Dispersal of Atlantic salmon fry from a natural redd: evidence for undergravel movements?

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In this paper we describe a modified version of a box trap used for bank-to-bank trapping during a study of dispersal of Atlantic salmon fry (*Salmo salar* L.). Two such traps were positioned 2 m upstream and downstream of a single isolated natural redd and a third was placed 20 m downstream. All fry captured in each trap were marked and released beyond the trap. Of the fish caught in the second downstream trap, 64% were unmarked. The seasonal patterns of trapping for marked and unmarked fish were identical, but the unmarked fish were significantly smaller than their marked peers. We argue that these unmarked captures represent fish that evaded capture in the first downstream trap, either by dispersing from the redd deep within the gravel or by leaving the water column and burrowing into the gravel on encountering the trap. Implications for the interpretation of trapping data on newly emerged salmonids are discussed.

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Nous avons utilisé une version modifiée de la nasse parallépipède ordinairement employée pour capturer les poissons d'une rive à l'autre, au cours d'une étude de la dispersion des alevins du Saumon atlantique (*Salmo salar*). Deux de ces nasses ont été installées à 2 m en amont et à 2 m en aval d'un nid naturel et une troisième a été installée à 20 m en aval. Tous les alevins capturés dans les nasses ont été marqués et relâchés au-delà de la nasse. Soixante-quatre pourcent des poissons capturés dans la seconde nasse placée en aval étaient des poissons non marqués. Les patterns saisonniers de capture étaient identiques chez les deux types d'alevins, marqués ou non, mais les poissons non marqués étaient significativement plus petits que les alevins marqués. Nous croyons que les alevins non marqués sont des poissons qui ont échappé à la première nasse placée en aval, soit en s'enfonçant profondément dans le gravier au sortir du nid, ou alors en quittant la colonne d'eau pour s'enfoncer dans le gravier au point de rencontre avec la nasse. L'interprétation des données de piégeage chez les salmonidés fraîchement émergés fait l'objet d'une discussion.

[Traduit par la rédaction]

Introduction

Patterns of dispersal of salmonid fry on emergence from natural redds have been extensively studied (e.g., Pritchard 1944; Bams 1969; Godin 1982; Bardonnet and Gaudin 1990). These studies have shown that over a period of several weeks, the fry emerge from the gravel, predominantly at night, and disperse downstream in the water column. The number of fish moving away from the redd on any given night correlates with certain environmental factors, such as stream flow (e.g., Nunan and Noakes 1987; Crisp and Hurley 1991).

This kind of information has been collected using a variety of techniques. In most studies of emergence under natural conditions, either special emergence traps placed over sections of redds have been used (e.g., Field-Dodgson 1988), or a proportion of downstream migrants have been caught in drift sample nets (e.g., Marty and Beall 1991). While these techniques provide information on relative rates of dispersal, complete characterisation of patterns of dispersal from natural redds requires bank-to-bank trapping. Bank-to-bank trapping is also necessary for partitioning losses into mortality and emigration. For obvious reasons this presents technical difficulties and this approach has been used in very few published studies. Elliott's (1986) study of brown trout (*Salmo trutta*) is a notable exception that has provided a wealth of information on dispersal and mortality in fry of this species. Bank-to-bank trapping of Atlantic salmon (*Salmo salar*) from a single natural redd has rarely been attempted, although Gustafson-Marjanen and Dowse (1983) enclosed entire artificially planted redds in a net to a depth of 30 cm and collected all emerging fry in a single box trap.

Here we describe a modified version of a box trap made of clear Plexiglas to minimise trap avoidance (Casselman and Harvey 1986). The traps were used (in conjunction with an underwater video camera) in a program of sequential trapping to capture young salmon dispersing from a single isolated redd.

Material and methods

This study was carried out in a small lade off the Girnock Burn, a tributary of the River Dee in Aberdeenshire. The lade is used by spawning salmon, but only at times of high flow. For this reason, redds found in the lade tend to be single at one end or the other. In the winter of 1989, only one salmon redd (approximately 2 m long) was found in the lade. This was at the upstream end, and so ideally placed for a study of patterns of dispersal in fry.

To investigate the timing of dispersal from the redd (as part of a wider scale study of the consequences of different dates of emergence; F. Huntingford, C. Garcia de Leaniz, and N. Fraser, in preparation), three identical traps of a modified box design were positioned across the whole width of the lade. One (trap 1) was positioned 2 m

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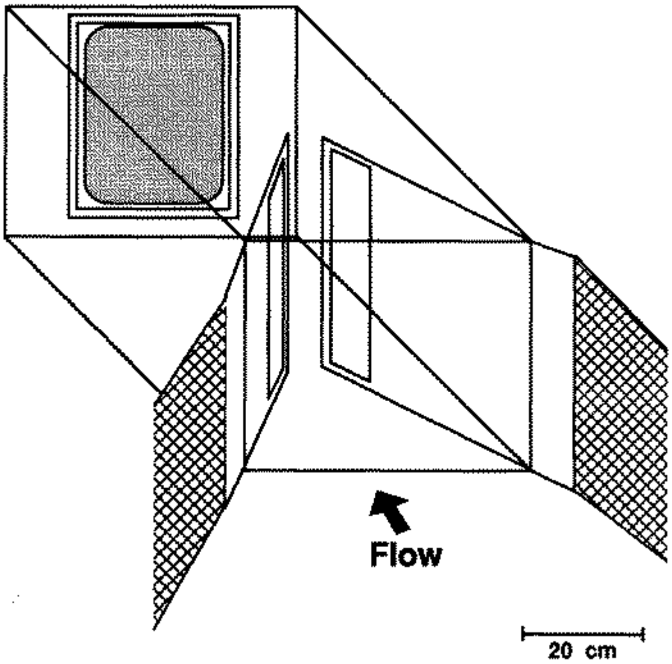

FIG. 1. Diagram of the box trap used in the study.

upstream of the upper border of the redd, another (trap 2) was placed 2 m downstream of the border, and a third (trap 3) was placed 20 m downstream. A conventional box trap (trap 4) was sited 120 m below the redd at the downstream confluence of the lade with the main river.

Each trap consisted of a Plexiglas box (70 × 50 × 50 cm; see Fig. 1) with transparent sides and a black floor. The back wall was fitted with a screen (10 × 30 cm) of 1-mm netlon mesh. The entrance comprised two vertical sheets of Plexiglas forming a V that funnelled water into the trap through a gap with an adjustable width of 4 cm, which was set, in this case, at 2 cm. A sliding lid of transparent Plexiglas prevented predators from entering the trap while allowing a clear view of its contents. A series of removable horizontal baffles at the back of the trap provided a region of low flow in which captured fish could avoid excessively strong currents. When required, flow into the trap could be cut off altogether by means of a sliding door across the front, allowing the trap to be fished with relative ease. Continuous screens of 1-mm netlon mesh were clamped to both sides of the trap by strips of Plexiglas and projected forwards to each bank at an angle to the axis of the stream. These screens were buried to a depth of 30 cm in the substrate and supported by a series of iron stakes driven into the stream bed. A panel of Inox wire mesh of similar gauge projected from the front edge of the trap; this was buried in the substrate and extensively overlapped the inside edges of the netlon side screens. These wings of the trap thus served as a bank-to-bank screen, directing fish moving downstream into the mouth of the trap.

The traps were established at the beginning of April 1990 and checked daily. Young salmon (with and without yolk sacs but all referred to here as fry) were caught every day between 90-04-26 and 90-06-30. Each fish caught in any of the traps was weighed and measured (standard length) and batch-marked, using either injection with alcian blue dye or attachment of small fin clips, depending on the trap in which they were caught. Marked fish were released upstream in the case of trap 1 (none of these were ever caught again, so all must have entered the main river) and downstream in the case of traps 2, 3, and 4. In addition, a sample of fish was collected for species identification by means of protein electrophoresis (GPI, PMG) as described by Verspoor (1988).

During a period of high emergence rates (90-05-13 to 90-05-16), a low-light underwater video 8 camera was used for 4 nights to film the entrance to trap 2. As the length of the video film limited us to 3 h of filming per night, filming was staggered on successive nights to cover all the hours of darkness.

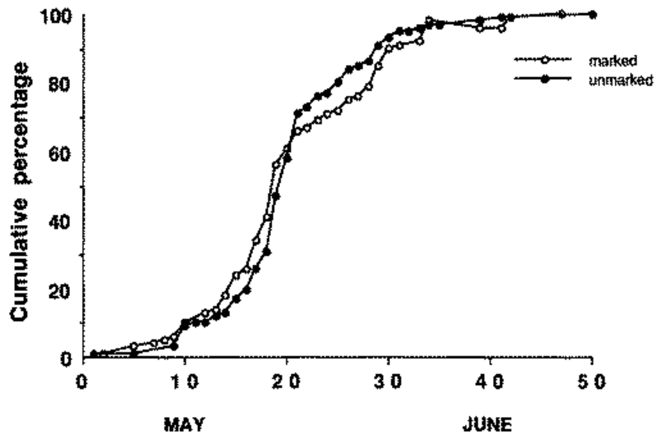

FIG. 2. Cumulative frequencies of marked and unmarked fry caught in trap 3 during the study period (day 1 is 90-04-26).

Water depth and flow rates were recorded continuously throughout the study at a station located 1 km downstream.

Results

In this article, we concentrate on the catch records from trap 3, since it is this data set that provides the clearest evidence that fish were evading capture. Over the entire trapping period, 311 fish were caught in trap 3; unexpectedly, 198 of these (64%) were unmarked. Both marked and unmarked fish were caught in trap 3 throughout the emergence period (Fig. 2), and the cumulative distributions for the two groups are identical (Kolmogorov–Smirnov two-sample test; $D_{m,n} = 10$, $P \gg 0.10$).

Marked fish (i.e., those that had previously been caught in trap 2) were significantly longer (median 25.0 vs. 24.0 mm; Mann–Whitney test, $W = 28256$, $P < 0.001$) and heavier (mean 0.157 ± 0.002 vs. 0.149 ± 0.001 g) than unmarked fish (which had evaded capture).

Over the 4 nights of video filming, 18 fry were recorded entering trap 2. Of these, 17 (94%) were swimming downstream in the water column, head first and moving faster than the current (as reflected by the rate of movement of air bubbles); the 1 remaining fish moved slowly into the trap along the substrate. The number of fry seen entering the trap during the 3-h filming session on a given night constituted about one-third of those collected from the trap the following morning. This suggests that we were able to observe a substantial proportion of the fish that entered the trap during the filming periods, and therefore that these observations are reasonably representative of the behaviour of the trapped fish.

Discussion

There are a number of possible reasons (which are not mutually exclusive) why so many unmarked fish were caught in trap 3:

1. It is possible that the unmarked fry might have passed through the mesh or over the screens when water levels were high. The mesh was fine, very robust, and buried deep in the substrate across the entire width of the lade. The traps were checked daily for holes and none was ever found. At the end of the trapping season, the underground sections of the screens

were found to be completely intact. We are confident, therefore, that the wings of the trap did indeed form a continuous fishproof screen from bank to bank down to a depth of 30 cm. The summer of 1990 was exceptionally dry, flow rates were low (approximately half full-bank discharge), and the trap never overflowed during the study period. For these reasons it is unlikely that trap leakiness explains the large number of unmarked fish captured in trap 3.

2. Although we can be certain that there were no other salmon redds in the lade, the unmarked fish might have been trout that had hatched between traps 2 and 3. However, the electrophoretic data showed that, of 63 fry captured in trap 3, 58 were salmon, 1 was a salmon × trout hybrid, 4 were unassignable, and none were trout. So this explanation can clearly be rejected.

3. Although the fry moved relatively quickly between traps 2 and 3 (a 7-day gap separates the 50% capture dates for all the fish caught in the two traps), it could be that marks were lost during this period. However, in a study of newly hatched fry housed in hatchery conditions, 31 of 33 dye marks and 73 of 75 fin clips were retained after 13 days (97% retention); retention rates after 33 days were 28 of 33 (85%) and 72 of 76 (95%), respectively. This degree of retention effectively rules out the possibility that the unmarked fish had been given marks that were subsequently lost.

4. A fourth possibility is that the unmarked fish had evaded capture as a result of movement through the gravel, either by making extensive horizontal movements away from the redd (to a point beyond trap 2) before emerging, or by emerging into the water column but burrowing into the gravel on making contact with the trap. In either case, the small size of unmarked fish would be expected, since this route is presumably more accessible to smaller fish.

The identical trapping patterns for unmarked and marked fish suggest that whatever the unmarked fish are doing, it does not take any longer than migration via trap 2. Since extensive undergravel migration before emergence is likely to be time-consuming (e.g., Godin 1982; Nunan and Noakes 1987), this favours the secondary burrowing as an explanation. We know that fish which had emerged and started feeding were capable of burrowing under trap 2, since a total of 17 fish marked and released downstream of this trap were subsequently recaptured upstream of it, and 5 of 16 (31%) of 0+ salmon caught in trap 4 were unmarked.

On the other hand, the video films showed no evidence of fish burrowing on reaching the trap. Extensive movements within the gravel have been documented for salmonids in artificial redds, in response to such stimuli as light (e.g., Dill 1969; Carey and Noakes 1981; Carey 1985); this suggests that such movements are well within the capabilities of Atlantic salmon around the time of emergence. Therefore, a real possibility remains that at least some of the unmarked fry evaded the trap because they had moved away from the redd for substantial distances well below the surface of the substrate before eventually emerging, perhaps in response to external conditions.

In conclusion, the box traps used in this study proved effective at capturing salmon fry dispersing through the water column in the conditions prevailing in the study lade. For this reason, although we can find no reference to undergravel dispersal from natural redds in the literature on juvenile salmonids (e.g., Godin 1982), we interpret the presence of unmarked fry in trap 3 as evidence that these fish moved past trap 2 within the gravel. According to this interpretation, the unmarked status of a substantial proportion of the fry captured in trap 3 suggests that undergravel migration may be an important means of dispersal from the redd. Current laboratory experiments, designed to examine this possibility more stringently, support this view.

In any event, the fact that so many fry evaded trapping (which only became apparent because captured fry were marked), and that these represent a nonrandom section of the size distribution, has implications for the interpretation of trapping data on newly emerged salmonids. In brief, the mean size of the migrants may have been overestimated (so that calculated growth rates, for example, may be on the low side) and their numbers underestimated. As a consequence, in partitioning losses of alevins and fry leaving redds containing known numbers of eggs, estimates of mortality may be inflated at the expense of estimates of emigration.

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