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### The Production of Juvenile Atlantic Salmon (*Salmo salar* L.) in the Upper Wye, Wales

by

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#### Introduction

Apart from the work of Eglishaw (1970) there are few data available on the production of Atlantic salmon (*Salmo salar* L.) in freshwaters. Stream studies on salmon are generally confined to the enumeration of smolts (Elson, 1957a; Meister, 1962; Jessop, 1975). In contrast, the production of brown trout (*S. trutta* L.), brook trout (*Salvelinus fontinalis* Mitchill) and coho salmon (*Oncorhynchus kisutch* Walbaum) is well documented (Allen, 1951; Hunt 1974; Chapman, 1965).

This paper reports estimates of salmon production (*sensu* Ivlev, 1966) in 16 study sites in 16 study sites in the upper catchment of the River Wye over a two year period and forms part of a broader study of fish populations in the Wye.

#### Methods

Quantitative sampling, using D.C. electrofishing apparatus based on the design of Moore (1968), was generally undertaken four times a year during 1975 and 1976 at all sites except W3 and W5 (Fig. 1) which were sampled in 1976 only. Additional sampling was undertaken in site W2 in April 1977. At each site a 50m reach was enclosed by stop-nets and fished three or four times. Fork lengths of all salmon were measured and scales were taken for ageing purposes. Samples of fish, weighed to the nearest 0.1g, were used to compute a length-weight relationship for the total study area, after it had been ascertained that there was no significant variation in this relationship between sites. Where possible the catch-depletion data were used to make abundance estimates for each age group using the method of Zippin (1956).

#### Description of the Study Area

The R. Wye, which is 250 km long and has a catchment area of 4183km<sup>2</sup>, rises at Plynlimon (667m O.D.) in Powys, mid-Wales. This study was confined to the upper catchment of the river which drains impermeable Ordovician and Silurian sediments, principally mudstones and shales.

Over the period of the study (February 1975 – November 1976) flows in the R. Wye were the lowest since records began (A. Tillotson, *pers. comm.*, Wright, 1976). Records from a gauging station on the lower Wye show that total flows for the 18 month period from April 1975 were 60% of the long term average (L.T.A.).

Of the 16 study sites, five were located on the main R. Wye and the remainder on tributaries of the Wye (Fig. 1, Table 1.). These sites are typical salmon nursery areas having a substrate of mixed coarse sand and gravel. Main river sites were predominantly riffle areas but tributary sites generally comprised a series of riffles and pools. Average widths of the 50m long study reaches ranged from 10.5 to 26.0m on the main river and from 4.0 to 6.5m on the tributaries: one the R. Elan, a tributary receiving 'compensation' discharge from an impoundment (Fig. 1), Site E1 was consistently 29m wide (Table 1).

Site D3 was 0.5 km below waterfalls impassable to migrating adult salmon whilst site C2 was 200m below and site M2 0.5km above waterfalls rarely negotiated by salmon.

Other fish species present in the study area included brown trout, bullheads (*Cottus gobio* L.), minnows (*Nemachilus barbatula* L.), brook lamprey (*Lampetra planeri* Bloch) and eel (*Anguilla anguilla* L.).

**Table 1**

**Physical dimensions of Sampling Sites**

<b>Station</b>	<b>Area m<sup>2</sup> Range 1975/76</b>	<b>Average depth, cm Range 1975/76</b>
<b>D1</b>	216-330	19-32
<b>D2</b>	300-368	22-40
<b>D3</b>	240-311	16-26
<b>B1</b>	189-267	9-37
<b>B2</b>	172-330	23-44
<b>B3</b>	157-230	13-31
<b>M1</b>	297-496	11-38
<b>M2</b>	277-446	15-49
<b>C1</b>	162-354	12-31
<b>C2</b>	255-379	14-26
<b>W1</b>	408-591	13-27
<b>W2</b>	575-948	21-37
<b>W3</b>	500-652	33-43
<b>W4</b>	635-1510	16-58
<b>W5</b>	612-701	24-35
<b>E1</b>	1149	36

## Results

### *Population size and structure*

Three year classes of juvenile salmon were generally present at all the study sites. The absolute and relative abundance of each of these age groups varied between sites and within each site with time (Table 2). The abundance of the 1975 year-class at each site has been shown to decline exponentially with time and the number of these parr surviving to their second birthday (1 March) is a function of the initial fry density (Gee and Milner, in prep). Data available for 1974 and 1976 year-class fish are more limited than for the 1975 year-class but show a similar pattern of exponential decline (e.g. site W2, Fig. 2).

Densities of 0+, 1+ and 2+ salmon in August 1976 are given in Table 2. 3+ parr were present in 7 of the 16 study sites in March 1976 but represented less than 10% of the total number of >0% parr. These were late migrants and had all disappeared by May. The densities of 1974 fish in Table 2 partly reflect their time of migration, for example, there were no 2+ parr in W5 in August 1976 whereas  $0.02\text{m}^{-2}$  were estimated in April 1976. 85% of the sites produced over  $0.025\text{m}^{-2}$  1975 year-class smolts (Gee & Milner, in prep). In July 1975 1+ parr densities were in the range  $0.0\text{m}^{-2}$  (W1) to  $0.39\text{m}^{-2}$  (D3) and 0+ parr densities  $0.08\text{m}^{-2}$  (W1) to  $4.26\text{m}^{-2}$  (D1). These are much higher than the corresponding August densities of the following year (Table 2).

Table 2

Densities (Numbers in m<sup>-2</sup>) of salmon parr in August 1976 (ISE)

Station	Year Classes		
	1974 (2+)	1975 (1+)	1976 (0+)
D1	0.0046 (0)	0.106 (0.0069)	1.153 (0.069)
D2	0.0030 (0)	0.083 (0.016)	0.450 (0.203)
D3	0.009 (0.0007)	0.044 (0.003)	1.481 (0.201)
B1	0.019 (0)	0.096 (0.003)	0.693 (0.107)
B2	0.035 (0.001)	0.151 (0.006)	0.581 (0.049)
B3	0.019 (0)	0.038 (0)	0.248 (0.046)
M1	0.003 (0)	0.199 (0.010)	1.441 (0.058)
M2	0.014 (0)	0.069 (0.001)	0.054 (0.016)
C1	0.012 (0)	0.111 (0.009)	1.253 (0.126)
C2	0.008 (0)	0.039 (0.003)	1.365 (0.138)
W1	0 (0)	0.027 (0.328)	0.118 (0.024)
W2	0.003 (0)	0.183 (0.066)	0.910 (0.081)
W3	0.004 (0)	0.154 (0.010)	1.160 (0.023)
W4	0.002 (0)	0.033 (0.001)	1.112 (0.186)
W5	0 (-)	0.028 (0.003)	1.972 (0.399)
E1	0 (-)	0.024	0.150

**Table 3**

**Mean length (cm) and 95% confidence limits for salmon in  
October – November 1976**

	Year-classes		
	1974	1975	1976
<b>D1</b>	-	13.0 (+8.4)	5.2 (+0.35)
<b>D2</b>	-	11.1 (+0.79)	5.7 (+0.21)
<b>D3</b>	13.8 (+3.60)	11.0 (+1.11)	5.4 (+0.14)
<b>B1</b>	12.9 (-)	10.5 (+0.52)	6.7 (+0.30)
<b>B2</b>	12/3 (+0.81)	9.9 (+0.32)	6.9 (+0.28)
<b>B3</b>	-	10.6 (-)	7.3 (-)
<b>M1</b>	15.7 (-)	10.7 (+0.63)	5.6 (+0.20)
<b>M2</b>	-	11.4 (+0.56)	5.7 (+1.07)
<b>C1</b>	12.5 (-)	10.0 (+0.75)	5.9 (+0.27)
<b>C2</b>	14.2 (+0.83)	11.2 (+1.88)	6.6 (+1.02)
<b>W1</b>	-	-	7.3 (-)
<b>W2</b>	-	10.3 (+0.31)	5.8 (+0.09)
<b>W3</b>	-	10.3 (+1.11)	5.9 (+0.24)
<b>W4</b>	-	12.3 (-)	5.2 (+0.24)
<b>W5</b>	13.7 (-)	10.0 (+0.92)	5.2 (+0.09)
<b>E1</b>	-	9.3 (+0.83)	5.3 (+0.05)

Growth

Mean lengths for each year-class were calculated for each of the 8 sampling periods in 1975-1976. Growth occurred throughout the year but was most rapid in the period April – September. There was very little growth between October and March (e.g. site D1, Fig. 3).

No meaningful comparison between sites can be made of the lengths of the 1974 year-class salmon in 1976 because faster growing smolts migrate earlier (Elson, 1957b). The mean length of the remaining fish is biased towards smaller individuals. The growth rates, as indicated by mean lengths, at the 16 study sites (Table 3) were similar and enabled most parr to smolt in their third year. October lengths of 0+ fish ranged from 5.2 cm (D1, W4, W5) to 7.3 cm (B3, W1,) and 1+ fish from 9.3 cm (E1) to 13.0 cm (D1) as shown in Table 3. The largest parr, found in D3, was 16.3 cm long and 29 months old.

Biomass

Mean lengths were converted to weights using the relationship:

$$\text{Log}_{10} \text{ weight} = 3.193 \text{ log}_{10} \text{ length} - 2.052$$

The biomass of each year-class was then calculated for each site.

The largest biomass of salmon, up to 60% of which was made up of 0+ fish, was recorded during the period July-August, ranging from 1.0 g.m<sup>-2</sup> (W1) to 12.1 g.m<sup>-2</sup> (D3). The smallest biomass was recorded in the period November to March ranging from 0.008 g.m<sup>-2</sup> (W1) to 0.8 g.m<sup>-2</sup> (D3).

### Production

As the abundance of juvenile salmon in the study area has been shown to decline exponentially with respect to time (Gee & Milner, in prep.) the mean biomass during the period  $t_1 - t_2$  can be expressed by

$$\bar{B} = \frac{\ln B_1 + \ln B_2}{2}$$

where  $B_1$  and  $B_2$  are the biomasses at times  $t_1$  and  $t_2$  respectively. The initial biomass of fry is assumed to be 1g. According to Ricker's formula (Ricker, 1946) production is then defined as:

$$P = G\bar{B}$$

where  $G$  = instantaneous growth rate in weight.

The initial growth rate,  $G$ , of fry was estimated assuming an initial length of 2.0 cm, equivalent to a weight of 0.08g.

In certain instances the loss of 2+ parr as smolts effectively reduced the mean weight of the population, resulting in apparent negative growth rate and negative production. Where this occurred an appropriate value for growth rate has been used to calculate production.

Comparison of the production of each year-class at 13 sites\* during the period March – November, when 06% of production takes place, indicates that 0+ and 1+ age classes contributed over 72% of the total production and 3+ salmon no more than 1% of the total (Table 4). The variation in the proportional contribution of year-classes between sites was large.

Values for average production during the study period are equivalent to annual production rates of 0.3 g.m<sup>-2</sup> and 11.0 g.m<sup>-2</sup> (Table 5). There is considerable variation between sites in the amount of production attained in the period March – November in 1975 and 1976; the ratio P1975/P1976 varies from 0.6 (W2) to 3.9 (D1).

\* insufficient data at W3, W5, E1.

**Table 4**

**Percentage contribution made by 0+, 1+, 2+ and 3+ year old fish to the total production of salmon in the period March – November in 1975 and 1976.**

**(\*production in period March 1975 – March 1976 in M1 and M2)**

Station	Year	Age Groups				Total Production (g)
		0+	1+	2+	3+	
<b>D1</b>	1975	70	28	2	0	3904
	1976	40	55	5	0	990
<b>D2</b>	1975	67	25	7	1	1951
	1976	48	37	15	0	1505
<b>D3</b>	1975	30	42	27	1	2568
	1976	51	35	14	0	1057
<b>B1</b>	1975	58	33	9	<1	1550
	1976	46	44	10	0	781
<b>B2</b>	1975	61	34	5	<1	1152
	1976	33	53	14	0	729
<b>B3</b>	1975	81	19	0	0	230
	1976	29	60	11	0	431
<b>M1</b>	1975	43	40	16	1	1838
	1976	40	41	19	0	2036
<b>M2</b>	1975	21	78	1	0	923
	1976	7	82	11	0	417
<b>C1</b>	1975	58	30	12	0	1062
	1976	54	33	13	0	1432
<b>C2</b>	1975	32	54	14	<1	1390
	1976	44	34	22	0	1512
<b>W1</b>	1975	90	10	0	0	77
	1976	76	24	0	0	111
<b>W2</b>	1975	68	29	3	0	1601
	1976	44	52	4	0	2658
<b>W4</b>	1975	61	36	3	0	1556
	1976	52	47	1	0	1204

Table 5 – The distribution of mean biomass  $\bar{B}$  ( $\text{g m}^{-2} \text{ day}^{-1}$ ) for juvenile salmon populations in the Upper Wye

Site	Time period ending November 1976 (days)		Year-classes					Total
			1972	1973	1974	1975	1976	
D1	637	B	0	0.415	1.696	1.462	0.377	3.05
		P	0	0.0005	0.0070	0.0200	0.0024	0.030
D2	599	B	0.057	0.625	0.800	1.289	0.819	2.62
		P	0.00007	0.0007	0.0038	0.0102	0.0038	0.019
D3	601	B	0.271	2.813	1.863	1.142	0.754	4.61
		P	0.00016	0.0049	0.0086	0.0079	0.0037	0.025
B1	573	B	0.072	0.785	1.113	1.477	0.569	3.06
		P	0.000017	0.0014	0.0056	0.0115	0.0032	0.022
B2	595	B	0.256	1.087	0.959	1.533	0.0029	2.67
		P	0	0.0006	0.0042	0.0094	0.0021	0.016
B3	600	B	0	0	0.180	0.295	0.120	0.53
		P	0	0	0.00073	0.0037	0.0011	0.006
M1	624	B	0.294	0.800	1.539	1.648	0.848	3.78
		P	0.00013	0.0016	0.0058	0.0083	0.0043	0.020
M2	630	B		0.039	0.545	0.616	0.039	1.10
		P		0.00005	0.0039	0.0027	0.00016	0.007
C1	629	B	0	0.483	1.225	0.179	0.858	2.88
		P	0	0.0010	0.0036	0.0078	0.0051	0.018
C2	584	B	0.055	0.996	1.776	0.765	0.812	3.36
		P	0.000013	0.0016	0.0082	0.0067	0.0044	0.021
W1	587	B	0	0	0.033	0.061	0.037	0.091
		P	0	0	0.00003	0.0005	0.0003	0.0008
W2	603	B	0	0.106	0.466	1.297	0.678	1.93
		P	0	0.00012	0.0015	0.0068	0.0030	0.011
W3	205	B	0	0	0.488	1.024	0.268	1.54
		P	0	0	0.0032	0.0085	0.0042	0.016
W4	599	B	0	0.065	0.122	0.169	0.394	0.43
		P	0	0.00005	0.0008	0.0020	0.0008	0.0036
W5	223	B	0	0	0.96	0.488	1.045	1.63
		P	0	0	0.0011	0.0042	0.0067	0.012
E1	583	B	0	0.205	0.189	0.191	0.136	0.413
		P	0	0.00013	0.0004	0.0011	0.0006	0.0022



Table 6

Regression parameters of  $\log_{10}P = a + b \log_{10} \bar{B}$  where P = production ( $\text{g.m}^{-2} \text{ day}^{-1}$ ) and  $\bar{B}$  = mean biomass ( $\text{gm}^{-2}$ ).  
 r = correlation co-efficient.

All data refer to composite year-classes except where indicated.

Period	a	95% ci (+)	b	95% ci (+)	r
Feb – May 1975	-2.3721	0.2000	0.9600	0.3762	0.8714
May – Jul 1975	-1.6830	0.1284	0.7910	0.2166	0.9305
Jul – Oct 1975	-2.3045	0.1484	1.0092	0.2179	0.9666
Oct 1975 – Mar 1976	-3.0482	0.3774	0.7332	0.4297	0.8362
Mar 1976 – Jun 1976	-1.9267	0.1185	1.2445	0.2468	0.9493
Jun 1976 – Aug 1976	-1.9069	0.1579	0.7777	0.3493	0.8138
Aug 1976 – Nov 1976	-2.2319	0.2643	0.7982	0.5731	0.6960
Feb 1975 – Nov 1976	-2.1332	0.0584	0.9106	0.1214	0.9740
* Jul 1975 – Nov 1976	-2.1327	0.0979	0.8836	0.2200	0.9350

\* (1975 year-class only)

The relationship between P and  $\bar{B}$  for all year-classes combined for each of the inter-sample periods and for the period March 1975 – November 1976 (Figs 4 and 5) can be expressed by the relationship.

$$P = a \bar{B}^{-b}$$

where a and b are constants.

A similar relationship holds when individual year-classes are considered and all values of b (Fig 4, Table 6) are not significantly different from the value of b (0.9106) calculated for pooled data (Fig 5) when compared by F-test ( $P = 0.05$ ). The value of a varies with the time of the year, generally being higher in the spring and summer and lower in the autumn and winter (Fig 4).

The relationship between P and  $\bar{B}$  for trout in the study area (unpublished data) during the period February 1975 to November 1976 is given by:

$$\text{Log } P = -2.4966 (\pm 0.1735) + 0.9797 (\pm 0.2055) \text{ log } \bar{B}$$

where P = production in  $\text{g.m}^{-2} \text{ day}^{-1}$

$$\bar{B} = \text{biomass in } \text{g.m}^{-2}$$

95% confidence limits for a and b are given in parentheses.

Neither a nor b is significantly different from the values obtained for salmon during the same period when compared by F-test ( $P = 0.05$ ).

### Discussion

Egglishaw (1970), in a three year study of a single stream, found that the production of salmon in each year was very different though there was limited variation between sites in any one year. The present study of a much wider range of habitat conditions clearly shows that there is much variation spatially as well as temporally. 1+ smolts have been recorded from the lower reaches of the R. Wye (Wye River Division Annual Reports) suggesting that there is greater variation in production in the Wye system that has been recorded in this study.

The population structure of juvenile salmon, unlike that of trout in the study area, is characterised by large numbers of 0+ fish whose abundance decreases with respect to time so that the numbers of each of the older year-classes is a function of the year-class strength of the original fry (Gee and Milner, in prep). Though there is likely to be much movement of fish, this migration is thought to be a prelude to death and such movement does not seem to affect the number of survivors in any part of the system. That some upstream movement occurs is illustrated by the fact that there were no salmon in B3 in March 1975 though 1+ fish were present in May 1975. such movement appears to be limited as no salmon were caught in three sites upstream of B3 in May. The production at B3 is much less than at B2, approximately 1km downstream (Table 5 and Fig. 1).

Mid-summer densities of parr were similar to those recorded for other rivers : in this study 0+ parr densities in 1975 and 1976 were in the range 0.05 – 4.26m<sup>-2</sup> compared with 0.17-0.25m<sup>-2</sup> in cove Brook (Meister, 1962), 0.25 – 1.01m<sup>-2</sup> in some Tweed tributaries (Mills, 1971) and 3-5m<sup>-2</sup> in Shelligan Burn (Egglshaw, 1970).

Without the use of traps the estimation of smolts can only be made from parr densities. In this study the mortality rate of parr was very high (annual instantaneous mortality rate  $z = 0.84 - 3.80$ ). It is likely therefore that some 1+ parr would die between the end of the growing season and the time of smolt migration in the spring of their third year. In this study the highest November density of 1+ parr was 0.17m<sup>-2</sup> in D3 but this had decreased to 0.05m<sup>-2</sup> by March. Egglshaw (1970) suggests that smolt production in the Shelligan Burn (0.10-0.22m<sup>-2</sup>) was much higher than in other streams. However, he equates smolt production with the number of parr over 9 cm in length at the end of the growth period of the second year. Yet, in November 1966 and 1968 1+ parr densities in the Shelligan Burn were in the range 0.03 – 0.15m<sup>-2</sup>. Meister (1962) found that only 17-25% of mid-summer parr were caught in smolt traps the following spring. Therefore, if it is assumed that an average 20% of mid-summer 1+ parr eventually migrate as smolts, the 1975 year-class in the study area would not be expected to produce more than 0.04 smolts per m<sup>2</sup> (Table 2). The empirical model proposed by Gee and Milner (in prep) suggested a maximum 0.042 smolts m<sup>-2</sup>. these estimates are similar to those for other rivers (Elson, 1957a; Meister, 1962; Mills, 1964; Jessop, 1975).

Le Cren (1969) argued that of all the population parameters the production is the best epitome of the population dynamics of a fish species. His comparison of a wide range of stream dwelling salmonids suggested that the production in natural small streams has a maximum of 12 g.m<sup>-2</sup> a<sup>-1</sup>. In the present investigation production ranged from 0.3 to 11.0 g.m<sup>-2</sup> a<sup>-1</sup>, indicating that in some parts of the system salmon production was approaching that regarded as maximal. High production was generally found in the smaller tributaries whilst in the main river and in the R. Elan salmon production was much lower. The curves of Fig. 4 and 5 indicate that the production was dependent on biomass, the P/B ratio, or growth rate (G) varying little between sites (see Table 3, equation 3, Appendix). The average specific growth rate G has the following relationship with biomass:

$$G = 0.0074 \bar{B}^{-0.089}$$

where  $\bar{B}$  = mean biomass density (g.m<sup>-2</sup>)

The factors which limit the standing crop of salmon therefore limit production. Consideration of the lowest standing stocks (Fig. 5) indicate that production is limited by density at W1, E1, W4, B3 and M2. W1 is the uppermost site on the main river and it is likely that production is limited by the number of spawners. B3 is 1km upstream of the nearest known spawning beds and M2 lies upstream of a series of steep waterfalls. Spawning intensity may have been low in W4 and E1, both of which are wide sites. The production of salmon in other parts of the Wye system accessible to spawners is typical of salmon nursery streams.

## Appendix

The mathematical relationship between P and B is a corollary of that between G and mean weight  $\bar{w}$  of individual fish:

$\bar{w}$

$$G = a\bar{w}^{-x} \text{ (Elliott, 1975)}$$

Mean biomass  $\bar{B} = N\bar{w}$  where N is the mean number of fish.

But  $P = G\bar{B}$  (Ricker, 1946)

Therefore  $P = a(N\bar{w})^{1-x}$

In this study  $(1-x) = b$  ranged from 0.73 to 1.2. Values of b for 6 of the 7 inter-sample period are not significantly different from 0.8 ( $P < 0.05$ ), the value of the exponent x in Parker and Larkin's (1956) generalized model for fish growth.

$$dw/dt = kw^x$$

where w = weight of fish; t = time, k and x are constants. Winberg (1956) showed that fish were characterised by a level of metabolism proportional to  $w^{0.8}$ . Similarly, the production of coarse fish in gravel-pit lakes in South-East England was found to be proportional to  $B^{0.82}$  (Gee, 1976). Therefore, it may be a general rule that  $P = aB^x$  where  $x = 0.8$  and  $a$  varies with species and environmental factors. In this study the value of  $a$  varied with the time of year, probably through temperature and food supply. For a single year-class of trout feeding on maximum rations Elliott (1975) found that  $a$  was a function of temperature ( $T^\circ\text{C}$ ):

$$a = x + BT$$

where x and B are constants whose values are different above and below  $13.0^\circ\text{C}$ .

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## Summary

1. The production of juvenile Atlantic salmon (*Salmo salar* L.) was investigated in 16 study sites in the upper Wye catchment during the period February 1975 to November 1976.
2. The population structure was characterised by large numbers of 0+ fish whose abundance decreased with respect to time so that the numbers of each of the older year-classes was a function of the year-class strength of the original fry.
3. The range of parr densities was similar to that recorded for other rivers; the estimates of 2+ smolts did not exceed about  $0.04\text{m}^{-2}$ .
4. Production ranged from 0.3 to  $11.0\text{ g}\cdot\text{m}^{-2}\text{ a}^{-1}$  0+ and 1+ fish contributed over 72% and 3+ fish less than 1% of the total annual production.
5. The relationship between production  $P(\text{g}\cdot\text{m}^{-2}\text{ a}^{-1})$  and mean biomass  $\bar{B}(\text{g}\cdot\text{m}^{-2})$  for all year-classes considered separately and in combination can be expressed by the relationship  $P = a \bar{B}^{-b}$ . The values for  $a$  vary with age composition and season but the values for  $b$  are not significantly different.
6. Differences in growth rate of salmon between sites are small and differences in production result principally from differences in standing crop. In most cases low values for salmon production can be attributed to poor spawning.

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## Figure Legends

- Fig 1 Map of the study area to show the sampling sites.
- Fig 2 The relationship between log population abundance ( $\pm$ S.E.) and time for three year-classes of salmon in site W2.
- Fig 3 The growth in length ( $\pm$ 95% confidence limits) of four year-classes of salmon in site D1.
- Fig 4 The relationship between production (P) and mean biomass ( $\bar{B}$ ) for all sites for salmon (all year-classes combined) during 1975 and 1976 indicating the range of values of  $\bar{B}$ .

a = Feb – May 1975;                      b = May – July 1975                      c = July – Oct 1975;  
d = Oct 1975 – Mar 1976;                      e = March – June 1976;                      f = June = Aug 1976;  
g = Aug = Nov 1976.

- Fig 5 The relationship between production (P) and mean biomass ( $\bar{B}$ ) for salmon for the period February 1975 – November 1976.



## Appendix

The mathematical relationship between P and B is a corollary of that between G and mean weight  $\bar{W}$  of individual fish:

$\bar{W}$

$$G = c\bar{W}^{-x} \text{ (Elliott, 1975)}$$

Mean biomass  $\bar{B} = N\bar{W}$  where N is the mean number of fish.

But  $P = G\bar{B}$  (Ricker, 1946)

Therefore  $P = cN(\bar{W})^{1-x}$

$$= \underline{a} B^{\underline{b}}, \bar{W}^{\underline{b}}$$

i.e. if  $(1-x) = \underline{b}$ ,  $c = \underline{a}N^{-x}$

In this study  $\underline{b}$  ranged from 0.73 to 1.2.

Values of  $\underline{b}$  of 6 of the 7 inter-sample periods are not significantly different from 0.8 ( $P < 0.05$ ), the value of the exponent x in Parker and Larkin's (1956) generalized model for fish growth.

$$dw/dt = kw^x$$

where w = weight of fish; t = time, k and x are constants. Winberg (1956) showed that fish were characterised by a level of metabolism proportional to  $w^{0.8}$ . Similarly, the production of coarse fish in gravel-pit lakes in South-East England was found to be proportional to  $B^{0.82}$  (Gee, 1976).

Therefore, it may be a general rule that  $P = aB^b$  where  $b = 0.8$  and  $\underline{a}$  varies with species and environmental factors. In this study the value of  $\underline{a}$  varied with the time of year, probably through temperature and food supply. For a single year-class of trout feeding on maximum rations Elliott (1975) found that c was a function of temperature ( $T^\circ\text{C}$ ):

$$c = x + BT$$

where x and B are constants whose values are different above and below  $13.0^\circ\text{C}$ .

Figure 1

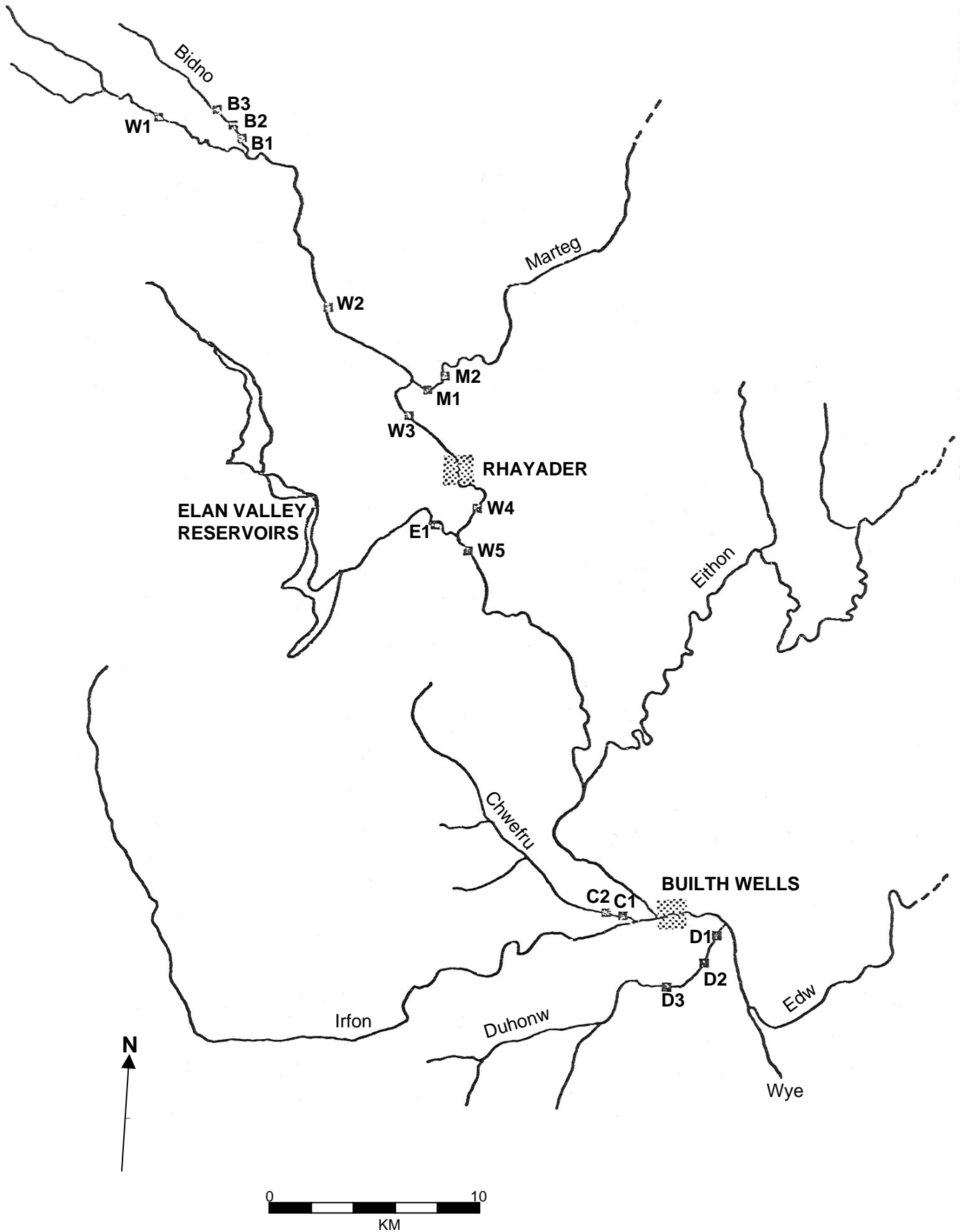


Figure 2

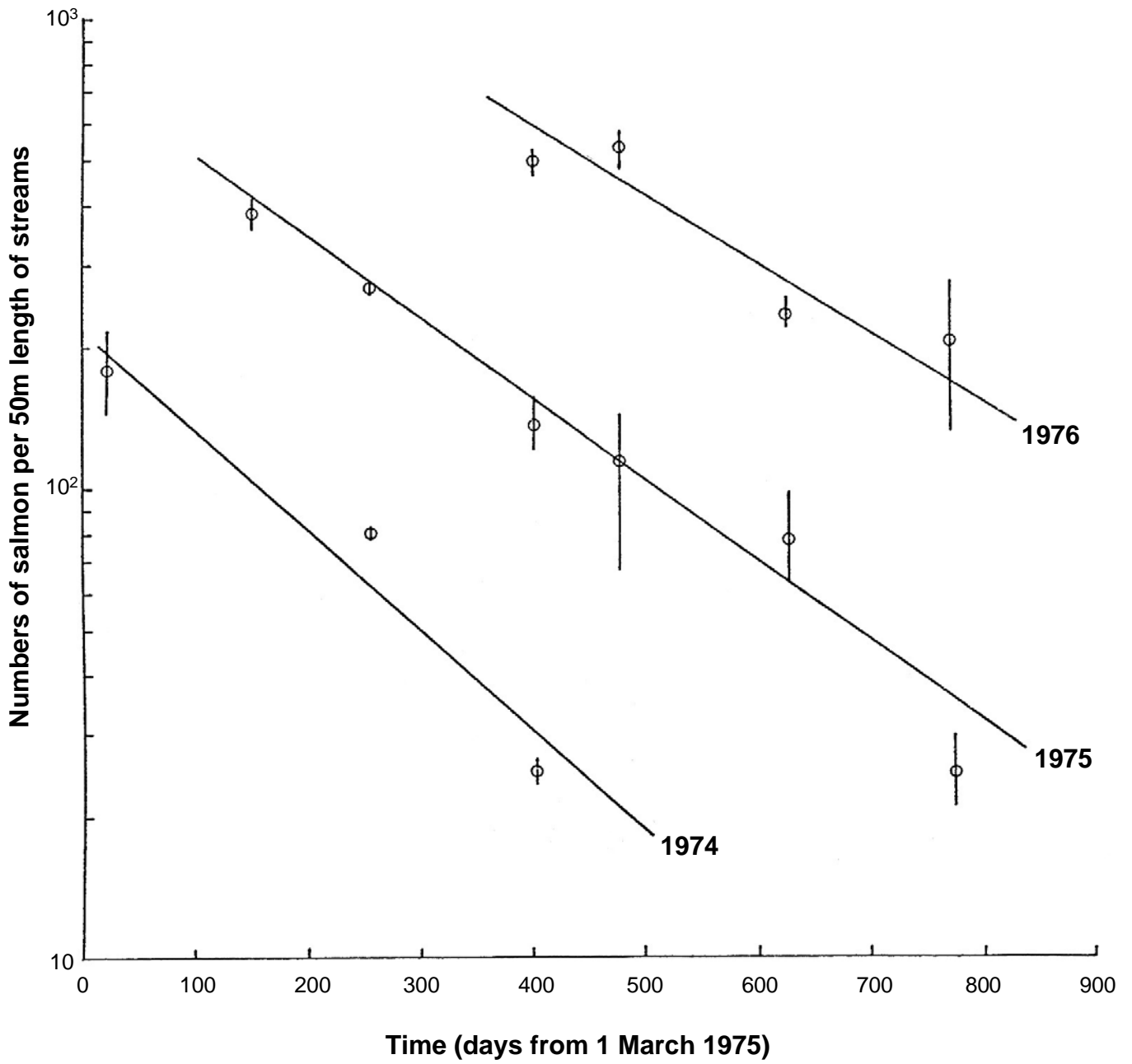
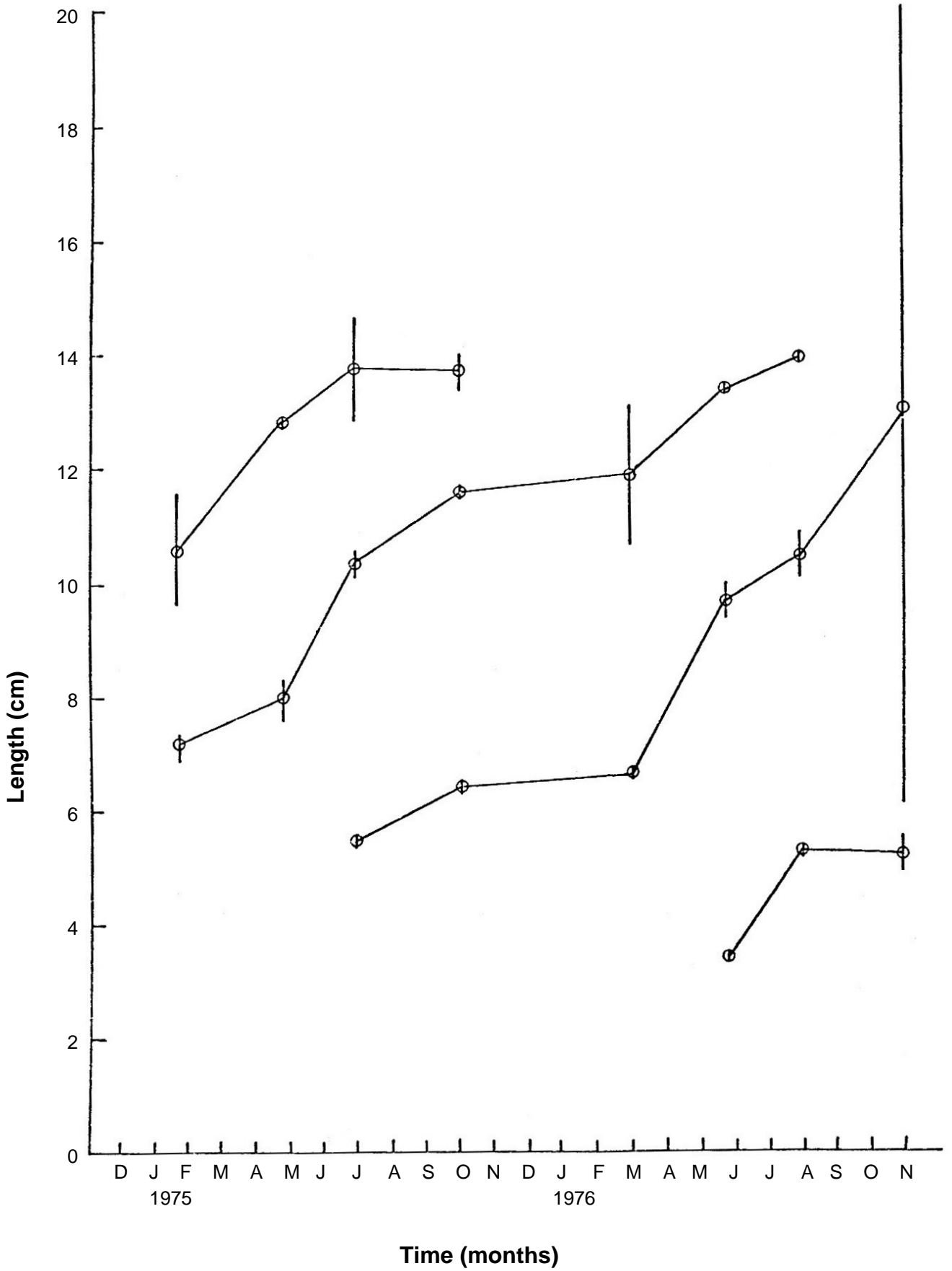


Figure 3



**Figure 4**

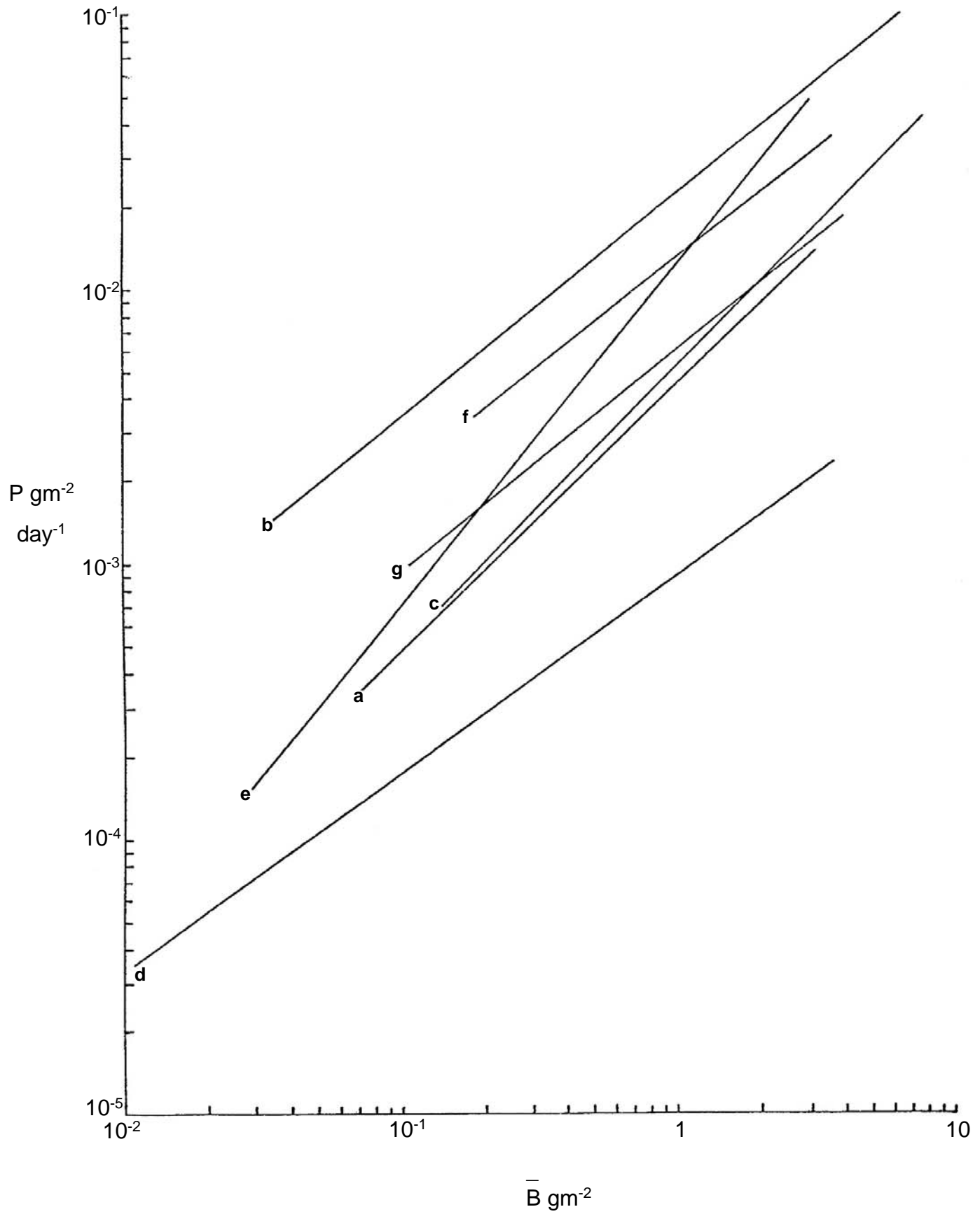


Figure 5

