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# APPENDIX TO THE REBUTTAL PROOF OF EVIDENCE

**OF**


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# Effects of hot dry summers on the loss of Atlantic salmon, Salmo salar, from estuaries in South West England

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**Abstract** Salmon, *Salmo salar* L., were radio tagged in four estuaries in South West England. At medium to high summer flows, most salmon entering the river did so within 10 days of tagging. Lower flows were associated with an increased tendency for fish to remain in tidal water for a protracted period, and for those delayed fish to fail to enter the river. The delay was correlated with low freshwater flow, but it was concluded that high water temperature, and in some situations low dissolved oxygen, were likely to be the major influences. The causes of failure to enter the river by the delayed fish include lethally low levels of oxygen in some situations, but a major factor may be missed physiological opportunity. Implications in terms of water resource management, fisheries management and climate change are discussed.

KEYWORDS: Atlantic salmon, estuaries, flow, migration, temperature, water resource management.

## Introduction

The association between elevated river flow following rainfall and upstream migration of adult Atlantic salmon, *Salmo salar* L. is well documented (e.g. Banks 1969; Alabaster 1970). Much less well described is a widespread phenomenon of many fish failing to enter the river at all in years with hot summers and extended periods of low freshwater flow. The most explicit review was that of Solomon, Sambrook & Broad (1999) based on 10 years of salmon telemetry studies (1986–1995). It concluded that more than 50% of a year's run of fish can be lost in this way in drought years, such as 1989 or 1995, and that 'this shocking conclusion clearly has major significance for management of water resources and for salmon fisheries management in general'.

This paper explores this phenomenon through examination of the literature and by further analysis of radio tracking data in four rivers in South West England described by Solomon *et al.* (1999).

The earliest specific reference to this phenomenon was by Alabaster (1970), who analysed trap catches of salmon and sea trout on the River Coquet in northern England. However, a major limitation of measures or estimates of total runs entering the river in this respect is that the size of the total returning stock approaching the coast is variable between years and is usually unknown. Thus the impact of estuary or river conditions on survival to enter the river is impossible to assess in quantitative terms, and may be difficult to detect, even qualitatively, unless the impact is great relative to the variation in stock size due to other factors. Tracking of individual fish fitted with transmitting tags in coastal waters or estuaries overcomes this limitation, as availability is defined as the total tagged stock. Although numbers are typically limited to tens or hundreds of fish, it is possible to follow the fate of each fish in detail to obtain a reliable picture to what is happening to the stock as a whole.

Salmon fitted with radio tags in the estuary of the River Tywi in 1988–1990 (Clarke, Purvis & Mee 1991;

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Clarke, Evans, Ellery & Purvis 1994) showed a correlation on a monthly basis between the probability of both prompt and eventual river entry and freshwater flow (positive correlation), estuary temperature (negative) and estuary oxygen concentration (positive). As there were close correlations between the environmental variables tested, it was not possible to identify the true contribution of each to the observed behaviour. None of the variables approached levels likely to be directly harmful to the fish.

The data used in this paper were obtained from separate studies of fish movement into the Rivers Avon, Exe, Tamar and Tavy in South West England. During these studies it became clear that in each case hot, dry summers were associated with a delay to river entry and a significant increase in the proportion of returning adult salmon that failed to enter the river. Location and hydrometric details of the four rivers are given in Table 1.

## Methods

The approach and methods used to tag and track the salmon are detailed in Solomon et al. (1999). In this analysis the fate of tagged fish is explored in relation to freshwater flow to the estuary, and associated environmental variables, at the time of capture and tagging and shortly afterwards, and the tendency to enter the river promptly (within 10 days of tagging), survival to enter the river later (more than 10 days after tagging), and failure to enter the river. The fail-to-enter category includes all individuals which were not recorded passing, or having passed, the tidal limit on the river in whose estuary the fish was tagged. It thus includes fish whose presence was recorded at some time after tagging in tidal water (but not subsequently entering the river), fish known to have been recaptured in estuary nets, fish reported or recorded in other rivers, and fish not detected after release.

Fish for tagging were obtained from seine nets operated by licensed commercial fishermen. On the Avon the netting was conducted at the narrow entrance to Christchurch Harbour, which forms the joint estuary of the rivers Avon and Stour. It is likely that most fish caught were entering the estuary for the first time, and that the subsequent observations included the whole of their estuary residence. On the other rivers the netting sites were within the estuary so the fish had passed an unknown part of their estuary residence before capture. However, from the appearance of the fish (bright silver with sea lice), and from patterns of migration and recapture, it is likely that most fish had arrived in the estuary shortly before capture.

Freshwater flows to each estuary (daily means, $m^3 s^{-1}$) were obtained from appropriate gauging stations in the lower reaches, adjusted as appropriate for downstream catchment and abstraction. On the River Avon, water temperature just upstream of the tidal limit was recorded daily (09.00hr) by West Hampshire Water Company. Daily readings for seawater temperature at Bournemouth Pier, about 10 km west of the entrance to Christchurch Harbour, were collected by Bournemouth Borough Council. A study was undertaken by the Environmental Agency (A. Frake, personal communication) to investigate conditions of temperature, salinity and dissolved oxygen (DO) in the tidal River Stour, which shares a joint estuary with the Avon, where many of the delayed Avon fish spent the period between tagging and river entry. Spot readings of water temperature, DO and ammonia concentration, at approximately monthly intervals, were available from the Environment Agency for one or two sites in each estuary.

Selection of the geographical location of the point which constitutes entry to the river is an important issue, and the results are sensitive to only minor variations in the selected location. For consistency of this analysis, passage landwards of the tidal limit was selected (Table 1).

Table 1. Statistics for the tidal limit of the rivers studied

| | Avon | Exe | Tamar | Tavy |
|---|---|---|---|---|
| Tidal limit NGR | SX 157933 | SX 930909 | SX 436709 | SX474650 |
| Tidal limit lat./long. | 50°44′19″N | 50°42′26″N | 50°30′59″N | 50°27′52″N |
| | 1°44′39″W | 3°30′56″W | 4°12′23″W | 4°9′1″W |
| Catchment area ($km^2$) | 1706 | 1195 | 928 | 210 |
| Mean flow ($m^3 s^{-1}$) | 19.85 | 24.61 | 22.45 | 7.25 |
| Q95 ($m^3 s^{-1}$) | 6.97 | 3.45 | 1.77 | 1.21 |

NGR, National Grid Reference; Q95, flow exceeded for 95% of the period of flow record, i.e. a measure of low flow. Flow statistics are 'naturalised', i.e. effects of abstraction and effluent discharges have been modelled out of the flow record.

Table 2. Percentage of radio-tagged fish in each estuary each year that were recorded entering that river at any time. Also shown is the flow for June, July and August each year at Thorverton, River Exe, as a percentage of the long-term average (1956–1994) for those months, and the ‘Central England mean surface temperature’ for June to August each year (Hulme & Barrow 1997) as general indicators of ‘dryness’ and warmth of the season

| Year | Avon | Exe | Tavy | Tamar (C'hele) | Tamar (W'Quay) | Exe flow % mean | Central England (temp. °C) |
|---|---|---|---|---|---|---|---|
| 1986 | 72.4 | | | | 66.7 | 266 | 14.8 |
| 1987 | 77.9 | | | | 46.2 | 72 | 14.8 |
| 1988 | 60.2 | | | 50.0 | | 131 | 14.8 |
| 1989 | 55.0 | | | 25.0 | | 39 | 16.5 |
| 1990 | 54.8 | | | 47.1 | | 58 | 16.2 |
| 1991 | | 66.7 | 46.2 | 25.9 | | 100 | 15.5 |
| 1992 | | 56.3 | 42.8 | 73.9 | 31.8 | 102 | 15.7 |
| 1993 | | 62.0 | 42.0 | 44.8 | 30.0 | 145 | 14.9 |
| 1994 | | 36.7 | 17.1 | | 39.2 | 60 | 16.2 |
| 1995 | | | 16.7 | | 29.5 | 37 | 17.4 |
| Mean | 63.7 | 55.4 | 28.9 | 42.2 | 37.3 | | |

## Results

On the River Avon the overall proportion of tagged fish ($n = 437$) entering the river within 10 days was 47.8%, with 15.9% entering at a later date and 36.3% failing to enter the river. The proportion of tagged fish entering the river was correlated with river flow on an annual (Table 2), monthly (Fig. 1) and daily (Fig. 2) basis. Higher flows were associated with a high level of entry of fish within 10 days of tagging, and lower flows with increased levels of fish entering the river after more than 10 days, and, more importantly, failing to enter the river.

Of the 251 fish tagged at flows to the Avon estuary $> 9\ m^3\ s^{-1}$, 162 (64.5%) passed the tidal limit within 10 days. A further 22 (8.8%) entered the river after more than 10 days, mostly on elevated flows later in the year (October to November). At flows $< 9\ m^3\ s^{-1}$ the proportion of fish entering the river within 10 days fell away sharply. Increased numbers entered later in the year, but this increase did not make up for the decline in numbers making prompt entry, and the total proportion entering the river fell. Of the 182 fish tagged $< 9\ m^3\ s^{-1}$, 45 (24.7%) passed the tidal limit within 10 days, with a further 47 (25.8%) doing so later in the year. Thus a total of just over 50% of the fish tagged below $9\ m^3\ s^{-1}$ eventually entered the river, compared with 73.3% of those tagged at higher flows. Of the 60 fish tagged at residual flows $< 6\ m^3\ s^{-1}$ only 15 (25%) entered the river; two in < 10 days, and 13 later.

It is suggested that the disappearance rate for tagged fish at residual flows $> 9\ m^3\ s^{-1}$ represents that rate at which tags fail, fish are recaptured in tidal waters, and

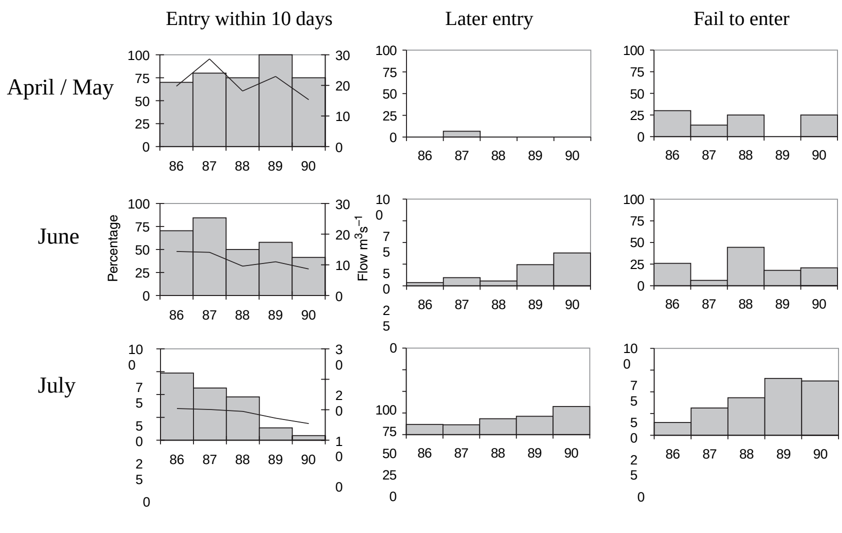


Figure 1. Fate of radio-tagged fish on the Avon, by month and year (histograms). Most ‘later entry’ fish entered the river in the autumn. Entry to the river is defined as passing the tidal limit. Also shown is the mean flow for each month at the tidal limit (line).

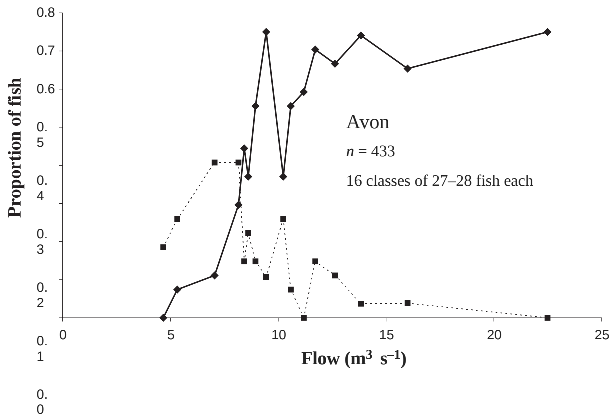


Figure 2. The relationship between river flow on the day of tagging, and the proportion of tagged fish that entered the river within 10 days of tagging (solid line) and after more than 10 days (dashed line), for fish tagged at the mouth of the Avon estuary. Each point represents the mean flow and proportions for a group of 27 or 28 fish.

fish go to rivers other than the Avon. As there is no obvious reason why these rates should increase at low discharges, it is reasonable to suggest that the increased loss rate of fish at lower flows is because of mortality of fish in the estuary or at sea between tagging and river entry, because of factors other than capture, handling and tagging. On the assumption that all Avon salmon approaching the river at flows > 9 $m^3 s^{-1}$ survive to enter the river, the equivalent figures for flows < 9 and 6 $m^3 s^{-1}$ are 68.9 and 34.1%, respectively.

There was also a relationship between river temperature on the day of tagging and the probability of river entry within 10 days (Fig. 3). Fewer fish enter the river promptly at high river temperatures and more at low temperatures, but there is a suggestion of a plateau in the relationship between about 13 and 19 °C, which

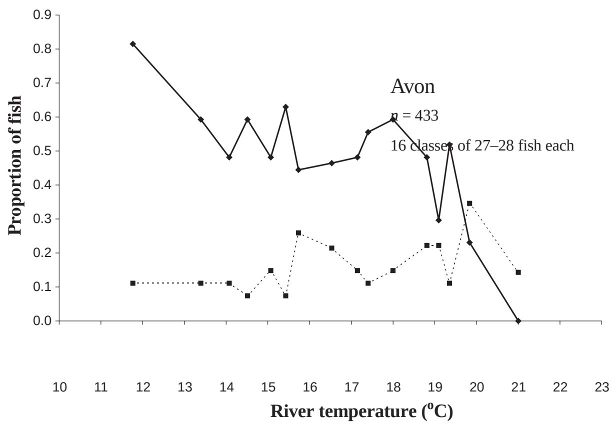


Figure 3. The relationship between river temperature on the day of tagging, and the proportion of tagged fish that entered the river within 10 days of tagging (solid line) and after more than 10 days (dashed line), for fish tagged at the mouth of the Avon estuary. Each point represents the mean flow and proportions for a group of 27 or 28 fish.

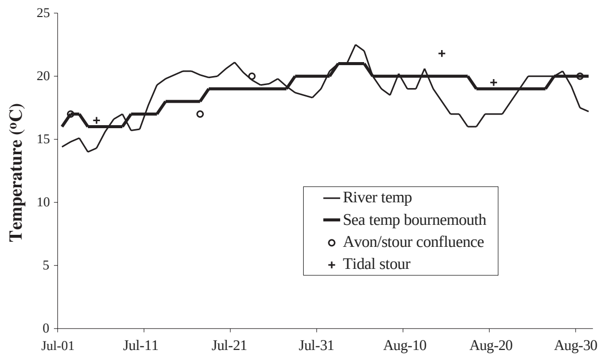


Figure 4. Daily readings of sea and river water temperature, and spot readings of estuary temperature, River Avon, July to August 1990.

includes the great majority of fish observations. It should be borne in mind that the temperatures that the fish experience within any 24-h period may vary from the single 09.00-hour reading. Regrettably, the opportunity was missed to make continuous records of estuary water temperature during the tracking studies. Daily figures for river and sea water temperatures for the River Avon for July to August 1989 (the period of the study with the highest tendency for delayed migration of tagged fish) are shown in Figure 4, with some spot readings from two locations in the estuary. The highest spot readings taken during the periods of tagging on the Avon (April to July, 1986–1990) were 21.6 °C in the upper Avon estuary and 22.2 °C in the tidal Stour, where many delayed fish spend the period between tagging and eventually passing the Avon tidal limit. The highest 09.00-hour reading of river temperature during this period was 21.8 °C.

A relationship was found between water temperature and the time of day of entry to the river. In summer, most fish reach the tidal limit in the early morning or late evening. However, this distribution was more marked at higher temperatures; of the 90 fish that reached the tidal limit on days when the 09.00-hour river temperature reading was in excess of 17 °C, only one (1.1%) did so between 09.00 and 21.00 hours. In contrast, 12 (21.4%) of the 56 fish reaching the tidal limit on days when the river temperature was below 15 °C did so between 09.00 and 21.00 hours.

Similar relationships between river flow and pattern of entry were apparent for the other rivers. Of the 318 fish tagged on the River Exe, 37.0% passed the tidal limit within 10days of tagging, 18.4% later, and 44.6% failed to enter the river (Fig. 5). At flows > 6 $m^3 s^{-1}$ about half (49.3%) of fish entered the river within 10 days of tagging, and a further 13.4% at a later date; 37.0% failed to enter (Fig. 6). At flows below that level, 29.4% entered within 10 days, a

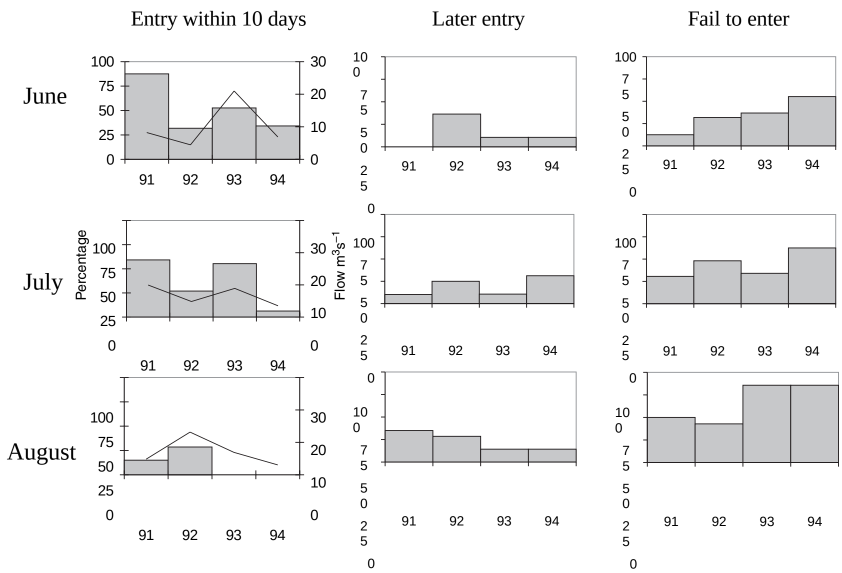


Figure 5. Fate of radio-tagged fish on the Exe, by month and year. Most ‘later entry’ fish entered the river in the autumn. Entry to the river is defined as ascending the weir that forms the tidal limit. Also shown is the mean flow for each month at the tidal limit (line).

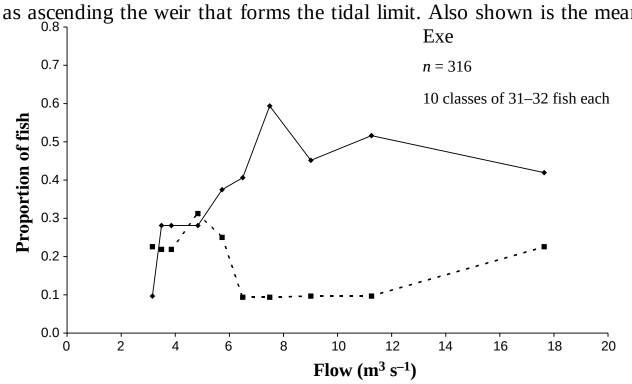


Figure 6. The relationship between river flow on the day of tagging, and the proportion of tagged fish that entered the river within 10 days of tagging (solid line) and after more than 10 days (dashed line), for fish tagged in the Exe estuary. Each point represents the mean flow and proportions for a group of 31 or 32 fish.

further 21.4% at a later date, and 49.2% failed to enter the river. At flows $< 4\ m^3\ s^{-1}$, only 24% of tagged fish entered the river within 10 days, a further 24.8% at a later date, with 51.2% failing to enter. Although no detailed temperature data were available, the tendency to delay entry and to fail to enter the river were associated with temperature on an annual basis (Table 2).

Although the River Tamar tagged fish showed a similar yearly pattern of river entry to the rivers Avon and Exe in terms of hot and dry summers (Table 2), comparison of monthly mean flows gave no clear pattern. This may have been a result of the flow not being uniform throughout any month; even generally dry and hot months may contain short periods of elevated flow and lower water temperatures. The pattern is somewhat clearer when the probability of entry within 10 days is considered against flow on day of tagging (Fig. 7), but while there was a trend for lower flows to be associated with a delay in river entry, some other factors appear to be operating that complicate the relationship.

Overall, the proportions of fish tagged on the Tamar estuary entering the river within 10 days and at any time were low, at 30 and 40% respectively (cf. 48 and 64% on the Avon; 37 and 55% on the Exe). One factor is that some of the fish tagged in the Tamar estuary are destined for the rivers Tavy and Lynher, which join the Tamar estuary seawards of the netting sites, but records of Tamar tagged fish entering the Tavy during the years when the two programmes were running together suggest that this cannot explain all of the difference between these results and those on the rivers Exe and Avon. It appears that losses from the Tamar estuary were relatively high, and more weakly correlated with low flows alone than are those on the Avon and Exe.

Once again, hot and dry summers were associated with a reduced tendency for fish tagged on the River Tavy to enter the river promptly (Table 2). As on the Tamar there was a downward trend in the line with falling flow but the relationship was not clear (Fig. 8). This, coupled with the very low tendency overall to enter the river within 10 days (18%) and at any time (29%), suggests that some other adverse factor is operating in this case, similar to that on the Tamar, but more extreme.

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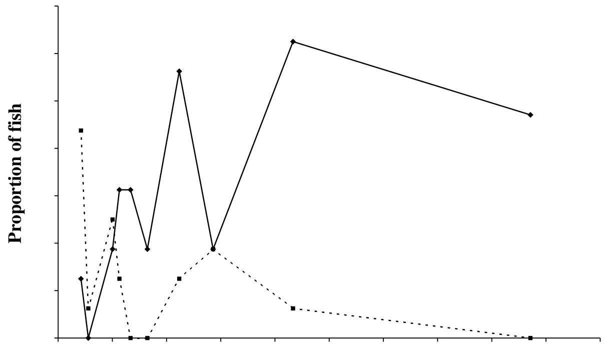


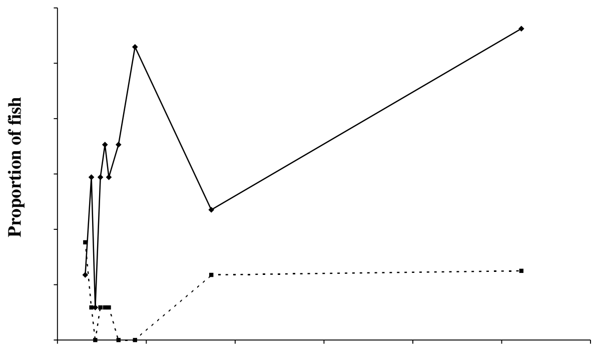


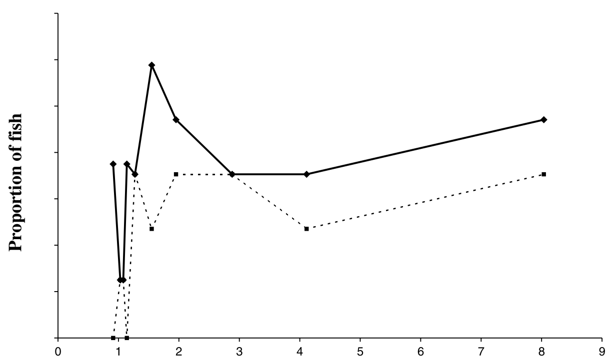

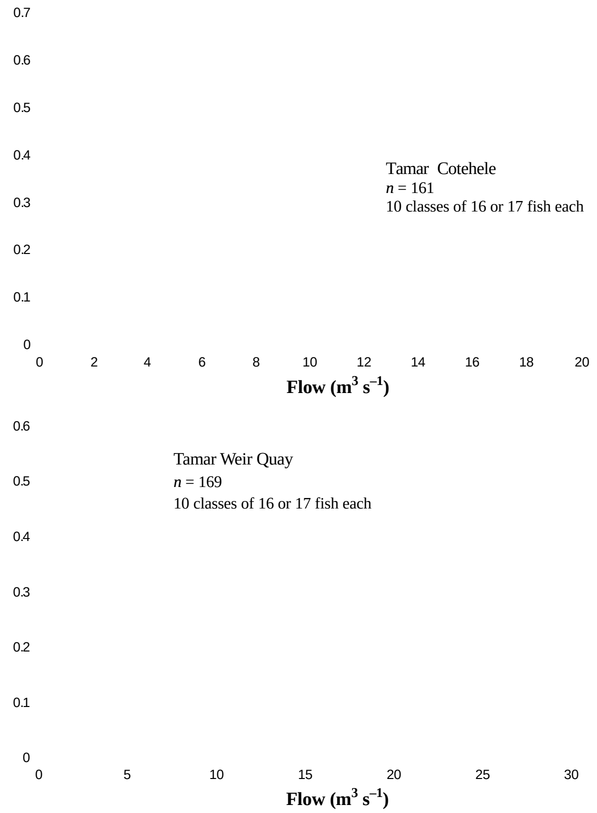


Figure 7. The relationship between river flow on the day of tagging, and the proportion of tagged fish that entered the river within 10 days of tagging (solid line) and after more than 10 days (dashed line), for fish tagged in the Tamar estuary at Cotehele (above) and Weir Quay (below). Each point represents the mean flow and proportions for a group of 16 or 17 fish.

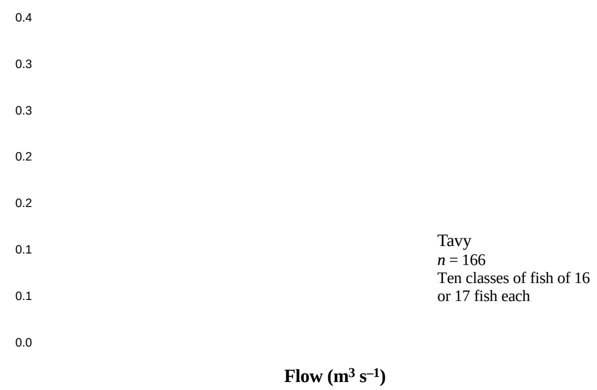


Figure 8. The relationship between river flow on the day of tagging, and the proportion of tagged fish that entered the river within 10 days of tagging (solid line) and after more than 10 days (dashed line), for fish tagged in the Tavy estuary. Each point represents the mean flow and proportions for a group of 16 or 17 fish.

## Discussion

### Summary of observations

At times of medium to high freshwater flow to the estuary, most fish arriving from the sea that are going to enter the river pass through the estuary and into the river with a minimum of delay. There appears to be no requirement for a period of physiological adjustment to the change in salinity, with fish often passing from sea water to fresh water within a matter of a few hours, and possibly less. Although some fish were not recorded entering the river even under apparently attractive conditions, this was probably because of fish being native to, and subsequently returning to, another river without passing the tidal limit of the river in which it was tagged; a minor proportion of fish tagged in each estuary were recorded in other rivers, although most fish going elsewhere would not be detected or caught and reported.

At times of low freshwater flow, most fish arriving from the sea did not pass promptly into fresh water, and many remained in the estuary or returned seawards for up to several months. Once freshwater flow increased in the autumn some of these delayed fish entered the river, but many failed to do so. It is likely that two distinct processes are involved in this overall phenomenon, the underlying causes of which may not be the same. The two processes are:

- delay in entry to the river from the estuary by more than 10 days; and
- compromise of the ‘delayed’ fish, causing direct mortality or at least apparently preventing them from subsequently entering the river.

Examination of the factors that are implicated is complicated by the correlation between likely contributory environmental conditions, such as freshwater flow to the estuary, water temperature and water quality parameters. A strong correlation does not necessarily indicate direct cause and effect, and it is likely that one or more of the contributory conditions are more critical than the others. It is also possible that the factors involved in the two processes are somewhat different in different rivers.

### Potential factors implicated in delayed entry

Low freshwater flow. Delay in passing through the estuary is strongly associated with low flows, particularly on the rivers Avon and Exe. However, it is difficult to see the direct cause and effect. In contrast to water temperature or DO concentration for example, fish have no means to sense directly the volume of freshwater flow, especially when in the estuary. In some situations low freshwater flow over a barrier at the tidal limit might make physical passage landwards difficult or impossible; this appears to be the case on the River Exe, for example, where large numbers of fish gather just below the weir that forms the tidal limit at times of very low flow. It does not appear to be the case on the other rivers, even those with tidal limit structures. It is also possible that changes in estuarine salinity, which would be affected by freshwater discharge, influence the behaviour of the fish, although estuary salinity fluctuates markedly with the state of tide. While water velocity varies with discharge, it also varies markedly with location within the river and estuary; salmon are willing to swim through areas of both slow and fast current to migrate upstream.

Another factor that suggests that low flow as such is not the major driver for the delays comes from a comparison of the low flows in the different rivers (Table 1). The rivers Avon, Exe and Tamar are of a similar size in terms of mean flow (19.85, 24.61 and 22.45 $m^3 s^{-1}$, respectively). However, their dry-weather flows are different due to differing contributions of groundwater, naturalised Q95 flow (the flow exceeded for 95% of the time, a widely used measure of dry-weather flow) being 6.97, 3.45 and 1.77 $m^3 s^{-1}$ on the Avon, Exe and Tamar respectively. Tendency to enter the River Avon within 10 days is greatly reduced as flows fall below the Q95 of 6.97 $m^3 s^{-1}$, yet on the Exe and Tamar the tendency is relatively high at this discharge volume. It thus appears that some factor associated with low flows, and not discharge volume itself, is responsible for the decreasing tendency for prompt entry.

**High water temperature.** High river and sea temperatures are associated with delay to migration into the river, but as already discussed, there is a correlation between freshwater discharge, river water temperature and estuary water temperature. This may partly be caused by freshwater flow affecting the hydraulics of the estuary. However, the dominant factor is likely to be that river flows are naturally lowest in late summer when temperatures tend to be highest, and that within this season, periods of settled high atmospheric pressure are associated with a lack of rainfall, reduced run-off (high evapo-transpiration) and strong solar radiation reaching the water surface of the river, estuary and mudflats exposed at low tide.

Given the infrequency of the readings from the Avon estuary, temperatures may at times have exceeded the highest recorded (22.2 °C). From the few data for river and estuary temperature available for the River Tamar, it appears that both may rise to well in excess of 20 °C. On the Avon, increased river temperature was associated with decreasing tendency to enter within 10 days of tagging, and virtually all fish entering the river on days when the 09.00-hour river temperature was in excess of 17 °C did so in the late evening and early morning, thus avoiding the time of day of highest water temperatures. It is therefore concluded that temperatures in the river and estuary were high enough to have contributed to the delays observed in this study. Temperature may be the predominant factor.

**Differential temperatures between the open sea, the estuary and fresh water.** Smith & Hawkins (1995) described a situation on the River Dee estuary in Aberdeen, Scotland, where stratification of saline and fresh water in the estuary meant that a difference in temperature of up to 10 °C between river and sea water might be experienced within a matter of metres by migrating salmon, and suggested that this might represent a barrier to free movement. Examination of the daily records for sea and river temperature, and spot readings from the estuary of the river Avon during a period when migration of tagged fish into the river was delayed (Fig. 4) indicated no major temperature differences between water bodies. Based on incomplete data, major temperature differences are unlikely to occur in the other rivers and it is therefore concluded that differential temperatures were not a major factor in the delay to migration in the rivers in this study.

**Poor water quality.** Deteriorating water quality, for example low DO or elevated ammonia concentration, may have a discouraging effect on migration at levels considerably more benign than those that cause mortality. Priede, Solbe, Nott, O'Grady & Cragg-Hine (1988) found avoidance behaviour of adult salmon in the Ribble estuary to oxygen levels falling < 5.5 mg $L^{-1}$.

Generally, DO levels in the Avon and Exe estuaries were high, and unlikely to have a major effect upon migration. Relatively few data for ammonia concentrations were available; the highest for the Avon estuary was 2.84 mg $L^{-1}$, which gives an unionised concentration in sea water of around the limit of 0.025 mg $L^{-1}$ set for salmonids in fresh water by the EC Directive (E. E. C. 1978), but very much less than the acutely toxic level for salmon smolts of 0.15 mg $L^{-1}$ suggested by Alabaster, Shurben & Knowles (1979). However, these authors recorded increased sensitivity to ammonia associated with low DO concentration. Alabaster & Lloyd (1982) found no evidence to suggest that fish exhibit avoidance behaviour with respect to sub-lethal levels of ammonia. Thus, while deteriorating water quality may contribute to conditions unattractive for migration during times of low flow and high temperature, there was no evidence that this is an over-riding factor in the estuaries of the Avon or Exe.

The situation on the Tamar is different. Here the concentration of oxygen can drop to lethal levels for salmon, the lowest recorded in a study involving 104 profiles along the estuary on a total of 87 separate days, being only 3% of air saturation (Morris, Bale & Howland 1982; Morris & Howland 1987). Such conditions occur when high temperatures, low freshwater flow and spring tides coincide, and they are associated with observed mortalities of salmon. The freshwater flow is generally high in oxygen, but a deep sag may develop in the upper estuary. The deepest point in the sag occurs just seawards of the freshwater/brackish water interface and coincides with the peak in suspended solids, typically 1–10 km seawards of the tidal limit at Gunnislake Weir, and thus lies between the netting sites where the tagged fish are released and the tidal limit. Uncles, Stephens & Woodrow (1988) reported that at high river flows there was a net seawards movement of sediment in the Tamar estuary; however, at low freshwater flows the sum of tidal pumping and gravitational circulation exceeded downstream advection, and the net sediment transport was back towards the tidal limit. The oxygen sag is most severe on spring tides, because of the suspension of organic detritus accelerating depletion; the lowest level recorded on neap tides was 67% of air saturation. There is little doubt that oxygen levels are low enough to act as a major behavioural barrier to migration over considerable periods in hot, dry summers, especially on spring tides.

### Potential factors implicated in the death of delayed fish

**High water temperature.** The ultimate upper lethal temperature for Atlantic salmon, in the absence of other stressors, is 27.8 °C (Garside 1973). This refers to the fish being progressively acclimated to temperatures approaching this limit, in otherwise ideal water quality conditions. There was no evidence of temperatures approaching this level in the situations being considered here. It is therefore concluded that high temperature on its own is not the primary cause of losses of salmon delayed in the estuary. However, high temperatures well below this level represent a stress on the fish and could be implicated alongside a range of other adverse environmental factors. In practice, high water temperatures are likely to coincide with deterioration in water quality, including lowered DO.

**Lowered dissolved oxygen.** Defining a lethal level for DO is complicated by the synergistic effects of other water quality parameters that are also likely to be deteriorating at the same time as DO, and variation in the length of time that fish will have to experience the worst conditions in an estuary. Alabaster & Lloyd (1982) suggested a value of 5 mg $L^{-1}$ for upstream migration. However, Alabaster & Gough (1986) observed some salmon successfully migrating through the Thames estuary when the median concentration over a 10 km length was 3.8 mg $L^{-1}$, although the situation was closely linked to water temperature. Alabaster, Gough & Brooker (1991) suggested that in the synergistic relationship on salmon migration, a reduction in DO of 1 mg $L^{-1}$ can be equated to a rise in water temperature of 4 °C. On the rivers Avon and Exe there was no evidence of general levels of DO falling to lethal level at any time, including years when many fish failed to enter the rivers. The lowest observed DO levels, down to 2.4 mg $L^{-1}$, occur in a saline sump on the Stour sub-estuary, between about 1 and 2 km seawards of the tidal limit, where many of the delayed Avon fish spent the intervening time between entering the estuary and entering the river. Oxygen levels in the fresh water lying over this sump were much higher, typically of the order of 7 mg $L^{-1}$ or more. Detailed tracking of the tagged fish indicated that they made frequent vertical movements between the two layers of water. It is therefore suggested that while low levels of DO may have contributed to a level of discomfort, it is unlikely that they were a direct cause of mortality, as the fish only had to make short vertical migrations to find more benign conditions.

The situation facing fish delayed on the River Tamar was quite different. As already described, lethally low levels of DO may occur over a discrete reach of several kilometres of the upper Tamar estuary under conditions of low freshwater flow, high temperatures and spring tides. This situation can develop rapidly on a flood spring tide with little opportunity for fish in the zone to escape. Major mortalities of salmon were recorded in the estuary in 1975, 1976, 1983, 1984, 1989 and 1995, all drought years with long periods of extreme summer conditions. It is therefore concluded that low DO was a major contributory factor in the mortality of fish delayed on the Tamar at times at least in the more extreme years. No other water quality parameter would appear to reach extreme enough levels to be a major factor in the mortality of delayed fish in the rivers in this study.

**Predation.** Fish remaining in the estuary or returning a short distance to sea could be vulnerable to natural predators in these waters. However, there are few predators large enough to tackle adult salmon in the estuaries and inshore waters of South West England. There are small numbers of grey seals and occasionally one will enter one of the estuaries, but this source of mortality is considered minor.

**Netting (legal or illegal).** All the estuaries studied have legal net fisheries catching salmon; indeed this was the source of most of the fish tagged. Numbers of tagged fish were reported recaptured by the nets, generally within a day or so of original capture and release; all tagged fish bore an external tag to facilitate reporting of recaptures, and the local commercial fishermen were familiar with their appearance. While it is likely that there were also unreported recaptures of tagged fish in these fisheries it is thought unlikely that this was the major component of the losses.

Illegal netting takes place on occasions in the estuaries of most salmon rivers, and it is unlikely that tagged salmon caught in such activities would be reported. The level of illegal fishing is not known, but local knowledge and experience suggest that it is not high enough to explain more than a small part of the apparent losses.

**Missed physiological opportunity.** The high losses of salmon from estuaries, which are for the most part considered to have high water quality, raises the possibility of some physiological explanation. It is known that smolts are pre-adapted to make the transition from fresh to salt water, and that they do not have the same physiological ability to make the transition outside the period of weeks normally associated with smolt migration. It is possible that returning adult fish also have a Ôwindow of opportunityÕ to make the transition from the salt to freshwater environment, and that if the fish are delayed making the transition then they are less able to make it at all. On the rivers Tamar and Exe at least, during years of high losses of delayed fish, the nets operating in the estuary start to catch fish which appear to be returning seawards from the upper estuary. These fish are generally fairly coloured which indicates that they are not fresh from the sea, and the occurrence of radio-tagged fish among them supports this. These fish appear lethargic and have soft flesh, and are considered by the netsmen to be barely marketable. It is suggested that these represent compromised fish that are unlikely to make a contribution to the river stock even when conditions improved.

## Conclusions

It is concluded that while the tendency to delay in the estuary is associated with low flows, the main driver is likely to be some associated factor. High water temperature appears to be a major influence, as does reduced levels of DO in some estuaries. Failure of these delayed fish to enter the river subsequently appears to be linked with poor water quality in some situations (e.g. reduced DO in the Tamar), but a major factor may be missed physiological opportunity.

These conclusions have important implications for the management of salmon stocks and water resources. Estuary conditions associated with a low rate of salmon migration and subsequent poor survival coincide with periods of low natural flow, but the exact role of flow is unclear. Low flows are also associated with high river and estuary temperatures and a decline in water quality parameters, particularly DO, but the exact causal relationships are not straightforward. The fundamental issue for water resource management is whether removal of a volume of water at (say) the tidal limit at times of low to medium natural flow will have the same effect on salmon movement and survival as would conditions that were associated with such a reduced flow occurring naturally. Small numbers of fish arrive at the tidal limit even at very low flows on most of the rivers, indicating that passage is possible at such times, and suggesting that the failure of the majority to do so is through inclination rather than compulsion. It could be argued that the precautionary principle should be applied, and that low flows should be protected at all costs. However, to do this unnecessarily could represent a misuse of resources in that it would require alternative or additional sources to be used to make up the shortfall in supply, representing a further range of potential environmental impacts elsewhere. These observations also have implications for the use of fisheries water banks, storage in reservoirs specifically for fisheries purposes and sometimes used to make releases to encourage salmon to migrate from estuaries at times of low flow. Failure to recognise the importance of water temperature and DO for example, might explain why artificial freshets have generally been ineffective.

It would appear that poor estuary survival associated with hot dry summers is a largely natural phenomenon and not solely the result of habitat degradation because of human activities, although the latter may exacerbate the problem. In the southern part of the natural range of the salmon, on the Iberian Peninsula in Europe and the Connecticut River in North America, summer conditions in coastal waters and estuaries are more extreme than those being considered here. In these rivers summer-running fish are rare and the great majority of the run passes through the estuary between March and June, before the estuaries reach their highest temperatures, and the fish spend the several months before spawning in the cooler middle and upper reaches of the river (Garcia de Leaniz, Hawkins, Hay & Martinez, 1987). Modelled climate change predictions for South West England include warmer and drier summers (e.g. HADCM2; Hulme & Barrow 1997), which will make poor summer estuary conditions more frequent and more extreme. Metcalf, Chambers, Charlesworth, Forrest, Hunt, McEwen, Russell & Schofield (2003) predicted that by the 2050s the South West of England will be 1.5–3.5 °C warmer and 15–30% drier in the summer than at present, depending upon the emission scenario used. If these predictions are substantially correct, it is likely that earlier (spring) and later (autumn) running may become more prevalent in salmon populations through natural selection. Run timing has been shown to have both environmental and genetic components (Saunders, Henderson, Glebe & Loudenslager 1983; Hansen & Jonsson 1991; Stewart, Smith & Youngson 2002). Historically, spring running has dominated on the rivers Avon (Solomon 1992) and Exe (Salmon Advisory Committee 1994), and the present strong tendency to return in summer appears to be a widespread phenomenon associated with long-term cycles in marine conditions (Salmon Advisory Committee 1994). However, other rivers in South West England (e.g. Fowey and Camel in Cornwall, and Plym in Devon) have predominantly autumn runs entering the rivers between October and December. Both spring and autumn running would appear to be effective at avoiding the damaging estuary conditions in hot dry summers, although warmer and drier summers may make the freshwater reaches of the rivers of South West England less favourable for spring-running salmon or even marginal for the species as a whole.

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