Review of Sea Trout Fecundity

D. J. Solomon

R&D Technical Report W60.

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Statement of Use
This report consists of a review of sea trout fecundity studies to be used as the basis for determining the need for further work on this subject. It is also available for information to Fisheries staff involved in the management of sea trout stocks.

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CONTENTS

SUMMARY

1. Data on the fecundity of sea trout from the British Isles, Norway and France are reviewed. British Isles data are available for six stocks in England and Wales, three in Scotland and one in Ireland.

2. The data were compared by use of a formula to link number of eggs per female with fish length for each stock, and for the stocks of each area. Comparisons are made based on predictions for fish of a range of standard lengths from 270 – 700 mm.

3. The length/fecundity relationships for different stocks were clearly different, but in most cases the raw data were not available to establish the statistical significance of these differences. If the differences are real, the use of a "mean British Isles" formula to predict fecundity of different stocks could lead to errors of up to 30%. The scope for derivation of a range of formulae for different regions or stock groupings is discussed.

4. Only one study presented data from different years analysed separately and this indicated considerable variation. Inter-annual variability is clearly an important issue and could explain at least part of the apparent differences between stocks.

5. Other aspects examined are the effect of spawning history on fecundity, the relationship between total fecundity and number of eggs in the redd, the relationship between fecundity and weight, relationships between total fecundity and the number of eggs yielded by manual stripping, variation of fecundity within catchments and the relationship between adult size and egg viability.

6. In view of the uncertainty surrounding other inputs to egg deposition estimates and spawning targets it is concluded that further refinement of our understanding of sea trout fecundity is not of overwhelming urgency. However, acquisition of further data on an opportunistic basis, and by "adding on" to existing investigations is recommended as in input to the developing science of management of spawning targets.

7. Recommendations are made with regard to gathering of further data on sea trout fecundity with particular reference to geographical and annual variation, a framework for integrating work on all aspects of spawning target R+D a review of data on salmon fecundity and a review of the opportunities represented by events such as fish kills for gathering data on a wide range of biological variables including fecundity. Suggestions are also made on approaches to gathering and storing samples.

1. INTRODUCTION

1.1 Background

With the development of the concept of potential egg deposition and spawning targets for the management of salmonid stocks, a need for a method of determining fecundity of individual fish and populations has become apparent. This must be non-destructive i.e. must be determined using characteristics such as size, age and stock origin.

The overall aim of this note is therefore to review the results of fecundity studies on sea trout conducted to date, consider the extent and patterns of variation, consider the adequacy of the available information for fisheries management purposes, and recommend appropriate further investigation.

1.2 Terms of reference

The specific TOR of this study are:

General aim.

To review and present the results of all available studies on the fecundity of sea trout.

Specific aims.

To present the mathematical formulae for, and prepare graphs of, fecundity against weight and length, and if the data is available, age-class, for each stock for which data are available.

To describe how fecundity varies with length, age, and sea-age-class, and between stocks.

To comment on potential variation caused by considering results from total ovary contents, and fish stripped in a hatchery, as indicators of natural egg production.

To report on any evidence of variation in viability of eggs from fish of different sizes or ages.

To advise on the potential for derivation of a single relationship of fecundity for weight/length/sea age class for general application, including an assessment of the errors that might arise.

To comment upon the criteria for a sampling programme to determine if any given river stock has a pattern of fecundity that is significantly different from a generalised relationship.

2. THE BASIS OF FECUNDITY

Eggs produced by any one species of fish tend to have a fairly limited range of size, and it is generally a truism that larger females produce more eggs than smaller ones. In a review of the subject Bagenal and Braum (1978) used the simple formulae

$$N = a L^b \qquad \text{(Equation 1)}$$

or its linear transformation

$$\log N = \log a + b \log L \qquad \text{(Equation 2)}$$

where N = number of eggs produced, L = length of fish, and a and b are constants for a particular population. As weight is clearly related to length, fecundity too may be quoted in relation to weight. Indeed, it might be thought that a better relationship would be apparent, as it is reasonable to suppose that fat fish would contain more eggs than a thin one of the same length. There is a fundamental problem, however, regarding the considerable weight loss that adult sea trout may experience between ceasing heavy feeding in the sea and spawning (which may be up to 6 months or more for large fish). Length, on the other hand, changes little or not at all once the fish is in freshwater (this is true at least for females, though males may undergo minor elongation due to kype development). For this reason most studies have concentrated on a length/fecundity relationship. Some have also quoted a weight/fecundity relationship, and this is given in section 4.4.

This basic length/fecundity relationship in Equations 1 and 2 have been used in all reported studies on fecundity in sea trout (and indeed most other salmonids), so a comparison of results should be straightforward. There are, however, a number of complicating factors.

First, the number of maturing eggs within the ovary may change during development. Prouzet et al (1984), working on Atlantic salmon on the Elorn River in France, examined the numbers of eggs in various months among spring-run salmon. When entering the river early in the year the fish contained large numbers of eggs of uniform size, between 1.5 and 2 mm in diameter. However, the number that matured was generally considerably lower; mean numbers per kg of body weight fell from 2359 to 1662 between fist entry to the river and spawning. This process of atresia of part of the egg load means that samples for fecundity determination for egg deposition estimates should be taken after the stage when the atretic eggs can be differentiated from those that are maturing; based on these observations of Prouzet et al, several of the sea trout investigations considered here used only samples from fish caught after August 1.

Even when the eggs are mature and ovulation has taken place to release the eggs to the body cavity, the quantification of fecundity is vulnerable to the approach used to determine it. Three approaches have been used:

1. Complete count of maturing eggs in sacrificed fish. This is the most usual approach. Totally reliable counts can be made, but not all such eggs are expelled during natural spawning, as evidenced by retained eggs observed in kelts and remains of resorbed eggs (particularly shells) found in subsequent years. Thus this approach may overestimate effective fecundity.

2. Count of egg "stripped" from fish for artificial spawning. Three studies used this approach for all or some of their samples. Investigations have shown that a significant and variable proportion of the eggs may not be ejected during this process, making the count somewhat inaccurate and imprecise as an index. Thus this approach may underestimate true fecundity.

3. Count of eggs in natural redds produced by a female of known dimensions. Only one study has used this approach. From the viewpoint of the aim of this exercise (actual egg deposition) this is the most valid concept, but its practicality is severely limited at most sites.

These three approaches would give different answers for the "fecundity" of the same fish so care is needed in comparing and applying the results of each.

Studies for sea trout providing data for a length/fecundity relationship for sea trout have been identified for ten catchments or sub-catchments for the British Isles, nine for Norway and three for France. These results are discussed in Section 3.

3. LENGTH/FECUNDITY RELATIONSHIPS DERIVED FROM DISSECTION OF DEAD FISH

3.1 Results for British Isles stocks

The values for the intercept ($\log_{10}a$) and slope (b) for equation 2 for studies identified for sea trout are given in Table 3.1. In some cases these have been transformed from other formats so that all constants are appropriate for $\log_{10}$ and length in mm. Virtually all studies provided a value for the correlation coefficient (r). Where available, the 95% CL on the slope and intercept figures are quoted.

Table 3.1. Values of constants obtained for the fecundity formula based on $\log_{10}$ transformations for a range of stocks. Where appropriate to the formulae have been adjusted for L in mm, and the intercept as $\log_{10}a$. Also shown are the numbers of fish involved in the investigations and their length range.

No	River	Dates	Length range (mm)	n	Intercept ($\log_{10}a$)	Slope (b)	r	Source
a) Dissection of dead fish								
1	Dyfi	1967-70	255-740	52	-3.622±0.596	2.603±0.227	0.954	Harris 1970
2	Erriff 1983-86	1983-86	c.240-550	150	-3.006	2.32		O'Farrell et al 1989
3	Tweed	1980-93	480-725	30	-5.268±1.702	3.196±0.267	0.89	Walker 1994
4	Earn System	1980-93	255-650	70	-4.179±0.737	2.804±0.121	0.93	Walker 1994
5	Ewe System	1980-93	284-615	58	-4.433±0.891	2.842±0.149	0.91	Walker 1994
6	Leven (Cumbria)	1966-68	c.300-500	61	-2.749±0.234	2.278±0.091	0.988	Elliott 1995
7	Dale Park Beck	1970-83	c.260-440	22	-2.827±1.008	2.309±0.395	0.939	Elliott 1995
8	Duddon	1966-68	c.310-430	20	-2.952±0.660	2.359±0.257	0.977	Elliott 1995
9	Enningdalselva	1983-86	250-630	22	-3.498	2.565	0.97	L'Abée Lund + Hindar
10	Langangselva	1984	250-510	19	-2.740	2.220	0.89	L'Abée Lund + Hindar
11	Eio	1982-89	290-590	18	-3.106	2.396	0.94	L'Abée Lund + Hindar
12	Korsbrekkelva	1986	330-770	16	-2.700	2.265	0.97	L'Abée Lund + Hindar
13	Gaula lower	1988-89	310-590	29	-3.371	2.518	0.89	L'Abée Lund + Hindar
14	Gaula upper	1986-89	400-630	28	-2.006	2.010	0.84	L'Abée Lund + Hindar
15	Fættenelva	1986-89	340-530	14	-2.858	2.340	0.86	L'Abée Lund + Hindar
16	Namsen lower	1989	320-490	23	-3.816	2.673	0.92	L'Abée Lund + Hindar
17	Namsen upper	1986-89	240-570	37	-4.256	2.764	0.99	L'Abée Lund + Hindar
18	Bresle, Touques, Orne	1983-88	c.320-820	92	-4.39	2.92	0.97	Euzenat et al 1991
b) From stripping live fish								
19	Dyfi	1967-70	345-710	22	-2.550±1.384	2.161±0.508	0.88	Harris 1970
20	Kent + Leven	1981	c.350-690	17	-3.211	2.42		Aprahamian + Farooqi
c) From excavation of redds								
21	Black Brows Beck	196 -	c.260-450	29	-2.203±0.332	2.048±0.131	0.987	Elliott 1995

Notes: "C" before the length range indicates approximate range deduced from graphed data.

With the exception of Harris (1970) the raw data were not included in the publications reviewed so it has no been possible to re-work most of the data sets. Other details, including numbers of fish involved, length-range of the sample, years covered by the samples, location, method used for collection of fish, and months of collection of samples are also presented in Tables 3.1 and 3.2. Studies, which involved dissection of dead fish (18 stocks or stock-groups), are listed separately from those based upon stripping of live fish (two stocks) and redd excavation (one stock). Although most studies involved fish collected over two or more years, only for the Erriff in Ireland are the data for different years presented separately (O'Farrell et al 1989).

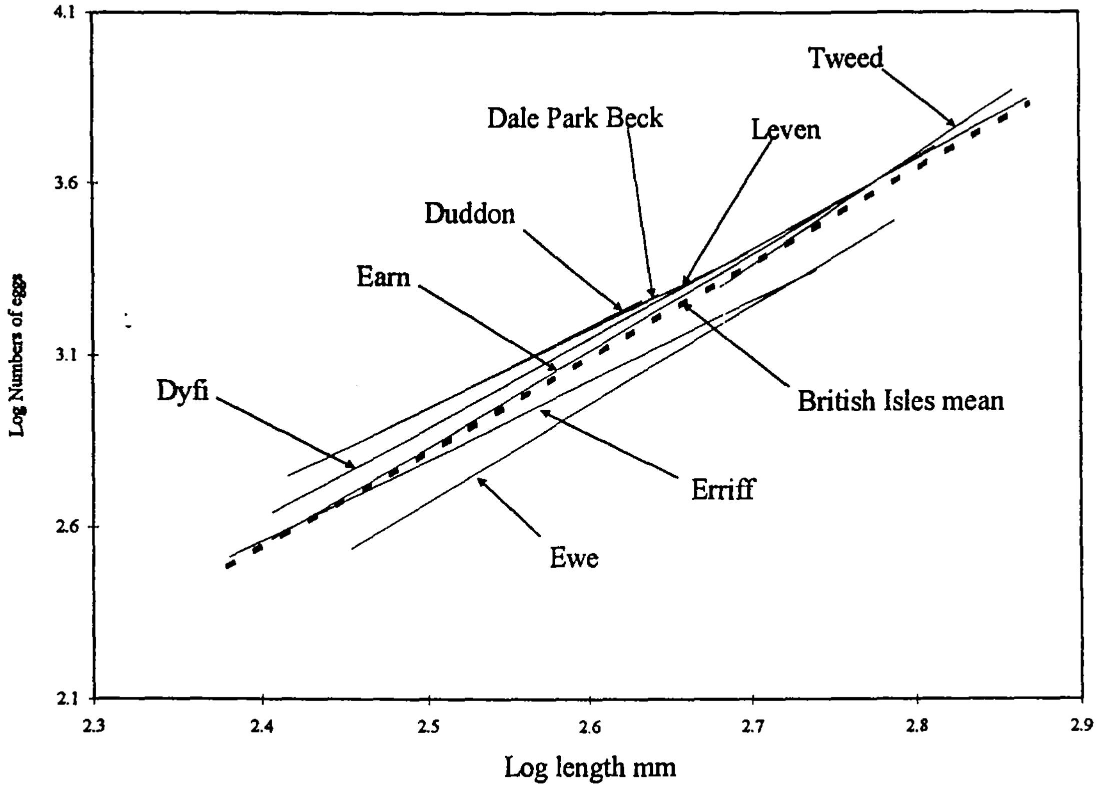
Table 3.2. Details of investigations of sea trout fecundity.

No	River	Dates	n	Location	Method of capture	Months	Maturity stage	Source
a) Dissection of dead fish								
1	Dyfi	1967-70	52	Wales	A, D	Aug on	IV-V	Harris 1970
2	Erriff	1983-86	150	Ireland	A	Aug on		O'Farrell et al 1989
3	Tweed	1980-93	30	Scotland	(3)		IV-VI	Walker 1994
4	Earn system (1)	1980-93	70	Scotland	E, T		IV-VI	Walker 1994
5	Ewe system (2)	1980-93	58	Scotland	E, F		IV-VI	Walker 1994
6	Leven	1966-68	61	Cumbria	A	Aug on		Elliott 1995
7	Dale Park Beck	1970-83	22	Leven trib.	A	Oct-Nov		Elliott 1995
8	Duddon	1966-68	20	Cumbria	A	Aug on		Elliott 1995
9	Enningdalselva	1983-86	22	Norway	E		IV-VI	L'Abée Lund + Hindar
10	Langangselva	1984	19	Norway	E		IV-VI	L'Abée Lund + Hindar
11	Eio	1982-89	18	Norway	E		IV-VI	L'Abée Lund + Hindar
12	Korsbrekkelva	1986	16	Norway	E		IV-VI	L'Abée Lund + Hindar
13	Gaula lower	1988-89	29	Norway	E		IV-VI	L'Abée Lund + Hindar
14	Gaula upper	1986-89	28	Norway	E		IV-VI	L'Abée Lund + Hindar
15	Fættenelva	1986-89	14	Norway	E		IV-VI	L'Abée Lund + Hindar
16	Namsen lower	1989	23	Norway	E		IV-VI	L'Abée Lund + Hindar
17	Namsen upper	1986-89	37	Norway	E		IV-VI	L'Abée Lund + Hindar
18	Bresle, Touques, Orne	1938-88	92	France	A,T,D	Aug on		Euzenat et al 1991
b) From stripping live fish								
19	Dyfi	1967-70	22	Wales		Nov?	V-VI	Harris 1970
20	Kent + Leven	1981	17	Cumbria		Nov?	V-VI	Aprahamian + Farooqi pc
c) From excavation of redds								
21	Black Brows Beck	196 -	29	Cumbria		Nov-Dec	VI	Elliott 1995

Notes:
(1) Includes samples for the Findhu Glen Burn.
(2) Includes samples for Loch Maree and Loch Coulin
(3) Seized illegal net catch.
A = angling; E = electric fishing; F = fyke nets; T = trap; D = found dead

The fecundity/length lines generated by these derived relationships for each stock in the British Isles are shown in Figure 3.1. The lines are shown only for the length-range of the fish actually sampled in each case i.e. they are not extrapolated. Also shown as a heavy dotted line is a calculated "mean" line for all the individual British Isles stocks combined. The derivation of this line warrants explanation.

Figure 3.1. Length/fecundity lines for the British Isles studies in Table 3.1 based on dissection of dead fish. The heavy dotted line is the mean line (Equation3).

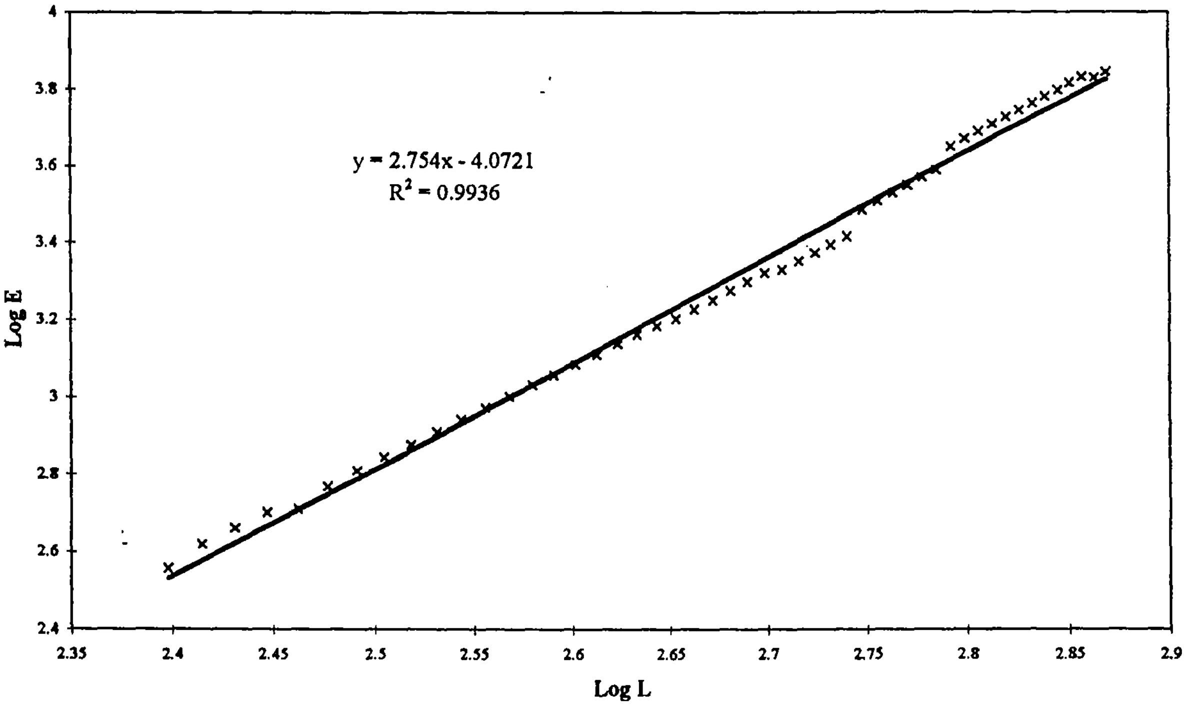


Perhaps the simplest way of deriving such a mean line would be to combine all the raw data and calculate an overall regression. However, as already explained, in most cases the raw data were not available. The line was therefore derived from a spreadsheet model based upon the predicted fecundity for each stock at 10 mm intervals, within the range of lengths sampled. A weighted geometric mean for each length interval was then calculated, and is plotted in Figure 3.2. The "steps" in the data points are due to different stocks entering and leaving the calculation according to their length ranges. A regression line was then calculated for these points, its formula being:

$$\mathrm{Log}_{10}\,N = 2.7514\,\mathrm{Log}_{10}\,L - 4.0623 \qquad \text{(Equation 3.)}$$

The geometric mean for each value was obtained by using an arithmetic mean of the $\log_{10} N$ value. The weighted mean was used so that relationships based on a larger number of fish carried more weight than those based on a few, as it is felt that the former are likely to represent more reliable relationships. It also prevents over-representation by samples from separate groups that might be considered to be drawn from the same stock e.g. Leven and Dale Park Beck.

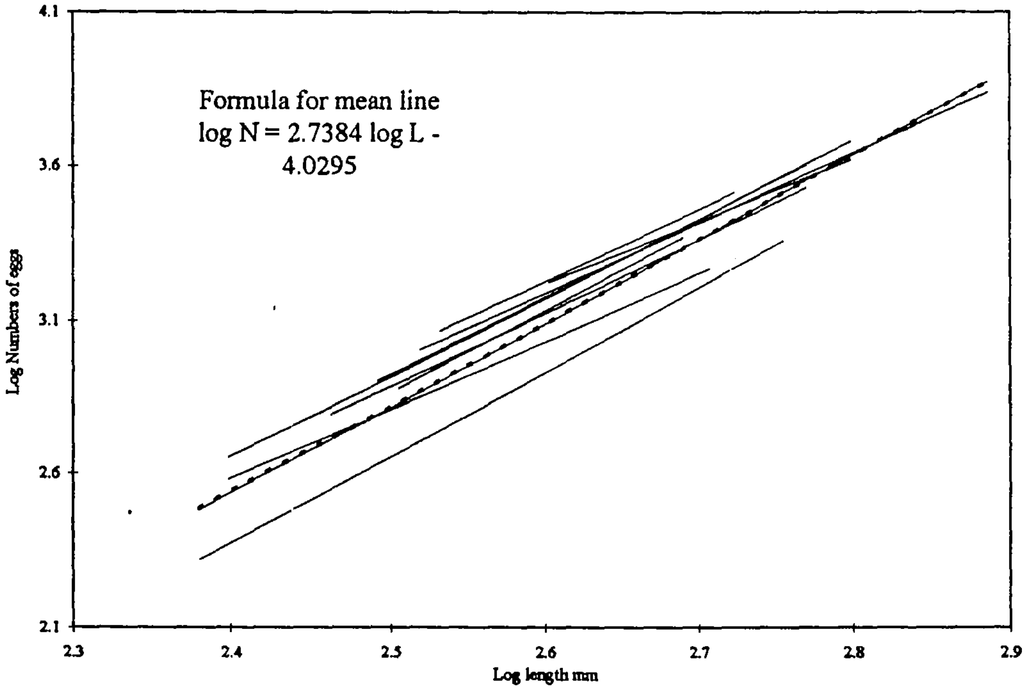
Figure 3.2. Derivation of British Isles mean line, based upon mean fecundities at 10mm intervals from Table 3.3.



3.2 Norwegian stocks

The length/fecundity lines for the nine Norwegian stocks listed in Table 3.1 are shown in Figure 3.3, along with the calculated mean line. This was derived in the same way as that for the British Isles stocks described above.

Figure 3.3. Length/fecundity lines for the Norwegian stocks in Table 3.1.



3.3 Comparison of British Isles stocks

In order to compare the fecundity of the British Isles stocks more directly, the formulae are used to generate predicted numbers of eggs in females at 270 mm (the lowest value that lies within the range of the majority of stocks), 300 mm and then at 50 mm intervals throughout the length ranges represented by samples (Table 3.3). This highlights the range of values obtained. The greatest relative range is at a length of 300 mm, with the Ewe stock indicating 405 eggs and the Cumbrian Leven 783, a factor of 1.93. These two stocks are consistently at the extremes throughout their length ranges (Table 3.3, Fig 3.1).

Table 3.3. Calculated fecundity at standard lengths

			Length (mm)									
	River	**l range**	**270**	**300**	**350**	**400**	**450**	**500**	**550**	**600**	**650**	**700**
1	Dyfi	255-740	509	670	1000	1416	1924	2532	3245	4069	5012	6078
2	Erriff	c.240-550	431	551	787	1073	1411	1801	2247			
3	Tweed	480-725						2280	3092	4083	5273	6682
4	Earn System	255-650	435	585	901	1310	1822	2449	3199	4083	5110	
5	Ewe System	284-615		405	627	916	1281	1728	2265	2901		
6	Leven (Cumbria)	c.300-500		783	1113	1508	1973	2508				
7	Dale Park Beck	c.260-440	612	781	1115	1518	1992					
8	Duddon	c.310-430			1121	1536						
	British Isles	**240-740**	**421**	**562**	**860**	**1242**	**1717**	**2295**	**2984**	**3793**	**4728**	**5798**
9	Enningdalselva	250-630	548	717	1065	1501	2030	2660	3396	4246		
10	Langangselva	250-510	455	574	809	1088	1413	1785				
11	Eio	290-590		675	976	1344	1783	2295	2883			
12	Korsbrekkelva	330-770			1154	1562	2040	2589	3213	3913	4691	5548
13	Gaula lower	310-590			1084	1517	2041	2661	3382			
14	Gaula upper	400-630				1675	2123	2624	3178	3785		
15	Fættenelva	340-530			1245	1701	2241	2868				
16	Namsen lower	320-490			964	1378	1888					
17	Namsen upper	240-570	291	390	597	863	1195	1599	2081			
	Norway	**250-770**	**425**	**567**	**865**	**1247**	**1722**	**2298**	**2983**	**3786**	**4714**	**5775**
18	**France**	**c.320-820**			**1093**	**1614**	**2277**	**3097**	**4091**	**5275**	**6664**	**8273**

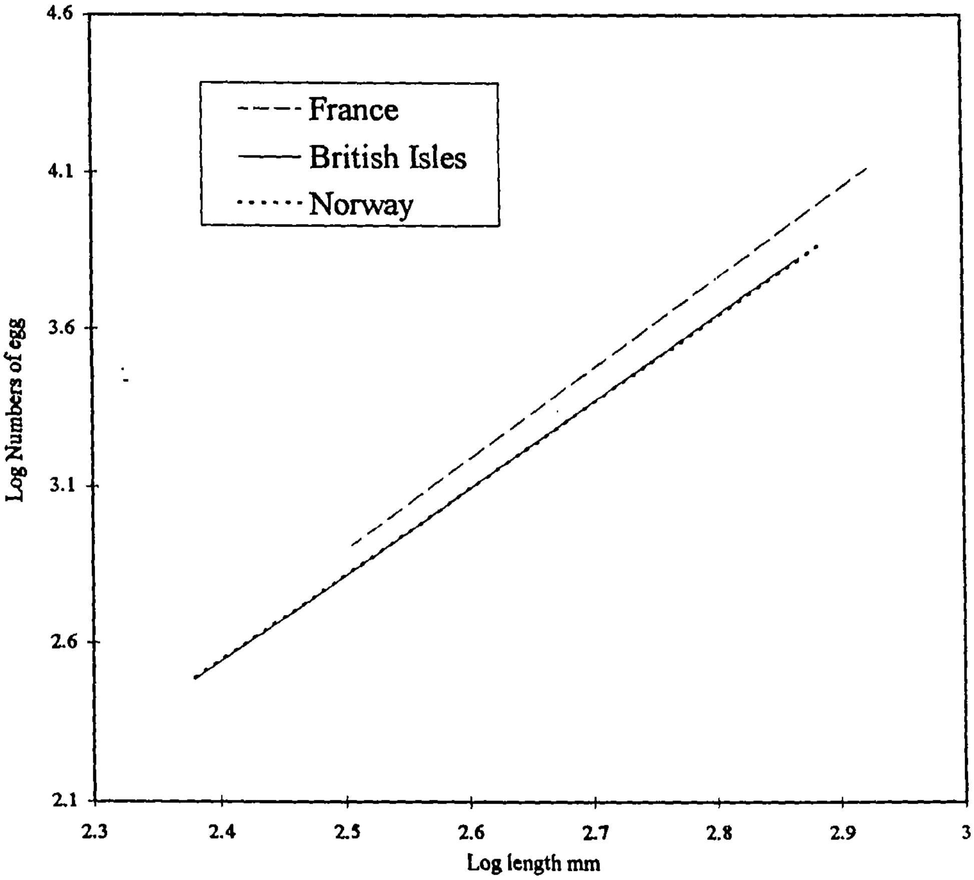
3.4 Comparison between British Isles and other European stocks.

Figure 3.4 compares the mean lines for the British Isles and Norwegian groups of stocks, and the line for the French stocks from Table 3.1.

The Norwegian mean line is remarkably similar to that for the British Isles stocks, and the ranges of numbers of eggs for standard lengths for the two groups of stocks is also similar (Table 3.3). On the other hand the group of French stocks have a mean fecundity well above the means for the other countries. From a length of 450 mm upwards the French stocks have a fecundity above any single stock in the British Isles and Norway. The samples from the

French stocks also contained some remarkably large fish, with a maximum length of 870 mm and weight of 9.05 kg. The largest number of eggs recorded in a single fish was in excess of 13,000.

Figure 3.4. Mean length/fecundity lines for the studies in the British Isles (Equation 3), Norway (Figure 3.3) and France (Table 3.1).



4. ASPECTS OF SEA TROUT FECUNDITY

4.1 How real are the apparent differences between stocks?

Two mechanisms may contribute to the apparent differences between stocks:

- a true, genetically-determined, tendency towards a particular level of fecundity;
- environmental conditions experienced by the fish, for example feeding opportunities, and its resulting physiological state, may influence fecundity.

There are clear geographic patterns in levels of fecundity, with stocks from rivers entering the open Atlantic (e.g. Erriff, Ewe) having lower fecundity than those entering the Irish Sea or North Sea. Fahy (1985) comments on this phenomenon:

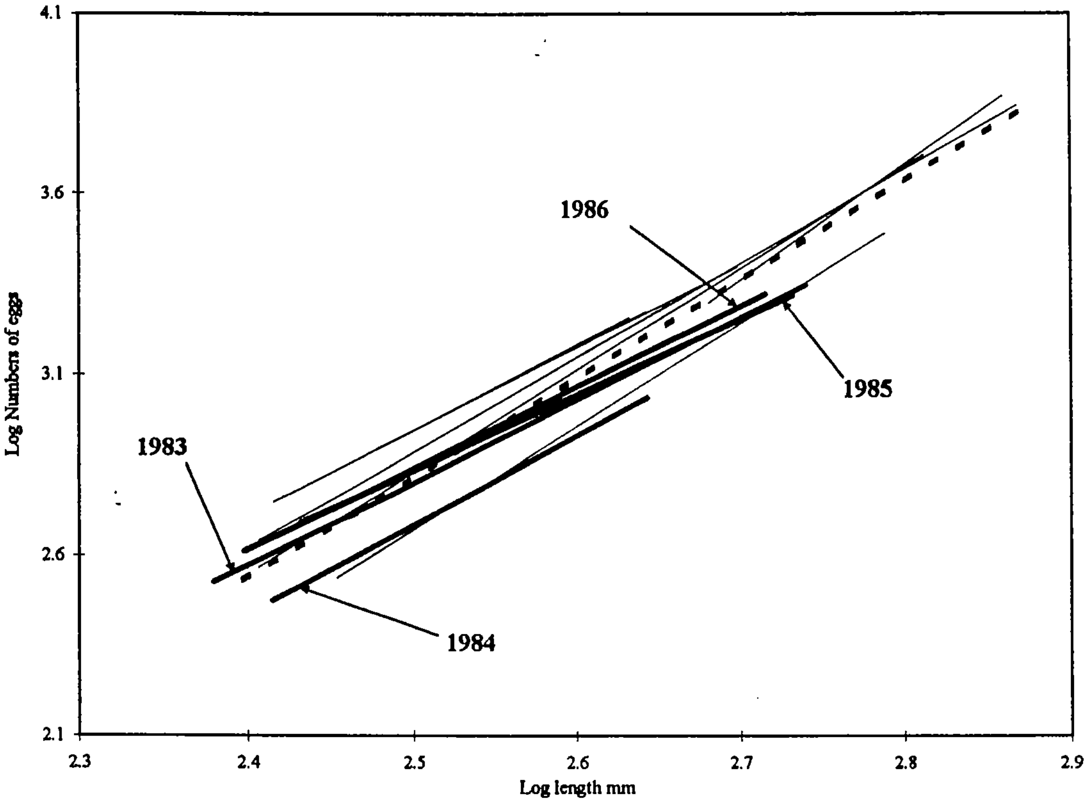
> "A sea trout from rich Irish Sea feeding conditions of 500mm fork length would contain about 2,700 eggs but a fish of the same length from Atlantic surroundings would yield only slightly more than 2,000...."

Regrettably this appears to be the only observation of sea trout fecundity made by Dr Fahy, who has worked on Irish Sea Trout for many years. These figures are certainly consistent with the range of egg numbers for various stocks shown in Table 3.3, but this takes us little further in determining the exact mechanism responsible for the differences. However, evidence for an environmental influence upon fecundity comes from the investigation on the Erriff in Ireland (O'Farrell et al 1989). The length/fecundity relationships were different in each of the four years, (Table 4.1, Fig 4.1), and in the case of 1984 and 1986 this difference was statistically significant. It will be noted from Fig 4.1 the variation between years on the Erriff is as great as the apparent difference between many separate stocks. Although most other studies involved samples collected over more than one year, the data are not available in a form, which would allow analysis of inter-annual variation. Elliott (1995) found no significant differences between years in his study involving samples from the Leven and Duddon collected over 3 years or over 9 years for the Dale Park Beck, but stated that the sample sizes were too small to allow firm conclusions to be drawn.

Table 4.1. River Erriff length/fecundity relationships, 1983-86, including constants for Equation 2 and predictions of egg numbers for standard lengths.

					Length mm						
River	**l range**	**n**	**log10a**	**b**	**270**	**300**	**350**	**400**	**450**	**500**	**550**
Erriff 1983	c.240-550	34	-2.9	2.28	440	560	795	1078	1410	1793	2229
Erriff 1984	c.260-440	36	-3.44	2.45	329	426	621	861			
Erriff 1985	c.270-540	40	-2.39	2.09	492	613	845	1118	1430	1782	
Erriff 1986	c.250-520	40	-2.76	2.24	486	615	868	1171	1525	1931	
Erriff mean	c.240-550	150	-3.006	2.32	431	551	787	1073	1411	1801	2247

Figure 4.1. Length/fecundity lines for the four years of Erriff data plotted separately (heavy solid lines), other British Isle stocks (thin lines) and the British Isles mean line (broken line).



There is also good experimental evidence that food abundance can influence fecundity in salmonids (e.g. for rainbow trout, Scott 1962; and for brown trout, Bagenal 1969). It appears that salmonid fish have the potential to produce a larger number of eggs than usually mature, and that a physiological "decision" is taken during the development of the ova regarding the number that will continue to be nurtured. The remainder are resorbed by a process termed atresia; a detailed description is given by Scott (1962). As already described in Section 2, observations on the number of eggs in spring-run salmon in France showed a mean number of eggs of about 2359 per kg body weight in fish entering the river; at this time the ova were about 1.5-2 mm in diameter. By spawning time, the mean number of maturing eggs averaged 1662 per kg body weight. The process of atresia is apparently difficult to detect in ovaries at stage III (see Table 4.2), but atresic eggs are readily identifiable at stage IV. A number of studies of fecundity have indicated that the differentiation becomes apparent a few months before spawning, and have used the beginning of August as a start date for gathering reliable samples. However, it is likely that the physiological decision regarding the number of eggs that will mature is taken only when heavy feeding in the sea ceases and the fish can assess the energy resources available to it; thus fish entering the river later in the season could be expected to show differentiation of atresic eggs later in the year than one entering the river earlier.

4.2 Effect of age and spawning history on fecundity.

None of the published studies have presented the raw data on age, spawning history, length, weight and fecundity of individual fish that would allow any further analysis. We must therefore depend upon the conclusions of the individual studies.

Table 4.2. Stages of maturity of female sea trout. Based upon Dahl (1943) and Orton et al (1938).

Stage	Description
I	Ovaries very small. Ova difficult or impossible to differentiate by eye.
II	The ovaries have grown, but do not occupy more than one third of the length of the body cavity. Ova about the size of a pin head
III	Ova larger than a pin head, and the ovaries occupy about half the body cavity.
IV	Ovaries almost fill the body cavity, but the ova are still attached.
V	The ova are starting to loosen from the ovary.
VI	Spawning condition or spawning
VII	Spawned.

Harris (1970) and Euzenat (1991) offer no comment on the effect of age and spawning history on fecundity. O'Farrell et al (1989) stated that fish derived from 3-year old smolts had a significantly lower fecundity per unit length than those derived from two-year olds. Previously spawned fish were found to be less, but not significantly less, fecund than maiden fish of the same length. These authors also noted that fish first spawned as finnock (whitling) were significantly less fecund than fish that first spawned as one or two-sea-winter maidens, but this effect appears to be due to the lower overall length of the early spawners and not to a different length/fecundity relationship. L'Abée-Lund and Hindar (1990) found no significant effect of spawning history on fecundity in their study of Norwegian stocks. Walker (1994) observed a relationship between fecundity at standard lengths (e.g. 300 mm) and age, with older (i.e. slower growing) fish producing fewer eggs than younger fish. However, this relationship was based on a large number of stocks of which only a few were sea trout, and the analysis was therefore dominated by slower-growing brown trout. Elliot (1995) makes no observation on the effect of age and spawning history on fecundity in his studies on Lake District streams.

4.3 Relationship between total fecundity and eggs in the redd.

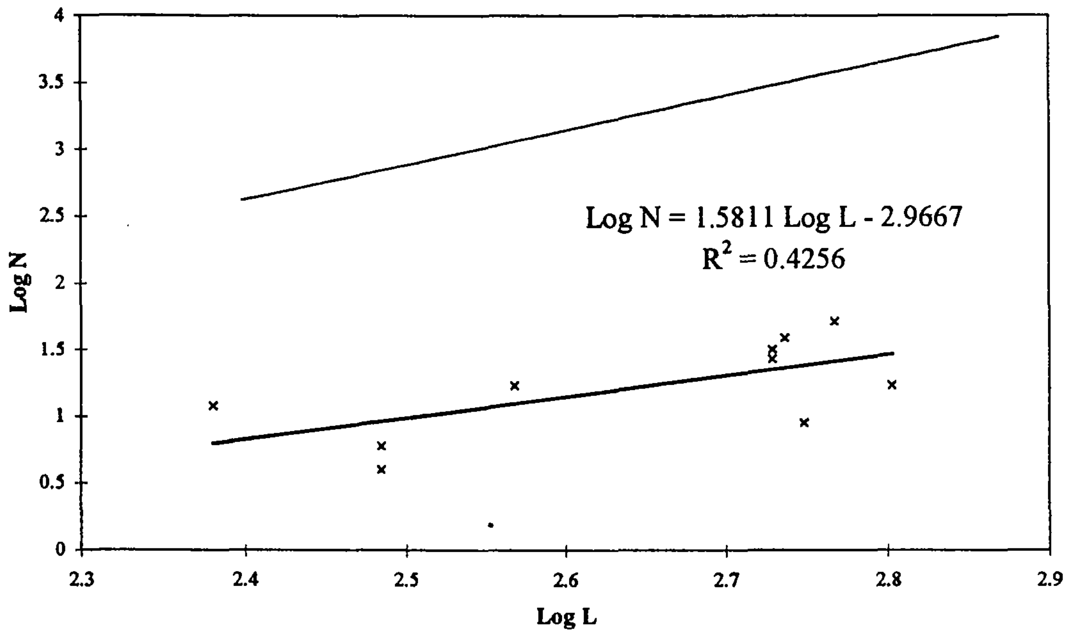
As discussed in Section 2, from the viewpoint of effective egg deposition rates it is the number of eggs in the redd that is strictly more relevant than the number of mature eggs in the pre-spawned female. There are two obvious mechanisms that might contribute to a discrepancy between these two parameters:

- not all mature eggs are voided from the female during spawning

- some eggs that are voided during spawning may be washed away by the current - such eggs are likely to experience virtually 100% mortality.

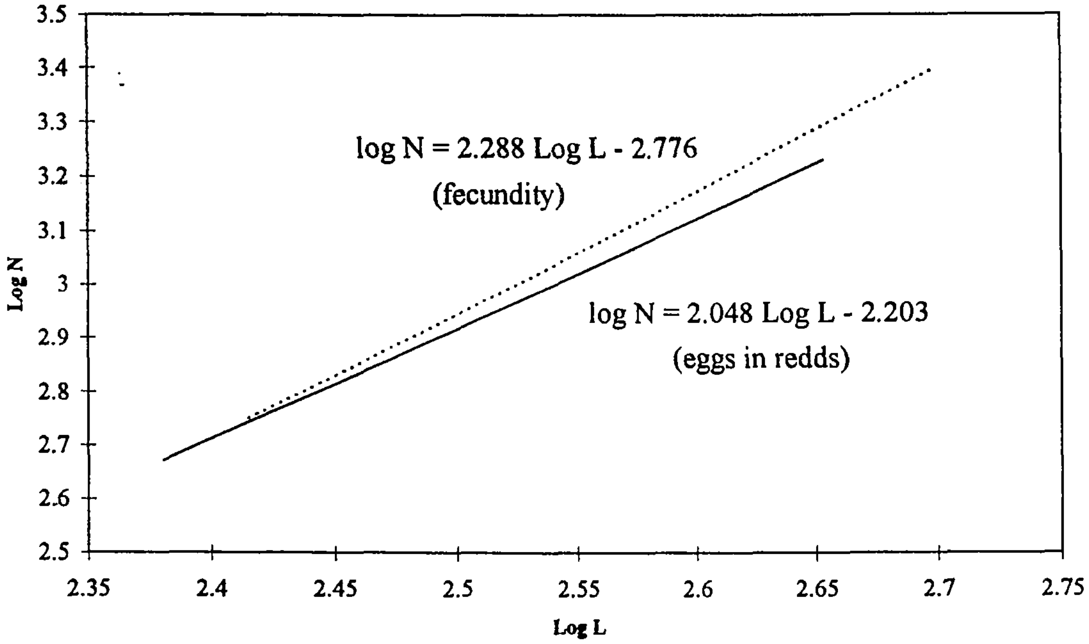
The first phenomenon was examined by Harris (1970), who examined the numbers of eggs retained within the body cavity of ten naturally-spawned kelts on the Dyfi. The results are shown in Fig 4.2, along with the line for the length/fecundity relationship derived from pre-spawned fish. The mean number of eggs retained (22) represents on average only about 0.9% of the egg load of the pre-spawned fish, suggesting that natural spawning is very effective in achieving a high level of voiding of mature eggs. The calculated proportion of retained eggs appears to be size dependent, being 1.6% for fish of 250 mm and 0.7% for 600 mm fish, but the small sample size and scatter of results means that this observation must be viewed with caution. There is of course a possibility that some residual eggs were shed between effective spawning and collection of the samples.

Fig 4.2. Relationship between fish length and numbers of eggs retained in the body cavity of ten naturally-spawned kelts on the Dyfi. Also shown (thin line) is the length/fecundity relationship. Data from Harris (1970).



Elliott (1984, 1995) related the number of eggs in redds determined by excavation, with the length of the female which was netted after spawning was believed to be complete. The work was conducted on the Black Brows Beck which flows into the Dale Park Beck a tributary of the River Leven in Cumbria. The following observations were made by Elliott (1984) reporting on the excavation of 22 redds; a female was never seen to construct more than one redd; there was never more than one female per redd; some eggs were lost from the redd during spawning, but catches in the nets used to trap the spawning female showed that these losses never exceeded 2% of the total eggs in the redd. Elliott (1995) added a further 7 excavated redds to the data, but stated that the net used to catch females after they had spawned had too wide a mesh to trap eggs drifting from the redd during spawning, but few eggs were seen moving downstream. After measuring, the females were "squeezed" to check for any readily-expelled residual eggs, but none were apparent. The fish were then released alive, so no direct check for retained eggs was made. In order to compare total fecundity with eggs in the redd, Elliott (1995) used the length/fecundity relationship derived for female sea trout from the Leven (61 fish taken by anglers) and from the Dale Park Beck (22 fish taken by electric fishing). The two derived lines are plotted in Fig 4.3. The mean discrepancy between predicted total fecundity and eggs excavated from the redd varied with size of fish from 0% at 240 mm to 16% at 500 mm. Higher egg retention by larger fish has also been reported by O'Farrell et al (1989), though they suggested that the link was with multiple spawning rather than with size *per se*.

Figure 4.3. Comparison of the length/fecundity relationship for sea trout from the Leven and Dale Park Beck (Leven tributary, dotted line), and the relationship between fish length and number of eggs in redds on the Black Brows Beck (Dale Park Beck tributary, solid line). Data from Elliott (1995).



4.4 Fecundity and weight

As discussed in Section 2, weight is a less satisfactory determinant of fecundity than length. Studies have derived a weight/fecundity relationship in addition to a length/fecundity one. Harris (1970) presented the following fecundity formulae for the length/weight regressions of Dyfi sea trout:

$\text{Log } N = 0.865 \text{ Log } W + 0.780$ (for dissected dead fish)

$\text{Log } N = 0.681 \text{ Log } W + 1.967$ (for manually stripped fish)

Walker (1994) presented a linear (non-log transformed) regression for Scottish trout:

$N = 1.597\,W + 105.1$

It is stressed however that this last equation was based on samples of both brown and sea trout.

4.5 Fecundity and egg size

There is a relationship between fecundity and egg size, though not all studies have been able to supply appropriate data. There is clearly a danger interpreting the size of eggs before they are fully developed, and the safest approach is to consider measurements made only after the eggs become loose from the ovary (stage V). Hindar and L'Abée-Lund (1990) observed a positive correlation between fish length (and hence fecundity) and egg size within stocks, though not all the relationships were statistically significant. Walker (1994) observed that trout stocks with higher fecundity per unit length tended to have smaller eggs, and discussed the "trade-off" in life history strategy terms of a larger number of smaller eggs and a smaller number of larger eggs. There is good evidence that larger eggs are associated with larger fry and a higher survival (Bagenal 1969; Elliott 1984). The latter study noted a doubling in survival time of alevins kept without food associated with an increase in alevin wet weight from 140 mg to 210 mg.

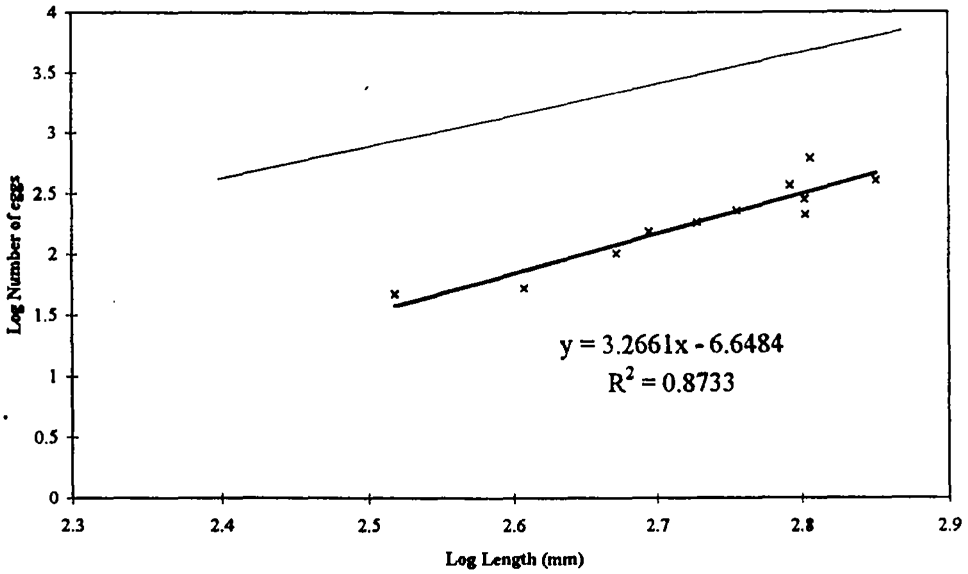
While outside the terms of reference of this study, egg size is clearly a potentially important factor in the survival of the young fish under certain circumstances, and may be a factor that should be taken into consideration in development of spawning targets.

4.6 Stripped fish

Three studies listed in Table 3.1 used stripping of live fish for all or part of their samples. Two of these provided a comparison of the total fecundity and the numbers of eggs expressed during manual stripping.

Harris (1970) killed and dissected 11 female sea trout after manual stripping, and counted the residual eggs. The results are shown in Fig 4.4, along with the length/fecundity relationship for the Dyfi stock.

Figure 4.4. Relationship between fish length and numbers of eggs retained in the body cavity after manual stripping of 11 fish on the Dyfi. Also shown (thin line) is the length/fecundity relationship. Data from Harris (1970).



Numbers of retained eggs averaged 6.8% of the predicted egg load. There appears to be a relationship with length; the mean retention at 250 mm being 3.7%, and at 700 mm about 7.3%. This trend is the reverse of that noted for natural kelts in the Dyfi (Section 4.3) but the small sample sizes and scatter of values suggest that this difference may be an artefact. Overall, the proportion of eggs retained by manually stripped fish was about 7.5 times that recorded in natural kelts.

Walker (1994) used manually-stripped fish for some of his samples, including some sea trout. To provide a multiplier to estimate total fecundity he sacrificed 35 fish after stripping, dissected them and counted the retained eggs. Retention varied from 0.9% - 19.9%, with a mean of 9.0 ± 5.3%. This average includes both brown and sea trout.

As the proportion of eggs retained after manual stripping is variable and may be partly dependent upon the individual operator, it is not safe to use multipliers derived from other studies to calculate total fecundity for investigations where no independent assessment of retention was made. For this reason the result of study 20 in Table 3.1 were not incorporated into Equation 3.

4.7 Variation in fecundity within catchments

Several studies involved separate collections of fish from separate sections of the same catchment, allowing examination of possible differences.

Elliott (1995) found no significant differences between samples from the River Leven (collected by angling), its tributary the Park Dale Beck (by electric fishing), and the nearby River Duddon (collected by angling) even though they represented different years.

Hindar and L'Abée Lund (1990) did however find a significant difference between fecundity of the samples from the Upper and Lower River Namsen in Norway, with prediction of egg numbers in a 400 mm fish of 863 (upper river) and 1378 (lower river) (Table 3.3). The mean egg size was also significantly different, with the fewer eggs from females in the upper river being larger. The discussion of possible reasons for these differences was inconclusive, though production of larger eggs (at the expense of numbers) might be considered an appropriate strategy for the harsher environment of high-altitude streams. If these variations are truly adaptive, the survival of the larger eggs must be in excess of 1.6 times that of the smaller in order to outweigh the disadvantage of the lower numbers produced.

4.8 Relationship between fish size and egg viability

O'Farrell et al (1989) reported a personal observation based on hatchery experience in the West of Ireland that ova from very large sea trout were not as viable as those from middle size fish and that a high percentage of ova from these large fish did not become fertilised. If this is a widespread phenomenon among wild stocks than it has significant implications for effective egg deposition estimates. However, Elliott (1984) and Dr Andy Walker, (pers. comm.) noted high egg survival rates throughout the range of fish sizes under hatchery conditions. Poole et al (1994) similarly noted uniformly high survival rates of eggs derived from previously-spawned sea trout reconditioned in captivity. There is thus little evidence of a widespread phenomenon of reduced egg viability from large or previously-spawned fish.

5. CONCLUSIONS

5.1 Variability between stocks, and use of predictive formulae.

Given the variability in individual fecundity and the small sample sizes involved there is some doubt whether the formulae given in Table 3.1 accurately describe the situation for the stocks from which they are drawn even for the years in which the samples were collected. Unfortunately, the reports on most of the studies did not present the raw data and it has not been possible to undertake analysis of the statistical significance of the apparent differences between stocks. However, if we for the moment assume that the differences apparent are real and stable, we can examine what sort of errors that various predictive formulae would lead to.

We consider first the British Isles mean line (Equation 3) as a predictor for each individual stock. The numbers of eggs for various lengths of fish, as generated by the individual stock formulae and by the British Isles mean line, were given in Table 3.3. If we now consider the British Isles mean line prediction as a percentage of the individual stock prediction for each length (Table 5.1) we can see what percentage error the use of the generalised line would generate as a predictor for each stock. The greatest overestimation is the case of 300 mm fish in the Ewe (+39%), while the greatest underestimate (-31.3%) is for 270 mm fish on the Dale Park Beck. It will be noted that the estimates for these two stocks are at or near the extremes throughout their length ranges.

Table 5.1. Fecundity predictions for various standard lengths of fish produced by the British Isles mean line (Equation 3) as a percentage of the predictions produced by the individual stock relationships.

			Length (mm)									
	River	**l range**	**270**	**300**	**350**	**400**	**450**	**500**	**550**	**600**	**650**	**700**
1	Dyfi	255-740	82.6	83.9	85.9	87.7	89.2	90.7	92	93.2	94.33	95.39
2	Erriff	c.240-550	97.5	102	109	116	122	127	133			
3	Tweed	480-725						101	96.5	92.9	89.66	86.77
4	Earn System	255-650	96.7	96.2	95.4	94.8	94.2	93.7	93.3	92.9	92.52	
5	Ewe System	284-615		139	137	135	134	133	132	131		
6	Leven (Cumbria)	c.300-500		71.8	77.2	82.3	87.1	91.5				
7	Dale Park Beck	c.260-440	68.7	72	77.1	81.8	86.2					
8	Duddon	c.310-430			76.7	80.9						
9	British Isles mean	c. 240-740	100	100	100	100	100	100	100	100	100	100

Given that this approach consistently over, or under, estimates egg numbers for some stocks, while producing a good fit for others, there is clearly scope for grouping stocks and using a number of predictive formulae. The fact that some stocks have higher or lower levels of fecundity throughout their length range arises because the lines are fairly close to being, parallel , i.e. it is the intercept that varies to a greater extent than the slope. O'Farrell et al (1989) discussed a modified format for equation 2:

$$\mathrm{Log}_{10}\, N = \mathrm{Log}_{10}\, a + b\, \mathrm{Log}_{10}\, L + \mathrm{Log}_{10}\, C. \qquad \text{(Equation 4)}$$

where C is a stock-specific constant that acts as a modification to the intercept. The British Isles stocks are "covered" by a range of values of Log_{10} C of -0.149 to +0.158 in relation to Equation 3. Three lines based on equation 4 with values of Log_{10} C of –0.1, 0 and +0.1 would thus represent a better series of predictions than using Equation 3 for all stocks. Data on more stocks is needed however to establish whether the adoption of a single (mean) slope is justified and to establish its value, to assess the range of values of C that occurs, and to develop guidelines for a regional (or other) basis of allocation of a value of C to particular stocks.

5.2 Requirements for further information

The extent to which the use of a generalised fecundity relationship (Equation 3), which may under or over estimate the total fecundity of stocks by up to 30% or more, is acceptable will depend upon the reliability of the other inputs to an egg deposition rate model. The other main variables are:

- the length-frequency distribution of the spawning stock in question, each year.
- the total spawning stock size, each year.
- the sex ratio of each length-class.
- the proportion of each length class of females that will mature and spawn in the current year.
- the habitat and effectiveness of spawning distribution with respect to availability of spawning and rearing habitat.

At present, the lack of reliable measures of for these variables for any single stock suggests that the requirement for a better indicator of fecundity is not of overwhelming urgency. Nevertheless, steady progress in all these areas is clearly highly desirable. Future work on any of these aspects should take place in an integrated framework of development of spawning targets to ensure that work is correctly prioritised and that opportunities for work to examine more than one area are optimised. It is therefore recommended that future work in these areas be considered as part of a structured programme that is overseen and reviewed by a committee of practitioners. The possibility of combining similar work on salmon and sea trout, to the extent that is appropriate, should be carefully considered.

It is appropriate to note that the understanding of the variability of fecundity of salmon is at a similarly uncertain stage. Egg deposition targets and estimates are already being tentatively applied as a management tool, based upon a single fecundity estimator of a number of eggs per unit body weight. Clearly development of a more critical approach is desirable for salmon as well as for sea trout, and it is possible that any programme of further development could most beneficially cover both species. However, it would be prudent to undertake an assessment of current knowledge on salmon fecundity (an equivalent exercise to this report) before specific recommendations for gathering further data on salmon fecundity are made.

What, then, is it that we need to know to advance our understanding of variation in fecundity of sea trout? The questions fall into three classes:

1. How do stocks vary in their length/fecundity relationships, and can we establish any meaningful patterns (e.g. on a regional or environmental parameter basis) to allow extrapolation and interpolation from stocks with known relationships?

2. What are the temporal (between year) variations in the length/fecundity relationship within stocks, and can we link them in a predictive manner to direct environmental observations e.g. inshore sea-water temperatures?

3. What is the pattern of onset of detectable atresia of non-maturing ova in fish entering the river at different times of year? The earlier in the year we can establish reliably the effective egg contribution of individual fish the easier will be the task of gathering adequate samples to describe each stock or year.

The requirement for a greater geographical range of data is probably most realistically addressed on an opportunistic basis. Dedicated collection of samples with reliable records is likely to be expensive in terms of man-power and may be difficult to justify. On the other hand, collection of samples as and when they become available could, in the medium term, result in a most effective collection. Opportunities that spring to mind are fish kills, seizures of illegal catches, collection of fish poisoned in poaching incidents, collection of fish "found dead" due to natural causes, fish accidentally killed or damaged during trapping or broodstocks collection exercises, and collections by EA staff who happen to be sea-trout anglers. It is likely that, eventually, it will be desirable to fill gaps in the coverage by dedicated collection, but this need should be addressed as and when it becomes apparent.

Addressing the annual variation in relationships is likely to require a dedicated programme on a single river system.

5.3 Recommendations

The recommendations for a future programme are therefore:

1. The establishment of an integrated framework for planning and developing R+D on all aspects of spawning targets for sea trout and salmon. This should be undertaken by a small committee which should also adopt the role of overseeing progress.

2. Where authors of earlier work in the British Isles are willing, the raw data for individual fish should be collected together. This will allow a thorough statistical analysis of the whole data set in the future; the lack of raw data significantly limited the analyses that could be undertaken in the current exercise.

3. Gathering ovaries from sea trout from as wide a range of rivers as possible, on an opportunistic basis, as suggested in Section 5.2. Appropriate EA staff should be appraised of the desirability of gathering samples and of the appropriate methods for gathering, storing, and recording details (see Section 5.4). In particular, large samples that might become available, without warning, from events such as fish kills are potentially very valuable.

4. Arising from (i) there is need for establishment of an immediate response mechanism for events such as fish kills of which all relevant EA staff should be aware. This is of course far wider than the subject of sea trout fecundity alone and should be the subject

of a specific R+D initiative. It is recommended that a short review be commissioned on the opportunities for gathering of biological data represented by events such as fish kills and seizures of illegal catches. This should cover all species and develop recommendations for practical implementation of an approach to optimise potential benefits. It is understood that an earlier (NRA) R+D project looked at assessments of fish-kills in terms of mitigation requirements but no specific recommendations regarding R+D data-collecting opportunities have been implemented.

5. In order to investigate the annual variations in the length/fecundity relationships a longer-term study on a single catchment is recommended. Such a programme should be located on a catchment where there is some expectation, in the short to medium term, of obtaining good quality data on other aspects of the sea trout population with a view to developing egg deposition rate estimates. Obvious possibilities are the Welsh Dee and the Lune, both of which have adult trapping programmes in progress. A programme to gather ovaries from (say) 50 fish per year and to count the eggs should be relatively inexpensive though of course every opportunity should be taken to integrate such an exercise with other initiatives and opportunities e.g. scale-collecting and routine bailiff operations.

6. It is recommended that a brief review be commissioned, equivalent to this one covering sea trout, examining the current knowledge of the fecundity of salmon. This should consider the opportunities for development of a programme to gather further data required for both species.

5.4 Collection and storage of samples

Regarding the approach to obtaining samples the following points are made

1. Apart from the "opportunistic" events discussed in Section 5.3, the most realistic source of samples is from fish caught by anglers. It may be feasible to train anglers to collect the samples and record details for a reward payment, but care would be needed regarding quality control of length measurements. The ovaries could be kept frozen until collection could be arranged.

2. Ideally complete ovaries should be removed and placed into 4% formalin to preserve and harden the eggs. They can then be stored almost indefinitely. Similarly, if the eggs are already loose in the body cavity they should be collected and stored in the same way. In a continuing study described by Euzenat et al (1991), the ovaries are stored frozen, and then lightly boiled to harden and separate the eggs for counting (Gilles Euzenat and Francoise Fournel, pers. comm).

3. Other information that should be gathered is the fork length to the nearest mm, the stage of maturity, the exact location and date of capture/collection, and the circumstances of death. A sample of scales should also be taken. Needless to say care should be taken to cross-reference the stored ovaries, the scale samples and the other information.

4. When complete counts are made of the egg numbers, measurements should also be made of the mean egg diameter, and observations made on any apparent bimodal distribution of egg sizes that would indicate detectable differentiation of maturing and

atresic ova. It is likely that treatment during storage and handling could have an effect on subsequent egg diameter measurements so care would be needed in analysing such data; nevertheless they should be adequate for the detection of atresia.

5. All future studies of fecundity should, unless the sample sizes are prohibitively large, include the raw data for individual fish in their reports (see recommendation 2 in section 5.3).

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