

Variability in performance in wild Atlantic salmon, *Salmo salar* L., fry from a single redd

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Abstract Dispersal and growth were studied in Atlantic salmon, *Salmo salar* L., fry from a natural isolated redd. The distribution of fry leaving the redd was strongly peaked, 80% being caught within a 2-week period. Early in the dispersal period, all fry leaving the redd had remnants of yolk sac and had not fed; by half way through the dispersal period, no fry had any visible yolk, but 35% still had empty stomachs. Fry leaving the redd during the first half of the dispersal period tended to settle in different first feeding sites than those dispersing later. Predation on fry by larger salmonids was frequent, especially during dispersal. Coefficients of variation for length, weight and condition factor increased significantly over the study period and for individually recognised fry, growth rates varied markedly. Thus, individual salmon fry differ in physical status on emergence from the redd and these differences are amplified during the first few weeks after emergence.

KEYWORDS: dispersal, growth, salmon, variability.

Introduction

Studies of differential success of individuals at critical life-history stages can promote understanding of the way in which natural selection acts. One such critical period for salmonid fishes is the time during which alevins emerge and disperse from the redd and in their first few months of life (Elliott 1994). Studies under experimental conditions in the laboratory have shown that within a single clutch, individuals differ in the date on which they start first feeding and in basal metabolic rate. These two variables interact to determine dominance in subsequent social encounters (Metcalfe & Thorpe 1992; Metcalfe, Taylor & Thorpe 1995) and consequently, at high densities at least, subsequent

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growth rates (Metcalf, Huntingford, Thorpe & Adams 1990). Variation in early performance has profound effects on subsequent life history events, since age of smolting is determined by rates of growth over the first summer of life (see Thorpe, Mangel, Metcalfe & Huntingford 1998), and age of maturation is determined by body size and lipid reserves at critical periods in the year (Thorpe 1989).

To put these laboratory data into context, it is important to establish the nature and origin of individual variation in performance in the wild, but this is much more difficult to estimate. There is an extensive literature on emergence, dispersal and first feeding in salmonids in natural and semi-natural conditions (reviewed by Godin 1982). Emergence from the redd is generally associated with the initiation of exogenous feeding (Dill 1977), but fry may also disperse with substantial amounts of unabsorbed yolk sack (Mason 1976; Elliott 1986; Brannas 1987). Early competition for food and space can be severe and, at least in brown trout, *Salmo trutta* L., large numbers of fry may simply drift downstream and starve (LeCren 1973a,b; Elliott 1994). Timing of emergence in salmonids is influenced by environmental conditions during egg development, most notably water temperature (e.g. Brannon 1965; Rimmer, Paim & Sanders 1984; Brannas 1987; Crisp 1988; Elliott & Hurley 1998). Emergence is typically clumped (e.g. Mason 1976; Gustafson-Marjanen & Dowse 1983; Gustafson-Greenwood & Moring 1990; Bardonnet & Godin 1991) and most salmon and trout alevins disperse at night (e.g. Godin 1982, Gustafson-Marjanen & Dowse 1983; Crisp 1991; Crisp & Hurley 1991; Johnstone 1997). The number of alevins emerging on any given night depends on flow rates (Field-Dodgeson 1988; Marty & Beall 1989) and on ambient light levels (Field-Dodgeson 1988).

Accurate studies of individual variation in wild salmonids during the early life stages have been hampered by the difficulty of trapping and marking of very small fish, although the extended series of studies of brown trout in a small stream in the English Lake District demonstrated what can be achieved in favourable field conditions (Elliott 1994). Some variation in the behaviour of newly emerged salmonids may relate to gender; in masu salmon, *Onchorhynchus masou* (Brevoort), male fry were more likely than female fry to remain on (artificial) redds, the latter being more likely to move downstream (Nagata & Irvine 1997). Using a combination of dye marking and fin clipping, Bradford & Taylor (1997) demonstrated repeatable individual differences in propensity for downstream movement in chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in an experimental stream channel and suggested that such small behavioural differences may have large effects on patterns of dispersal at the population level.

The present paper describes a study of dispersal and growth in Atlantic salmon, *Salmo salar* L., alevins from a natural redd, using exhaustive, bank-to-bank trapping, batch marking and a photographic method for individual identification of a proportion of dispersing fry (García de Leániz *et al.* 1994). This approach enabled the following questions to be addressed.

1. What is the temporal pattern of dispersal from a natural redd?
2. To what extent do alevins vary in condition when they leave the redd?

3. How variable is their subsequent performance?

Materials and methods

Study site

This work was carried out in the Girnock Burn, a tributary of the River Dee, Aberdeenshire, Scotland, situated 460 m above sea level in an area that sustains juvenile salmon densities of 1–2 fish m⁻². The study section had an average width of 1.2 m, a total length of 135 m and a gradient of about 4%. The substratum consisted mainly of gravel (1–10 cm diameter) and partly-submerged boulders (30–75 cm diameter). In the autumn of 1989, a single isolated salmon redd was located in the study section, close to its upstream end and emergence from this redd was studied until the following July. During the period of study (April–June 1990) daily mean water temperatures ranged from 5.6 to 12.7 °C. Daily mean flow rates ranged from 0.03 to 3.4 m³ s⁻¹.

Trapping dispersing fry

To investigate patterns of dispersal, four box traps were positioned at different distances from the redd: 2 m upstream (trap 1) and 2, 20 and 130 m downstream (traps 2–4). Traps 1–3 were based on a modified box design (García de Leániz, Fraser & Huntingford 1993), consisting of a clear perspex cube (70 × 50 × 50 cm) with a 10 × 30 cm back screen of 1 mm netlon mesh. Water was funnelled into the trap by two angled vertical sheets of perspex, a sliding lid of transparent perspex prevented land-based predators from entering the trap and a series of removable horizontal baffles at the back provided a region of low flow. A continuous bank-to-bank screen of 1 mm netlon mesh buried within the gravel to a depth of 30 cm was attached securely to each side of the trap and to its base. Trap 4 was a conventional box trap (Mills 1964), also fitted with a bank-to-bank screen of 1 mm mesh buried in the gravel. Trap retention efficiency was estimated at 87%, with fish escaping upstream through the entrance. The traps were established on 12 April 1990 and were fished at least every morning up to 1 July. During the period of peak dispersal (11–24 May) the traps were fished several times throughout the day and night to obtain data on the timing of dispersal. Dispersal from the redd was deemed to have finished following 5 consecutive days with zero catches in trap 2. Dispersing alevins were caught every day between 26 April 1990 and 30 June 1990. A sub-set of fish were killed and preserved for species identification based on protein electrophoresis; all were found to be salmon, except for one salmon-trout hybrid (Verspoor 1988).

A major proportion of the fry caught at trap 3 (198/311, 64%) and at trap 4 (5/16, 31%) were unmarked, despite all fish caught leaving the redd at trap 2 being marked (see below). It was shown that such unmarked fish represent fish that evaded capture at trap 2 (and in some cases at trap 3 also) by dispersing undergravel from the redd to a depth of at least 30 cm. Although undergravel migrants were significantly smaller and lighter

than fry dispersing through the water, they showed identical patterns of trapping over the study period and took the same time to disperse (García de Leániz *et al.* 1993).

Processing dispersing fry

Each fish caught in any of the traps was anaesthetised (MS222), measured (fork length, mm) and those caught alive were weighed (to the nearest 0.001g, wet weight). The data were used to calculate the somatic condition factor (Weatherley 1990). All newly caught fish were batch marked using a combination of fin clipping and dye marking (Hart & Pitcher 1969). All fish captured before the 18 May were designated as early emergers and all those emerging subsequently were designated late emergers; these two categories of fry were batch marked accordingly. Fry were also photographed for individual identification based on melanophore pattern (García de Leániz, Fraser, Huntingford & Mikheev 1994). Presence or absence of a visible yolk sac and of food in the fish's stomach (visible through the body wall) were noted. Several hours were allowed for recovery before the fish were released, upstream in the case of trap 1 and downstream in the case of traps 2–4. The traps were established in early April 1990 and checked at least once daily until emergence had ceased (in early June).

Sampling first feeding sites On 4 and 5 July 1990, the entire length of the study stream was point electric fished (Hearn & Kynard 1986) in 20-m sections, using a small, battery-powered back pack unit with a direct pulsed current of 5 A, frequency 80 Hz, 500–700 volts and a maximum range of 1 m. One pass only was made to ensure that the fish were caught *in situ*. All captured fish were weighed and measured and their mark status assessed. In addition, the nature of the habitat in which any marked fry was captured was classified as follows (García de Leániz 1990):

- pools – areas of low water velocity and smooth flow, including small side waters near the stream margins;
- cascades – areas of fast, turbulent flow with eddies and back-currents adjacent to an area of dead or slack water;
- glides – areas of non-turbulent, fast flow without surface rippling;
- riffles – areas of fast surface currents with surface rippling.

The availability of these different habitat types was also assessed for the whole stream at the end of the study.

Observations of predation on fry

Predation on fry was monitored opportunistically. All fish other than 0+ salmon (including older salmonids) caught either in the traps or by electric fishing were killed, measured (fork length, mm) and their stomach contents examined for salmonid fry.

Results

Timing of dispersal from the redd

Dispersal began on 26 April and finished on 30 June (Fig. 1). Altogether, 345 salmon alevins were caught in the trap sited 2 m below the redd (trap 2) and 311 in the trap 20 m further downstream (trap 3). Only 16 fry were caught in the trap 132 m below the redd (trap 4), suggesting that most fry either remained within the available habitat or died during their first 2 months of life. Dispersal was highly synchronous and strongly clumped (Fig. 1a), with 80% of all trapped fry being caught within 14 days for trap 2 and within 18 days for trap 3. Comparison of night-time and day-time catches during the period of peak dispersal ($n = 199$ fish) indicated that fry dispersed exclusively by night ($\chi^2 = 53.8$, d.f. = 1, $P < 0.001$).

Direction of dispersal

The majority of fry leaving the redd dispersed in a downstream direction (95%); upstream migrants were few (18) and only started appearing late in the season (Fig. 1b), when fry became larger. Analysis of fry caught from 23 May onwards (when fish were dispersing in both directions) showed no difference in length, weight, or condition factor between upstream and downstream migrants (mean weight = 0.17 g in both cases; mean length = 24.9 and 25.1 mm for upstream and downstream dispersers, respectively; mean condition factor = 10.8 and 10.6 for upstream and downstream dispersers respectively; t -tests, d.f. = 35, $P > 0.2$ for all variables).

Rates of dispersal

The time elapsing between the dates on which 50% of the fry were captured in traps 2 and 3 was 8 days, giving a mean rate of dispersal of 2.5 m day⁻¹ over the first 20 m from the redd. Dispersal rates appear to increase further downstream, as the time elapsing between 50% catches in traps 3 and 4 was 21 days (giving a mean rate of dispersal of 5.24 m day⁻¹), although sample sizes for fish caught in trap 4 were small. Direct information on the 35 fry captured in the trap 22 m below the redd (trap 3) that were identified on the basis of photographs taken at the trap just below the redd (trap 2; Fig. 2a) showed marked variability in rates of movement between the two traps. The modal number of days taken for these fish to move between traps 2 and 3 was 6, with a range of 2–24 days and a hint of a second mode at circa 21 days.

Yolk sac retention and first feeding

For the first 20 days into the dispersal period, all the fish caught in the trap just below the redd (trap 2) had some remaining yolk (Fig. 4), but the proportion with visible yolk declined to 0% by day 30. A similar pattern was observed 20 m downstream from the redd (trap 3), where all dispersing fry had some remaining yolk up to day 20, and none

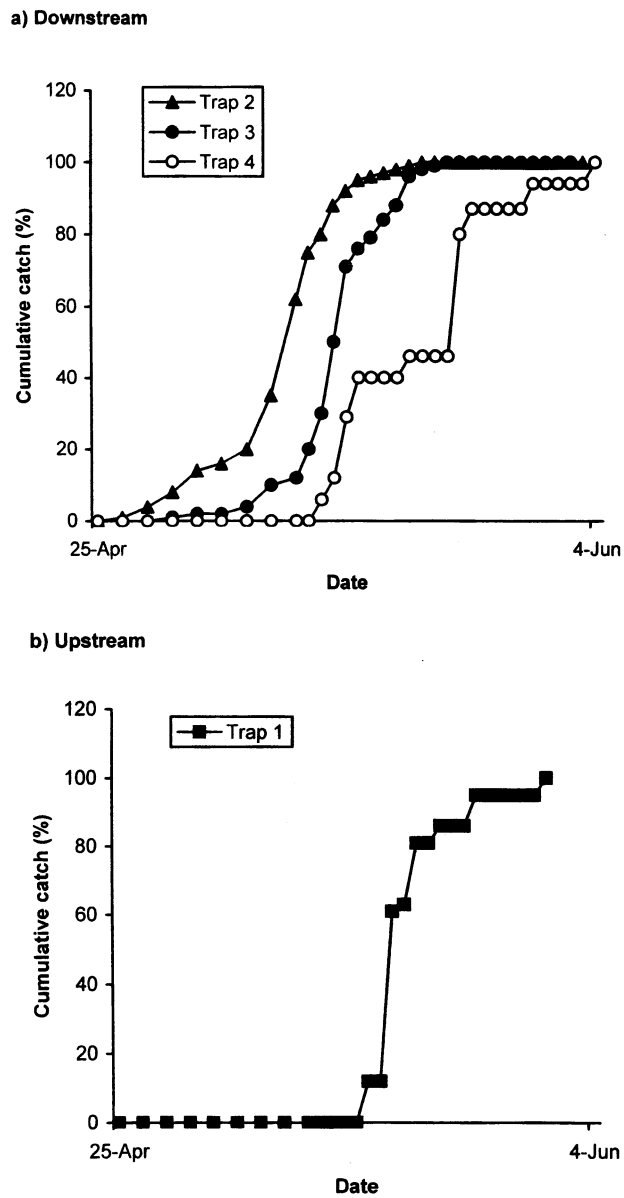


Figure 1. Cumulative percentages of the total number of dispersing Atlantic salmon fry over the whole study period captured on each day a) in traps 2, 3, and 4 (2 m, 23 m and 132 m downstream of the redd) and b) in trap 1 (2 m upstream of the redd).

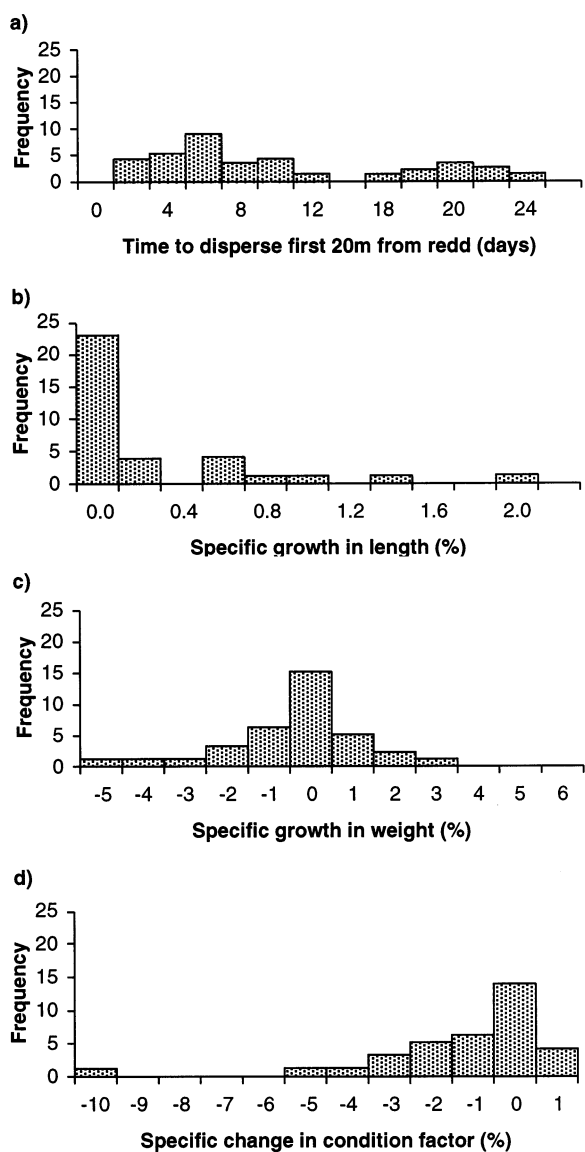


Figure 2. Frequency distribution in individually identified fry of: a) time taken to move between traps 2 and 3; b) daily specific growth rate for length; c) daily specific growth rate for weight; and d) daily rate of change in condition factor.

had any yolk left by day 40. Although complete reabsorption of the yolk sack coincided with the initiation of exogenous feeding in most fish (Fig. 4), 35% of all fry captured in trap 2 and 17% of those captured in trap 3 had no remaining visible yolk sac, but had empty stomachs.

Growth rates

No clear increase in the size (in length and weight) of dispersing fry was evident during the first 2–3 weeks of the study, but size increased dramatically from mid-May (Fig. 5). These two growth stanzas were reflected in changes in their condition factor, which fell initially as alevins exhausted their lipid reserves, but then increased again. Growth rates based on average values at the 50% catches between traps 2 and 3 were 0.48% day⁻¹ for length and 1.31% day⁻¹ for weight. Daily rate of increase in condition factor was 0.53% day⁻¹.

Coefficients of variation of body measurements (Fig. 5) were high and, after an initial dip in weight and condition (probably due to variability in yolk sac volume in very young fish), increased significantly with time (Spearman Rank order coefficients of CV against time period = 0.67, 0.89 and 0.66 for length, weight and condition factor, respectively, $n = 10$, $P < 0.05$, < 0.01 , < 0.05 , respectively). The individually-identified fish also show striking variation (Fig. 3b–d). Thus, during dispersal between traps 2 and 3, mean daily specific growth rate for length was 0.26%, but with minimum rates of zero and maximum rates of 2.08%. Equivalent figures for growth in weight were a mean of -0.41% day⁻¹, with a minimum of -4.39% day⁻¹ and a maximum of 2.10% day⁻¹.

First feeding habitat

High mortalities and fading of marks during the study period meant that the number of fish recaptured was very small (19 marked fry overall). Fry were captured throughout the length of the study stream, more being found in areas of riffle than expected given the availability of this habitat type (Fig. 5; $\chi^2 = 9.56$, d.f. = 3, $P < 0.05$). Whereas all the recaptured late emergers were found in riffles (9) or cascades (2), the early emergers were found in glides (6) and riffles (2; Fisher's Exact test $P < 0.02$).

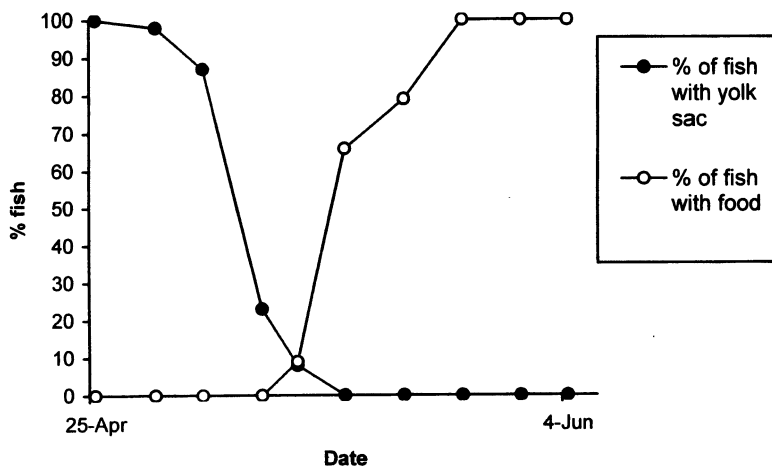
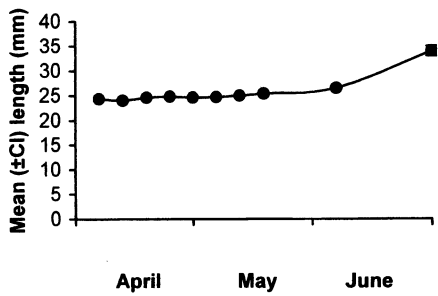
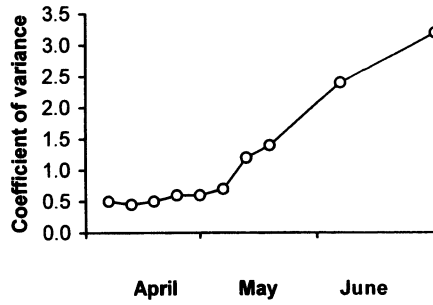


Figure 3. Proportion (%) of dispersing fry captured in trap 2 (2 m from the redd) with remaining yolk sac and with food visible through the body wall.

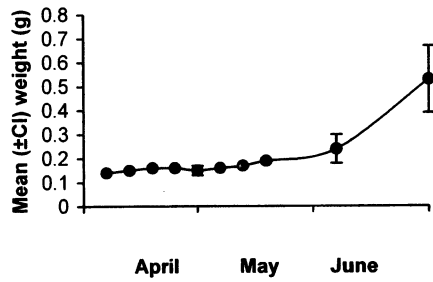
a) mean length



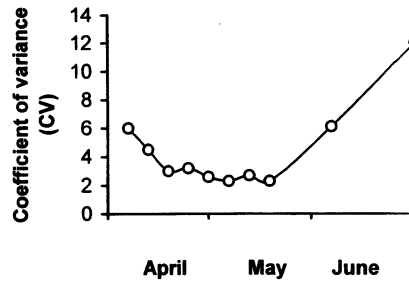
b) length CV



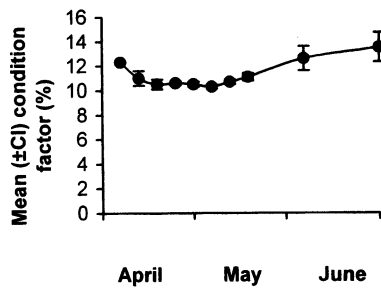
c) mean weight



d) weight CV



e) mean condition factor



f) condition factor CV

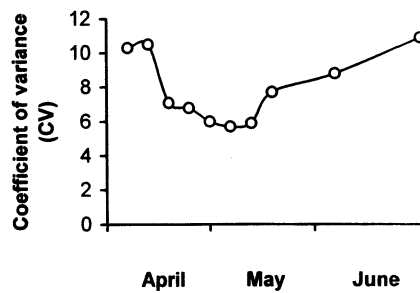


Figure 4. Mean (\pm 95% CI) length, weight and condition factor of all fry captured in the study section in relation to date, together with coefficients of variation.

Predation on fry

During trapping and electric fishing, 32 juvenile salmonids aged 1+ and over were captured; 34% of these had fry in their stomachs. The incidence of alevin predation in relation to predator size (fork length) was 0% (0/9) for predators of 50–69 mm, 40%

(4/10) in predators of 70–89 mm and 54% (7/13) for predators of 90 mm or larger ($\chi^2 = 7.04$, d.f. = 2, $P < 0.05$). All identified cases of predation occurred during May, when 52% of the captured yearling or older salmonids (11/21) had been eating fry; none of the 10 larger salmonids captured after May had fry in their stomachs ($\chi^2 = 8.78$, d.f. = 1, $P < 0.01$).

Discussion

This study confirmed the essentially nocturnal nature of dispersal from the redd in Atlantic salmon (e.g. Gustafson-Marjanen & Dowse 1983; Brannas 1987; Crisp 1991; Johnstone 1997) and that it is seasonally clumped (e.g. Gustafson-Marjanen & Dowse 1983; Gustafson-Greenwood & Moring 1990; Brannas 1995). Leaving the redd at night, together with undergravel movements in smaller fish (García de Leániz *et al.* 1993), may well provide protection against predators. Opportunistic observations at the study site suggest that the incidence of predation at the study sites was high, especially during the period of initial dispersal.

Use of serial bank-to-bank trapping, together with batch marking and, in favourable cases, sequential samples from identified individuals, demonstrated marked variability in several aspects of the biology of newly emerged salmon fry, even though these were almost certainly half-sibs or full-sibs. For example, both the date on which fry left the redd and the developmental stage at which they did so were variable. Early in the season, dispersing fry all had remnants of yolk and so had opted to leave the redd some time before being forced to do so by lack of nourishment. Later on, dispersing fry had fully depleted yolk sacs; while many had food in their stomachs, some fry with no remaining yolk sac had failed to feed. Similar results have been described for trout (Elliott 1986),

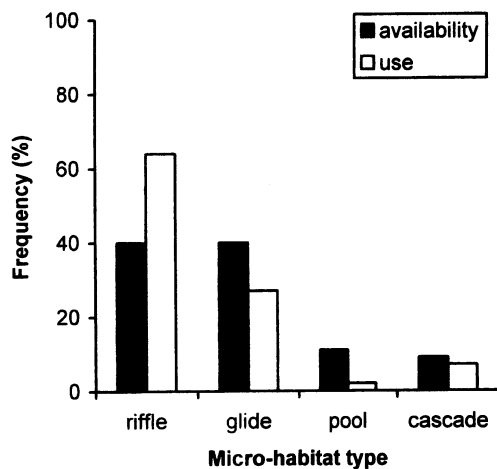


Figure 5. The percentage of fry recaptured in different habitat types, together with the percentages expected on the basis of habitat availability.

coho salmon (*Onchorhynchus kisutch* (Walbaum), Mason 1976) and Atlantic salmon (Brannas 1987). Within-clutch variability in rate of yolk sac depletion and in age at first feeding have also been reported in studies under highly controlled conditions in the laboratory (e.g. Metcalfe & Thorpe 1992).

The great majority of fry left the redd in a downstream direction, apparently moving continuously (if slowly) at least 20 m away from the redd. The observed rates of dispersal (2.5 m day^{-1} on average) were much lower than expected if alevins had simply drifted downstream with the prevailing current ($\sim 0.3 \text{ m s}^{-1}$ or 26 km day^{-1}). Individuals varied in the speed at which they moved downstream, although the origin of this variation was not clear.

Both the increasing coefficients of variation in body dimensions and the data from identified fish indicate marked differences in growth between fry. The period during which variability increased most rapidly coincided with the date at which fish with food in their stomachs began to be caught in significant numbers. Individual fish achieved strikingly different performances during the period of dispersal from the redd, some growing well and others apparently starving. Marked and increasing differences in growth rates between sibling Atlantic salmon have been reported in many laboratory-based studies and in some cases their origin is known; for example, differences in competitive ability are a key determinant of growth rate in first feeding fry (e.g. Metcalfe 1989; Metcalfe *et al.* 1995). In addition, their consequences for subsequent life history processes is also well documented under laboratory conditions (e.g. Metcalfe, Huntingford & Thorpe 1987; Metcalfe *et al.* 1990).

It is much more difficult to identify causes of individual differences in performance in the wild, although date of emergence may be an important factor. Steelhead fry, *Onchorhynchus mykiss* (Walbaum), from early redds outcompeted those from late redds in stream channels (Chandler & Bjornn 1988) and coho salmon emerging early from a single redd were more likely to establish residency and grow faster in artificial stream channels than those that emerge later (Mason & Chapman 1965). The present study suggests that in nature early emergers may settle in more favourable first feeding habitat, but early emerging Atlantic salmon run a greater risk of predation than late emerging fish, at least when predators are present through emergence (Brannas 1995). Whatever its origin, since body size is an important determinant of performance at several key points in the life cycle of Atlantic salmon, such marked variability in performance is likely to have strong effects on fitness.

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