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The Effect of Density on Mortality in Juvenile Atlantic Salmon (*Salmo salar* L.)

By

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Introduction

Le Cren (1973) suggested that the most likely population-regulating process in salmonid populations is density-dependent territorial behaviour. Thus, in trout (*Salmo trutta* L.) populations aggressive territorial behaviour was manifested in density-dependent mortality and the size of the adult stock was largely dependent on the area of suitable rearing ground for the fry (Le Cren, 1973). Ricker (1954) also concluded that in most fish populations compensatory mortality in the juvenile stages, rather than in the mature stock, was of greatest importance as a regulator of population size. The nature of such regulating mechanisms in juvenile populations is, therefore, of fundamental importance in the understanding of the dynamics of fish populations and the implementation of management policies.

This paper considers mortality rates of young Atlantic salmon (*Salmo salar* L.) in the upper catchment of the R. Wye over a two year period. The work forms part of a broader study of fish populations in the R. Wye.

Description of the Study Area

The R. Wye, which is 250 km. long and has a catchment area of 4183 km³, rises at Plynlimon (667 m. 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 (Fig. 1).

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 for the 18 month period from April 1975 flows were 60% of the long term average (L.T.A.). The range during the study period was very large being 2% of the L.T.A. in June, July and August 1976 and 218% in October 1976.

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: the R. Elan (E1), a tributary receiving 'compensation' discharge from an impoundment (Fig. 1) was consistently 29m. wide (Table 1).

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 W4 and W5. These sites were sampled in 1976 only. 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.

Where possible the catch-depletion data were used to make abundance estimates for each size-age group using the method of Zippin (1956). Mortality rates were calculated from abundance estimates at successive sampling dates.

Results

Mortality rates of 1975 year-class salmon only are considered because of the limited data available for other age-classes. June was the earliest time at which fry were large enough to sample efficiently. Within each site the mortality rate remained remarkably constant over the period June 1975 to November 1976 (Fig. 2). Estimated abundance at each site declined exponentially with respect to time according to the standard expression:

$$N_t = N_0 \exp (-Zt) \quad (1)$$

where N_t = number present at time t (days)
 N_0 = number present at beginning of the period ($t = 0$)
 Z = exponential rate of decrease or mortality.

Using the method of at least squares regression the line of best fit was calculated and Z estimated for each site (Fig. 2). It was then possible to estimate the numbers of salmon fry (N_0) at each site at a common time, 1 June 1975 (t_0), and hence, knowing the area (A_0) of each site at this time, fry density (N_0/A_0). The relationship between the instantaneous rate of mortality, Z , over the 18-month period and the density of fry on 1 June 1975 is significant at the 0.001 level ($r = 0.827$, d.f. = 15) (Fig. 3). If sites W4 and E1, which were substantially larger than the other sites (Table 1) are excluded from the analysis the relationship (fitted by the least squares method) is best expressed by (Fig. 3):-

$$Z = 0.0026 + 0.0021 (N_0/A_0) \quad (2)$$

Combining equations (1) and (2) the numbers of 1975 year-class salmon (N_t) surviving to time t can be calculated from:

$$N_t = N_0 \exp \left(- \left(0.0026 + 0.0021 \frac{N_0}{A_0} \right) t \right) \quad (3)$$

Assuming a fry density on 1 June 1975 and using 1 March as a convenient birthday for salmon it is possible to estimate, using Equation (3), the number of salmon surviving until the second birthday (March 1977) (Fig. 4). Since most 2 year-old salmon (parr) in the

Wye are in fact pre-smolts at this time (Hutton, 1937) their abundance can be considered a good estimate of smolt production for the area during the year.

It is clear that optimum smolt production in the upper Wye catchment results from fry densities (1 June) in the region of 0.75m^{-2} (Fig. 4). Of the sites sampled, three (W2, M1 and D3) have fry densities likely to produce maximum smolt production, three (W1, M2 and B3) have fry densities too high (Fig. 4). The range of expected smolt densities is $0.005 - 0.052\text{m}^{-2}$, with 85% of the sites producing over 0.025 smolts m^{-2} .

Discussion

Juvenile salmon and trout are strongly territorial (Kalleberg, 1958; Le Cren, 1973). The expected relationships between the mortality rate and the initial density would, therefore, be semi-logarithmic; the mortality rate would be asymptotic at high initial densities (see Fig. 3), as found for trout by Le Cren (1973). However, in this study this was not the case. Above initial densities of 0.75m^{-2} the relationship between mortality and density is over-compensatory (Fig. 3) such that the number of survivors decreases as density increases above the optimum density. In this study and Le Cren's (1973) experiments, post-June mortality rates within each site were constant and a function of the June density. It appears, therefore, that initial high densities ($> 0.75 \text{m}^{-2}$) confer some disadvantages even to those individuals that survive the initial period of higher mortality. This disadvantage was not manifested in growth rates, which followed the normal pattern of being inversely density-dependent (unpublished data). There may well be stress effects, resulting from the initial high density conditions, which continue to operate even at lower densities. Miller (1958) found that transplanted hatchery-reared trout accumulated high blood lactate levels and died either from acidosis or starvation as a result of aggression in competition with native trout. A similar decrease in fitness may occur in young salmon at high densities as a result of an increase in the number of intra-specific encounters.

In contrast to the observations of Le Cren (1973) on brown trout, variations in the abundance of coexisting species both within and between studies over the period of study (Table 1) did not significantly affect mortality rates (Fig. 2): this is presumably because changes in such wetted areas are much lower than the differences in population densities between sites. This is of relevant importance in interpreting the effects of changes in wetted areas, whether natural or artificial, on the survivorship of salmon populations.

Data from the two sites, W4 and E1, were not in close agreement with those collected at other sites and it may be significant that the river at these two sites is considerably wider (approx. 100%) than any of the other sites. Clearly, there are difficulties in adequately sampling such wide river sites which may have resulted in biased abundance estimates. Alternatively, the general density-dependent relationship (Fig. 3 Equation [2]) may not be the best description of the relationships pertaining at these sites, although data from a nearby site W5, fitted the relationship well.

This is evidence that under favourable conditions the mortality of salmonid eggs and alevins is low and that high mortality does not occur until the fry stage (Hobbs, 1940; Allen, 1951; Jones 1959). In the absence of destruction of previously laid eggs by later spawners ('overcutting') fry density measured on 1 June, is, therefore, likely to be proportional to spawning intensity. Since variation in adult mortality is small compared

with that in the juvenile stages and less likely to affect recruitment (Ricker, 1954; Le Cren, 1965). The model depicted in Fig. 4 can be regarded as a reproduction or stock-recruitment curve and is similar to observed curves for non-territorial species, including *Oncorhynchus gorbusha* Walbaum (Ricker, 1954) and *Melanogrammus negliffinus* L. (Cushing & Harris, 1973).

Expected smolt densities in the Wye catchment calculated from Equation (3) are similar to density estimates from migrating smolts caught in traps in other rivers (Elson, 1957; Mills, 1964; Meister, 1962; Jessop, 1975). Many sites on the R. Wye appear to sustain fry densities which are too high for optimum smolt production (Fig. 4).

More work of the kind done in North American rivers (Elson, 1957; Wickett, 1958; Meister, 1962) is needed before salmon stocks in Britain can be managed by manipulation of the spawning escapements. The more immediate fishery management implications are that, assuming hatchery reared fish behave as native fry, the optimum stocking density should be such as to produce about 0.75 fry m^{-2} , considerably lower than the density of $2\text{-}5 \text{ m}^{-2}$ recommended for moorland streams by Mills (1969).

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Summary

1. The mortality of juvenile Atlantic salmon (*Salmo salar* L.) was investigated in 16 study sites in the upper Wye catchment during the period June 1975 to November 1976.
2. Within each site the instantaneous mortality rate remained remarkably constant over the period of study and the mortality rate at each site was directly related to the density of fry on 1 June. Thus, knowing the fry density on 1 June it was possible to predict the survivorship of juvenile salmon.
3. The number of survivors decreased above the optimum initial density as indicated by a dome-shaped recruitment curve atypical of territorial species.
4. Assuming that smolt production is equivalent to the numbers of juvenile salmon surviving to 2 years of age, the maximum smolt production of 0.052 m^{-2} is estimated to be attained from a fry density on 1 June of 0.75 m^{-2} . Many sites on the R. Wye appear to sustain fry densities which are too high for maximum smolt production. The optimum stocking density for unfed fry is 1 m^{-2} , considerably lower than is common practice.

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Table 1

Physical dimensions of Sampling Sites

Station	Area m ⁻²		Average depth, cm.	
	June 1975	Range 1975/76	June 1975	Range 1975/76
D1	260	216-330	26	19-32
D2	315	300-368	25	22-40
D3	240	240-311	18	16-26
B1	195	189-267	14	9-37
B2	195	172-330	23	23-44
B3	200	157-230	27	13-31
M1	310	297-496	16	11-38
M2	310	277-446	21	15-49
C1	240	162-354	24	12-31
C2	255	255-379	20	14-26
W1	538	408-591	24	13-27
W2	633	575-948	25	21-37
W3	500	500-652	33	33-43
W4	1270	635-1270	32	16-58
W5	627	612-701	31	24-35
E1	1149	-	36	-

Figure Legends

- Fig. 1. Map of the study area to show the sampling sites.
- Fig. 2. Mortality curves for the 1975 year-class salmon in 16 study sites indicating the magnitude of the instantaneous mortality rate (per day) Z .
- Fig. 3. The relationship between the instantaneous mortality rate (Z) and fry density as estimated for each site from the mortality curves of Fig. 2. the 'line of density-dependence' indicates the relationship between Z and fry density necessary to produce asymptotic recruitment.
- Fig. 4. Expected 'smolt' production at varying fry densities as predicted from equation (3). The observed densities of fry on 1 June 1975 for sites in the Wye catchment are indicated.

Figure 1

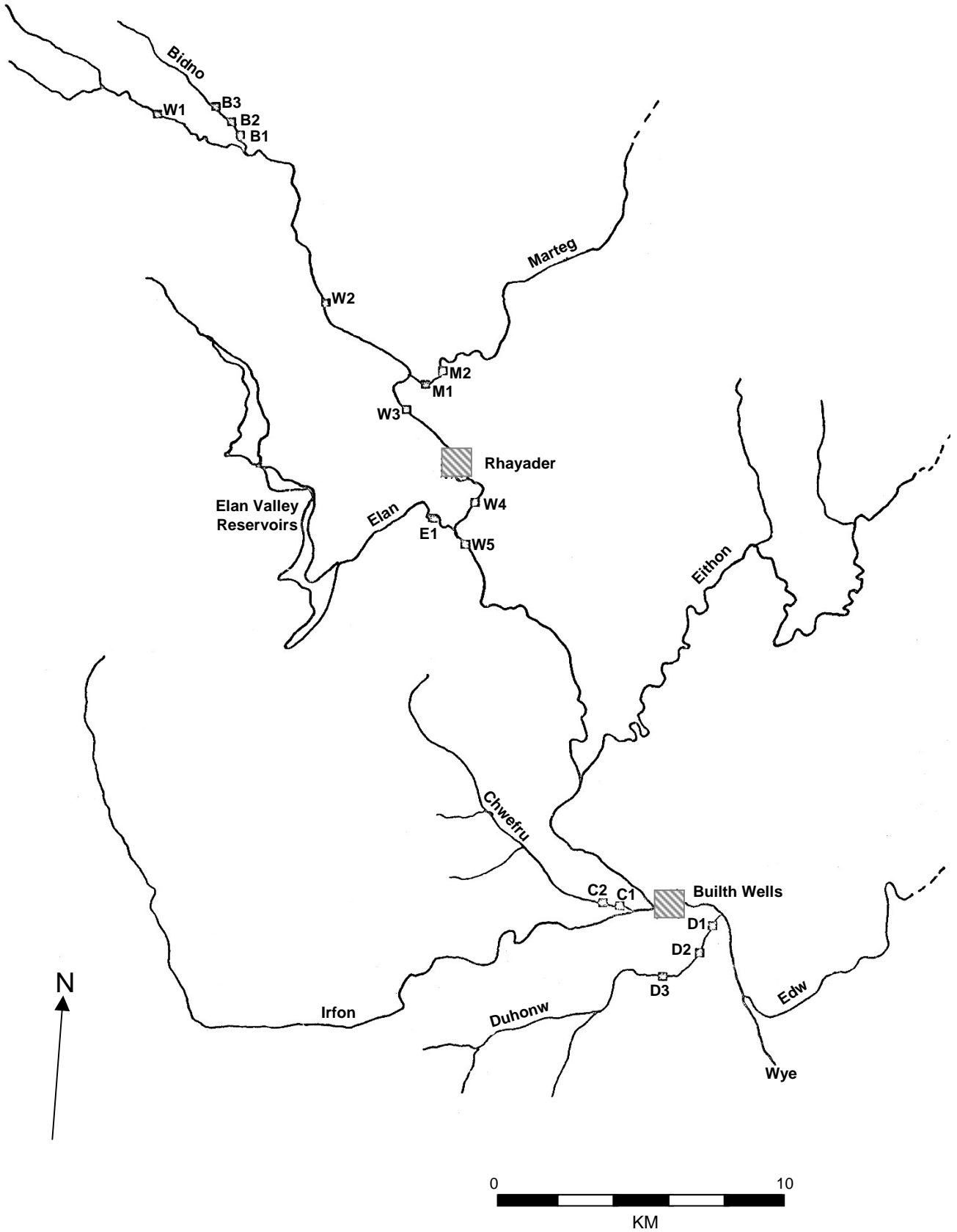


Figure 2

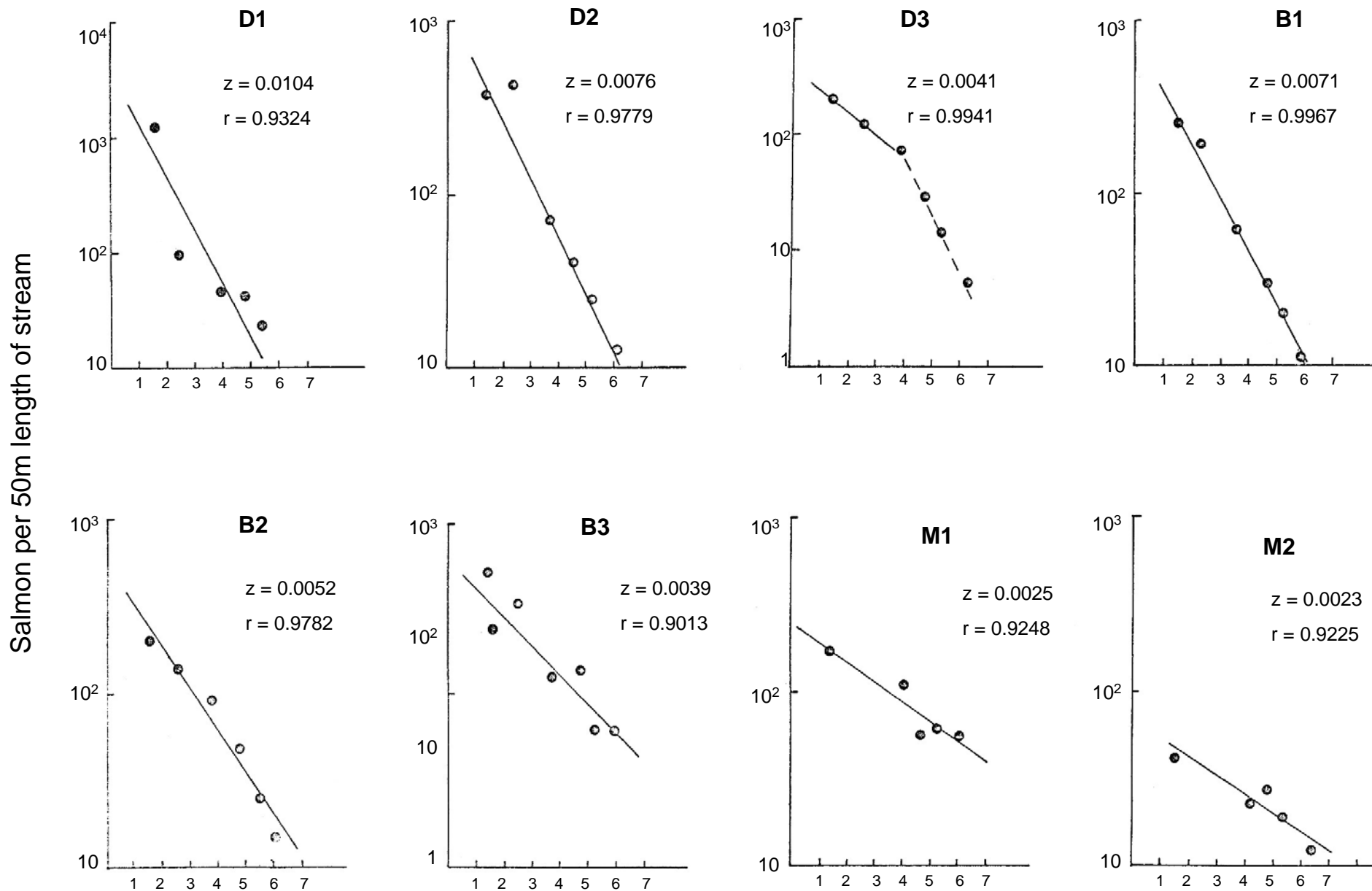


Figure 2 cont.

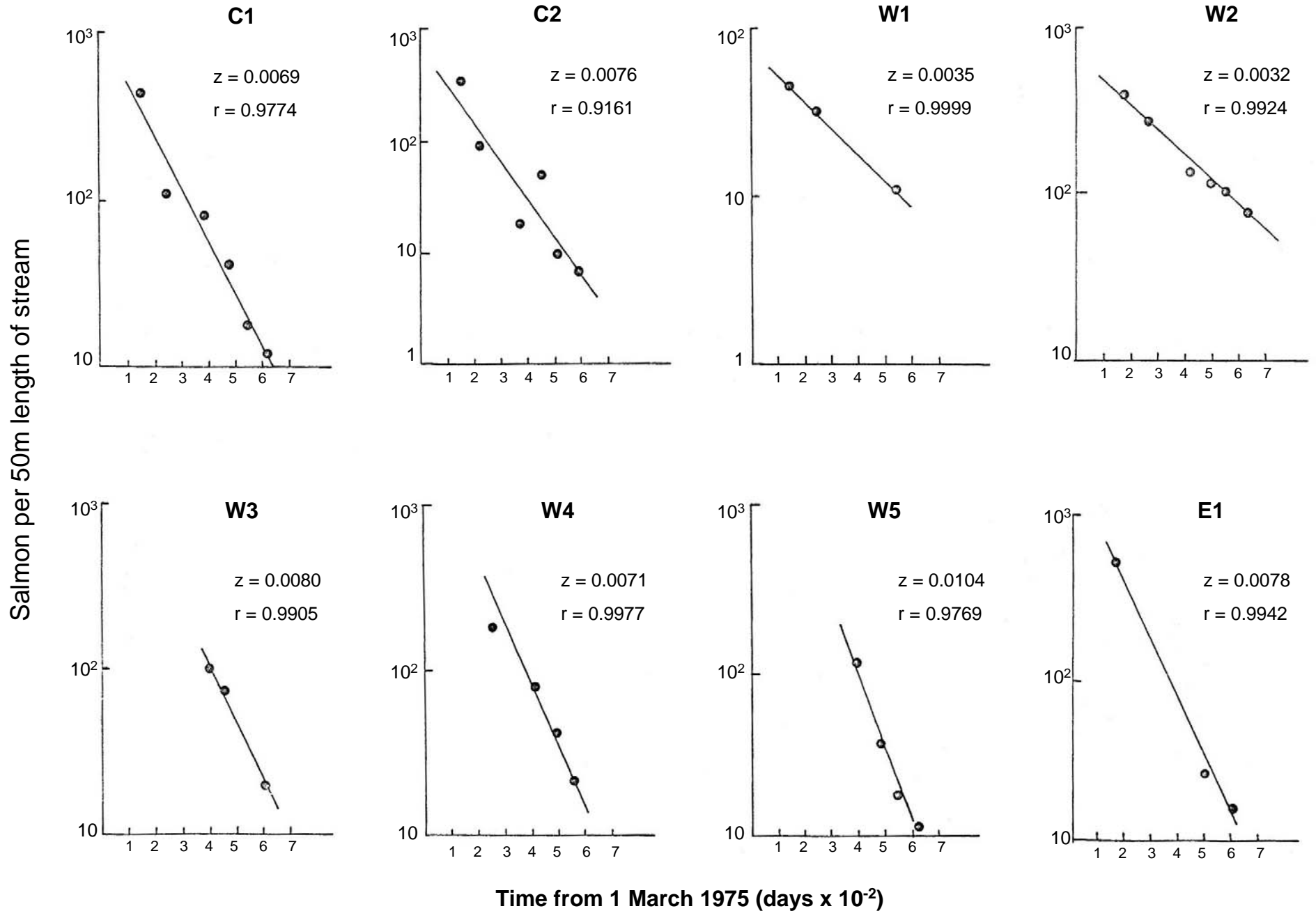


Figure 3

Instantaneous mortality rate (per day) z ($\times 10^3$)

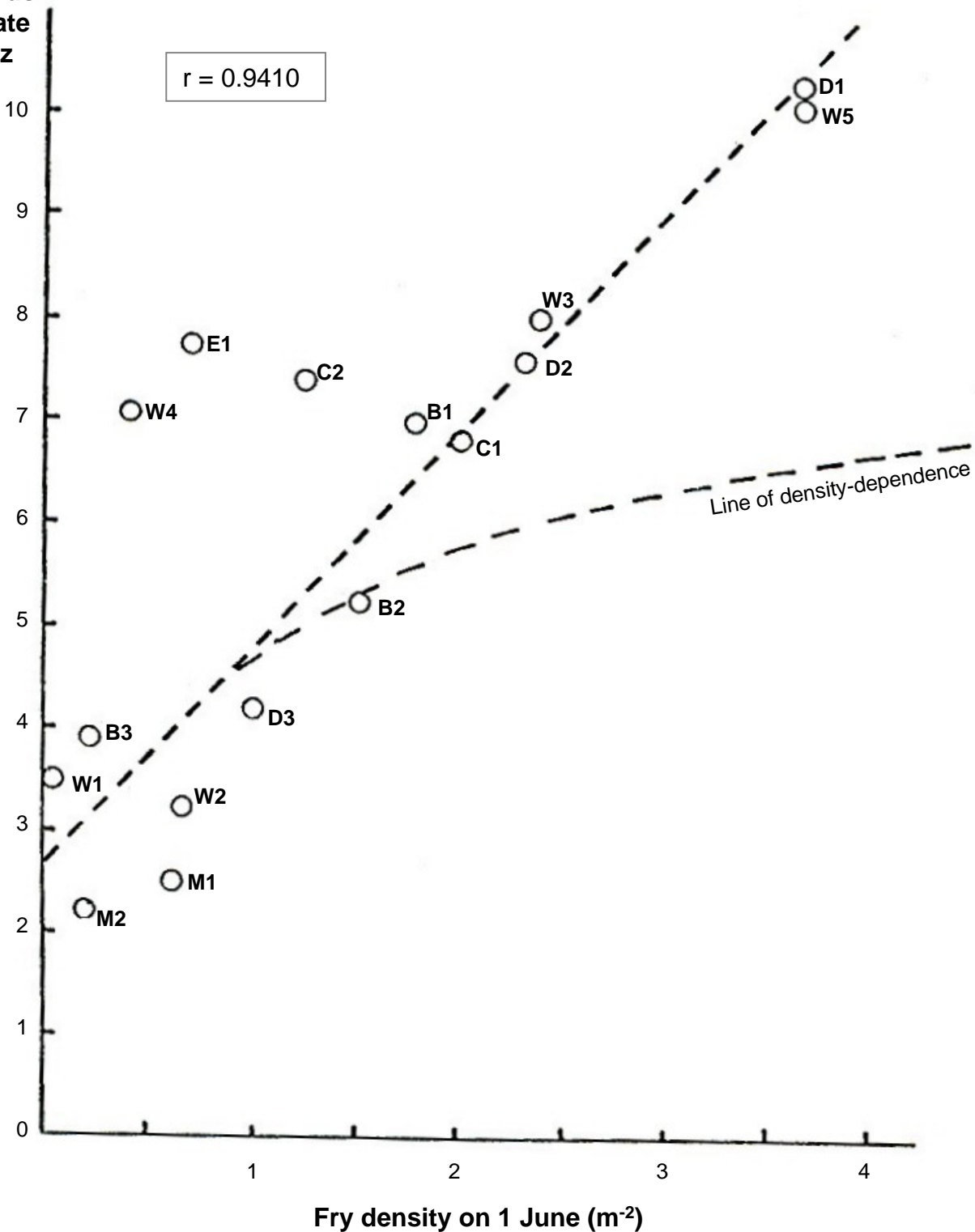


Figure 4

