyn.

Wessex (1960-1989); 4 rivers: Avon, Stour, Piddle, Frome.

North East (1964-1989); 5 rivers: Aln, Coquet, Tyne, Wear, Yorkshire Esk.

Commercial catches

North West (1978-1989); 6 rivers: Ribble + Hodder, Lune, Kent, Leven + Crake, Duddon, Eden + Border Esk.

Welsh (1974-1989); 16 rivers: Usk, Tywi, Taf, E + W Cleddau, Nevern, Teifi, Dyfi, Dysynni, Mawddach, Glaslyn, Dwyfawr, Seiont, Ogwen, Conwy, Clwyd, Dee.

South West (1953-1989); 10 rivers: Exe, Teign, Dart, Tavy, Tamar, Lynher, Fowey, Camel, Lyn, Taw & Torridge.

Wessex (1951-1989); 2 sites: Avon + Stour, Poole Harbour.

North East (1965-1989); Northumbrian total coastal catch, Yorkshire total coastal catch.

Table 2.2 - Summary of data matrix used in analyses

	Year 1	Year 2	Year 3	Year i	
River 1	x_{11}	x_{12}	x_{13} -----	x_{1i}	\bar{x}_1, s_1^2 for River 1
River 2	x_{21}	x_{22}	x_{23} -----	x_{2i}	\bar{x}_2, s_2^2 for River 2
River 3	x_{31}	x_{32}	x_{33} -----	x_{3i}	\bar{x}_3, s_3^2 for River 3
River k	x_{k1}	x_{k2}	x_{ki} -----	x_{ki}	\bar{x}_k, s_k^2 for River k
	\bar{x}_1, s_1^2 for Year 1	\bar{x}_2, s_2^2 for Year 2	\bar{x}_3, s_3^2 ----- for Year 3	\bar{x}_i, s_i^2 for Year i	

\bar{x}_s = spatial mean catch

\bar{x}_t = temporal mean catch

s_s^2 = spatial variance

s_t^2 = temporal variance

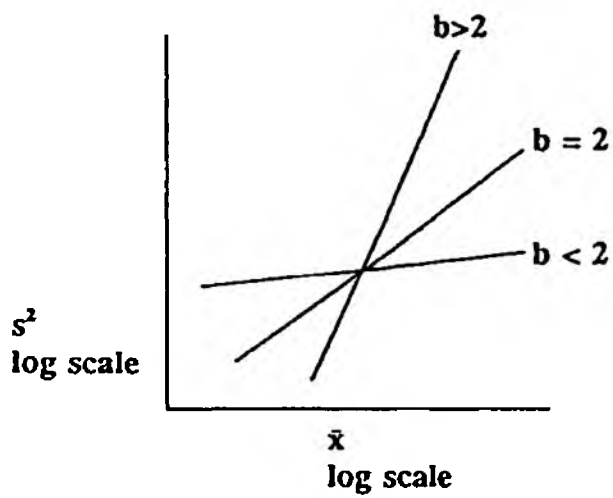
n_i years = total number of
pairs of \bar{x}_s, s_s^2 in data set

n_k rivers = total number of
pairs of \bar{x}_t, s_t^2 in data set

x_{ki} = total catch in Year i
for River k

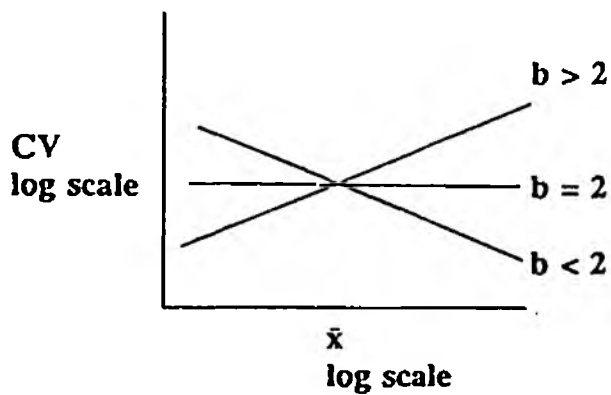
$$\bar{x} = \frac{\sum x}{n}$$

$$s^2 = \frac{\sum (x - \bar{x})^2}{n - 1}$$



$$s^2 = a \bar{x}^b$$

$$\log s^2 = \log a + b \log \bar{x}$$



$$CV = \frac{\sqrt{s^2}}{\bar{x}} = \frac{s}{\bar{x}}$$

$$= a^{0.5} \bar{x}^{(0.5b-1)}$$

Figure 2.1 - Relationships between variance (s^2) and arithmetic mean (\bar{x}) and between coefficient of variation (CV) and mean (\bar{x})

3. RESULTS

3.1 Spatial and temporal variability of rod catches

For the analyses of spatial variability, equation 1 was an excellent fit to all five data sets and the r^2 values indicated that 78-99 % of the spatial variance could be explained by variations in mean catch (Table 3.1). Values of the constant a were not significantly different ($P>0.05$) between data sets or from one (i.e. $\log_{10}a$ not significantly different from zero). Values of the power b were not significantly different ($P>0.05$) from two or between data sets from the North West, Welsh and South West regions. They were, however, significantly higher ($P<0.05$) than two for the Wessex and North East regions.

For the analyses of temporal variability, equation 1 was an excellent fit to three sets (North West, Welsh, South West) and a significant fit to the set for Wessex even though the latter was restricted to four rivers (Table 3.1). The high r^2 values indicated that 92-98% of the temporal variance could be explained by variations in mean catch. Equation 1 just failed to fit significantly the data set for the five North East rivers. Values of the constant a were again not significantly different ($P>0.05$) from one, but the power b was close to two for only the Wessex region and was significantly less ($P<0.05$) than two for the North West, Welsh and South West regions (and also for the North East region if the regression had been a significant fit).

These analyses have shown that both spatial and temporal variability of rod catches were density-dependent on mean catch. The excellent fits of the power function to all data sets, except one, are illustrated by Figures 3.1, 3.2, 3.3, 3.4, 3.5, and complementary relationships between the CV and the mean catch provide alternative views of the analyses.

With $b=2$ for spatial variability in the North West, Welsh and South West regions, the CV remained fairly constant with changes in mean catch and therefore the relative spatial variability of catches from the different rivers was roughly constant over time (Figures 3.1, 3.2, 3.3). With $b<2$ for temporal variability in these three regions, the CV decreased with increasing mean catch and therefore the relative temporal variability of catches was lower for good rivers with a high mean catch than for poor rivers with low mean catches. This means that poor rivers will be subject to years of 'boom or bust' whereas catches from good rivers vary less between years.

With $b>2$ for spatial variability in the Wessex and North East regions, the CV increased with increasing mean catch (Figures 3.4, 3.5). This relationship, together with $b=2$ for temporal variability, in the Wessex region indicates that the relative temporal variability of catches was roughly constant from river to river, but that the relative spatial variability of catches increased in good years when catches were high and decreased in bad years when catches were low. It also implies that in good years with high catches, good rivers tend to do superproportionally well, and/or in bad years with low catches, poor rivers are less affected than good rivers. All these conclusions for spatial variability are also applicable to North East rivers but the absence of a significant relationship for temporal variability makes it difficult to interpret the data further.

3.2 Spatial and temporal variability of commercial catches

As data were obtained for only two sites for each of the North East and Wessex regions (Table 2.1), analyses were restricted to three regions. For all data sets, equation 1 was an excellent fit and therefore both spatial and temporal variability of commercial catches were density-dependent on mean catch (Table 3.2, Figures 3.6, 3.7, 3.8). The high r^2 values indicated that 84-93 % of the spatial variance and 95-99 % of the temporal variance could be explained by variations in mean catch. Although they were not included in the analysis, the two Wessex values for temporal variability were remarkably similar to those obtained for South West rivers (Figure 3.8).

Values of the constant $\log_{10}a$ were not significantly different ($P>0.05$) between data sets or from zero (Table 3.2). Values of the power b were not significantly different ($P>0.05$) between the three regions, and were also not significantly different from two for spatial variability and 1.7 for temporal variability (Table 3.2). Therefore the slight increases in the CV with increasing mean catch for spatial variability in the North West and South West regions (Figures 3.6, 3.8) were not significant but, in contrast, there was a significant decrease in the CV for temporal variability with increasing mean catch in all three regions (Figures 3.6, 3.7, 3.8). These relationships are similar to those obtained for rod catches from these three regions and therefore reinforce the conclusions already drawn from the analyses of rod catches (see section 3.1).

3.3 Mean catches and coefficients of variation as a time series

As spatial variability (variation between rivers for each year) for both rod and commercial catches was strongly density-dependent on mean catch, catches from different rivers in a region varied in a synchronised manner. Therefore the overall mean catch for all rivers in a region provided a useful summary of temporal changes in catch. The relative spatial variability was measured by the coefficient of variation (CV) and this was also expressed as a time series. A large amount of data was thus reduced to a more succinct form (Figures 3.9, 3.10, 3.11, 3.12, 3.13).

It has already been concluded that the relative spatial variability of rod catches was fairly constant between years in each of the North West, Welsh and South West regions (section 3.1). This stability was well illustrated by the generally small fluctuations in CV with time (see CV for rod catches in Figures 3.9, 3.10, 3.11). There were, however, some years in which the CV was more extreme than in other years (e.g. 1981, 1982 for North West rivers; 1984, 1987, 1989 for Welsh rivers), and the stability of CV for Welsh rivers appears to have deteriorated since 1982. It is not known if any of these discrepancies are important and it must be stressed that the overall picture is one of stability.

As expected, there were no obvious relationships between fluctuations in CV and mean rod catch, and the latter varied markedly in time (see mean rod catch in Figures 3.9, 3.10, 3.11). Although rod catches were all low in 1989, the time series showed that low catches have also occurred in previous years (e.g. 1976-78 for Welsh rivers).

Fluctuations in CV for commercial catches were similar (North West, Wales) or slightly greater (South West) than those for rod catches, but once again indicated a general stability over time (see CV for commercial catches in Figures 3.9, 3.10, 3.11). Temporal changes in the mean commercial catch for South West rivers were very similar to those for rod catches (Figure 3.11) but this was not the case for North West and Welsh rivers (Figures 3.9, 3.10). There is no obvious explanation for this discrepancy. Once again, the time series showed that the low catch in 1989 was not unique; mean commercial catches were lower than the 1989 value in 1978, 1979, 1981, 1986 in the North West, 1985-87 in Wales, 1953, 1970, 1972, 1986 in the South West.

In marked contrast to the three previous regions, the relative spatial variability of rod catches in Wessex and North East regions was not fairly constant between years but was positively related to mean catch (section 3.1). It was therefore not surprising that temporal changes in CV often reflected the larger fluctuations in mean catch (Figures 3.12, 3.13). Once again, the low rod and commercial catches in 1989 in Wessex were not unique and both time series showed that similar or lower values have occurred in previous years. In contrast to other regions, the 1989 rod and commercial catches in the North East were amongst the highest recorded and the overall trend in mean catch has been upward since 1971-72 (Figure 3.13). These differences between the North East and other regions reinforce the suggestion from previous analyses that the North East rivers are different from those in the rest of England and Wales.

Although they were not used in the analyses, 1990 catches have been added for comparison (Figures 3.9 to 3.13). Rod and commercial catches for the North West, Welsh and South West regions were all very low but there was little corresponding change in the CV's (Figures 3.9, 3.10, 3.11). The mean rod catch for Wessex rivers was also low with a corresponding fall in the CV as in previous years, but the mean commercial catch was slightly higher than in 1989 (Figure 3.12). Although the mean rod and commercial catches for North East rivers fell slightly from recent values, they remained high compared with many previous values (Figure 3.13). North East catches in 1990 were therefore relatively higher than those in other regions, once again supporting the conclusion that these rivers are different from those in other regions.

3.4 Temporal variability of rod catches from all 67 rivers

The variation in catches between years for each river (s^2) was strongly density-dependent on the overall mean annual catch (\bar{x}) for each river (Figure 3.14a), the relationship being well described by a power-function (Table 3.3). The coefficient of determination (r^2) indicates that 93% of the between-years-variation in catch could be explained simply by variations in the overall mean catch for each river. As the power b was significantly less than two ($P < 0.001$), there was an expected decrease in the Coefficient of Variation (C.V.) with increasing mean catch (Figure 3.14b). The relative temporal variability of catches therefore decreased from a high value for poor rivers with low catches to a low value for good rivers with high catches.

As there was such a strong relationship between temporal variance and mean catch, it was not surprising that there were no obvious outliers, i.e. no data points departed significantly from the regression line (Figure 3.14a). A suitable and simple discriminating function was the logarithmic difference between observed and expected s^2 expressed as a percentage of log

expected s^2 , i.e. $100 (\log \text{ observed } s^2 - \log \text{ expected } s^2) / (\log \text{ expected } s^2)$. Observed values were 18.6% higher than expected for the Neath, 14.4% higher for the Tyne, 11.1% higher for the Wye, 10.4% higher for the Avon, and 12.1% lower than expected for the Ehen, 11.4% lower for the Yealm. The discrepancy for the remaining 61 rivers was less than 10%. If this was increased slightly to 11%, then the number of rivers increased to 64 to reduce the exceptions to the Neath, Tyne and Ehen.

3.5 Temporal variability of commercial catches from all 36 rivers

The variance to mean and C.V. to mean relationships were similar to those for rod catches (Figure 3.15 a,b), the former being well described by a power-function (Table 3.3). The coefficient of determination (r^2) was even higher than that for rod catches and indicates that 98% of the between-years-variation in catch could be explained by variations in the overall mean catch for each river.

Once again there were no obvious outliers, but the discriminating function used for rod catches was also applied to the commercial catches. Observed values were 15.6% higher than expected for the Mawddach, 18.0% lower than expected for the Dee, and 15.6% lower for the Cledau. The discrepancy for the remaining 33 rivers was 11% or less.

3.6 Classification of sea-trout rivers

The rivers were classified according to overall mean catch and their relative variability in catch between years, the latter being expressed as the Coefficient of Variation (C.V.%). As the power-function was the model used in the analyses, the divisions for mean catch and C.V. were on logarithmic scales. The natural break-points for mean annual catch were 105 and 1000 so that all rivers could be classified into those with a low annual catch (<105 fish/year), those with a medium annual catch (105-1000 fish/year) and those with a high annual catch (>1000 fish/year). Similarly, the break-points for C.V. were 50% and 86% so that rivers could be classified into those with high temporal variability (C.V.>86%), with medium variability (C.V. 50-86%) and with low variability (C.V.<50%). The results of this classification are summarised for rod catches from 67 rivers in Table 3.4 and commercial catches from 36 rivers in Table 3.5.

For rod catches (Table 3.4) there were: 11 rivers with high variability (C.V.>86%), and these were subdivided into 10 with low annual catches (<105 fish), one with a medium catch (105-1000 fish) and none with a high annual catch (>1000 fish); 32 rivers with medium variability (C.V. 50-86%), and these were subdivided into 9 with low catches, 20 with medium catches and 3 with high catches; 24 rivers with low variability (C.V.<50%), and these were subdivided into 15 with medium catches and 9 with high catches. It is obvious that high and low catches were associated predominantly with low and high temporal variability respectively.

For commercial catches (Table 3.5) there were: 4 rivers with high variability (C.V.>86%), all with low annual catches (<105 fish); 15 rivers with medium variability (C.V. 50-86%), and these were subdivided into 10 with low catches and 5 with medium catches (105-1000 fish);

17 rivers with low variability (C.V.<50%), and these were subdivided into only one with a low catch, 7 with medium catches and 9 with high catches (>1000 fish). Once again, high and low catches were associated predominantly with low and high temporal variability respectively.

Table 3.1 - Summary of statistics for rod catches of sea-trout

Spatial variability	$\log_{10}a$ (95%CL)	b (95%CL)	r^2	n	P
North West	0.592 (1.314)	1.830 (0.520)	0.831	14	<0.001
Welsh	0.203 (1.147)	2.033 (0.404)	0.893	16	<0.001
South West	-0.209 (0.411)	2.098 (0.153)	0.957	37	<0.001
Wessex	-0.141 (0.258)	2.217 (0.104)	0.986	30	<0.001
North East	-1.583 (1.321)	2.491 (0.561)	0.778	26	<0.001
Temporal variability					
North West	0.587 (0.490)	1.481 (0.214)	0.955	13	<0.001
Welsh	0.637 (0.475)	1.555 (0.182)	0.922	28	<0.001
South West	0.142 (0.487)	1.765 (0.194)	0.962	17	<0.001
Wessex	-0.197 (2.046)	2.012 (0.934)	0.977	4	<0.05
North East	0.398 (6.758)	1.679 (2.858)	0.538	5	>0.05 (N.S.)

Table 3.2 - Summary of statistics for commercial catches of sea-trout

Spatial variability	$\log_{10}a$ (95%CL)	b (95%CL)	r^2	n	P
North West	-0.086 (1 .456)	2.205 (0 .481)	0.912	12	<0.001
Welsh	0.270 (0 .869)	2.021 (0 .325)	0.927	16	<0.001
South West	-0.254 (0 .959)	2.271 (0 .344)	0.839	37	<0.001
Temporal variability					
North West	0.217 (0 .437)	1.693 (0 .186)	0.994	6	<0.001
Welsh	0.046 (0 .528)	1.715 (0 .223)	0.951	16	<0.001
South West	0.220 (0 .375)	1.714 (0 .156)	0.988	10	<0.001

Table 3.3 - Summary of statistics for temporal variability of sea-trout catches

	$\log_{10}a$ (+95%CL)	b (+95%CL)	r^2	n	P
Rod Catches	0.416 <u>+0.278</u>	1.636 <u>+0.112</u>	0.930	67	<0.001
Commercial Catches	0.0864 <u>+0.217</u>	1.733 <u>+0.0864</u>	0.980	36	<0.001

Equation: $\log_{10} s^2 = \log_{10} a + b \log_{10} \bar{x}$

$$s^2 = a \bar{x}^b$$

where s^2 = temporal variance, \bar{x} = temporal mean catch

TABLE 3.4 - Rod catches: Classification of 67 rivers

	I. High Temporal Variability (CV>86%)				II. Medium Temporal Variability (CV50-86%)				III. Low Temporal Variability (CV<50%)			
	River (region)	\bar{x}	year ⁻¹	CV% n	River (region)	\bar{x}	year ⁻¹	CV% n	River (region)	\bar{x}	year ⁻¹	CV% n
(a) Low Annual Catch (<105)	1 Ellen (NW)	12.9	101	14	1 Duddon (NW)	26.9	66	14				
	2 Exe (SW)	17.3	122	37	2 Yealm (SW)	36.5	57	37				
	3 Wye (W)	17.6	131	16	3 Usk (W)	43.6	71	16				
	4 Wyre (NW)	27.9	90	14	4 Otter (SW)	59.2	70	37				
	5 Piddle (Wx)	35.9	89	36	5 Itt (NW)	69.1	58	14				
	6 Stour (Wx)	58.3	105	39	6 Frome (Wx)	74.9	70	40				
	7 Gwyrfaï (W)	67.1	95	16	7 Dee (W)	83.2	60	15				
	8 Neath (W)	99.3	154	15	8 Axe (SW)	97.5	66	37				
	9 Esk (NW)	101.4	101	14	9 Aln (NE)	97.8	75	26				
	10 Lyn (SW)	104.3	106	37								
(b) Medium Annual Catch (105-1000)	1 Tyne (NE)	264.6	121	26	1 Artro (W)	132.9	53	16	1 Ehen (NW)	149.1	37	14
					2 Looe (SW)	135.3	54	31	2 Dwyryd (W)	151.1	45	16
					3 Loughor (W)	168.5	79	15	3 Lynher (SW)	236.9	43	37
					4 Ogwen (W)	184.7	51	16	4 Coquet (NE)	251.3	45	26
					5 Leven/ Crake (NW)	231.4	64	14	5 Kent (NW)	252.6	45	14
					6 Dysynni (W)	250.6	63	16	6 Avon/Erne (SW)	271.2	44	37
					7 Plym (SW)	259.5	64	37	7 Derwent/ Cocker (NW)	281.2	47	14
					8 Nevern (W)	280.6	81	16	8 Conwy (W)	430.6	40	16
					9 Wear (NE)	298.2	57	26	9 Ribble/ Hodder (NW)	529.8	36	14
					10 Yorks Esk (NE)	315.6	55	26	10 Glaslyn (W)	530.3	38	16
					11 Taf (W)	343.4	54	16	11 Aeron (W)	670.4	45	16
					12 Ogmore (W)	359.2	86	15	12 Esk Border (NW)	671.9	31	14
					13 Ystwyth (W)	373.0	57	16	13 Eden (NW)	721.6	41	14
					14 Tamar (SW)	418.7	58	37	14 Tavy (SW)	767.7	48	37
					15 Seiont (W)	428.6	53	16	15 Rheidol (W)	781.0	30	16
					16 Tawe (W)	486.3	51	14				
					17 Llyfni (W)	598.1	77	16				
					18 Dart (SW)	690.9	59	37				
					19 E/W Cloddau (W)	812.9	61	16				
					20 Torridge (SW)	879.4	72	37				
(c) High Annual Catch (>1000)					1 Camel (SW)	1124.5	60	37	1 Clwyd/Elwy (W)	1049.1	40	16
					2 Avon (Wx)	1148.9	86	40	2 Mawddach (W)	1078.8	46	16
					3 Taw (SW)	1369.4	61	37	3 Teign (SW)	1153.5	45	37
									4 Lune (NW)	1394.0	28	14
									5 Fowey (SW)	1441.1	46	37
									6 Dwyfawr (W)	1596.4	44	16
									7 Dyfi (W)	1880.0	29	16
									8 Teifi (W)	2499.9	38	16
									9 Tywi (W)	4750.3	42	16

Table 3.5 - Commercial catches: Classification of 36 rivers

I. High Temporal Variability (CV>86%)					II. Medium Temporal Variability (CV50-86%)					III. Low Temporal Variability (CV<50%)				
River (region)		\bar{x} year ⁻¹	CV%	n	River (region)		\bar{x} year ⁻¹	CV%	n	River (region)		\bar{x} year ⁻¹	CV%	n
(a) Low Annual Catch (<105)	1 Mawddach (W)	24.1	113	16	1 E/W Cleddau (W)	10.3	58	16		1 Usk (W)	77.5	40	16	
	2 Kent (NW)	31.2	92	12	2 Leven (NW)	19.2	82	11						
	3 Lyn (SW)	42.1	93	36	3 Ribble (NW)	26.3	61	12						
	4 Nevern (W)	55.2	92	13	4 Exe (SW)	28.4	78	37						
					5 Frome/Fiddle (Wx)	51.2	61	39						
					6 Lynher (SW)	54.1	62	37						
					7 Camel (SW)	79.5	80	35						
					8 Duddon (NW)	82.5	66	12						
					9 Conwy (W)	84.3	51	16						
					10 Ogwen (W)	99.7	67	16						
(b) Medium Annual Catch (105-1000)					1 Fowey (SW)	123.0	50	37		1 Dee (W)	132.7	26	16	
					2 Taf (W)	134.0	53	16		2 Dysynni (W)	194.6	47	16	
					3 Tavy (SW)	241.5	66	37		3 Seiont (W)	305.0	46	16	
					4 Glastyn (W)	241.6	52	16		4 Dwyfawr (W)	352.3	45	16	
					5 Tamar (SW)	287.6	62	37		5 Avon/Stour (Wx)	458.9	47	39	
(c) High Annual Catch (>1000)										6 Dart (SW)	529.5	46	37	
										7 Teifi (W)	972.2	47	16	
										1 Clwyd (W)	1136.8	47	16	
										2 Lune (NW)	1254.9	49	12	
										3 Teign (SW)	1299.0	44	37	
										4 Dyfi (W)	1387.9	37	16	
										5 Tywi (W)	2503.3	31	16	
										6 Taw/Torridge (SW)	3737.4	43	37	
										7 Eden/Border Esk (NW)	5108.9	31	12	
										8 Yorks Coastal (NE)	15512.6	40	25	
										9 Northum/ Coastal (NE)	30128.3	26	25	

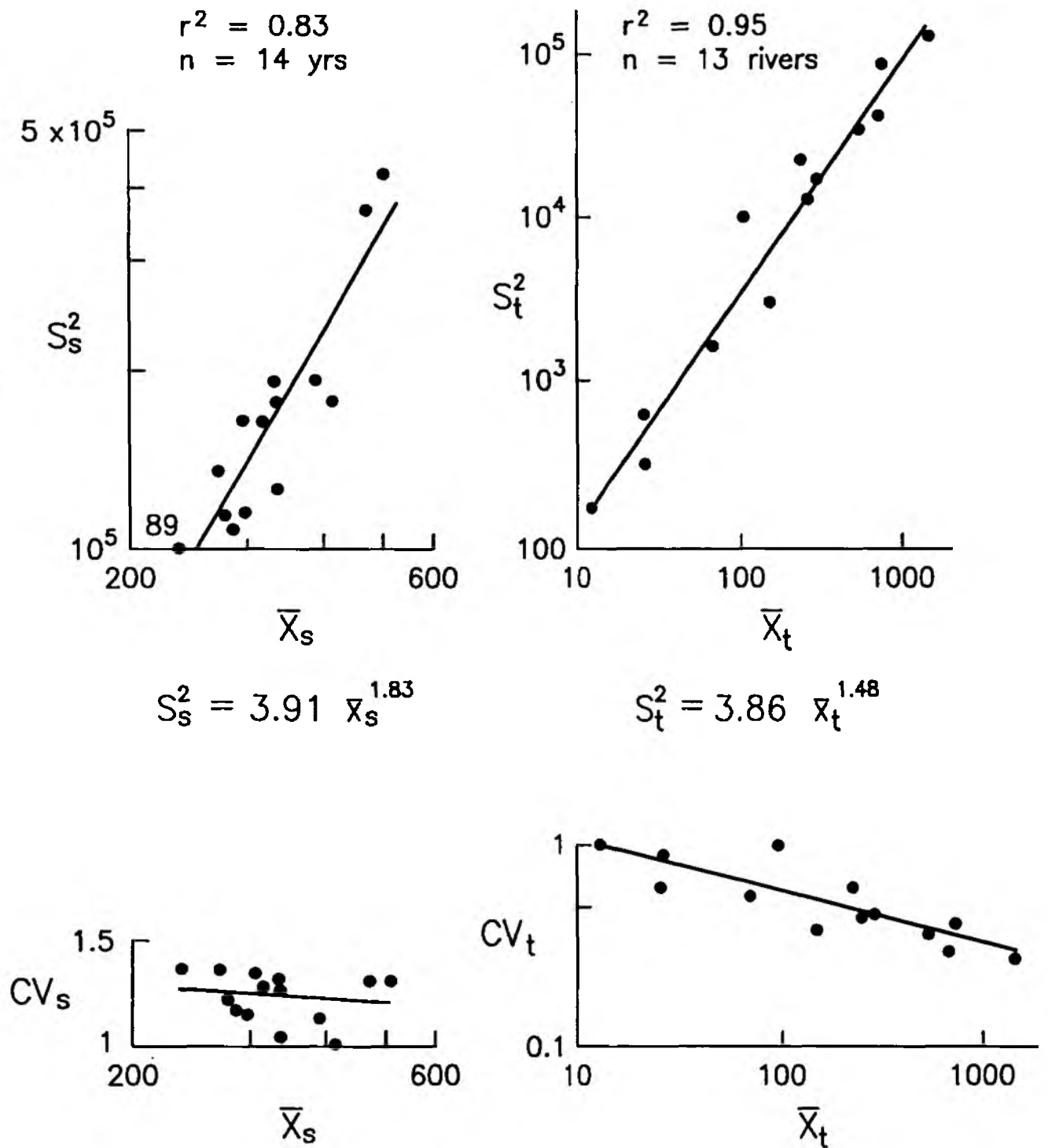
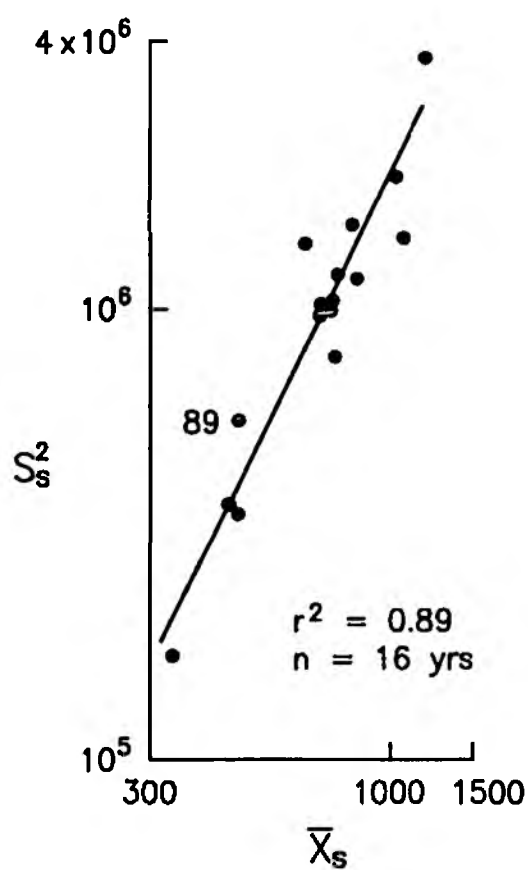
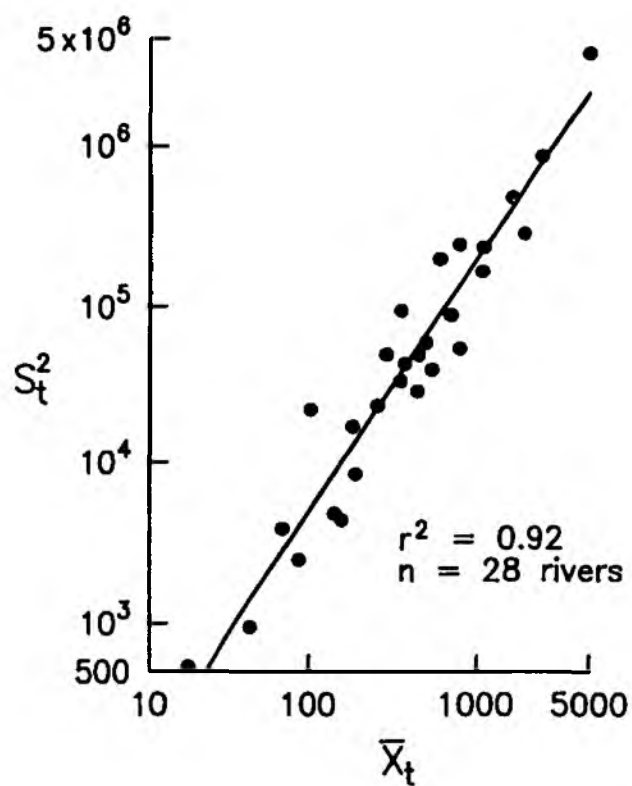


Figure 3.1 - Rod catches for North West rivers: relationships between variance and mean, and between CV and mean for spatial variability (s_s^2 , \bar{x}_s) and temporal variability (s_t^2 , \bar{x}_t).



$$S_s^2 = 1.59 \bar{X}_s^{2.03}$$



$$S_t^2 = 4.34 \bar{X}_t^{1.55}$$

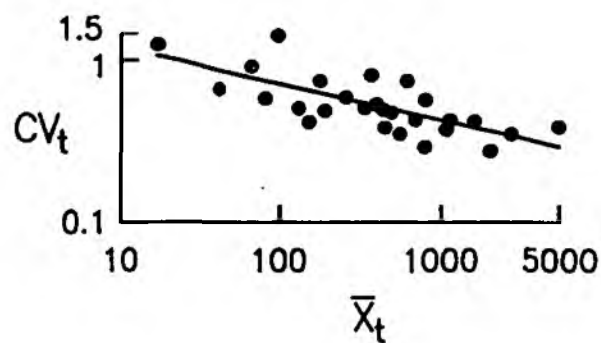
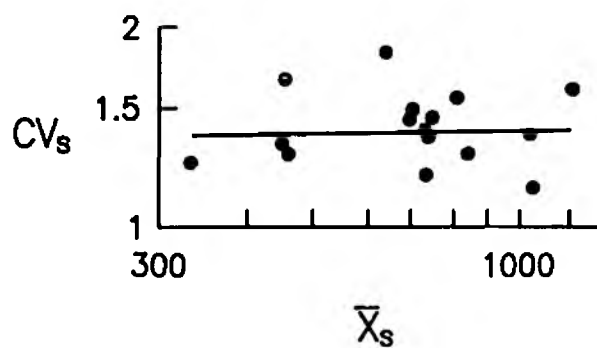


Figure 3.2 - Rod catches for Welsh rivers: legend as in Figure 3.1

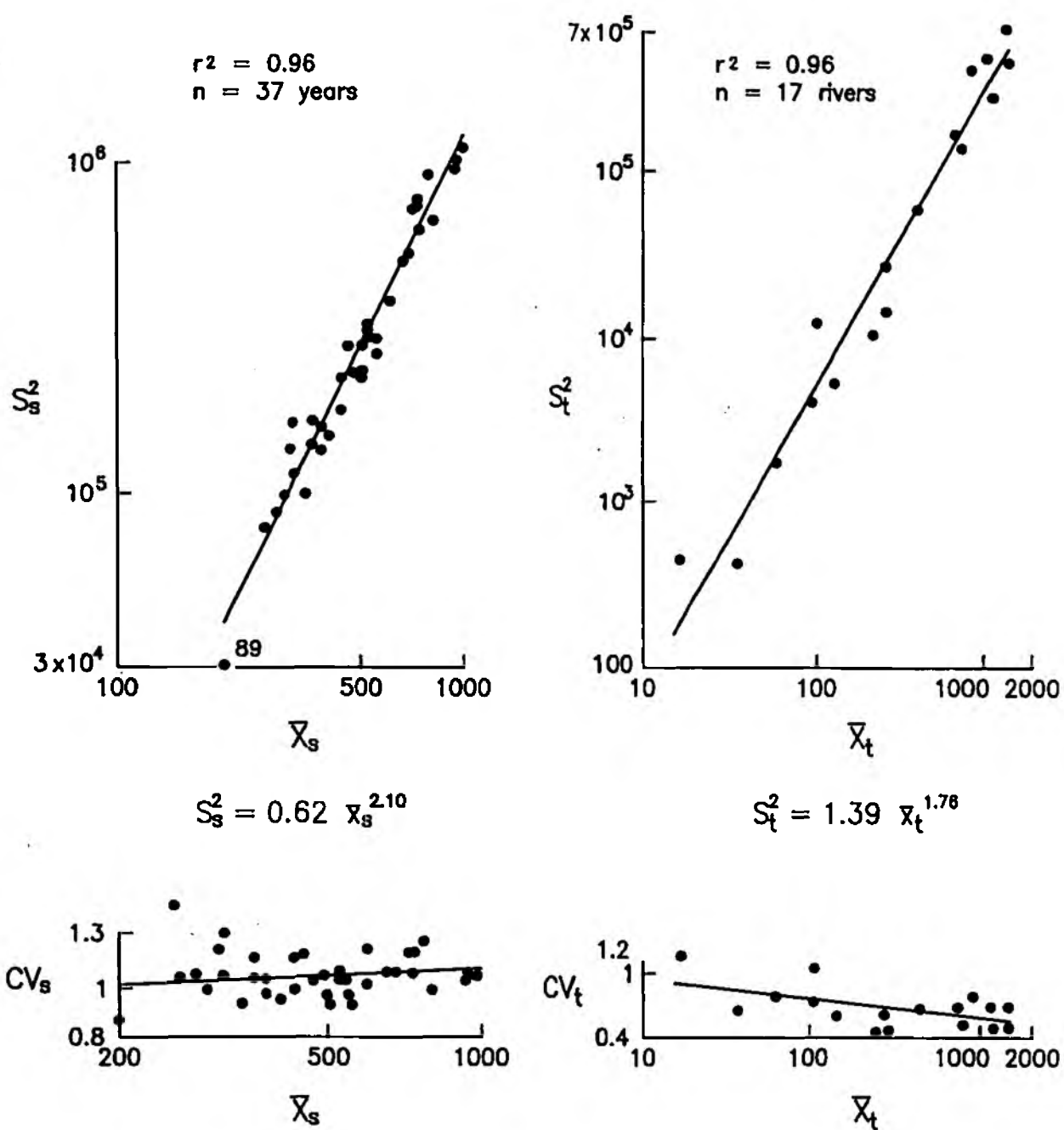
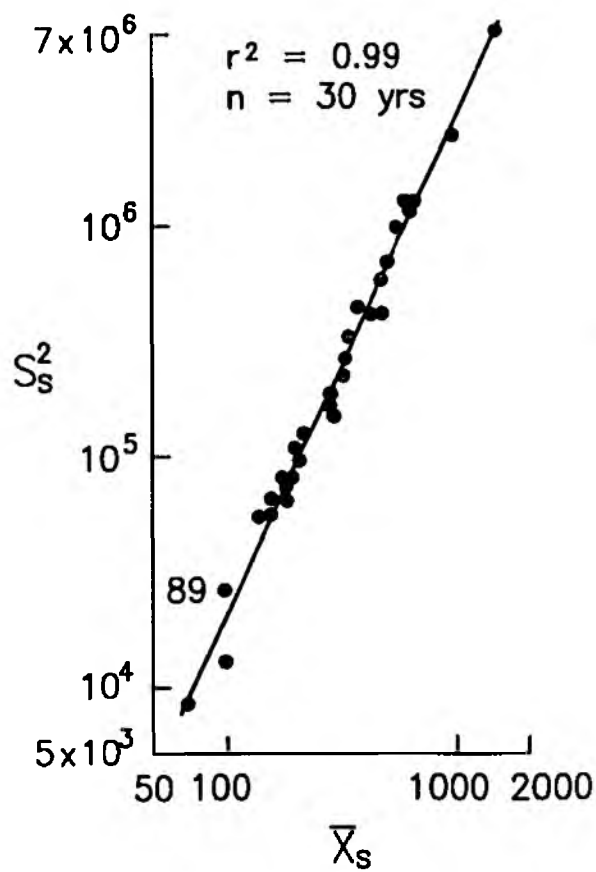
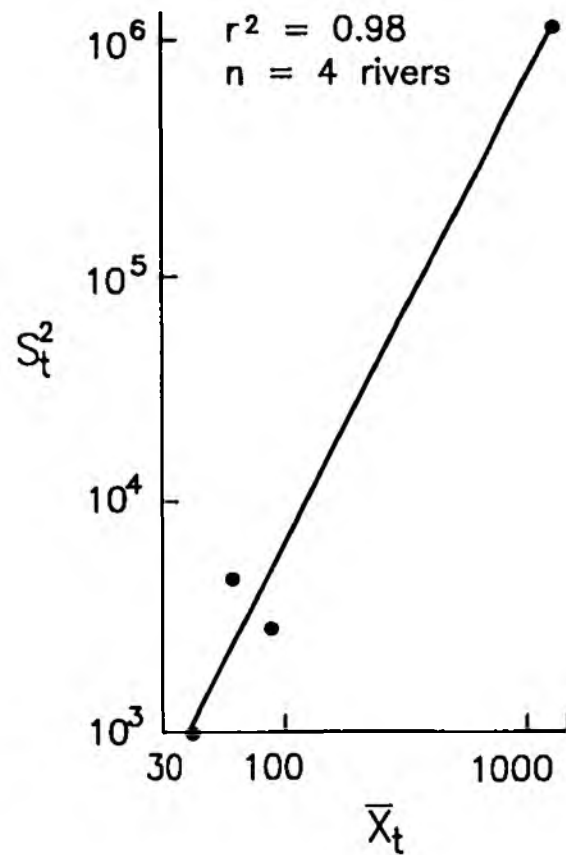


Figure 3.3 - Rod catches for South West rivers: legend as in Figure 3.1



$$S_s^2 = 0.723 \bar{X}_s^{2.22}$$



$$S_t^2 = 0.635 \bar{X}_t^{2.012}$$

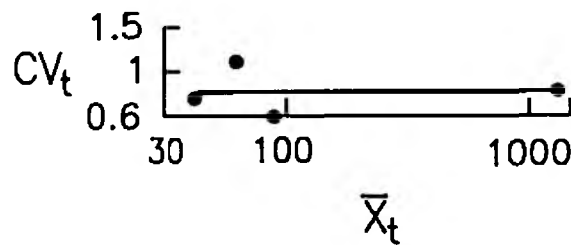
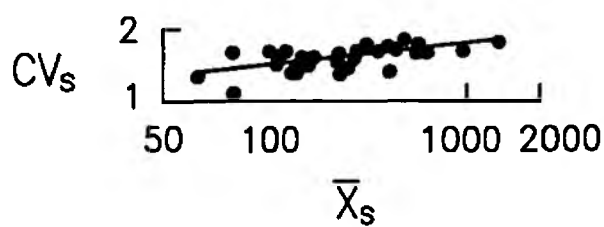


Figure 3.4 - Rod catches for Wessex rivers : legend as in Figure 3.1

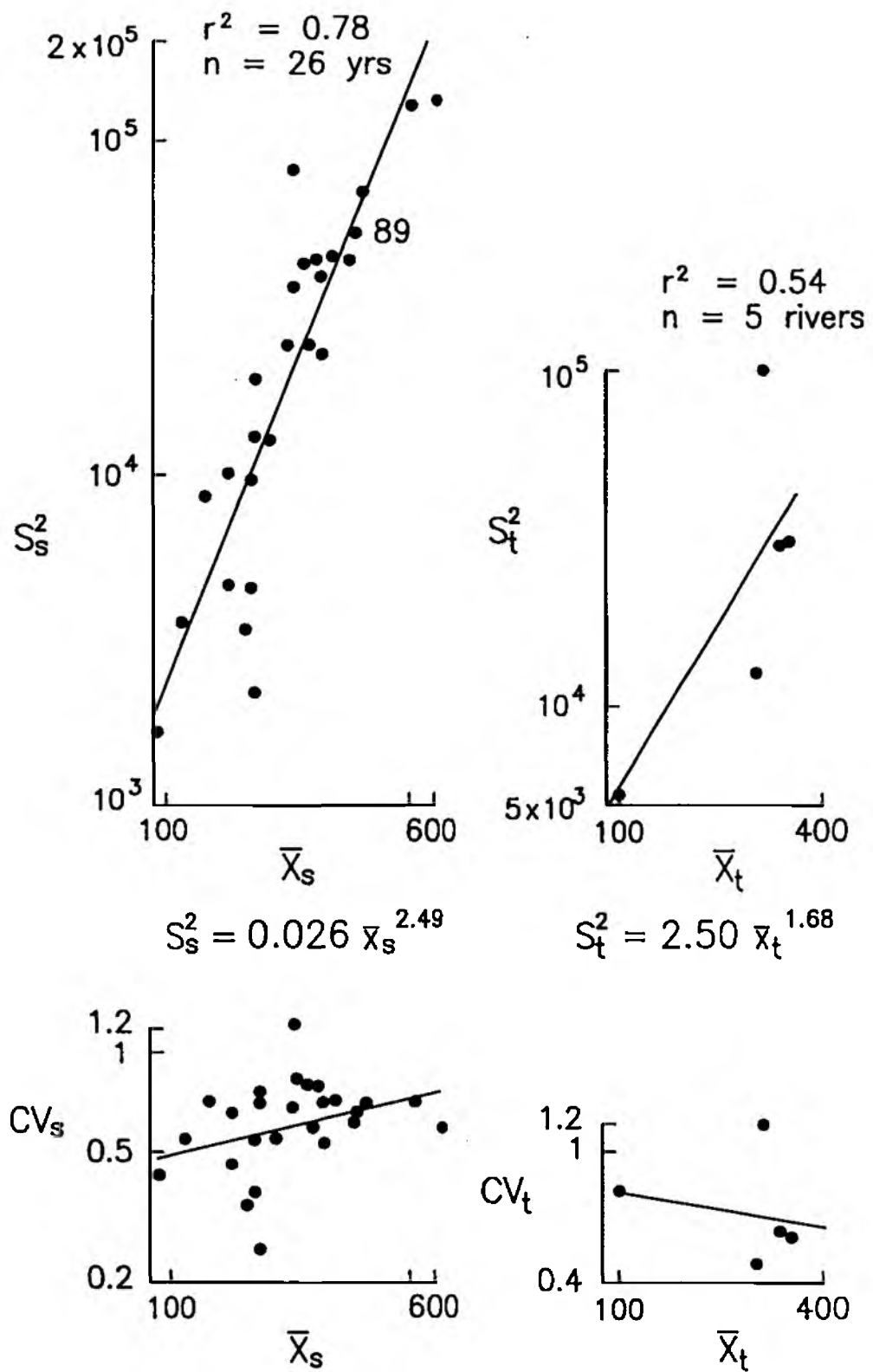


Figure 3.5 - Rod catches for North East rivers : legend as in Figure 3.1

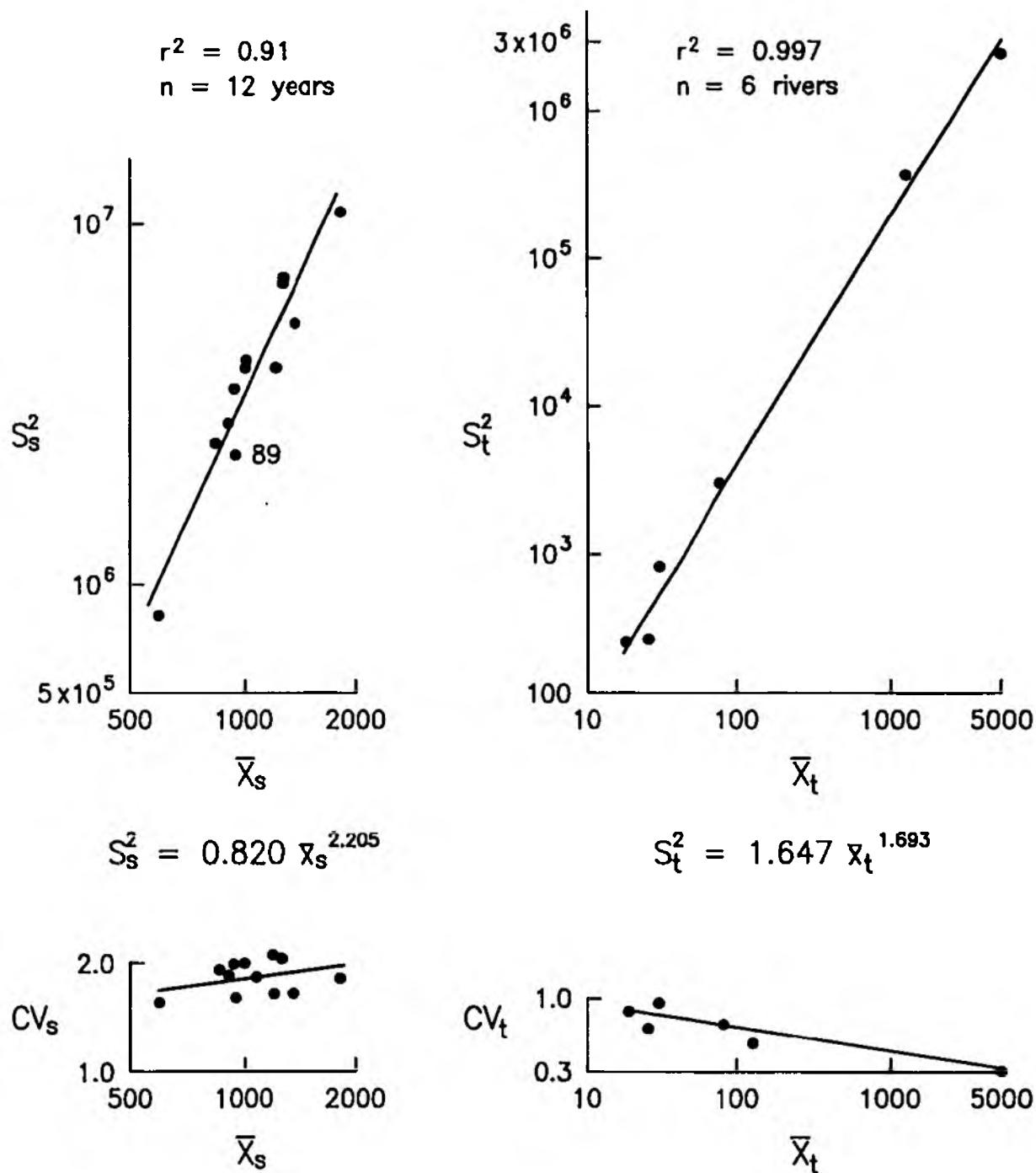


Figure 3.6 - Commercial catches for North West rivers: legend as in Figure 3.1

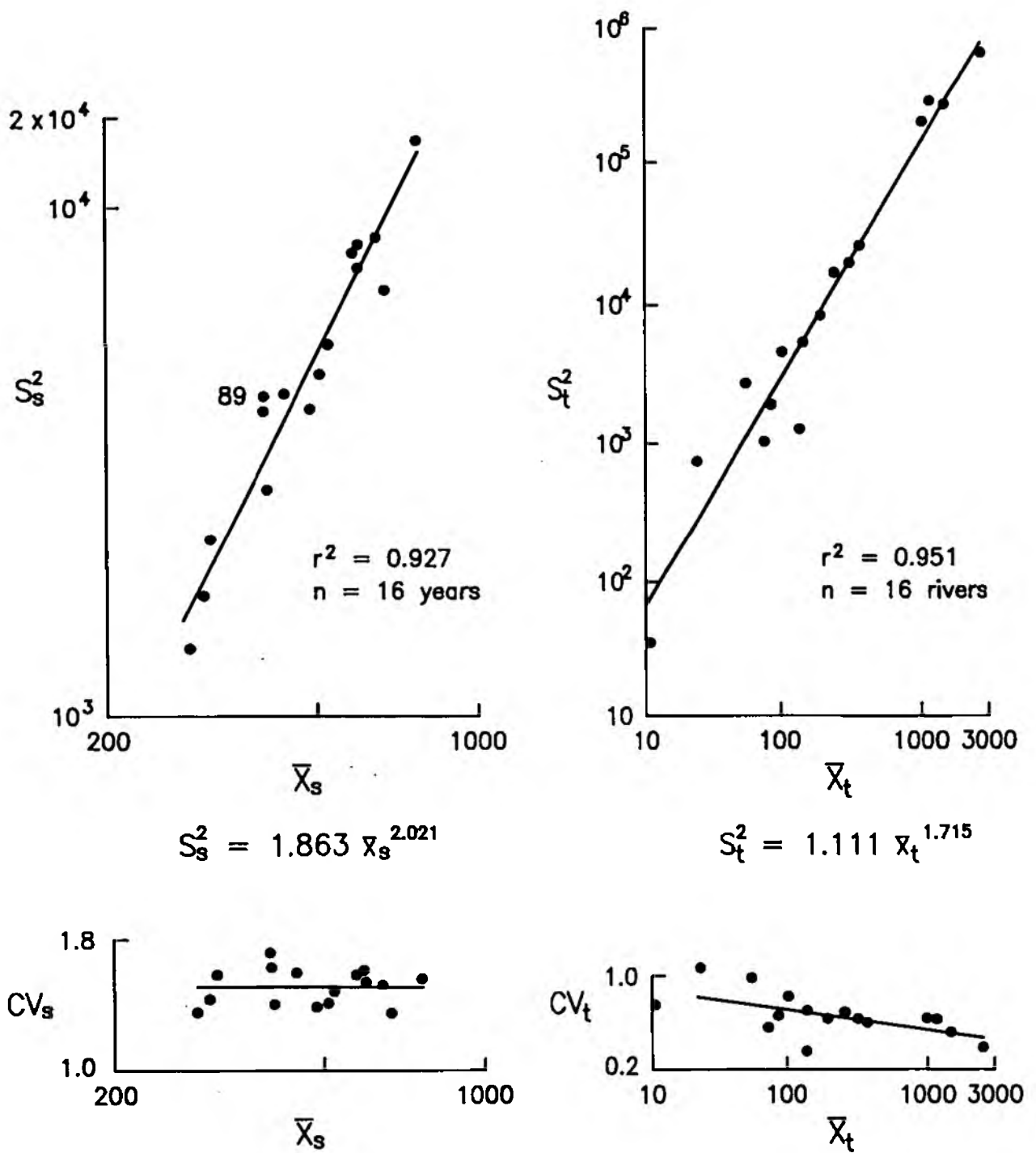
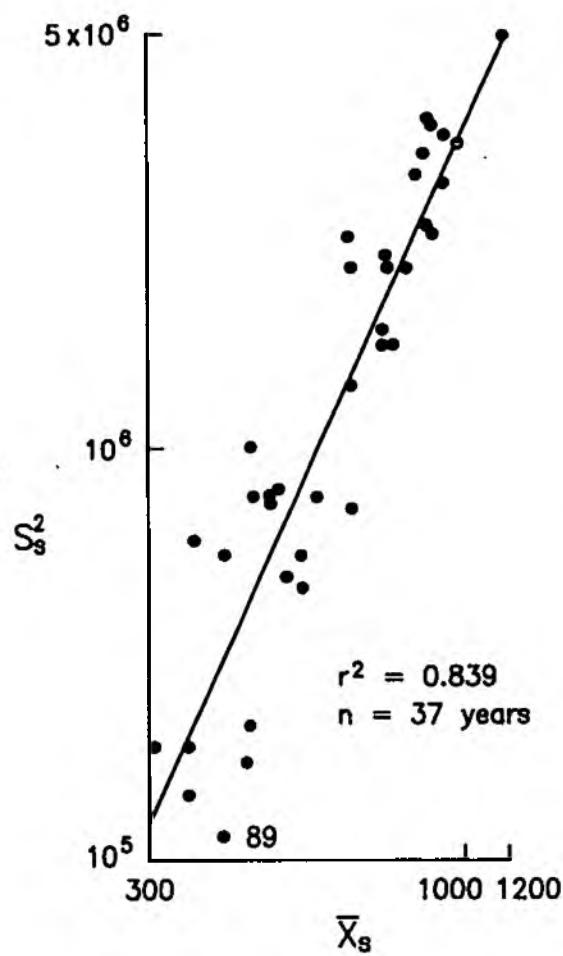
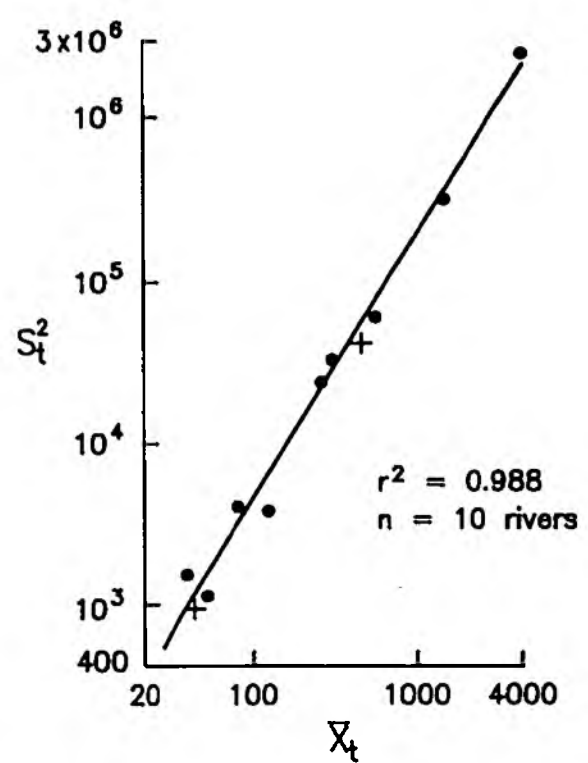


Figure 3.7 - Commercial catches for Welsh rivers: legend as in Figure 3.1



$$S_s^2 = 0.557 \bar{X}_s^{2.271}$$



$$S_t^2 = 1.660 \bar{X}_t^{1.714}$$

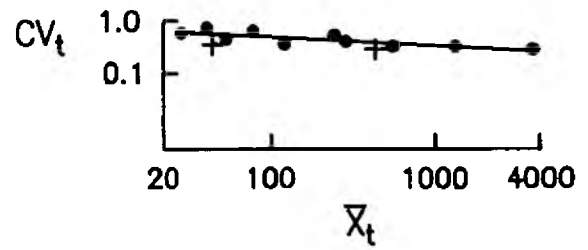
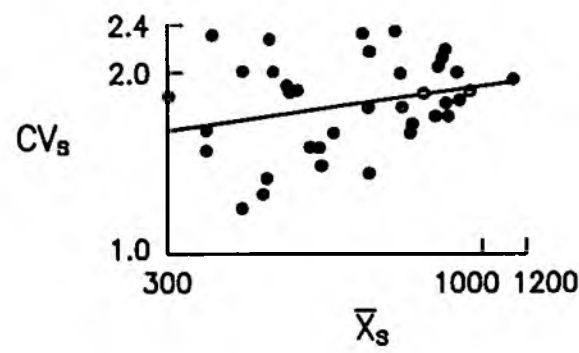


Figure 3.8 - Commercial catches for South West rivers: legend as in Figure 3.1 (note that two values from Wessex have been added for comparison to right hand figure but were not included in the analysis)

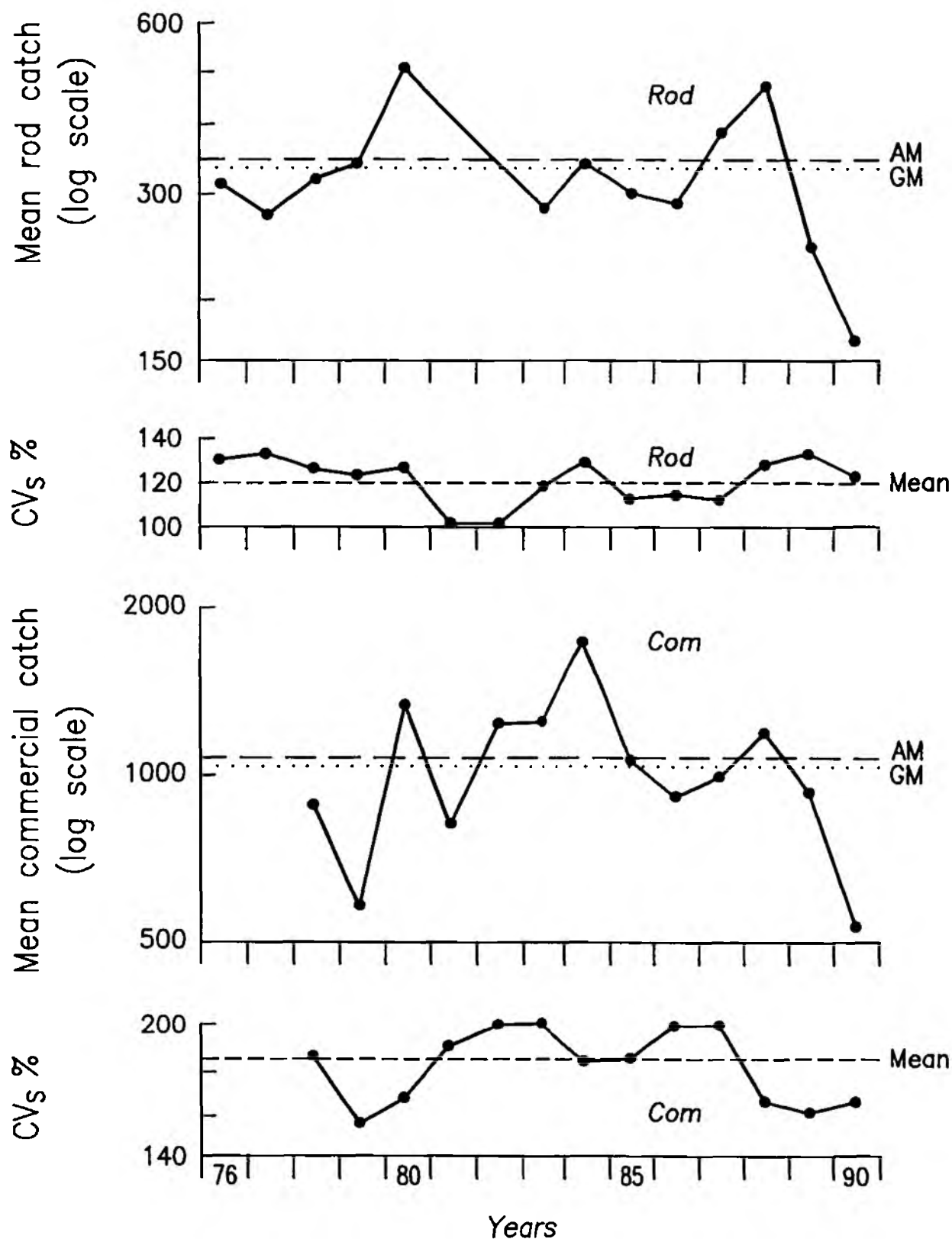


Figure 3.9 - North West rivers : temporal changes in the mean rod catch per river, mean commercial catch per river and their corresponding coefficients of variation (CV); mean catch is on log scale with overall arithmetic mean (AM) and geometric mean (GM).

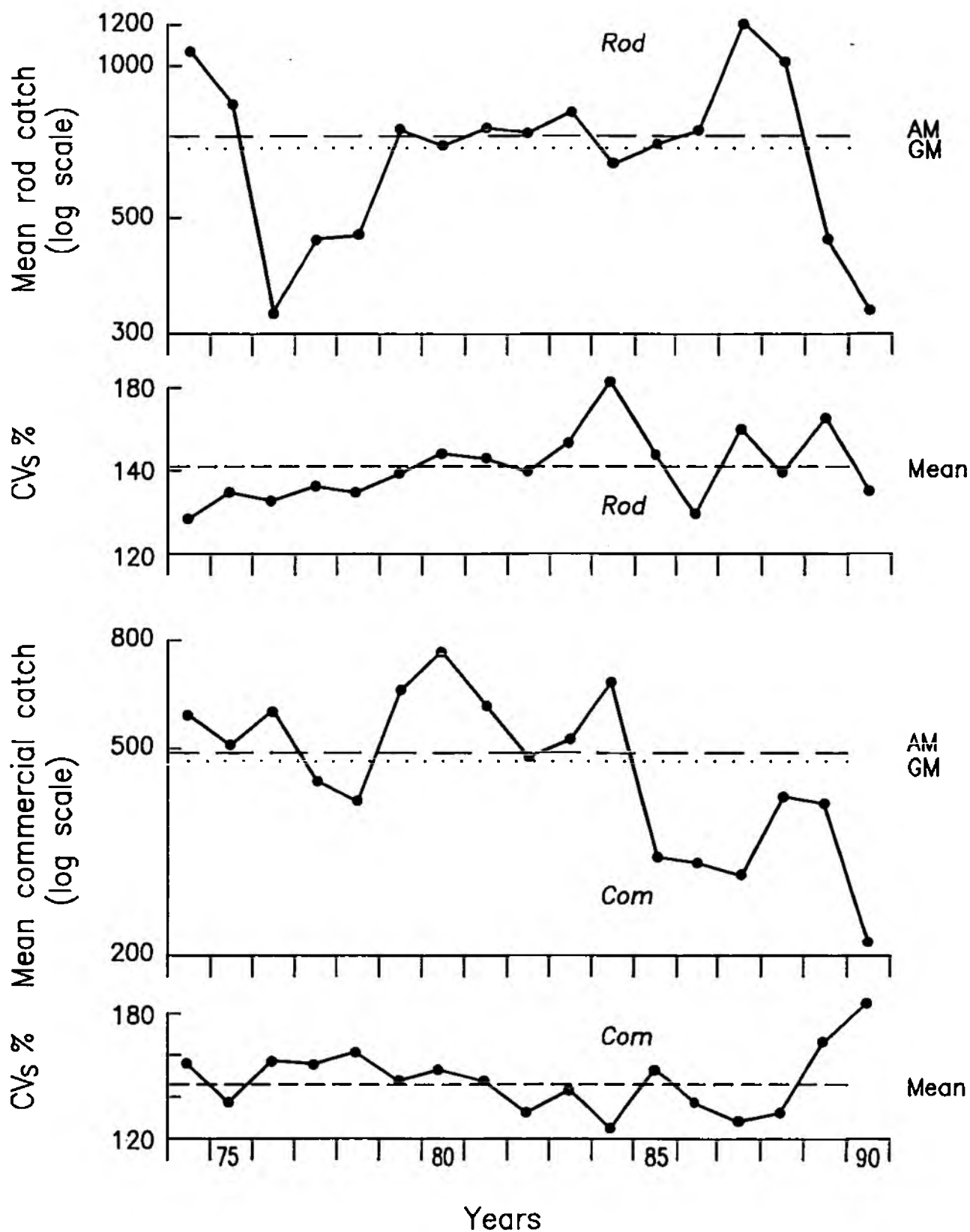


Figure 3.10 - Welsh rivers : legend as in 3.9

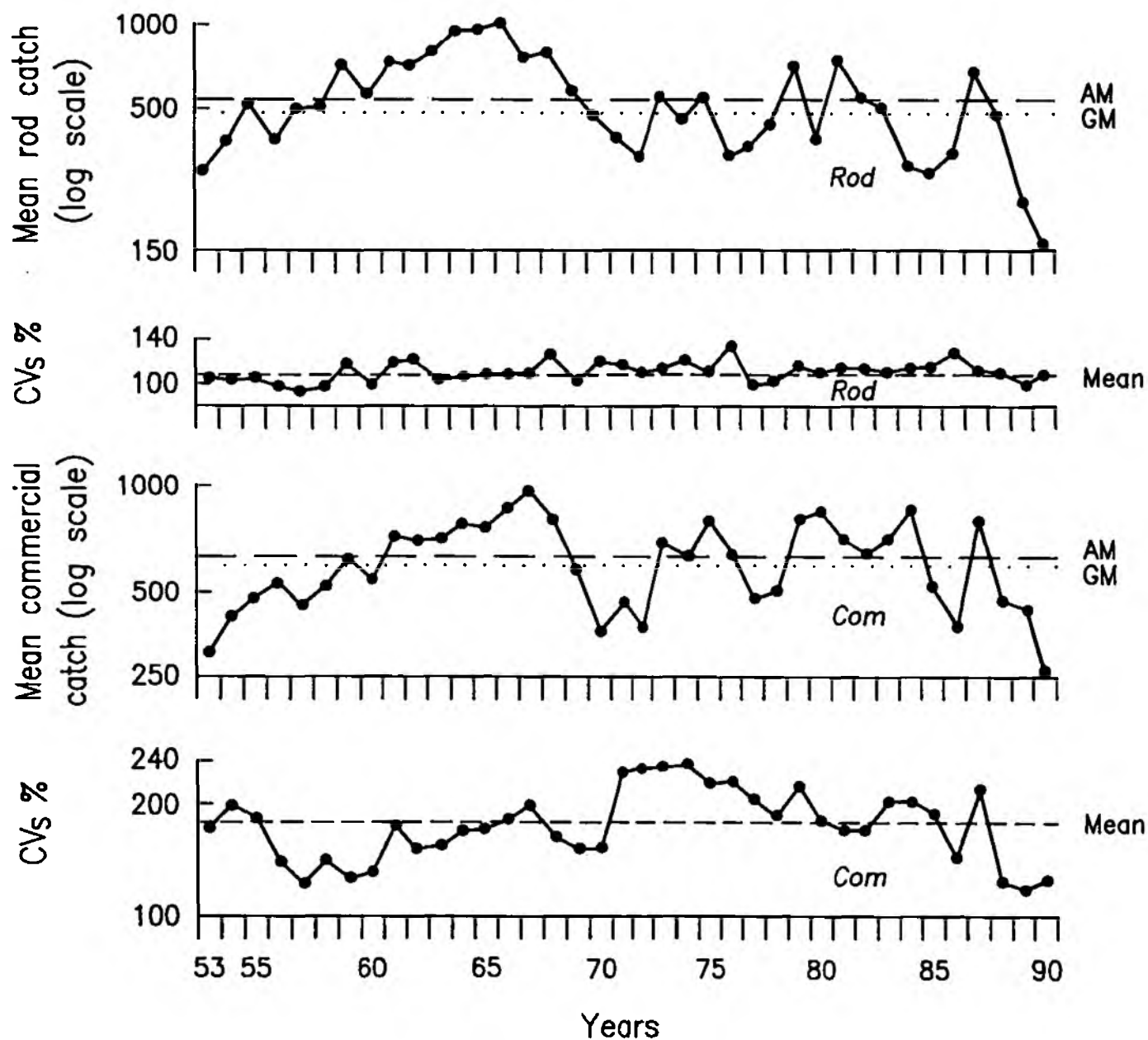


Figure 3.11 - South West rivers : legend as in 3.9

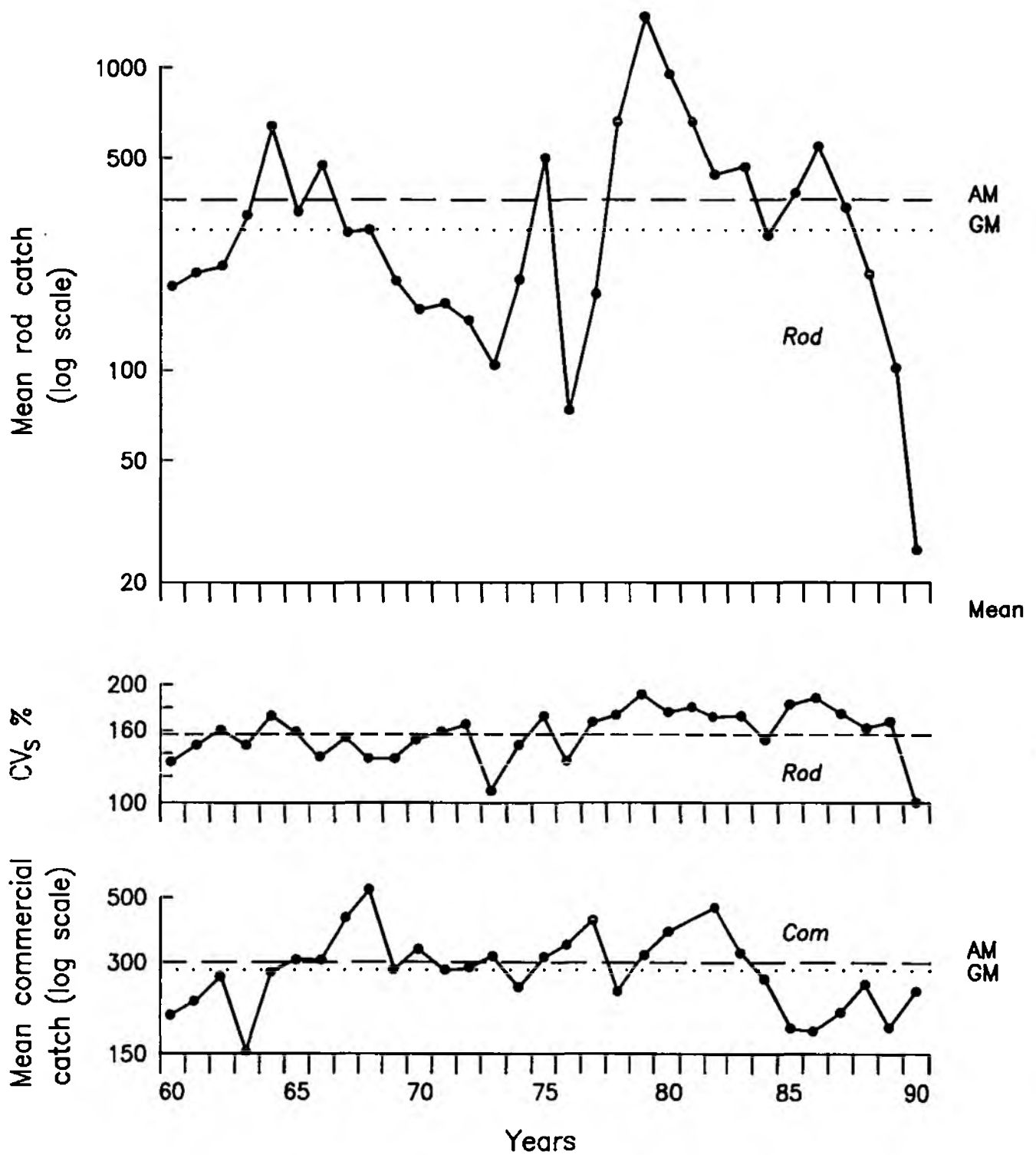


Figure 3.12 - Wessex rivers : legend as in 3.9

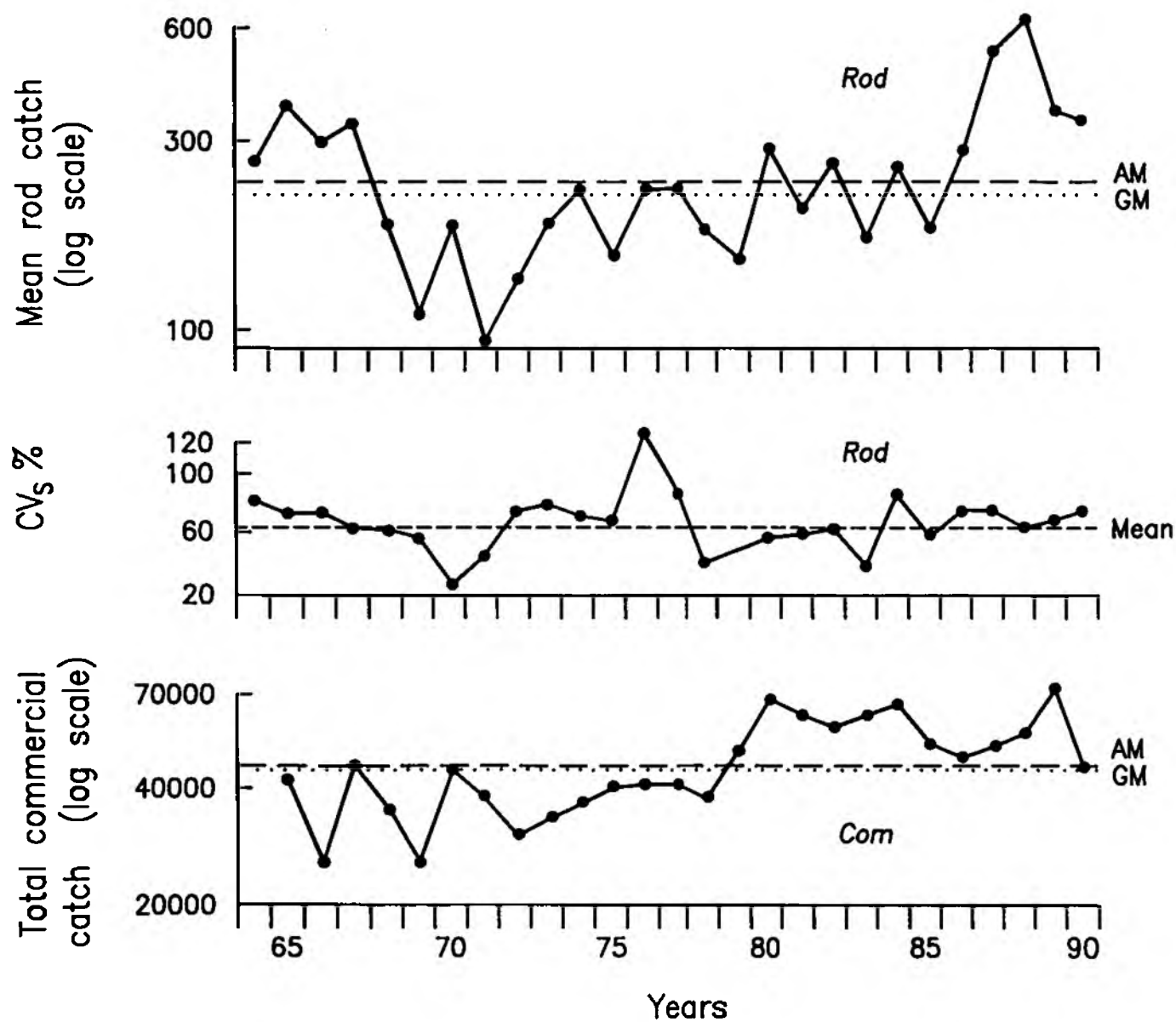


Figure 3.13 - North East rivers : legend as in 3.9

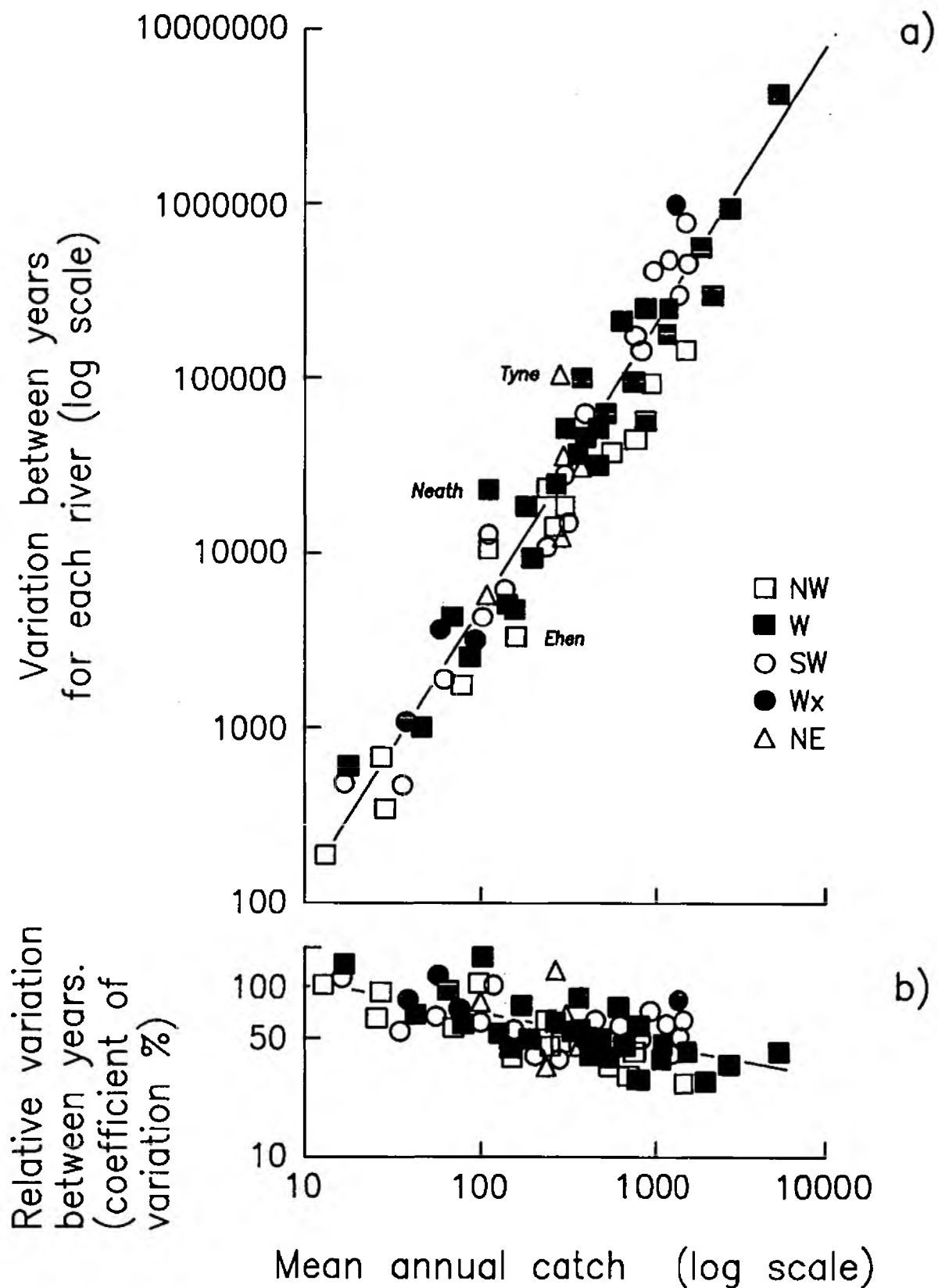


Figure 3.14 - Rod catches : relationships between variance and mean and between C.V. and mean annual catch.

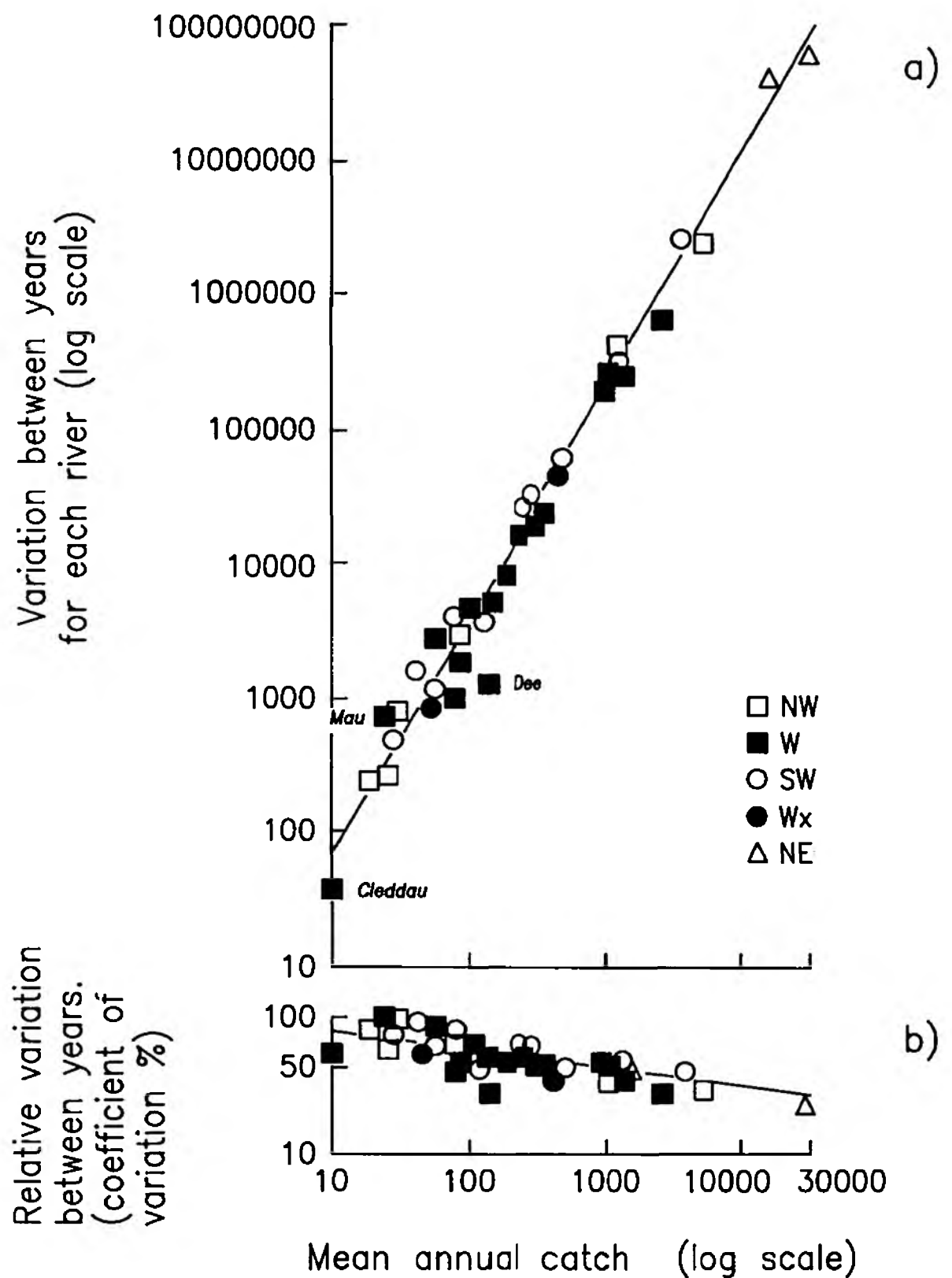


Figure 3.15 - Commercial catches : relationships between variance and mean and between C.V. and mean annual catch.

4. DISCUSSION

These analyses have shown that both spatial and temporal variability of both rod and commercial catches was strongly density-dependent on mean catch. The remarkably good fit of the power function to all, except one, of the data sets (Tables 3.1, 3.2) clearly indicated the strong synchronicity of catches from different rivers in each region. There were no significant differences between parameter estimates for the data sets from the three regions (North West, Wales, South West) and therefore catch data from these regions could be treated as a single set in future analyses. Although parameter estimates from two regions (Wessex, North East) were significantly different from those for other regions, this discrepancy could be due to only one or two rivers rather than the whole data set.

As the power b for spatial variability was not significantly different from two for both rod and commercial catches from three regions (North West, Wales, South West), the relative spatial variability (measured by CV) remained fairly constant between years in spite of wide fluctuations in mean catch (see Figures 3.1 to 3.3, 3.6 to 3.11). Such a result is valuable because it means that, for log-transformed data, there will be effectively no relationship between the variance (or standard deviation or CV) and the mean, a most desirable property for subsequent analyses. For example, factors other than mean catch could be examined by analysis of variance on the log-transformed catches and the conclusions would not be invalidated by the variance-mean relationship. Analysis of the variance or standard deviation of the log-transformed data has one major disadvantage; it cannot deal with zero catches except by adding one to all catches before transformation and this practice is not without risk (Anscombe 1948). The CV is not subject to this problem and is often easier to interpret and analyze (van Valen 1978, Sokal and Braumann 1980, McArdle et al. 1990).

The interpretation of spatial variability for rod catches in the Wessex and North East regions was more complicated because the power b was significantly greater than two. Relative spatial variability (measured by CV) therefore increased with mean catch so that it was low in bad years with low catches and high in good years with high catches (see Figures 3.4, 3.5, 3.12, 3.13). Therefore catch differences between rivers will be much higher in good years because rivers with the highest catches will do superproportionally well. Conversely, catch differences between rivers will be relatively small in poor years and rivers with the highest catches will do superproportionally badly. It is again important to discover if these generalisations are applicable to all rivers in the two regions or if they are simply due to only one or two rivers.

Parameter estimates for temporal variability were similar not only for rod and commercial catches from North West, Welsh and South West rivers but also for rod catches from the North East, even though the power function was not a significant fit in the latter case (Tables 3.1, 3.2). For these seven data sets, the power b was clearly less than two with a mean value of 1.66 (range 1.56-1.76). Variations in catch between years will be therefore much greater for poor rivers with a generally low mean catch than for good rivers with a higher mean catch. Catches in the latter rivers will be more stable from year to year whilst catches in poor rivers will be subject to years of 'boom or bust'. The Wessex region was the exception with $b=2$ suggesting that the relative temporal variability of rod catches in this region was fairly constant between rivers. As only four rivers were included in the analysis, it is possible that this exception was due to only one or two rivers.

The analyses of catch data from all regions combined showed that temporal variability of both rod and commercial catches was strongly density-dependent on the mean catch for each river (Figures 3.14, 3.15). The remarkably good fit of the power-function to both data sets showed that none of the rivers is markedly different from the rest. Only the Rivers Neath, Tyne and Ehen for rod catches and Mawddach, Dee and Cleddau for commercial catches could be regarded as possible outliers but, for these 6 rivers, the departure from the expected value never exceeded 19% of the latter. It can therefore be concluded that the density-dependent relationship could explain nearly all the variation in temporal variance (variation in catches between years for each river), the actual percentage being 93% for rod catches and 98% for commercial catches.

The classification of the rivers (Tables 3.4, 3.5) revealed a clear relationship between mean annual catch and the relative variability in catches between years, the latter being expressed as the C.V. For both rod and commercial catches, rivers with a high relative variability in catches (C.V.>86%) are nearly all those with low annual catches (<105 fish), the exception being the Tyne with its medium annual rod catch. Catches in these rivers must vary considerably, with years of 'boom or bust', and the variation is probably chiefly due to density-independent factors, especially those associated with fluctuations in climate.

At the opposite extreme, rivers with a low relative variability in catches (C.V.<50%) include nearly all those with high annual rod catches (>1000 fish) (exceptions: Camel, Avon, Taw) and all those with high annual commercial catches. This low variability category also included some rivers with medium annual catches (105-1000 fish), but only one river (Usk) with a low commercial catch (<105 fish) and none with a low rod catch. Catches in these rivers vary only moderately between years and are essentially stable, the variation in catches being chiefly due to density-dependent factors rather than density-independent factors.

Finally, there are a group of rivers with a medium relative variability in catches (C.V. 50-86%). These rivers are chiefly those with low (<105 fish) and medium (105-1000 fish) annual catches but three rivers with high rod catches (>1000 fish) are also in this category. Variation in catches between years is probably due to the combined effects of density-dependent and density-independent factors.

Although this classification scheme does provide a basis for the management of sea-trout populations, especially the almost opposite management schemes required for low variability and high variability rivers, it can only serve as a starting point. It is obvious, for example from Tables 3.4 and 3.5 that rivers do not always occur in the same category on the basis of rod and commercial catches. For those rivers with commercial fisheries, it may be preferable to analyze total catches, rather than rod and commercial catches separately and to discover if any relationship exists between the relative sizes of the rod and commercial catches. The latter are probably more affected by fishing effort and therefore an analysis of catch data expressed as catch per unit effort (CPUE) could be revealing. There are clearly many other possibilities, but these analyses and the earlier ones have shown that catch data for sea-trout can produce meaningful results and are worthy of further analysis.

5. CONCLUSIONS AND RECOMMENDATIONS

1. Both spatial and temporal variability of rod catches were density-dependent on mean catch, the relationship being well-described by a power-function ($s^2 = a\bar{x}^b$ where s^2 is the spatial or temporal variance, \bar{x} is the spatial or temporal mean catch, and a and b are constants). For spatial variability (variation in catches between rivers for each year), this function was an excellent fit to all five data sets and 78-99% of the between-years-variation in spatial variance could be explained by variations in the annual mean catch. For temporal variability (variation in catches between years for each river), this function was an excellent fit to three data sets (North West, Welsh, South West), a significant fit to one (Wessex), and just failed to fit one (North East). For the significant fits, 92-98% of the between-rivers-variation in temporal variance could be explained by variations in the mean catch for each river.
2. There were no significant differences between the power functions for the North West, Welsh and South West data sets for rod catches. Both the power b and coefficient of variation (CV) showed that the relative spatial variability of catches was fairly constant between years whilst the relative temporal variability of catches decreased with increasing mean catch. Therefore variability of catches was higher for poor rivers with a low mean catch (years of 'boom and bust' occur) than for good rivers with a high mean catch (more stable from year to year).
3. In contrast to the previous results, the relative temporal variability of rod catches in the Wessex region was fairly constant between rivers whilst the relative spatial variability of catches increased with increasing mean catch so that it was low in bad years with low catches and high in good years with high catches. The same pattern was shown for relative spatial variability in North East rivers but the lack of a significant relationship for temporal variability negated any further comparisons. Therefore in good years with high catches, good rivers tend to do superproportionally well but in bad years with low catches, poor rivers are less affected than good rivers.
4. Analyses of commercial catches for the North West, Welsh and South West regions generated results similar to those obtained for rod catches and therefore reinforced the previous conclusions. Although only two values for temporal variability were available from Wessex, they were very similar to those obtained for South West rivers.
5. The analyses of spatial variability demonstrate that catches from different rivers in a region varied synchronously in time. The mean catch for all rivers in a region and the corresponding CV therefore provide succinct summaries of temporal changes in catch size and the relative variability between catches from different rivers. The latter was fairly stable between years for catches from the North West, Welsh and South West regions, but varied considerably for catches from the Wessex and North East regions, usually reflecting the larger fluctuations in mean catch. Mean catch varied considerably between years in all regions and although 1989 catches were low in all except the North East, similarly low values have occurred in previous years. Although they were not used in the analyses, 1990 catches were included for comparison and were low compared with previous catches.

6. When all rod catches from 67 rivers were treated as a single data set and all commercial catches from 36 rivers were also treated as a single set, the temporal variance of both rod and commercial catches was density-dependent on mean catch, the relationship being well described by a power-function. This function was an excellent fit to both data sets and the proportion of the between-years-variation in catches that could be explained simply by variations in the overall mean catch for each river was 93% for rod catches and 98% for commercial catches.
7. With such strong relationships, it was not surprising that there were no obvious outliers, i.e. data points that departed significantly from the regression line. A suitable discriminating function was the logarithmic difference between observed and expected s^2 expressed as a percentage of log expected s^2 . Observed values for rod catches were 18.6% higher than expected for the River Neath, 14.4% higher for the Tyne and 12.1% lower than expected for the Ehen. The discrepancy for the remaining 64 rivers was 11% or less. Observed values for commercial catches were 15.6% higher than expected for the Mawddach, 18.0% lower than expected for the Dee and 15.6% lower for the Cleddau. The discrepancy for the remaining 33 rivers was 11% or less.
8. The rivers were classified according to their overall mean catch and their relative variability in catches between years, the latter being expressed as the Coefficient of Variation (C.V.%). For rod catches there were: 11 rivers with high variability (C.V.>86%) divided into 10 with low catches (<105 fish per day) and only one (Tyne) with a medium annual catch (105-1000 fish); 32 rivers with medium variability (C.V. 50-86%) divided into 9 with low catches (<105 fish), 20 with medium catches (105-1000 fish) and 3 with high catches (>1000 fish); 24 rivers with low variability (C.V.<50%) divided into 15 with medium catches (105-1000 fish) and 9 with high catches (>1000 fish). For commercial catches there were: 4 rivers with high variability (C.V.>86%), all with low annual catches (<105 fish); 15 rivers with medium variability (C.V. 50-86%) divided into 10 with low catches (<105 fish) and 5 with medium catches (105-1000 fish); 17 rivers with low variability (C.V.<50%) divided into only one (Usk) with a low catch (<105 fish), 7 with medium catches (105-1000 fish) and 9 with high catches (>1000 fish).
9. Therefore rivers with high variability in catches between years (C.V.>86%) usually provide low annual rod/commercial catches (<105 fish), the exception being the medium rod catch for the Tyne. Rivers with medium variability in catches (C.V. 50-86%) usually provide low or medium (105-1000) catches, exceptions being rod catches for the Camel, Avon and Taw (>1000 fish). Rivers with low variability in catches (C.V.<50%) usually provided medium or high (>1000 fish) catches, the exception being commercial catches for the Usk (<105 fish).
10. These differences support the conclusion that populations of sea-trout in rivers with low catches will be regulated chiefly by density-independent factors (chiefly fluctuations in climate) whilst those in rivers with medium to high catches will be regulated chiefly by density-dependent factors (see discussion in Elliott 1987, 1988, 1989). Such differences have implications for the management of the different sea-trout populations. For example, in a population regulated chiefly by density-dependent factors, stocking in a year with good recruitment of young trout would actually reduce

the number of survivors and decrease variation in their size (Elliott 1985, 1989).

11. Finally it is worth iterating the point that catch data for salmonids are frequently said to be inaccurate because of factors such as wrong identification of a fish (sea-trout confused with lake trout, resident trout or salmon), failure to return records of fish caught, inadequacies in the fishing methods and variations in the fishing effort. The excellent fits obtained in the present investigation suggest that if these factors do affect catch records, the effects must be of similar relative magnitude for all catches. It is therefore concluded that an annual catch record does reflect the number of adult sea-trout in a river and that such records can be used as the basis for comparisons between rivers and years. Further work could include an analysis of catch statistics as a time series in relation to several factors (e.g. weight of fish caught, total discharge, number of smolts). It would also be useful to repeat these analyses for salmon catches. Sea-trout and salmon are sympatric in most of the rivers used in the present study and it would be interesting to discover if the relationships established for sea-trout are also true for salmon. Comparisons could then be made between the two species to discover if fluctuations in their catches are synchronous or complementary.

6. REFERENCES

- Anscombe, F.J. (1948) The statistical analysis of insect counts based on the negative binomial distribution. Biometrics, 5, 165-173.
- Elliott, J.M. (1985) Population dynamics of migratory trout, Salmo trutta, in a Lake District stream, 1966-83, and their implications for fisheries management. Journal of Fish Biology, 27 (Supplement A), 35-43.
- Elliott, J.M. (1987) Population regulation in contrasting populations of trout Salmo trutta in two Lake District streams. Journal of Animal Ecology, 56, 83-98.
- Elliott, J.M. (1988) Growth, size, biomass and production in contrasting populations of trout Salmo trutta in two Lake District streams. Journal of Animal Ecology, 57, 49-60.
- Elliott, J.M. (1989) The natural regulation of numbers and growth in contrasting populations of brown trout, Salmo trutta, in two Lake District streams. Freshwater Biology, 21, 7-19.
- McArdle, B.H. (1988) Structural relationship: regression in biology. Canadian Journal of Zoology, 66, 2329-2339.
- McArdle, B.H., Gaston, K.J. and Lawton, J.H. (1990) Variation in the size of animal populations: patterns, problems and artefacts. Journal of Animal Ecology, 59, 439-454.
- Perry, J.N. (1981) Taylor's power law for dependence of variance on mean in animal populations. Applied Statistics, 30, 254-263.
- Ricker, W.E. (1973) Linear regressions in fishery research. Journal of the Fisheries Research Board of Canada, 30, 409-434.
- Sokal, R.R. and Braumann, C.A. (1980) Significance tests for coefficients of variation and variability profiles. Systematic Zoology, 29, 50-66.
- Taylor, L.R. (1984) Assessing and interpreting the spatial distribution of insect populations. Annual Review of Entomology, 29, 321-357.
- Taylor, L.R. (1986) Synoptic dynamics, migration and the Rothamsted insect survey. Journal of Animal Ecology, 55, 1-38.
- Taylor, L.R. and Woiwod, I.P. (1980) Temporal stability as a density dependent species characteristic. Journal of Animal Ecology, 49, 209-224.
- Taylor, L.R. and Woiwod, I.P. (1982) Comparative synoptic dynamics. 1. Relationships between inter- and intra- specific spatial and temporal variance/mean population parameters. Journal of Animal Ecology, 51, 879-906.
- Taylor, L.R., Woiwod, I.P., Harrington, R., Nicklen, J. and Dupuch, M.J. (1985) Synoptic monitoring for migrant insect pests in Great Britain and Europe. VI Revised nomenclature for aphids and moths, analytic tables for spatial and temporal species parameters and light trap sampling site distributions. Report Rothamsted Experimental Station for 1984, 251-285.
- Taylor, L.R. Woiwod, I.P. and Perry, J.N. (1980) Variance and the large scale spatial stability of aphids, moths and birds. Journal of Animal Ecology, 49, 831-854.
- van Valen, L. (1978) The statistics of variation. Evolutionary Theory, 4, 33-43.

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