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BIOLOGICAL AND CLIMATIC INFLUENCES ON THE DACE *LEUCISCUS LEUCISCUS* IN A SOUTHERN CHALK-STREAM

R. H. K. Mann & C. A. Mills

Introduction

The dace, *Leuciscus leuciscus* (L.), is a member of the Cyprinidae or carp family. It is widely-distributed in England, Wales and mainland Europe, and typically it inhabits clear, fast-flowing rivers and streams that provide clean gravel areas for spawning. It is the most important cyprinid, in terms of population biomass, in the chalk-streams of southern England. In the upper reaches of these waters it is often culled (usually by electrofishing) to reduce its supposed, but unproven, competition for food and space with the brown trout, *Salmo trutta* L. Such a management regime is less prevalent in fisheries for salmon, *S. salar* L., further downstream. Here the dace contributes, often substantially, to the coarse fishing practised during the salmon close season.

Many aspects of the ecology of the dace have been examined at the River Laboratory, principally in the River Frome, Dorset but also in the neighbouring rivers to the east, the Stour and Avon (Mann 1967, 1971, 1974, 1979, 1982; Mann & Mills 1985; Mills 1980, 1981a, b, 1982; Mills & Mann 1985; Mills et al. 1985; Scott in press). The dace thrives in all three catchments and a 709 g specimen was reputedly caught in the Frome in 1902 (Lonsdale & Parker 1930). This must have been an impressive fish, for the largest two caught in our studies were 261 g (Frome) and 321 g (Avon). The current British rod-caught record is 680 g for a specimen from the River Ivel, Bedfordshire.

A characteristic of chalk-streams is their relatively stable flow regime, unlike more upland rivers where sudden spates are often encountered. Similarly the temperature regimes of chalk-streams do not show such wide diel or seasonal fluctuations as occur in some other river systems. For example, minimum and maximum flows in the River Frome over twelve years were 0·92 and 18·58 $m^3 s^{-1}$ respectively. This twenty-fold difference compares with a thousand-fold difference for the River Tees, an upland Pennine river where other FBA fish studies have been made (e.g. Crisp et al. 1975). The absence of sudden large increases in discharge in the Frome is because most of the river water comes from the chalk aquifer through springs and boreholes, and relatively little originates as run-off from surrounding land after rain.

It is often argued that fish populations in upland streams are controlled principally by abiotic (= non-living) features of the environment, whereas biotic features, such as competition for food, plant cover and predation, are of greater importance in more benign habitats (e.g. Zalewski et al. in press). In reality, the situation is highly complex, partly because the biotic factors themselves will be influenced by abiotic ones. There is clear evidence that, even in these apparently stable ecosystems in which we work, quite small variations in abiotic factors can have a very marked effect on the distribution, growth and survival of the dace.

Population fluctuations

A characteristic feature of dace in chalk-streams (and many other waters) is their variation in recruitment success from year to year. In Fig. 1 the age-structure of Frome dace is shown separately for samples taken in twelve successive winters, 1973/74 to 1984/85. It is evident that dace which were spawned in some years (e.g. 1973, 1976) are prominent in the various samples. Conversely, some other year-classes (e.g. 1972, 1977, 1978) are very poorly represented. Because the strength of a particular year-class is established by the end of the first year of life and is maintained throughout the life of the cohort, we can conclude that the mechanism determining it acts on the very young stages. We can conclude, also, that those factors which influence the survival of older dace do not vary markedly from year to year. Hence, many of our studies of the Frome dace have focused on the egg and larval stages. These investigations have included both field observations and experimental studies.

To compare the strength of year-classes with environmental variables, it is useful to determine an index of year-class strength (*YCS*). This can be calculated by dividing the percentage frequency of a particular cohort in any one year's sample by the average frequency of fish of that age in several years' samples. For River Frome dace the means were based upon the twelve years shown in Fig. 1. Thus, the 1979 cohort formed 42 per cent of the 1980/81 winter's catch, compared with an average of 23 per cent for all fish in their second year of life, and the *YCS* index for

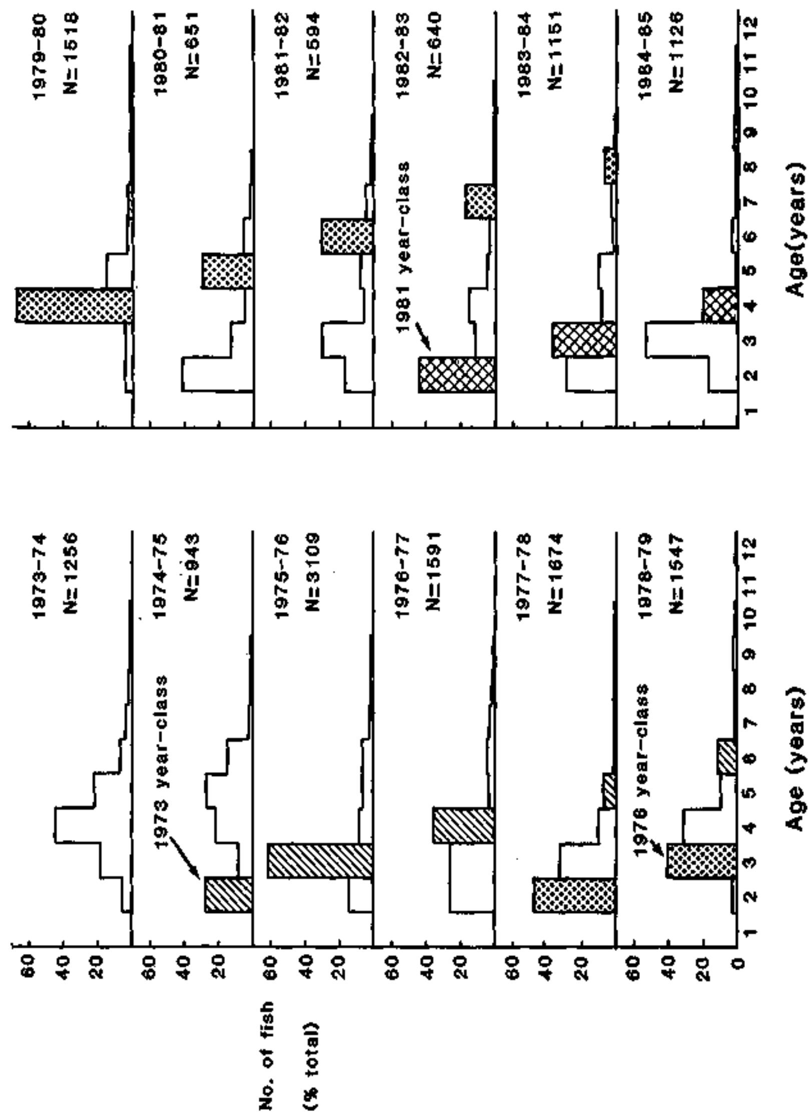

FIG. 1. The age-structure of dace from the River Frome based on samples collected in twelve successive winters.

that year was 1·8. This procedure was repeated for each year in the life of a cohort to derive a mean index (Table 1). Data for dace aged nine years or more were excluded because the numbers of fish involved were very small. Also, to improve reliability, data for a particular cohort were obtained from at least three successive years before it was included in the analysis. Even so, it should be noted that, after a sequence of weak year-classes, an average year-class will appear initially to be very strong. An example is the 1981 year-class of Frome dace. Our prediction (see later) from the low summer temperature in 1981 and the small over-winter size of the O group dace (52 mm) is that the *YCS* is not above average. We expect that further data for this cohort in the coming years will reduce the present *YCS* from 1·38 to 1·00 or less. The value and limitations of data of this type emphasize clearly the importance in ecology of long-term data sets.

Spawning and egg population dynamics

River Frome dace lay their adhesive eggs on gravel beds, usually over a two or three week period in March or early April. Both sexes are mature after four years' growth (age 3+), though some faster-growing individuals may spawn one year earlier. Maturing females aged 2+ had a mean length of 160 mm (95% CL ± 9 mm) compared with 143 (±3) mm for immature females of the same age (Mann 1974). Each female lays a single batch of eggs each year, but may spawn annually for up to seven successive years (Mann & Mills 1985). Some gravel beds may be visited regularly, and dace have spawned on a site in the River Frome mill-stream at East Stoke for at least 10 successive years (Mills 1981a, b). During each of these spawning periods mature dace were caught by electric fishing at 2–3 day intervals and marked by fin-clipping. Using the pelvic and pectoral fins in sequence over four years enabled us to identify the year that recaptured fish had been marked initially. The data showed that fewer dace returned to the East Stoke spawning site than would be expected from the estimate of natural mortality based on mean age structure (see later). The mean instantaneous rate of disappearance of marked fish from the annual samples was 1·06, compared with a mean instantaneous natural mortality rate of 0·76. This suggests that the fish spawning in the mill stream are being diluted by emigration of marked fish and immigration of new individuals from a much larger population. Such evidence of dace movement is emphasized by the recapture of marked individuals in the Tadnoll Brook, a tributary of the River Frome approximately 7 km upstream of East Stoke.

From the moment that they are released from the parent, dace eggs are vulnerable to several sources of mortality. In 1979 the overall mortality from release to hatching at the East Stoke site was estimated to be in the range 78·2 to 91·4 per cent (instantaneous rate Z, 1·52–2·45). Eggs that were washed away during spawning, or after being detached from the substratum during floods, accounted for less than 2 per cent (Z = 0·02) of total mortality. There was some predation by macroinvertebrates but, from feeding experiments in the laboratory and estimates of the abundance of macroinvertebrates on the spawning site during March and April, we concluded that those invertebrates that could eat dace eggs, either preferred dead eggs (*Gammarus pulex, Brachycentrus subnubilis, Isoperla grammatica*), or were relatively scarce (*Rhyacophila dorsalis, Perloides microcephala*). The results suggested that invertebrate predation caused only a 5 per cent (Z = 0·05) loss of live dace eggs. Predation by fish is a strong possibility, though we found only one egg (in a stone loach, *Noemacheilus barbatulus*) in a mid-April sample from the spawning site of 3 stone loach, 4 bullheads (*Cottus gobio*), 2 eels (*Anguilla anguilla*), 6 minnows (*Phoxinus phoxinus*) and 2 brown trout (*Salmo trutta*).

Most egg mortality was attributed to the effects of silt and other fine sediments, either through eggs being deposited on an unfavourable substratum or by silt deposition during the incubation period. In either case the eggs probably died as a result of oxygen starvation. Fig. 2 illustrates variation in the proportion of live eggs within the spawning area in relation to the proportion of fine material in the substratum.

The period of egg incubation is strongly correlated with water temperature:

$$\log \text{Days} = 2{\cdot}06 - 0{\cdot}06 \text{ Mean temperature (°C)}, \; r^2 = 0{\cdot}99, \; n = 11$$

However, the differences in water temperature between years are not great and, with egg development lasting about thirty days, any increased risk to the eggs of predation or siltation is insufficient to account for the wide variation that occurs in year-class strengths.

O group dace

Dace larvae, approximately 9 mm long, first appear in the River Frome during mid-April to early May. On hatching they are washed passively downstream into marginal areas where the current speed is low (<20 mm s^{-1}). Exogenous feeding commences after 2–3 days, before the yolk-sac has been fully absorbed. Rotifers and diatoms form the initial prey together with occasional nauplii and copepodites. As the dace grow, larger planktonic crustacea (Cladocera, Copepoda), larval Chironomidae and other small aquatic invertebrates are included in the diet. The availability of food is not a limiting factor in productive chalk-streams such as the Frome, for no density-dependent growth was observed from field data. But it did occur when extremely high densities

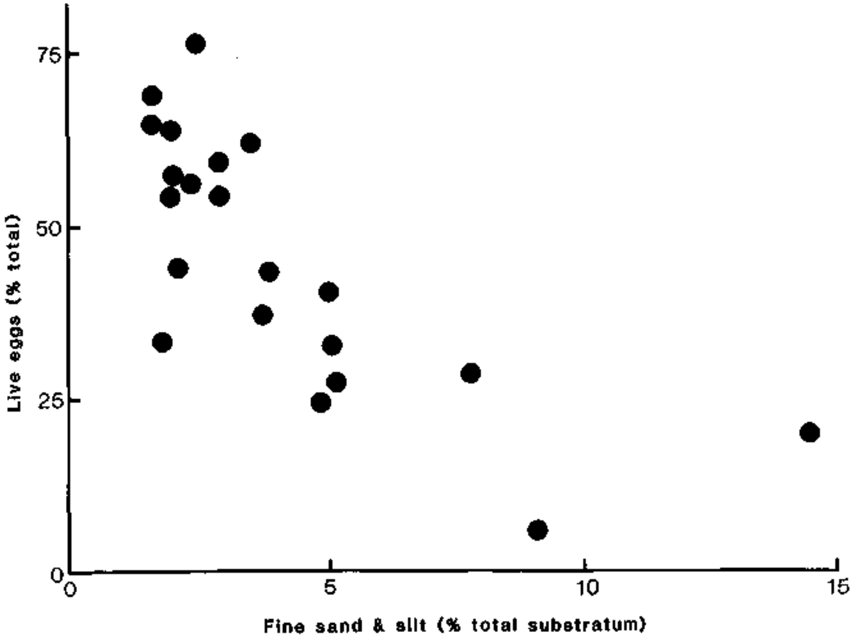

FIG. 2. The relationship between the percentage of live dace eggs and the occurrence of fine sediment (particle size <0·25 mm) in the top 50 mm of the gravel spawning substratum.

of dace larvae were maintained in fine-mesh cages placed in backwaters of the River Frome.

However, the growth of O group dace did vary considerably from year to year (Table 1). During the 1970–84 study period the mean lengths of overwintering O group dace ranged from 47 mm (1972) to 64 mm (1975); these values represent more than a three-fold difference in mean weight (1·3 g – 4·0 g). In general, warm summers produced faster growth rates than cool summers (Fig. 3) and, in a correlation between mean over-winter length and degree days >12°C for the whole year, water temperature accounted for 66 per cent of the variance in length. But other factors are clearly involved because two years of intermediate warmth (1972, 1975) produced widely different growth rates (Table 1). Water temperature during the first weeks of larval life (May-July) was also correlated with year-class strengths between 1968 and 1981, but only accounted for 32 per cent of the variance.

During the early summer, many dace larvae fall victim to invertebrate predators. We have observed the hemipteran *Notonecta* sp. successfully

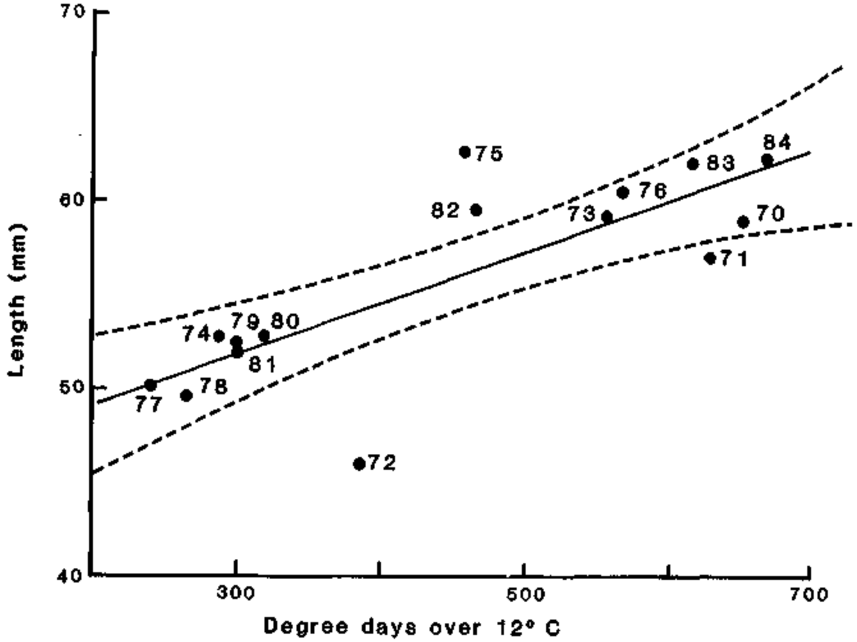

FIG. 3. The relationship between the overwinter length of O group dace and water temperature (degree days over 12°C) in the previous year.
Dotted lines indicate 95 per cent CL.

attack dace larvae in a backwater of the Frome, and aquatic Coleoptera and Odonata nymphs are also known to attack young fish. Indirect evidence of heavy losses through predation was provided by the very high survival rates of dace larvae kept at low densities in floating, fine-mesh cages in the River Frome. In aquarium experiments the nymphs of three species of Odonata (*Calopteryx splendens, Pyrrhosoma nymphula, Coenagrion* spp.) ate significantly more small dace larvae than larger larvae. In other experiments *C. splendens* ate 144 newly-hatched larvae (mean length 9 mm) compared with only 19 older larvae (mean length 10 mm).

How can these various relationships involving O group dace explain the mechanism whereby the strength of a particular year-class is determined? Growth rate is an important factor, as indicated by a regression of *YCS* on the size of overwintering O group dace:

$$\ln YCS = -6{\cdot}24 + 0{\cdot}107\ L\ (\text{mm}),\ n = 11$$

This regression accounted for 67 per cent of the variation between

TABLE 1. Indices of year-class strength (*YCS*) and overwinter lengths of O group dace from the River Frome, with data on water temperature.

Year	YCS	Mean overwinter length (mm)	No. of fish	Degree days >12°C May-July	Degree days >12°C Calendar year
1968	0·70			314	569
1969	1·24			321	566
1970	1·29	60	132	403	658
1971	0·67	58	855	368	634
1972	0·25	47	88	228	389
1973	1·13	60	427	308	561
1974	0·65	53	66	196	289
1975	1·15	64	638	266	459
1976	3·21	62	64	402	572
1977	0·49	50	15	138	240
1978	0·30	50	61	146	265
1979	0·96	53	46	179	300
1980	0·42	53	51	151	320
1981	1·38	52	116	140	303
1982		60	58	290	470
1983		63	5	386	621
1984		64	81	344	674

length and *YCS*. Our experiments indicate that, in the River Frome, the predation rate on dace larvae by macroinvertebrates could be an inverse function of larval growth rate. As the latter depends upon water temperature (as is characteristic of poikilotherms), recruitment success will tend to be highest in warm summers and least in cool summers. However, the regressions involved do not account for all the variance in year-class strength, partly because of some lack of precision in determining the *YCS* index, but also because other variables are involved.

For instance, newly-hatched dace larvae can swim only at about two body lengths per second (c. 17 mm s^{-1}). Even larger O group dace hold station only if the flow is less than 20 mm s^{-1}. During the summer, only 2 to 3 per cent of the surface area of the River Frome at East Stoke has water current speeds under 20 mm s^{-1}. Refuge areas are, therefore, of vital importance. Their availability may vary from year to year according to river discharge and there is some evidence, from Frome data (Mills & Mann 1985) and other rivers (Philippart 1981), of an inverse relationship between dace *YCS* and precipitation. However, the situation is complicated because of the connection between precipitation and temperature, i.e. wet summers tend to be cooler than dry summers. Refuge areas may also be affected by weed-cutting operations, especially when the latter causes a sudden fall in water level (Mills 1981c). Other factors affecting *YCS* may include the different diets of dace larvae in some backwater areas as compared with river margins, and the enhanced water temperatures which can occur in shallow, slow-flowing backwater habitats. Both these factors could influence the growth of O group fish.

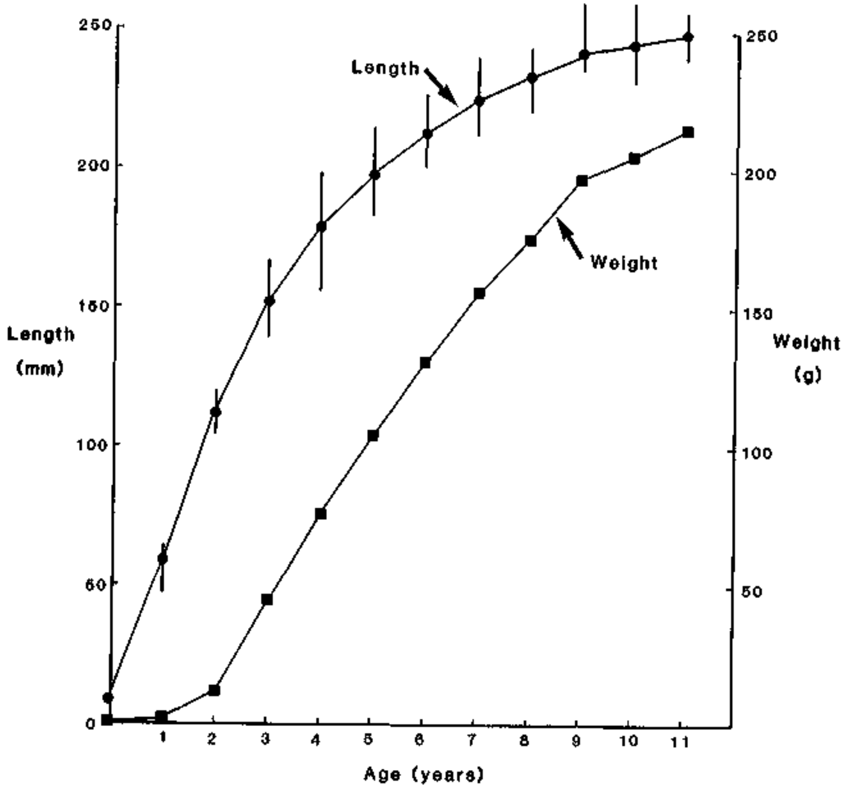

FIG. 4. Mean lengths and weights at each age (both sexes combined) for R. Frome dace over twelve successive years.
The bars indicate minimum and maximum annual mean lengths.

Older dace

The mean year-to-year pattern of dace growth (Fig. 4) in the River Frome conforms to the asymptotic model described by von Bertalanffy (1957):

$$L_t = L_\infty\ (1 - \exp\ (-K(t-t_0)))$$

where L_t is the length at age t years, L_∞ is the asymptotic length (for Frome dace L_∞ = 260 mm), K is a growth coefficient (Frome dace = 0·29), t_0 is the hypothetical age at which length is zero (Frome dace = 0·03 year). Growth rates vary annually in relation to water temperature and such variations are exhibited in wide and narrow growth zones on the fish scales. Generally, high water temperatures result in fast growth rates but, in 1976, water temperatures approaching 24°C in June coincided with the appearance of a false check on Frome dace scales, indicating an interruption in growth. Even so, growth in 1976 was greatly in excess of that in other years, although it appeared to be at the expense of gonad development for the spring 1977 spawning. In other years from 1974 to 1980 the weight of eggs produced by a particular size of fish was constant, but there was variation between many, small eggs and fewer, large eggs. However, in the 1977 spawning both fecundity and egg size

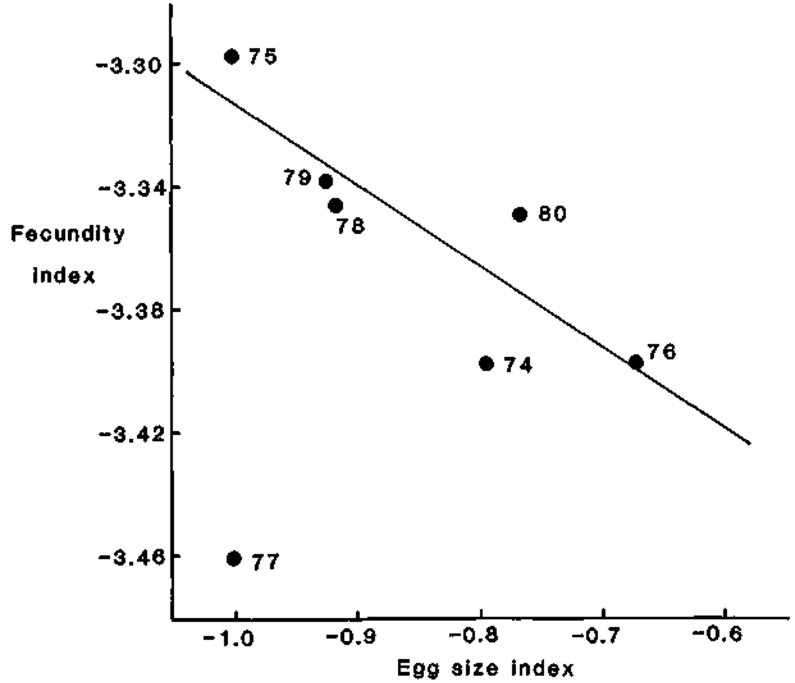

FIG. 5. The relationship between the indices of mean egg volume and fecundity; the 1977 datum point is not included in the regression calculation. For details of the computation of indices see Mann & Mills 1985.

were low; this is illustrated in Fig. 5, where indices have been calculated to show the data for each year as a single point by removing the variance due to fish length (Mann & Mills 1985).

Imposed upon this picture is the general increase, in any year, of mean egg size with fish length, and of ovary weight with fish length i.e. we found that older dace put proportionately more energy into gonad

growth and less into somatic growth, compared with smaller, younger fish. Thus, the mean weight of eggs produced by a 160 mm (age 4 years) female was 14 per cent of total body weight compared with 20 per cent for a 230 mm (age 8 years) fish. Increased reproductive effort in fish has often been linked with increased mortality rate (Mann & Mills 1979;

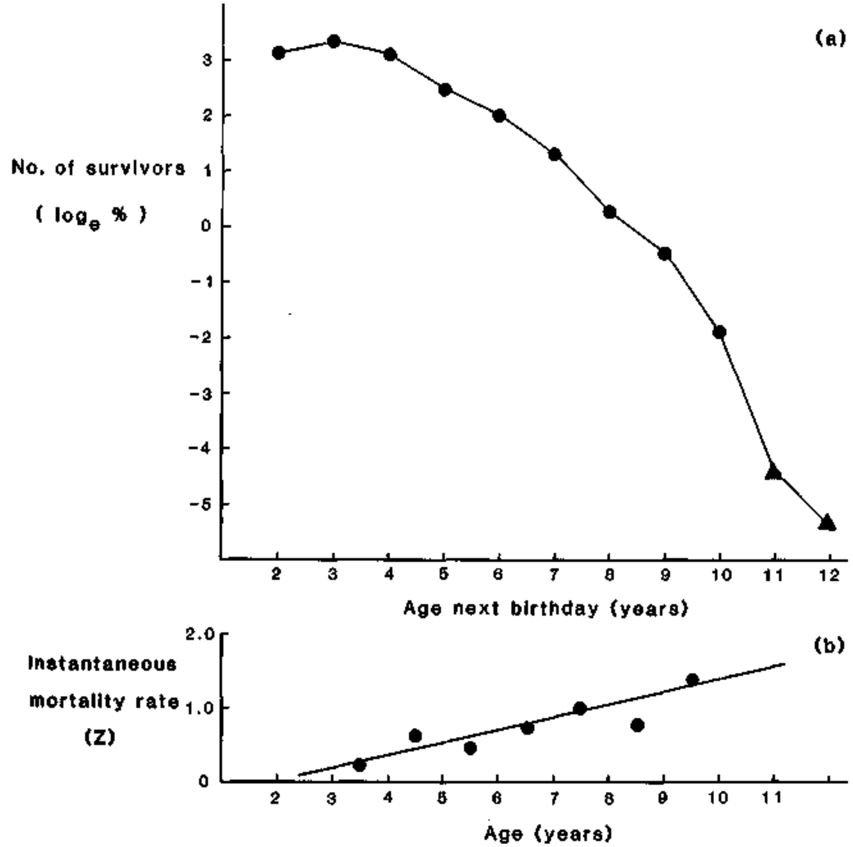

FIG. 6. Survival and mortality of River Frome dace. (a) Survival curve, (b) Mortality rate. Based on mean percentage age-composition over twelve years, 1973/74–1984/85, and the relationship between mean annual mortality rate and age.

Mann et al. 1984). Fig. 6 shows a survival curve for Frome dace based on the mean percentage age-composition over twelve years. The main right-hand limb of the curve illustrates the decrease in numbers of fish with age, whereas the slight rise of the left-hand limb reflects the relatively lower catchability of younger dace to electric fishing. The second part of Fig. 6 shows an increase in the annual rate of mortality (*Z*) with increasing age in the dace, and may portray the consequences of an increasing commitment of energy resources to gonad development at the expense of somatic tissue.

In the River Frome, predation by pike *Esox lucius* L. is a major contributor to the mortality of dace over one year old. Approximately 34 per cent by weight of fish prey of Frome pike are dace and they constitute the principal prey species. Most are eaten in the summer months, and comparatively few during the spring when the pike have moved into backwaters to spawn and dace are congregating on gravel areas for the same purpose. The size of dace eaten increases with pike size but no dace are too large to be taken. Although large numbers of dace are eaten (c. 1420 ha^{-1} yr^{-1}, range 1130–1960), the population of pike is relatively stable and the variation in numbers of dace consumed from year to year is likely to be small (Mann 1980, 1982).

Life-history strategy

Largely as a result of the influence of abiotic factors, chiefly water temperature, dace recruitment varies widely from year to year. From 1968 to 1981 there was a thirteen-fold difference in the *YCS* index between the minimum index (0·25 in 1972) and the maximum (3·21 in 1976). The problems of such variation, especially those that could ensue from a succession of poor year-classes, are offset by the spread of reproductive effort by each female over several years. Earliest maturity can occur just before the third birthday (age 2+) and the oldest female caught in the Frome study was aged 11+ years.

The emphasis on growth *vis-a-vis* gonad development among the younger, mature dace probably enhances their chances of survival, and ensures that they can reproduce over several years. A strategy of this type has been predicted for organisms in which the range of variation in the survival of pre-adults is greater than that for adults (Stearns 1976). In the case of the Frome dace, therefore, selection pressures operating through the high and variable mortality rate of newly-hatched larvae may have resulted in the evolution of an iteroparous species. However, the life-history strategy of the dace still embodies a degree of flexibility, as demonstrated by the variable trade-off between the development of few large, or many small, eggs. We do not know the relative advantages and disadvantages of these two options but it seems clear that, for a given level of reproductive effort, the optimum compromise may vary with environmental conditions. It is also pertinent that the dace genotype can be expressed phenotypically in a variety of ways, with the precise position being determined at any one time or place by environmental factors. However, it is interesting to note that another prominent cyprinid in the River Frome, the minnow *Phoxinus phoxinus* (L.) has evolved reproduction early in life and an extended spawning season. The minnow lays eggs, similar in size to those of the dace, on a gravel substratum and each female develops and releases a series of egg batches in one year. This strategy appears to be at the cost of a much reduced life-span, with most fish dying in the year when they reach maturity. The establishment of many temperate freshwater fishes in a range of habitats has resulted, at least in part, from such inter- and intra-specific flexibility in life-history tactics.

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APRIL 1986

Additions to the Membership since publication of the 53rd Annual Report

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